

DISTRIBUTION OF FISHES IN SEAGRASS MEADOWS: ROLE OF MACROPHYTE BIOMASS AND SPECIES COMPOSITION¹

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ABSTRACT

Large spatial variation was found in the abundance and species composition of ichthyofauna in seagrass meadows of Apalachee Bay and Indian River lagoon, Florida. Abundance of fishes was a direct function of aboveground seagrass biomass in Apalachee Bay where seagrass meadows were dominated by turtlegrass, *Thalassia testudinum*, but the relationship did not hold across monospecific beds of *T. testudinum*; manatee grass, *Syringodium filiforme*; and shoal grass, *Halodule wrightii*, in Indian River lagoon. Rather, the shoal grass site, with lowest seagrass biomass, yielded the largest number of fishes, while manatee grass, with biomass near that of shoal grass, had fewest fishes. Across seagrass species, blade density was a better predictor of fish abundance than seagrass biomass. Seasonal patterns of fish abundance at all of the sites were related to macrophyte biomass. Although lowest numbers of fish species were collected at an unvegetated site, species richness was not related to seagrass biomass or blade density; habitat heterogeneity appeared to be more important. Abundance of prey and protection from piscivorous predators were hypothesized as the best explanations for high fish abundance associated with high seagrass biomass and with shoal grass. Differential distribution in pinfish, *Lagodon rhomboides*, of various size classes was related to foraging behavior of individual trophic stages.

The great abundance and diversity of ichthyofauna in seagrass meadows are well established (Hoese and Jones 1963; Kikuchi 1966; Adams 1976; Weinstein and Heck 1979; Robertson 1980), but little is known concerning the mechanisms which control the distribution and diversity of fishes within beds. Although a few researchers have compared the ichthyofauna of vegetated and unvegetated substrata (Briggs and O'Connor 1971; Weinstein et al. 1977; Orth and Heck 1980) and changes in fish communities associated with pollution-induced reductions in seagrass cover have been examined (Kikuchi 1974; Livingston 1975), studies have not been designed specifically to test the role of seagrass biomass in the organization of fish assemblages. Only one study has examined ichthyofauna of different seagrass species (Martin and Cooper 1981). Such investigations require seagrass beds of different blade density or species composition within a restricted geographic range and beds which are characterized by similar physical and chemical conditions.

In this study I first discuss the ichthyofauna of four beds which have different seagrass biomass. Then, I compare the fish assemblages collected at three beds characterized by monotypic stands of three seagrass

species. The criteria for similar physical-chemical conditions were met within each of the two systems studied (Apalachee Bay and Indian River lagoon, Florida). Patterns of abundance, species composition, species richness, and fish size are discussed in terms of the life history of individual fish species, abundance of prey at the sites, and foraging behavior of numerically dominant species.

METHODS

Sampling Sites

Trawl surveys were made in two Florida localities: Apalachee Bay in the northern Gulf of Mexico and Indian River lagoon, 8 km north of Fort Pierce, on the east coast of Florida. Apalachee Bay is shallow and open to the Gulf of Mexico with seagrass beds (primarily turtle grass, *Thalassia testudinum*, and lesser amounts of manatee grass, *Syringodium filiforme*) which cover hundreds of square kilometers. Four stations were chosen on the basis of long-term macrophyte data for the area (Zimmerman and Livingston 1976, 1979) and are identical to the stations discussed by Stoner (1980a). Fenholloway station 11 (F-11) was characterized by a very sparse and patchy seagrass flora with a mean aboveground biomass of only 9.3 g dry wt/m². Station F-11 will be termed the unvegetated site. Fenholloway 12 (F-12) had a mean macrophyte biomass of 141 g dry wt/m²;

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the seagrass cover here was occasionally broken by a bare sand substratum. Econfina 10 (E-10) and 12 (E-12) had standing crops of 215 and 320 g dry wt/m², respectively, and were characterized by continuous, uniform seagrass cover. All of the stations were polyhaline, about 1.2 m in depth, and characterized by low levels of water color and turbidity. The physical-chemical and sedimentological similarity of the Apalachee Bay stations was established in an earlier report (Stoner 1980a).

Seagrass beds in Indian River lagoon are composed of three different species. Large monospecific stands of *Thalassia testudinum* (110 g dry wt/m²), *Syringodium filiforme* (48 g dry wt/m²), and shoal grass, *Halodule wrightii* (34 g dry wt/m²) were sampled near the western shore of the lagoon in shallow (1.0 m) polyhaline water. The beds were adjacent to one another and biomass values were representative of beds in the lagoon. Biweekly sampling showed that the Indian River stations were statistically similar to each other in depth, salinity, temperature, and other water conditions (Stoner 1983).

Biological Collections

In Apalachee Bay, fishes were collected with a 5 m otter trawl (1.9 cm mesh wing; 0.6 cm mesh liner) which was towed in a straight line near permanent station markers at a speed of 2 kn for 2 min. Seven replicate tows were made at each bed on a monthly basis from December 1976 through November 1977. The seven-trawl strategy was found to be appropriate for an asymptotic accumulation of species (Livingston 1975). In Indian River lagoon, a smaller net and a more rigid trawl strategy were required so that only monospecific seagrass beds were sampled. A 3 m otter trawl, with mesh identical to that used in Apalachee Bay, was towed at 2 kn in a straight line between floats at the ends of a 70 m transect or in a line close to and parallel to the line of the floats. Seven replicate tows were made at each bed on a quarterly basis after preliminary analysis showed that the seven replicates yielded an asymptotic species accumulation curve for fishes. Despite the restricted area of a trawl site, replicate tows did not overlap in the area covered and no change in species composition was observed over the collection period which normally spanned several hours. Collections were made at midday in October 1979, and in January, April, and July 1980. Because the efficiency of capturing fishes (Ryan 1981) and invertebrates (Greening and Livingston 1982) varies diurnally and because certain species move to and from seagrass beds on a diurnal basis (Randall 1965; Ogden and

Buckman 1973; Ogden and Zieman 1977), midnight collections were made at the Indian River stations. Two tows were made at each bed in January and in July. All fishes reported in this study were preserved in a Formalin³-seawater mixture, identified to species, counted, and measured for standard length (SL).

