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FISH ASSEMBLAGES IN SEAGRASS HABITATS OF THE FLORIDA KEYS, FLORIDA: SPATIAL AND TEMPORAL CHARACTERISTICS

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ABSTRACT

Seagrass beds of the Florida Keys National Marine Sanctuary (FKNMS) have global renown, yet their fish populations require study. A 24-mo trawl survey determined that *Haemulon plumierii* (Lacépède, 1801), *Lagodon rhomboides* (Linnaeus, 1766), *Monacanthus ciliatus* (Mitchill, 1818), and *Eucinostomus* spp. constituted nearly 70% of small-bodied fishes in FKNMS seagrasses. Mean abundance and species richness were significantly higher in areas containing larger, denser, and more structurally complex seagrass beds on the Gulf of Mexico side, especially in the middle and lower Keys, than in the sparser and less complex Atlantic seagrass beds, which are much closer to the Florida reef tract. There was limited seasonal variation in fish-assemblage composition. Abiotic factors (water temperature, salinity, and dissolved oxygen) appeared less important in defining assemblages than biotic characteristics (i.e., seagrass structure). The only prevalent, economically important reef-associated fishes using the seagrass beds as nurseries were *H. plumierii*, *Lutjanus synagris* (Linnaeus, 1758), and *Lachnolaimus maximus* (Walbaum, 1792). Many coral-reef-associated families were absent and most members of the locally important snapper-grouper complex (Lutjanidae and Serranidae) were captured infrequently. This may be attributable to distance from the reefs and also because some of these species inhabit seagrasses nocturnally and so were not collected by the diurnal trawling.

Seagrass beds are an important, often dominant, component of the benthic habitat in many coastal marine environments. Seagrass habitats generally support higher fish density and diversity than adjacent bare substratum (Sogard et al., 1987; Bell and Pollard, 1989; Tolan et al., 1997; Travers and Potter, 2002). Although seagrass beds are used by various fish species of different age classes and at different trophic levels (Bell and Pollard, 1989; Rooker and Dennis, 1991; Sheridan et al., 1998; Thayer et al., 1999), fish assemblages in seagrass beds are largely composed of juvenile and immature individuals, which use the area until they undergo ontogenetic migrations to reefs, offshore habitats, or other areas (Rooker and Dennis, 1991; Nagelkerken et al., 2000a; Ley and McIvor, 2002). Therefore, seagrass beds have often been described as nurseries for many marine species, including commercially important fishes (Arrivillaga and Baltz, 1999). There are few locations in the world where seagrass beds are as prevalent in the hydroscape as in south Florida (Fourqurean et al., 2002), yet in the Florida Keys ichthyological research has been limited to how fishes use seagrasses in the shallow waters of Florida Bay (Fourqurean and Robblee, 1999; Matheson et al., 1999; Thayer et al., 1999; Fourqurean et al., 2001, 2002).

Many studies in the Caribbean have documented the ecological importance of seagrass beds and mangroves as nursery areas for reef fishes of recreational and commercial importance (Rooker and Dennis, 1991; Acosta, 1997; Nagelkerken et al., 2000b, 2001). In the Indo-Pacific, however, the importance of seagrass beds and mangrove systems as nursery areas is apparent only in some locales (Thollot and Kulbicki, 1988; Friedlander and Parrish, 1998).

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This study describes the results of a 2-yr trawling project conducted from February 1999 through January 2001 throughout a large area of the Florida Keys National Marine Sanctuary's (FKNMS) seagrass meadows. The FKNMS has been recognized by the U.S. Congress as an ecologically sensitive environment, with 18 fully protected ("no-take") Sanctuary Preservation Areas and one Ecological Reserve. We evaluated the extent to which the seagrass habitats in the FKNMS are used by fishes, in particular the reef-associated species that support local fisheries. Our goals were to: (1) compare the fish density, taxon richness, and assemblage structure in seagrass habitats among three geographic regions (east–west) and the gulf and Atlantic sides of the FKNMS; (2) assess the evidence for seasonal changes in fish-assemblage structure; and (3) assess correlations of fish abundance with environmental variables (temperature, salinity, and dissolved oxygen).

Methods

Study Area

The study was conducted in the seagrass beds of the Florida Keys National Marine Sanctuary (FKNMS), a 9500-km^2 area that includes coastal and oceanic waters surrounding the entire Florida Keys (Fig. 1). The Florida Keys are a chain of limestone islands extending 120 km southwest from Key Biscayne to the Dry Tortugas. The coastal and marine areas adjacent to the Keys contain many mangrove islands and extensive seagrass meadows. On the Atlantic Ocean side is the Florida reef tract, the third-largest barrier reef system in the world (Jaap and Hallock, 1990). The reef tract parallels the island chain for its entire length, generally about 6–8 km offshore, and is separated from the islands by Hawk Channel, a broad, relatively shallow (4–13 m water depth) area consisting of mostly bare sediments.

Sampling was conducted in three geographical areas of the FKNMS, designated as zones U (upper Keys), M (middle Keys), and L (lower Keys) (Fig. 1). Zones were arbitrarily designated for logistical purposes. On the Atlantic Ocean side of the Keys, all three zones extended out over the reef tract. On the Gulf of Mexico side, zone U contained a limited portion of Florida Bay between the Keys and Everglades National Park (ENP), whereas zone M, which was not confined by ENP boundaries, extended farther into Florida Bay. Zone L is a unique region in the Keys because the longer axis of the islands arc is oriented perpendicular, rather than parallel, to the main axis of the island chain; the result is that long channels and numerous shallow embayments are contained between the islands. Each zone was divided into Gulf of Mexico (G) and Atlantic Ocean (O) strata based on a dividing line represented by U.S. Highway 1, giving a total of six zone-stratum combinations that we refer to as subzones: U_G, U_L, M_G, M_O, L_G, and L_O. Published data show that the densest seagrass beds in the study area are located on the Gulf of Mexico side of the middle Florida Keys (Fig. 2) (Fourqurean et al., 2001, 2002), i.e., corresponding to subzones M_G and L_G of the present study area. Seagrass species diversity is relatively high on the Gulf side of both the middle and lower Keys; *Syringodium filiforme* Kuetz., *Thalassia testudinum* Banks and Soland. ex Koenig, *Halodule wrightii* Aschers., *Halophila decipiens* Ostenf., and *Halophila engelmanni* Aschers. are found there (Fourqurean et al., 2001, 2002). In contrast, seagrass beds on the Ocean side of the Florida Keys are generally less dense, much less diverse, and mostly composed of *T. testudinum* (Fourqurean et al., 2001, 2002).

