

FEEDING RELATIONSHIPS AMONG NINE SPECIES OF SEAGRASS FISHES OF TAMPA BAY, FLORIDA

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ABSTRACT

Dietary analysis was conducted on nine, numerically abundant fishes of sub-tropical, seagrass beds of Tampa Bay, Florida. *Floridichthys carpio*, *Harengula jaguana*, and *Anchoa hepsetus* formed a group with relatively high overlap values due to the importance of copepods in the diet. These three species had the most diverse diets of the nine species studied, with relatively low evenness due to the preponderance of a few abundant prey items. Apart from these species there was generally low dietary overlap among the fishes. A second dietary group included *Chilomycterus schoepfi*, *Fundulus similis*, and *Eucinostomus gula*, with overlap values considerably less than the first group. Dietary overlap was primarily due to bivalve molluscs being abundant in the diet of each species. *Arius felis*, *Lagodon rhomboides* and *Syngnathus scovelli* had low dietary overlap with the other species and among themselves, with the exception of *S. scovelli* and *H. jaguana*, in which cypris larvae and amphipods were both abundant in the diets. Among all species there was generally a low degree of herbivory, with *L. rhomboides* accounting for much of the plant material consumption. Contrary to findings from other studies on seagrass fishes, copepods and bivalve molluscs predominated in the cumulative diet of all species, with amphipods ranking third in overall consumption.

Seagrass beds have long been recognized as important feeding grounds for juvenile and adult fishes (Randall, 1965; Carr and Adams, 1973; Adams, 1976; Ogden and Zieman, 1977; Weinstein and Heck, 1979; Livingston, 1982; Bell and Harmelin-Vivien, 1983; Robblee and Zieman, 1984; Stoner and Livingston, 1984). In Tampa Bay, Florida, seagrass meadows of *Thalassia testudinum* (turtle grass), *Syringodium filiforme* (manatee grass), *Halodule wrightii* (shoal grass), *Ruppia maritima* (widgeon grass), and *Halophila engelmannii* (star grass), presently cover approximately 5,750 ha of the benthos, with turtle and shoal grass dominating (Lewis et al., 1985). In addition to providing foraging grounds, the seagrass habitat serves as a nursery for many fish species (Pollard, 1984; Comp, 1985). In Tampa Bay this habitat has been reduced by 81% from its historical coverage of approximately 30,970 ha (Lewis et al., 1985).

Fishes inhabiting seagrass meadows can be categorized on the basis of micro-habitat and/or temporal occurrence (Kikuchi and Peres, 1977). Sogard et al. (1989) recognized two major micro-habitat components, the epibenthos and the water column. Epibenthic fishes are relatively sedentary, permanent residents that occur within the seagrass canopy; water column species are more pelagic in behavior, occurring throughout the water column (Sogard et al., 1987; Sogard et al., 1989).

We investigate the feeding relationships among nine species of fishes that are among the numerically abundant epibenthic and water column seagrass associated fishes of Florida and Tampa Bay (Springer and Woodburn, 1960; Livingston, 1976; Brook, 1977; Livingston, 1982; Stoner, 1983; Comp, 1985; Thayer et al., 1987). Diet, dietary diversity, and dietary overlap are examined, and the utilization of these seagrass beds as foraging grounds is discussed.

MATERIALS AND METHODS

Study Site.—The Tampa Bay system is a large, shallow (<4 m), subtropical estuary on Florida's west coast. Seagrass beds, macroalgae, and benthic microflora contribute to the total primary production of

Table 1. Species names and size distribution of fishes investigated (N = 30)

Species	Common name	Size range*
<i>Chilomycterus schoepfi</i>	Striped Burrfish	119–210 mm
<i>Floridichthys carpio</i>	Goldspotted Killifish	46–87 mm
<i>Lagodon rhomboides</i>	Pinfish	123–159 mm
<i>Eucinostomus gula</i>	Silver Jenny	64–89 mm
<i>Fundulus similis</i>	Longnose Killifish	73–114 mm
<i>Harengula jaguana</i>	Scaled Sardine	82–122 mm
<i>Syngnathus scovelli</i>	Gulf Pipefish	91–149 mm
<i>Anchoa hepsetus</i>	Striped Anchovy	86–100 mm
<i>Arius felis</i>	Hardhead Catfish	280–377 mm

* Standard length range for *F. carpio* is only approximate as lengths were collected for only six specimens.

this system (Johansson et al., 1985). The estuary is lined by mangrove forests and salt marsh areas which contribute detritus and consequently particulate and dissolved materials (Johansson et al., 1985). Fishes were collected from a seagrass habitat in Boca Ciega Bay, near the entrance to Lower Tampa Bay, Florida (27°41'N, 82°41'W). The site is a gently-sloping sandy beach leading to a shallow (0.5 m to 2.0 m) seagrass bed dominated by *Thalassia testudinum*, with intervening sandy patches. Dense mats of macroalgae dominated by *Gracilaria* sp. and *Hypnea* sp. were often present. Maximum tidal fluctuations resulted in a 94 cm change of depth, although collections were primarily made at high tide.

Collection and Data Analysis.—Thirty individuals of nine species found in and around the seagrass beds were examined: *Chilomycterus schoepfi*, *Floridichthys carpio*, *Lagodon rhomboides*, *Eucinostomus gula*, *Fundulus similis*, *Harengula jaguana*, *Syngnathus scovelli*, *Anchoa hepsetus* and *Arius felis* (Table 1). Only sexually mature individuals were sampled. Choice of species was determined by numerical abundance as caught by the following procedures. Collecting gear included a 0.95-cm (square mesh) 23-m long nylon beach seine; 2.5 cm, 3.75 cm, and 5.0 cm (square mesh) 33-m long monofilament gill nets; and a 3-m otter trawl with 0.32-cm mesh cod end pulled by a power boat, in and above the seagrass beds.