Macrophyte collections were made at each bed and on each date of fish collection. As described by Livingston et al. (1976), aluminum hoops (0.25 m by 0.25 m) were thrown haphazardly into the sampling site and all macrophytes within each hoop were collected by diving. Eight replicates were collected including leaves, stems, roots, and rhizomes. Samples were placed in plastic bags and taken to the laboratory for identification and weighing. Plants were divided into aboveground and belowground parts, dried at 80°-100°C for 12 h, and weighed by individual species and fractions. For an estimate of blade density at Indian River beds, the number of seagrass blades in each sample was determined and extrapolated to yield numbers of seagrass blades per square meter.

Certain limitations are inherent in the present study. The inefficiency of trawl sampling is known (Kjelson and Johnson 1978), and it is not possible to provide abundance data in absolute terms; only a comparison of collections is valid. It may also be argued (correctly) that trawl efficiencies decrease with seagrass biomass. Although visual surveys of ichthyofauna, made in Apalachee Bay and in Indian River lagoon during the surveys, helped to confirm the spatial patterns of abundance for large, mobile species, visual surveys are rarely quantitative and underestimate the abundance of cryptic species. Low water transparency further restricted the value of visual surveys in the two sampling areas.

RESULTS

Role of Seagrass Biomass

A total of 8,002 fishes representing 53 species were collected in the 12-mo survey in Apalachee Bay. The total number of individuals collected at a given station, however, varied from 714 to 3,171 (Table 1) and was a direct function of mean macrophyte biomass ($r = 0.988$; $P < 0.001$) (Table 2). The close linear relationship was largely a result of a linear increase in abundance of pinfish, *Lagodon rhomboides* ($r = 0.998$; $P < 0.001$); however, when all other species

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Abundance of the 20 most numerous fishes at four seagrass sites in Apalachee Bay, Fla. Values are the total number of fish collected and percentages (in parentheses) of the total catch for each station. Macrophyte biomass (g dry wt/m²) for each station is given in parentheses.

Species	Station			
	F-11 (9.3)	F-12 (141)	E-10 (215)	E-12 (320)
<i>Legodon rhomboides</i>	122 (17.1)	1,050 (57.0)	1,568 (68.9)	2,131 (67.2)
<i>Leiostomus xanthurus</i>	364 (51.0)	92 (5.0)	153 (6.7)	15 (0.5)
<i>Bairdiella chrysoura</i>	15 (2.1)	204 (11.1)	116 (5.1)	148 (4.7)
<i>Diplodus holbrooki</i>	0	97 (5.3)	87 (3.8)	179 (5.6)
<i>Syngnathus floridae</i>	0	40 (2.2)	47 (2.1)	145 (4.6)
<i>Monacanthus ciliatus</i>	5 (0.7)	52 (2.8)	4 (0.2)	127 (4.1)
<i>Centropristis melana</i>	0	58 (3.1)	23 (1.0)	98 (3.1)
<i>Orthopristis chrysoptera</i>	11 (1.5)	48 (2.6)	17 (0.8)	42 (1.3)
<i>Haemulon plumieri</i>	0	27 (1.5)	19 (0.8)	61 (1.9)
<i>Pareclinus fasciatus</i>	34 (4.8)	17 (0.9)	37 (1.6)	13 (0.4)
<i>Micrognathus crinigerus</i>	8 (1.1)	17 (0.9)	44 (1.9)	4 (0.1)
<i>Eucinostomus argenteus</i>	6 (0.8)	11 (0.6)	30 (1.3)	19 (0.6)
<i>Monacanthus hispidus</i>	0	20 (1.1)	7 (0.3)	35 (1.1)
<i>Chilomycterus schoepfi</i>	6 (0.8)	21 (1.1)	4 (0.2)	25 (0.8)
<i>Gobiosoma robustum</i>	32 (4.5)	7 (0.4)	15 (0.7)	2 (0.1)
<i>Cynoscion nebulosus</i>	10 (1.4)	10 (0.5)	13 (0.6)	11 (0.3)
<i>Opsanus beta</i>	15 (2.1)	9 (0.5)	19 (0.8)	0
<i>Urophycis floridana</i>	16 (2.2)	14 (0.8)	7 (0.3)	4 (0.1)
<i>Syngnathus scovalli</i>	20 (2.8)	8 (0.4)	5 (0.2)	1 (0.05)
<i>Eucinostomus gula</i>	8 (1.1)	8 (0.4)	2 (0.1)	1 (0.05)
Other species	42 (6.0)	31 (1.8)	59 (2.6)	110 (3.5)
Total number of individuals	714	1,841	2,276	3,171
Total number of species	34	36	33	32

TABLE 2.—Summary of statistics from regression analyses for Apalachee Bay, Fla., fishes. *R* values are Pearson correlation coefficients; *N* is the total number of fish collected; *F* values are for tests of regression significance by analysis of variance.

Regression	<i>R</i>	<i>N</i>	<i>F</i> value	Significance
Tested as a function of mean macrophyte biomass				
Total number of fishes	0.988	4	576.21	<i>P</i> < 0.001
Number of pinfish	0.998	4	440.25	<i>P</i> < 0.001
Number of non-pinfish	0.882	4	7.00	<i>P</i> < 0.10
Tested as a function of macrophyte biomass, all dates examined separately				
Total number of fishes	0.572	48	22.31	<i>P</i> < 0.001
Number of pinfish	0.565	48	21.52	<i>P</i> < 0.001
Number of non-pinfish	0.380	48	7.75	<i>P</i> < 0.01

were combined, a similar positive relationship with seagrass biomass was found ($r = 0.882$; $P < 0.10$). The dominant fish at the unvegetated site (F-11) was spot, *Leiostomus xanthurus*, most of which were juveniles (10-20 mm SL). Silver perch, *Bairdiella chrysoura*, was most abundant at station F-12; the same was true for pigfish, *Orthopristis chrysoptera*, although numerical differences among the stations were small (Table 1). Fishes that increased in abundance with seagrass biomass or were most abundant at the most heavily vegetated site (E-12) included spot-tail pinfish, *Diplodus holbrooki*; dusky pipefish, *Syngnathus floridae*; fringed filefish, *Monacanthus ciliatus*; planehead filefish, *M. hispidus*; southern sea bass, *Centropristis melana*; and white grunt, *Haemulon plumieri* (Table 1); of these six species, only *M. ciliatus* was collected at the unvegetated site.

