BENTHIC HABITATS, FISH ASSEMBLAGES, AND RESOURCE PROTECTION IN CARRIBEAN MARINE SANCTUARIES

by

CHRISTOPHER FRANCIS GABRIEL JEFFREY

(Under the Direction of Eugene S. Helfman)

ABSTRACT

Reef fishes and benthic habitats of the Florida Keys National Marine Sanctuary (FKNMS) were studied to examine spatial patterns in fish occurrence, effectiveness of volunteers in assessing fish species richness, spatial patterns in habitat occurrence, and the influence of habitats on reef fishes. Distinct regional patterns in fish composition were observed, with unique assemblages occurring in the Upper Keys, Middle, and Lower Keys, and Dry Tortugas. Mean species richness was higher in the Upper and Lower Keys than in the Middle Keys or Dry Tortugas.

Three factors (diver, location, and dive time) explained 95% of the variation in mean fish species richness. Divers and dive time explained 70-94% and 41-74% of the variation in richness at Molasses Reef and in the FKNMS. Inexperienced volunteers detected greater among-site differences in richness but provided more variable and probably less reliable data than experienced volunteers. Survey location explained 32-57% of the variation in richness but only after the effects of diver and dive time were reduced by random selection of surveys.

Habitat types varied among subregions and between protected and unprotected areas of the FKNMS. Seagrass habitats dominated the Upper and Lower Keys, whereas hardbottom habitats dominated the Dry Tortugas and Middle Keys. The Dry Tortugas had higher mean habitat richness and evenness than the Upper, Middle, and Lower Keys. Protected areas had greater habitat evenness but lower habitat richness than unprotected areas.

Significant relationships existed between fishes and habitats. Assemblage trophic structure was most affected by habitat composition and abundance. Occurrence of generalized carnivores was negatively correlated, whereas occurrences of piscivores and herbivores were positively correlated with habitat richness and evenness. Occurrences of fishes, e.g., mahogany snapper, longfin damselfish, epinepheline and mycteropercine groupers, and small pelagic species were influenced by abundance of seagrass and hardbottom habitats but varied in the direction of the relationship, with some being positive and others negative. When coupled with geographic information systems based on accurate environmental maps, species-occurrence data from effective volunteer-monitoring programs could help identify important linkages between ecosystem components that are crucial to the successful implementation and management of marine protected areas.

INDEX WORDS: Florida Keys, FKNMS, benthic habitats, coral reef fish, marine protected area, spatial pattern, richness, diversity, evenness, trophic structure, generalized carnivore, herbivore, piscivore, snapper, grouper, damselfish

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DEDICATION

Dedicated to the following people who are most important to me:

My adorable, patient, and longsuffering wife, Chrystel, who stood by me throughout this entire ordeal; my son Jían – the Strong One; my daughter Jolie – a pretty little angel; my mother Mary Jeffrey, who believed in me when my confidence waned; my loving sister Jennifer, who’s strength and resourcefulness I admire; and to all those who never had an opportunity to pursue higher education.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Reef fishes are a major component of tropical and subtropical marine ecosystems. Fishes dominate the top of coral reef food webs and play an important role as herbivores; their presence and abundance can reflect the overall condition of an area (Ogden and Lobel, 1978). Reef fishes also support important commercial and recreational fisheries, and because these fishes represent a large proportion of the biomass in coastal environments, intense fishing pressure may have significant effects on ecosystem processes (Bohnsack 1993, Rogers and Beets 2001, Roberts et al. 2001).

Successful management of coral reef fisheries has become a challenging and complex balance between resource protection and exploitation. Much of the decline in fishery resources has been blamed on overexploitation and habitat degradation resulting from anthropogenic and natural causes (Roberts and Polunin 1991, Roberts 1995, Lauck et al. 1998, Aronson and Precht 2001, Rogers and Beets 2001). Caribbean reef fisheries are highly stressed, and increased documentation of declining fisheries and marine environments has prompted the use of marine protected areas (MPAs) to protect these important resources (Bohnsack and Ault, 1996; NOAA, 1996; Allison et al., 1998; Ault et al., 1998 Rogers and Beets 2001, Roberts et al. 2001). MPAs are useful management and conservation tools because they enhance biodiversity and protect both fishery stocks and the habitats upon which they depend (Plan Development Team 1990, Roberts and Polunin 1991, Bohnsack 1993, Roberts 1995, Russ and Alcala 1996a, 1996b, Sluka et al. 1997, Guennette et al. 1998, Appeldoorn 2001, Roberts et al. 2001). The inclusion of representative and critical habitats within MPAs can provide spatial protection for fishery stocks, enhance stock abundance in adjacent areas because of “spill-over” effects, and preserve ecosystem components critical to fish growth and survival (Parrish 1989, Sluka et al. 1997, Bohnsack 1998, Appeldoorn 2001, Roberts at al. 2001).

Understanding the fundamental role of habitats in determining the structure and dynamics of fish populations is crucial to the successful implementation of MPAs. Coral reef fishes associate with habitats that are complex biologically and architecturally, and are dynamic temporally and spatially (Jackson 1991, Jones and Syms 1998). In addition, these habitats vary temporally and spatially in their distribution because of disturbances that range in scale and intensity from the destruction of individual coral heads to the destruction of vast areas by hurricanes (Jackson 1991, Hughes 1994, Jones and Syms 1998). The structure and quality of underlying habitats can influence demographic and ecological processes such as rates of recruitment, settlement, and the outcomes of competition and predation, all of which ultimately determine patterns in the distribution, abundance, and structure of post-settlement fish assemblages (Helfman 1978, Sale et al. 1984, Hixon and Menge 1991, Hixon and Beets 1993, Caley and St. John 1996, Jones 1998).

Strong associations between fishes and their habitats imply that successful implementation of marine reserves requires a knowledge of the location, distribution, and extent of habitats necessary for successful recruitment, growth, feeding, and reproduction of fishes (Parrish 1989, Friedlander and Parrish 1998). Recent evidence suggests that reef fishes are dependent on systems that comprise a mosaic of habitats, including not only reef structure but also a mixture of seagrasses, mangroves, and unconsolidated sand flats as well (Christensen et al. 2003, Kendall et al. 2003, Mumby et al. 2003). Each of these habitats contains biotic communities that vary differently depending on the scale at which individual or community-level processes are observed (Williams 1991, Sale 1998).

This dissertation examined the influence of benthic habitats on patterns in abundance, composition, and distribution of adult coral reef fish assemblages in the Caribbean. Chapter two describes patterns in fish community structure and assemblage composition among geographic regions of the Florida Keys National Marine Sanctuary (FKNMS) based on data collected by volunteer divers of the Reef Environmental Education Foundation (REEF). In chapter three, the effectiveness of REEF volunteers as assessors of fish species richness is analyzed. Such an assessment was necessary to determine what factors were affecting the variability of data on fishes reported by REEF. Chapter four presents an analysis of the spatial patterns in the distribution and abundance of benthic habitats in the FKNMS. Spatial patterns are based on data derived from digitized benthic maps that were developed from aerial photography of a 160-km^2 area (scale = 1:48,000, FMRI and NOAA 1998). A set of GIS-based metrics were developed to describe spatial patterns in the distribution and abundance of benthic habitats among subregions, among protected areas, and between protected and unprotected areas. In chapter five, relationships between fish assemblages and benthic substrates that occur in the FKNMS were examined to determine if spatial patterns in fish distributions were driven by spatial patterns in the distribution of underlying habitats. Finally, chapter six concludes this dissertation and presents a summary of the influence of benthic habitats on Caribbean coral reef fish assemblages.

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CHAPTER 2

SPATIAL PATTERNS IN FISH ASSEMBLAGE COMPOSITION OF THE FLORIDA KEYS NATIONAL MARINE SANCTUARY[1]

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[1] Jeffrey, C.F.G., C. Pattengill-Semmens, S. Gittings, and M.E. Monaco. To be submitted to *Bulletin of Marine Science*

Abstract

Spatial patterns in fish assemblage composition among geographic regions were examined between 1993 and 1999 in the Florida Keys National Marine Sanctuary (FKNMS). Species richness was generally highest in Upper Keys sites with a maximum of 220 species at Molasses Reef and lowest at Dry Tortugas sites, where as few as 16 species occurred per site. Hierarchical clustering of species presence and absence produced three main site clusters that reflected patterns of similarities in species composition among sites within and across regions. Correspondence analysis explained only 25% of the variation in composition of site clusters but revealed significant associations between the site clusters and regions based on fish assemblage structure. Five species had significantly lower mean sighting frequency (% SF) in the Dry Tortugas; six species had significantly higher mean (% SF) in the Dry Tortugas compared with other regions. Three other species showed a gradual eastward or westward increase in % SF across regions. Regional and site differences in the structure, variety, and extent of habitats coupled with specific habitat requirements of fishes strongly influenced the patterns in assemblage composition in the FKNMS. Factors affecting reef fish composition appear to operate at three different spatial scales: 1) a Keys-wide biogeographic scale that characterizes the Florida Keys; 2) a regional scale (~50-100 km) that includes meso-scale oceanographic processes and regional variation in the abundance, structure, and variety of reef-associated habitats; and 3) a local scale that includes level of protection, cross-shelf location, and the physical characteristics of a given reef. The importance of habitats in structuring fish populations indicates the need to investigate factors that operate at regional and sub-regional scales. An increased understanding of fish-habitat relationships over large spatial scales will help in the development of sound ecosystem-based strategies for managing large biogeographic regions, such as those encountered within the FKNMS.

Introduction

Reef fish assemblages are a major component of tropical and subtropical marine ecosystems. Fishes dominate the top of coral reef food webs and play an important role as herbivores, and their presence and abundance reflect the overall condition of an area (Ogden and Lobel 1978). Reef fishes also support important commercial and recreational fisheries, and because these fishes represent a large proportion of the biomass in coastal environments, intense fishing pressure may have significant effects on ecosystem processes (Richards and Lindeman 1987).

Reef fishery resources of the Florida Keys are highly stressed, and increased documentation of declining fisheries and marine environments has prompted the use of no-take marine reserves to protect these important resources (Bohnsack and Ault 1996, NOAA 1996, Allison et al. 1998, Ault et al. 1998). Additionally, the 1990 amendment of the Magnuson Fishery Conservation and Management Act (H.R. 2061) has increased focus on fishery habitat protection within the United States coastal waters.

Implementing marine protected areas to enhance fishery resources (e.g., increased biomass) requires an understanding of the complex interactions among several physical and biological factors (e.g., ocean currents, habitat distribution, and reproductive behavior) that determine broad-scale patterns of fish abundance and distribution. Specifically, resource managers need a better understanding of the natural spatial and temporal variability exhibited by marine populations as well as the ecological relationships among the ecosystems, habitats, and living resources they contain. Reef fish populations and assemblages often vary greatly among habitat patches at varying scales such as physiographic reef zones or reef types (Williams 1991). Thus, designing effective monitoring or resource management programs requires an understanding of a population's spatial and temporal patterns of distribution.

This study describes large-scale spatial patterns in the composition and community structure of reef fish assemblages within the Florida Keys National Marine Sanctuary (FKNMS) reef ecosystem. The specific objectives were 1) to identify patterns in the diversity and distribution of fishes within the FKNMS, and 2) to compare the community structure of fish assemblages among four regions of the

Florida Keys. Data for this study were obtained from the Reef Environmental Education Foundation (REEF), a volunteer fish-monitoring program (REEF 2001).

Methods

Study area

The Florida Keys comprise an island archipelago that extends 320 km southwest from Soldier Key in Biscayne Bay to the Dry Tortugas (Figure 2.1). To the north and west, the Keys are bounded by Biscayne Bay and the Gulf of Mexico; to the east and south, they are bounded by the Straits of Florida. Submerged aquatic habitats include extensive seagrass beds and an extensive coral reef tract that extends 8 km offshore toward the Atlantic Ocean. The study area was divided into four regions based on geomorphologic properties that may affect the degree of exchange among the Gulf of Mexico, Florida Bay, and the Atlantic Ocean (FMRI 1998). The regions are the Upper Keys (Key Largo to Upper Matecumbe Key), Middle Keys (Upper Matecumbe Key to Pigeon Key), Lower Keys (Little Duck Key to Marquesas Key), and the Dry Tortugas (Figure 2.1).

Collection of data on fishes in the FKNMS

REEF volunteer divers used the Roving Diver Technique (RDT) to collect data on fish distribution and abundance (Schmitt and Sullivan 1996, REEF 2001). The RDT involved divers swimming freely about a dive site within a 100-m radius of the starting point and recording every fish species that was positively identified. The survey began as soon as the diver entered the water. At the conclusion of each survey, the diver assigned each recorded species to one of four log_{10} abundance categories (single [1]; few [2-10]; many [11-100]; and abundant [>100]) based on the approximate number of individuals seen. Location, time, depth, temperature, and logistic information pertinent to the survey were also noted. Data were recorded and later transferred to standardized scan sheets for upload into an online database. A series of quality assurance and control procedures, such as verifying previously unrecorded species from known species lists and checking for misidentification of species that are similar morphologically, occurred before data were uploaded into an online database.

RDT survey data files obtained from REEF were imported into JMP statistical software (Version 5.1, SAS Institute Inc. 2003) for processing and analysis. Each survey was assigned a unique identification number and was used as a replicate within survey sites. Site (point sample) locations were identified by unique geographic zone codes and by latitude and longitude. Five hundred and eighteen REEF divers conducted 4,431 surveys at 119 sites in the Florida Keys and Dry Tortugas from July 1993 to August 1999. Recorded survey time varied significantly, ranging from 10 minutes to 245 minutes (4.75 hr), and were normally distributed around a mean of 59.4 min ± 0.2 min. Approximately 96% (4,331) of the surveys ranged between 30 and 100 minutes. Because species richness data may be influenced by observation time, surveys shorter than 30 minutes or greater than 100 minutes were considered outliers, and data from these surveys were not used in statistical analyses. Additionally, sites with fewer than three replicate surveys were excluded. As a result, 4,324 surveys from 112 sites were used for analysis of species richness and sighting frequency. Species richness (R), defined as the total number of species documented, was calculated for each survey, site, and region. Percent sighting frequency (% SF) was calculated for each species, by site, and by region. Percent sighting frequency was the percentage of all survey dives in which a particular species or family was recorded. The number of RDT surveys used in this study ranged from 2,603 surveys in the Upper Keys to 377 surveys in the Dry Tortugas.

Statistical analysis and development of species distribution maps

Similarity in species assemblage composition among sites and regions was determined by hierarchical clustering (Ward's minimum variance) and correspondence analysis. Hierarchical clustering was used to group sites based on species composition (presence-absence) such that sites that were most similar clustered more closely than sites that were more dissimilar. Resulting site clusters were plotted as dendrograms so that regional patterns of assemblage composition could be detected more easily. Site clusters were determined with a fixed-stopping rule by drawing a line across the nodes of the resulting dendrogram (Boesch 1977, Gauch 1995). The line was drawn at the node where the sharpest change in slope occurred in a line plot of the distance between the clusters against the number of remaining clusters. Clustering analysis included only 97 sites, each of which had at least five surveys; all species were included. Correspondence analysis was used to determine if any significant associations existed between the site clusters and the four geographic regions of the FKNMS. If species composition differed among regions, then each site cluster should consist predominantly of sites from a single region that would associate strongly with that region in canonical space.

Mean estimates of 1) species richness and 2) sighting frequency of the 20 most commonly observed species in the FKNMS and the ten most commonly observed species in the Dry Tortugas were calculated for each site and region. Kruskal-Wallis non-parametric rank sums tests and modified Tukey multiple comparisons were used to determine differences in mean estimates among sites and regions (Sokal and Rohlf 1995, Zar 1999). Surveys were considered replicates, whereas location, region, and other factors (e.g., diver experience and habitat types) were considered treatment effects. Statistical analyses, including comparisons of means among treatments, were done with $\alpha = 0.05$ to test for significant differences.

Finally, distribution maps for the most frequently observed species were created using four equal % SF quartiles to classify fish distribution (Figure 2.2). Geographic coverages for the most frequently observed species were created by plotting sighting frequency data on a base map of the FKNMS region in ArcView GIS© software (Version 3.2a, Environmental Systems Research Institute, Inc., ESRI 2000).

Results

Patterns of species richness

The Florida Keys and Dry Tortugas REEF data set contained sighting information on 341 fish species comprising 68 families (see Appendix 2). Molasses Reef in the Upper Keys (25° 0.5' N, 87°

22.4' W) had 220 species, the highest number of species observed per location. Molasses Reef also had the greatest number of surveys (277 surveys; approximately 261 h). Overall, cumulative species richness at survey sites increased log-linearly with increasing cumulative survey time such that time accounted for 82% of the variation in richness ($r^2 = 0.82$, $P < 0.0001$, Figure 2.3). Approximately 90% of the species were observed only after 130 h of surveying had been conducted (Figure 2.3). The rate of increase in cumulative species richness did not vary significantly among regions, nor were species encounter rates relative to the total number of species observed significantly different among regions ($F = 8.36$, df = 3, 363, $P = 0.89$).

However, significant patterns were observed when mean species richness was compared among regions after accounting for differences in survey time. Chi-square comparisons of mean richness among regions showed significantly fewer species in the Dry Tortugas compared with other regions ($P < 0.0001$, Figure 2.4). The number of species observed per survey was similar among the Upper, Middle, and Lower Keys but was significantly lower in the Dry Tortugas ($P < 0.0001$, Figure 2.5). Observer-related differences among regions were not evident, and patterns of species richness among regions were similar between novice and expert divers ($F = 69.9$, df = 1, 369, $P = 0.99$).

Patterns in species composition and sighting frequency

Hierarchical clustering produced three main site clusters that reflected patterns of similarities in species composition among sites within and across regions (Figure 2.6). Correspondence analysis explained only 25% of the variation in species composition but revealed significant associations between the site clusters and regions (Figure 2.6). Site cluster I associated strongly with the Dry Tortugas in the c1 dimension and consisted mainly of sites from the Dry Tortugas (Figure 2.6). Cluster I also contained a few sites from the Upper, Middle, and Lower Keys (2.6B). Site cluster II had an equal number of sites from the Upper and Lower Keys, a few sites from the Middle Keys and the Dry Tortugas, and was associated with the Middle and Lower Keys. Site cluster III associated with the Upper Keys in both c1 and c2 dimensions and consisted of 23 sites (85%) from the Upper Keys, one site from the Lower Keys, and no sites from the Dry Tortugas (Figure 2.6B).

Regional patterns in species distribution

Ranking of species by sighting frequency revealed differences in species composition between the Dry Tortugas and other regions of the Florida Keys. Ten of the 20 most frequently observed species in the Florida Keys did not rank among the 20 most observed species in the Dry Tortugas (Table 2.1). Conversely, nine of the 20 most frequently observed species in the Dry Tortugas did not rank among the 20 most observed species in other regions of the Florida Keys (Table 2.2). Blue tang[1] was the most frequently observed fish in both the Florida Keys and the Dry Tortugas, 91% and 93% respectively. Other frequently observed species included the stoplight parrotfish, yellowtail snapper, sergeant major, bluehead wrasse, and the French grunt. Grunts and damselfishes were more highly represented among the top 20 species in both the Florida Keys and the Dry Tortugas (Table 2.3). Groupers were not ranked among the top 20 most frequently observed species for any region.

Kruskal-Wallis tests and modified Tukey multiple comparisons of species % SF among regions showed significantly lower mean % SF of five species in the Dry Tortugas compared with other regions ($P < 0.05$; Table 2.4). Bluestriped grunt was significantly less frequent at Dry Tortugas sites (38.0 % ± 8.2) compared with the Lower (81.2 % ± 3.2), Middle (87.1% ± 4.3), and Upper Keys (86.1 % ± 2.6), but differences among the Lower, Middle, and Upper Keys were not significant (Tukey HSD, $P < 0.05$; Figure 2.7A). Similarly, four other species were less frequent in the Dry Tortugas than other regions of the Florida Keys. These species were the yellowtail damselfish, sergeant major, porkfish, and the foureye butterflyfish.

Six species were consistently observed more frequently in the Dry Tortugas than other regions of the Keys (Table 2.4). Barred hamlets occurred almost twice as often at Dry Tortugas sites than at sites in

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[1] Common and scientific names for fish species are given in Appendix 2.2

other regions, and were not observed at 47% and 20% of sampled sites in the Middle and Upper Keys, respectively (Figure 2.7B). Other species that occurred more frequently in the Dry Tortugas than elsewhere were the blue hamlet, butter hamlet, cocoa damselfish, blue angelfish, and the neon goby.

Three other species showed a general increase or decrease in % SF across the four regions, with significant differences occurring only between the Dry Tortugas and the Upper Keys. Sharpnose puffer was observed less frequently in the Dry Tortugas compared with the Upper Keys but not when compared with the Lower or Middle Keys (Figure 2.8A). Striped parrotfish were observed more frequently in the Upper Keys compared with the Dry Tortugas but observed at similar levels in the Lower and Middle Keys (Figure 2.8B). Threespot damselfish had a pattern of distribution similar to that of striped parrotfish but were observed the least in the Middle and Lower Keys compared with the Upper Keys or the Dry Tortugas. Interestingly, none of these species were observed more frequently in the Middle and Lower Keys compared with either the Dry Tortugas or the Upper Keys.

Discussion

Distinct regional patterns in monitoring effort, species richness, and assemblage composition were observed in the FKNMS, and an understanding of these patterns is critical to the design of effective monitoring programs. Estimates of parameters such as encounter rates of species and levels of sample variance provide information that can be used to determine the effort required to test specific hypotheses or to detect changes of varying magnitude. This study utilized a database generated by a large, volunteer-based survey effort intended to provide such background. In addition, the study extends the effort by other researchers to determine regional patterns in the diversity and abundance of fishes within the FKNMS (Bohnsack and Ault 1996, Ault et al. 1998).

The species/effort curve shown in Figure 2.3 suggests that visual sampling by REEF volunteers provided adequate measures of species richness for the FKNMS. After 150 h, most species (90%) were observed, with few additional species being seen with additional sampling. Furthermore, the rate of increase in species richness with time did not vary significantly among regions, which suggests that differences in sampling effort among regions had minimal effect on regional estimates of species richness. Thus, differences in measures of species richness and species composition among regions may be related to differences in environmental factors rather than to differences in sampling effort among regions.

Patterns in sighting frequency and species richness suggest that reefs in the Dry Tortugas are different from those in other regions of the Florida Keys. Six species (barred, blue and butter hamlets, cocoa damselfish, blue angel fish, and neon goby) were observed more frequently in the Tortugas than in other regions. Five other species (bluestriped grunt, yellowtail damselfish, sergeant major, porkfish, and foureye butterflyfish) were less frequently encountered in the Tortugas.

Hierarchical clustering and correspondences analysis further supported differences in species assemblages among regions, but also identified site groupings that appeared to contradict regional patterns in fish assemblage structure. Most sites in the Dry Tortugas clustered together and separately in site cluster I, which indicated that the Dry Tortugas had fish assemblages that were different from those of other regions. Likewise, several sites in the Upper Keys clustered separately and contained fish assemblages that differed from those of other regions. However, 13 sites from the Upper, Lower, and Middle Keys were grouped with sites from the Dry Tortugas in site Cluster I. These 13 sites either were deep reefs (e.g., Dixie Reef, Hammerhead Reef, and Herman’s Behind Reef, all 18-24 m) or shipwrecks (e.g., the Duane and Wreck of Eagle), and had fish assemblages that were more similar to the deeper reefs of the Dry Tortugas than to the shallower reefs of other regions in the Florida Keys. Interestingly, site cluster II contained two distinct sub-clusters (i.e., Upper and Lower Keys) in which sites within the same region associated more closely with each other than with sites from other regions. These sub-clusters further indicate that locations from the same region within site cluster II had fish assemblages that were more similar with each other than with those from the other regions.

Alternatively, these sub-clusters could have resulted from similarities in species composition among sites because of environmental variables such as cross-shelf location of sites or underlying habitat type. For example, an inshore patch reef in the Upper Keys (Canon Patch/Garrett's Reef) associated most closely with inshore patch reefs from other regions (Cheeca Rocks, Middle Keys and Newfound/Captain's Coral Reef, Lower Keys). Similarly, offshore bank reef sites such as Fish Bowl (Upper Keys), Herman's Hole and Delta Shoals (Middle Keys), and No Name Reef (Lower Keys) clustered closely together. Such site groupings suggest that further stratification of fish assemblages by these environmental variables is needed to understand patterns of fish assemblage composition in the Florida Keys.

Oceanographic and ecological processes affecting reef fish composition in the FKNMS may be operating at multiple spatial scales. Beyond the biogeographic scale that defines the character of the region as a whole (the reefs contain tropical species of the Caribbean Province), processes operating on a scale of the order of ~50-100 km may account for differences between the Tortugas and the rest of the Florida Keys. Meso-scale current circulation patterns, such as those identified by Lee et al. (1992, 1994), may localize some recruitment within several areas of the Keys and could result in fish assemblage differences among regions. Additionally, the influence of Florida Bay may operate at similar scales because passes, which allow the exchange of seawater between the bay and the Gulf of Mexico, are numerous in the Middle and Lower Keys but are uncommon the Upper Keys.

Regional differences in the structure, variety, and extent of habitats coupled with specific habitat requirements of fishes strongly influenced the patterns in assemblage composition revealed in this study. Reefs in the Upper Keys tend to be more structurally complex than those in the Middle and Lower Keys. Seagrass beds and other aquatic vegetation – habitats utilized by fishes during early life history stages – are abundant in the Upper Keys, less so in the Middle and Lower Keys, and are rare in the Dry Tortugas (see chapter 4). The presence or absence of aquatic vegetation in an area has been shown to affect fish assemblage composition on nearby reefs (Nagelkerken *et al.* 2000, Kendall 2003, Christensen et al.

2003). The importance of specific characteristics of habitats in structuring fish populations indicates the need to investigate factors that operate at a sub-regional scale, such as the proximity of reefs to seagrass beds and to shore-associated habitats (e.g. mangroves). Also, the relationship between the abundance of reef habitats and fish assemblage composition should be examined because reef size may affect fish richness, abundance, and size (Parrish 1989, Chittaro 2004).

Two previous studies conducted on smaller spatial scales have identified regional patterns in fish assemblage structure in the Florida Keys. Schmitt and Sullivan (1996) analyzed data collected from 27 sites by four trained volunteers during 130 h of sampling in summer of 1994. They found that species richness was highest in the Upper Keys, followed by the Lower Keys, and the Dry Tortugas. Furthermore, a cluster analysis of reefs based on the Jaccard index of similarity showed that reefs within regions were more similar in species composition than reefs from other regions (Schmitt and Sullivan 1996). In an even earlier study, Jones and Thompson (1978) compared reef fish assemblages at four sites in Key Largo (Upper Keys) with those at four sites in the Dry Tortugas (total survey time per region = 25 h). Jones and Thompson observed more species and a higher diversity of fishes at Key Largo than in the Dry Tortugas. Additionally, species composition was more similar among sites within regions than among sites across regions based on the Bray-Curtis index of dissimilarity (Jones and Thompson 1978). In this study, data from a much larger survey effort (119 sites, 518 divers, > 4000 surveys, and > 7000 h of survey time) confirmed regional patterns in fish species richness and assemblage composition similar to those observed by others. The similarity in the results of these three studies across the spatial and temporal scales indicates that regional patterns in fish assemblage structure and composition in the FKNMS are real.

The results of this study provide a benchmark for the current status of the reef fishes in the FKNMS. These data provide the basis for analyses on reserve effects and the biogeographic coupling of benthic habitats and fish assemblages. Further analyses of these data include identifying patterns in the distribution of benthic habitats within the FKNMS (Chapter 4) and correlating these patterns with spatial trends in fish assemblage structure and composition (Chapter 5). Ultimately, an increased understanding of fish-habitat relationships over large spatial scales will only help guide the development of sound ecosystem-based management of large biogeographic regions, such as those encountered within the FKNMS.

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TABLES

Table 2.1. Percent sighting frequency (% SF) of the most common fishes observed in the Florida Keys (excluding the Dry Tortugas) by volunteer divers of the Reef Environmental Education Foundation (REEF). Data are from REEF (2000). A pound symbol (#) indicates species that are not ranked among the 20 most commonly observed species in the Dry Tortugas. Scientific species names are given in Appendix 2.1.