Collections were made in the day between 1000 and 1600 from May to October, 1989 and 1990. Collections spanned both years for all species. For schooling species such as *A. hepsetus* and *H. jaguana*, collection was completed after a few net deployments (2–3), whereas collection of the other species required multiple samplings.

Fishes were gutted immediately after capture. Guts were preserved in 10% buffered formalin with Rose Bengal, and fishes were frozen for subsequent morphological analysis. For species with a distinct stomach, only prey items in the stomach were included. For species without a distinct stomach the anterior 1/2 of the intestine was evacuated. Specimens with empty stomachs or anterior intestines were not utilized.

Gut contents from each fish were identified and counted. Like items were pooled for each species, and wet weight was taken. Pooled items were aspirated for a period of one minute in a Buchner funnel attached to an Erlenmeyer flask and suction pump, then weighed with a Mettler balance to the nearest 0.001 g.

In most cases prey items were identified to order. In all calculations species were replaced by taxa (copepods, amphipods, isopods etc.). When an organism's parts, such as pieces of a single crab or bivalve, could be reconstructed with reasonable certainty, it was scored as one organism. In certain cases parts were treated as separate categories (e.g., crab and crab parts, shrimp and shrimp parts). Such categories were chosen to reflect differential prey processing by the predators. For example, whole crabs could be procured via suction feeding whereas single chelipeds suggest biting. Bites on algae and seagrass were scored individually by number if the pieces in the gut appeared to be bitten off separately (e.g., small individual pieces with apparent bite marks). Nematodes were excluded from the dietary analysis because they constitute gut fauna of questionable nutritional value to fishes. In addition, nematodes appear to be of importance only to such fish as mullet which feed by nonselective scooping up and consuming sediment (Gee, 1989).

In a few cases very abundant prey (Hill's N2, below) were identified to lower taxonomic levels. Bivalves consumed by *C. schoepfi* were identified to genus or species, widths measured, and approximate percentage by number visually estimated. Crushed shells prohibited accurate numerical counts. Similarly, gastropod prey of *C. schoepfi* were identified to family, and opercular diameter measured. Because gastropod shells were less fragmented, actual counts were taken. Very small bivalves from *A. hepsetus*, *F. similis*, and *E. gula* could not be accurately identified. They were subsampled haphazardly and widths taken.

Table 2. Hill's (1973) diversity numbers and Shannon's diversity index based on IRI values for nine species of fishes in Tampa Bay, Florida. N0 equals the number of prey taxa, N1 the number of abundant species in the sample, N2 the number of very abundant species in the sample, E5 the evenness, and H' Shannon's diversity index (N = 30).

Species	N0	N1	N2	H'	E5
<i>Syngnathus scovelli</i>	10	2.41	1.93	0.88	0.66
<i>Fundulus similis</i>	15	2.90	1.85	1.06	0.45
<i>Lagodon rhomboides</i>	19	3.39	2.10	1.22	0.46
<i>Chilomycterus schoepfi</i>	10	3.69	3.27	1.31	0.84
<i>Arius felis</i>	11	3.92	3.08	1.37	0.71
<i>Floridichthys carpio</i>	16	4.80	2.77	1.57	0.47
<i>Anchoa hepsetus</i>	16	4.69	3.45	1.55	0.66
<i>Harengula jaguana</i>	19	6.51	3.79	1.87	0.51
<i>Eucinostomus gula</i>	19	6.38	5.24	1.85	0.79

An Index of Relative Importance (IRI) (Pinkas et al., 1971) was calculated for each prey taxa for each species:

$$IRI = (\%N + \%V)(\%F)$$

where %N is percent number of items, %V is percent volume, and %F is proportion of guts containing the taxa. Percent wet weight was substituted for percent volume. Since there is no one method of stomach analysis that gives a complete picture of dietary importance (Hyslop, 1980) this cumulative index was utilized.

Hill's (1973) diversity numbers were calculated using the IRI values for each species (Table 2). The units for these indices are number of species (or the number of prey taxa, in this case); they are measures of the number of prey taxa in the sample where each taxon is weighted by its abundance. The indices are:

$$N0 = S$$

where S is the total number of taxa present, regardless of abundance;

$$N1 = e^{H'}$$

where H' is Shannon's Index. N1 is the number of abundant prey taxa; and

$$N2 = 1/\lambda$$

where λ is Simpson's Index. N2 is the number of very abundant taxa in the sample. N2 is a subset of N1. For example, if N1 = 10 and N2 = 5, five of the ten abundant species are very abundant. Ludwig and Reynolds believe Hill's diversity numbers are probably the easiest to interpret ecologically. The evenness index E5, or modified Hill's ratio, was calculated using IRI values for each species:

$$E5 = ((1/\lambda) - 1)/(e^{H'} - 1)$$

alternately,

$$E5 = (N2 - 1)/(N1 - 1)$$

where λ is Simpson's index, H' is Shannon's index, and N1 and N2 are Hill's diversity numbers. E5 approaches zero as a single species becomes more dominant (Alatalo, 1981 in Ludwig and Reynolds, 1988), and tends to be relatively independent of sample size (Ludwig and Reynolds, 1988). Hill's diversity numbers and the evenness index (E5) were calculated with the Statistical Ecology computer package (SPDIVERS program) of Ludwig and Reynolds (1988).

