Epibenthic fish communities on Florida Bay banks: relations with physical parameters and seagrass cover

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ABSTRACT: Epibenthic fish communities residing in seagrass beds on shallow (<0.5 m) mudbanks in Florida Bay, USA, were quantitatively sampled with a throw trap method. The overall average density of 11 fish m^{-2} was substantially higher than most previously reported densities for seagrass habitats. Four sites, representing 4 different subenvironments of Florida Bay, differed widely in species composition and densities of individual species; results of discriminant function analysis indicated that fish communities at the 4 sites were relatively distinct. Species composition at different sites is proposed to be a result of complex interactions between the deterministic influence of habitat quality and the stochastic influence of larval availability. Restricted water circulation, effected by the network of banks, and different sources of water mass exchange are proposed as constraints on larval availability. Differences in species richness and fish densities across individual banks corresponded to gradients in depth, sediment structure, detrital loads, and various measures of seagrass structural complexity. The greater physical stress on top of a bank appeared to limit species richness, while fish densities across individual banks were regulated by habitat gradients. Multiple regression analysis indicated that the standing crop of seagrasses and the accumulation of vegetation litter were important determinants of fish densities; physical factors, such as depth and sediment structure, were also influential.

INTRODUCTION

An extensive body of information has been published regarding ecological relations of fishes inhabiting seagrass ecosystems (see Pollard 1984 for recent review). One area of particular interest concerns the role of the structural complexity of a seagrass bed in determining faunal densities. The functional means by which seagrass structure enhances densities is thought to be a reduction in predation risk and/or increased food availability (e.g. Heck & Orth 1980, Orth & Heck 1980, Stoner 1983).

While the importance of the architectural structure of the seagrass canopy has been examined for several infaunal and epifaunal invertebrates (Orth et al. 1984 and references therein), only limited information is available for fishes. Martin & Cooper (1981), Huh (1984), and Middleton et al. (1984) noted contrasts in the fish communities in meadows dominated by different seagrass species, but did not quantify differences in the physical structure of the grassbeds. Orth & Heck (1980) found an association of both species richness and total abundance with eelgrass biomass in Chesapeake Bay, but did not separate this effect from regular seasonal cycles in abundance. Stoner (1983) specifically examined different aspects of the seagrass canopy, and found fish density most correlated with seagrass biomass in one location, but with blade density in another location. Bell & Westoby (1987a) found fish densities associated with canopy height and seagrass density on a narrow scale, but the relationship weakened when examined on a broader scale (Bell & Westoby 1987b).

In addition to mechanisms of predation and food availability (as reflected in correlations of fish density with seagrass architecture), the grassbed fish community is also structured by physical characteristics, including water temperature, salinity, and depth (Livingston 1982), the presence of additional algal and sponge microhabitats (Weinstein & Heck 1979, Heck & Orth 1980), and water circulation patterns (Adams 1976). In

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a North Carolina estuary, Adams (1976) found that seagrass beds located near an oceanic inlet had more subtropical species and earlier arrivals of recruits than did interior grassbeds. Stoner (1986) also noted a greater species richness closer to the inlet of an estuary, although this difference disappeared when samples were rarefied to balance differences in fish abundance. Circulation patterns are likely to be especially important to South Florida faunas, where mixing of West Atlantic, Gulf of Mexico, and Caribbean forms occurs (Robins et al. 1986).

Examination of the influence of both physical and vegetational (seagrass) factors requires a range of conditions within a single geographic location. The unique system of shallow (<0.5 m), seagrass-covered mudbanks running throughout Florida Bay provides an excellent opportunity for such study, due to strong intra- and inter-bank habitat variability. Gradients in seagrass cover, depth, and sediment structure occur within individual banks as a result of bank contour and wind stress patterns (Powell et al. 1987b). The network of banks divides the Bay into discrete basins of increasingly restricted circulation with distance from open ocean waters (Ginsburg 1956, Fleece 1962), resulting in relative isolation of water masses and marked differences in tidal range and salinity (Powell et al. 1987b). Subenvironment delineations for Florida Bay have been proposed based on tidal flux (Ginsburg 1956), sources of water mass exchange (reflected in mollusk distributions, Turney & Perkins 1972), and distributions of seagrass and algae (Zieman & Fourqurean 1985).

The fauna of a seagrass meadow can be subdivided into several categories, dependent on microhabitat (Kikuchi & Peres 1977). For fishes, perhaps the most useful distinction is between epibenthic species, typically small fish residing within the seagrass canopy, and pelagic species, typically larger, more active fishes present in the water column above the grass canopy. In this paper we concentrate on the epibenthic component, with the following objectives: (1) Characterize the fish community inhabiting seagrass meadows on Florida Bay banks and examine intra-bank zonation. (2) Determine the variability in species composition and densities across subenvironments in Florida Bay and assess the distinctiveness of bank communities in different subenvironments. (3) Analyze the relative contribution of a suite of physical and vegetational parameters in determining the densities of fish on the banks.

METHODS

Study sites. Florida Bay's banks differ from most previously examined seagrass ecosystems due to their shallow depth and near exposure at low tide or during seasonal periods of low water level. Resident fishes must adapt to stresses not present in permanently submerged grassbeds, including wading bird predation, temperature extremes, wave turbulence, and potential desiccation.

Physical layout and sedimentary characteristics of carbonate mudbanks in Florida Bay have been described by Ginsburg (1956), Scholl (1966), and Schomer & Drew (1982). The banks are generally flat on top, sloping on either side into basins of up to 3 m in depth. A predominant pattern of easterly trade winds, with a strong northerly component in winter (Echternacht 1975, Warzeski 1976, Schomer & Drew 1982, Powell et al. 1987b), results in different water turbulence patterns on either side of a bank, i.e. a windward and leeward side (Ginsburg 1956). Sediment granulometric properties, the growth form of seagrasses, and detrital loads vary considerably across individual banks (Powell et al. 1987b).