Sample Collection

Trawl sampling was conducted on a monthly basis for a 2-yr period (February 1999–January 2001) in seagrass habitats in zones U and M (Fig. 1). During the second year of this survey, sampling was extended westward to include zone L. Sampling sites were randomly selected using a grid subdivided into one-longitudinal-by-one-latitudinal-minute (approximately 1

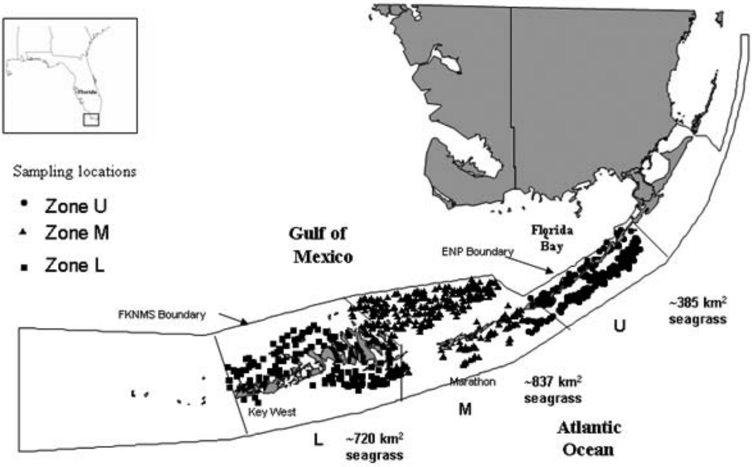

Figure 1. Map of the sampling areas in the Florida Keys National Marine Sanctuary (FKNMS) showing sampling locations by zone. Sampling zones are labeled U (eastern zone, upper Keys), M (central zone, middle Keys), and L (western zone, lower Keys).

square nautical mile—nm^2) cells. The grid-selection process was limited to grids containing bottom habitat mapped as "continuous seagrass" or "patchy seagrass" in the Florida Keys Benthic Habitat Geographical Information System (GIS) (FDEP and NOAA, 1998). We excluded cells characterized as "patchy seagrass" habitat immediately adjacent to the back-reef (landward) side of the reef tract, because they contained numerous corals and sponges that prohibited efficient trawling operations. Each cell chosen for sampling was further subdivided into one hundred 0.1′ × 0.1′ "micro-grids" (~0.01 nmi) so that we could determine the nominal trawl location within the grid, providing that the micro-grid contained seagrass habitat adequate for sampling purposes and that water depth was > 1 m to allow proper operation of the gear. If this was not the case, a nearby micro-grid with the desired habitat was located by spiraling in a randomly selected direction.

The number of sites sampled monthly within each subzone was approximately proportional to the total trawlable habitats defined by the GIS system within each subzone (Fig. 1). During all of the 1999 sampling season (February–December), 30 sites per month were sampled in zones U (11 sites) and M (19 sites). During January 2000, sampling was extended to include zone L, and 45 sites were proportionately sampled in the three zones. However, during the remainder of 2000, sampling was reduced to a total of 40 sites per month in the three zones due to logistical considerations. Monthly sampling intensity during the second year within zones U and M was decreased to 9 and 16 sites, respectively, whereas 15 sites were sampled in zone L. Total sample sizes by subzone were as follows: 321 (M_G), 142 (U_O), 141 (L_G), 100 (M_O), 96 (U_G), and 53 (L_O) (Fig. 1).

Fish collections at each selected site were made using a 6.1-m otter trawl constructed of 38-mm stretched mesh with a 3.2-mm stretched-mesh cod-end liner. The net was towed over the bottom at a speed of approximately 1.2 kt (2.2 km hr^{-1}) for 3 min, giving a mean tow distance of 0.06 nmi (0.11 km). One tow was conducted at each site. Beginning and ending tow positions were recorded using a differential Global Positioning System receiver, and the area sampled and resultant fish densities (number of fish 100 m^{-2}) were calculated according to tow distance and the estimated average net-opening width (4 m). The trawl tends to catch small-bodied fishes and was assumed to have reasonable consistency between tows over seagrass habitats of differing structural complexity. Petrik and Levin (2000) reviewed sampling methods in the seagrass beds of North Carolina and concluded that trawl sampling is a useful tool for detecting spatial and temporal trends in biodiversity because trawls sample a much greater area and, consequently, capture many more species and individuals than other types

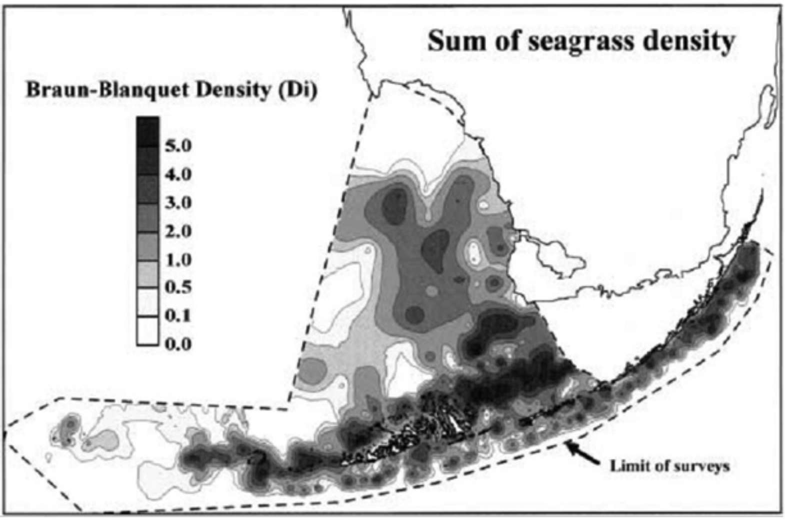

Figure 2. Seagrass distribution in a 17,000-km^2 area of south Florida. Data from 874 mapping sites studied from 1995 to 1998 were interpolated using a kriging algorithm to generate contours of the sum of Braun-Blanquet densities for five seagrass species (Fourqurean et al., 2001). Reproduced with kind permission of Springer Science and Business Media and J. Fourqurean. © Springer-Verlag 2001.