Rank	Species	Family	% SF
1	Blue tang	Acanthuridae	91.1
2	Stoplight parrotfish	Scaridae	87.7
3	Yellowtail snapper	Lutjanidae	84.1
4	Sergeant major #	Pomacentridae	83.4
5	Bluehead wrasse #	Labridae	83.4
6	French grunt	Haemulidae	82.4
7	Bicolor damselfish	Pomacentridae	81.6
8	Ocean surgeonfish #	Acanthuridae	77.5
9	Bluestriped grunt #	Haemulidae	77.3
10	Yellowtail damselfish #	Pomacentridae	74.8
11	Porkfish	Haemulidae	74.2
12	Foureye butterflyfish #	Chaetodontidae	73.9
13	White grunt #	Haemulidae	73.9
14	Redband parrotfish	Scaridae	71.1
15	Spotfin butterflyfish	Chaetodontidae	70.5
16	Yellowhead wrasse	Labridae	70.1
17	Great barracuda #	Sphyraenidae	68.5
18	Gray angelfish	Pomacanthidae	68.0
19	Bar jack #	Carangidae	66.4
20	Sharpnose puffer #	Tetraodontidae	62.4

Table 2.2. Percent sighting frequency of the most common species observed in the Dry Tortugas by volunteer divers of the Reef Environmental Education Foundation. Asterisks denote species that were not ranked among the twenty most frequently observed species in other areas of the Florida Keys. Data are from REEF (2000). Scientific species names are given in Appendix 2.1.

Rank	Species	Family	% SF
1	Blue tang	Acanthuridae	93.4
2	Bluehead wrasse	Labridae	89.5
3	Stoplight parrotfish	Scaridae	83.9
4	Gray angelfish	Pomacanthidae	83.7
5	Yellowtail snapper	Lutjanidae	83.2
6	White grunt	Haemulidae	78.8
7	Cocoa damselfish*	Pomacentridae	78.1
8	Spotfin butterflyfish	Chaetodontidae	77.1
9	Threespot damselfish*	Pomacentridae	75.9
10	Neon goby*	Gobiidae	74.9
11	Redband parrotfish	Scaridae	69.6
12	Butter hamlet*	Serranidae	68.6
13	Blue angelfish*	Pomacanthidae	68.4
14	French grunt	Haemulidae	64.0
15	Striped parrotfish*	Scaridae	63.8
16	Bicolor damselfish	Pomacentridae	63.5
17	Blue hamlet*	Serranidae	63.0
18	Yellowhead wrasse	Labridae	61.6
19	Slippery dick*	Labridae	59.9
20	Barred hamlet*	Serranidae	57.4

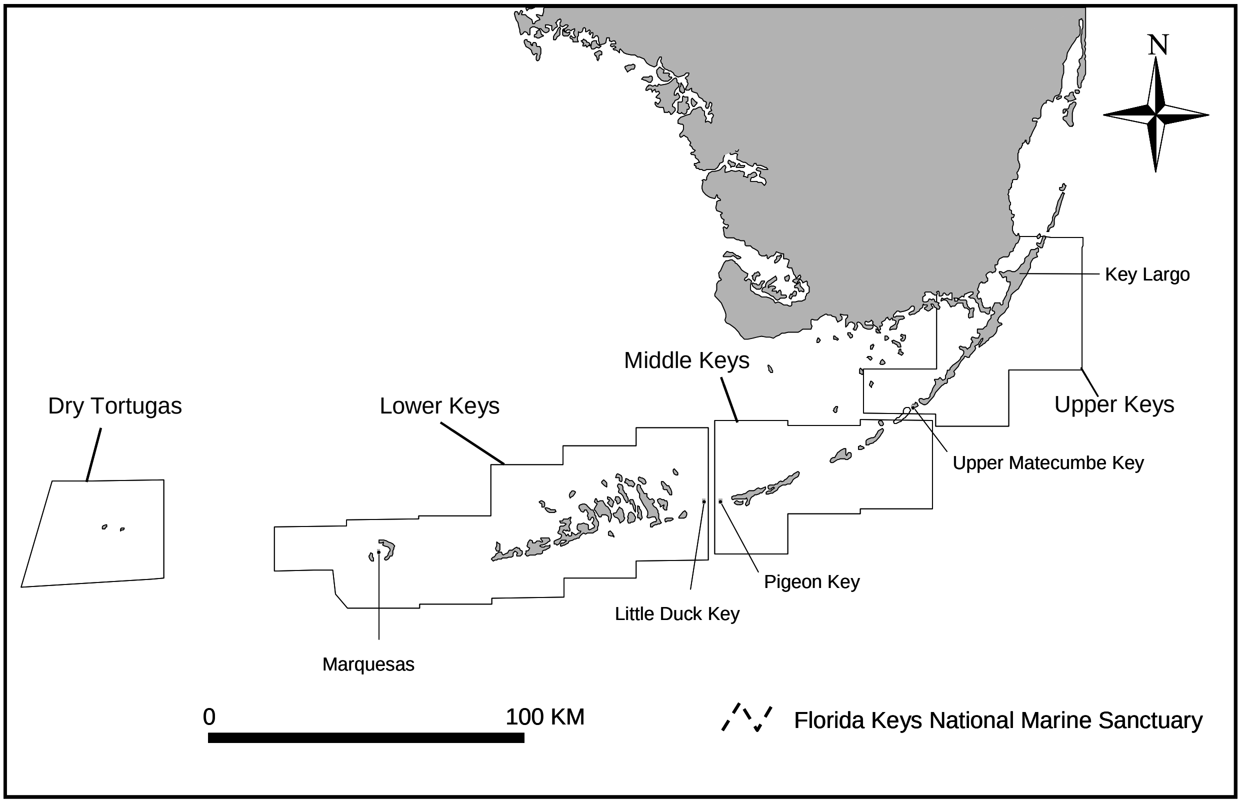
Table 2.3. Number of species per fish family ranked among the twenty most frequently observed species in the Florida Keys and Dry Tortugas. Data are from REEF (2000).

Fish Family	Common name	# of species
Haemulidae	Grunts	4
Pomacentridae	Damselfishes	3
Scaridae	Parrotfishes	2
Labridae	Wrasses	2
Chaetodontidae	Butterflyfishes	2
Acanthuridae	Surgeonfishes	2
Tetradontidae	Puffers	1
Sphyraenidae	Barracudas	1
Pomacanthidae	Angelfishes	1
Lutjanidae	Snappers	1
Carangidae	Jacks	1

Table 2.4. Results of Wilcoxon / Kruskal-Wallis and Tukey type tests for significant differences in mean percent sighting frequency of 29 species among regions of the Florida Keys and the Dry Tortugas (alpha = 0.05, df = 3). Asterisks indicate species ranked in the Dry Tortugas but not among the twenty most observed species in the Florida Keys. Frequency classes are based on equal quantiles determined from the distribution of the mean sighting frequencies (n = 112 site means). DT = Dry Tortugas, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys. P values < 0.05 were considered significant. HF: highly frequent; F: frequent; C: common; U: uncommon. Scientific species names are given in Appendix 2.1.

Species	χ^2	P	Frequency			
			DT	LK	MK	UK
Bluestriped grunt	21.00	**0.00**	C	HF	HF	HF
Yellowtail damselfish	20.52	**0.00**	C	F	HF	F
Sergeant major	18.42	**0.00**	C	HF	HF	HF
Porkfish	14.85	**0.00**	C	HF	HF	HF
Sharpnose puffer	11.29	**0.01**	C	F	F	F
Foureye butterflyfish	7.86	0.05	F	HF	HF	F
Barred hamlet*	23.57	**0.00**	C	UC	UC	UC
Blue angelfish*	29.65	**0.00**	F	C	C	UC
Neon goby*	19.41	**0.00**	F	F	C	C
Butter hamlet*	18.72	**0.00**	F	C	C	F
Blue hamlet*	15.66	**0.00**	F	C	C	C
Cocoa damselfish*	13.03	**0.00**	F	F	F	F
Threespot damselfish*	11.49	**0.01**	F	F	C	F
Striped parrotfish*	9.48	**0.02**	F	F	F	F
Redband parrotfish	7.68	0.06	F	F	F	HF
Bar jack	7.35	0.06	F	F	HF	F
Ocean surgeonfish	6.77	0.08	F	HF	HF	HF
French grunt	6.50	0.09	F	HF	HF	HF
Bluehead	6.34	0.10	HF	F	HF	HF
Gray angelfish	6.12	0.11	HF	F	HF	F
Yellowhead wrasse	5.05	0.17	F	F	HF	HF
Spotfin butterflyfish	4.87	0.18	HF	F	HF	F
Yellowtail snapper	4.63	0.20	HF	HF	F	HF
Bicolor damselfish	4.40	0.22	F	F	HF	HF
Great barracuda	3.05	0.38	F	F	F	F
Blue tang	1.68	0.64	HF	HF	HF	HF
White grunt	1.28	0.73	HF	HF	HF	HF
Stoplight parrotfish	1.17	0.76	HF	HF	HF	HF
Slippery dick*	1.31	0.73	F	F	F	F

FIGURES


N
Key Largo
Middle Keys
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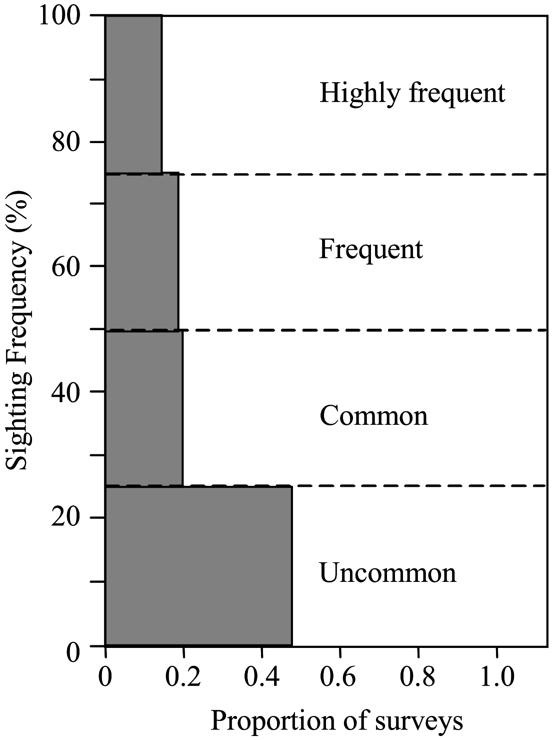


Figure 2.2. Classification scheme used in mapping fish abundance and summary statistics for fish data obtained from the Reef Environmental Education Foundation (REEF, 2000). Shaded bars indicate the proportion of surveys in each category of sighting frequency.

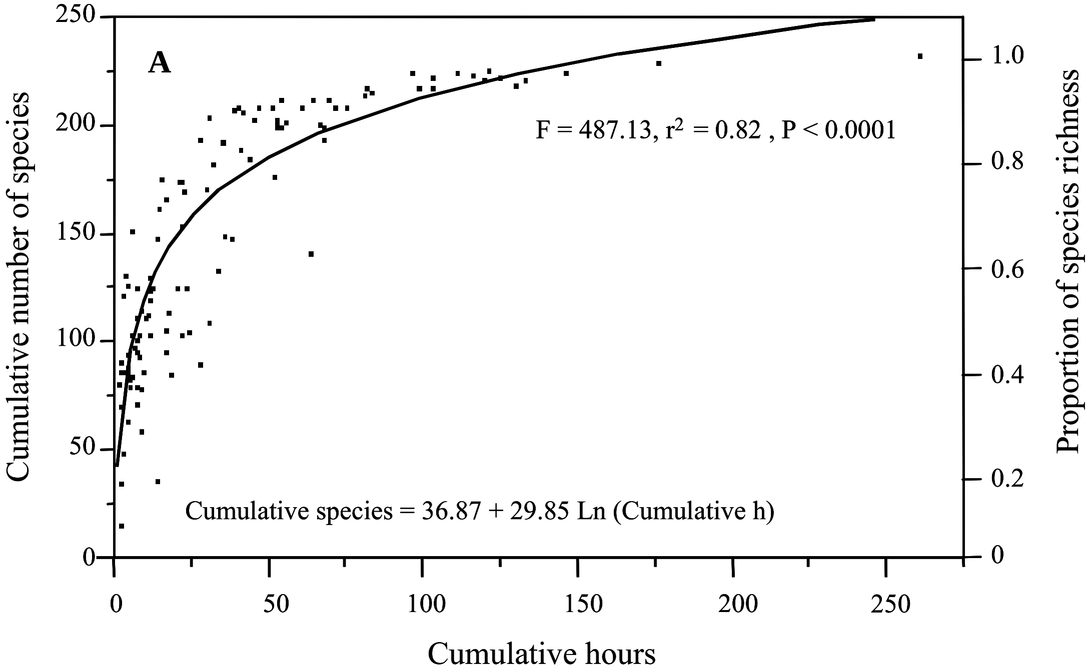


Figure 2.3. Scatter plot and regression of cumulative fish species richness against dive time for sites in the Florida Keys. Data were collected by volunteers of the Reef Environmental Education Foundation between July 1993 and July August 1999.

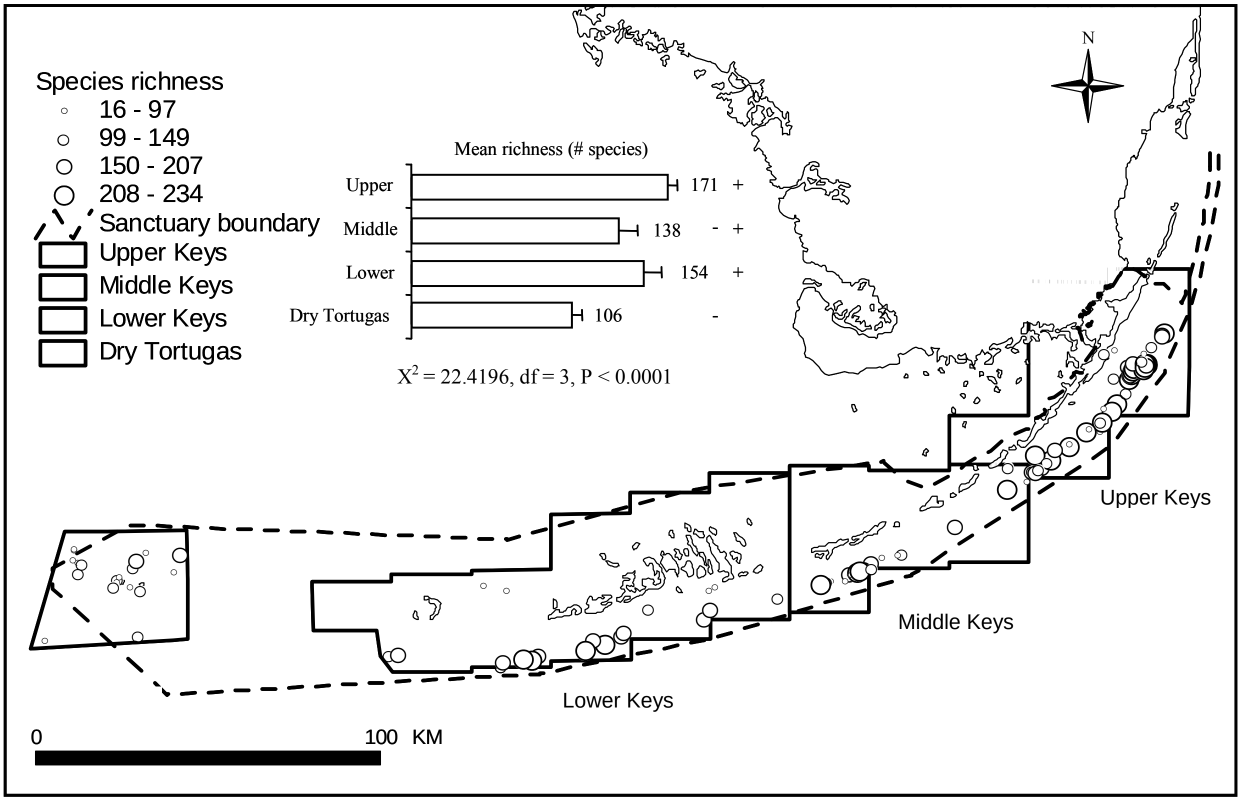
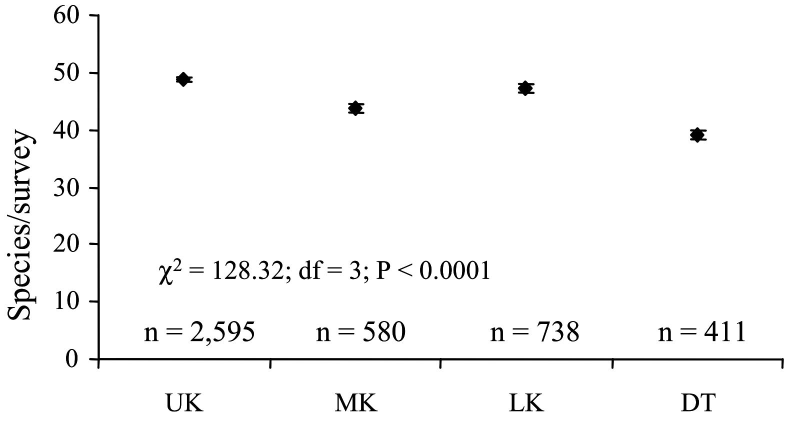


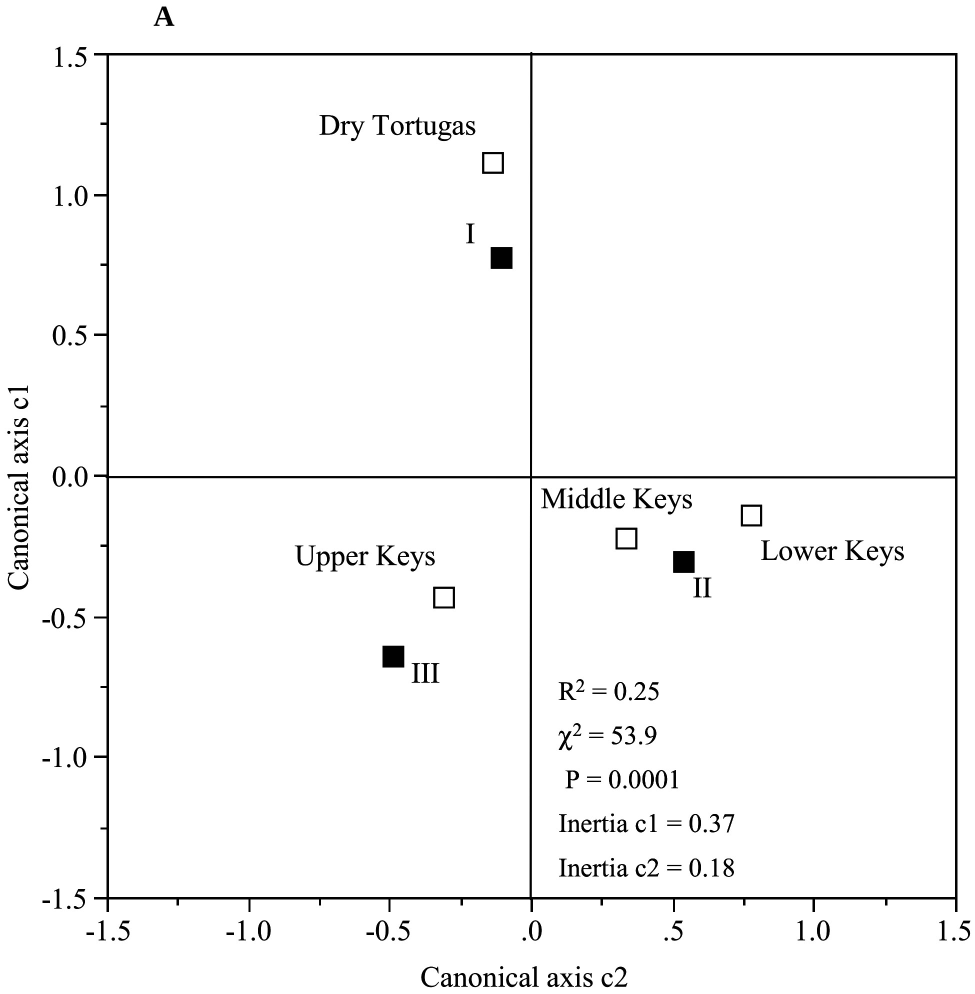
Figure 2.4. Distribution map of overall species richness for four regions of the Florida Keys. The bar graph shows regional differences in the mean number of species and tests for significant differences among regional means (Kruskal-Wallis χ^2 test, $\alpha = 0.05$; modified Tukey multiple comparisons, $\alpha = 0.05$). Means with the same symbols (+ or -) were not significantly different.



	UK	LK	MK	DT
UK	-	-	+	+
LK	-	-	+	+
MK	+	+	-	+
DT	+	+	+	-

UK = Upper Keys
MK = Middle Keys
LK = Lower Keys
DT = Dry Tortugas

Figure 2.5. Mean species richness per diver survey for four regions of the Florida Keys. Differences between means are significant. Means were tested with a Wilcoxon / Kruskal-Wallis one-way Chi-Squared (Rank Sums) test. The table shows the results of pairwise comparisons among regions using modified Tukey-Kramer comparisons ($\alpha = 0.05$; $q^* = 2.57003$). A '+' indicates significant differences among paired means; a '-' shows no significant differences among paired means.



B

	Cluster		
	I	II	III
Upper Keys	9 (30)	13 (37.2)	23 (85.2)
Middle Keys	3 (5)	7 (20)	3 (11.1)
Lower Keys	4 (10)	13 (37.1)	1 (3.7)
Dry Tortugas	19 (55)	2 (5.7)	0 (0)
Total	35 (100)	35 (100)	27 (100)

Figure 2.6. Correspondence analysis plot (A) and contingency table (B) of the association between site clusters and regions of the Florida Keys. Site clusters were identified from hierarchical clustering (Ward's minimum variance technique) of fish species composition (i.e. the presence or absence of species) of each site. The figure (A) shows Chi-square (χ^2), P, and Inertia values of a –log likelihood test of a significant correlation between site clusters and regions of the Florida Keys. The proportion of sites within each cluster that belongs to each region is given as a percent in parentheses (Table B). Data were collected by volunteers of the Reef Environmental Education Foundation (REEF) between July 1993 and July August 1999.

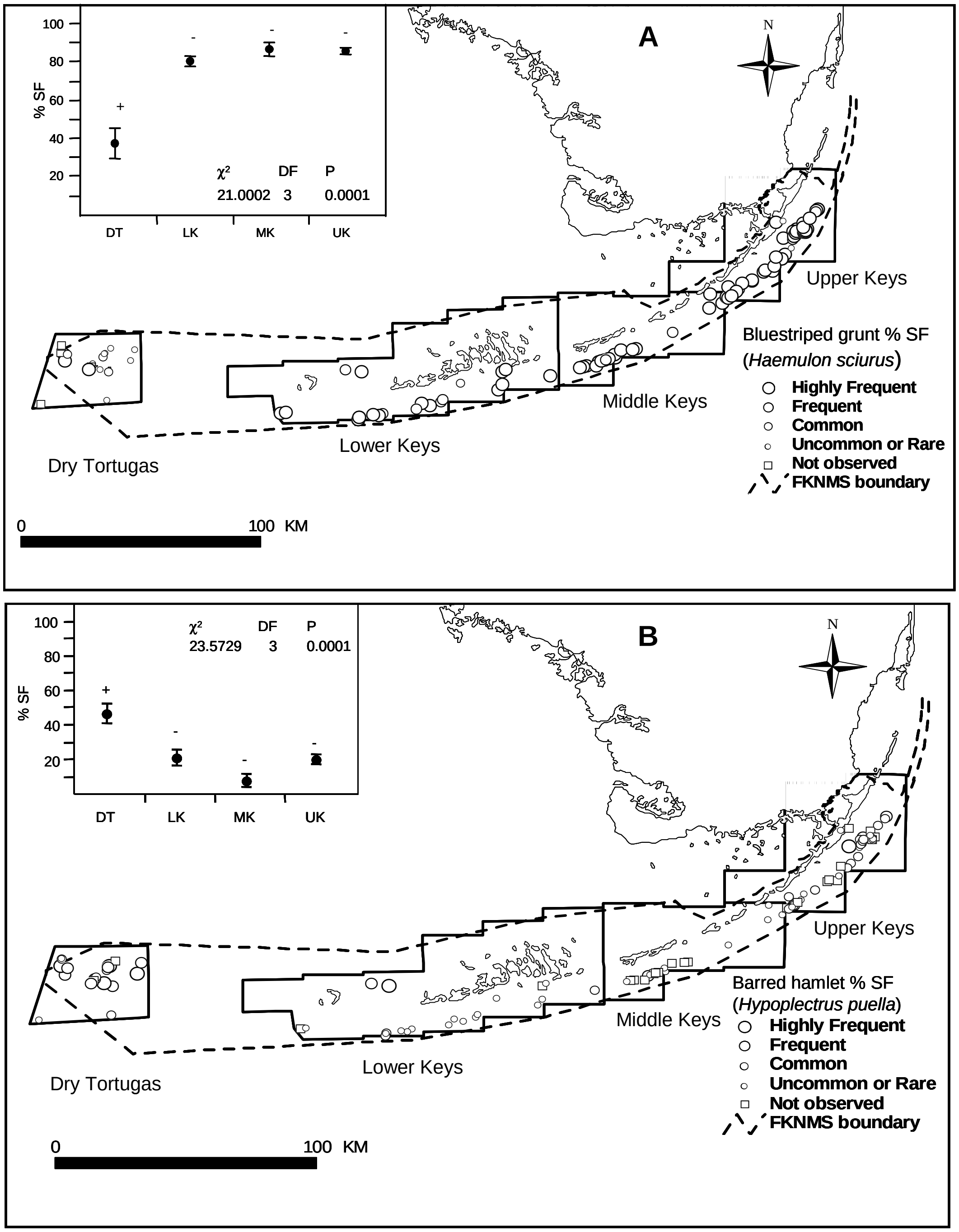


Figure 2.7. Spatial distribution and relative %SF of bluestriped grunt (A) and barred hamlet (B) among regions of the Florida Keys. The scatter plots show regional differences in mean % SF and tests for significant differences among means (Kruskal-Wallis χ^2 test, $\alpha = 0.05$; modified Tukey multiple comparisons, $\alpha = 0.05$). Means with the same symbols (+ or -) were not significantly different. Other species with a pattern of distribution similar to bluestriped grunt were: yellowtail damselfish , sergeant major, porkfish, and the foureye butterflyfish. Species with a pattern of distribution similar to barred hamlet were: blue hamlet, butter hamlet, cocoa damselfish, blue angelfish, and the neon goby. Scientific species names are given in Appendix 2.1.