The total number of fishes collected per unit effort

(seven trawls) was lowest in winter months (December, January, and February) and highest between May and August, except at the unvegetated site where peak fish abundance occurred in February (Fig. 1). A brief abundance of juvenile spot and pinfish at station F-11, as they moved from offshore spawning sites to the marshes of the Fenholloway estuary, was responsible for the winter peak in total fish abundance at that station. After the brief transience of early juveniles, a consistently low number of fishes characterized the unvegetated site. At vegetated stations, the abundance of pinfish and spot continued to increase after initial recruitment of juveniles until midsummer.

Because of major seasonal patterns in the abundance of fishes and macrophytes in Apalachee Bay (Figs. 1, 2), two tests of the relationship between these biotic components were made. In the first test, using the 48 points available for 12 collections at four stations, total numbers of fishes, numbers of pinfish, and numbers of non-pinfish all proved to be weak linear functions of macrophyte biomass (Table 2). The second test, using the four stations as separate points on a month-by-month basis, found significant positive correlations between fish abundance and seagrass biomass during certain periods (Table 3). Pinfish abundance was closely related to seagrass biomass between May and October, the season during which first-year pinfish use the benthic habitat for a nursery ground. Total fish abundance showed a similar positive correlation with seagrass standing crop from

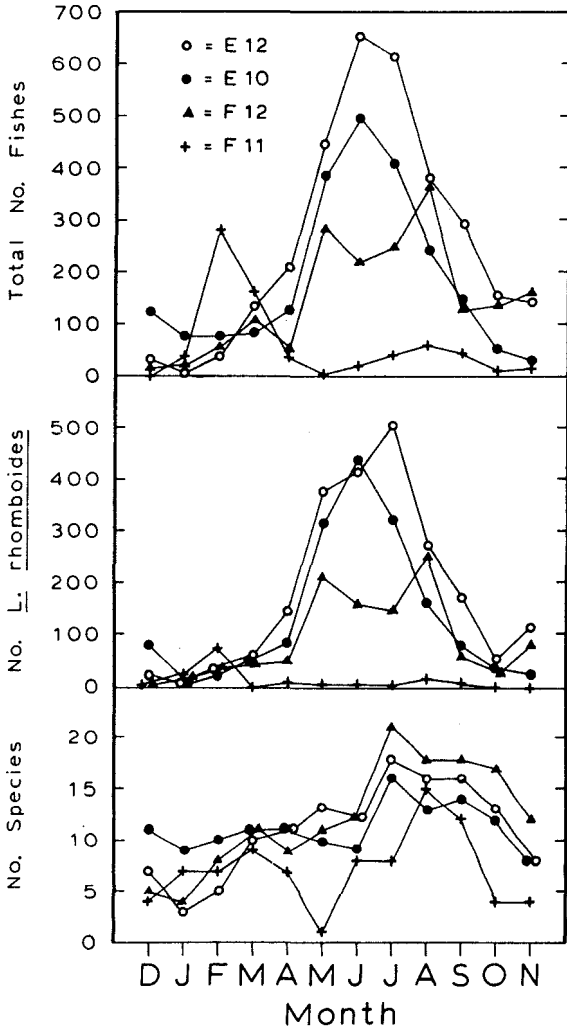


FIGURE 1.—Seasonal patterns of fish abundance and species richness at four seagrass sites in Apalachee Bay, Fla. Station F-11 (mean macrophyte biomass = 9.3 g dry wt/m²); F-12 (141 g dry wt/m²); E-10 (215 g dry wt/m²); E-12 (320 g dry wt/m²).

May to September, and non-pinfish abundance was significantly correlated with macrophyte biomass from June to September. Curiously, with all three fish categories, correlation coefficients gradually changed from negative in January to positive in the summer and fall when fishes and macrophytes were most abundant, and back to insignificant in December (Table 3).

Seasonality of fishes in Apalachee Bay was also a function of water temperature (Fig. 2) at the three vegetated sites. The correlation was strongest at station E-12 ($r = 0.857$; $F = 24.79$; $P < 0.001$) but was also significant at stations F-12 ($r = 0.717$; $F = 9.51$;

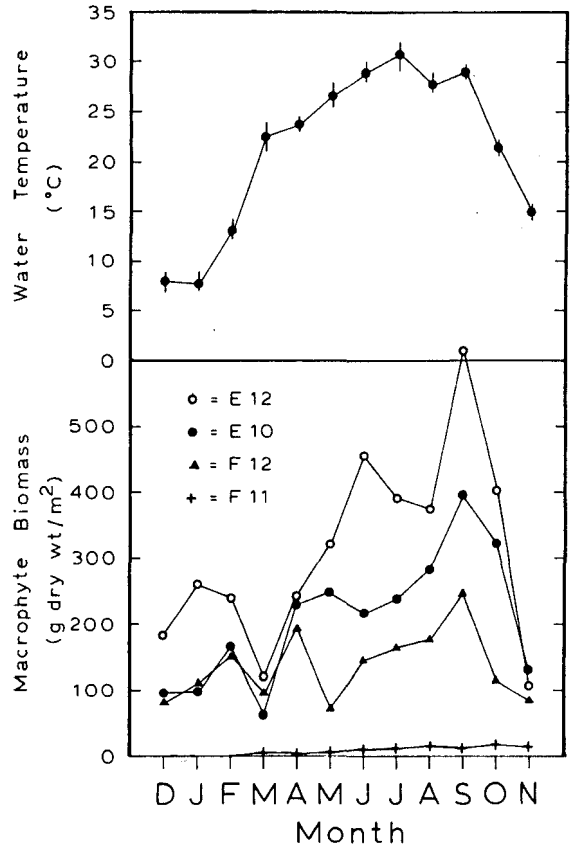


FIGURE 2.—Seasonal patterns in water temperature (mean and range) and seagrass biomass at four sites in Apalachee Bay, Fla.

TABLE 3.—Summary of statistics from regression analyses for abundance of fishes tested as a function of macrophyte biomass at four seagrass stations in Apalachee Bay, Fla. R values are Pearson correlation coefficients, with significance indicated; F values are for tests of regression significance using analysis of variance; n equals 4 for all regressions.