of gears do (e.g., throw traps, minnow traps, seines, visual observations). It must be noted that our sampling was limited to seagrass beds of sufficient depth (> 1 m) to allow trawling operations. Whereas the vast majority of seagrass beds within our region are > 1 m deep, there are some small areas of shallow-water seagrass beds close to the shoreline that were outside of our sampling limits, and these beds could be preferentially inhabited by some juvenile fishes instead of the deeper seagrass beds. Subsequent experimental seine sampling that we have conducted in these shallow seagrass areas has indicated that this may indeed be the case for some snapper species, including mutton snapper [*Lutjanus analis* (Cuvier, 1828)], gray snapper [*Lutjanus griseus* (Linnaeus, 1758)], and yellowtail snapper (*Ocyurus chrysurus* Bloch, 1791) (Bartels and Ferguson, 2006). We also caution that our trawl sampling was limited to daylight hours and so may have underestimated densities of reef-associated species (principally grunts and snappers) inhabiting the seagrass beds at night (Weinstein and Heck, 1979; Nagelkerken et al., 2000b). Daytime trawling was the only practical option available and was used consistently across all sites; however, we concede that this method does not describe the entire fish assemblage living within the sampled habitats.

All fishes collected were identified and enumerated, and a randomly selected subsample (up to 40 individuals from each trawl) of each species was measured in the field to the nearest mm standard length (SL). Specimens for which field identification was uncertain and representative specimens of each other taxon from each sampling day were brought back to the laboratory to confirm field identifications. All remaining specimens were released. All identifications were made to species level, with the exception of small juveniles of a few genera that could not be classified to species level in the field without the aid of a microscope. These fish, consisting primarily of small grunts (*Haemulon* spp.) and mojarras (*Eucinostomus* spp.), were recorded to the genus level in the field. All *Eucinostomus* that were < 40 mm SL were recorded as *Eucinostomus* spp. because of the difficulties involved in identifying such small sizes (Matheson, 1983). Because the vast majority of *Eucinostomus* collected were small juveniles, all members of this genus were treated as *Eucinostomus* spp. for analytical purposes.

Temperature (°C), salinity, and dissolved oxygen (mg L^{-1}) were measured on the surface with Hydrolab$^{®}$ Surveyor series water quality instruments.

STATISTICAL ANALYSIS.

Spatial Patterns in Fish Density and Species Richness.—General linear models (GLM; SAS Institute Inc., 1999) were used to determine the statistical significance of differences in mean fish density (number of fish per 100 m^2 trawled for all species combined, and also for each of the ten most abundant species) and mean taxon richness (number of taxa per 100 m^2 trawled) between zones (U, M, or L), strata (Gulf or Ocean), and their interaction (i.e., subzone). A conservative P of 0.01 for the full model was adopted to judge statistical significance given the increased likelihood of type 1 error caused by non-normality and heterogeneity of variance. A second GLM assessed differences in abundance between the six subzones (i.e., the zone × stratum interaction). A posteriori Bonferroni tests were used to determine pairwise differences when statistical significance had been established. An adjusted P of 0.01 per n was used to account for n multiple comparisons.

Spatial Patterns in Fish-assemblage Structure.—We conducted various multivariate analyses to complement the univariate single-species analyses of fish distribution and further examine possible differential occupation of subzones by two or more size classes within the same species (Baltz and Jones, 2003). These analyses used data collected from January 2000 to January 2001 to ensure that there was no temporal pseudoreplication among zones. Monthly length-frequency plots of abundant and frequently collected species were examined in order to assign size classes. Size classes were based on the observed range of sizes for each species and the number of individuals across the range of sizes. For example, *Haemulon plumierii* (Lacépède, 1801) (white grunt) was classified into three size classes (< 50, 50–80, and > 80 mm SL), whereas *Sphoeroides spengleri* (Bloch, 1785) (bandtail puffer fish) was left as a single size class because no obvious size-class divisions existed.

The null hypothesis that there was no significant difference in fish-assemblage structure between the different subzones was tested by a two-way crossed Analysis of Similarities (ANOSIM; Clarke, 1993) with zone and stratum as main effects, and differences between subzones (i.e., the zone-stratum interaction) included as pairwise comparisons. The similarity matrix used in the ANOSIM test was calculated based on Bray-Curtis coefficients of pairs of individual samples (Bray and Curtis, 1957). A Bonferroni-adjusted probability level of 0.0033 (i.e., 0.05/15, where 15 is the number of subzone-pair comparisons) was used to determine statistical significance following 999 random permutations of the sample labels. Subzone pairs that ANOSIM separated at the $P < 0.0033$ and $R > 0.25$ levels (i.e., above the "barely separable at all" threshold suggested by Clarke and Gorley, 2001) were included in similarity percentages analysis (SIMPER; Clarke, 1993) to determine principal size classes discriminating the fish assemblages between subzones.

Seasonal Patterns in Fish-Assemblage Structure.—We tested the null hypothesis that there was no annual cycle in fish assemblage structure in each subzone, using the non-parametric Mantel-like test RELATE (Somerfield et al., 2002). Data were treated in the same way as above and Bray-Curtis similarity matrices were calculated. The values in these biotic matrices of fish-assemblage similarity were ranked and compared to theoretical matrices of Euclidean distances representing annual cycles in fish assemblage structure. In these theoretical matrices of Euclidean distance, adjacent samples (e.g., samples collected in January and February or January and December) were assigned values of 1, while those furthest apart (e.g., samples collected in January and July or March and September) were assigned values of 6; intermediate values ranged from 2 to 5. The values in these theoretical matrices were ranked, and the Spearman Rank correlation coefficient (r_S) between biotic and theoretical matrices was calculated based on corresponding elements of each matrix. The values in the biotic matrix were then randomly rearranged 999 times and r_S calculated between biotic and theoretical matrices for each of the 999 permutations. This allowed statistical significance of the true r_S to be determined. We rejected the null hypothesis if $P < 0.05$ (i.e., ≥ 50 permuted correlation coefficients were greater than the actual value).