Horn's index of overlap (R_0) was used to calculate the amount of dietary overlap among species based on IRI values. This index was utilized because it is effected very little by sample size, and because it is appropriate when data are expressed as proportions. Furthermore, we were interested in the differential utilization of prey among species rather than the differences in availability of the prey themselves (Horn, 1966; Krebs, 1989). Because no data on prey availability were collected, it was necessary to assume that all resources were equally abundant. Horn's Index was calculated as:

$$R_0 = ((p_{ij} + p_{ik})\log(p_{ij} + p_{ik}) - p_{ij}\log p_{ij} - p_{ik}\log p_{ik})/(2 \log 2)$$

where R_0 = Horn's index of overlap for species j and k, p_{ij} = proportion resource i is of the total resources utilized by species j, p_{ik} = proportion resource i is of the total resources utilized by species k (Krebs, 1989). This index varies from 0 when the samples are completely distinct to 1 when prey

Table 3. Horn's (1966) index of niche overlap based on IRI values for nine species of fishes in Tampa Bay, Florida (N = 30)

Species	1	2	3	4	5	6	7	8	9
1. <i>A. felis</i>	1.000	0.064	0.190	0.006	0.287	0.065	0.104	0.073	0.015
2. <i>A. hepsetus</i>		1.000	0.372	0.253	0.128	0.788	0.529	0.735	0.359
3. <i>C. schoepfi</i>			1.000	0.004	0.059	0.175	0.490	0.157	0.333
4. <i>S. scovelli</i>				1.000	0.129	0.279	0.062	0.325	0.190
5. <i>L. rhomboides</i>					1.000	0.196	0.136	0.168	0.114
6. <i>F. carpio</i>						1.000	0.261	0.796	0.250
7. <i>F. similis</i>							1.000	0.352	0.384
8. <i>H. jaguana</i>								1.000	0.283
9. <i>E. gula</i>									1.000

are consumed in equal proportions (Horn, 1966). The index was calculated using the NICHE program of the statistical package "Ecological Methodology" by Krebs (1989).

RESULTS

Dietary overlap data separated the nine species into three groups; one with relatively high overlap, a second with intermediate overlap levels, and a third group comprised of species with relatively little dietary overlap (Table 3).

The first group comprised of *F. carpio*, *H. jaguana*, and *A. hepsetus*, had overlap values of 0.796 for *F. carpio* and *H. jaguana*, 0.788 for *F. carpio* and *A. hepsetus*, and 0.735 for *H. jaguana* and *A. hepsetus*. Copepods had the highest IRI values for all species in this group. Copepods dominated the diet of *F. carpio*, with ostracods, eggs, gastropods, and amphipods also abundant (N1 = 4.80, N2 = 2.77, Appendix A).

Harengula jaguana had 6.51 (N1) abundant prey taxa dominating its diet: copepods, cypris larvae, cladocerans, trematodes, amphipods, bivalves, and eggs (Appendix A). Of the very abundant taxa, copepods dominated, followed by cypris larvae, cladocerans, and trematodes (N2 = 3.79).

Anchoa hepsetus primarily fed on copepods, with bivalves, shrimp, shrimp parts, and gastropods of lesser importance (N1 = 4.69) (Table 2, Appendix A). Three very abundant prey categories (N2 = 3.45) dominated: copepods, bivalves and shrimp. Bivalves consumed by this species were small, the average length being 0.39 mm with a range of 0.21–1.37 mm, and consumed whole (not crushed). While there was high overlap in their diets (Table 3), these three species had among the most diverse diets of the nine species studied ($H' = 1.57, 1.87, 1.55$ respectively), but relatively low evenness (Table 2) due to the preponderance of a few abundant prey items.

A second dietary group was composed of *C. schoepfi*, *F. similis*, and *E. gula*. The overlap values were: *C. schoepfi* and *F. similis*, 0.490; *C. schoepfi* and *E. gula*, 0.333; *F. similis* and *E. gula*, 0.384. *Chilomycterus schoepfi* had the most evenly distributed diet ($E5 = 0.84$) and primarily consumed gastropods, and secondarily bivalves, barnacles, and crabs (N1 = 3.69) (Appendix A). The former three were very abundant in its diet (N2 = 3.27). Several families of molluscs were exploited by this fish (Table 4). The majority of hard-shelled molluscs (e.g., Turbinidae and Modulidae) were crushed.

Bivalves were the predominant prey of *F. similis*, with trematodes and eggs contributing more than other categories but substantially less than bivalves (N1 = 2.90). Bivalves, to a greater extent, and eggs, to a lesser extent, were very abundant (N2 = 1.85, Appendix A). The majority of the bivalves were crushed.

Table 4. Molluscan prey, relative sizes and percentage contribution to the gut contents of the Striped Burrfish, *Chilomycterus schoepfi* (o = opercular diameter; l = shell length or shell height) (N = 30)

Family	% of all molluscs	Size
Gastropoda		
Modulidae	50	o = 3.5 mm
Turbinidae	20	o = 3.0 mm
Olividae	20	l = 9.72 mm
Turridae	8	o = 3.2 mm
Buccinidae	<1	
Hydrobidae	<1	
Bivalvia		
<i>Cardita</i>	40	l = 3 cm
<i>Periglyta</i>	10	l = 1-2 cm
<i>Diplodonta</i>	10	l = 0.5-1.0 cm
<i>Ostrea</i>	10	l = 2 cm
<i>Modiolus</i>	10	l = 2 cm
<i>Solen</i>	10	l = 2 cm

The average shell length was 1.25 mm, ranging from 0.43 to 2.00 mm. Its diet had the lowest evenness ($E5 = 0.45$).