Sample period	All fish species		Pinfish		Non-pinfish	
	R	F	R	F	R	F
January	-0.385	0.35	-0.773	2.96	-0.242	0.12
February	-0.978***	43.18	-0.964***	26.35	-0.981***	50.24
March	-0.408	0.40	-0.808	3.76	0.609	1.18
April	0.699	1.91	0.776	3.03	0.443	0.49
May	0.900**	8.48	0.929**	12.55	0.709	2.02
June	0.950**	18.49	0.930**	11.79	0.959***	22.93
July	0.997***	305.96	0.988***	85.28	0.907**	8.46
August	0.870*	6.32	0.893*	7.31	0.848*	5.42
September	0.965***	27.30	0.976***	40.58	0.923**	11.53
October	0.481	0.60	0.836*	4.63	0.241	0.12
November	0.342	0.27	0.429	0.45	0.128	0.03
December	0.236	0.12	0.197	0.08	0.302	0.02

* = $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$.

$P < 0.01$) and E-10 ($r = 0.611$; $F = 5.29$; $P < 0.05$). The relationship was not observed at the un-vegetated site ($r = -0.165$; $F = 0.251$; $P > 0.10$)

because of the heavy winter passage of juvenile spot and pinfish.

The number of fish species collected in Apalachee Bay was highest in July and August, concurrent with peaks in total abundance (Fig. 1). Total number of species, however, ranged only from 32 at station E-12 to 36 at F-12, and there was no significant relationship between macrophyte biomass and species richness on either a spatial or seasonal basis.

Analysis of length-frequency data for pinfish, using ontogenetic stages discussed in earlier studies of the species (Stoner 1980b; Stoner and Livingston 1984) revealed differences in size-frequency distribution among the populations found at the four stations in Apalachee Bay (Table 4). At the unvegetated site, the pinfish population was dominated by fish in the 11-15 mm class (51.6% of the total) which appeared primarily in February and March. Among the vegetated sites, however, the number of small juveniles (16-35 mm) increased with seagrass biomass, as did the number of large juveniles (36-80 mm). The number of pinfish >80 mm decreased with seagrass biomass at the vegetated sites, but were also relatively uncommon at the unvegetated site.

TABLE 4.—Distribution of *Lagodon rhomboides* at four seagrass sites in Apalachee Bay, Fla., based on size class. SL is standard length of fish; *N* is the total number of fish collected in a size class.

SL (mm)	Station							
	F-11		F-12		E-10		E-12	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
11-15	63	51.6	12	1.1	35	2.2	30	1.4
16-35	15	12.3	299	28.3	569	36.3	884	41.5
36-80	35	28.7	649	61.3	881	56.2	1,181	55.4
>80	9	7.4	99	9.4	83	5.3	36	1.7

Role of Seagrass Species

A total of 2,580 fishes representing 37 species were collected during daytime sampling at three stations in Indian River lagoon (Table 5). Unlike collections made in Apalachee Bay, spatial variation in the abun-

dance of fishes was not related to seagrass biomass (Tables 6, 7); rather, fish abundance varied widely with seagrass species, independent of macrophyte biomass. The lowest number of individuals was found in beds of *Syringodium filiforme* (Table 5). Two and one-half times more fish were collected in *Halodule wrightii* where seagrass biomass was always lowest (Table 6), and an intermediate number of fishes were collected in *Thalassia testudinum* where highest macrophyte abundance occurred consistently. Analyzed by individual collection date, the *Halodule* bed supported greater total numbers of fishes than did the other two seagrass beds, except in October when equal numbers were collected in *Halodule* and *Thalassia* (Table 8). *Thalassia* and *Syringodium* beds supported statistically similar numbers of fishes except in October. As in Apalachee Bay, *Lagodon rhomboides* was the numerically dominant species in seagrass meadows of Indian River lagoon (Table 5). Except in October, the *Halodule* bed supported a significantly greater number of pinfish than the other two beds (Table 8). The *Syringodium* bed consistently yielded fewest pinfish, but mean values per trawl were similar to those from the *Thalassia* bed in January and July.

TABLE 5.—Abundance of the 10 most numerous fishes at three seagrass beds in Indian River lagoon, Fla. Values are the total number of fish collected and percentages (in parentheses) of the total catch for each bed type. Mean macrophyte biomass (g dry wt/m²) for each bed type is shown in parentheses.

Species	Syringodium	Thalassia	Halodule
	(48)	(110)	(34)
<i>Lagodon rhomboides</i>	265 (51.0)	576 (76.4)	898 (69.0)
<i>Eucinostomus gula</i>	45 (8.6)	16 (2.1)	145 (11.1)
<i>Orthopristis chrysoptera</i>	35 (6.7)	58 (7.6)	86 (6.6)
<i>Gobiosoma robustum</i>	100 (19.2)	12 (1.6)	14 (1.0)
<i>Syngnathus scovelli</i>	32 (6.2)	18 (2.4)	38 (2.9)
<i>Bairdiella chrysoura</i>	5 (1.0)	19 (2.5)	23 (1.8)
<i>Lutjanus griseus</i>	8 (1.5)	7 (0.9)	10 (0.8)
<i>Chilomycterus schoepfi</i>	1 (0.2)	12 (1.6)	4 (0.3)
<i>Eucinostomus argenteus</i>	2 (0.4)	1 (0.1)	12 (0.9)
<i>Syngnathus louisianae</i>	2 (0.4)	3 (0.4)	10 (0.8)
Other species	25 (4.8)	33 (4.4)	62 (4.8)
Total no. of individuals	520	758	1,302
Total no. of species	24	26	32

TABLE 6.—Aboveground biomass and blade density of macrophytes at three seagrass beds in Indian River lagoon, Fla. Values are mean \pm SD (*n* = 8).

Seagrass bed	October	January	April	July
Seagrass biomass (g dry wt/m ²)				
<i>Halodule</i>	25.7 \pm 6.5	17.8 \pm 1.9	23.2 \pm 8.3	66.8 \pm 19.8
<i>Thalassia</i>	69.4 \pm 9.2	73.0 \pm 20.3	99.4 \pm 25.7	197.4 \pm 52.4
<i>Syringodium</i>	49.9 \pm 7.9	28.4 \pm 8.5	23.4 \pm 4.2	86.8 \pm 27.1
Seagrass blade density (no./m ²)				
<i>Halodule</i>	8,389 \pm 1,878	6,111 \pm 1,878	10,589 \pm 2,752	11,611 \pm 3,029
<i>Thalassia</i>	2,044 \pm 218	1,856 \pm 296	2,344 \pm 493	2,400 \pm 734
<i>Syringodium</i>	3,767 \pm 489	2,722 \pm 455	2,411 \pm 206	4,178 \pm 1,065

TABLE 7.—Summary of statistics from regression analyses for Indian River fishes. *R* values are Pearson correlation coefficients; *N* is the total number of fish collected; *F* values are for tests of regression significance by analysis of variance.