Four sampling sites, corresponding to the Northeast, East Central, Atlantic, and Gulf vegetational subdivisions of Zieman & Fourqurean (1985), were selected for this study (Fig. 1). The 4 sites differed broadly with regard to several physical and vegetational parameters (Table 1). For complete description of the sites, see Powell et al. (1987b). The Northeast site, near Eagle Key, had a minor tidal range ($\bar{x}$ = 3.3 cm d^{-1}) and relatively sparse growth of turtle grass *Thalassia testudinum*. This area experienced a wide range in salinity, with low salinities a result of freshwater input from the Everglades and high salinities a result of high evapotranspiration rates (Powell et al. 1987b). We sampled 2 stations (3 km apart) along this bank to examine heterogeneity within a subenvironment. The East Central site, near Cowpens Keys, had no direct terrestrial freshwater input, a minor salinity range, a minor tidal range ($\bar{x}$ = 4.5 cm), and relatively dense growth of *T. testudinum*. This bank was also sampled at 2 stations (2 km apart). The Atlantic site, near Buchanan Key, had a significant tidal range ($\bar{x}$ = 17.3 cm), no terrestrial freshwater input, a minor salinity range, and dense growth of *T. testudinum*. This site had some coverage by finger coral (*Porites* sp.) and relatively high coverage by several species of green algae, particularly on the windward side of the bank. The Gulf site, near Oyster Keys, had some terrestrial freshwater input, a minor salinity range, a marked tidal range ($\bar{x}$ = 68.9 cm), and mixed seagrass meadows of *T. testudinum*, shoal grass *Halodule wrightii*, and manatee grass *Syringodium filiforme*. The seagrass *Halophila englemanni* and several species of green algae occurred sporadically across the bank. While the first 3 banks were narrow, between 140 and 230 m in breadth, the Gulf bank was 1 km wide.

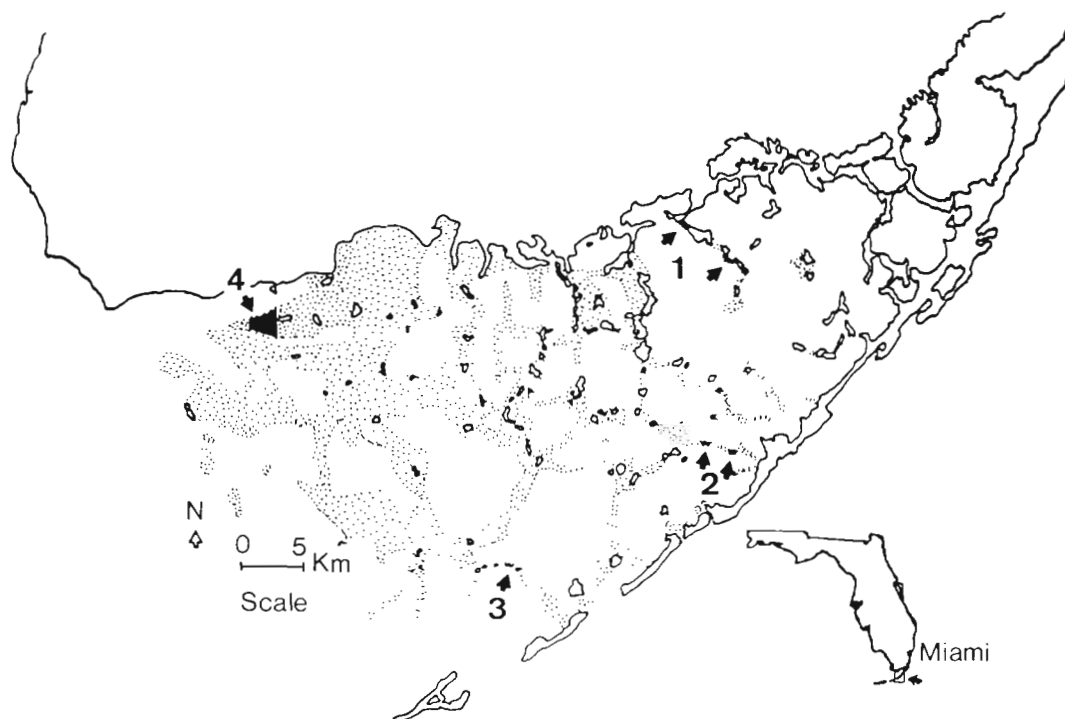At both the Northeast and East Central sites, rela-

Fig. 1. Florida Bay. Pattern of bank development and location of sampling sites. Solid lines: emergent land; stippled areas: shallow banks. 1 = Northeast site, 2 = East Central, 3 = Atlantic, and 4 = Gulf

tively minor differences in seagrass parameters and fish densities occurred between the 2 stations (Powell et al. 1987b). The 2 stations within each site, therefore, were combined for further analysis.

Sampling regime. Temperature and tide data were provided by continuous water temperature recorders placed on top of each site and water level recorders in deeper water adjacent to each site. Sediments on each

transect of each site were analyzed for size structure and percent organic content (Powell et al. 1987b).

We sampled the epibenthic fishes 3 times a year during 1984 and 1985, with the sampling periods corresponding to the 3 ecologically distinct seasons of Florida Bay (Powell et al. 1987b). The first (Jan–Mar), in the middle of the dry season, has low water temperatures, salinities, and mean water levels. The second

Table 1. Mean values (total range for salinity) of physical and vegetational parameters at 4 sampling sites in Florida Bay, USA. Tide, temperature, and salinity values were averaged over 2 yr (1984, 1985), sediment parameters are from Aug, 1985 sampling, and seagrass values were averaged over the 6 sampling series

	Gulf	Atlantic	East Central	Northeast
Daily tidal range (cm)	68.9	17.3	4.5	3.3
Daily temp range (°C)	4.9	3.5	5.0	4.6
Salinity (ppt)	35.3	37.4	36.3	28.4
Salinity range	28–40	35–42	27–44	17–43
Sediment silt (%)	64.6	35.7	42.0	67.1
Sediment organics (%)	11.6	8.7	8.8	8.7
Standing crop m^{-2}	36.7	79.5	55.3	30.0
Thalassia shoots m^{-2}	99	1074	872	663
Halodule shoots m^{-2}	548	25	16	23
Thalassia length (mm)	166.3	70.1	74.9	71.8
Thalassia width (mm)	9.3	5.8	5.0	4.4
Total blade density m^{-2}	1854	2903	2185	1757
Leaf area ($m^2 m^{-2}$)	0.71	1.22	0.87	0.56
Canopy height (mm)	209	92	98	94
Seagrass litter m^{-2} (g)	264	443	1246	397

(May–Jul), in the first half of the wet season, is characterized by low mean water level, high water temperatures, and increasing salinities. The third (Sep–Nov), in the second half of the wet season, has high mean water levels, high temperatures and falling salinities.

This sampling regime was designed primarily to examine spatial distribution of fishes in conjunction with variability in structural characteristics of the seagrass habitat. The 3 series per year were not intended to assess seasonal cycles but rather to provide replicates of our sampling effort that would cover the range of environmental characteristics encountered in Florida Bay.

Sampling procedure. A 1 m^2 throw trap (Kushlan 1981) was used to collect quantitative fish samples. The effective depth of the trap, a 45 cm deep box without top or bottom, was extended to 1 m with a net (3 mm square mesh) surrounding the top edges. A float cord around the top raised the net to the water's surface, preventing entry or exit of animals.