Spatial and Temporal Patterns in Environmental Variables and Correlations with Fish Density.—General linear models were used to determine whether mean temperature, salinity, and dissolved oxygen differed among seasons (spring [March–May], summer [June–August], fall [September–November], and winter [December–February]), years (1999 and 2000), strata (Gulf and Ocean), zones (U, M, and L), and subzones (i.e., the interaction of zone with stratum). Seasons, years, strata, zones, and subzones were considered fixed factors because they were chosen as representing different periods or different zones of the Florida Keys. Models were considered significant at $P \leq 0.01$, with a posteriori Bonferroni tests conducted as detailed above. The Pearson correlation coefficient was used to determine the significance of each environmental variable to the observed fish densities (Zar, 1984). This statistical technique allowed us to analyze the linear relationship between species densities and individual environmental parameters and thus to determine the independent variable most likely to affect the distribution of each species and the nature of that effect (Marshall and Elliot, 1998). Analyses were conducted for total density (all species combined) and for densities of the ten most abundant species (Table 1). A Bonferroni-adjusted P of 0.017 (0.05/3) was used to judge statistical significance, with the adjustment based on the multiple correlations calculated for each species.

RESULTS

FISH ABUNDANCE

In total, 26,617 fishes, representing 156 species ranging in size from 5 to 520 mm SL, were collected in 853 trawl collections during the study period. The most abundant taxa in the Gulf strata, accounting for about 69% of the total catch, were *H. plumierii* (27.6%), *Monacanthus ciliatus* (Mitchill, 1818) (finged filefish) (13.7%), *Lagodon rhomboides* (Linnaeus, 1766) (pinfish) (14.3%), and *Eucinostomus* spp. (13.1%), whereas on the ocean side the most abundant taxa were *M. ciliatus* (28.0%), *H. plumierii* (18.9%), *Stephanolepis hispidus* (Linnaeus, 1766) (planehead filefish) (5.4%), and *Eucinostomus* spp. (4.5%), accounting for 56.8% of the total catch. The ten most abundant taxa caught in trawls constituted 81.7% of the total number of fish collected during the 2 yrs of sampling (Table 1).

FISH DENSITY AND TAXON RICHNESS

Seasonal Patterns.—Mean densities of all fish combined ranged from about 4.6 to 9.0 fish 100 m^{-2} during the first year and from about 2.2 to 10.1 fish 100 m^{-2} during the second year (Fig. 3). There was only slight seasonal variation in fish abundance, with lower mean density values observed in the late spring than during the rest of the year; there was a marked decline in fish density in all three zones in April 2000. Overall mean densities and density by zone showed both greater month-to-month variation and a broader range of values during the second year of the study. For the ten most abundant species, mean densities of *H. plumierii*, *Acanthostracion quadricornis* (Linnaeus, 1758) (scrawled cowfish), *Opsanus beta* (Goode and Bean, 1880) (gulf toadfish), and *Calamus arctifrons* Goode and Bean, 1882 (grass porgy) fluctuated throughout the 2 yrs without showing consistent seasonal trends. In contrast, mean densities of *M. ciliatus* were lowest in spring and summer (March through May 1999; April through August 2000) and increased to a high in January. Mean densities of *Eucinostomus* spp. were lowest during the winter months and showed multiple peaks in the warmer months that were not consistent across either sampling years or zones. *Lutjanus synagris* (Linnaeus, 1766) (lane snapper) had higher mean densities during fall and winter of both years. Densities of the emerald parrotfish, *Nicholsina*

Table 1. Total number (n), percent of catch (%), percent occurrence (% Occur.), and mean density of the ten most abundant species and all others collected in 855 6.1-m trawls in the Florida Keys by strata from February 1999 through January 2001.

		Gulf			Ocean			Total		
Species	Family	n	%	% Occur.	n	%	% Occur.	n	%	% Occur.
Haemulon plumierii	Haemulidae	6,644	28.4	64.7	621	18.9	33.0	7,265	27.3	60.5
Monacanthus ciliatus	Monacanthidae	3,220	13.7	66.2	919	28.0	61.2	4,139	15.6	68.9
Lagodon rhomboides	Sparidae	3,343	14.3	54.5	81	2.4	15.8	3,424	12.9	44.3
Eucinostomus spp.	Gerreidae	3,071	13.1	49.1	145	6.1	13.0	3,216	12.1	36.4
Acanthostracion quadricornis	Ostraciidae	785	3.3	50.1	121	3.6	28.8	906	3.4	46.1
Lutjanus synagris	Lutjanidae	537	2.3	32.8	106	3.2	29.6	643	2.3	27.8
Opsanus beta	Batrachoididae	569	2.4	42.5	31	0.9	7.4	600	2.3	32.2
Calamus arctifrons	Sparidae	561	2.4	34.6	20	0.6	7.6	581	2.2	26.1
Nicholsina usta	Scaridae	427	1.8	26.4	68	2.0	12.9	495	1.9	26.1
Lachnolaimus maximus	Labridae	384	1.6	21.5	49	1.4	8.8	433	1.6	22.3
Total		19,541	83.7		2,161	66.0		21,702	81.5	
All other species		3,799	16.3		1,116	34.0		4,915	18.4	
Grand total		23,340	100		3,277	100		26,617	100	

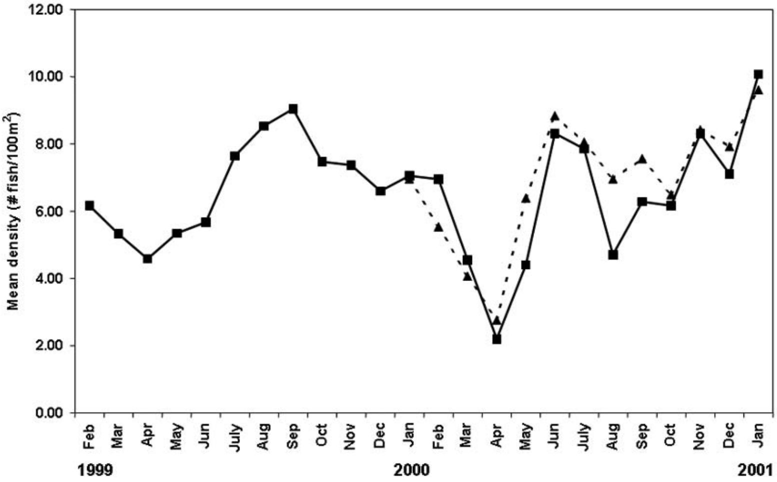

Figure 3. Mean density (# fish 100 m^{-2}) of fish caught each month from February 1999 through January 2001 in zones U and M (combined) (—■—) and zones U, M, and L (combined) (···▲···).

usta (Valenciennes in Cuvier and Valenciennes, 1840) dropped in April and were higher in summer and late fall (peaking in November) of both years. Finally, during both years, densities of *Lachnolaimus maximus* (Walbaum, 1792) (hogfish) were highest in summer and fall, with peaks in June and September–October.