Regression	<i>R</i>	<i>N</i>	<i>F</i> value	Significance
Tested as a function of macrophyte biomass				
Total number of fishes	-0.021	12	0.005	<i>P</i> > 0.10
Tested as a function of macrophyte blade density				
Total number of fishes	0.769	12	14.42	<i>P</i> < 0.01
Number of pinfish	0.733	12	11.58	<i>P</i> < 0.01
Number of non-pinfish	0.596	12	5.51	<i>P</i> < 0.05
Total number of fishes				
October	0.318	3	0.11	<i>P</i> < 0.10
January	0.989	3	43.88	<i>P</i> < 0.01
April	0.998	3	199.39	<i>P</i> < 0.001
July	0.916	3	5.18	<i>P</i> < 0.10

TABLE 8.—Daytime abundance of fishes and fish species in three seagrass beds in Indian River lagoon, Fla. Values are mean numbers per trawl sample \pm SD (*n* = 7). * and + indicate mean values that were not statistically different on a given date (ANOVA and Duncan's multiple range test, *P* < 0.05; *F* values are provided).

Seagrass bed	October	January	April	July
Number of individuals, all species				
<i>Halodule</i>	*53.1 \pm 15.5	24.1 \pm 10.3	50.1 \pm 18.2	63.4 \pm 19.2
<i>Thalassia</i>	*51.1 \pm 9.9	* 3.9 \pm 1.5	*21.3 \pm 7.3	*31.9 \pm 13.9
<i>Syringodium</i>	25.6 \pm 11.0 (<i>F</i> = 9.21)	* 4.9 \pm 2.7 (<i>F</i> = 20.13)	*19.1 \pm 6.8 (<i>F</i> = 11.01)	*22.0 \pm 11.1 (<i>F</i> = 12.49)
Number of pinfish				
<i>Halodule</i>	*34.7 \pm 8.4	13.2 \pm 7.4	36.6 \pm 10.8	44.7 \pm 17.1
<i>Thalassia</i>	*39.3 \pm 9.1	* 2.3 \pm 1.4	15.0 \pm 6.9	*26.0 \pm 9.5
<i>Syringodium</i>	17.4 \pm 6.5 (<i>F</i> = 12.33)	* 1.1 \pm 0.9 (<i>F</i> = 13.78)	2.3 \pm 1.6 (<i>F</i> = 12.53)	*17.0 \pm 5.4 (<i>F</i> = 8.73)
Number of individuals, excluding pinfish				
<i>Halodule</i>	*18.4 \pm 9.8	10.9 \pm 5.5	*13.6 \pm 5.7	14.0 \pm 8.0
<i>Thalassia</i>	*11.9 \pm 3.1	* 1.6 \pm 1.4	6.3 \pm 3.8	* 5.9 \pm 4.2
<i>Syringodium</i>	8.1 \pm 5.2 (<i>F</i> = 3.63)	* 3.7 \pm 1.9 (<i>F</i> = 11.64)	*16.9 \pm 6.2 (<i>F</i> = 6.15)	* 7.9 \pm 3.2 (<i>F</i> = 3.5)
Number of species				
<i>Halodule</i>	* 6.0 \pm 1.8	* 4.7 \pm 0.7	* 5.7 \pm 1.2	6.9 \pm 2.8
<i>Thalassia</i>	* 5.9 \pm 2.4	+ 2.4 \pm 1.3	** 4.0 \pm 1.9	* 3.7 \pm 1.1
<i>Syringodium</i>	* 5.0 \pm 2.1 (<i>F</i> = 0.40)	+* 3.7 \pm 1.4 (<i>F</i> = 5.79)	+ 3.0 \pm 0.7 (<i>F</i> = 10.13)	* 4.1 \pm 1.6 (<i>F</i> = 4.30)

The number of species collected per trawl varied little among the stations (Table 8); however, certain compositional differences were evident in the collections from different sites. *Orthopristis chrysoptera*, *Bairdiella chrysoura*, and *Syngnathus louisianae* increased in abundance from *Syringodium* to *Thalassia* to *Halodule* beds; however, because of wide variation in the numbers collected in replicate trawls, differences in catch among the beds were not significant statistically (ANOVA, *P* > 0.10). The gerreids, *Eucinostomus gula* and *E. argenteus*, were most abundant in *Halodule* beds in October and January (ANOVA, *P* < 0.05), the only months during which they were caught in large numbers. Both species were uncommon at the *Thalassia* bed. Code goby, *Gobiosoma robustum*, was abundant only at the *Syringodium* bed. Although other species were collected in nearly equal numbers in the three seagrass species, *Halodule* yielded mean abun-

dances of non-pinfish higher than those from *Thalassia* and *Syringodium* in January and July (Table 8). *Thalassia* and *Syringodium* yielded statistically similar numbers of non-pinfish in October, January, and July.

Despite major differences in the gross morphology of the three seagrass species, blade density (Table 6) proved to be a better predictor of fish abundance than macrophyte biomass. Using all station-date combinations, there was a significant positive correlation between total number of fishes collected, number of pinfish, and number of non-pinfish (Table 7). Despite low sample numbers (*n* = 3), collections made in January, April, and July showed surprisingly close, and statistically significant, correlations between total number of fishes collected at a given site and macrophyte blade density (Table 7).

Although the *Halodule* bed yielded a higher total number of species (32) than the *Thalassia* and *Syringodium* beds (26 and 24, respectively), the number of species collected was a direct function of the number of individuals collected and may be artifactual. Differences in number of species collected per trawl were rarely significant (Table 8).

Length-frequency analysis of pinfish populations at Indian River stations (Table 9) showed that each of the three smallest size classes increased in total numbers from *Syringodium* to *Thalassia* to *Halodule* beds, but relatively small populations of fish > 80 mm were uniformly distributed over the three habitats. Within-site analysis indicated that nearly 95% of the pinfish population on the *Syringodium* bed were > 35 mm; numerically, smaller fish were much more important at the *Thalassia* and *Halodule* beds, making up 14 and 23.1% of the total, respectively. Consequently, mean pinfish size decreased from *Syringodium* to *Thalassia* to *Halodule* beds, and numbers of individuals increased.