To collect a sample, the trap was thrown so that it landed evenly on the bank, and it was immediately pushed into the sediment. Fish were removed from the trap with a 1 m wide, framed net (bar seine) with 3 mm mesh. All vegetation litter (primarily dead seagrass leaves) and drift algae inside each trap were removed and weighed separately (wet weight). Each trap was seined a minimum of 10 times and until 3 successive passes encountered no organisms. The bar seine was typically forced 2 to 4 cm into the sediment during final seining efforts to remove shallow burrowers.

With each throw trap, 2 seagrass samples at opposite outside corners were collected with 15.3 cm diameter cores. Seagrass species, shoot density, standing crop (dry weight), leaf surface area, and mean blade length and width were determined from core samples.

To assess within-bank heterogeneity, we used a stratified random design. Six throw trap samples were randomly collected along 70 m transects located along the long axis of the bank on the top and on either side about 50 cm deeper than the top. A fourth, deeper transect was sampled on the north side of the wide Gulf bank, with its greater topographic relief.

All 3 transects at the Atlantic site and the shallowest transect at the Gulf site were sampled at both low and high tide in an effort to account for animal movements that were mediated by tidal flux. Nearly all species tested showed no difference in density between high and low tide at any of the transects where comparisons were made (ANOVA, $p < 0.05$, Powell et al. 1987b). Data from the 2 tidal stages were therefore combined for all further analyses.

As a preliminary test to determine if species composition and/or abundances differed between day and

night, we collected 8 throw traps by day (0900 to 1700 h) and 8 traps by night (2100 and 0400 h) within a 24 h period in November 1986. All traps were collected from the leeward transect of the East Central site. Traps thrown at night were pushed into the sediment and closely covered with 1 mm mesh screening to prevent entry or escape. Fish were collected the following day, using the regular sampling procedure; this ensured visual detection of all individuals.

Data analysis. All statistical analyses were performed with the SPSS/PC+ package (Norusis 1986). To reduce problems of non-normality and heteroscedasticity all data were log-transformed prior to analyses. Due to the large number of samples (828 throw traps), further minor violations of assumptions were considered insignificant relative to the robustness of the selected statistical tests (Tabachnick & Fidell 1983).

The distinctiveness of the fish community across sites was assessed using discriminant function analysis and subsequent classification of each trap sample. Transformed densities of all species with at least 12 individuals caught were used as discriminating variables. Because group covariance matrices were not equal, classification was based on separate group covariance matrices (Tabachnick & Fidell 1983). Percentages of classification into each site were then determined for each site and each transect (leeward, top, and windward sides of banks).

The relative importance of physical and vegetational habitat parameters were examined with multiple regression techniques, using a 2-step process. Dummy variables incorporating season and year of collection were initially forced as a set into the equation to control for density differences caused by seasonal variation. Habitat parameters were then entered into the equation stepwise, with a $p = 0.01$ criterion of entry into the equation. At each step habitat variables already in the equation were removed if p rose above 0.10 due to entry of other factors. The following measured habitat variables were available for entry:

Standing crop = mean dry weight of seagrass m^{-2}
Canopy height = mean length of longest blade of each seagrass shoot
Total shoot density = density of all seagrass shoots m^{-2}
Thalassia shoots = density of *Thalassia* shoots m^{-2}
Blade density = shoot density × mean number of blades per shoot
Leaf area = mean length × mean width × blade density
Litter = mean wet weight of seagrass litter m^{-2}
Percentage silt = percentage of sediment in silt/clay fraction (<63 μm)
Percentage organics = percentage organic content of sediment, or AFDW dry weight^{-1}

Depth = mean water depth at each transect during each sampling series

Temperature = water temperature

Temperature range = mean daily range in water temperature for the month

Salinity = mean salinity for the month

For each species, results of multiple regression analysis were examined for normality, linearity, homoscedasticity of residuals and absence of outliers (Tabachnick & Fidell 1983). Only those species that did not show obvious violations of these assumptions are presented in the results. Other species were not abundant enough to meet the assumptions.

The most useful indicator of the importance of individual independent variables, according to Tabachnick & Fidell (1983), is the squared semi-partial correlation (sr^2). In the format used in this study, the sr^2 values reveal the additional percentage of variation in density explained by a variable after all other variables in the equation have been taken into account (in contrast to the typically reported form for stepwise regression, where the sr^2 value is adjusted only for the variables preceding it in entry).

RESULTS

Results from day-night comparisons indicated no difference for any of the species tested (ANOVA, $p > 0.05$). Total numbers caught were similar between day and night for all species (Table 2); by day 10

Table 2. Total number of individuals per species listed caught by day and night at a single location of the East Central site within a 24 h period. n = 8 throw traps for each time period

Species	Day	Night
Opsanus beta	11	21
Floridichthys carpio	9	13
Lucania parva	9	4
Anarchopterus criniger	26	28
Cosmocampus albirostris	2	0
Syngnathus scovelli	3	1
S. floridae	0	1
Hippocampus zosterae	1	0
Paraclinus fasciatus	6	1
Chasmodes saburrae	0	1
Diplogrammus pauciradiatus	15	16
Gobiosoma robustum	25	23

species and 107 individuals were caught, while night totals were 10 species and 109 individuals. Based on these results and similar results of Huh (1983), we concluded that daytime sampling alone provided quantitative assessment of epibenthic fish densities on bank grassbeds.

A total of 56 species of fish was collected over the 2 yr

period (Table 3). Species richness varied considerably among the 4 sites, with 35 species caught at the Gulf site, 33 at the Atlantic, 21 at the East Central, and 18 at the Northeast site. Densities of the 10 most abundant species were all significantly different among sites (ANOVA, all $p < 0.001$, Table 4). While the density of all species combined was higher at the 2 southern bay sites (Atlantic and East Central) than the 2 northern bay sites (Gulf and Northeast), there was no consistent pattern among individual species. The populations of the 2 most abundant species overall (goldspotted killifish *Floridichthys carpio* and rainwater killifish *Lucania parva*) were most dense at the East Central site. The Atlantic site had the highest densities of code goby *Gobiosoma robustum*, fringed pipefish *Anarchopterus criniger*, and spotted dragonet *Diplogrammus pauciradiatus*; the highest densities of gulf pipefish *Syngnathus scovelli*, dwarf seahorse *Hippocampus zosterae*, and mojarras *Eucinostomus* spp. were at the Gulf site. While the Northeast site had the lowest species richness, 2 of the top 10 species were most abundant there (bay anchovy *Anchoa mitchilli*, and gulf toadfish *Opsanus beta*).

There was a large difference in the structure of the seagrass canopy within individual banks (Fig. 2). The leeward transect generally had more luxuriant seagrass, with a higher standing crop, taller canopy height, and more litter accumulation than the top or windward transects. A gradient in these parameters from leeward to windward side was clear at the 2 southern sites (Atlantic and East Central), but was less well defined at the 2 northern sites. Additional differences in vegetational parameters across and within sites were presented in Powell et al. (1987b).