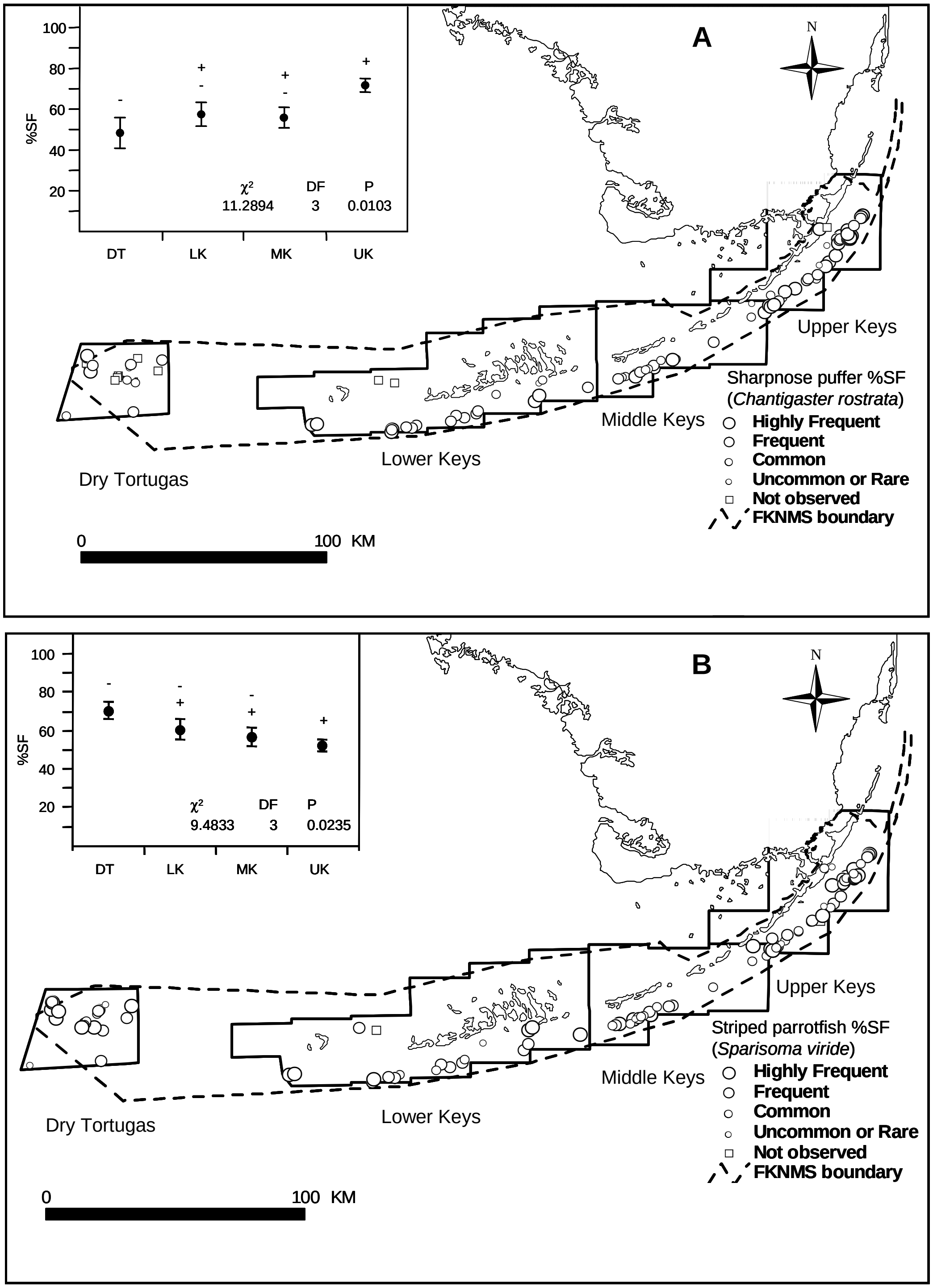


Figure 2.8. Spatial distribution and relative % SF of sharpnose puffer (A) and striped parrotfish (B) among regions of the Florida Keys. The scatter plot shows regional differences in mean %SF and tests for significant differences among means (Kruskal-Wallis χ^2 test, $\alpha = 0.05$; modified Tukey-multiple comparisons, $\alpha = 0.05$). Means with the same symbols (+ or -) were not significantly different. Threespot damselfish had a pattern of distribution that was similar to that of striped parrotfish. Scientific species names are given in Appendix 2.1.

Appendix 2.1. List of sites in the Florida Keys and Dry Tortugas surveyed by the Reef Environmental Education Foundation (REEF) volunteers between July 1993 and August 1999.

Location	°N	°W	Surveys (no.)	Hours (tot.)	Species (tot.)
Upper Keys					
Carysfort Reef	25.2200	80.2123	63	60.2	209
Carysfort Deep Ledge	25.2200	80.2112	26	21.5	175
Carysfort Reef Johnny's Spot	25.2135	80.2168	49	52.5	200
South Carysfort Reef	25.2105	80.2172	65	66.6	202
Watson's Reef	25.1860	80.2425	3	3.0	132
Toadfish Flats (Hawks Ch.)	25.1792	80.3403	15	13.5	37
N. Carysfort - Fishbowl	25.1707	80.3680	12	11.7	120
Triple North (off Elbow)	25.1525	80.2673	7	7.1	102
Elpis Grounding Site	25.1483	80.2525	8	8.4	116
South-South Ledges E1	25.1473	80.2610	89	96.2	225
Civil War Wreck (Elbow)	25.1473	80.2577	8	6.3	99
City of Washington-E7/8	25.1460	80.2558	84	81.9	219
Anchor Chain E6	25.1450	80.2563	141	145.7	225
Mike's Wreck E4/5	25.1447	80.2568	87	83.3	216
The Fingers E3	25.1423	80.2577	46	44.7	204
Train Wheel E2	25.1420	80.2578	44	43.6	186
South Ledges E9	25.1403	80.2590	94	98.5	219
The Elbow	25.1388	80.2610	56	53.6	213
Horseshoe Reef	25.1387	80.3050	31	30.6	205
Spanish Anchor (Elbow)	25.1382	80.2600	4	4.0	127
NN Dry Rocks	25.1363	80.2903	84	80.5	215
Pecks Place / Cap Happy's	25.1343	80.2638	37	40.1	210
Spikes Ridge (off Elbow)	25.1333	80.2585	19	19.9	126
Minnow Caves/North Dry Rocks	25.1307	80.2943	64	64.1	213
Key Largo Dry Rocks	25.1225	80.2975	177	175.7	230
Little Grecian	25.1190	80.3002	48	52.6	201
Cannon Patch/Garret's Reef	25.1118	80.3417	22	21.3	104
Grecian Rocks	25.1098	80.3042	123	119.6	222
Dixie Ledge	25.0773	80.3110	16	11.1	131
Benwood Wreck	25.0527	80.3337	114	110.9	226
White Banks	25.0417	80.3700	29	27.2	91
French Reef	25.0353	80.3473	123	121.2	227
Molasses Reef	25.0090	80.3737	277	261.0	234
Wellwood Grounding Site	25.0083	80.3750	11	11.4	125
The Pillars	24.9922	80.4085	3	3.1	87
Duane	24.9880	80.3805	7	3.6	87
Pickles Reef	24.9862	80.4157	52	46.5	209
Horseshoe (Near Conch)	24.9567	80.4570	2	1.4	82
Conch Reef	24.9518	80.4595	106	102.5	219
Mutton Snapper Reef	24.9435	80.4953	26	27.3	195
Hens and Chickens	24.9317	80.5483	72	75.3	210
Davis Reef	24.9220	80.5060	123	132.9	222
Pleasure Reef	24.9135	80.5158	11	10.7	114
Crocker Ridges	24.9032	80.5302	15	14.7	176
Crockers Wall	24.9002	80.5313	47	34.6	193

Appendix 2.1 continued

Location	Lat. (^{o} N)	Long. (^{o} W)	Surveys (no.)	Hours (tot.)	Species (tot.)
Upper Keys continued					
Pocket, The	24.8982	80.5363	14	13.5	149
Fish Bowl	24.8933	80.5527	15	16.1	107
Aquarium Reef	24.8912	80.5555	20	22.3	171
Hammerhead Reef	24.8888	80.5468	6	5.5	152
Middle Keys					
Cheeca Rocks	24.9045	80.6155	28	30.5	110
Wreck of the Eagle	24.8695	80.5702	12	7.0	97
Alligator Reef	24.8512	80.6202	108	129.9	220
Tennessee Reef	24.7617	80.7550	57	67.6	195
Porkfish	24.7002	80.8938	5	5.3	104
Rusty's	24.6953	80.9058	4	4.3	89
Donut Reef	24.6918	80.9478	2	1.9	92
Coffins Patch	24.6767	80.9750	63	68.0	200
Horseshoe	24.6612	80.9942	14	14.5	163
Samantha's Ledge	24.6592	81.0040	66	71.3	210
Joanie's Reef	24.6563	81.0095	36	38.2	208
Joanie's Rock	24.6560	81.0098	4	4.3	95
Pot Holes	24.6517	81.0247	4	4.2	89
Hermans Behind	24.6510	81.0290	7	4.4	90
Herman's Hole	24.6505	81.0313	16	16.7	167
Boom Ledge	24.6353	81.0793	2	1.7	71
Lucille's Reef	24.6348	81.0415	4	4.2	86
Delta Shoals	24.6327	81.0900	18	17.2	115
Sombrero Reef	24.6283	81.1050	130	124.5	223
Lower Keys					
The Alexander	24.6232	81.9822	3	2.5	50
Newfound Open/Captain's Coral	24.6215	81.3805	12	8.3	79
Newfound Harbor Spa	24.6138	81.3953	12	9.2	87
Cottrel (Stingray)	24.6137	81.9213	2	2.0	36
No Name Reef	24.5965	81.2140	12	12.5	126
Nine Foot Stake	24.5683	81.5517	32	33.0	134
Looe Key - Research	24.5667	81.3933	32	31.6	183
Looe Key - East	24.5450	81.4083	48	52.4	204
Widow Fingers	24.5117	81.6172	38	40.5	190
Pelican Shoals	24.5020	81.6230	39	41.2	207
Middle Sambo	24.4952	81.6965	50	53.8	200
Eastern Sambo	24.4848	81.6648	63	69.4	213
Western Sambo	24.4730	81.7143	114	116.1	224
Research Site #1	24.4612	82.2047	18	21.8	155
Eastern Dry Rocks	24.4583	81.8407	57	55.1	203
Sand Key	24.4508	81.8778	100	102.8	223
Rock Key	24.4490	81.8563	51	50.5	210
Western Dry Rocks	24.4443	81.9305	39	35.5	150
Lost Reef	24.4433	81.9325	7	5.4	85
Trinity Cove	24.4338	81.9330	9	6.9	126

Appendix 2.1 continued

Location	Lat. (^{o} N)	Long. (^{o} W)	Surveys (no.)	Hours (tot.)	Species (tot.)
Dry Tortugas					
The Wall (before Carysfort)	25.1693	80.2663	2	2.2	87
Shark's Reef	25.1475	80.2927	20	20.7	175
Sherwood Forest	24.7115	83.0468	8	5.1	80
Robins Hood	24.7072	83.0475	7	4.0	64
Squid Row	24.7030	82.8593	10	8.5	60
Pulaski	24.6955	82.7713	31	29.4	172
Big Johnson	24.6843	82.8832	21	22.7	126
Oklahoma	24.6840	83.0505	7	6.8	81
Texas Rock	24.6817	82.8847	54	51.7	177
Cessies Peak (aka Bird In Hand)	24.6782	83.0375	6	5.0	84
Wreck Reef (Tortugas Banks)	24.6765	83.0242	13	9.9	113
Juanita's Reef	24.6672	82.8920	37	38.0	149
The Gap	24.6660	80.9718	4	2.9	123
Blenny flats	24.6553	82.7877	16	17.7	86
G-Spot (near Pinnacles)	24.6538	83.0333	13	11.2	120
Oasis	24.6442	82.9295	18	16.8	97
Loggerhead Nursery	24.6385	82.9320	20	23.4	106
SW Loggerhead	24.6318	82.9362	2	2.0	16
Garlic Gardens (near Bird Key)	24.6217	82.9005	6	7.2	73
Windjammer Site	24.6212	82.9430	7	8.0	105
Bird Key	24.6128	82.8713	72	63.2	142
Simon's Hump	24.5077	82.8775	18	11.7	105
Riley's hump	24.4937	83.1218	13	7.9	94
Cuda Reef/Marquesas Rock	24.4593	82.2245	6	7.1	113

Appendix 2.2. Species list for the Florida Keys and Dry Tortugas. Data were collected by the Reef Environmental Education Foundation (REEF) between July 1993 and August 1999.

Family	**Species**	**Common species**
Acanthuridae	*Acanthurus coeruleus*	blue tang
Acanthuridae	*Acanthurus chirurgus*	doctorfish
Acanthuridae	*Acanthurus bahianus*	ocean surgeonfish
Antennariidae	*Antennarius multiocellatus*	longlure frogfish
Apogonidae	*Apogon binotatus*	barred cardinalfish
Apogonidae	*Apogon townsendi*	belted cardinalfish
Apogonidae	*Apogon affinis*	bigtooth cardinalfish
Apogonidae	*Apogon aurolineatus*	bridle cardinalfish
Apogonidae	*Apogon maculatus*	flamefish
Apogonidae	*Apogon planifrons*	pale cardinalfish
Apogonidae	*Apogon robinsi*	roughlip cardinalfish
Apogonidae	*Apogon quadrisquamatus*	sawcheek cardinalfish
Apogonidae	*Apogon pseudomaculatus*	twospot cardinalfish
Apogonidae	*Apogon lachneri*	whitestar cardinalfish
Apogonidae	*Astrapogon puncticulatus*	blackfin cardinalfish
Apogonidae	*Astrapogon stellatus*	conchfish
Apogonidae	*Phaeoptyx pigmentaria*	dusky cardinalfish
Apogonidae	*Phaeoptyx xenus*	sponge cardinalfish
Atherinidae, Clupeidae, Engraulidae (silversides, herrings, anchovies)		
Aulostomidae	*Aulostomus maculatus*	trumpetfish
Balistidae	*Aluterus schoepfi*	orange filefish
Balistidae	*Aluterus scriptus*	scrawled filefish
Balistidae	*Balistes capriscus*	gray triggerfish
Balistidae	*Balistes vetula*	queen triggerfish
Balistidae	*Cantherhines pullus*	orangespotted filefish
Balistidae	*Cantherhines macrocerus*	whitespotted filefish
Balistidae	*Canthidermis sufflamen*	ocean triggerfish
Balistidae	*Canthidermis maculata*	rough triggerfish
Balistidae	*Melichthys niger*	black durgon
Balistidae	*Monacanthus ciliatus*	fringed filefish
Balistidae	*Monacanthus hispidus*	planehead filefish
Balistidae	*Monacanthus setifer*	pygmy filefish
Balistidae	*Monacanthus tuckeri*	slender filefish
Batrachoididae	*Opsanus tau*	oyster toadfish
Belonidae	*Playbelone argalus*	keeltail needlefish
Belonidae	*Strongylura marina*	Atlantic needlefish
Belonidae	*Strongylura notata*	redfin needlefish
Belonidae	*Tylosurus crocodilus*	houndfish
Blenniidae	*Hypleurochilus bermudensis*	barred blenny
Blenniidae	*Ophioblennius atlanticus*	redlip blenny
Blenniidae	*Parablennius marmoreus*	seaweed blenny
Blenniidae	*Scartella cristata*	molly miller
Bothidae	*Bothus ocellatus*	eyed flounder
Bothidae	*Bothus lunatus*	peacock flounder
Bothidae	*Paralichthys albigutta*	Gulf flounder
Bothidae	*Syacium micrurum*	channel flounder

Appendix 2.2. continued.

Family	**Species**	**Common species**
Callionymidae	*Diplogrammus pauciradiatus*	spotted dragonet
Callionymidae	*Paradiplogrammus bairdi*	lancer dragonet
Carangidae	*Alectis ciliaris*	African pompano
Carangidae	*Caranx ruber*	bar jack
Carangidae	*Caranx lugubris*	black jack
Carangidae	*Caranx crysos*	blue runner
Carangidae	*Caranx hippos*	crevalle jack
Carangidae	*Caranx latus*	horse-eye jack
Carangidae	*Caranx bartholomaei*	yellow jack
Carangidae	*Decapterus macarellus*	mackerel scad
Carangidae	*Elagatis bipinnulata*	rainbow runner
Carangidae	*Seriola rivoliana*	almaco jack
Carangidae	*Seriola dumerili*	greater amberjack
Carangidae	*Trachinotus goodei*	palometa
Carangidae	*Trachinotus falcatus*	permit
Carcharhinidae	*Carcharhinus limbatus*	blacktip shark
Carcharhinidae	*Carcharhinus perezi*	reef shark
Centropomidae	*Centropomus undecimalis*	common snook
Chaetodontidae	*Chaetodon striatus*	banded butterflyfish
Chaetodontidae	*Chaetodon capistratus*	foureye butterflyfish
Chaetodontidae	*Chaetodon aculeatus*	longsnout butterflyfish
Chaetodontidae	*Chaetodon sedentarius*	reef butterflyfish
Chaetodontidae	*Chaetodon ocellatus*	spotfin butterflyfish
Cirrhitidae	*Amblycirrhitus pinos*	redspotted hawkfish
Clinidae	*Acanthemblemaria chaplini*	papillose blenny
Clinidae	*Acanthemblemaria aspera*	roughhead blenny
Clinidae	*Acanthemblemaria maria*	secretary blenny
Clinidae	*Acanthemblemaria spinosa*	spinyhead blenny
Clinidae	*Chaenopsis limbaughi*	yellowface pikeblenny
Clinidae	*Coralliozetus bahamensis*	blackhead blenny
Clinidae	*Emblemaria pandionis*	sailfin blenny
Clinidae	*Hemiemblemaria simulus*	wrasse blenny
Congridae	*Heteroconger halis*	brown garden eel
Coryphanidae	*Coryphaena hippurus*	dolphin (mahi-mahi)
Dasyatidae	*Dasyatis americana*	southern stingray
Echeneidae	*Echeneis naucrates*	sharksucker
Echeneidae	*Echeneis neucratoides*	whitefin sharksucker
Echeneidae	*Remora remora*	remora
Elopidae	*Megalops atlanticus*	tarpon
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish
Exocoetidae	*Hemiramphus brasiliensis*	ballyhoo
Exocoetidae	*Hirundichthys speculiger*	mirrorwing flyingfish
Fistulariidae	*Fistularia tabacaria*	bluespotted cornetfish
Gerreidae	*Eucinostomus jonesi*	slender mojarra
Gerreidae	*Gerres cinereus*	yellowfin mojarra
Gobiidae	*Bollmannia boqueronensis*	white-eye goby
Gobiidae	*Coryphopterus glaucofraenum*	bridled goby
Gobiidae	*Coryphopterus dicrus*	colon goby

Appendix 2.2. continued.

Family	Species	Common species names
Gobiidae	*Coryphopterus personatus*	masked goby
Gobiidae	*Coryphopterus eidolon*	pallid goby
Gobiidae	*Coryphopterus lipernes*	peppermint goby
Gobiidae	*Coryphopterus punctipectophorus*	spotted goby
Gobiidae	*Gnatholepis thompsoni*	goldspot goby
Gobiidae	*Gobionellus saepepallens*	dash goby
Gobiidae	*Gobionellus stigmalophius*	spotfin goby
Gobiidae	*Gobiosoma illecebrosum*	barsnout goby
Gobiidae	*Gobiosoma prochilos*	broadstripe goby
Gobiidae	*Gobiosoma genie*	cleaning goby
Gobiidae	*Gobiosoma saucrum*	leopard goby
Gobiidae	*Gobiosoma oceanops*	neon goby
Gobiidae	*Gobiosoma dilepsis*	orangesided goby
Gobiidae	*Gobiosoma grosvenori*	rockcut goby
Gobiidae	*Gobiosoma evelynae*	sharknose goby
Gobiidae	*Gobiosoma louisae*	spotlight goby
Gobiidae	*Gobiosoma macrodon*	tiger goby
Gobiidae	*Gobiosoma horsti*	yellowline goby
Gobiidae	*Gobiosoma randalli*	yellownose goby
Gobiidae	*Gobiosoma xanthiprora*	yellowprow goby
Gobiidae	*Ioglossus calliuris*	blue goby
Gobiidae	*Ioglossus helenae*	hovering goby
Gobiidae	*Lophogobius cyprinoides*	crested goby
Gobiidae	*Microgobius microlepis*	banner goby
Gobiidae	*Microgobius carri*	Seminole goby
Gobiidae	*Nes longus*	orangespotted goby
Gobiidae	*Priolepis hipoliti*	rusty goby
Gobiidae	*Risor ruber*	tusked goby
Grammatidae	*Gramma melacara*	blackcap basslet
Grammatidae	*Gramma loreto*	fairy basslet
Haemulidae	*Anisotremus surinamensis*	black margate
Haemulidae	*Anisotremus virginicus*	porkfish
Haemulidae	*Haemulon bonariense*	black grunt
Haemulidae	*Haemulon sciurus*	bluestriped grunt
Haemulidae	*Haemulon carbonarium*	caesar grunt
Haemulidae	*Haemulon melanurum*	cottonwick
Haemulidae	*Haemulon flavolineatum*	french grunt
Haemulidae	*Haemulon parra*	sailors choice
Haemulidae	*Haemulon chrysargyreum*	smallmouth grunt
Haemulidae	*Haemulon macrostomum*	spanish grunt
Haemulidae	*Haemulon striatum*	striped grunt
Haemulidae	*Haemulon aurolineatum*	tomtate
Haemulidae	*Haemulon plumieri*	white grunt
Haemulidae	*Haemulon album*	white margate
Haemulidae	*Orthopristis chrysoptera*	pigfish
Holocentridae	*Holocentrus vexillarius*	dusky squirrelfish

Appendix 2.2. continued.

Family	Species	Common species names
Holocentridae	*Holocentrus marianus*	longjaw squirrelfish
Holocentridae	*Holocentrus rufus*	longspine squirrelfish
Holocentridae	*Holocentrus coruscum*	reef squirrelfish
Holocentridae	*Holocentrus adscensionis*	squirrelfish
Holocentridae	*Myripristis jacobus*	blackbar soldierfish
Holocentridae	*Plectrypops retrospinis*	cardinal soldierfish
Inermiidae	*Emmelichthyops atlanticus*	bonnetmouth
Inermiidae	*Inermia vittata*	boga
Kyphosidae	*Kyphosus sectatrix/incisor*	Bermuda chub
Labridae	*Bodianus rufus*	spanish hogfish
Labridae	*Bodianus pulchellus*	spotfin hogfish
Labridae	*Clepticus parrae*	creole wrasse
Labridae	*Doratonotus megalepis*	dwarf wrasse
Labridae	*Halichoeres poeyi*	blackear wrasse
Labridae	*Halichoeres maculipinna*	clown wrasse
Labridae	*Halichoeres radiatus*	puddingwife
Labridae	*Halichoeres pictus*	rainbow wrasse
Labridae	*Halichoeres bivittatus*	slippery dick
Labridae	*Halichoeres cyanocephalus*	yellowcheek wrasse
Labridae	*Halichoeres garnoti*	yellowhead wrasse
Labridae	*Hemipteronotus splendens*	green razorfish
Labridae	*Hemipteronotus novacula*	pearly razorfish
Labridae	*Hemipteronotus martinicensis*	rosy razorfish
Labridae	*Lachnolaimus maximus*	hogfish
Labridae	*Thalassoma bifasciatum*	bluehead
Lutjanidae	*Lutjanus buccanella*	blackfin snapper
Lutjanidae	*Lutjanus cyanopterus*	cubera snapper
Lutjanidae	*Lutjanus jocu*	dog snapper
Lutjanidae	*Lutjanus griseus*	gray snapper
Lutjanidae	*Lutjanus synagris*	lane snapper
Lutjanidae	*Lutjanus mahogoni*	mahogany snapper
Lutjanidae	*Lutjanus analis*	mutton snapper
Lutjanidae	*Lutjanus apodus*	schoolmaster
Lutjanidae	*Ocyurus chrysurus*	yellowtail snapper
Malacanthidae	*Malacanthus plumieri*	sand tilefish
Mugilidae	*Mugil cephalus*	striped mullet
Mullidae	*Mulloidichthys martinicus*	yellow goatfish
Mullidae	*Mullus auratus*	red goatfish
Mullidae	*Pseudupeneus maculatus*	spotted goatfish
Muraenidae	*Echidna catenata*	chain moray
Muraenidae	*Enchelycore carychroa*	chestnut moray
Muraenidae	*Enchelycore nigricans*	viper moray
Muraenidae	*Gymnothorax miliaris*	goldentail moray
Muraenidae	*Gymnothorax funebris*	green moray
Muraenidae	*Gymnothorax vicinus*	purplemouth moray
Muraenidae	*Gymnothorax moringa*	spotted moray
Myliobatidae	*Aetobatus narinari*	spotted eagle ray
Ogcocephalidae	*Ogcocephalus radiatus*	polka-dot batfish

Appendix 2.2. continued.

Family	Species	Common species names
Ophichthidae	*Myrichthys ocellatus*	goldspotted eel
Opistognathidae	*Opistognathus macrognathus*	banded jawfish
Opistognathidae	*Opistognathus whitehursti*	dusky jawfish
Opistognathidae	*Opistognathus aurifrons*	yellowhead jawfish
Ostraciidae	*Lactophrys trigonus*	buffalotrunkfish
Ostraciidae	*Lactophrys polygonia*	honeycomb cowfish
Ostraciidae	*Lactophrys quadricornis*	scrawled cowfish
Ostraciidae	*Lactophrys triqueter*	smooth trunkfish
Ostraciidae	*Lactophrys bicaudalis*	spotted trunkfish
Pempheridae	*Pempheris schomburgki*	glassy sweeper
Pomacanthidae	*Centropyge argi*	cherubfish
Pomacanthidae	*Holacanthus bermudensis*	blue angelfish
Pomacanthidae	*Holacanthus ciliaris*	queen angelfish
Pomacanthidae	*Holacanthus tricolor*	rock beauty
Pomacanthidae	*Holacanthus sp. (Hybrid)*	Townsend angelfish
Pomacanthidae	*Pomacanthus paru*	French angelfish
Pomacanthidae	*Pomacanthus arcuatus*	gray angelfish
Pomacentridae	*Abudefduf taurus*	night sergeant
Pomacentridae	*Abudefduf saxatilis*	sergeant major
Pomacentridae	*Chromis cyanea*	blue chromis
Pomacentridae	*Chromis multilineata*	brown chromis
Pomacentridae	*Chromis scotti*	purple reeffish
Pomacentridae	*Chromis insolata*	sunshinefish
Pomacentridae	*Chromis enchrysura*	yellowtail reeffish
Pomacentridae	*Microspathodon chrysurus*	yellowtail damselfish
Pomacentridae	*Stegastes leucostictus*	beaugregory
Pomacentridae	*Stegastes partitus*	bicolor damselfish
Pomacentridae	*Stegastes variabilis*	cocoa damselfish
Pomacentridae	*Stegastes fuscus*	dusky damselfish
Pomacentridae	*Stegastes diencaeus*	longfin damselfish
Pomacentridae	*Stegastes planifrons*	threespot damselfish
Priacanthidae	*Priacanthus arenatus*	bigeye
Priacanthidae	*Priacanthus cruentatus*	glasseye snapper
Rachycentridae	*Rachycentron canadum*	cobia
Rhincodontidae	*Ginglymostoma cirratum*	nurse shark
Rhinobatidae	*Rhinobatos lentiginosus*	Atlantic guitarfish
Rhinobatidae	*Rhinobatos percellens*	southern guitarfish
Scaridae	*Cryptotomus roseus*	bluelip parrotfish
Scaridae	*Nicholsina usta*	emerald parrotfish
Scaridae	*Scarus coeruleus*	blue parrotfish
Scaridae	*Scarus coelestinus*	midnight parrotfish
Scaridae	*Scarus taeniopterus*	princess parrotfish
Scaridae	*Scarus vetula*	queen parrotfish
Scaridae	*Scarus guacamaia*	rainbow parrotfish
Scaridae	*Scarus croicensis*	striped parrotfish
Scaridae	*Sparisoma radians*	bucktooth parrotfish
Scaridae	*Sparisoma atomarium*	greenblotch parrotfish
Scaridae	*Sparisoma aurofrenatum*	redband parrotfish

Appendix 2.2. continued.