Night collections in Indian River lagoon yielded much larger numbers of fish per trawl than daytime collections in all three of the seagrass beds (Table 10); mean values for all fish species were between two and five times greater at night. The same was true for pinfish as well as non-pinfish. Although only two

TABLE 9.—Distribution of *Lagodon rhomboides* at three seagrass beds in Indian River lagoon, Fla., based on size class. SL is standard length of fish; *N* is the total number of fish collected in a size class.

SL (mm)	<i>Syringodium</i>		<i>Thalassia</i>		<i>Halodule</i>	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
11-15	1	0.3	2	0.3	7	0.7
16-35	13	4.9	79	13.7	201	22.4
36-80	217	81.9	460	79.4	659	73.4
>80	34	12.9	38	6.8	31	3.5

trawls were made for night collections, as opposed to seven in the daytime, variation around the mean values was low; the three beds yielded no statistically similar collections of pinfish or total number of individuals. There were, however, no significant differences among the three beds in numbers of non-pinfish individuals or numbers of species collected. Although night collections yielded higher numbers of individuals than daytime collections, there were few qualitative differences between samples. In January, the relative abundance of pinfish was slightly greater in night collections than in daytime collections in *Halodule* and *Syringodium*; there were slight decreases at all stations in July (<14%) (Tables 8, 10). Certain cryptic species, such as *Syngnathus scovelli*, *Gobiosoma robustum*, and *Myrophis punctatus*, were more abundant in night collections than in daytime samples, but only one species, sea catfish, *Arius felis*, was captured only at night.

DISCUSSION

Comparisons of vegetated and unvegetated habitats have demonstrated the importance of seagrass habitats to a wide variety of juvenile fishes (Reid 1954; Livingston 1975; Weinstein et al. 1977; Orth and Heck 1980). From the present study, it is clear that there is a close relationship between structural complexity of a seagrass bed and patterns of fish abundance. Aboveground biomass was a good indicator of ichthyofaunal abundance in one type of meadow (*Thalassia*), but when examining monotypic

TABLE 10.—Nighttime abundance of fishes and fish species in three seagrass beds in Indian River lagoon, Fla. Values are mean numbers per trawl \pm SD ($n = 2$). * indicate mean values that were not statistically different on a given date (ANOVA and Duncan's multiple range test, $P < 0.05$; F values are provided).

Seagrass bed	January	July
Number of individuals, all species		
<i>Halodule</i>	43.0 \pm 7.0	126.0 \pm 20.0
<i>Thalassia</i>	21.5 \pm 7.5	88.0 \pm 8.0
<i>Syringodium</i>	12.0 \pm 3.0	49.0 \pm 9.0
	($F = 6.62$; $P < 0.10$)	($F = 8.78$)
Number of pinfish		
<i>Halodule</i>	30.0 \pm 7.0	89.0 \pm 11.0
<i>Thalassia</i>	12.0 \pm 2.0	60.0 \pm 7.0
<i>Syringodium</i>	5.0 \pm 1.0	28.5 \pm 5.5
	($F = 9.24$)	($F = 13.72$)
Number of individuals, excluding pinfish		
<i>Halodule</i>	*13.0 \pm 0	*37.0 \pm 9.0
<i>Thalassia</i>	* 9.5 \pm 5.5	*28.0 \pm 1.0
<i>Syringodium</i>	* 7.0 \pm 2.0	*20.5 \pm 3.5
	($F = 0.80$)	($F = 2.17$)
Number of species		
<i>Halodule</i>	*3.5 \pm 0.5	* 5.5 \pm 0.5
<i>Thalassia</i>	*2.5 \pm 0.5	* 4.0 \pm 1.0
<i>Syringodium</i>	*3.0 \pm 0	* 3.5 \pm 0.5
	($F = 1.50$)	($F = 2.17$)

beds of several seagrass species, blade density, rather than biomass, proved to be best correlated with fish abundance.

The observed relationships between fish abundance and structural complexity or type of seagrass meadow are governed by the dispersal of fishes to the beds, habitat preferences of the fishes, and their survival in the meadows. Because most of the fishes on temperate seagrass beds are seasonal residents (Kikuchi and Pères 1977) and because the majority are juveniles, seasonal abundance is related to time of spawning. Many of the most numerous seagrass associates, including *Lagodon rhomboides*, *Leiostomus xanthurus*, *Bairdiella chrysoura*, and *Diplodus holbrookii*, spawn offshore in midwinter (Brady 1981). Differential dispersal of larvae to various field sites, therefore, could have a major influence on the abundance of fishes at a given field location. In a study of ichthyoplankton in Apalachee Bay, Brady (1981) found highest numbers of fish eggs and larvae at station F-12 which yielded the smallest trawl collections of all vegetated sites. Lowest numbers of eggs and larvae were collected at station E-12 where juvenile and adult fishes were most abundant. Similarly, there was no correlation between the abundance of eggs and larvae as determined by Brady and the number of juveniles and adults collected by trawl for species such as *L. rhomboides* and *L. xanthurus*. Clearly, differential dispersal of eggs and larvae does not explain the distributional pattern for juvenile and adult fishes in Apalachee Bay. Because late postlarval fish were collected at all stations in Indian River lagoon and because the sites were in very close proximity (all within a radius of 300 m), differential dispersal of fishes seems unlikely to explain ichthyofaunal differences among sites in the lagoon.

Individual fish species or age groups may actively seek particular habitat types. Two characteristics of seagrass meadows attract fishes—abundance of food and shelter. In earlier studies (Stoner 1980a) it was shown that spatial patterns in the abundance of benthic macroinvertebrates in Apalachee Bay are directly related to seagrass biomass. Because the benthic samples were taken concurrently with fish collections, and on the same stations, strong circumstantial evidence exists for a functional relationship between food abundance and fish distribution. Also, experimental data on the foraging behavior of *Lagodon rhomboides* (Stoner 1982) provide support for the hypothesis that predator and prey distribution may be related to predatory efficiencies of the fishes. *Lagodon rhomboides* was found to be most successful in capturing amphipod prey in habitats composed of *Halodule*; capture rate

was significantly lower in *Thalassia*; and lowest efficiency of predation occurred in *Syringodium*. Therefore, low biomass and high predatory success in the *Halodule* bed would make it the habitat of choice for pinfish and probably other consumers of small invertebrates. Herbivorous pinfish adults, which show a distinct dietary preference for *Syringodium* over other seagrasses (Stoner 1980b), showed largest relative abundance at the *Syringodium* site.