Species richness tended to follow consistent patterns among transects within sites. At all 4 sites fewer species were collected on the top (shallowest) transect of a bank than on the side transects (Fig. 3). When collections were rarefied to n = 200 individuals (using the explicit method of Heck et al. 1975), thus controlling for differences in total fish abundance, the pattern of species richness differed little from that of the original data (Fig. 3).

The mean density of all species combined and the mean total biomass of fish per m^2 followed a different pattern from that of species richness. Both were typically highest on the leeward side, intermediate on top, and lowest on the windward side (Fig. 3). Individual species generally followed this pattern (Fig. 4), although *Floridichthys carpio* was consistently more abundant on top of the banks, and *Anarchopterus criniger* was typically less abundant on top than on either side of a bank.

Discriminant function analysis resulted in 3 significant functions separating the 4 sites (Table 5). Com-

Table 3. Number of species and number of individuals caught in throw traps at 4 sites in Florida Bay. Values are summed across 6 sampling series. n = total throw trap samples at each site

	Northeast n = 216	East Central n = 216	Atlantic n = 216	Gulf n = 180	Total n = 828
Number of species	18	21	33	35	56
Ophichthidae					
Ahlia egmontis	0	0	2	0	2
Myrophis punctatus	0	0	3	3	6
Clupeidae					
Harengula jaguana	0	0	0	2	2
Jenkinsia lamprotaenia	0	1	0	0	1
Opisthonema oglinum	6	0	0	0	6
Engraulidae					
Anchoa mitchilli	126	0	0	5	131
Synodontidae					
Synodus foetens	0	0	2	2	4
Batrachoididae					
Opsanus beta	508	471	391	100	1470
Antennariidae					
Histrio histrio	0	2	0	0	2
Exocetidae					
Hemiramphus sp.*	0	0	1	0	1
Belonidae					
Strongylura notata	4	3	2	2	11
Cyprinodontidae					
Cyprinodon variegatus	2	3	0	0	5
Floridichthys carpio	582	1243	465	197	2487
Lucania parva	277	1076	148	287	1788
Poeciliidae					
Poecilia latipinna	0	0	0	1	1
Atherinidae					
Atherinomorus stipes	1	8	8	0	17
Hypoatherina harringtonensis	0	0	1	0	1
Menidia penisulae	5	0	0	0	5
Syngnathidae					
Anarchopterus criniger	61	94	367	75	597
Cosmocampus albirostris	0	0	13	0	13
Hippocampus zosterae	66	11	89	232	398
Syngnathus floridae	2	1	8	14	25
S. louisianae	0	0	1	1	2
S. scovelli	59	34	20	152	265
Serranidae					
Diplectrum bivittatum	0	0	0	1	1
Carangidae					
Trachinotus falcatus	0	1	0	0	1
Lutjanidae					
Lutjanus griseus	0	3	3	0	6
L. synagris	0	0	0	3	3
Gerreidae					
Eucinostomus spp.**	4	23	37	101	165
Haemulidae					
Haemulon parrai	0	0	1	0	1
H. plumieri	0	0	0	3	3
H. sciurus	0	0	6	16	22
Haemulon sp.*	0	0	0	2	2
Orthopristes chrysoptera	0	0	0	7	7
Sparidae					
Archosargus probatocephalus	0	0	0	2	2
Lagodon rhomboides	3	32	18	29	82
Sciaenidae					
Bairdiella chrysoura	0	0	0	1	1
Cynoscion nebulosus	0	0	0	1	1

Table 3 (continued)

	Northeast	East Central	Atlantic	Gulf	Total
Scaridae					
Sparisoma sp [*]	0	0	2	0	2
Clinidae					
Chaenopsis ocellata	0	0	1	0	1
Paraclinus fasciatus	1	12	29	1	43
P. marmoratus	0	0	10	0	10
Blenniidae					
Chasmodes saburrae	0	3	3	1	7
Callionymidae					
Diplogrammus pauciradiatus	0	6	232	1	239
Gobiidae					
Barbulifer ceuthoecus	0	0	2	0	2
Gobionellus saepepallens	0	0	1	0	1
Gobiosoma robustum	4	255	706	290	1255
Microgobius gulosus	71	24	0	0	95
Soleidae					
Achirus lineatus	0	0	0	5	5
Trinectes maculatus	0	0	0	1	1
Cynoglossidae					
Symphurus plagiusa	0	0	1	46	47
Balistidae					
Monacanthus ciliatus	0	0	0	15	15
M. hispidus	0	0	0	1	1
Ostraciidae					
Lactophrys quadricornis	0	0	0	1	1
Tetraodontidae					
Sphoeroides nephelus	0	0	1	0	1
Diodontidae					
Chilomycterus schoepfi	0	0	3	0	3

[*] Unidentifiable juveniles
[**] Primarily *Eucinostomus gula*, with some *E. harengulus* and possibly *E. jonesii*

Table 4. Mean density (geometric means) of fish m^{-2} at 4 sites in Florida Bay, and results of 1-way ANOVAs comparing densities across sites. Sites with the same superscript were not significantly different (SNK, $\alpha = 0.05$). All statistical analyses were performed on log-transformed data. All F values were significant at $p < 0.01$

Species	Gulf	Atlantic	East Central	Northeast	F
All species combined	6.48[1]	9.37[2]	11.91[2]	6.47[1]	19.1
Lucania parva	0.66[1]	0.31	2.11	0.80[1]	44.0
Floridichthys carpio	0.51	1.02	3.08	1.64	47.9
Gobiosoma robustum	1.10	1.99	0.65	0.01	114.1
Opsanus beta	0.39	1.16[1]	1.37[1,2]	1.58[2]	31.8
Anarchopterus criniger	0.22[1]	1.01	0.24[1]	0.16[1]	50.8
Syngnathus scovelli	0.49	0.06[1]	0.11[1]	0.19	33.1
Hippocampus zosterae	0.86	0.26[1]	0.03	0.18[1]	68.8
Diplogrammus pauciradiatus	0.00[1]	0.61	0.02[1]	0.00[1]	106.9
Anchoa mitchilli	0.01[1]	0.00[1]	0.00[1]	0.12	9.7
Eucinostomus spp.	0.34	0.10[1]	0.07[1]	0.01	31.2

parison of the scores of each site (evaluated at group centroids) on the 3 functions and the correlations of individual species indicated that Function 1 separated the Atlantic site from the other 3, and Function 2 separated the Gulf site from the East Central and Northeast,