Polychaetes dominated the diet of *E. gula*. Bivalves, cumaceans, amphipods, and gastropods ($N2 = 5.24$) were also very abundant in the diet, with copepods of lesser importance ($N1 = 6.38$). Bivalves were not crushed during ingestion. The average length of the bivalves was 0.66 mm, ranging from 0.5 to 1.0 mm.

Overlap values in this second dietary group were less than in the first group (Table 3). Bivalve molluscs were very abundant in the first two species, however, the relatively lower overlap index (0.490) between these two species was due to differences in other very abundant prey; gastropods and barnacles were also abundant for *C. schoepfi*, and eggs and trematodes for *F. similis* (Appendix A). *Eucinostomus gula* overlapped with the other two species to a lesser extent (*C. schoepfi* 0.333; *F. similis* 0.384) reflecting the fact that five very abundant prey dominated the diet of *E. gula* ($N2 = 5.24$), including bivalves and cumaceans, but with polychaetes having the highest IRI.

A third group consisted of *A. felis*, *S. scovelli*, and *L. rhomboides* with relatively low dietary overlap values (range 0.006 to 0.287, Table 3), and generally little overlap with the other species (range 0.015 to 0.279) with the exception of *S. scovelli* and *H. jaguana* at 0.325 (Table 3). Tunicates were very abundant for both *A. felis* and *L. rhomboides* resulting in an overlap of 0.287. Three very abundant prey taxa ($N2 = 3.08$) dominated the diet of *Arius felis* (Table 2): crabs, tunicates, crab parts, and fish to a lesser extent (Appendix A).

Syngnathus scovelli had a diet dominated by amphipods, and secondarily by shrimp and cypris larvae ($N1 = 2.41$, $N2 = 1.93$) (Appendix A). Three abundant prey taxa, algae, tunicates, and seagrass ($N1 = 3.39$) dominated the diet of *L. rhomboides*, with algae and tunicates being very abundant ($N2 = 2.10$) (Appendix A).

When the sixteen very abundant prey taxa ($N2$) were ranked according to total IRI values for all fish species, copepods (17,787) and bivalve molluscs (16,768) had the largest cumulative IRI values (Table 5). The dominance of copepods was primarily due to group 1 fishes (17,265): *F. carpio*, *H. jaguana*, and *A. hepsetus*. High IRI values for bivalve molluscs were due primarily to the high percent number and frequency of occurrence recorded for several species including both fishes feeding on large robust molluscan prey and those consuming large quan-

Table 5. Cumulative IRI values of all nine species of fishes for prey taxa considered very abundant, that is, those delineated by Hill's Index N2

Prey taxa	IRI total
Copepods	17,787*
Bivalves	16,768
Amphipods	9,746
Algae	7,588†
Gastropods	6,688
Shrimp + shrimp parts	6,585
Crabs + crab parts	6,203
Polychaetes	5,906‡
Tunicates	4,820
Eggs	3,129
Cypris larvae	2,480
Trematodes	2,228
Barnacles	2,104
Cumaceans	1,479
Cladocerans	1,266
Ostracods	1,194

* Mostly group 1 fishes: *F. carpio*, *H. jaguana*, *A. hepsetus*.

† Mostly *L. rhomboides*.

‡ Mostly *E. gula*.

tities of small, weakly armored prey. The IRI total for algae (7,588), higher than expected, was primarily due to one species, *L. rhomboides* (7,514); and the total for polychaetes (5,906) was due primarily to *E. gula* (5,769).

DISCUSSION

Tampa Bay supports a diverse community of resident and transient fishes and is an important nursery area for immature fishes. At least 203 species of fishes inhabit the bay (Comp, 1985). A small percentage of common species dominate the ichthyofauna of the bay (Comp, 1985) and similar seagrass beds around Florida (Springer and Woodburn, 1960; Livingston, 1976; Brook, 1977; Livingston, 1982; Stoner, 1983; Thayer et al., 1987). The nine species investigated are among the most numerically abundant species in these seagrass beds.

The present study investigating trophic relationships among nine sympatric species within a seagrass community in Tampa Bay yielded dietary information coincident with many previous studies (Carr and Adams, 1973; Adams, 1976; Brook, 1977; Robertson, 1978, 1980; Stoner, 1980a; Bell and Harmelin-Vivien, 1983). However, the type of dietary analysis performed here has been used by relatively few investigators (Bell and Harmelin-Vivien, 1983). Many studies present dietary data either by weight, volume, numbers or frequency of occurrence. Any single measure by itself can be potentially misleading. For example, relative number of each food item reflects how many of a particular prey item are consumed but is highly correlated with food size. It is therefore biased towards smaller food items, which, if commonly used by a fish predator must be more numerous than large food items (Cailliet et al., 1986; Hyslop, 1980). The index of relative importance (IRI) attempts to yield a more accurate picture of dietary importance by taking into account bulk, amount, and frequency of occurrence of all prey items (Hyslop, 1980). Compound indices such as IRI are not widely used, so comparisons between studies are limited (Hyslop, 1980). Combinations of the three separate measures (frequency, number, and weight) of prey importance may allow a more representative feeding habit data summary, yet still allow each

measure to be evaluated individually, increasing their usefulness for comparison between studies (Cailliet et al., 1986).