Predation experiments also showed that predatory efficiency is less affected by dense seagrass for small juvenile pinfish than for large juvenile and subadult size classes (Stoner 1982); therefore, the inverse relationship between abundance of large pinfish and seagrass biomass in Apalachee Bay may be a function of decreasing predatory efficiency in heavy seagrass. Conversely, small pinfish, adept at picking small prey from among seagrass blades, show an abundance pattern directly related to seagrass biomass and, hence, food abundance. In correspondence with these observations, it is interesting to note that negative correlations of fishes with seagrass biomass in January, February, and March occurred with numerical dominance by early juvenile fishes which feed in the water column or on small invertebrates of the sediment such as harpacticoid copepods (Stoner 1980b; Livingston 1982). Positive correlations occurred during months when collections were dominated by benthic carnivores (May to October). This observation provides more evidence for the utility of the "ontogenetic trophic unit" concept proposed by Livingston (1980) and Stoner (1980b).

As a more parsimonious explanation of the apparent relationship between fish abundance and seagrass biomass or species, individual fishes may simply prefer areas of high blade density, regardless of seagrass species. The selective advantage of such a habitat preference would be obvious if heavy losses to predation or shortages of appropriate food types occur outside the beds. Careful experimentation will be required to determine which mechanisms are involved in the choice of habitat by seagrass-associated fishes.

Heck and Orth (1980) have suggested that high abundance and species richness of fishes and motile invertebrates in seagrass meadows are, at least, partially due to protection offered by seagrass blades. Experimental evidence for this conclusion exists for crustaceans (Nelson 1979; Coen et al. 1981; Stoner 1982), and it is likely that small fishes are rapidly removed from unvegetated and sparsely vegetated habitats by large, piscivorous predators. Large piscivores are abundant in the seagrass meadows of Apalachee Bay (e.g., *Cynoscion nebulosus*) and are

known to consume juvenile fishes such as *Lagodon rhomboides* (Ryan 1981). The predatory efficiency of most fishes would be reduced with increasing seagrass biomass or blade density. Seine hauls conducted by Gilmore⁴ near the trawl stations in Indian River also yielded large numbers of piscivorous fishes which could have a significant effect on populations of smaller fishes such as *L. rhomboides*, *Eucinostomus* species, and *Orthopristis chrysoptera*. Fifty-three percent of all seine hauls yielded snook, *Centropomus undecimalis*, 41% contained great barracuda, *Sphyraena barracuda*, and 62% contained large grey snapper, *Lutjanus griseus*. Because these piscivores found in the seagrass meadows are visual predators relying on high speed, increasing blade density probably hinders both prey detection and capture. The relatively low density of thin *Syringodium* blades undoubtedly increases foraging efficiency of large predators. Despite low biomass, high blade density in *Halodule* beds (often over 10,000 blades/m²) may provide excellent protection for small and/or juvenile fishes. High biomass and long, wide blades of *Thalassia* may provide better protection for juveniles than *Syringodium*, despite low blade densities.

Seagrass biomass had very little effect on the species richness of ichthyofauna in Apalachee Bay, unlike the relationship shown for invertebrates (Heck and Wetstone 1977; Stoner 1980a). Rather, species richness and occurrence of certain species appeared to be related to the presence of particular microhabitats. Highest species richness was found at the site with low plant biomass (station F-12), where there is a patchy distribution of grasses with occasional clumps of red algae and sponges. The importance of the red algal microhabitat has been reported for fishes from both Apalachee Bay (Stoner and Livingston 1980) and Indian River lagoon (Kulczycki et al. 1981). Similarly, Weinstein and Heck (1979) found that latitudinal variation in the richness of seagrass-associated ichthyofauna was related to the presence of non-seagrass habitats such as coral reefs and mangroves. Consequently, increasing habitat heterogeneity within beds may be more important than seagrass biomass, species, or blade density in determining species richness in fish communities.

Although certain, highly mobile predators such as sharks are known to move into seagrass meadows of Apalachee Bay and the total number of fishes collected per trawl increases, the smaller resident species appear not to leave the beds at night (Ryan 1981) as some do in tropical regions where regular diurnal

⁴R. G. Gilmore, Staff Scientist, Harbor Branch Foundation, Inc., R.R. 1, Box 196, Fort Pierce, FL 33450, pers. commun. April 1981.

movement of fishes and invertebrates between seagrass beds and coral reefs is common (Randall 1965; Ogden and Buckman 1973; Ogden and Zieman 1977). In Apalachee Bay, lack of diurnal change in species composition probably relates to the enormous size of the meadow (continuous for hundreds of square kilometers) and the fact that no alternative habitats are in close proximity except for occasional patches of bare sand or mud. Despite the smaller, band or patchlike nature of seagrass beds in Indian River lagoon, the ichthyofauna found there were also full-time residents. An examination of the food habits of temperate seagrass-associated fishes (Carr and Adams 1973; Livingston 1982) indicates that most consume prey items normally found among the macrophytes. Also, most appear to be visual predators which rest near bottom at night (pers. obs.), taking advantage of the shelter provided by the seagrass blades. It would appear, therefore, that fishes in the temperate regions examined do not move to and from seagrass beds, except for a few species of nocturnal predators which move into the beds at night. Increased catches at night are most likely related to inactivity of many species and the resultant elevation in capture efficiency.

Because trawl efficiency probably decreases with seagrass biomass, fish populations in Apalachee Bay would have been underestimated most severely at the most heavily vegetated station E-12 and least at station F-11; therefore, the relationship between seagrass biomass and fish abundance is probably even more pronounced than that demonstrated. In Indian River lagoon, seagrass biomass was similar at the *Syringodium* and *Halodule* beds, but the high density of *Halodule* blades might serve to reduce trawl efficiency as would high biomass at the *Thalassia* bed. Estimates of fish abundance at the *Halodule* and *Thalassia* beds, therefore, may be low, in relative terms. Because the limited collections made at night yielded much higher numbers of fishes and more clearly separated the stations in Indian River lagoon, future trawl studies should be conducted at night despite the inherent difficulties. New surveys in other areas would be particularly valuable in establishing the universality of relationships observed between fishes and seagrass biomass and seagrass species.