Spatial Differences.—Significant differences in mean fish density existed among zones, between strata, and among subzones. Mean density was highest in zones M and L (Fig. 4A) and mean density in the Gulf stratum was higher than the Ocean stratum (Fig. 4B). This pattern was driven by high mean densities in subzones M_G and L_G (Fig. 4C). Mean density in zone M was significantly higher than in both other zones for several taxa (*H. plumierii*, *L. rhomboides*, *N. usta*, and *L. maximus*). Mean fish densities were lowest in Zone L. *Eucinostomus* spp. was the only species found in significantly higher densities in zone L compared to zones U and M.

One of the limitations of this study was the inability to sample the upper area of subzone U_G located within Florida Bay (Everglades National Park). The unsampled seagrass area was estimated to be approximately 164 km^2 (based on Zieman et al., 1989). These Atlantic and East-Central zones in Florida Bay are characterized by sparse, patchy *T. testudinum* (Zieman et al., 1989). Fish density values obtained from these two zones during pilot studies in 1997 were compared with the results of the present study, and they indicated that the mean density for the U_G subzone and unsampled seagrass areas of Florida Bay were not significantly different (Mean fish density was 4.31 fish 100 m^{-2} for U_G zone and 4.14 fish 100 m^{-2} for Florida Bay). Even with the inclusion of the seagrass areas from Florida Bay, the seagrass cover in subzones M_G and L_G is considerably greater than in subzone U_G.

Mean taxon richness in zone M was significantly greater than richness in zone L, which in turn was significantly greater than richness in zone U (Fig. 5A). The Gulf stratum had more than twice the mean number of taxa per 100 m^2 than the Ocean stratum (Fig. 5B). The interaction of zone and stratum (subzone) on richness was clear: no significant difference in mean richness existed among zones in the Ocean stratum, whereas mean richness increased significantly from subzones U_G to M_G and from L_G to M_G (Fig. 5C).

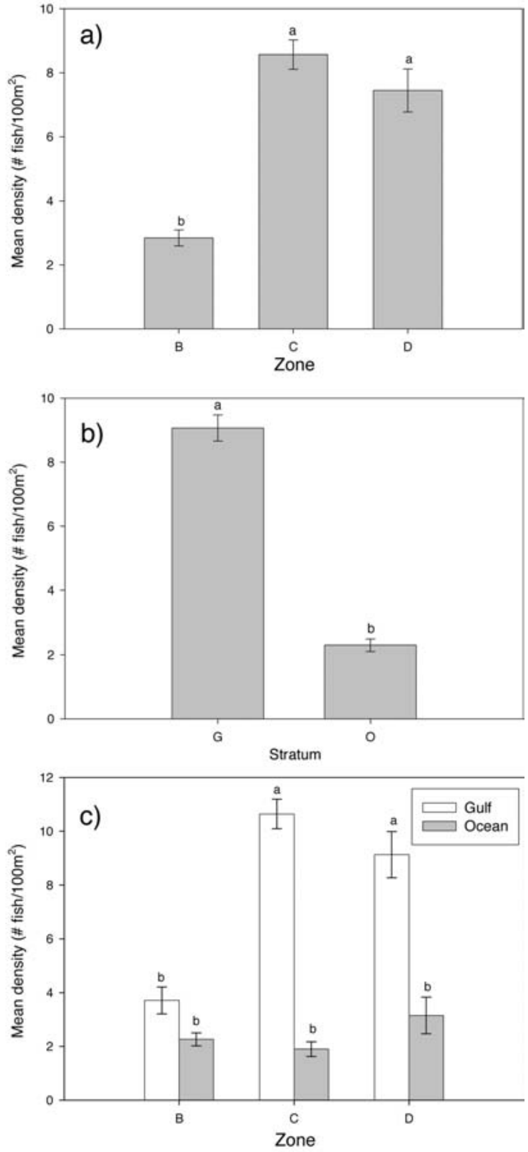

Figure 4. Mean density (± SE) per trawl in each of the subzones of the Florida Keys National Marine Sanctuary. Letters above bars indicate significant differences (A posteriori Bonferroni test following general linear model). Means with the same letter were not significantly different.

The zone × stratum interaction was not significant for only two taxa (*Eucinostomus* spp. and *O. beta*). In most cases there was no difference in mean density among zones in the Ocean stratum (Fig. 6), with the exceptions of *M. ciliatus* and *L. synagris* (Fig. 6B,F). In the Gulf stratum, mean fish density was significantly greater in subzone M_G for *H. plumierii*, *L. rhomboides*, *N. usta*, and *L. maximus* (Fig. 6A,C,I,J), and greater in subzone L_G for *Eucinostomus* spp. (Fig. 6D). Mean densities of fish in subzone U_G were often significantly lower than in the other two zones in the Gulf stratum; exceptions were *M. ciliatus*, *Eucinostomus* spp., *L. synagris*, *O. beta*, *N. usta*, and *L. maximus* (Fig. 6C,D,F,G,I,J).