Dietary Analysis.—In contrast to our finding that copepods, ostracods, eggs, gastropods, and amphipods predominated in the diet of *F. carpio*, Springer and Woodburn (1960) reported a diet of small crustaceans, molluscs, and annelids in Tampa Bay. For individuals in the North River Estuary in southwest Florida, Odum and Heald (1972), examining 81 specimens sized from 14 to 59 mm, identified the following prey items by decreasing percent volume: detritus (fecal pellets, root material, leaf material, bark, and conglomerates), amphipods, unrecognizable material, filamentous algae, ostracods, benthic diatoms, harpacticoid copepods (only 6%), chironomid larvae, isopods, polychaetes, and nematodes. These findings may not be directly comparable to our study since killifish in our study were 46–87 mm. Brook's (1977) analysis of 125 individuals in Card Sound, Florida, was more consistent with those reported here. By percent frequency of occurrence, Brook found that copepods and amphipods dominated the diet (42 and 32% respectively). Our restricted spatial and temporal sampling regime could lead to discrepancies in dietary analysis as compared to other studies. Furthermore, there appear to be important seasonal (Stoner, 1980a; Livingston, 1982; Huh and Kitting, 1985) and ontogenetic (Stoner, 1980a; Stoner and Livingston, 1984) effects which may be responsible for differences among studies.

In contrast to our findings Springer and Woodburn (1960) reported that *H. jaguana* consumed gammarid amphipods, copepods, ostracods, and small crustaceans. However, their qualitative dietary analysis was limited. In the North River basin, a Florida mangrove estuary, amphipods and mysids comprised 65% of the diet and harpacticoid copepods 5% by volume of 64–96 mm SL fish (Odum and Heald, 1972). In southwest Florida the diet of *H. jaguana* was primarily comprised of copepods for 21–35 mm SL fish, and crab zoea for all size classes larger than 35 mm (Kinch, 1979). Amphipods were taken by smaller fish (21–30 mm SL), but not by fish larger than 30 mm SL. Similarly, Carr and Adams (1973) found *H. jaguana* consumed mainly veliger larvae and crab megalops larvae (42% and 55% dry weight, respectively). Copepods were taken by only the smallest size class. In our sample (fish of 82–122 mm SL) copepods dominated by IRI value, although based on percent weight as others have done, gastropods, amphipods, and isopods predominated (Appendix A).

Our feeding data for *A. hepsetus* are in general agreement with those of others (Adams, 1976). Qualitative studies by Hildebrand and Schroeder (1928) found that this species consumed primarily small crustaceans, especially copepods, mysids, isopods, and occasionally small molluscs and fish. Hildebrand and Cable (1930) reported that adults fed on copepods, but the diet also included ostracods, annelids, small crustaceans and mysids. Similar qualitative studies by Springer and Woodburn (1960) reported a diet of primarily copepods, isopods, mysids, caridean shrimp, and pelecypods.

The diet of *C. schoepfi* was composed almost entirely of hard-shelled prey (gastropods, bivalves, barnacles, crabs), the majority of which were crushed. These findings concur with Adams (1976) who found that scallops and gastropods comprised approximately 95% of the diet by weight. Because of their large size and beak-like jaws, diodontids can feed on some of the larger molluscs and crustaceans that smaller fishes would be unable to eat (Randall, 1983).

Dietary information for *Fundulus similis* is limited. Springer and Woodburn (1960) qualitatively reported copepods, ostracods, small molluscs, and annelids in the guts of the species collected in Tampa Bay. In the Indian River salt marsh

this species consumed 2% cyclopoid copepods, 2% harpacticoid copepods, 76% *Aedes* mosquito larvae, and 19% dipteran larvae by volume (Harrington and Harrington, 1961). At our site, bivalves dominated the diet in all categories, with eggs playing a secondary role in dietary importance.

We found that *E. gula* consumed primarily polychaetes, which is consistent with other studies. Copepods dominated the diets of smaller size classes and were gradually replaced by polychaetes as size increased (Springer and Woodburn, 1960; Carr and Adams, 1973; Brook, 1977; Livingston, 1984). Copepods were absent from the diets of larger size classes (>40 mm SL, Carr and Adams, 1973; >45 mm SL Springer and Woodburn, 1960).

The pinfish, *L. rhomboides* is the numerically dominant species within *T. testudinum* beds along subtidal areas of the Gulf of Mexico (Hansen, 1969). It is an important predator on macrobenthic organisms within these seagrass beds (Young and Young, 1978). Available data on this species suggest that it undergoes several ontogenetic dietary shifts which may correspond with food availability (Huh and Kitting, 1985), although the data are conflicting. An increased tendency towards carnivory with growth was reported by Subrahmanyam and Drake (1975), and Carr and Adams (1973). This contrasts with the shift to herbivory with growth cited by Darnell (1958), Hansen (1969), Stoner (1980a), and Stoner and Livingston (1984).

Algae dominated the diet of the relatively large pinfish (123–159 mm SL) sampled here. Our findings of increased herbivory with size, rather than increasing carnivory, may be due to geographical and seasonal differences in prey availability and abundance (Stoner, 1980a).

According to Sheridan et al. (1984), *A. felis* (150–298 mm SL) in the West Mississippi Delta fed mainly on polychaetes (8–33% of the diets), stomatopods, shrimp, shallow water crabs, and bones and scales of estuarine fishes. In Texas, this species consumed large quantities of commercial penaeid shrimp (Knapp, 1949; Harris and Rose, 1968). Springer and Woodburn (1960) found that the diet of *A. felis* in the Tampa Bay area consisted mostly of annelids and fish scales. Our study revealed crabs, tunicates, and fish remains to be most predominant in its diet.