Family	Species	Common species names
Scaridae	*Sparisoma rubripinne*	yellowtail parrotfish
Scaridae	*Sparisoma chrysopterum*	redtail parrotfish
Scaridae	*Sparisoma viride*	stoplight parrotfish
Sciaenidae	*Bairdiella sanctaeluciae*	striped croaker
Sciaenidae	*Equetus umbrosus*	cubbyu
Sciaenidae	*Equetus acuminatus*	highhat
Sciaenidae	*Equetus lanceolatus*	jackknife-fish
Sciaenidae	*Equetus punctatus*	spotted drum
Sciaenidae	*Odontoscion dentex*	reef croaker
Scombridae	*Acanthocybium solandri*	wahoo
Scombridae	*Scomberomorus regalis*	cero
Scombridae	*Scomberomorus maculatus*	spanish mackerel
Scorpaenidae	*Scorpaena plumieri*	spotted scorpionfish
Scorpaenidae	*Scorpaenodes caribbaeus*	reef scorpionfish
Serranidae	*Alphestes afer*	mutton hamlet
Serranidae	*Diplectrum bivittatum*	dwarf sand perch
Serranidae	*Diplectrum formosum*	sand perch
Serranidae	*Epinephelus fulvus*	coney
Serranidae	*Epinephelus cruentatus*	graysby
Serranidae	*Epinephelus itajara*	Goliath grouper
Serranidae	*Epinephelus striatus*	Nassau grouper
Serranidae	*Epinephelus morio*	red grouper
Serranidae	*Epinephelus guttatus*	red hind
Serranidae	*Epinephelus adscensionis*	rock hind
Serranidae	*Epinephelus nigritus*	Warsaw grouper
Serranidae	*Hypoplectrus puella*	barred hamlet
Serranidae	*Hypoplectrus nigricans*	black hamlet
Serranidae	*Hypoplectrus gemma*	blue hamlet
Serranidae	*Hypoplectrus unicolor*	butter hamlet
Serranidae	*Hypoplectrus gummigutta*	golden hamlet
Serranidae	*Hypoplectrus (Hybrid)*	hybrid hamlet
Serranidae	*Hypoplectrus indigo*	indigo hamlet
Serranidae	*Hypoplectrus sp.*	masked hamlet
Serranidae	*Hypoplectrus guttavarius*	shy hamlet
Serranidae	*Hypoplectrus sp.*	tan hamlet
Serranidae	*Hypoplectrus aberrans*	yellowbelly hamlet
Serranidae	*Hypoplectrus chlorurus*	yellowtail hamlet
Serranidae	*Liopropoma carmabi*	candy bass
Serranidae	*Liopropoma rubre*	peppermint bass
Serranidae	*Mycteroperca bonaci*	black grouper
Serranidae	*Mycteroperca rubra*	comb grouper
Serranidae	*Mycteroperca microlepis*	gag
Serranidae	*Mycteroperca phenax*	scamp (salmon rockfish)
Serranidae	*Mycteroperca tigris*	tiger grouper
Serranidae	*Mycteroperca venenosa*	yellowfin grouper
Serranidae	*Mycteroperca interstitialis*	yellowmouth grouper
Serranidae	*Paranthias furcifer*	creole-fish
Serranidae	*Rypticus bistrispinus*	freckled soapfish

Appendix 2.2. continued.

Family	Species	Common species names
Serranidae	*Rypticus saponaceus*	greater soapfish
Serranidae	*Rypticus subbifrenatus*	spotted soapfish
Serranidae	*Rypticus maculatus*	whitespotted soapfish
Serranidae	*Serranus subligarius*	belted sandfish
Serranidae	*Serranus tortugarum*	chalk bass
Serranidae	*Serranus tigrinus*	harlequin bass
Serranidae	*Serranus baldwini*	lantern bass
Serranidae	*Serranus annularis*	orangeback bass
Serranidae	*Serranus tabacarius*	tobaccofish
Sparidae	*Archosargus rhomboidalis*	sea bream
Sparidae	*Archosargus probatocephalus*	sheepshead
Sparidae	*Calamus bajonado*	jolthead porgy
Sparidae	*Calamus nodosus*	knobbed porgy
Sparidae	*Calamus proridens*	littlehead porgy
Sparidae	*Calamus pennatula*	pluma
Sparidae	*Calamus calamus*	saucereye porgy
Sparidae	*Calamus penna*	sheepshead porgy
Sparidae	*Diplodus argenteus*	silver porgy
Sparidae	*Diplodus holbrooki*	spottail pinfish
Sparidae	*Lagodon rhomboides*	pinfish
Sphyraenidae	*Sphyraena barracuda*	great barracuda
Sphyraenidae	*Sphyraena picudilla*	southern sennet
Sphyrnidae	*Sphyrna tiburo*	bonnethead
Sphyrnidae	*Sphyrna mokarran*	great hammerhead
Sphyrnidae	*Sphyrna lewini*	scalloped hammerhead
Syngnathidae	*Cosmocampus elucens*	shortfin pipefish
Syngnathidae	*Micrognathus ensenadae*	harlequin pipefish
Synodontidae	*Synodus saurus*	bluestriped lizardfish
Synodontidae	*Synodus foetens*	inshore lizardfish
Synodontidae	*Synodus synodus*	red lizardfish (rockspear)
Synodontidae	*Synodus intermedius*	sand diver
Tetraodontidae	*Canthigaster rostrata*	sharpnose puffer
Tetraodontidae	*Chilomycterus antennatus*	bridled burrfish
Tetraodontidae	*Chilomycterus schoepfi*	striped burrfish
Tetraodontidae	*Chilomycterus antillarum*	web burrfish
Tetraodontidae	*Diodon holocanthus*	balloonfish
Tetraodontidae	*Diodon hystrix*	porcupinefish
Tetraodontidae	*Sphoeroides spengleri*	bandtail puffer
Tetraodontidae	*Sphoeroides greeleyi*	Caribbean puffer
Tetraodontidae	*Sphoeroides testudineus*	checkered puffer
Tetraodontidae	*Sphoeroides nephelus*	southern puffer
Torpedinidae	*Narcine brasiliensis*	lesser electric ray
Tripterygiidae	*Enneanectes altivelis*	lofty triplefin
Tripterygiidae	*Enneanectes pectoralis*	redeye triplefin
Urolophidae	*Urolophus jamaicensis*	yellow stingray
Stromateidae	*Nomeus gronovii*	man-of-war fish
Carapidae	*Carapus bermudensis*	pearlfish

Appendix 2.2. continued.

Family	Species	Common species names
Labrisomidae	*Labrisomus kalisherae*	downy blenny
Labrisomidae	*Labrisomus nuchipinnis*	hairy blenny
Labrisomidae	*Labrisomus gobio*	palehead blenny
Labrisomidae	*Labrisomus bucciferus*	puffcheek blenny
Labrisomidae	*Malacoctenus versicolor*	barfin blenny
Labrisomidae	*Malacoctenus boehlkei*	diamond blenny
Labrisomidae	*Malacoctenus macropus*	rosy blenny
Labrisomidae	*Malacoctenus triangulatus*	saddled blenny
Labrisomidae	*Starksia hassi*	ringed blenny
Istiophoridae	*Makaira nigricans*	blue marlin

CHAPTER 3

EFFECTIVENESS OF VOLUNTEERS AS ASSESSORS OF FISH SPECIES RICHNESS ON CORAL REEFS[1]

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[1] Jeffrey, C.F.G. To be submitted to *Environmental Monitoring and Assessment Journal*

Abstract

A series of multiple linear regression (MLR) models was used to determine factors that may have influenced measures of species richness in surveys conducted by expert (conducted ≥ 35 surveys) and novice (conducted < 35 surveys) volunteers of the Reef Environmental Education Foundation (REEF) at the Florida Keys National Marine Sanctuary (FKNMS). MLR models were developed for surveys from expert, novice, and pooled volunteers (experts and novices together) and were run for the entire FKNMS and a single reef tract (Molasses Reef) to determine consistency in model results across spatial scales. Models based on pooled surveys explained 80-94% of the variation in species richness measures, whereas those for expert data and novice data explained 73-75% of the observed variation. Models based on data collected by novices explained 78-95% of the observed variation. Overall, site location explained 32-58% of the variation in estimates of species richness but only after the effects of sampling artifacts such as diver and dive time were reduced by random selection of surveys. These results were consistent across spatial scales (sanctuary-wide and at a single site), suggesting that the observed correlations are not spurious nor are they artifacts of the analysis. Data collected by novices had greater statistical power to detect significant differences in species richness among sites because of a larger sample size. Measures of species richness from novices were, however, much more variable than those collected by experts and indicated that data from experts may be more reliable. Reducing the effects of observers and dive time by randomly selecting surveys in future analyses of these data, or controlling for these artifacts when designing volunteer-based monitoring efforts, certainly would increase the probability of differentiating between the effects of sanctuary management on fish assemblage structure and those related to environmental variation. Successful identification of site-related environmental factors that affect reef fish assemblages over large areas such as the FKNMS would provide useful information and help guide decision makers on the placement and management of other marine protected areas.

Introduction

Species richness of fishes at several sites in Florida Keys National Marine Sanctuary (FKNMS) was investigated to identify potential factors that may have affected observed patterns. Species richness, defined as the total number of species at a site and given time, was based on data collected by the Reef Environmental Education Foundation (REEF). REEF is a nonprofit organization that educates and trains recreational divers and snorkelers to identify fishes and report data on their presence and abundance. REEF has been monitoring fishes in the Florida Keys since 1993; 1,103 of its members have completed about 11,810 surveys to characterize fish fauna at 300 sites that are widely distributed over an area of 9000 km^2 (Figure 3.1). As part of a long-term monitoring and research program, managers of the FKNMS contracted REEF to monitor reef fishes in 16 no-take zones and 15 reference areas annually since 1997. The REEF data set is extensive spatially and temporally and has become an important source of information on reef fishes for managers of the FKNMS (Bohnsack 1996, REEF 2003, FKNMS 2003).

In November 1990, the United States Congress enacted the Florida Keys National Marine Sanctuary and Protection Act (HR 5909), which established the FKNMS to manage and protect the marine resources of the Florida Keys. The FKNMS comprises approximately 9,500 km^2 of coastal and oceanic water and submerged lands organized into five management areas: Wildlife Management Areas (WMA), Ecological Reserves (ER), Sanctuary Preservation Areas (SPA), Existing Management Areas (EMA), and Special Use/Research Only Areas (SA/RO). In 1997, the FKNMS management plan, which included a large-scale marine zoning plan, became effective and closed 23 areas (eighteen SPAs, four SAs, and one ER) to all extractive use (NOAA 1996). These zones aim to protect the biological diversity and integrity of the marine environment in the Keys. Additionally, these no-take zones were planned as replenishment zones where the total abundance of fishes, their average size, and their overall egg production might increase (NOAA 1996).

Determining the zoning plan's effectiveness at protecting fishes and increasing their diversity, species richness, and abundance is a major goal. This goal requires (i) the design and implementation of suitable and effective monitoring programs, (ii) an understanding of the natural spatial and temporal variability exhibited by fish populations, and (iii) characterization of the variability of the data generated through monitoring activities. The use of members of REEF to monitor fishes within the FKNMS represents a logical, effective, and cost-efficient method.

Species composition of reef fish assemblages often varies greatly among habitat patches at varying scales because of complex interactions among physical and biological factors such as ocean currents, habitat distribution, and reproductive behavior that determine broad-scale patterns of fish abundance and distribution (Williams 1991). Additionally, observed species richness can vary temporally and spatially because of natural variation and because of differences in methods used to collect data. Because several volunteers collected data over a large spatial area, characterizing and identifying sources of variability inherent in the REEF data set before invoking correlations or causations between zone effectiveness and biological effects of protection is crucial. More specifically, FKNMS resource managers and other users of the REEF data set should distinguish among the following: (1) environmental variation, i.e., natural variation in the observed patterns of fish distribution and occurrence; (2) observer-based variation; and (3) management-based variation, i.e., variability correlated with differing levels of resource protection. This paper describes a series of “Standard-Least- Squares” regression models that attempt to identify the relative influence of these sources of variation on apparent patterns of fish assemblage structure. The analyses focused on species richness at 237 sites in the Florida Keys as determined by the REEF data set. The models tested the hypothesis that variation in mean species richness was related to the regressor terms or factors used in the model rather than to random error.

Methods

Study area

The Florida Keys comprise an island archipelago that extends 320 km southwest from Soldier Key in Biscayne Bay to the Dry Tortugas (Figure 3.1). To the north and west, the Keys are bounded by Biscayne Bay and the Gulf of Mexico; to the east and south, they are bounded by the Straits of Florida.

Submerged aquatic habitats include expansive seagrass beds and a coral reef tract that extends 8 km offshore toward the Atlantic Ocean.

Statistical analyses

A series of multiple linear regression (MLR) models were developed to determine if species richness varied non-randomly among sites at two spatial scales: the entire FKNMS and a single reef tract (Molasses Reef). The goal was to determine if factors that were significant at a single reef tract were also important sanctuary-wide. Data from Molasses Reef would be most likely to show significant effects because that reef was sampled the most by volunteers. Three models were developed separately for data from (1) experts (volunteers who conducted ≥ 35 surveys and achieved a score of 90% or greater on the REEF Advanced Exam), (2) novices (the first 34 surveys of any volunteer regardless of exam score), and (3) pooled data (expert and novice data combined). Skill levels of volunteers were defined by Pattengill and Semmens (1998). The data were separated to determine if the models would perform differently among the three data sets. Species richness was chosen as a response variable because it is a readily understood measure of community structure and was easily determined from data on species composition. Species richness was calculated as the total number of species observed during a Roving Diver Technique (RDT) survey, with surveys being considered replicate samples within sites. The factors used as main effects in the (MLR) models included temporal, spatial, and diver-related variables (Table 3.1).

A series of Lack-of-Fit (LOF) tests was used to determine if MLR models needed additional factors or interaction terms to explain the observed variation in species richness. The tests determined the error resulting from a poor fit of the statistical model by comparing random error to the total residual error after fitting the model (Sokal and Rohlf 1995). Random error in species richness was determined by the equation:

$$\sum_{i=1}^{s}\left(\overline{Y}-Y_i\right)$$

where $\overline{Y}$ is the mean species richness calculated from replicate surveys for each independent variable and Y_i is the species richness of the i^{th} survey for that variable. Significant P values from LOF tests ($P_{lack\text{-}of\text{-}fit} < 0.05$) were used to determine if the form of the model was inappropriate and did not adequately explain the observed variation in species richness. A lack of fit could have resulted from the inclusion of too few independent variables, the use of the wrong functional form of the model, or interactions among factors that were ignored in the model.

To determine if differences in the number of surveys conducted by experts and novices would affect model results, pooled, expert, and novice MLR models were repeated with 150 randomly selected expert and novice surveys. Finally, distribution plots of the residuals were examined to determine if they met the assumptions of normality and heteroscedasticity. The residuals appeared normally distributed with the mean centered at zero, which suggested that model assumptions of normality and equal variances among means were met.

Selection of surveys and independent variables for inclusion in MLR models

Only surveys that occurred during daylight hours were included in this study. Daylight was defined as the period between sunrise and sunset based on astronomical data for Key West, Florida; the data were obtained from the United States Naval Observatory, Washington D.C. (http://aa.usno.navy.mil/data/docs/RS_OneYear.html, accessed: 4/23/2004). Data for Key West were representative of the entire Florida Keys because there was only a 4-minute difference in time of sunrise and sunset between Key West, the island furthest west, and Key Largo, the island furthest east.

REEF volunteer divers recorded information on 11 independent variables that may have affected the collection of data on species composition during RDT surveys. Bottom time, depth, and temperature were measured with standard gauges found on SCUBA regulators. Visibility was estimated as the horizontal distance (ft) a diver could see underwater. Current flow was estimated and recorded as being strong, weak, or absent. The benthic substrate over which a survey occurred was determined by the diver based on a set of habitats predefined by REEF. Other ancillary information included the type of survey e.g., species identification or species abundance), REEF geographic zone code and member identification number, name and regional location of the dive site, and the date on which the survey was done. All data were transferred to standardized data scan sheets, returned to REEF headquarters for review, and optically scanned into a database. Data were passed through a series of quality assessment and quality control procedures, such as verifying previously unrecorded species from known species lists and checking for misidentification of species that are similar morphologically, before being made available online (REEF 2003).

Power – the probability of detecting significant differences (an effect) – is positively correlated with sample size for a given p-value of alpha and standard deviation of the error (Sokal and Rolhf 1995). Likewise, the potential for spurious relationships increases with the number of hypotheses and variables tested (Cohen and Cohen 1983). Nine of the 11 independent variables in the REEF data set contained three or more categories. The number of categories within independent variables was reduced through hierarchical clustering, before those variables were used as factors in MLR models (Boesch 1977, Figure 3.2). Reduction in the number of categories per variable 1) minimized the potential for spurious relationships and confounding interactions between factors; and 2) increased the per-category sample size and the statistical power to detect significant differences among variable categories.

The average depth, type of benthic substrate, and visibility at sites during surveys were recorded as categorical independent variables. Depth, benthic substrate, and visibility had 16, 11, and 7 categories respectively. Plots of the statistical distributions of these variables by categories were examined to exclude outlier surveys based on the criteria listed in Table 1 and to identify under-sampled categories of each independent variable. Under-sampled categories were combined to increase their sample size. Adequate sample size was defined as the minimum number of samples per category needed to detect a significant difference in mean species richness among categories of an independent variable at $\alpha = 0.05$. Aggregation of under-sampled categories also reduced the number of categories, the number of statistical parameters, and the potential for interactions among and within independent variables during MLR analysis. Hierarchical clustering based on Ward’s minimum variance was used to determine similarities in the relative abundance of species among categories for each variable (Boesch 1977). This procedure grouped together categories of variables (rows) by minimizing the within-category variance in species abundance codes (columns) such that categories with similar species abundance codes were grouped together (Figure 3.2a).

Bias was minimized when selecting the final categories by using a fixed stopping rule, which was a line drawn across the nodes of the resulting dendrograms (Boesch 1977, Gauch 1995). The line was drawn at the node where the sharpest change in slope occurred in a line plot of the distance between clusters against the number of remaining clusters (Figure 3.2b). Resulting cluster groups were used as categories of the independent variables in the MLR models (Figure 3.2c). Additionally, a series of power analyses determined the minimum number of surveys needed to detect a significant difference in mean species richness among the categories of each variable. Categories with fewer surveys than the minimum required for detecting a significant difference in mean species richness were excluded.

Surface and bottom temperatures recorded by volunteers during surveys were compared with data on sea surface temperature (SST) collected by moored buoys to identify outlier temperature values in the REEF data set. Moored buoys were located at Molasses Reef, Long Key, Sand Key, and the Dry Tortugas and were operated by NOAA National Data Buoy Center (National Oceanographic Data Center 1998). Several surveys had surface and bottom temperatures below 50 ^{O}F during the summer months. Data from these surveys were excluded from the analysis because such low summer temperatures are unlikely in the Florida Keys at depths above 30 m. Additionally, new estimates of surface and bottom temperature were predicted from an orthogonal regression of bottom against surface temperature recorded during surveys. Predicted bottom temperature was used as a continuous independent variable in MLR models. Statistical analyses were done with JMP 4.0 statistical software ($\alpha = 0.05$, SAS Institute 2000).

Results

Eleven hundred and nine divers conducted 9,340 surveys at 305 sites in the Florida Keys (including the Dry Tortugas) from July 1993 to July 2002. Of these, 8,274 surveys met the criteria listed in Table 3.1. The number of surveys conducted per site ranged from 1 to 639, with highest number of surveys being conducted at Molasses Reef. The mean number of surveys per site was 37±4. The maximum number of surveys per diver was 478, with a mean of 8±1. Recorded survey time ranged from 3 min to 11 h with a mean of 56.4±0.2 min; only surveys with bottom time between 15 min and 2 h were used in MLR analyses. The mean number of sites surveyed by a diver was 5±1 but ranged from 1 – 120 surveys, with 90% of the divers visiting fewer than 11 sites. Novice volunteers conducted 77% and 59% of the surveys at Molasses Reef and the FKNMS respectively (Table 3.2).

Species richness in the FKNMS

Mean species richness varied significantly among sites and ranged from 1 species per survey at Bob's Check Out Reef (25^{O} 13.17' N, 80^{O} 12.65' W) to 108 species per survey at Toadfish Flats (25^{O} 06.59' N, 80^{O} 18.25' W, Figure 3.2). The MLR models explained most of the variation in species richness measures ($P < 0.01$, Table 3.3). The model based on expert data explained 75% of the variation in species richness, whereas the models based on novice and pooled data explained 78% and 80% of the observed variation respectively. The results of the LOF tests indicate that the regressor terms adequately accounted for the variation in mean species richness measures for all models ($P_{lack\ of\ fit} > 0.05$, Table 3.3).

Although 10 of 11 factors affected species richness significantly, three factors accounted for about 95% of the variability in species richness measures in regressions based on expert, novice, and pooled surveys ($P < 0.01$, Table 3.3). Site location, diver, and dive time respectively accounted for 53%, 31%, and 9% of the observed variation in species richness measured by experts (Table 3.4). In contrast, diver, site location, and dive time respectively explained 74%, 16%, and 9% of the variation in species richness measured by novices (Table 3.4). When surveys were pooled, MLR results were similar to those based on species richness measured by novices (Table 3.4). Other main factors in the models – year, benthic substrate, diver experience, visibility, month, depth, temperature, and water current – cumulatively explained < 5% of the variation in species richness measures (Table 3.4).

Species richness at Molasses Reef

A similar suite of variables affected species richness significantly ($P < 0.01$) when data for Molasses Reef was analyzed separately (Table 3.5). The MLR models explained 73%, 95%, and 94% of the variability in species richness measures for expert, novice, and pooled data respectively (Table 3.5). Results from the Lack-of-Fit tests show that the factors adequately explained the variation in species richness at Molasses Reef ($P_{Lack\text{-}of\text{-}Fit} > 0.05$, Table 3.5). The factors that affected species richness measures the most were different among the three models (Table 3.6). Whereas three factors (diver, dive time, and month) accounted for 85% of the variability in expert species richness measures, only one factor (diver) accounted for 92% and 87% of the variability in novice and pooled models respectively (Table 3.6). The diver factor was most important in all three models but accounted for different amounts of variability among expert, novice, and pooled data (Table 3.6). In the model based on expert data, divers accounted for only 53% of the variability in species richness measures, whereas in models based on novice and pooled data, divers explained 92% and 87% of the variability respectively (Table 3.6). Dive time contributed 17% of the variability in expert species richness measures but less than 2% and 6% of the variability in novice and pooled models (Table 3.6). Interestingly, diver experience accounted for the smallest proportion of the variability of pooled species richness measures (0.04%, $F = 0.66$, $P = 0.42$).

Effects of sample size on MLR models

Models based on a random selection of expert, novice, and pooled surveys were significant ($P < 0.05$) and explained most of the variability in species richness measures ($R_{expert} = 0.84$, $R_{novice} = 0.92$, and $R_{pooled} = 0.92$, Table 3.7). Site location and diver were the most important variables that affected species richness measures when randomly selected surveys were analyzed; this finding was consistent with previous results (Table 3.8). Randomization of surveys had the greatest effect on novice species richness measures, however. The diver factor explained 33% of the variability in species richness measures in randomly selected novice surveys compared to 74% for the FKNMS overall (Table 3.8).

Randomly selecting surveys also reduced the importance of divers on species richness measures obtained from pooled surveys from 62% to 37% when all surveys were included in the MLR analyses (Table 3.8).

Discussion

A major starting premise of this analysis was that species richness measures varied non-randomly among sites in the FKNMS and could be related to several different factors. The results of multiple linear regressions successfully demonstrated this assertion and were consistent across spatial scales (sanctuary-wide and at a single site), and types of data (pooled, expert, and novice). This suggests that the observed correlations are not spurious nor are they artifacts of the analysis.

The effectiveness of the REEF monitoring program lies in its ability to rapidly generate through its large member base a tremendous wealth of accurate data on species composition and relative abundance over a large spatial area. Several studies have examined spatial and temporal trends in fish distribution and species composition based on such data (Schmitt and Sullivan 1996, Semmens et al. 2000, Jeffrey et al. 2001, Schmitt et al. 2002, Pattengill-Semmens and Semmens 2003). Generally, these studies analyzed data collected by novices and experts separately but minimized the potential of other factors, such as those identified in this study to affect observed patterns in various biological metrics derived from these data. In contrast to previous conclusions, the results presented here indicate that divers, site location, dive time, and the level of diver experience may all be affecting the number of species observed during a census. Further distinction of diver ability is needed because the binary distinction for level of experience, namely novice versus experts, did not account for the variability associated with divers.

Unquestionably, separating data collected by experienced and inexperienced divers is necessary. Models based on pooled and novice surveys explained more of the variability in species richness measures than models based on expert surveys and had greater statistical power to detect differences among sample units. However, most of the variability in species richness measures from pooled and novice data was explained by the diver factor, whereas site location was the biggest contributor to the variability in species richness measures from expert surveys. Ideally, location and other environmental variables should have greater effects on species richness measures than diver-related factors, which could be considered artifacts of the sampling design. Site location was the most important factor in models based on expert surveys and when equal samples of randomly selected expert and novice surveys were pooled (Table 3.8). These findings suggest that measures of species richness collected by novice divers are more variable and prone to diver error than data collected by experts. Pooling data collected by experts and novices is cost-efficient and may result in greater power, but biological estimates based on expert surveys or equal numbers of randomly selected expert and novice surveys would be more reliable than those based on pooled surveys.

The factors that significantly affected species richness measures can be categorized into four groups that operate at various spatial and temporal scales and may affect differently the validity of data on species composition. First, observer-based factors such as the divers themselves (i.e., their ability to identify species), the time spent surveying, and the diver's level of experience directly affect the probability of fish being seen, counted, and correctly identified; this can introduce variance in species composition data at all spatial and temporal scales. Second, local variation in environmental factors such as visibility and water-current strength can influence an observer's ability to see or his or her comfort level during a dive, and hence may affect the likelihood of successfully seeing, properly identifying, and counting fishes that are present. Third, variation in other environmental factors such as temperature, habitat structure, and depth over small and large spatial scales may have direct effects on the occurrence, distribution, and abundance of fishes (Luckhurst 1978, Friedlander and Parrish 1998, Christensen *et al.* 2003). Non-random variation in these environmental factors could result in the occurrence and detection of fishes in a non-random manner. Fourth, all these factors may vary through time systematically (e.g., monthly and annual cycles), resulting in a temporal component of variation that affects 1) the occurrence of species and, 2) the probability of a fish being identified and counted during a census.

Traditionally, reef fish researchers have handled the inherent variation in fish census data in one of several ways. Observer-based variation is minimized typically by either using a single observer, or by averaging the results of two divers (Bohnsack and Bannerot 1986). Temporal variation usually is handled by sampling within the same month or season within a given year, or in the same month or season in different years if the identification of annual variation is important. Variation resulting from habitat and other environmental factors typically can be reduced by the *a priori* identification of known categories within the variables of interest. However, the use of such approaches to minimize inter-observer and temporal variation in REEF's data would have yielded very few data for analysis because most volunteers conducted only a few surveys at a few sites. About 1,100 divers collected data on fishes in the Florida Keys, but only 12% visited more than 18 sites and conducted 20 or more surveys.

Volunteer-based estimates of species richness in the Florida Keys were explained in large part by site location and artifacts such as diver and dive time. The effect of site location on reef fish species richness, especially for data collected by novices, became evident only after the effects of these artifacts were reduced through randomized selection of surveys. Ideally, only data from well-trained expert divers should be used in assessing management actions, but this would severely limit the power of the analysis because of the smaller number of available expert divers and surveys. Therefore, reducing the effects of observers and dive time through random selection of surveys is the next best alternative. Additionally, controlling for these artifacts when volunteer-based monitoring programs are designed would certainly increase the probability of differentiating between the effects of sanctuary management on fish assemblage structure and those related to environmental variation. The observed effect of site location on reef fish assemblage structure suggests two logical questions. First, what environmental factors are affecting reef fish assemblage structure and composition in the Florida Keys as indicated by differences in site-specific estimates of species richness? Second, are the effects of environmental factors detectable at spatial scales of 1-10 km^2 that are characteristic of marine protected areas? Successful identification of site-related environmental factors that affect reef fish assemblages over large areas would provide useful information and help guide decision makers on the placement and management of marine protected areas.

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TABLES

Table 3.1. Summary of factors and criteria used to select surveys for multiple linear regression (MLR) models.