with Function 3 separating the latter. Classification based on predictor variables (densities of each species) resulted in an overall correct classification rate of 74 %, indicating consistent differences in the 4 resident fish communities (Table 6). In addition, it was evident that
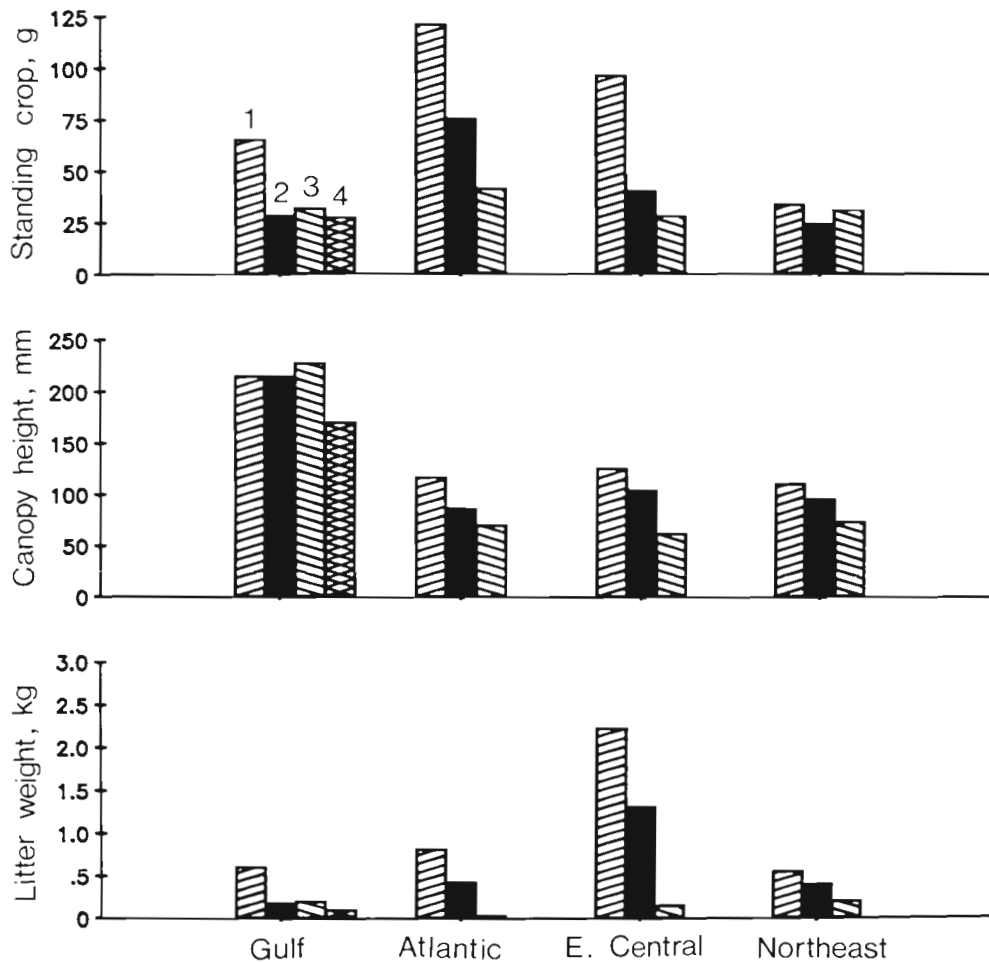
Fig. 2. Mean seagrass standing crop (g m^{-2}), canopy height (mm), and litter accumulation (kg m^{-2}) along each transect (1 to 4) of each site. Transect 1 = sheltered or leeward side of bank, 2 = top, 3 = exposed or windward side. A deeper windward transect (Transect 4) was sampled only at the Gulf site. n = 72 grass samples and 36 litter samples on Transects 1, 3, and 4 at the Gulf site; n = 146 grass samples and 72 litter samples on all other transects

Table 5. Results of discriminant function analysis of fish species among 4 sampling sites. All 3 functions were significant at p < 0.001 and all were included in the classification process

Function	1	2	3
Eigenvalue	1.32	1.06	0.25
Variance explained (%)	50.0	40.4	9.6
Scores at group centroids			
Gulf	−0.01	1.95	0.04
Atlantic	1.80	−0.52	−0.15
East Central	−0.61	−0.60	0.75
Northeast	−1.18	−0.50	−0.62

there were greater similarities between some sites than between others. The Northeast and East Central sites were misclassified most often as each other and rarely as the Atlantic or Gulf sites. The latter sites were distinct from each other, with misclassification for both being to either the Northeast or East Central sites.

As a further comparison of intra-site differences, misclassification rates for discriminant function analysis were determined for each transect of each site (Table 7). At the Gulf site, throw trap samples from the leeward and top sides were misclassified more than the 2 windward transects, and most often fell into the Atlantic and East Central sites. Misclassification at the Atlantic site indicated different site affinities for each transect; traps on top of the bank tended to be misclassified as East Central, while leeward traps were classed as Gulf and windward traps as Northeast. At the East Central site, the windward transect was classified more as Northeast than correctly classified. While misclassifications on top also fell into the Northeast site, the leeward side was more similar to the Atlantic site. All 3 transects of the Northeast site were most often misclassified to the East Central site, with
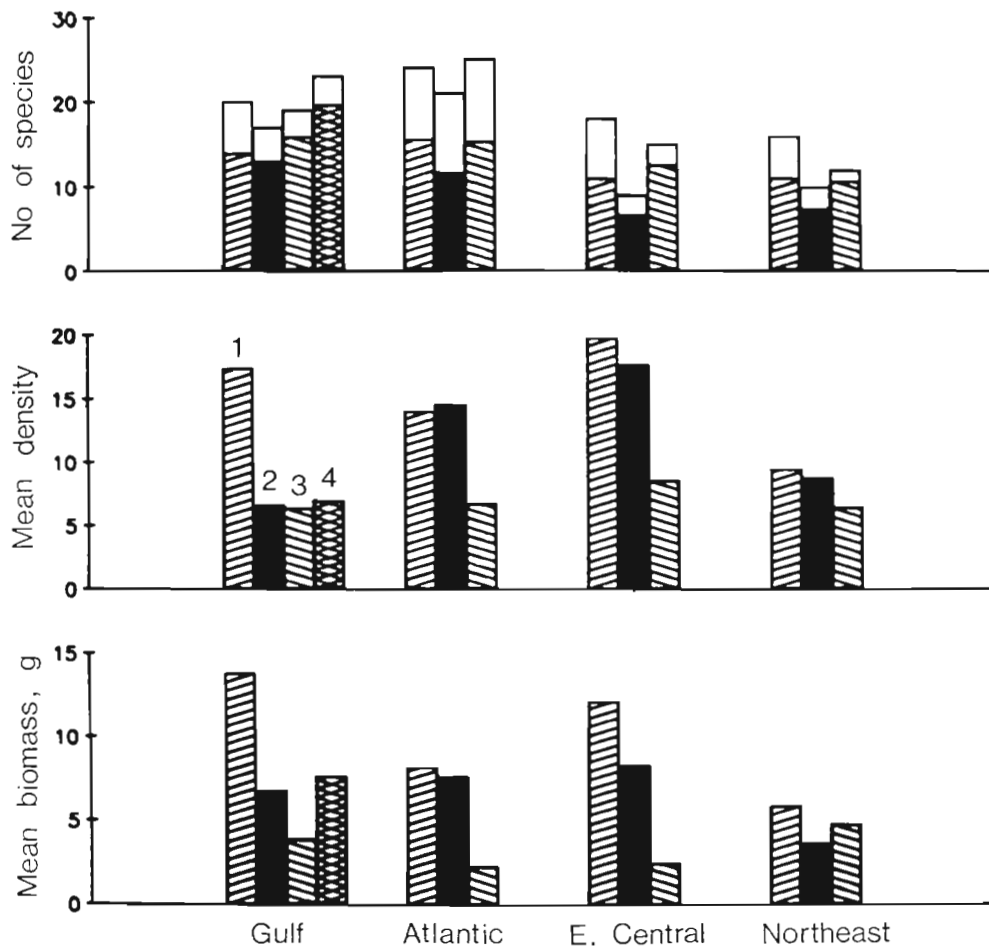
Fig. 3. Total number of species, mean density of fish m^{-2} (all species combined), and mean fish biomass (g m^{-2}) along each transect (1 to 4) of each site. Transect 1 = leeward side of bank, 2 = top, 3 = windward side. A deeper windward transect (Transect 4) was sampled only at the Gulf site. n = 36 throw trap samples on Transects 1, 3, and 4 at the Gulf site; n = 72 on all other transects. Hatched bars in top graph indicate the number of species collected on each transect after samples were rarefied to n = 200 individuals to control for differences in total abundance; open bars indicate the number of species without rarefaction