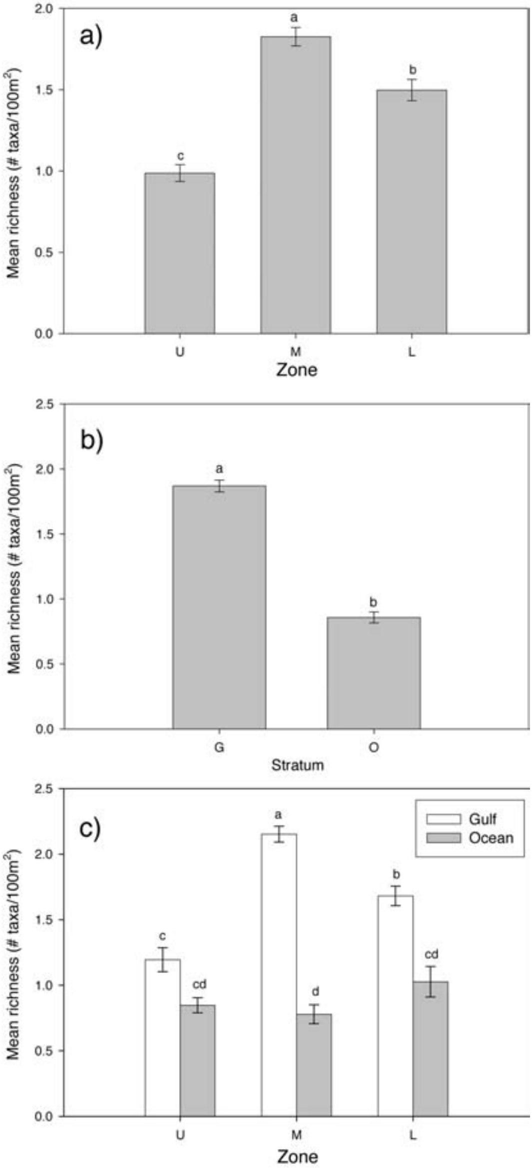

Figure 5. Mean taxon richness (± SE) per trawl in each of the subzones of the Florida Keys National Marine Sanctuary. Letters above bars indicate significant differences (A posteriori Bonferroni test following general linear model). Means with the same letter were not significantly different.

Seasonal and Spatial Patterns in Seagrass Fish Assemblages

Seasonal Differences.—We accepted the null hypothesis of no annual cycle in fish assemblage structure for four of six subzones. Very weak annual cyclicity in fish-assemblage structure was found in subzones U_O (r_S = 0.095, P = 0.001) and L_G (r_S = 0.042, P = 0.012).

Spatial Patterns.—The fish assemblages of the different subzones of the FKNMS overlapped to a considerable degree but were nonetheless sufficiently different to reject the null hypothesis of no difference among subzones (Global ANOSIM R =

0.271, $P < 0.001$). Bonferroni-adjusted pair-wise comparisons revealed that subzones M_G and L_G tended to be most different from the other areas, whereas the fish assemblages in U_G, U_O, M_O, and L_O were not greatly distinguishable from each other (Table 2).

Eight size classes were largely responsible for discriminating subzones M_G and L_G from the other areas: *H. plumierii* (< 50, 51–80, and > 80 mm), *M. ciliatus* (≤ 60 and > 60 mm), *Eucinostomus* spp. (≤ 38 and > 38 mm), and *L. rhomboides* (≥ 65 mm). In almost all pairwise comparisons, these size classes were generally found in much greater abundance in subzones M_G and L_G than in the other areas; the exceptions were the two *M. ciliatus* size classes, which were often similarly or more abundant in subzones U_G, U_O, M_O, and L_O. Other, less important discriminating size classes that were occasionally more abundant in subzones other than M_G and L_G included *S. hispidus* (≤ 60 and > 60 mm), *L. synagris* (< 85 and ≥ 85 mm), *O. beta* (< 140 mm), *Chilomycterus schoepfii* (Walbaum, 1792) (stripped burrfish) (≤ 110 and > 110 mm), *Hippocampus erectus* Perry, 1810 (lined seahorse), and *S. spengleri.* There was very little evidence of size classes within the same species differentially occupying separate strata within each zone, i.e., all sizes of individuals tended to occupy similar areas on the Gulf and Ocean sides.

Spatial and Temporal Patterns in Environmental Variables and Correlations with Fish Density

Surface temperatures ranged from 14.3 °C to 33.3 °C (mean = 26.0 °C; SD = 4.1), with monthly averages from 16.8 °C to 31.0 °C. Mean temperatures differed significantly among seasons (Table 3). Monthly mean salinities remained close to 35 during all months except November and December 1999, when they dropped to about 32. As a result, salinity differed significantly among seasons and zones, and between years (Table 3). Salinity was positively correlated with temperature throughout the study area. Individual salinity readings ranged from 22.2 to 41.0 (mean = 35.6; SD = 1.94). Dissolved oxygen ranged from 3.2 to 9.8 mg L^{-1} (mean = 6.5 mg L^{-1}; SD = 1.02), and monthly mean values showed the expected inverse cyclical pattern to temperature. As with temperature, mean dissolved oxygen values also differed significantly among seasons and zones (Table 3).

Temperature, salinity, and dissolved oxygen were not significantly correlated with total fish density. Only four of the 10 most abundant species showed statistically significant correlations between density and any of the three environmental variables ($P < 0.017$). Densities of *Eucinostomus* spp., *L. synagris,* and *O. beta* were positively correlated with temperature. ($P < 0.017$). Densities of *M. ciliatus* were inversely correlated with temperature ($P < 0.017$) and positively correlated with dissolved oxygen ($P < 0.017$). Densities of *L. synagris* were inversely correlated with salinity ($P < 0.017$). Fish densities of *H. plumierii*, *L. rhomboides, A. quadricornis, L. maximus*, *C. arctifrons,* and *N. usta* were not significantly correlated with any environmental variables. In total, one-fifth (6/30) of all correlations were significant.

Discussion

Many studies have stressed the crucial role seagrass beds play in sustaining the biodiversity of fish assemblages and have emphasized the need for their protection (Bell and Pollard, 1989; Guidetti, 2000). South Florida has the largest document-