Factor type	Factor	Variable type	Criteria for inclusion
Environmental	Benthic substrate	Categorical	Identifiable
	Current	Categorical	≥ 0 m/s
	Depth	Categorical	< 40 m
	Temperature	Continuous	> 0
	Visibility	Categorical	> 0 m
Observer-related	Dive (bottom) time	Continuous	> 15 minutes
	Diver	Categorical	> 1 survey
	Level of experience	Categorical	> 1 survey
Spatial	Site location	Categorical	> 1 survey
Temporal	Month	Categorical	All months
	Year	Categorical	All years
	Pre- and post- no-take zone implementation	Categorical	All surveys that met above criteria

Table 3.2. The number of surveys conducted by experts, novice, and pooled (experts and novice combined) at Molasses Reef and the Florida Keys National Marine Sanctuary (FKNMS) between July 19, 1993 and August 12, 2002. Experts were volunteers who conducted ≥ 35 surveys and achieved a score of 90% or greater on the REEF Advanced Exam. Novices were volunteers who conducted < 35 surveys.

Site	Volunteer experience	N	Percent (%)
Molasses	Expert	163	23.5
	Novice	530	76.5
	Pooled	693	100
FKNMS	Expert	3385	40.9
	Novice	4889	59.1
	Pooled	8274	100

Table 3.3. Results of ANOVA and Lack-of-Fit tests from multiple regressions of species richness measures derived from expert, novice, and pooled surveys conducted by REEF in the Florida Keys National Marine Sanctuary. Diver experience categories are defined in Table 3.2.

								Lack-of-Fit	
Data set	Source	df	SSE	MSE	F	P	R	F	P
Expert	Model	259	529821	2045.64	30.72	<0.01	0.75	0.47	0.99
	Error	2609	173752	66.60					
	Total	2868	703573						
Novice	Model	709	950848	1341.11	15.65	<0.01	0.78	0.96	0.59
	Error	3094	265083	85.68					
	Total	3803	1215932						
Pooled	Model	759	1965603	2589.73	31.80	<0.01	0.80	0.76	0.91
	Error	5910	481232	81.43					
	Total	6669	2446836						

Table 3.4. Factors affecting the variability in species richness measures among expert, novice, and pooled surveys conducted by the REEF in the Florida Keys National Marine Sanctuary. Data were collected between July 19, 1993 and August 12, 2002. “Other” refers to factors listed in Table 3.1 that cumulatively explained less than 10% of the variability in species richness measures. Percent variation is the proportion of the ANOVA model sum of squared error (SSE) associated with each source of variability if there are no interactions between factors. Lack-of-Fit tests were not significant (P > 0.05) and indicated that the ANOVA model adequately explained observed variability without additional factors and interactions among factors. Diver experience categories are defined in Table 3.2.

Data set	Source	df	Percent variation	P
Expert	Site location	158	53.13	0.00
	Diver	70	31.47	0.00
	Dive time	1	9.27	0.00
	Other	30	6.13	0.00
Novice	Diver	503	73.75	0.00
	Site location	175	16.44	0.00
	Other	31	9.81	0.00
Pooled	Diver	531	62.41	0.00
	Site location	196	26.31	0.00
	Dive time	1	7.67	0.00
	Other	30	3.61	0.00

Table 3.5. Results of ANOVA and Lack-of-Fit tests from multiple regressions of species richness measures derived from expert, novice, and pooled surveys conducted by the REEF at Molasses Reef, Florida Keys National Marine Sanctuary. Diver experience categories are defined in Table 3.2.

								Lack of fit	
Data set	Source	df	SSE	MSE	F	P	R	F	P
Expert	Model	63	7826.12	124.22	3.49	<0.01	0.73	1.60	0.46
	Error	82	2921.91	35.63					
	Total	145	10748.03						
Novice	Model	293	255066.28	870.53	14.35	<0.01	0.95	3.37	0.09
	Error	210	12735.08	60.64					
	Total	503	267801.36						
Pooled	Model	236	256724.33	1087.81	19.61	<0.01	0.94	4.94	0.06
	Error	270	14979.28	55.48					
	Total	506	271703.61						

Table 3.6. Factors affecting the variability in species richness measures among expert, novice, and pooled (expert and novice combined) surveys conducted by the REEF at Molasses Reef, Florida Keys National Marine Sanctuary. “Other” and “percent variation” are defined in Table 3.6. Diver experience categories are defined in Table 3.2.

Data set	Source	df	Percent variation	P
Expert	Diver	33	53.47	0.00
	Dive time	1	17.47	0.00
	Month	11	14.47	0.07
	Site location	3	7.13	0.03
	Other	27	7.47	>0.05
Novice	Diver	264	91.70	0.00
	Other	46	8.30	<0.05
Pooled	Diver	205	87.18	0.00
	Dive time	1	6.45	0.00
	Other	30	6.37	<0.42

Table 3.7. Results of ANOVA from multiple linear regressions of species richness measures derived from randomly selected expert, novice, and pooled surveys conducted by the REEF in the Florida Keys National Marine Sanctuary. Diver experience categories are defined in Table 3.2.

Data set	Source	df	SSE	MSE	F	P	R
Expert	Model	102	27448.79	269.11	5.66	<.0001	0.92
	Error	49	2328.48	47.52			
	Total	151	29777.26				
Novice	Model	111	26259.30	236.57	4.22	<.0001	0.92
	Error	38	2130.84	56.08			
	Total	149	28390.14				
Pooled	Model	157	56624.16	360.66	5.80	<.0001	0.85
	Error	166	10314.40	62.14			
	Total	323	66938.55				

Table 3.8. Factors affecting the variability in species richness measures among randomly selected expert, novice, and pooled surveys conducted by the REEF at Molasses Reef, Florida Keys National Marine Sanctuary. "Other" and "percent variation" are defined in Table 3.6. Diver experience categories are defined in Table 3.2.

			Percent variation		
Data set (N)	Source	df	Sample	*(all surveys)*	P
Expert (150)	Site location	47	56.73	*(53.13)*	0.00
	Diver	24	26.3	*(31.47)*	0.00
	Year	9	5.96	*(3.06)*	0.16
	Visibility	1	3.22	*(0.24)*	0.01
	Other	21	7.79		>0.05
Novice (150)	Diver	26	33.02	*(73.74)*	0.00
	Site location	54	31.91	*(16.44)*	0.14
	Month	11	9.55	*(0.61)*	0.05
	Dive time	1	8.32	*(5.91)*	0.00
	Year	9	8.15	*(2.17)*	0.05
	Other	10	9.05		>0.05
Pooled (300)	Site location	72	44.25	*(26.31)*	0.00
	Diver	43	35.66	*(62.41)*	0.00
	Year	9	7.31	*(1.58)*	0.01
	Diver time	1	6.83	*(7.67)*	0.00
	Other	22	5.95		>0.05

FIGURES

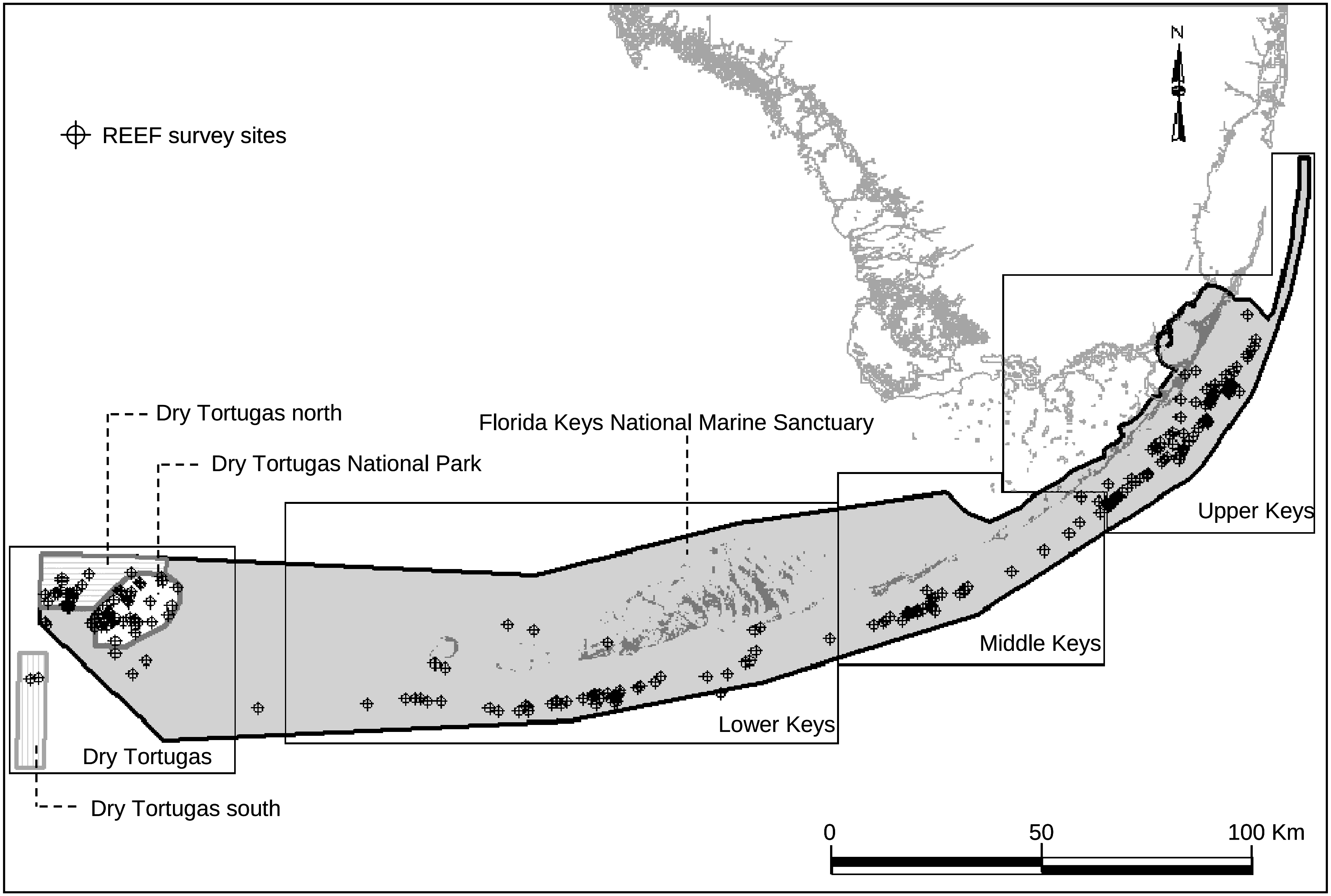
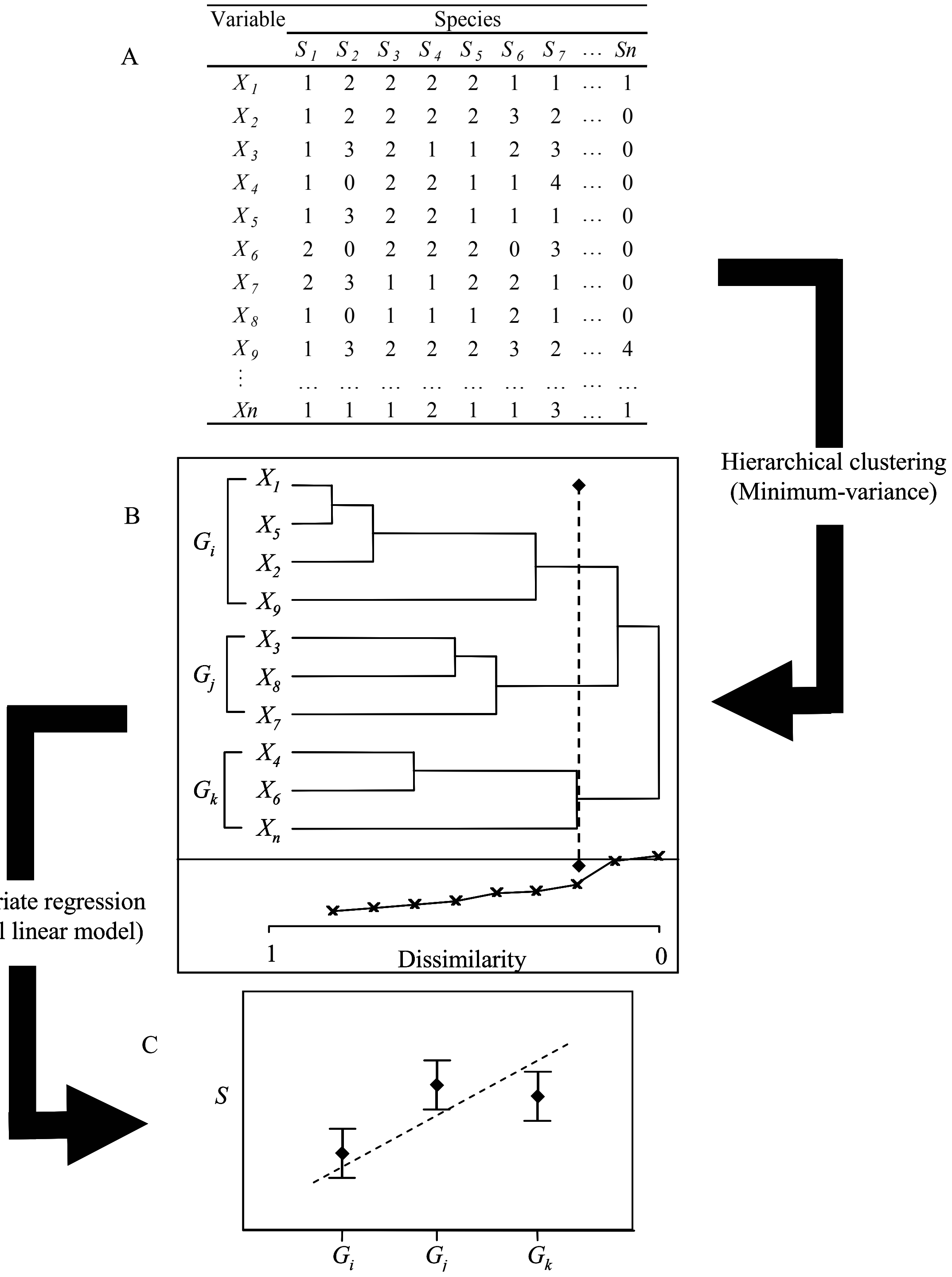


Figure 3.1. Map of the Florida Keys showing the location of sites and management jurisdictions surveyed by volunteers of the Reef Environmental Education Foundation (REEF) between July 1993 and August 2002. Darker site markers represent areas where numerous surveys were conducted.



Variable	Species								
	S_1	S_2	S_3	S_4	S_5	S_6	S_7	…	Sn
X_1	1	2	2	2	2	1	1	…	1
X_2	1	2	2	2	2	3	2	…	0
X_3	1	3	2	1	1	2	3	…	0
X_4	1	0	2	2	1	1	4	…	0
X_5	1	3	2	2	1	1	1	…	0
X_6	2	0	2	2	2	0	3	…	0
X_7	2	3	1	1	2	2	1	…	0
X_8	1	0	1	1	1	2	1	…	0
X_9	1	3	2	2	2	3	2	…	4
⋮	…	…	…	…	…	…	…	…	…
Xn	1	1	1	2	1	1	3	…	1

Figure 3.2. A graphic representation of the selection of independent variables for use as factors in the multiple linear regression models used in this study. **A**: Table of species abundance with categories of an independent variable (e.g., depth, $X_{1\text{-}n}$) as rows and species ($S_{1\text{-}n}$) as the columns (data source: REEF 1999-2002). **B**: A dendrogram of cluster groups ($G_{i\text{-}k}$) resulting from hierarchical clustering of Table A. **C**: The results of multiple linear regression of species richness against depth cluster groups.

CHAPTER 4

SPATIAL VARIATION IN BENTHIC HABITATS OF THE FLORIDA KEYS SEASCAPE[1]

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[1] Jeffrey, C.F.G. To be submitted to *Ecological applications*

Abstract

Island biogeographic and landscape mosaic approaches was used to identify patterns in the distribution and arrangement of benthic habitats among four subregions, 23 protected areas, and unprotected seascapes of the Florida Keys National Marine Sanctuary (FKNMS). Spatial patterns in benthic habitats were quantified by computing three GIS-based metrics: habitat frequency, relative habitat richness, and habitat evenness. Delineated habitats were considered homogeneous and point-in-time estimates of areas of ecological and environmental conditions at specific spatial scales. Identifiable and significant patterns occurred in the occurrence and distribution of some habitats among subregions and protected zones and between protected and unprotected areas of the FKNMS. Although no single habitat dominated the FKNMS seascape, seagrass habitats were most abundant; this suggested that the FKNMS comprises a mosaic of hardbottom habitat patches interspersed in a matrix of seagrass habitats. Two seagrass habitats dominated the Upper and the Lower Keys, whereas the Dry Tortugas and the Middle Keys abounded with hardbottom habitats. Patterns in habitat frequency among protected areas were less obvious, although two distinct groups of protected areas contained similar habitats. The Upper Keys and the Dry Tortugas on average contained more habitat types than the Middle or the Lower Keys, but habitats were least evenly distributed in the Upper Keys and most evenly distributed in the Dry Tortugas. Protected areas contained a greater variety of habitats than non-protected areas, suggesting that protected seascapes potentially house a greater variety of fish and invertebrate species than non-protected areas. Quantification of the variation in spatial patterns of habitat occurrence provides a basis for evaluating the protection afforded fish assemblages, assuming such variation influences the distribution, abundance, and assemblage structure of fishes in the FKNMS.

Introduction

A major constraint facing ecological studies is the quantification of spatial and temporal variability in ecosystems (Pielou 1977, Levin 1992, Ault and Johnson 1998, García-Charton and Perez-Ruzafa 1999, García-Charton et al. 2000). For example, distinguishing between the population effects of marine protected areas (MPAs) and the inherent variability of the fish populations being protected is difficult (García-Charton and Perez-Ruzafa 1999, García-Charton *et al*. 2000). Although MPAs are only a few hectares in size, many can encompass large biogeographic areas that contain highly variable ecosystems. This natural ecosystem variability, coupled with the effects of variable management measures, pose a major problem in detecting, explaining, and predicting the effects of MPAs (García-Charton and Perez-Ruzafa 1999, García-Charton et al. 2000).

The ecological linkages between habitats and the abundance and distribution of coral reef fishes have been reviewed by Parrish (1989), Williams (1991), Sale (1998), García-Charton and Perez-Ruzafa (1999) and García-Charton et al. (2000). These authors criticized the absence of a spatial dimension in the design of the studies they reviewed, a shortcoming also acknowledged by the original authors. Several studies have addressed small (meter) scale spatial variation in fish populations by focusing primarily on differences within and among reefs (Luckhurst and Luckhurst 1978, Williams 1991, McGhee 1994, Rakitin and Kramer 1996, Chabanet et al. 1997, Friedlander and Parrish 1998, Sale 1998, García-Charton and Perez-Ruzafa 1999, García-Charton et al. 2000). Although these studies have provided insight into the small-scale patterns of coral reef fish distributions, the factors affecting broad-scale variation and distribution of reef fishes are yet to be determined. Also, small-scale patterns frequently are extrapolated to imply regional and large scale patterns (Williams 1991, Sale 1998, García-Charton et al. 2000).

Recent studies have begun to focus on identifying the factors that affect large-scale variation in the abundance and distribution of coral reef fishes to address the link between anthropogenic factors and temporal changes in assemblage structure (Edmunds and Bruno 1996, Ault and Johnson 1998, García-Charton and Perez-Ruzafa 1999, Gonzalez-Gandara et al. 1999, Lindeman et al. 1999, García-Charton et al. 2000). Ecologists are becoming more aware of the importance of spatial and temporal heterogeneity of ecosystems for understanding ecological processes and how humans affect them. García-Charton et al. (2000) suggested that a conceptual and methodological framework was needed to deal with ecosystem variability in marine systems. The ecology of reef fish assemblages is multi-scalar because of ontogenetic succession of spatial scales used in daily activities and over the lifetime of reef fishes (Helfman 1978, Williams 1991, Sale 1998). A landscape approach similar to that used in terrestrial systems may provide the framework necessary for linking the effects of multi-scalar and spatial variability observed in marine ecosystems to the large-scale patterns of coral reef fish abundance and distribution.

Landscape ecology is the study of spatial variation across broad spatial scales. It focuses on spatial relationships among ecosystems and how they affect ecosystem processes (Turner et al. 2001). The basic premise of landscape ecology is that ecological processes are closely linked to ecological pattern (Pielou 1977, Urban et al. 1987, Haines-Young and Chopping 1996, Gustafson 1998). A landscape is considered a mosaic of patches forming patterns that are generated by disturbances, biotic processes, and environmental constraints at various scales (Urban et al. 1987). Additionally, the spatial arrangements (pattern) of elements in a landscape may also control the ecological processes that operate within it (Haines-Young and Chopping 1996).

Landscape ecology has developed as a tool for studying ecological-scale-dependent effects of spatial patterning of ecosystems (Urban et al. 1987). Although it has been applied widely to the study of terrestrial systems, the landscape approach has only recently been applied to the study of coral reef ecosystems (see reviews by Sale 1998 and Charton et al. 1999). Furthermore, landscape-type studies in coral reef systems have focused on the effects of functional habitat linkages on selected species or genera such as the transfer of energy between adjacent habitats by commuter species; studies on the effects of habitat patterns on reef fish assemblage structure are much less common (see reviews by Parrish 1989 and Charton et al. 1999).

Terrestrial ecologists commonly use landscape ecology to quantify spatial patterns in the distribution and abundance of organisms, but this approach has only been applied recently to marine systems. In general, two approaches have been used in quantifying spatial patterns in landscapes: the island biogeographic model and the landscape mosaic model. The island biogeographic model represents the landscape as a series of suitable island-like vegetation types in the sea or matrix of surrounding unsuitable areas that are unimportant or are barriers to the species or populations of concern (MacArthur and Wilson 1967, Urban and Keitt 2001). The underlying premise of the 'island' model is that the organism of interest has identifiable dependencies only on the focal vegetation or habitat type, and will be affected by changes in the abundance or isolation of that focal habitat type. This approach has provided the basis for studying the effects of habitat fragmentation on threatened or endangered species in terrestrial systems (Saunders et al. 1991). Alternatively, the landscape can be represented as a complex mosaic of heterogeneous habitat types, in which adjacent habitats may be similar or dissimilar, and all habitat types are of some relevance to the organism or species of concern (Forman 1995). The landscape 'mosaic' model assumes that the organism of interest uses the habitat types within the landscape proportionately to the fitness conferred by the habitats rather than being dependent on a single habitat type.

This study used the island-biogeographic and landscape-mosaic approaches to identify patterns in the distribution and arrangement of benthic habitats in the FKNMS. The premises were that 1) quantifiable spatial patterns exist in the arrangement of benthic habitats, with gradients existing among subregions and between protected areas and non-protected areas of the FKNMS, and 2) these patterns may influence the distribution and abundance of fishes. If patterns in benthic habitat influence fish distribution and these patterns vary within the landscape, then successful evaluation of resource protection will depend in part on the quantification of such patterns among protected and non-protected sites. The objectives of this study were to determine patterns of variation in GIS-based benthic habitat variables among subregions and protected zones, and select suitable variables as potential factors that help explain the variation in fish populations within the FKNMS. Patterns in benthic habitats were examined at the scale of variation (1) among four sub-regions, (2) among 23 protected areas within the sanctuary system, and (3) variation between protected and unprotected areas within subregions.

Methods

Study area

The area of study was the seascape included within the FKNMS and the Dry Tortugas National Park (DTNP) (Figure 4.1). The Florida Keys comprise an island archipelago that extends 320 km southwest from Soldier Key in Biscayne Bay to the Dry Tortugas (Figure 4.1). To the north and west, the Keys are bounded by Biscayne Bay and the Gulf of Mexico; to the east and south, they are bounded by the Straits of Florida. The study area measured 4,305 km^2 and included seagrass beds, sand flats, hardbottom areas, and a coral reef tract that extends 8 km offshore into the Atlantic Ocean.

The Florida Keys National Marine Sanctuary and the Dry Tortugas Ecological Reserve

In November 1990, the United States Congress passed the Florida Keys National Marine Sanctuary and Protection Act (HR 5909) that designated the FKNMS. The Act authorized the National Oceanic and Atmospheric Administration (NOAA) to develop and implement a comprehensive management plan to manage and protect Sanctuary resources for the enjoyment of present and future generations. The FKNMS is organized into five management areas: Wildlife Management Areas (WMA), Ecological Reserves (ER), Sanctuary Preservation Areas (SPA), Existing Management Areas (EMA), and Special Use/Research Only Areas (SA/RO). On July 1, 1997, the FKNMS Management Plan, which included a large-scale marine zoning plan, became effective and closed 23 areas (eighteen SPAs, four SAs, and one ER) to all extractive use (NOAA, 1996). These zones aim to protect the biological diversity and integrity of the marine environment in the Keys. In addition to providing areas that are limited to non-extractive recreation, these no-take zones are intended to act as replenishment zones where the total abundance of fishes, their average size, and their overall larval production may increase. State and Federal managers are reevaluating the use of zones as a management tool and are supporting a wide-scale, three-tiered monitoring program to evaluate the effects of the zones on biodiversity and human activities (FKNMS 2002). Monitoring projects include research on coral, algae, fish, lobster, and human values, and focus on three levels: ecosystem, human-ecosystem interface, and volunteer-based monitoring of ecosystem health.

The Dry Tortugas Ecological Reserve is a 391-km^2 no-take area set aside to protect the critical coral reef ecosystem of the Tortugas, a remote area in the Western Part of the Florida Keys. The reserve consists of two sections: Tortugas North, and Tortugas South. The Dry Tortugas Ecological Reserve expands the Florida Keys National Maine Sanctuary boundaries westward to protect important coral reef resources in the areas of Sherwood Forests and Riley's Hump. Currently, detailed benthic habitat maps do not exist for the protected areas of the Dry Tortugas.

GIS coverages – benthic habitats and bathymetry

Data on benthic communities were summarized from digitized benthic maps (FMRI and NOAA 1998). In 1998, a six-year collaborative effort between NOAA and the Florida Marine Research Institute (FMRI) culminated in the production of an atlas and a CD-ROM containing data on the types, location, coverage, and depths of benthic habitats within the FKNMS (FMRI and NOAA 1998). Benthic habitats were identified from 450 natural color aerial photographs of the Florida Keys region acquired by remote sensing from December 1991 through March 1992. The photographs were at a scale of 1:48,000 and covered an area of approximately 160 km^2 or 3% of the FKNMS.

A hierarchical classification scheme was used to interpret and delineate the benthic communities seen on the aerial photographs. The hierarchical classification consisted of four major categories (coral, seagrasses, hardbottom, and bare substrate) and 22 known subcategories (Table 4.1). The minimum habitat area delineated was 0.05 km^2; however, smaller identifiable patch reefs were delineated also because of their ecological significance as critical habitat (FMRI and NOAA 1998). Delineated habitats are static point-in-time estimates of coral reef ecosystems presented as a mosaic of patches. Although marine seascapes may contain complex spatial patterns in the distribution of temporally dynamic resources, habitat patches were assumed to be areas of homogeneous ecological and environmental conditions with discrete and discontinuous boundaries at specific spatial and temporal scales.

Depths of benthic habitats were based on 109 hydrographic surveys conducted by NOAA National Ocean Service between 1851 and 1965 that contained *c.* 1.4 million depth soundings of the study region (NOAA NGDC 2003, http://www.ngdc.noaa.gov/mgg/bathymetry/hydro.html, accessed: 1/10/2003). The original point soundings were used to generate bathymetric Digital Elevation Models (DEM) from which maximum and minimum depth contours were created (FMRI and NOAA 1998). The contoured GIS depth layer was converted to a 40 x 40 m grid and used to determine the depth of benthic habitats. The maximum error associated with depth contours was 2 m for depths shallower than 100 m (FMRI and NOAA 1998).