Table 6. Results of classification of each throw trap using discriminant functions derived from all traps. n = number of traps collected from each site. Diagonal elements show the percentage of traps correctly classified at each site

Actual group	Predicted membership (%)			
	Gulf	Atlantic	East Central	Northeast
Gulf (n = 180)	76.7	7.2	6.7	9.4
Atlantic (n = 216)	5.6	77.3	10.2	6.9
East Central (n = 216)	3.7	12.5	61.1	22.7
Northeast (n = 216)	4.6	0.5	14.4	80.6

the greatest frequency of misclassification occurring for bank top samples.

Results of multiple regression analysis indicated that a variety of habitat parameters were significant determinants of fish densities (Table 8). Each final equation incorporated several habitat variables after season and year had been taken into account, suggesting a com-

plex relation of fish densities with the physical environment and various aspects of seagrass architecture.

Floridichthys carpio was generally limited to the more shallow areas of the banks, resulting in a strong negative relationship with water depth, which explained 25.7 % of the variation in the fish's density (Table 8). For *Lucania parva* the highest sr^2 value was
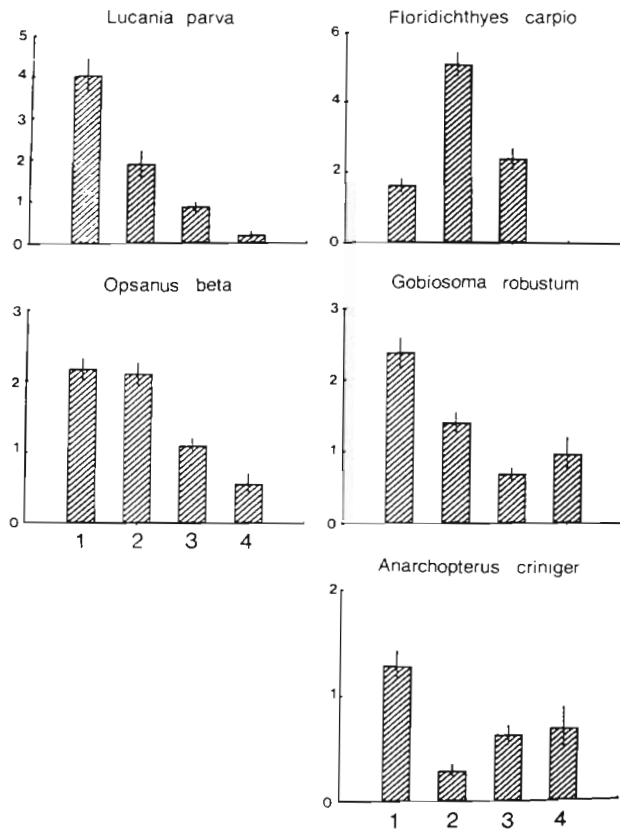
Fig. 4. Mean density of fish on each sampling transect (all sites combined). Transect 1 = leeward, 2 = top, 3 = windward, and 4 = deeper windward transect (sampled only at the Gulf site). n = 252 throw traps on Transects 1 and 3, 288 on Transect 2, and 36 on Transect 4. Error bars are standard errors

with litter, which explained 12.1 % of the variance in density. There was a positive relationship with litter for the other species as well, except *Hippocampus zosterae*. For *Anarchopterus criniger* and *Gobiosoma robustum* the highest sr^2 was with seagrass standing crop. The highest sr^2 for *H. zosterae* was with *Thalassia* density, and the relationship was negative. This effect was probably due to the high density of *H. zosterae* at the Gulf site (Table 4), where *Thalassia* was sparse but *Halodule* and *Syringodium* were common, resulting in relatively high densities of all seagrass shoots (Table 1).

Once the negative relationship with *Thalassia* density had been taken into account, total shoot density had a positive relationship with *H. zosterae* densities. For *Opsanus beta*, the highest sr^2 was with *Thalassia* density, reflecting its low abundance at the Gulf site. The combined influence of the habitat variables resulted in regression equations explaining from 24.8 % (*H. zosterae*) to 42.7 % (*F. carpio*) of the variance in fish densities.

DISCUSSION

The species composition of fishes in Florida Bay differed from that of seagrass beds on the Atlantic side of the Florida Keys (Springer & McErlean 1962, Powell et al. unpubl.) and nearby Biscayne Bay (Low 1973, Sogard 1982, Berkeley 1984), primarily due to the absence of tropical species. Notably missing in Florida Bay were the parrotfishes (Scaridae), scorpionfishes (Scorpaenidae), cardinalfishes (*Astrapogon* spp.), surgeonfishes (Acanthuridae), clingfishes (Gobiesocidae), wrasses (Labridae) and additional species of the Gobiidae and Clinidae. Tabb et al. (1962) and Schmidt (1979) also noted a dominance of the Bay fauna by Gulf temperate species. Winter temperatures in the shallow, minimally flushed waters of the Bay are much colder than those of oceanic waters exposed to the same air temperatures (Hudson et al. 1976, Roberts et al. 1982). In addition, temperature stress is greater on Florida Bay banks than in adjacent basins (Powell et al. 1987b). Thus, despite its subtropical geographic location, Florida Bay is apparently too harsh an environment for tropical species.