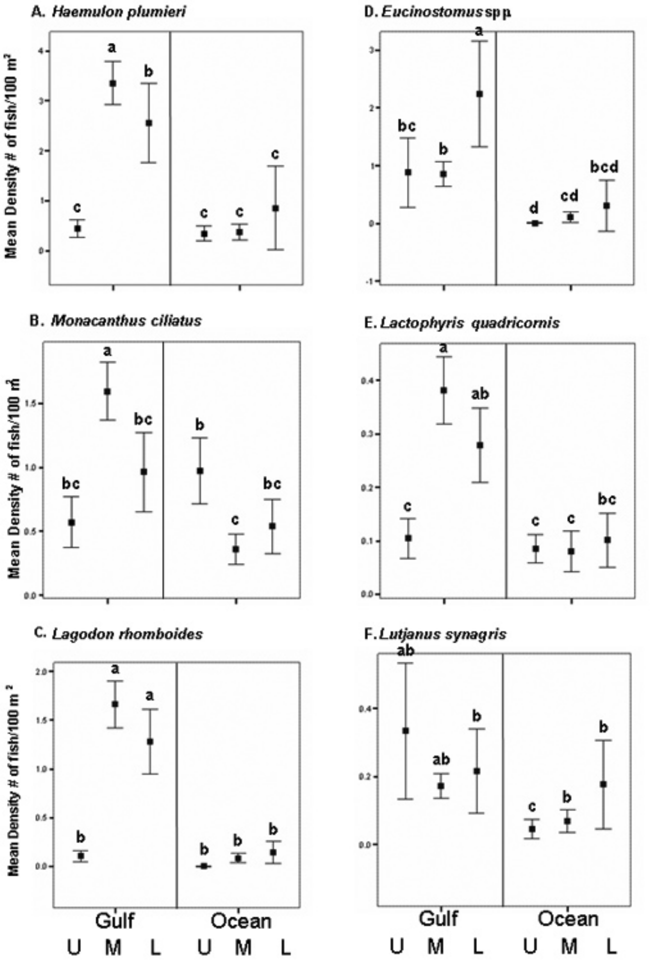

Figure 6. Mean density (± SE) of the ten most abundant species collected per trawl in zones U, M and L in the Gulf of Mexico and Atlantic Ocean strata of the Florida Keys: (A) *Haemulon plumierii*, (B) *Monacanthus ciliatus*, (C) *Lagodon rhomboides*, (D) *Eucinostomus* spp., (E) *Lactophrys quadricornis*, (F) *Lutjanus synagris*, (G) *(Opposite page) Opsanus beta*, (H) *Calamus arctifrons*, (I) *Nicholsina usta*, and (J) *Lachnolaimus maximus*. Letters above bars indicate significant differences (a posteriori Bonferroni test following general linear model). Means with the same letter were not significantly different.

ed semi-continuous seagrass assemblage in the world (Fourqurean et al., 2001). It was beyond the scope of this study to assess and characterize seagrasses in detail at the sampling sites; visibility was such that even simple visual assessment of seagrass or substrate identity could not be made reliably. Nevertheless, spatial patterns of fish density, taxon richness, and fish-assemblage structure correspond well with the known spatial patterns of seagrass abundance and distribution throughout the Florida Keys. Clearly, the seagrass beds sampled in the middle and lower Keys on the Gulf side supported considerably higher fish densities and taxon richness than seagrass beds in other areas of this study. This may be not only because the sea-

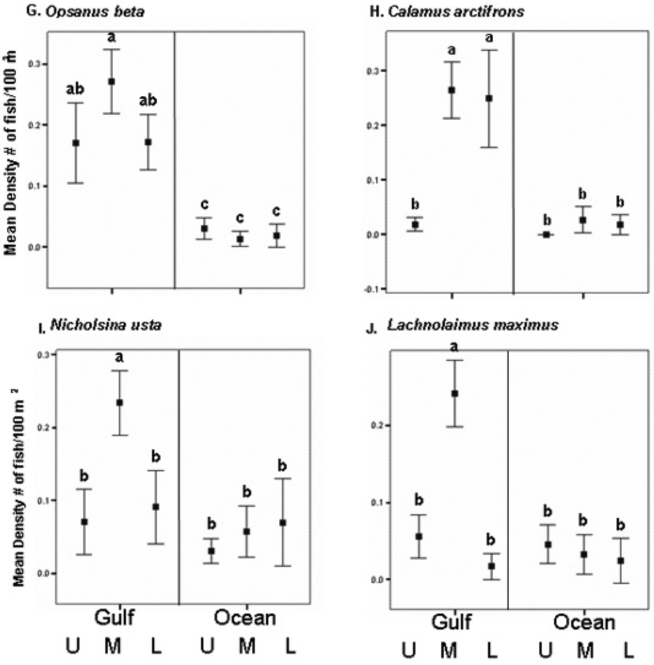

Figure 6. Continued.

grass beds are denser (Fourqurean et al., 2001, 2002) but also because they occupy a much larger area (approximately 1557 km^2 in zones C and D combined vs approximately 385 km^2 in zone B (FDEP and NOAA, 1998), therefore providing more available habitat to fish assemblages (Connolly and Hindell, 2006). Thayer et al. (1999) demonstrated that mixed-species and higher-density seagrass beds support higher densities of fishes than homogeneous and less dense seagrass beds. Our results suggest that large, dense, and complex seagrass beds on the Gulf side of the middle and lower Florida Keys, particularly subzone M_G, may be exceptionally important finfish nursery areas. This importance stems from the high likelihood that these beds make an above-average contribution to the adult populations of many species of finfishes in the FKNMS, both because of their large area relative to other seagrass beds in the FKNMS (Dahlgren et al., 2006) and also because of the high density of fish within them (Beck et al., 2001).

Haemulon plumierii, *L. rhomboides*, *A. quadricornis, O. beta,* and *C. arctifrons* showed no consistent seasonal trends in abundance, and a wide range of sizes were consistently collected, indicating that these species may be using this habitat for an extended period of their life cycle and not principally as a larval settlement area and nursery zone for early juveniles. In contrast, *Eucinostomus* spp.—believed to be almost exclusively *Eucinostomus gula* (Quoy and Gaimard, 1824)—is clearly selectively using this habitat during a limited portion of the early juvenile phase, as evidenced by the fact that abundances showed annual pulses of very small juveniles in the summer and fall and that catches consisted almost entirely of individuals < 50 mm long. The remaining species were prevalent in highest densities from summer to early fall (*L. maximus* and *N. usta)* or from early fall through winter (*M. ciliatus* and *L. synagris*), reflecting seasonal recruitment of early juveniles, but these species tended to

Table 2. Results of Analysis of Similarities (ANOSIM; Clarke, 1993) comparing fish assemblages in six seagrass areas of the Florida Keys Marine Sanctuary arranged by R value. Zones are Upper (U), Middle (M), and Lower (L), strata are Gulf (G) and Atlantic Ocean (O). Subzones are designated as $\text{Zone}_{\text{stratum}}$. Statistical significance at the Bonferroni-adjusted $P < 0.0033$ is denoted in bold.