Computation of GIS metrics to measure habitat patterns within seascapes

The benthic map for the entire Florida Keys seascape was divided into 40 x 40 m grid cells (1600 m^2) and each cell was coded with one of the 22 habitat categories listed in Table 4.1. Habitat-coded grid cells were sampled with a larger 200 x 200 m polygon grid, which was equivalent to sampling the FKNMS habitat map with a 0.2-km^2 quadrat. Habitat frequency, relative habitat richness, and habitat evenness were computed for each 200 x 200 m grid. Habitat frequency ($\%f$) describes the relative abundance of each habitat and is the proportion of the seascape covered by each habitat within the sampling grid. Relative habitat richness ($\%R$) is the number of habitats expressed as a percent of the maximum number of possible habitats such that $\%R = \frac{S}{S_{\max}} \times 100$. Habitat evenness ($J'$) describes habitat diversity as well as how evenly similar-sized habitat patches are distributed. Similar to species evenness that describes the number of species present and how equally individuals are distributed among species, J' was based on the Shannon-Weaver diversity index (H') and defined as follows:

$$J' = \frac{H'}{\ln(s)} = \frac{\sum_{i=1}^{s} (p_i)\ln(p_i)}{\ln(s)}$$

where p_i is the proportion of each habitat, and s is the total number of habitats within the FKNMS seascape (Shannon and Weaver 1949, Pielou 1977). Higher values of H' indicate greater diversity;

division by *ln*(s) normalizes H' such that $0 \leq J' \leq 1$, where higher values of J' indicate greater habitat evenness. GIS metrics were computed with Fragstats software (Ver. 3.3, McGarigal *et al*. 2002).

Study design and GIS analysis

The FKNMS was divided into four distinct regional seascapes: the Upper Keys, the Middle Keys, the Lower Keys, and the Dry Tortugas. Each region was further divided into protected and non-protected seascapes based on the FKNMS 1997 zoning plan. Means and standard errors of each GIS metric were computed for each region, protected area, and 10% of non-protected areas within each region. Non-protected areas comprised 95% of the mapped area in the FKNMS. Therefore, 10% of the non-protected area within each subregion was randomly selected to estimate means and standard errors of GIS metrics for comparison with protected areas. The use of only 10% rather than all of the unprotected areas 1) provided a more conservative estimate of the variance around the mean of each GIs-based metric, and 2) minimized probability of finding significant differences between protected and non-protected areas (Type I error) when a true difference did not exist. Where appropriate, non-parametric Kruskal-Wallis rank sums tests and modified Tukey-type multiple comparisons were used to determine significant differences in mean estimates of GIS-based metrics among subregions and protected areas (Sokal and Rohlf 1995, Zar 1999). Significant differences between protected areas and non-protected areas were tested with a series of Student’s *t*-tests that compared mean estimates of derived metrics (Sokal and Rohlf 1995, Zar 1999). Statistical analyses were done with the JMP 4.0 statistical software ($\alpha = 0.05$, SAS Institute 2000).

Results

Patterns in frequency of habitats

The FKNMS habitat map contained 11,450 habitat polygons (hereafter patches). Patch size was highly variable and ranged from 0.00001 to 421.85 km^2 ($\overline{X}$ = 0.37 km^2, SD = 7.12 km^2, CV = 1931%).

Most patches (99.5%) were less than 7 km^2. Mean patch size also varied among habitat types, with macro algae with scattered seagrass (S07) and hardbottom with perceptible seagrass (H01) having the highest mean patch size per habitat (Figure 4.2). Seagrasses dominated the FKNMS seascape. Seagrasses accounted for 69.1%, hard substrates 25.7%, and uncolonized sediments 4.4% of the mapped area (Table 4.1). The three most dominant habitats were moderate to dense continuous seagrass (41.8%), hardbottom (<50% perceptible seagrass -19.9%), and patchy seagrass (moderate to dense with blowouts - 18.3%, Table 4.1). Thirteen of 22 habitat types had *%f* < 1% (Table 4.1).

PCA of regions based on habitat frequency showed differences in the frequency of five habitats among regions. Three principal components (P1, P2, and P3) explained 99.7% of the variation in habitat frequency among regions. P1 explained 62.1% of the regional variation in habitat frequency and separated moderate to dense continuous seagrass (S01) and moderately dense patchy seagrass with blowouts (S02), habitats that were associated with the Upper and the Lower Keys (Figure 4.3). P2 explained 22.7% of the regional variation in habitat frequency, and further separated remnant low profile reef (H02) and coral-rock patches with sand (H04), habitats that were most frequent in the Dry Tortugas (Figure 4.3). The third factor (P3) explained 14.9% of the regional variation in habitat frequency, and separated hardbottom with perceptible seagrass (H01), habitat that was associated with the Middle Keys (Figure 4.3).

Non-parametric rank sums tests and modified Tukey multiple comparisons confirmed significant regional differences in the mean *%f* of five habitats (Figure 4.4). The frequency of hardbottom with perceptible seagrass (habitat H01) was significantly higher in the Middle Keys than in the Upper or the Lower Keys and was absent from the Dry Tortugas (Figure 4.4). Remnant low profile reef (habitat H02) and coral-rock patches with sand (habitat H04) were significantly more abundant in the Dry Tortugas but did not vary significantly among other regions of the FKNMS (Figure 4.4). Moderate to dense continuous seagrass habitat (S01) was significantly different among all regions and was most abundant in the Upper Keys, followed by the Lower Keys, the Middle Keys, and the Dry Tortugas (Figure 4.4).

Moderately dense patchy seagrass with blowouts (habitat S02) was highest in the Middle Keys, followed by the Lower Keys, and lowest in the Upper Keys and the Dry Tortugas (Figure 4.4).

Nine principal components explained about 92.6% of the variation in the frequency of 16 habitats among protected areas of the FKNMS (Table 4.2). The first three principal components explained only 55% of the variation, with P1, P2, and P3 respectively accounting for 23%, 20%, and 12% respectively of the variability in habitat frequency (Table 4.2). There were no strong associations between protected areas and any single habitat type along P1, P2, and P3. Rather, several habitat types contributed to the variability in habitat abundance among protected areas (Table 4.2, Figure 4.5). PCA separated two groups of protected areas along P2 based on habitat abundance (Figure 4.5).

Patterns in richness, diversity, and evenness of habitats

Total relative habitat richness *(%R*) of habitats was highest in the Lower Keys (100%) and lowest in the Dry Tortugas (55%) but similar in the Upper and Middle Keys (91%, Figure 4.6A). In contrast, mean relative habitat richness was highest in the Dry Tortugas, followed by the Upper, the Lower, and the Middle Keys (Figure 4.6A). Overall habitat diversity (H') and evenness (J') of the FKNMS was 1.75 and 0.56 respectively. H' was directly and positively correlated with J' ($\rho = 0.81$, $P < 0.001$), thus only patterns in evenness are reported. Although the range in evenness was small, mean habitat evenness varied significantly among subregions and was lowest in the Upper Keys, followed by the Middle and Lower Keys, and highest in the Dry Tortugas (Figure 4.6B).

Relative habitat richness varied among protected areas; different spatial trends existed among the Upper, the Middle, and the Lower Keys (Figure 4.7A). Protected areas had lower relative habitat richness and contained fewer habitats than surrounding non-protected areas in each region (Figure 4.7A). In the Upper Keys, relative habitat richness ranged from about 40% at Carysfort Reef – the northernmost protected area – to about 10% at Hens and Chickens Reef further south (Figure 4.7A). In the Middle Keys, relative habitat richness of protected areas was 18-27%. Relative habitat richness in the protected areas of the Lower Keys was 68% at Western Sambos Reef, the largest protected area in the region, and 18% at Newfound Harbor Key and Looe Key II, the two smallest protected areas of the region.

Evenness of habitats varied among protected areas and was highest at Molasses Reef, Coffins Patch Reef, Western Sambos Reef, Looe Key II, and Eastern Dry Rocks (Figure 4.7B). Additionally, habitat evenness was consistently higher in protected areas compared with surrounding non-protected areas except at Conch Reef and Newfound Harbor Key, where evenness between protected and non-protected areas was similar (Figure 4.7B). Evenness of habitats in protected areas showed no other discernable patterns within or among regions (Figure 4.7B).

Patterns in bathymetry

Depths in the FKNMS ranged from 0.1 – 99.7 m ($\bar{X}$ = 5.2 m, SD = 8.3 m). The mean depth of the Upper, the Middle, and the Lower Keys was shallow ($\bar{X}$ = 5.0 ± 0.01 m) compared with the average depth of the Dry Tortugas (32 ± 0.2 m). The mean depth of protected areas in the Upper Keys was 5.3 ± 0.07 m except for Conch Reef II with a mean depth of 15.4 ± 0.67 m (Figure 4.8). Protected areas of the Middle and Lower Keys were more variable in mean depth than protected areas of the Upper Keys or the Dry Tortugas (Figure 4.8). Differences in the mean depths of protected and non-protected areas were greatest in the Middle Keys where protected areas were on average 1.5 m deeper than non-protected areas (Figure 4.8).

Discussion

Spatial patterns in benthic habitats

Assuming that variation in habitat distribution affects fishes (see chapter 5), quantifying variation in the distribution and spatial pattern of benthic habitats between protected and non-protected seascapes is important as we evaluate management efforts aimed at protecting fish assemblages via habitat protection. The results of this study indicate that regions and protected areas of the FKNMS have distinct and quantifiable benthic seascape properties that ultimately can be used to develop a spatial framework for assessing spatial heterogeneity in the distribution and abundance of fish populations. Additionally, analysis of GIS-based metrics revealed identifiable and significant patterns in the occurrence and distribution of some habitats among subregions and protected zones in the FKNMS. Although any single habitat type did not cover more than 50% of the FKNMS seascape overall, analysis of habitat frequency data revealed that seagrass habitats together were most abundant and suggests that the FKNMS consists of a mosaic of hardbottom habitat patches interspersed in a matrix of seagrass habitats. A few habitats dominated the seascape regionally, however. Two seagrass habitats dominated the seascape of the Upper and the Lower Keys, whereas the Dry Tortugas and the Middle Keys abounded with hardbottom habitats.

Patterns in habitat frequency among protected areas were less obvious, although two protected areas – Western Sambos and Newfound Harbor Key – contained mainly hardbottom and seagrass habitats respectively. The Upper Keys and the Dry Tortugas on average contained more habitats than the Middle or the Lower Keys, but habitats were least evenly distributed in the Upper Keys and most evenly distributed in the Dry Tortugas. This pattern in habitat evenness reflects the dominance of one or two seagrass habitats in the Upper Keys compared with the Dry Tortugas. Protected areas contained fewer habitats than non-protected areas, but habitats were more evenly distributed in protected areas than in non-protected areas. These differences in the habitat richness and evenness between protected and non-protected areas result from differences in size and location of protected areas. Protected areas represent < 1% of the FKNMS, and therefore will contain fewer habitats than unprotected areas by random chance alone. Unprotected areas in the Upper, Middle and Lower Keys are characterized by large areas of contiguous, seagrass habitats. Many of the grids sampled randomly from unprotected areas probably were monotypic, which resulted in low measures of evenness. In contrast, coral reefs and hardbottom areas are patchy in their spatial distribution, and they are highly variable in shape and structure. Protected areas were designed to protect the coral reef ecosystems of the FKNMS and are located along the main reef tract where the most developed coral reefs occur. Thus, sample grids from protected areas were much less likely to be monotypic, and thus had higher evenness compared with grids from unprotected areas.

Relevance to fish assemblage composition

The goal of this study was to quantify spatial patterns in the distribution, abundance, and arrangement of habitats and to determine ultimately if such patterns may influence fish assemblages in the FKNMS seascape. Two approaches were used to quantify spatial patterns in the FKNMS seascape: the island biogeographic model and the landscape mosaic model.

Based on the 'island' model, the seascape was represented as a series of island-like habitats in a sea or matrix of surrounding areas, and the abundance and frequency of each habitat was computed. The underlying premise is that fishes have direct and identifiable species-specific linkages with habitats. If such linkages exist, then fish assemblage structure could be affected by changes in the occurrence and abundance of those habitats on which fishes depend. PCA identified two seagrass and three coral-reef/hardbottom habitat types that explained 100% of the variability in habitat frequency among regions of the FKNMS. Regional differences in the amounts of seagrasses and specific coral-reef/hardbottom types could determine how fishes that show preferences for these habitats are spatially distributed throughout the FKNMS. Quantification of the abundance and frequency of habitats then could be important when fish assemblages of different seascapes are compared. Preferential habitat selection has been demonstrated only for a few coral reef species, such as newly settled stoplight parrotfish, damselfishes, and juvenile grunts (Ormond et al. 1996, Tomlieri 1998, Kendall et al. 2003). However, whether such preferences are detectable in adult populations after stochastic post-recruitment and post-juvenile processes have operated is still unknown.

Although the distribution of species with particular habitat requirements may be affected the habitat abundance and frequency, overall spatial variation in the populations of coral reef fishes may be more correlated with metrics such as habitat richness and evenness that are based on the "mosaic" model. Most coral fishes utilize several habitats over the course of their lifetime rather than being dependent on a single habitat type (Helfman 1978, Sale 1998, Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2003). More specifically, variation in the assemblage structure of fishes may be more strongly linked to patterns of habitat richness and evenness than to patterns of the abundance of specific habitats. Thus, one can reasonably expect for example that a seascape with a greater variety of habitats or greater habitat diversity will also have more diverse fish assemblages than a seascape with a dominant habitat type that lacks variability.

Significant regional differences in benthic habitat richness and evenness were identified by using, the landscape mosaic model. Protected areas also varied considerably in habitat richness and evenness and contained fewer habitats that were more evenly distributed than unprotected areas. PCA results highlights further the usefulness of these indices. PCA of habitat abundance did not identify strong associations between protected areas and any single habitat type. Instead, protected areas appeared to contain several types of coral reef and hard bottom habitats that contributed to the variability in habitat abundance. In fact, a different suite of habitat types contributed to the variability measured along P1, P2, and P3 during PCA (see Table 4.2). These findings suggest that measures of habitat richness and evenness may be more useful than measures of habitat frequency in characterizing differences in benthic composition among protected areas in the FKNMS.

Parrish (1989) advocated the development of a spatial framework to address the effects of interactions among adjacent habitats on coral reef fishes. Several recent studies have used a spatial approach to describe habitat use by fishes or to quantify spatial variability in fish populations (García-Charton and Perez-Ruzafa 1999, Lindeman et al. 1999, Christensen et al. 2003, Kendall et al. 2003). Additionally, defining the spatial scales at which populations of coral reef fishes operate may be very important for the effective management of coral reef fisheries, but this issue still represents a large gap in our understanding of the ecology of coral reef fishes (Sale 1998, 2002). This study presents two approaches to quantify spatial patterns in seascape structure of the FKNMS that may provide a basis for assessing the effects of habitats on fish assemblage structure and for evaluating the effects of marine protected areas on fish populations in the FKNMS.

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TABLES

Table 4.1. Percent cover of habitat types in the Florida Keys assessed in this study.

Substrate	Percent cover	Habitat type	Code	Percent cover
Seagrass	69.1	Continuous seagrass - moderate to dense	S01	41.81
		Patchy seagrass - moderate to dense with blowouts	S02	18.27
		Patchy seagrass - predominantly sand or mud with small, scattered seagrass patches (<50%)	S03	4.51
		Patchy seagrass - dense patches in a matrix of hardbottom	S04	4.31
		Continuous seagrass - dense patches in a matrix of sparse seagrass (<50%)	S05	0.67
		Continuous seagrass - sparse	S06	0.42
		Patchy seagrass - predominantly macroalgae cover with scattered seagrass patches	S07	0.13
Hardbottom	27.5	Hardbottom - perceptible seagrass (<50%)	H01	19.95
		Platform margin reefs - remnant - low profile	H02	2.78
		Platform margin reefs - drowned spur and groove	H03	2.04
		Patch reefs - coral or rock patches with bare sand	H04	1.27
		Patch reefs - aggregated	H05	0.56
		Hardbottom - soft corals, sponges, algae	H06	0.24
		Platform margin reefs - reef rubble	H07	0.23
		Patch reefs - individual	H08	0.19
		Patch reefs - aggregated with halo	H09	0.16
		Platform margin reefs - shallow spur and groove	H10	0.07
		Patch reefs - halo	H11	0.02
		Platform margin reefs - back reef	H12	0.01
Uncolonized sediment	4.4	Bare substrate - carbonate sand	U01	4.32
		Bare substrate - carbonate mud	U02	0.03
		Bare substrate - organic mud	U03	0.01

Table 4.2. Eigenvectors for 9 of 16 principal components that explained 93% of the variation in the frequency of 16 habitats occurring in protected areas of the Florida Keys National Marine Sanctuary. Values in bold indicate the most important source of variability for each of the nine factors.

Variation	P1	P2	P3	P4	P5	P6	P7	P8	P9
Percent	23.29	20.39	11.56	9.79	8.46	6.05	5.04	4.39	3.66
Cumulative	23.29	43.68	55.24	65.03	73.49	79.54	84.58	88.97	92.63
Habitat									
H01	0.31	0.37	0.28	0.13	0.05	0.08	0.00	0.04	0.01
H02	0.23	0.15	0.21	0.25	0.41	0.11	0.42	0.11	0.26
H03	0.25	0.28	0.14	0.14	0.34	0.13	0.30	0.26	0.28
H04	0.28	0.05	**0.39**	0.19	0.08	0.01	0.30	0.20	**0.52**
H05	0.15	0.27	0.04	0.41	0.18	0.15	0.32	**0.55**	0.12
H07	0.32	0.24	0.35	0.19	0.14	0.10	0.04	0.27	0.13
H08	0.19	0.35	0.20	0.41	0.07	0.00	0.11	0.13	0.13
H09	**0.46**	0.18	0.17	0.06	0.00	0.01	0.00	0.08	0.06
H10	0.02	**0.38**	0.21	0.27	0.21	0.39	0.13	0.06	0.20
H11	0.16	0.36	0.24	**0.44**	0.06	0.12	0.01	0.00	0.03
H12	0.05	0.22	0.36	0.07	0.42	0.20	0.17	0.40	0.42
S01	0.00	0.23	0.37	0.31	0.25	0.20	0.43	0.01	0.32
S02	0.40	0.06	0.14	0.11	0.30	0.03	0.12	0.29	0.27
S03	0.15	0.06	0.31	0.15	**0.51**	0.20	**0.44**	0.24	0.29
S04	0.36	0.22	0.17	0.23	0.05	0.05	0.03	0.34	0.25
U01	0.08	0.21	0.06	0.14	0.09	**0.81**	0.31	0.25	0.00

FIGURES

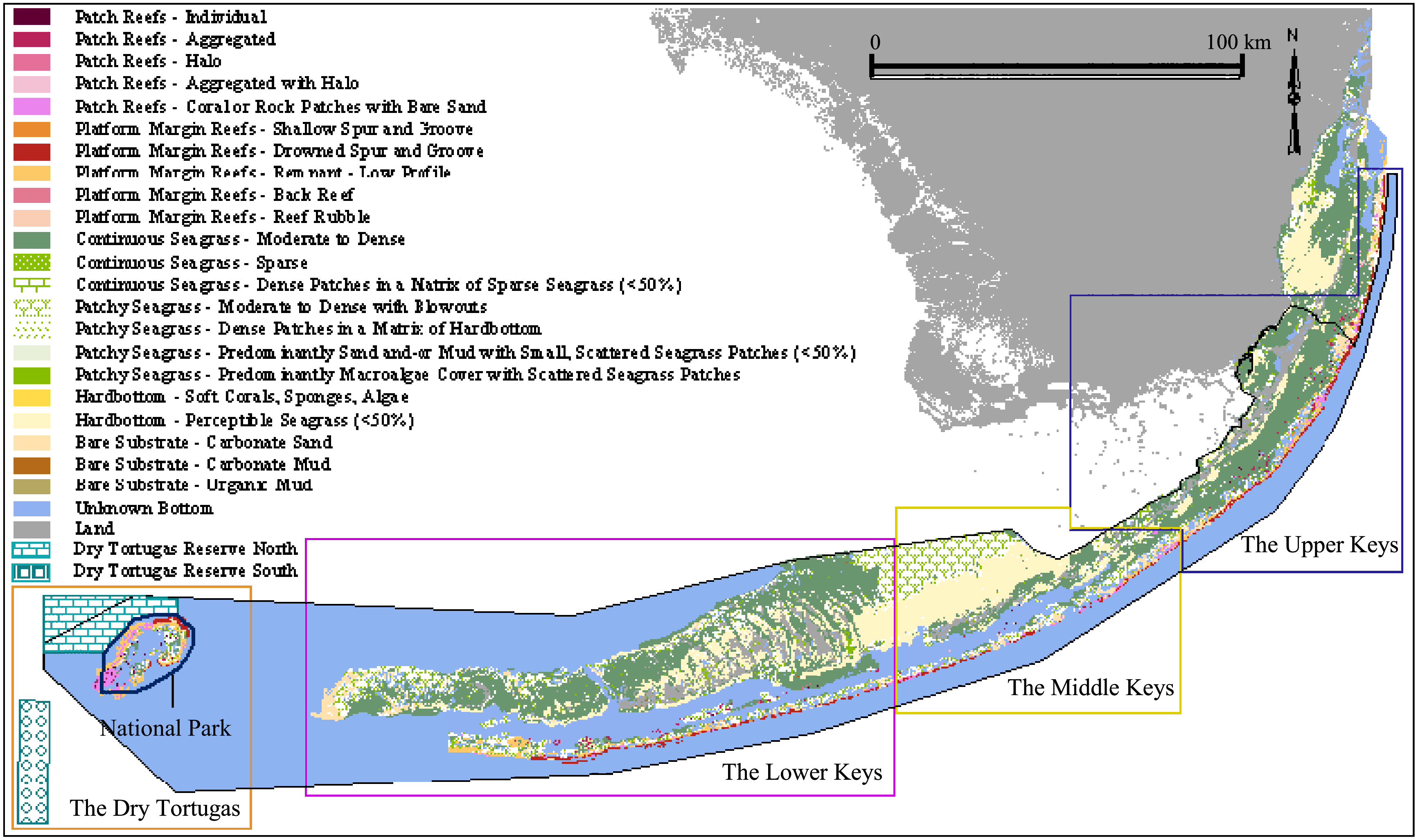

Figure 4.1. Benthic habitats and regions of the Florida Keys National Marine Sanctuary (FMRI and NOAA 1998).

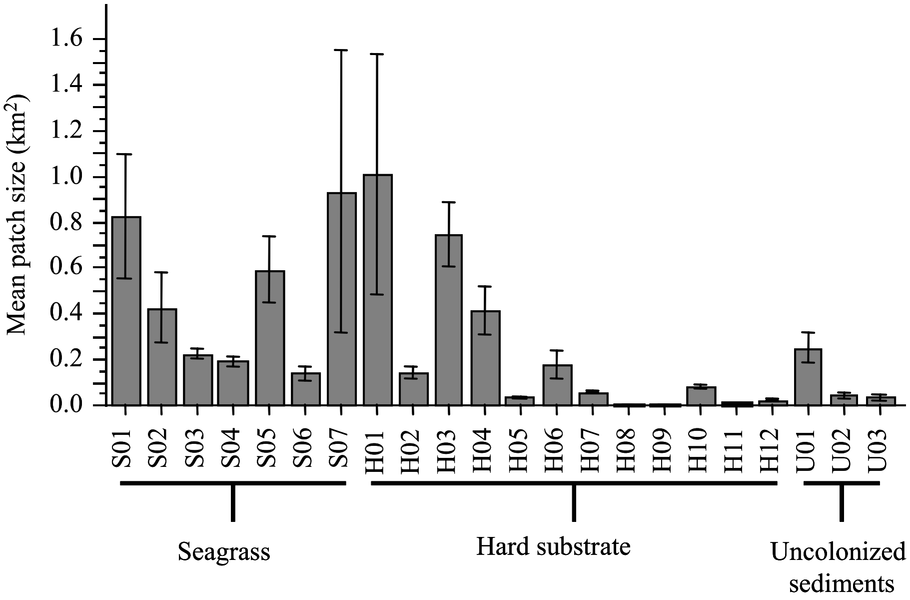

Figure 4.2. Mean patch size of habitats types occurring in the Florida Keys National Marine Sanctuary. Vertical bars represent the standard error of the mean. Habitats are defined in Table 4.1.

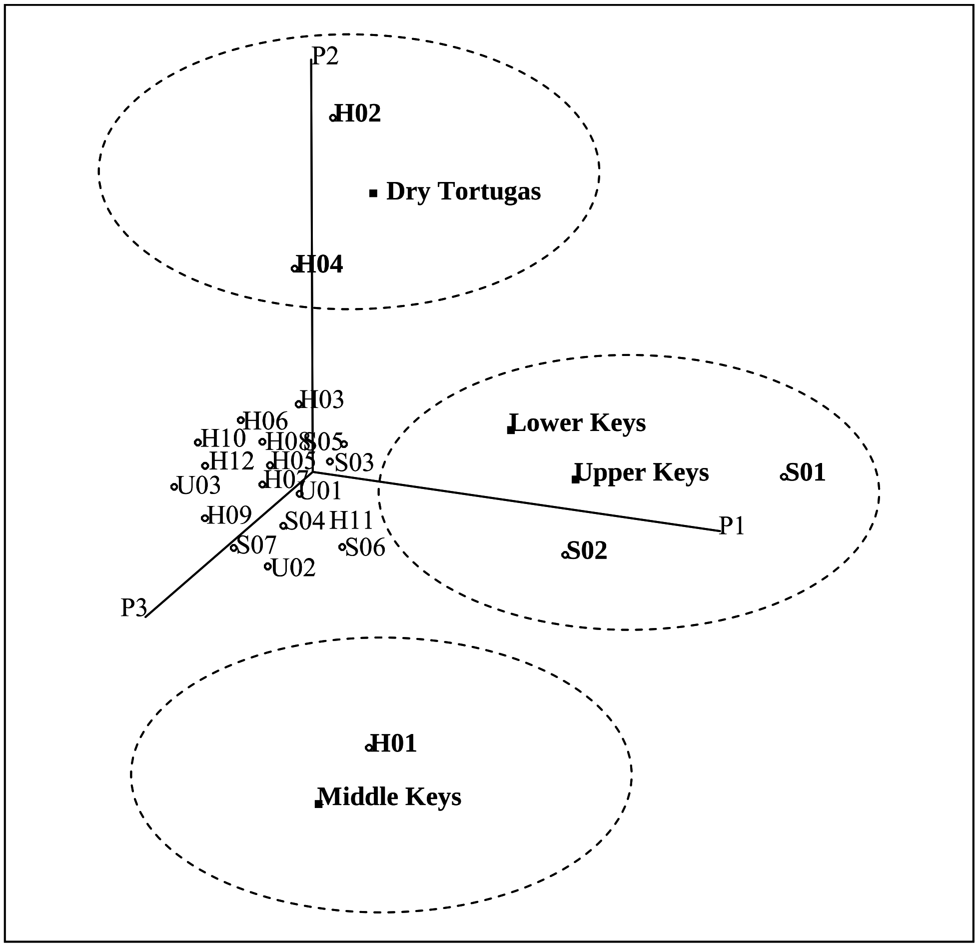

Figure 4.3. Results of principal component analysis (PCA) of habitat frequency data to determine the associations among regions and benthic habitats in the Florida Keys National Marine Sanctuary. Habitat frequency was defined as the percent area of a 200 x 200 m grid covered by benthic habitats in a region (N = 1000 per region). Habitats are defined in Table 4.1.