Densities of fish inhabiting seagrass beds on Florida Bay banks (overall mean = 11 fish m^{-2}) well exceeded those reported for some other seagrass habitats (0.08 to 6.55 fish m^{-2}, Adams 1976; 1 m^{-2}, Robertson 1980; 0.2 to 2.0 m^{-2}, Sogard 1982; 0.01 to 1.5 m^{-2}, Stoner 1983 [our calculations based on his reported methods and total fish captured]; 0.0 to 3.4 m^{-2}, Weinstein & Brooks 1983). While Florida Bay appears to be a relatively rich environment, some of the differences in density are

Table 7. Percentage of throw trap samples misclassified by discriminant function analysis on each transect of each site. Code in parentheses indicates site to which majority of incorrectly classified samples were classified. Transect 4 was a deeper transect sampled only at the Gulf site

| | % Misclassified | | | |
Transect	Gulf	Atlantic	East Central	Northeast
1 (leeward)	0.28 (A, EC)	0.12 (G)	0.33 (A)	0.19 (EC)
2 (top)	0.30 (A, EC)	0.32 (EC)	0.22 (NE)	0.29 (EC)
3 (windward)	0.11 (NE)	0.24 (NE)	0.62 (NE)	0.08 (EC)
4 (windward)	0.17 (NE)			

Table 8. Results of stepwise multiple regression of habitat variables on fish densities (n = 828 throw trap samples). Values reported are the squared semi-partial correlation coefficients (sr^2, the proportion of total variance in density accounted for by each habitat variable after accounting for all other variables in the equation). Only those variables entered in the final equation are listed; all others did not meet a criterion of p = 0.01 for entry. Negative signs indicate negative relationships. All Multiple R values resulting from final equations were significant at p < 0.001

				sr^2		
	O. beta	F. carpio	L. parva	A. criniger	H. zosterae	G. robustum
Litter	0.057	0.014	0.121	0.011		0.046
Standing crop			0.015	0.091		
Canopy height			0.008	0.014 (−)	0.015	
Shoot density					0.014	
Thalassia density	0.089				0.051 (−)	0.007 (−)
Depth		0.257 (−)		0.073	0.037	
% Silt	0.031	0.010 (−)				0.011 (−)
% Organics						0.019
Temp. range	0.005 (−)			0.009 (−)		
Salinity						0.026
Multiple R	0.586	0.657	0.543	0.538	0.504	0.642
Adjusted R^2	0.338	0.427	0.289	0.282	0.248	0.406

likely due to varying efficiencies of the different types of sampling gear. Seines and trawls are particularly ineffective for small, epibenthic species (Gilmore et al. 1978, Gray & Bell 1986). Using a 2-boat, high speed trawl, Thayer et al. (1987) found a mean density of only 0.22 fish m^{-2} (geometric mean) in Florida Bay grassbeds adjacent to mangroves. Although Thayer et al. (1987) suggest that the fish densities they calculated for mangrove prop roots (geometric mean = 8.0 fish m^{-2}) are much higher than densities in seagrass beds of Florida Bay, our results indicate that the 2 habitats are similar, at least for bank grassbeds (geometric mean = 8.2 fish m^{-2}). Trawl efficiencies of 4 to 5 % for epibenthic shrimp were found by Howard & Lowe (1984) and Campos & Berkeley (1986), and may be similar for epibenthic fishes. In contrast, throw trap efficiencies of over 70 % were found by Kushlan (1981) for grassbed and freshwater marsh fishes. Densities in our study were similar to those reported by Huh (1984) for Texas grassbeds sampled with 1 m^2 throw cages ($\bar{x}$ = 6 fish m^{-2} in Thalassia meadows and 15 fish m^{-2} in Halodule meadows).

Although we are confident that throw traps were efficient in sampling most of the species listed in Table 3, this method is limited in its ability to capture pelagic species (except those that show a behavioral response of diving into the grassbed when disturbed, e.g. pinfish, mojarras, and juvenile snappers and grunts [Shulman 1985]). Species more pelagic in behavior and probably not sampled quantitatively included the Clupeidae, Engraulidae, Exocetidae, Belonidae, and Atherinidae.

Several previous studies of grassbed fish communities have found higher abundances at night (Adams 1976, Livingston 1976, Weinstein & Heck 1979,

Orth & Heck 1980, Stoner 1983, Gray & Bell 1986). Using methods similar to ours, however, Huh (1983) also found few day-night differences. Again, differing results of this study and others may be largely due to sampling methods and a resulting emphasis on either demersal or pelagic species. Increased night catches with trawling methods may be due to combined effects of decreased net avoidance, migration into seagrass beds by larger, more mobile species from adjacent habitats (Sogard et al. unpubl.), and increased fish activity with subsequent movement into the water column from the grass canopy. Because trawls tend to skim over a grass canopy (Klumpp & Nichols 1983), they would incorrectly show diel differences if a species hides within the grass cover by day or by night. Capture efficiencies of throw traps are unlikely to vary between day and night, and small, epibenthic residents are unlikely to show major diel migrations in and out of grassbeds. In contrast, pelagic species using Florida Bay banks do show obvious diel patterns, with capture rates of several species increasing at night (Sogard et al. unpubl.).

An additional contrast between the epibenthic species emphasized in this study and the pelagic species emphasized in trawling studies lies in the relative importance of these fish in the grassbed fish community. The importance of grassbeds as nursery grounds for larger and/or economically valuable fishes has been stressed (e.g. Phillips 1960, Carr & Adams 1973, Thayer et al. 1975, Kikuchi & Peres 1977, Pollard 1984), and Stoner (1983) states that the majority of fishes in temperate seagrass beds are juveniles. Length-frequency distributions and temporal abundance patterns of the epibenthic species collected in this study (Powell et al. 1987b) confirm their status as

permanent residents, and their high density ($\bar{x} = 11$ fish m^{-2}) indicates that seagrass beds are a lifetime habitat for a substantial portion of the fish community. The proportion of the grassbed fish community comprised of permanent residents may increase with decreasing latitude, as the extent of winter migrations out of grassbeds (Adams 1976, Orth & Heck 1980) declines. The common view of seagrass meadows as primarily nursery grounds and the corollary assumption that fish inhabitants are predominantly juveniles are probably inaccurate for warm temperate to tropical systems, and result in a misunderstanding of grassbed community structure and function.