Amphipods and secondarily shrimp were very abundant in the diet of *S. scovelli* (Appendix A). This species had the narrowest diet of the species investigated ($N_0 = 10$) and the lowest diversity ($H' = 0.88$). Similar results by Livingston (1982) revealed that *Syngnathus sp.* specialized on shrimp in the fall and amphipods in winter and spring, emphasizing the importance of seasonality as a determinant of diet. Algae comprised a substantial portion of the diet in terms of percent frequency of occurrence (Appendix A). However, the prevalence of shrimp and amphipods, both known to inhabit drift algae, suggests that the consumption of algae may be incidental. By contrast, Huh and Kitting (1985) found that this species had very consistent feeding habits throughout the year, regardless of food availability in Redfish Bay, Texas. Copepods dominated the diet of 31–70 mm fish, and amphipods of 71–120 mm pipefish. Prey size selectivity was not investigated in our study, however, Nelson (1979a) found that *S. fuscus* (110–130 mm) selected small amphipods in controlled experiments, being essentially unable to consume large amphipods whole.

Trophic Utilization.—Trends in resource (food) partitioning as well as degree of carnivory in these fishes are consistent with previous studies. We found a low incidence of herbivory with the sparid, *L. rhomboides*, accounting for most of the consumption of plant material. Of 49 species studied by Bell and Harmelin-Vivien

(1983) only one species was omnivorous, and as in our study, it was a sparid. Robertson (1984), working in Western Port, Australia found that 9 of 11 seagrass associated fishes were carnivorous. In *Zostera* beds in Australia, Robertson (1978, 1980) reported a low incidence of herbivory (1 out of 10 species) in addition to low dietary overlap among fishes. Of 21 species of fishes inhabiting seagrass beds in Crystal River, Florida, only three species, one being *L. rhomboides*, exhibited herbivorous feeding stages (Carr and Adams, 1973).

The relatively high levels of herbivory we observed in *L. rhomboides* may be related to reduced abundance of amphipods in these *Thalassia* dominated beds, or to decreased predation on amphipods due to habitat complexity. Numerous studies have found that small crustaceans such as amphipods may be limited in abundance in seagrass meadows by predators during seasons of predator abundance (Young et al., 1976; Young and Young, 1977, 1978; Reise, 1978; Nelson 1979a, 1979b; Orth and Heck, 1980; Stoner, 1980b, 1982; Nelson et al., 1982). Predation by fishes and invertebrates is perhaps the single most important factor organizing the amphipod community in eelgrass beds (Nelson, 1979a). Stoner (1982) found that amphipods were most readily detected by *L. rhomboides* on the narrow blades of *Halodule* than on wider blades of *Thalassia* and cylindrical blades of *Syringodium*. He believes that increased herbivory of *L. rhomboides* may be directly related to the type of seagrass beds they inhabit. *Halodule*, which is a poor refuge for crustaceans, permits pinfish to take high energy animal prey (primarily amphipods and shrimp), whereas *Thalassia* (such as in Tampa Bay) and *Syringodium* habitats protect crustaceans from consumption resulting in the pinfish diet being composed of the less nutritionally valuable plant material.

Increased habitat complexity may decrease predation of fishes on amphipods (Ware, 1972; Vince et al., 1976; Nelson, 1979a) and on invertebrate prey in general (Heck and Thoman, 1981), resulting in decreased importance of amphipods in the diet of these seagrass fishes. Nelson found that small (20–30 mm) and large (35–45 mm) pinfish responded differently to increased density of artificial eelgrass. The feeding efficiency of small fish was impaired by increasing seagrass density, whereas large fish had lower feeding efficiency only for higher blade densities. This could also account for increased herbivory in *L. rhomboides*.

Low dietary overlap with considerable resource partitioning has been reported within *Posidonia* beds in Australia by Scott and Dybdahl (in Pollard, 1984) and Scott et al. (in Pollard, 1984). Low dietary overlap was also characteristic of fishes within our study. The only fishes which displayed a high level of dietary overlap were those species in the first group that primarily fed on copepods (*Floridichthys carpio*, *Harengula jaguana*, *Anchoa hepsetus*). However, this conclusion must be interpreted with caution because, (1) this study only examined a subset of the seagrass inhabiting fishes in Tampa Bay, (2) had prey items been identified to species, the dietary overlap indices would likely decrease, (3) diel trophic interactions between these fishes and their prey, for example vertically-migrating zooplankton, were not investigated (Robertson and Howard, 1978), and (4) seasonality in diet was not examined. Seasonality of predation of invertebrate prey (particularly amphipods) by seagrass inhabiting fishes has been found by Adams (1974), Heck and Orth (1980), Heck and Thoman (1981), and Huh and Kitting (1985). The latter found seasonal peaks in amphipods, polychaetes, isopods and other benthic animals in shoalgrass and turtlegrass meadows on Redfish Bay, Texas. Greatest dietary overlap among four abundant seagrass fishes (pinfish, *L. rhomboides*; darter goby, *Gobionellus boleosoma*; code goby, *Gobiosoma robustum*; gulf pipefish *S. scovelli*) occurred in spring when foods became abundant. During this season all species became carnivorous and preyed heavily on amphi-

pods. Summer had the lowest dietary overlap. During winter there was relatively high overlap, with copepods being the important food item for all species.

Pollard (1984) recognized a number of generalizations describing trophic relationships within seagrass habitats worldwide. One was that small seagrass-canopy inhabiting crustaceans were one of the predominant prey items in the diets of many of the fish communities. Another was that infaunal benthos, especially molluscs and polychaetes, were relatively unimportant in overall community diets. These generalizations are echoed by Bell and Harmelin-Vivien (1983) as well as Robertson (1978, 1980, 1984). In worldwide studies researchers have found that amphipods (and other infaunal and epifaunal crustaceans) are the predominant prey item in most seagrass fish species (Brook, 1977; Robertson, 1978, 1980, 1984; Bell and Harmelin-Vivien, 1982, 1983; Scott and Dybdahl, in Pollard, 1984; Scott et al., in Pollard, 1984; Heck and Weinstein, 1989). Our study differs considerably from those of previous investigators due to the relative importance of copepods and bivalve molluscs as prey for these adult fishes, with reduced importance of amphipods in the diet. Copepods have been noted to be of great importance to juvenile fish within seagrass meadows, however, the continued importance of this food item in adults is atypical. The occurrence of the transient, water column foraging species *H. jaguana* and *A. hepsetus*, and the epi-benthic foraging *F. carpio* account for the predominance of copepods in the diet.