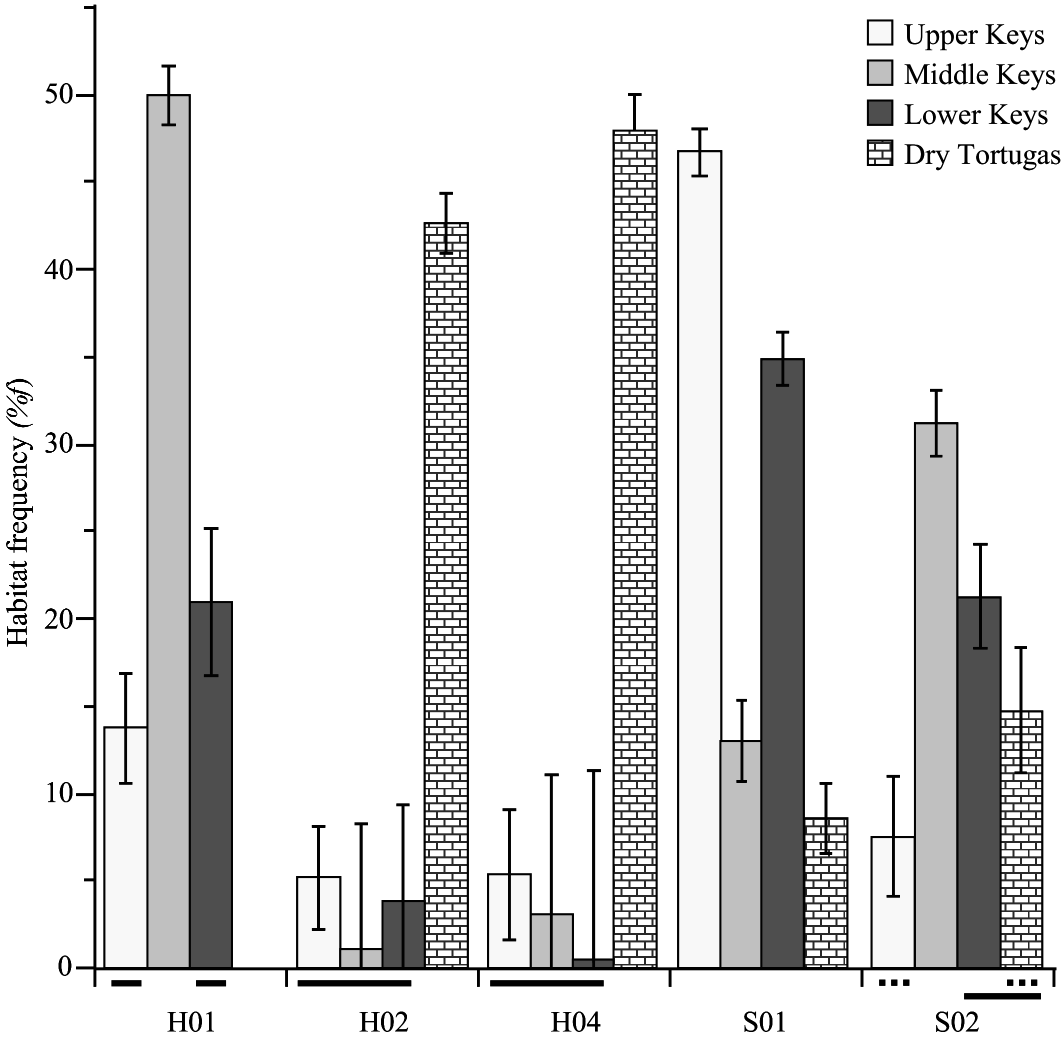

Figure 4.4. Mean habitat frequency for regions of the Florida Keys National Marine Sanctuary. Solid and dotted lines show results of modified Tukey-Kramer comparisons and join means that are not significantly different from each other (P > 0.05). Habitats are defined in Table 4.1.

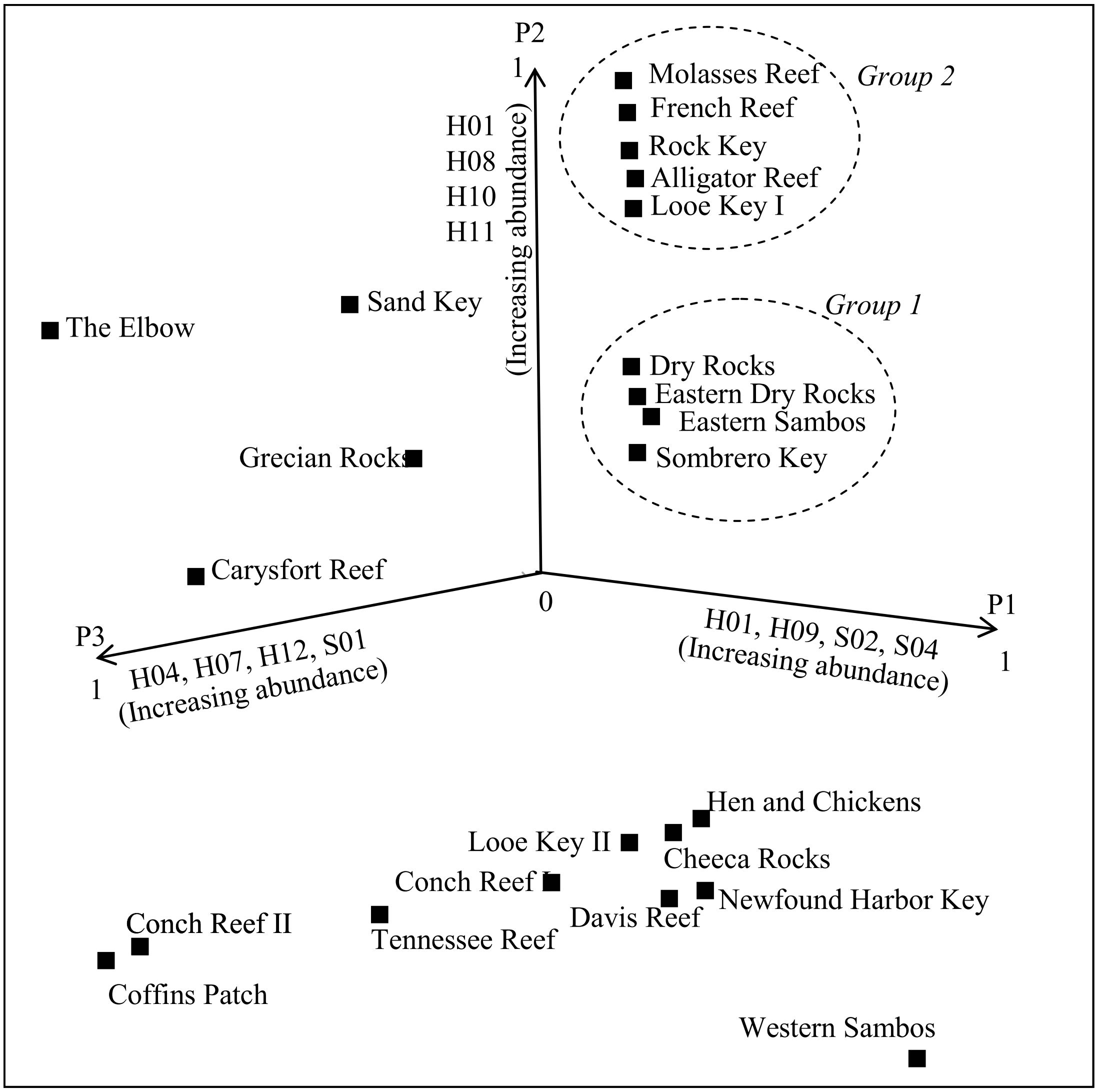

Figure 4.5. Results of principal component analysis (PCA) of protected areas in the Florida Keys National Marine Sanctuary. The habitats contributing the most to the variability in protected areas are given along each PCA axis. PCA was based on the frequency of 16 habitats in the Habitat frequency was defined as the percent area of a 200 x 200 m grid covered by benthic habitats in region (N = 16-50 per protected area). Habitats are defined in Table 4.1.

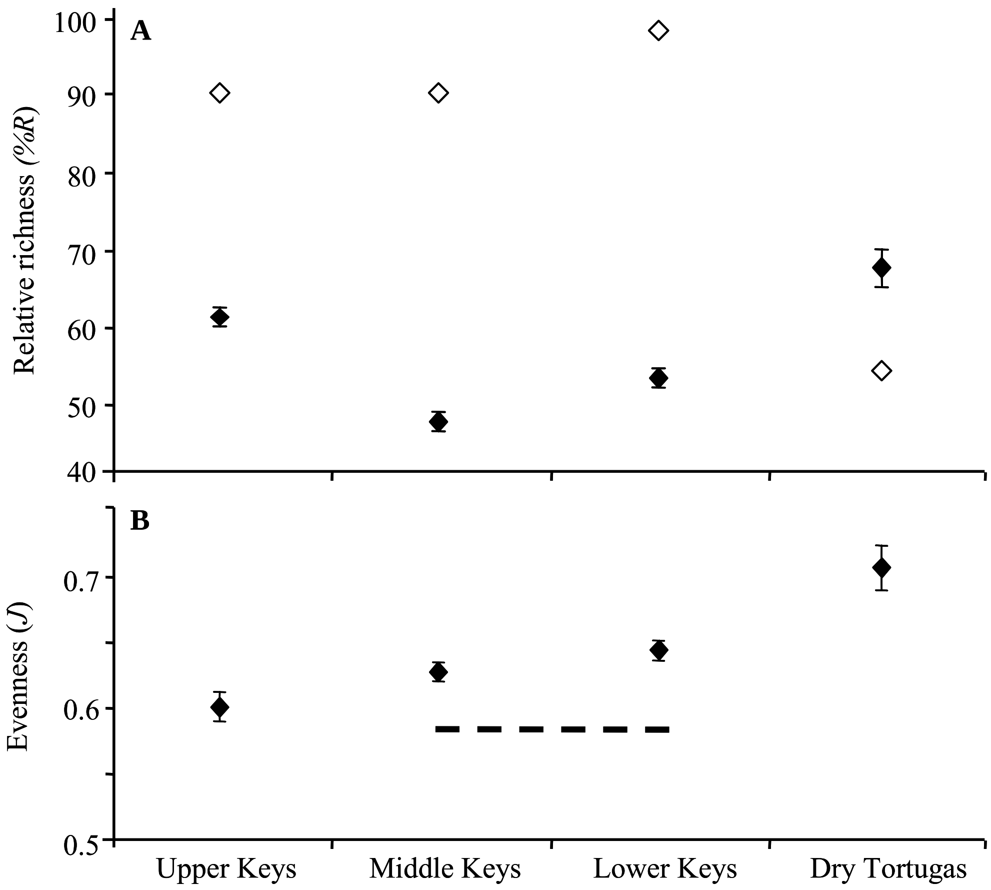

Figure 4.6. Relative richness and evenness of habitats in four regions of the Florida Keys National Marine Sanctuary. **A**: Total (unfilled) and mean (filled) relative habitat richness. **B**: Mean habitat evenness. Means and standard errors (vertical bars) were estimated through bootstrapping (n = 1000). The broken line joins means that are not significantly different from each other ($P > 0.05$).

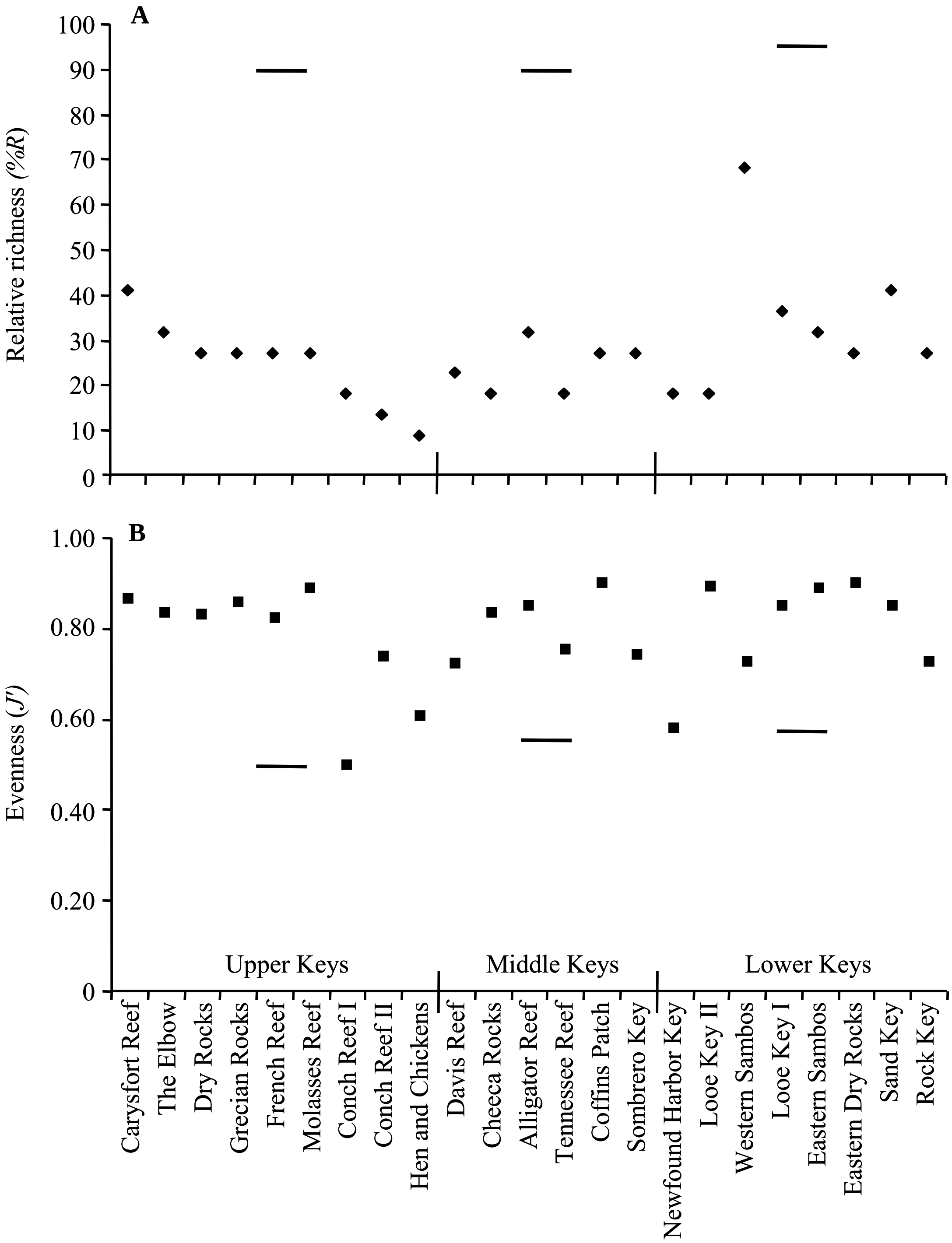

Figure 4.7. Percent relative richness (**A**) and evenness (**B**) of habitats in protected areas of the Florida Keys National Marine Sanctuary (FKNMS). The thin horizontal bars indicate relative richness and evenness of habitats in randomly sampled unprotected areas in each region of the FKNMS.

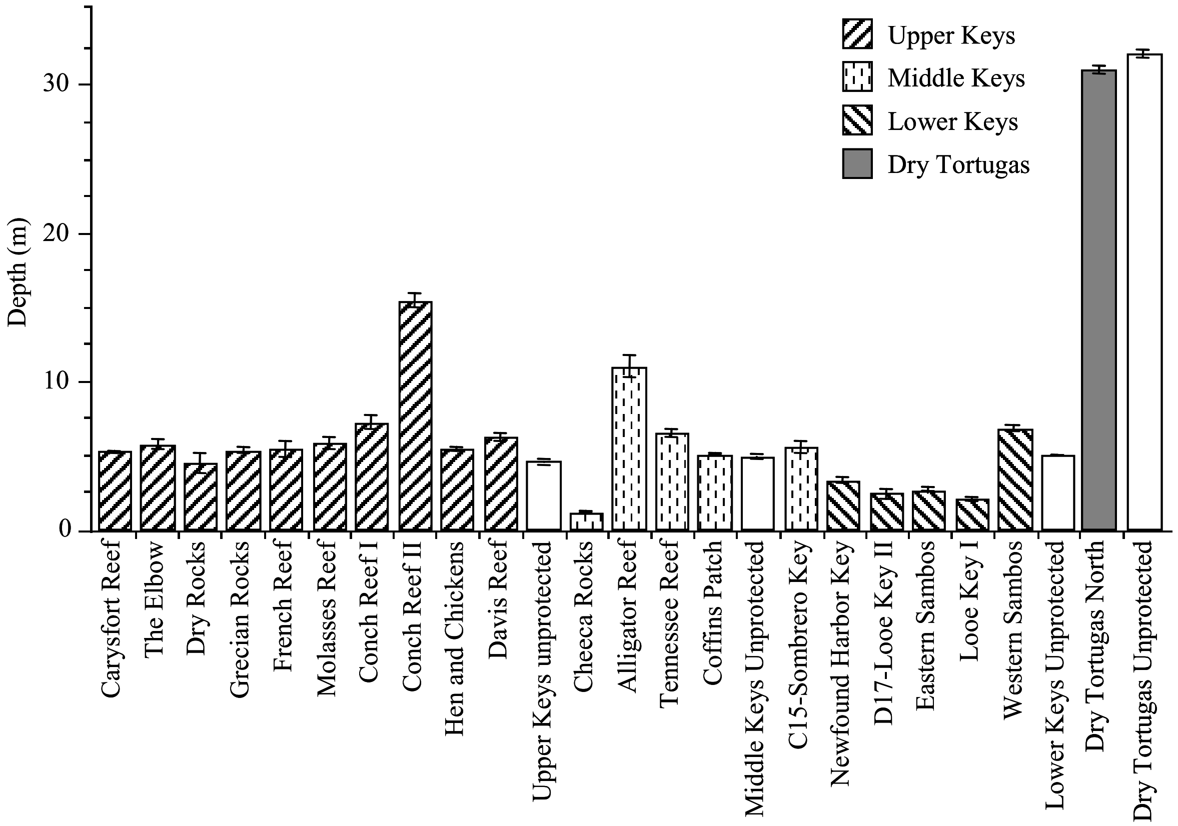

Figure 4.8. Mean depth of protected (shaded bars) and randomly sampled unprotected areas (unshaded bars) of the Florida Keys National Marine Sanctuary. Vertical bars are the standard errors of means.

CHAPTER 5

RELATIONSHIPS BETWEEN BENTHIC HABITATS AND REEF FISHES IN THE FLORIDA KEYS[1]

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[1] Jeffrey, C.F.G. To be submitted to *Coral Reefs.*

Abstract

The relationship between benthic habitats and reef fish assemblages were examined to correlate spatial patterns in fish assemblage structure with variation in benthic habitats for the Florida Keys National Marine Sanctuary (FKNMS). The abundance of 15 benthic habitats, habitat richness, habitat evenness, and fish assemblage variables were determined for 67 sites. Data on habitats were derived from benthic maps of the FKNMS. Fish census data were collected visually by volunteer divers of the Reef Environmental Education Foundation. Three trophic variables showed strong correlations with habitat richness and diversity. Occurrence of generalized carnivores was correlated negatively with habitat richness and evenness, and with abundance of two hardbottom and two seagrass habitats. Piscivore occurrence was correlated positively with habitat richness and evenness, but negatively with abundance of "drowned spur and groove" habitat. Herbivore occurrence correlated positively with habitat richness and abundance of "shallow spur and groove" habitat. Six fish species were correlated positively with habitat richness. Two species were correlated positively, and one species was correlated negatively with habitat evenness. The relative abundance of groupers was correlated positively with abundance of "drowned spur and groove" habitat but was correlated negatively with abundance of "patchy seagrass" and "aggregated patch reefs" habitats. The highest numbers of red grouper occurred at sites with low abundance of "drowned spur and groove" compared with sites that had higher abundance of that habitat. Occurrence of 23 species was correlated positively, whereas occurrence of three species was correlated negatively with abundance of several habitats types. The results of this study support the broad hypothesis that fish assemblages are affected by underlying habitats, and that particular species and guilds occur more frequently in particular habitat types. By quantifying the spatial patterns in abundance and composition of benthic habitats, this study further demonstrates the role of benthic habitats in determining spatial patterns in the structure and composition of coral reef fish assemblages.

Introduction

Spatial variation in the structure and composition of reef fish assemblages are of concern to managers of coral reef ecosystems. Generally, managers are mandated by law to conserve fishery resources, while exploiting them sustainably; fulfilling this mandate requires an understanding of the complex ecological interactions among fish assemblages and several environmental factors. Yet, the factors that affect the distribution and abundance of fishes are not understood fully, and the spatial scales at which these factors operate still are largely undefined (Parrish 1989, Williams 1991, Jones and Syms 1998, Sale 1998).

Several studies have shown that small-scale (meters) variation in the structure of underlying habitats may influence the structure, composition, and distribution of reef fish assemblages (Luckhurst and Luckhurst 1978, Williams 1991, McGhee 1994, Rakitin and Kramer 1996, Chabanet *et al*. 1997, Friedlander and Parrish 1998, Sale 1998, García-Charton and Perez-Ruzafa 1999, García-Charton *et al*. 2000). Other studies have described differences in fish assemblage structure and composition that may have been driven by ontogenetic differences in the use of adjacent habitats, such as mangroves, seagrasses, and coral reefs (Lindeman *et al*. 1999, Christensen *et al*. 2003, Kendall *et al*. 2003). These studies demonstrate that reef fishes are linked strongly to the habitats over which they occur, and these linkages may operate at different scales.

At much larger scales, disturbances such as hurricanes, climate change, and coral diseases adversely affects benthic communities in coral reef ecosystems and can result in drastic changes in the structure, abundance, and heterogeneity of habitats available to reef fishes (Jones and Syms 1998). The effects of broad-scale changes in habitat structure and abundance on reef fish assemblages are yet to be determined, although fish-habitat associations identified from small-scale studies have been extrapolated to imply large-scale patterns (Williams 1991, Sale, 1998, García-Charton *et al*. 2000). Therefore, understanding that fish-habitat associations occur at broad spatial scales, the scale at which coral reefs ecosystems are managed and are affected by disturbances is crucial.

This study determined broad-scale variation in associations between benthic habitats and reef fish assemblages in the Florida Keys National Marine Sanctuary (FKNMS). Data for this study were collected prior to establishment of no-take areas (July 1993 to July 1997) to test for natural variation in habitats and fish assemblages, and to avoid potential confounding effects of protection. My objectives were to identify relationships between habitat and fish assemblage variables, correlate spatial patterns of fish distribution and abundance with variation in benthic variables, and provide a basis for evaluating differences in fish assemblages between protected and non-protected areas. My underlying assumptions were that (1) the ecology of reef fish assemblages was affected by the benthic substrates over which they occur, (2) differences in the composition and structure of reef fish assemblages were associated with composition and structure of habitats, and that (3) differences in the composition and structure of both habitats and reef fish assemblages are measurable at broad spatial scales on the order of thousands of square meters. Large-scale patterns in fish assemblage variables and benthic substrates have been described separately in chapters 2 and 4 respectively.

Methods

Derivation of habitat variables

Metrics of habitat variables at fish census locations were computed with ArcView GIS 3.2a© software (Version 3.2a, Environmental Systems Research Institute, Inc., ESRI 2000) and (Table 5.1). The geographic locations of 67 reef fish censuses were plotted on a 40 x 40 m rasterized habitat map of the FKNMS (FMRI and NOAA 1998). The abundance of 15 habitat types (A_{bh}), habitat richness (S_{bh}), and habitat evenness (J_{bh}) was calculated by placing a 40,000 m^2 (200 x 200 m) sampling grid around the centroid of each reef fish census location. A_{bh} was defined as the area of each habitat type and S_{bh} was the number of habitats that occurred within the sampling grid. If a habitat type did not occur within the sampling grid, its abundance value was zero for that fish census location. J_{bh} was based on the on Shannon's diversity index (H) and computed as follows:

$$J_{bh} = \frac{H}{\ln(s)} = \frac{\sum_{i=1}^{s}(p_i)\ln(p_i)}{\ln(s)}$$

where p_i is the proportion of each habitat, and s is the total number of habitats within the sample grid (Shannon and Weaver 1949, Pielou 1977). Higher values of H indicate greater diversity; division by *ln*(s) normalizes H such that $0 \leq J \leq 1$, where higher values of J indicate greater diversity and evenness (Pielou 1977).

Collection of fish data and derivation of reef fish assemblage variables

Data on the presence and relative abundance of reef fishes were obtained from the Reef Environmental Education Foundation (REEF), a non-profit volunteer-based organization that has been monitoring fishes within the FKNMS since 1993. Trained volunteers used the Roving Diver Technique (RDT), in which the identity and relative abundance of species observed within a circular area with a radius of 100 m (survey area = 31,400 m^2) were recorded while swimming freely about a dive site (Schmitt and Sullivan 1996, REEF 2003, http://www.reef.org/data/research.htm, accessed: 10/5/2003). An RDT survey began as soon as divers entered the water and ended when they exited. At the end of the survey, the diver assigned each recorded species to one of four $\log_{10}$ relative abundance categories [single (1); few (2-10); many (11-100); and abundant (>100)]. The geographic coordinates of each site, the duration of the survey (minutes), and other environmental data pertinent to the survey or site were also noted. RDT surveys occurred between July 19, 1993 and July 1, 1997, the date on which the FKNMS zoning plan was implemented.

Several variables were derived to describe the reef fish assemblage of each site (Table 5.1). Fish species richness (S_f) was estimated for each site with a multiple linear regression model in which the number of species seen during a RDT survey was the response variable and site location, diver, and the duration of the survey (minutes) were main factors (see Chapter 3). The model significantly explained about 75% of the variation in S_f among sites ($F_{model} = 30.72$, $P_{model} < 0.01$, $R_{model} = 0.75$). A modified index of fish evenness (J_f) based on the Shannon-Weaver index of diversity was computed as follows:

$$J_f = \frac{\sum_{i=1}^{s}\left(\frac{a}{A}\right)\ln\left(\frac{a}{A}\right)}{\ln(A)}$$

where a is the frequency of each species' relative abundance value at a site. A is the cumulative frequency of all species' relative abundance values at a site, and s is the number of species at a site. The frequency of each species' relative abundance values was used to determine the proportional occurrence of each species and thereby provided information on the relative abundance of each species in the index. Thus, J will be greater at a site with a higher relative abundance score when two sites with equal number of species but different relative abundance scores are compared.

The mean trophic level (T_{mean}) of each site was determined by averaging the trophic ranking of species occurring at a given site. Data on the trophic ecology of reef fishes in the Gulf of Mexico and the Caribbean were obtained from FishBase 2000 and used to assign species to trophic positions within a food web. FishBase 2000 is an information system with data on the biology of most fishes (Froese and Pauly 2000). Estimates of the trophic levels of fishes in FishBase were derived from mass-balance trophic models of ecosystems (Ecopath) based on the known diet composition of consumer species and the trophic level of their prey (Pauly and Christensen 1995). Cross-validation of trophic estimates from Ecopath models have correlated strongly with estimates based on isotope ratios (Kline and Pauly 1998). The values of trophic levels for species in the Gulf of Mexico and the Caribbean ranged from 2 (herbivores) to 5 (piscivores).

Trophic sighting frequency was the proportion of all survey dives at a site in which a trophic group to which a fish species belonged was recorded. Fish species occurring at each site were assigned to one of three trophic groups. Trophic groups were defined based on Randall's (1967) trophic classification scheme as follows: 1) plant and detritus feeders (H); 2) generalized carnivore, macro-invertebrate, zooplankton, and sessile-invertebrate feeders (GC); and 3) fish and macro-invertebrate only feeders (P). Median relative abundance of commercially important groupers (RA_{emy}, *Epinephelus* spp. and *Mycteroperca* spp. only) and snappers (RA_{lut}, Lutjanidae) was the mean relative abundance score assigned by divers to grouper and snapper species each site. Percent sighting frequency ($\%_{sf}$), the proportion of all survey dives at a site in which a species was recorded, was determined for each species. Silversides, herrings, and anchovies were often indistinguishable during visual censuses and were treated as a single taxonomic species group for analysis, even though they belong to three different families.

Statistical analyses

The Reef dataset used for this study consisted of 247 species, of which 21% (52 species) occurred only at 1 or 2 sites. These 52 species were considered rare and were excluded from this study. A nonparametric correlation coefficient, Spearman's Rho (ρ), and its associated probability value (P) were computed to determine the strength of linear relationships between paired benthic habitat and fish assemblage variables. A nonparametric approach was better suited to these data because assumptions of normality and homoscedasticity necessary for parametric analyses were not met for habitat or fish assemblage variables. Spearman's ρ was computed on the ranks of data values and ranged from 1 to -1, with a value of 1 indicating a strong positive relationship and a value of -1 indicating a strong negative relationship between paired variables (SAS 2002). Values near zero (i.e., $|\rho| < 0.3$) were assumed to indicate the absence of linear relationships between paired variables.

Several tests for statistically significant pair-wise correlations were possible between fish and benthic habitat variables (Table 5.1). For all $|\rho| \geq 0.3$, the level of alpha (α) associated with a test of significance for each pair-wise correlation obtained from multiple correlation analysis was determined with the sequential Bonferroni technique (Holmes 1979, Rice 1989). After selecting an initial $\alpha = 0.05$, corresponding P values from each set of pair-wise correlations were ranked in ascending order from *i* to *k*.