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LITERATURE CITED

- ADAMS, S. M.
1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. *J. Exp. Mar. Biol. Ecol.* 22:269-291.
- BRADY, K. D.
1981. Seasonal and spatial distribution of ichthyoplankton in seagrass beds of Apalachee Bay. M.S. Thesis, Florida State Univ., Tallahassee, 169 p.
- BRIGGS, P. T., AND J. S. O'CONNOR.
1971. Comparison of shore-zone fishes over naturally vegetated and sand-filled bottoms in Great South Bay. *N.Y. Fish Game J.* 18:15-41.
- CARR, W. E. S., AND C. A. ADAMS.
1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Am. Fish. Soc.* 102:511-540.
- COEN, L. D., K. L. HECK, JR., AND L. G. ABELE.
1981. Experiments on competition and predation among shrimps of seagrass meadows. *Ecology* 62:1484-1493.
- GREENING, H. S., AND R. J. LIVINGSTON.
1982. Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities. *Mar. Ecol. Prog. Ser.* 7:147-156.
- HECK, K. L., JR., AND R. J. ORTH.
1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile invertebrate assemblages. *In* V. S. Kennedy (editor), *Estuarine perspectives*, p. 449-464. Acad. Press, N.Y.
- HECK, K. L., JR., AND G. S. WETSTONE.
1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J. Biogeogr.* 4:135-142.
- HOESE, H. D., AND R. S. JONES.
1963. Seasonality of larger animals in a Texas turtle grass community. *Publ. Inst. Mar. Sci. Univ. Tex.* 9:37-47.
- KIKUCHI, T.
1966. An ecological study on animal communities of the *Zostera marina* belt in Tomioka Bay, Amakusa. *Kyushu Univ. Publ., Amakusa Mar. Biol. Lab.* 1:1-106.
1974. Japanese contributions on consumer ecology in eelgrass (*Zostera marina* L.) beds, with special reference to trophic relationships and resources in inshore fisheries. *Aquaculture* 4:145-160.
- KIKUCHI, T., AND J. M. PÉRÈS.
1977. Consumer ecology of seagrass beds. *In* C. P. McRoy and C. Helfferich (editors), *Seagrass ecosystems: a scientific perspective*, p. 147-193. Marcel Dekker, N.Y.

- KJELSON, M. A., AND G. N. JOHNSON.
1978. Catch efficiencies of a 6.1-meter otter trawl for estuarine fish populations. *Trans. Am. Fish. Soc.* 107:246-254.
- KULCZYCKI, G. R., R. W. VIRNSTEIN, AND W. G. NELSON.
1981. The relationship between fish abundance and algal biomass in a seagrass—drift algae community. *Estuarine Coastal Mar. Sci.* 12:341-347.
- LIVINGSTON, R. J.
1975. Impact of kraft pulp-mill effluents on estuarine and coastal fishes in Apalachee Bay, Florida, USA. *Mar. Biol. (Berl.)* 32:19-48.
1980. Ontogenetic trophic relationships and stress in a coastal seagrass system in Florida. In V. A. Kennedy (editor), *Estuarine perspectives*, p. 423-435. Acad. Press, N.Y.
1982. Trophic organization of fishes in a coastal seagrass system. *Mar. Ecol. Prog. Ser.* 7:1-12.
- LIVINGSTON, R. J., R. S. LLOYD, AND M. S. ZIMMERMAN.
1976. Determination of sampling strategy for benthic macrophytes in polluted and unpolluted coastal areas. *Bull. Mar. Sci.* 26:569-575.
- MARTIN, F. D., AND M. COOPER.
1981. A comparison of fish faunas found in pure stands of two tropical Atlantic seagrasses, *Thalassia testudinum* and *Syringodium filiforme*. *Northeast Gulf Sci.* 5:31-37.
- NELSON, W. G.
1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.* 38:225-245.
- OGDEN, J. C., AND N. S. BUCKMAN.
1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* 54:589-596.
- OGDEN, J. C., AND J. C. ZIEMAN.
1977. Ecological aspects of coral reef-seagrass bed contacts in the Caribbean. *Proc. Third Int. Coral Reef Symp.*, p. 377-382. Univ. Miami.
- ORTH, R. J., AND K. L. HECK, JR.
1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—fishes. *Estuaries* 3:278-288.
- RANDALL, J. E.
1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255-260.
- REID, G. K., JR.
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. *Bull. Mar. Sci. Gulf Caribb.* 4:1-94.
- ROBERTSON, A. I.
1980. The structure and organization of an eelgrass fish fauna. *Oecologia (Berl.)* 47:76-82.
- RYAN, J. D.
1981. Nocturnal predator-prey relationships of some fishes in a temperate seagrass meadow. M.S. Thesis, Florida State Univ., Tallahassee.
- STONER, A. W.
1980a. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.* 30:537-551.
1980b. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses. *Fish. Bull., U.S.* 78:337-352.
1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 58:271-284.
1983. Distributional ecology of amphipods and tanaidaceans associated with three seagrass species. *J. Crustacean Biol.* 3:505-518.
- STONER, A. W., AND R. J. LIVINGSTON.
1980. Distributional ecology and food habits of the banded blenny, *Paraclinus fasciatus* (Clinidae): a resident in a mobile habitat. *Mar. Biol. (Berl.)* 56:239-246.
1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* 1984:174-187.
- WEINSTEIN, M. P., C. M. COURTNEY, AND J. C. KINCH.
1977. The Marco Island estuary: a summary of physicochemical and biological parameters. *Fla. Sci.* 40:97-124.
- WEINSTEIN, M. P., AND K. L. HECK, JR.
1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panamá and in the Gulf of Mexico: composition, structure and community ecology. *Mar. Biol. (Berl.)* 50:97-107.
- ZIMMERMAN, M. S., AND R. J. LIVINGSTON.
1976. Seasonality and physico-chemical ranges of benthic macrophytes from a north Florida estuary (Apalachee Bay). *Contrib. Mar. Sci. Univ. Tex.* 20:33-45.
1979. Dominance and distribution of benthic macrophyte assemblages in a north Florida estuary (Apalachee Bay, Florida). *Bull. Mar. Sci.* 29:27-40.