Subzone pairs		R	P
M_G	**M_O**	**0.413**	**0.001**
M_G	**U_G**	**0.397**	**0.001**
M_O	**L_G**	**0.396**	**0.001**
M_G	**L_O**	**0.386**	**0.001**
M_G	**U_O**	**0.372**	**0.001**
U_O	**L_G**	**0.36**	**0.001**
L_G	**L_O**	**0.326**	**0.001**
U_G	**L_G**	**0.291**	**0.001**
U_G	**U_O**	**0.15**	**0.001**
M_G	**L_G**	**0.121**	**0.001**
U_O	**L_O**	**0.104**	**0.001**
M_O	**U_O**	**0.092**	**0.003**
M_O	**U_G**	**0.075**	**0.001**
U_G	L_O	0.051	0.009
M_O	L_O	0.011	0.177

remain in this habitat for a protracted portion of the juvenile phase, as evidenced by far fewer fluctuations in seasonal abundance and the presence of a wide range of sizes. The general lack of seasonality in fish assemblages of the FKNMS agreed with the results from the single-species analyses.

Clear relationships between densities of juvenile fish and environmental factors have been demonstrated in many other studies (Wagner and Austin, 1999; Kupschus and Tremain, 2001), but total fish densities in the FKNMS were not found to be correlated with mean water temperature, salinity, or dissolved oxygen. Because our study was conducted in a subtropical area well removed from freshwater influences, both the seasonal and spatial variations in these parameters were much smaller than those commonly observed in more temperate regions with greater estuarine influences.

Only three species of recreational or commercial importance (*H. plumierii*, *L. synagris*, and *L. maximus*) appeared to be heavily using the seagrass beds sampled in our study as settlement areas and nursery grounds, based on the presence of appreciable numbers of very small individuals. Three other species of reef-dwelling lutjanids (*L. griseus*, *L. analis*, and yellowtail snapper, *O. chrysurus*) are abundant in the local fishery (Chiappone and Sluka, 1996) and have been reported to use seagrass habitat as a primary nursery area in south Florida waters (Lindeman et al., 1998; Bartels and Ferguson, 2006). *Lutjanus griseus* was collected in moderate numbers (n = 384), but the great majority of these fish were late juveniles (> 70 mm, Lindeman et al., 1998) and no newly settled individuals (< 25 mm) were collected. *Ocyurus chrysurus* was relatively rare in our collections (n = 66), and only one juvenile *L. analis* was encountered. Several other locally abundant species of *Haemulon*, however, were either present in only moderate numbers [*Haemulon sciurus* (Shaw, 1803) (bluestriped grunt); n = 218] or were rare in our samples [*Haemulon aurolineatum* (Cuvier, 1830) (tomtate), *Haemulon carbonarium* Poey, 1860 (Caesar grunt), *Haemulon flavolinea-*

Table 3. Analysis of variance of log transformed salinity, dissolved oxygen, and temperature by season, zones, and years. Bonferroni test: $P < 0.01$. Zones are Upper (U), Middle (M), and Lower (L), Wi = winter, Sp = spring, Su = summer, Fa = fall; df = degrees of freedom, MS = mean square.

Source		df	MS	F	P	Bonferroni
Season	Salinity	3	0.212	401.7	< 0.0001	Su and Sp > Fa and Wi; Wi = Fa
	Dissolved oxygen	3	3.75	5,626.4	< 0.0001	Wi > Sp > Su > Fa
	Temperature	3	8.97	1,158.2	< 0.0001	Su > Sp > Fa > Wi
Zone	Salinity	2	0.213	380.5	< 0.0001	L > M and U; M = U
	Dissolved oxygen	2	0.007	1.29	< 0.0001	M > U and L; L > U
	Temperature	2	0.386	80	0.274	
Year	Salinity	1	0.929	1,920.8	< 0.0001	2000 > 1999
	Dissolved oxygen	1	0.0057	6.4	0.011	
	Temperature	1	0.036	0.117	0.732	

tum (Desmarest, 1823) (French grunt), and *Haemulon parra* (Desmarest, 1823) (sailors choice)].

Proximity to coral reefs or other more complex habitats may influence the distribution and abundance of certain reef-associated species in seagrass beds (Dorenbosch et al., 2005, 2006); the seagrass beds that we sampled throughout the Florida Keys apparently serve as nursery areas for only a limited number of reef-associated fishes. This tentative conclusion is made without any supporting synoptic sampling of nearby reefs, however, and highlights a potential future research direction. Baelde (1990) found that seagrass beds near reefs were used as foraging areas by species that normally found shelter among coral reefs and that seagrass beds in close proximity to mangroves provided a nursery zone for small juveniles. Our results are consistent with other studies that have been unable to demonstrate major linkages between seagrass and reef habitats (Dennis, 1998; Chittaro et al., 2005). Dorenbosch et al. (2004) also found that the relation between fish density on coral reefs and the proximity of seagrass beds and mangroves was only evident for some species. Many of the fish commonly residing on coral reefs throughout their lives ("reef residents", to use the terminology of Dorenbosch et al., 2005), such as chaetodontids, acanthurids, and pomacentrids, were not collected at all in our study, and negligible numbers of other reef residents (e.g., pomacanthids and serranids) were collected in our trawls. This may be because many of these species have specific needs (e.g, particular food sources or spatial complexity) that are not met by seagrass beds alone and reside mainly on the reef tract, patch reefs, or nearby hardbottom habitats. The large distance between seagrass beds on the gulf side and reefs may also limit potential migration between the two habitats or prevent the reef species from establishing permanent residence in seagrass beds, a scenario consistent with that reported by other authors in the Florida Keys and adjacent systems (Robblee and Zieman, 1984; Sogard et al., 1989). In any case, our results indicated that we did not sample in, or effectively sample nursery habitats of many reef-associated species.

The present study identifies seagrass beds on the Gulf of Mexico side of the middle Keys as important habitat for small and juvenile fishes. Describing the relationship between seagrass habitats and fish assemblages, especially in environmentally sensitive areas such as the FKNMS, is critical for evaluating patterns and trends in the ecosystem and evaluating the recovery of impacted areas. Future research is needed to ascertain the extent to which newly settled and juvenile fishes are using habitats other than seagrass beds as nursery grounds, and the connectivity between seagrass beds and these habitats. Ultimately, managers must consider a suite of habitats that may be accommodating the life stages of a wide variety of fish species when making management decisions (Friedlander and Parrish, 1998) especially as they relate to zoning (e.g., establishment of protected areas).

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