While studies focusing on resource availability have suggested that infauna are abundant within the benthos, this potential food source is largely under-utilized by seagrass fishes (Pollard, 1984). Brook (1977) found that molluscs, which contributed significantly to the benthic biomass of *T. testudinum* beds in Card Sound, south-eastern Florida, were not a preferred food for the animals frequenting the study site. Heck and Weinstein (1989) generally agreed with this, however, similar to our study they found that infaunal crustaceans (stomatopods) were a significant portion of the diet of several seagrass fishes in Panamanian seagrass beds. In our study bivalve molluscs comprised a significant portion of the diet in several of the seagrass fishes investigated here.

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Appendix A. Indices of Relative Importance for nine species of fishes from Tampa Bay, Florida. Percent number, percent wet weight, and percent frequency of occurrence given for each prey category present in the stomach, or anterior third of the intestine in fishes without a stomach. The average number and weight of prey items per prey taxa is indicated (N = 30 individuals per fish species). To calculate number, weight, and frequency of occurrence of each prey taxa an example for amphipod prey in *F. carpio* is as follows: average # of prey (68.438) × number of prey taxa (16) × percent number (0.049315) = 54 amphipods; average weight (0.044 g) × number of prey taxa (16) × percent weight (0.03004) = 0.021 g cumulative weight; percent frequency (0.60) × number of fish sampled (30) = 18 fish.

Prey	% No.	<i>F. carpio</i> % Weight	% Freq	IRI
Amphipods	4.932	3.004	60.000	476.148
Bivalves	1.005	4.149	20.000	103.067
Bryozoans	0.091	2.861	3.333	9.842
Copepods	52.877	9.442	80.000	4,985.502
Crab parts	0.183	8.155	6.667	55.581
Cypris larvae	0.274	5.866	10.000	61.395
Eggs	15.251	12.589	23.333	649.613
Gastropods	3.562	9.156	40.000	508.703
Larval fish	0.091	9.299	3.333	31.301
Mites	0.731	0.000	10.000	7.306
Ostracods	11.872	4.006	60.000	952.672
Polychaetes	0.822	3.147	3.333	13.231
Seagrass	1.461	5.293	16.667	112.574
Shrimp	2.101	12.732	23.333	346.102
Shrimp parts	4.110	5.866	26.667	266.003
Trematodes	0.640	4.435	10.000	50.742

Average number of prey items per prey taxa = 68.438; Average weight of prey per prey taxa = 0.044 g.

<i>H. jaguana</i>				
Prey	% No.	% Weight	% Freq	IRI
Amphipods	3.100	9.692	66.667	852.785
Bivalves	2.604	4.789	76.667	566.776
Cladocerans	7.586	5.929	93.333	1,261.397
Copepods	60.505	8.666	100.000	6,917.087
Crab larvae	1.184	0.000	76.667	90.735
Crab parts	0.068	0.000	10.000	0.676
Cypris larvae	11.835	6.842	96.667	1,805.394
Eggs	1.138	6.499	70.000	534.649
Gastropods	0.158	16.876	20.000	340.670
Isopods	0.248	9.464	23.333	226.615
Mites	0.135	0.000	30.000	4.058
Ostracods	0.169	1.140	30.000	37.280
Seagrass	0.147	1.254	16.667	23.347
Shrimp	0.845	7.184	43.333	347.921
Shrimp larvae	0.034	0.912	6.667	6.307
Shrimp parts	0.970	7.298	43.333	358.234
Sponges	0.023	5.131	3.333	17.179
Trematodes	9.029	0.684	96.667	938.880
Tunicates	0.225	7.640	20.000	157.302

Average number of prey items per prey taxa = 466.947; Average weight of prey per prey taxa = 0.046 g.

Appendix A. Continued

Prey	% No.	<i>A. hepsetus</i> % Weight	% Freq	IRI
Amphipods	1.296	4.592	33.333	196.254
Bivalves	36.250	2.857	76.667	2,998.230
Cladocerans	0.304	0.102	13.333	5.413
Copepods	46.473	23.469	76.667	5,362.217
Crab larvae	0.176	0.102	13.333	3.707
Cypris larvae	0.288	0.102	6.667	2.600
Eggs	1.184	3.980	33.333	172.113
Fish larvae	0.368	6.633	10.000	70.006
Gastropods	2.560	8.061	50.000	531.041
Isopods	0.080	0.102	10.000	1.820
Mites	0.016	0.102	3.333	0.394
Ostracods	1.760	0.510	43.333	98.363
Shrimp	1.264	25.714	50.000	1,348.904
Shrimp parts	1.632	21.531	43.333	1,003.702
Scaphopods	0.048	0.102	6.667	1.000
Tunicates	6.303	2.041	10.000	83.438

Average number of prey items per prey taxa = 390.688; Average weight of prey per prey taxa = 0.061 g.