Results of multiple regression analysis brought out several vegetational and physical parameters that influence fish densities on Florida Bay banks (Table 8). Although the various seagrass variables were often intercorrelated (Powell et al. 1987b), their differential importance to individual species indicated that the fish were discriminating among different structural aspects of the seagrass canopy. Due to intercorrelations, however, additional seagrass parameters added little to variance explanations once the most important variable had been taken into account.

The importance of seagrass litter to grassbed inhabitants has not been previously reported. Litter should be valuable both as a rich detrital food source and in providing protection from predation, due to the large surface area. The dead blades form a dense layer that may be equivalent to the cover provided by mats of drift algae, also correlated with high fish densities (Stoner & Livingston 1980, Kulczycki et al. 1981). In Florida Bay, drift algae is common on banks, but typically occurs in small clumps (less than 0.1 m^3 in volume) rather than the dense mats present in Indian River (Gore et al. 1981) and other locations. Drift algae was not encountered frequently enough in throw traps to allow adequate analysis of its contribution to fish abundance in this study.

In comparing the long-term effects of variation in physical parameters on seagrass ecosystems in Apalachee Bay, Livingston (1984) concluded that aspects of the seagrass canopy are of primary importance in structuring the grassbed community, with physical processes important in determining habitat quality and productivity cycles. On the shallow banks of Florida Bay, several physical parameters were included as determinants of fish densities even after the structure of the seagrass canopy had been taken into account. The importance of water depth was likely related to tolerance of conditions on the top transects of banks. Fewer species colonized bank tops (Fig. 3), although seagrass growth was generally more lush on top than on windward sides (Fig. 2). *Floridichthys carpio*, however, appeared to thrive in very shallow

waters, and may exploit areas avoided by other species.

Previous attempts to correlate faunal densities with habitat parameters (both vegetational and physical) in seagrass meadows have had limited success when considered on a broad scale (Brook 1978, Nelson 1980, Livingston 1982, Stoner 1983, Virnstein et al. 1984, Bell IN RUHE Westoby 1987b). In Florida Bay, despite the large number of samples (828 throw traps) and the wide range of measured habitat variables, multiple regression equations accounted for only 24.8 % *(Hippocampus zosterae)* to 42.7 % *(Floridichthys carpio)* of the variance in fish densities. Using correlation or regression techniques, which assume linear relationships, may result in overly conservative estimates if the actual relationships are non-linear (Tabachnick & Fidell 1983). A step function more accurately describes the relation of seagrass structure with protection from predation (Nelson 1979, Heck & Thoman 1981), and step functions or curvilinear relationships may better relate fish densities to physical parameters. Dependence on seagrass structural complexity or physical parameters may, therefore, be stronger than implied by the sr^2 values derived in this study.

Our use of concurrently measured salinity and temperature values may also limit the accuracy of the regression model if the recent history of salinity and temperature regimes has a greater influence on fish densities than current conditions. The salinity range we recorded (17 to 43 ppt, Powell et al. 1987b) was conservative compared to previously reported ranges, particularly in northern Florida Bay, with salinities up to 64.8 (1974–1976, Schmidt 1979) and over 65 ppt (1965–1966, Tabb pers. comm.). In contrast, there was an extended period of relatively low salinities near our Northeast site prior to initiation of this study (Everglades National Park, unpubl.). If recolonization rates are slow following local salinity- or temperature-related extinctions (see below), local population densities would reflect past, not present physical conditions.

Despite the broad heterogeneity in seagrass structural complexity within sites (Fig. 2), epibenthic fish communities were relatively distinct and maintained a certain site integrity, according to discriminant classification results (Table 6). Site differences in species composition and abundance may be explained by 2 factors, variation in habitat characteristics (those listed in Table 1 and others we did not measure) and variation in the availability of recruits from the plankton, with the latter constrained by water circulation processes in Florida Bay. Results of multiple regression analysis indicate the importance of habitat for the more common species. With regard to species composition and densities of the less common species, the role of circulation warrants further attention. We do not have data

on flushing rates and residence times, but the severe damping of tides in Florida Bay with distance from open ocean water (Powell et al. 1987b) implies correspondingly reduced circulation.

The majority of the epibenthic residents on Florida Bay banks are small species that likely have short life spans of 1 or 2 yr, and presumably have a limited home range as adults. Maintaining populations on individual banks requires continually successful recruitment, and localized extinctions are probably common. In areas with limited water mass exchange, such as the Northeast site, colonization by individuals spawned in other parts of the Bay or outside the Bay may be rare. The major families common across the 4 sites all have reproductive strategies that minimize planktonic dispersal, from demersal or attached eggs (Cyprinodontidae, Gobiidae) to parental brooding (Syngnathidae) to elimination of a pelagic stage (Batrachoididae). This retentive strategy may increase juvenile survival by ensuring that post-larvae recruit to areas known to be favorable to adults (evidenced by their spawning success).

Colonization by occasional species that may not be adapted to Bay conditions is more likely along the Gulf and Atlantic sections of Florida Bay, where tidal exchange could increase availability of larvae. The few tropical species we caught (*Diplogrammus pauciradiatus*, *Barbulifer ceuthoecus*, *Cosmocampus albirostris*, *Sparisoma* sp., *Paraclinus marmoratus*) occurred primarily or exclusively at the Atlantic site, where there is substantial exchange with Atlantic water. At the Gulf site, exchange with Gulf of Mexico water was reflected in a high diversity of fishes, dominated by temperate species. Larval availability, based on planktonic species composition, differs markedly from the Gulf to Atlantic sides of Florida Bay and between the ocean side and bay side of the Florida Keys (Powell et al. 1987a), implying that the potential source of recruits varies according to geographic location. Stoner (1983) concluded that dispersal of eggs and larvae was of minor importance in determining adult densities in Apalachee Bay, as there was little correlation of the 2 groups. In Florida Bay, however, dispersal may be a major limiting factor for the grassbed fauna in areas isolated from open Gulf and Atlantic waters by the network of banks.

We are presently unable to resolve the relative roles of habitat heterogeneity and differences in the pool of available colonizers in structuring species composition on the banks. Further information on larval species composition in interior sections of Florida Bay and knowledge of circulation patterns and residence times of water masses in the Bay are essential to understanding the probability of planktonic larval dispersal to the different subenvironments. In addition, basic life history information is lacking for most of the epibenthic residents. Knowledge of larval stage duration and tolerance of various salinity and temperature regimes would be valuable in understanding habitat relationships.

In conclusion, the Florida Bay epibenthic fish fauna contrasts as a whole from surrounding grassbed fish faunas in its lack of tropical species, presumably a function of its harsher physical environment. Within the Bay, heterogeneity in habitat quality acts in conjunction with widely varying patterns of water circulation, resulting in distinctive fish communities in different subenvironments. Finally, at the level of individual banks, fish densities are structured by gradients in sediment structure and seagrass architecture that are effected by the shallow depths and prevailing water turbulence patterns.

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