Prey	% No.	<i>C. schoepfi</i> % Weight	% Freq	IRI
Amphipods	0.376	0.016	6.667	2.611
Barnacles	25.376	23.056	43.333	2,098.721
Bivalves	15.226	33.058	60.000	2,897.032
Bryozoans	1.504	0.031	10.000	15.353
Crabs	6.015	24.643	33.333	1,021.946
Gastropods	43.797	18.940	73.333	4,600.709
Polychaetes	4.887	0.058	6.667	32.970
Seagrass	1.504	0.065	10.000	15.683
Shrimp	0.376	0.038	3.333	1.379
Tunicates	0.940	0.094	6.667	6.896

Average number of prey items per prey taxa = 53.200; Average weight of prey per prey taxa = 6.351 g.

Prey	% No.	<i>F. similis</i> % Weight	% Freq	IRI
Algae	0.904	1.645	6.667	16.993
Amphipods	0.904	1.645	30.000	76.467
Bivalves	45.200	56.555	83.333	8,479.630
Copepods	2.970	4.306	23.333	169.775
Crab larvae	2.798	1.597	20.000	87.893
Crabs	3.831	4.983	33.333	293.811
Eggs	23.031	9.966	36.667	1,209.879
Gastropods	1.378	0.677	30.000	61.645
Isopods	0.129	3.628	10.000	37.576
Ostracods	2.109	0.871	16.667	49.670
Polychaetes	0.775	0.387	23.333	27.111
Seagrass	0.172	3.338	10.000	35.104
Shrimp	0.603	1.645	16.667	37.460
Shrimp parts	1.033	1.597	13.333	35.062
Trematodes	14.163	7.160	53.333	1,137.219

Average number of prey items per prey taxa = 154.867; Average weight of prey per prey taxa = 0.138 g.

Appendix A. Continued

Prey	% No.	<i>E. gula</i> % Weight	% Freq	IRI
Algae	0.208	0.000	3.333	0.693
Amphioxus	0.208	0.093	3.333	1.004
Amphipods	14.137	4.762	43.333	818.962
Anemone	0.624	0.093	6.667	4.781
Bivalves	15.177	8.683	70.000	1,670.213
Copepods	3.534	4.482	26.667	213.763
Crab parts	0.416	0.000	6.667	2.772
Cumaceans	12.474	9.711	66.667	1,478.971
Eggs	0.208	0.000	3.333	0.693
Fish parts	0.416	0.000	3.333	1.386
Gastropods	12.474	1.681	40.000	566.187
Isopods	1.247	7.937	13.333	122.452
Horseshoe crab	0.208	0.280	3.333	1.627
Ostracods	1.871	0.000	6.667	12.474
Polychaetes	28.067	50.607	73.333	5,769.386
Shrimp parts	2.079	3.922	20.000	120.011
Sipunculids	0.208	0.934	3.333	3.805
Sponges	0.416	6.816	6.667	48.212
Trematodes	6.029	0.000	16.667	100.485

Average number of prey items per prey taxa = 25.316; Average weight of prey per prey taxa = 0.056 g.

Prey	% No.	<i>A. felis</i> % Weight	% Freq	IRI
Bivalves	0.559	0.327	3.333	2.954
Crabs	16.760	31.582	76.667	3,706.175
Crab parts	10.056	9.717	43.333	856.807
Eggs	5.028	4.917	6.667	66.299
Fish parts	6.145	13.476	26.667	523.242
Fish scales	37.430	0.752	6.667	254.548
Mites	0.559	0.000	3.333	1.862
Seagrass	4.470	1.776	10.000	62.451
Shrimp	0.559	0.064	3.333	2.076
Shrimp parts	2.793	2.890	16.667	94.729
Tunicates	15.643	34.499	60.000	3,008.473

Average number of prey items per prey taxa = 16.273; Average weight of prey per prey taxa = 17.04 g.

Prey	% No.	<i>L. rhomboides</i> % Weight	% Freq	IRI
Algae	64.300	16.211	93.333	7,514.404
Amphipods	5.112	0.235	60.000	320.764
Anemones	0.811	2.783	3.333	11.983
Barnacles	0.203	0.540	6.667	4.955
Bivalves	1.420	0.255	30.000	50.243
Bryozoans	1.907	0.367	13.333	30.317
Cladocerans	0.041	0.041	3.333	0.271
Copepods	2.110	0.510	26.667	69.849
Crab parts	0.852	7.932	30.000	263.527
Eggs	6.288	9.360	30.000	469.432
Gastropods	1.623	0.275	40.000	75.920
Isopods	0.243	0.510	16.667	12.553
Mites	0.162	0.000	6.667	1.082
Ostracods	1.501	0.010	23.333	35.262
Polychaetes	3.327	1.458	13.333	63.794
Seagrass	8.154	2.049	70.000	714.246
Shrimp	0.446	0.112	16.667	9.307
Sponges	0.162	0.051	3.333	0.711
Tunicates	1.339	57.300	26.667	1,563.704

Average number of prey items per prey taxa = 129.737; Average weight of prey per prey taxa = 0.516 g.

Appendix A. Continued

Prey	% No.	<i>S. scovelli</i> % Weight	% Freq	IRI
Algae	2.778	0.000	20.000	55.556
Amphipods	39.444	44.566	83.333	7,000.834
Copepods	0.833	9.298	6.667	67.541
Cypris larvae	35.000	10.805	13.333	610.730
Eggs	1.111	6.733	3.333	26.147
Gastropods	0.278	0.321	3.333	1.995
Hydroids	3.056	0.321	6.667	22.508
Isopods	0.556	0.481	6.667	6.910
Ostracods	0.833	0.000	6.667	5.556
Shrimp	16.111	27.477	60.000	2,615.272

Average number of prey items per prey taxa = 36.000; Average weight of prey per prey taxa = 0.031 g