Each ranked P value was sequentially compared to an alpha value such that $\alpha_i = 0.05/(1+k\text{-}i)$, where i denotes the P-value rank and k is the total number of pair-wise correlations being tested for significance. Pair-wise correlations were considered significant only if $p_i \leq \alpha_i$. The smallest value at which $P > \alpha_i$ was the level at which all subsequent pair-wise correlations were not considered significant.

For pair-wise correlations where $|\rho| > 0.3$, *a posteriori* Kruskall-Wallis tests and nonparametric Tukey-type multiple comparisons were used to determine if fish assemblage metrics varied significantly among strata based on habitat richness, evenness, and abundance (Sokal and Rohlf 1995, Zar, 1999). Fish survey sites were assigned to one of three strata based on the percentile rankings of habitat richness and evenness. For each habitat, two habitat abundance strata were determined based on whether the abundance of a habitat was less than or greater than the mean abundance of that habitat for the study area.

Results

Benthic habitat richness, evenness, and fish assemblage variables

Habitat richness (S_{bh}) at fish census locations was low ($S_{bh} < 5$), with 73% of sites containing only one or two types of habitat (Figure 5.1). Platform margin reefs comprised 72% of the area; further subdivision showed that "drowned spur and groove" habitat comprised 39%, "shallow spur and groove" made up 16%, and "low profile reef" accounted for 17% of these platform reef sites (Figure 5.2). Seagrasses accounted for 14% of the area, whereas patch reef, hardbottom, and bare substrate made up the remaining 11% of benthic habitats at fish survey sites (Figure 5.2). Habitat evenness (J_{bh}) ranged from 0 to 1.0 with a mean of 0.55 (± 0.05). On average, J_{bh} of sites increased with increasing S_{bh} (ρ = 0.62, P = 0.000).

Three of four variables that measured the trophic structure of fish assemblages showed significant linear relationships with S_{bh} (Table 5.2). Generalized carnivores (GC_{sf}) were strongly negatively correlated with S_{bh} ($\rho = -0.54$, $P < \alpha_i$), whereas piscivores (P_{sf}) and herbivores (H_{sf}) correlated positively but weakly with S_{bh} ($|\rho| < 0.50$, $P < \alpha_i$, Table 5.2). Mean trophic level (T_{mean}) was not correlated significantly with S_{bh} ($\rho = 0.21$, $P = 0.08$).

Two trophic variables, P_{sf} and GC_{sf}, showed weak linear relationships with habitat evenness; P_{sf} increased, whereas GC_{sf} decreased as J_{bh} increased ($p < \alpha_i$, Table 5.2). Herbivores and other fish assemblage variables such as fish species richness (S_f), evenness (J_f), mean trophic level, and mean relative abundance of groupers and snappers (RA_{emy} and RA_{lut}) showed no significant linear relationships with S_{bh} or J_{bh} ($|\rho| < 0.30$, $P > \alpha_i$).

Significant differences in trophic structure existed among site strata based on S_{bh} and J_{bh}. Mean GC_{sf} was significantly higher at sites with only one type of habitat than at sites with two or more types of habitat ($P = 0.002$, Figure 5.3A). Conversely, mean P_{sf} was lower at sites with only one habitat compared with sites having multiple habitat types (Figure 5.3A). Median GC_{sf} decreased, whereas median P_{sf} increased with an increase in J_{bh} (Figure 5.4).

The sighting frequency ($\%_{sf}$) of six species correlated positively and significantly with S_{bh} ($\rho \geq 0.3$, $P < \alpha_i$, Table 5.3). The $\%_{sf}$ of French angelfish[1] and the green razorfish showed the strongest positive relationships with S_{bh} ($\rho = 0.44$ and 0.43, $P < \alpha_i$ respectively, Table 5.3). Yellowtail parrotfish, tomtate, bar jack, and lancer dragonet also increased in frequency of occurrence with an increase in S_{bh} ($P < \alpha_i$, Table 5.3). Five other species correlated positively and three correlated negatively with S_{bh}, but those correlations were not significant ($P > \alpha_i$, Table 5.3).

Positive and negative significant correlations were observed between fish species $\%_{sf}$ and J_{bh} ($0.3 < |\rho| < 0.5$, $P < \alpha_i$, Table 5.3). The $\%_{sf}$ of common snook and French angelfish increased as J_{bh} increased, whereas $\%_{sf}$ of spotfin butterflyfish decreased as J_{bh} increased ($P < \alpha_i$, Table 5.3). The $\%_{sf}$ of yellowhead jawfish appeared negatively correlated with J_{bh}, but the correlation was not significant ($P > \alpha_i$, Table 5.3).

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[1] Common names of fishes are used here but scientific fish species names are given in Appendix 2.2.

Kruskal-Wallis tests and nonparametric multiple pair-wise comparisons revealed significant differences in $\%_{sf}$ among three levels of S_{bh} for only three fish species, although significant correlations between $\%_{\mathrm{sf}}$ and S_{bh} occurred for six species (Figure 5.5). French angelfish were observed significantly less frequently at sites with one habitat type than at sites with multiple habitats ($P < \alpha_i$, Figure 5.5A). Green razorfish and tomtate occurred more frequently at sites with four to five habitat types compared with sites that contained fewer habitats (Figure 5.5B and C). Lancer dragonet, bar jack, and yellowtail parrotfish did not vary significantly among site strata based on S_{bh} ($P > \alpha_i$, Figure 5.5D).

Significant differences in $\%_{sf}$ occurred among three levels of J_{bh} for only three species. French angelfish occurred less commonly at sites with low habitat evenness compared with sites of higher habitat evenness (Figure 5.6A). Conversely, sites with lower habitat evenness had higher occurrences of green razorfish than sites with higher habitat evenness (Figure 5.6B). Spotfin butterfyfish and common snook did not show significant variation between J_{bh} strata (Figure 5.6C and D).

Benthic habitat abundance and fish assemblage variables

Although fish survey sites contained 15 mapped benthic habitats, only 11 habitat types were present at three or more fish census sites and were included in the analysis of pair-wise correlations between habitat abundance and fish assemblage variables. Habitat abundance ranged from 0 m^2 where habitats were absent to 40,000 m^2 for monotypic grids. Four fish assemblage variables were significantly correlated with the abundance of benthic habitats (Table 5.4). Herbivores (H_{sf}) correlated positively with an increase in the abundance of “shallow spur and groove” habitat ($\rho = 0.34$, $P = 0.004$, Table 5.4). Generalized carnivores (GC_{sf}) were negatively correlated with the abundance of four habitats but positively correlated with one habitat – “drowned spur and groove” ($P < \alpha_i$, Table 5.4). Piscivores (P_{sf}) decreased weakly with increasing abundance of “drowned spur and groove” ($\rho = -30$, $P = 0.013$), but increased as the abundance of “aggregated patch reef” habitat increased ($\rho = 30$, $P = 0.017$), Table 5.4).

Grouper abundance (RA_{emy}) increased significantly with an increase in the abundance of "drowned spur and groove" ($\rho = 0.30$, $P < \alpha_i$) and decreased significantly with an increase in the abundance of "aggregated patch reef" and "patchy seagrass" ($\rho = -0.30$, $P < \alpha_I$, Table 5.4). Other fish assemblage variables did not correlate significantly with the abundance of benthic habitats $\rho < 0.30$, $P > \alpha_i$, Table 5.4).

Kruskall-Wallis tests and multiple pair-wise comparisons revealed significant differences in trophic structure among habitat abundance strata. Generalized carnivores were more prevalent at sites with lower abundance of "shallow spur and groove" compared with sites that had more "shallow spur and groove" habitat (Figure 5.7A). Likewise, the numbers of generalized carnivores also varied among abundance strata of "aggregated patch reefs" ($\chi^2 = 5.91$, $P = 0.015$), "patchy seagrass S02" ($\chi^2 = 10.26$, $P = 0.001$), and "patchy seagrass S03" ($\chi^2 = 10.26$, $P = 0.001$). Generalized carnivores occurred more frequently at sites with lower abundance of these three habitats than at sites where these three habitats were more abundant (Figure 5.7A). Patterns in the distribution of generalized carnivores between abundance strata were reversed for "drowned spur and groove" habitat (Figure 5.7B). Herbivores were more prevalent at sites with low abundance of "shallow spur and groove" habitat (Figure 5.7C). Piscivores were observed more frequently at sites with lower abundance of "drowned spur and groove" compared with sites that had higher abundance of that habitat (Figure 5.7D).

Groupers (RA_{emy}) varied significantly with the abundance of four habitats (Figure 5.8). Groupers were significantly more abundant at sites that contained less "patchy seagrass" or "aggregated patch reef" compared with sites that had more of these habitats (Figure 5.8 A, B). Coincidentally, sites with low abundance of "patchy seagrass" habitat also had significantly high abundance of other hardbottom habitats ($\chi^2 = 11.4$, $P = 0.001$). Likewise, abundance of "aggregated patch reef" habitat was inversely correlated with abundance of other hardbottom habitats ($\chi^2 = 9.83$, $P = 0.002$). Significant differences in mean RA_{emy} between abundance strata of shallow and drowned "spur and groove" habitats were undetectable, probably because differences in abundance among sites within strata were greater than differences in abundance between strata (Figure 5.8C, D).

Linear relationships were observed between the $\%_{sf}$ of 64 species and abundance of nine habitat types ($\rho \geq 0.30$, Table 5.5). Nineteen species showed positive relationships with abundance of "shallow spur and groove", of which only nine were significant ($\rho \geq 0.3$, $P \leq \alpha_i$, Table 5.5). Two species, mahogany snapper and longfin damselfish, correlated strongly and positively and occurred more frequently at sites with higher abundance of "shallow spur and groove habitat" ($\rho = 0.50\text{-}0.53$, $P \leq \alpha_i$, Table 5.5). Six species showed weaker and positive relationships with "shallow spur and groove" habitat ($\rho < 0.50$, $P < \alpha_I$, Table 5.5). Blue angelfish were negatively correlated with abundance of "shallow spur and groove" ($\rho = -0.42$, $P = 0.000$, Table 5.5).

Ten species showed positive relationships with "drowned spur and groove" ($\rho \geq 0.30$), but only four of those relationships were significant ($P < \alpha_i$, Table 5.5). Blue chromis, foureye butterflyfish, creole wrasse, and blue hamlet were more frequently observed at sites with higher abundance of "drowned spur and groove" habitat ($\rho > 0.30$, $P < \alpha_i$,Table 5.5). Six species correlated negatively with abundance of "drowned spur and groove", but only tomtate decreased significantly as the abundance of that habitat increased ($\rho = -0.43$, $P < \alpha_i$, Table 5.5). One species – beaugregory – correlated positively with abundance of "remnant low profile reef" habitat, but that relationship was not significant ($P > \alpha_i$, Table 5.5).

Few species showed relationships with "reef rubble," "hardbottom with seagrass", or "patch reef" habitats. Cubbyu correlated positively and significantly with the abundance of "reef rubble" habitat ($\rho = 0.53$, $P = 0.001$), but four other species did not (Table 5.5). Another sciaenid, jacknife-fish was one of two species that increased significantly as abundance of "hardbottom with perceptible seagrass" increased ($P < \alpha_i$, Table 5.5). Townsend angelfish correlated strongly and positively with abundance of "individual patch reef" habitat ($\rho = 0.60$, $P = 0.000$). Hybrid hamlet correlated weakly with "individual patch reef" habitat ($\rho = 0.40$, P = 0.001, Table 5.5). Small pelagic species (silversides, herrings, and anchovies) were strongly and positive correlated with "aggregated patch reef" habitat ($\rho = 0.55$, P = 0.000, Table 5.5).

Sighting frequency of nine species was significantly correlated with the abundance of three seagrass habitat types. Yellowprow goby, red grouper, and Townsend angelfish all were positively correlated with abundance of "continuous seagrass" ($\rho = 0.40$-0.43, $P < \alpha_i$, Table 5.5). Tomtate were seen more frequently as abundance of "patchy seagrass" habitats increased ($\rho = 0.45$, P = 0.000, Table 5.5). Small pelagic fishes (silversides, herrings, and anchovies), orange filefish, Seminole goby, and rosy razorfish all increased in $\%_{sf}$ as abundance of "patchy seagrass" increased ($\rho = 0.39$-0.45, P = 0.001, Table 5.5). Redlip blenny were positively correlated whereas queen angelfish were negatively correlated with bare sand, but those relationships were not significant ($P > \alpha_i$, Table 5.5).

Significant differences in fish species ($\%_{sf}$) among habitat abundance strata were observed in five species that showed strong positive relationships ($\rho \geq 0.50$) with habitat abundance. Longfin damselfish and mahogany snapper were seen less frequently at sites with less spur and groove habitat compared with sites that contained more spur and groove habitat (Figure 5.9). Cubbyu were seen less frequently at sites where abundance of "reef rubble" was low compared to sites where that habitat dominated ($\chi^2 = 9.09$, P = 0.003). Sites with low abundance of "individual patch reefs" had fewer Townsend angelfish than sites with high abundance of that habitat ($\chi^2 = 12.32$, P = 0.000). Small pelagic fishes (silversides, herrings, and anchovies) occurred more often where abundance of "aggregated patch reefs" and "patchy seagrass S03" was high relative to where these two habitats were low in abundance ($\chi^2 = 20.8$, P =0.000). Interestingly, the $\%_{sf}$ of red grouper varied among abundance strata of three habitats, although observed linear correlations between red grouper and these habitats were weak (Figure 5.10). Red grouper $\%_{sf}$ was highest at sites with low abundance of "drowned spur and groove" compared with sites that had higher abundance of that habitat. In two seagrass habitats, the $\%_{sf}$ of red grouper was significantly lower at sites with low abundance of seagrass when compared with sites having a greater abundance of seagrass (Figure 5.10). Significant associations between benthic habitat measures and fish species and groups are summarized in Table 5.6.

Discussion

The objectives of this study were to identify relationships between reef fish assemblages and the benthic habitats over which they occur, and to identify habitat variables that explained observed differences in fish assemblages among sites. The results presented here support the broad hypothesis that the structure and composition of fish assemblages are affected by the composition of the underlying benthic substrate:

- Significant relationships were found between several reef fishes and the habitat variables used in this study (Table 5.6). For example, sighting frequency of generalized carnivores was negatively correlated with habitat richness, and three species (blue angelfish, tomtate, and bridled goby) were correlated negatively with abundance of “shallow spur and groove”, “drowned spur and groove”, and “patchy seagrass S02” habitats. Conversely, sighting frequency of herbivores, piscivores, and 22 species were positively correlated with habitat richness and abundance, as well as abundance of nine habitat types (Table 5.6).
- The results also support the notion that differences in benthic habitat patterns and fish assemblage structure are measurable over thousands of square meters. For example, differences in habitat richness and evenness among fish census sites that measured 31,400 m^2 each correlated positively with the sighting frequency of herbivores, piscivores, and several fish species.
- A benthic habitat map provided a means of identifying similarities and differences in benthic structure among areas of the FKNMS. The seascape metrics used in this study varied among fish census locations and quantified differences in the spatial arrangement and patterns of categorized habitats over an area of 4,000 km^2. These differences were positively correlated with occurrences

of herbivores, piscivores, and eight species, and negatively correlated with occurrences of generalized carnivores and spotfin butterflyfish.

Hence, by categorizing fish census locations based on habitat abundance, richness, and evenness, determining significant correlations between fish assemblage variables and derived habitat metrics was possible; determining differences in fish assemblage structure among sites was also possible.

Habitat richness, evenness, and fish assemblage patterns

Strong negative and weaker positive associations occurred between habitat richness and trophic composition of fish assemblages, which resulted in significant patterns in trophic structure when sites were grouped based on habitat richness and evenness (Figure 5.4). Generalized carnivores dominated sites of low habitat richness and evenness, whereas piscivores dominated sites of higher habitat richness and evenness. These patterns in trophic structure may have resulted more from differences in habitat composition and structure between “habitat rich” and “habitat poor” sites rather than from differences in absolute habitat richness and evenness. For example, drowned spur and groove habitats comprised 70% of the sites that contained only one habitat, whereas most sites with higher habitat richness and evenness generally contained “shallow spur and groove” habitat. “Drowned spur and groove” habitats occur on the reef slope, in deeper water, typically are buried in sand, and are less structurally complex than “shallow spur and groove” habitats (FMRI and NOAA 1998). “Shallow spur and groove” habitats may have provided greater protection from large piscivores to small piscivores from large predators (e.g., small seabasses, wrasses, blennies, and gobies) and herbivores (e.g., damselfishes and small parrotfishes) compared with “drowned spur and groove” habitats. Additionally, “drowned spur and groove” habitats may have contained more soft bottom microhabitats (e.g., sand) and may have provided a wider variety of food resources to support generalized carnivorous species (e.g., grunts, porgies, and squirrelfishes).

Although benthic habitat richness and evenness were significantly and positively correlated, fish species that were positively correlated with habitat richness were uncorrelated with habitat evenness. Sighting frequencies of green razorfish, yellowtail parrotfish, tomtate, barjack, and lancer dragonet increased as habitat richness increased, yet these species showed no significant positive relationships with habitat evenness. Likewise, common snook increased, whereas spotfin butterflyfish decreased in sighting frequency as habitat evenness increased, but these two species showed no significant relationships with habitat richness. These fish relationships with habitat richness and diversity may reflect species-specific interactions with locally occurring habitats that could have resulted in differences in the occurrence of species among habitat "rich" and habitat "poor" sites. Characterizing sites based on either habitat richness or evenness alone would have revealed fewer habitat-fish interactions, suggesting that comparisons based on several metrics may be more productive than those based on a single variable for identifying interactions between fishes and the underlying benthic substrates.

Fish assemblage patterns relative to abundance of habitats

The outcomes of competitive and predator-prey interactions between species may be influenced by habitat structure (Jones 1991, Hixon and Beets 1993). Previous studies have shown that highly complex habitats tend to contain more diverse and speciose fish assemblages (Luckhurst and Luckhurst 1978, Carpenter *et al*. 1981, Friedlander and Parrish 1998). Recruitment, settlement, competition, and predation are major demographic and ecological processes that determine the structure and composition of pre- and post-settlement fish assemblages (Hixon and Menge 1991, Jones 1991, Caly *et al*. 1996). Where fishes recruit and settle can be determined by the underlying habitats (Sale *et al*. 1984, Green 1996).

Habitats such as "shallow spur and groove" contain complex structures with high vertical relief, may offer more resources and protection from predation, and may support more species than simpler habitats such as "drowned spur and groove" with less topographic complexity. In this study, trophic composition showed opposing patterns with abundance of these two habitats. Generalized carnivores were more prevalent in “drowned spur and groove” habitats where piscivores were less prevalent; herbivores occurred less often at sites with “shallow spur and groove habitats, where generalized carnivores were seen more frequently. These differences suggest that interactions between trophic groups were affected by fish-habitat interactions. The mediation of the effects of competition and predation by the underlying habitats may have resulted in the nonrandom distribution of species and trophic groups among sites in the Florida Keys. However, the effects of habitats on competitive and predatory interactions among species were indistinguishable from effects related to differences in recruitment and settlement of fishes among habitat types.

The non-random distribution of epinepheline and mycteropercine groupers and other species may have resulted indirectly from differences in habitat complexity or the abundance of available hardbottom between habitat abundance strata. The groupers occurred non-randomly among habitat abundance strata and favored sites that contained low abundance of “aggregated patch reef” or “patchy seagrass S03” habitats more than sites with high abundance of these habitats (Figures 5.10A, B). However, abundance of aggregated patch reef was inversely correlated with abundance of other hardbottom habitats and may have indirectly influenced the distribution of these groupers. Longfin damselfish and the mahogany snapper were relatively dominant at sites with high abundance of “shallow spur and groove” habitat compared to sites with low abundance of that habitat, which could indicate the dependence of these species on that habitat type. Likewise, the prevalence of cubbyu and Townsend angelfish where abundance of “reef rubble” and “individual patch reef” habitats dominated the seascape respectively, may indicate some dependence on these two benthic substrates.

Although silversides, herrings, and anchovies are not known to associate closely with benthic substrates, their prevalence at sites where “aggregated patch reefs” and “patchy seagrass S03” habitats dominated may be related to their foraging patterns. These fishes feed primarily on zooplankton (Randall 1967). Demersal zooplankton live within the reef by day but nocturnally migrate into the water column proportionally to the three-dimensional structure of the substrate (Porter and Porter 1977). Many planktivorous fishes – including silversides, herrings, and anchovies – form resting aggregations near reef edges and drop-offs adjacent to deeper water (Hobson 1991, Helfman 1993). Reef edges, drop-offs, and halos with patchy seagrass are features common to "aggregated patch reef" habitats (FMRI 1998, C. Jeffrey, personal observation). Proximity to nocturnal foraging regions could be determining the daytime distribution of small pelagic fishes observed during this study.

The overall approach presented here elucidated a number of significant relationships, but several pair-wise correlations between fish assemblage and benthic habitat variables showed little or no relationship. In particular, overall fish richness and evenness were poorly correlated with habitat richness or evenness. Why relationships did not exist between these general variables is not immediately obvious. One possible explanation is that opposing patterns in the occurrence of some fish species may have masked differences in these fish assemblage variables among sites. For example, some fish species, such as common snook, showed positive correlations with habitat evenness, whereas other fish species, such as spotfin butterfly fish were negatively correlated with habitat evenness. Thus, a gain in fish evenness caused by positive habitat correlations of some species would have been canceled by negative habitat correlations among other species, making differences in fish richness and evenness among habitat "rich" or habitat "poor" sites undetectable.

The effects of microhabitat variation and complexity within sites were not considered in this study. The minimum mapping unit, an indication of the minimum area of habitat delineated, was 50,000 m^2. The area of each sampling unit was 40,000 m^2 for benthic habitats and 31,400 m^2 for conducting fish census. These samples may have contained smaller, distinct microhabitats with which various coral reef fishes may have associated. Benthic substrates can vary considerably in depth, topographic structure and complexity, and in their abiotic and biotic composition over areas < 100 m^2; and may therefore contain distinct microhabitats (Friedlander and Parrish 1998, C. Jeffrey, personal observation). Several studies conducted at spatial scales < 100 m^2 have shown that species richness, diversity, and abundance of fishes are positively correlated with reef spatial complexity, microhabitat type or quality, and the amount of live coral (reviewed by Jones and Syms 1998, Friedlander & Parrish 1998; Wolff *et al.* 1999). Microhabitat variation within fish census sites may have caused high "within-site" variability in fish abundance that may have masked the detection of differences in fish assemblage variables among habitat types and strata. That significant relationships were found here between fish assemblage and habitat variables measured at relatively large spatial scales suggests fish respond to widely-distributed habitats as well as microhabitat characteristics. Resolution of the question of which spatial scale is more important will require direct observation of individuals and better data on movements and home ranges of species. This question is of specific relevance to issues concerning the size and location of protected habitats and areas (e.g., Kramer and Chapman 1999, Chitarro 2004).

The importance of accurate habitat assessments

The results presented here underscore the fundamental relationships between the occurrence and abundance of fishes and habitat structure and composition, information which could be critical for managing coral reef ecosystems. Caribbean-wide declines in the abundance of coral reef fishes and in the fisheries they support have been blamed in part on habitat degradation resulting from hurricanes, diseases, and other disturbances that change the underlying habitat structure (Rogers and Beets, 2001). In response, agencies responsible for managing coral reef ecosystems are now placing greater focus on understanding the role of benthic habitats in determining fish assemblage structure, composition, and abundance. For example, the U.S. Coral Reef Task Force – created by Presidential Executive Order 13089 – considered mapping of all U.S. coral reefs and associated habitats essential and prioritized mapping in its national action strategy for long term conservation of coral reef ecosystems (Monaco *et al*. 2001, NOAA 2002).

Three recent studies have used benthic maps to link observed patterns in the distribution and abundance of fishes to spatial patterns in the occurrence of habitats. Christensen *et al*. (2003) showed that coral reef fishes occurred non-randomly among reef, seagrass, and mangrove habitats occurring over a 200-km^2 area in southwestern Puerto Rico. Kendall *et al*. (2003) observed that the probability of encountering juvenile grunts was inversely proportional to the distance of reef sites from foraging habitats in Buck Island, St. Croix, and that juveniles were more common at reef sites within 300 meters of soft bottom foraging sites compared with sites further away. In Belize, the linear extent of mangrove habitats was the dominant factor structuring reef fish communities, and fish biomass was up to 25 times greater on reefs with adjacent mangroves than on reefs without adjacent mangroves (Mumby *et al*. 2003). These studies demonstrate that reef fishes rely on several habitats at different ontogenetic stages, and that degradation of any habitat can have serious adverse population effects. By quantifying the spatial patterns in abundance and composition of benthic habitats, the present study further demonstrates the role of benthic habitats in determining spatial patterns in coral reef fish assemblages.

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TABLES

Table 5.1. Variables used to determine linear relationships between benthic habitats and reef fish assemblage structure and composition in the Florida Keys. Benthic habitat variables were computed with ArcView GIS© software (Version 3.2a, Environmental Systems Research Institute, Inc., ESRI 2000) and Fragstats software (Ver. 3.3, McGarigal *et al*. 2002).

Habitat variable	Symbol	Fish assemblage variable	Symbol
Richness	S_{bh}	Species richness	S_f
		Species evenness	J_f
		Mean trophic level	T_{mean}
		Trophic sighting frequency	
		Herbivores	H_{sf}
		Piscivores	P_{sf}
		Generalized carnivores	GC_{sf}
		Grouper relative abundance	RA_{emg}
		Snapper relative abundance	RA_{lut}
		Species percent sighting frequency	$\%sf$
Evenness	J_{bh}	Species richness	S_f
		Species evenness	J_f
		Mean trophic level	T_{mean}
		Trophic sighting frequency	
		Herbivores	H_{sf}
		Piscivores	P_{sf}
		Generalized carnivores	GC_{sf}
		Grouper relative abundance	RA_{emg}
		Snapper relative abundance	RA_{lut}
		Species percent sighting frequency	$\%sf$
Abundance	A_{bh}	Species richness	S_f
		Species evenness	J_f
		Mean trophic level	T_{mean}
		Trophic sighting frequency	
		Herbivores	H_{sf}
		Piscivores	P_{sf}
		Generalized carnivores	GC_{sf}
		Grouper relative abundance	RA_{emg}
		Snapper relative abundance	RA_{lut}
		Species percent sighting frequency	$\%sf$

Table 5.2. Spearman coefficients r*ho* (ρ), associated probability values (p), and corrected alpha (α_i) levels from pair-wise correlations between fish assemblage and benthic habitat variables for 67 sites in the Florida Keys National Marine Sanctuary. Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ table-wise, Rice 1989). Fish assemblage variables are defined in Table 5.1 and were derived from 463 surveys conducted by divers of the Reef Environmental and Educational Foundation (REEF) between August 1993 and July 1997.

Habitat variable	Fish assemblage variable	rho (ρ)	p	α_i
Richness (S_{bh})	Generalized carnivores (GC_{sf})	-0.54	0.000	0.010
	Piscivores (P_{sf})	0.36	0.003	0.013
	Herbivores (H_{sf})	0.31	0.011	0.017
Evenness (J_{bh})	Piscivores (P_{sf})	0.34	0.006	0.025
	Generalized carnivores (GC_{sf})	-0.30	0.018	0.050

Table 5.3. Spearman coefficients *rho* (ρ) computed for pair-wise correlations between sighting frequency of fish species ($\%_{sf}$) and benthic habitat variables for 67 sites in the Florida Keys National Marine Sanctuary. Bold type indicates significant correlations ($\rho \geq 0.30$, $p \leq \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ table-wise, Rice 1989).

Habitat variable	Fish species	Common name	rho (ρ)	p	α_i
Richness	***Pomacanthus paru***	**French angelfish**	**0.44**	**0.000**	**0.003**
	Hemipteronotus splendens	**green razorfish**	**0.43**	**0.000**	**0.003**
	Sparisoma rubripinne	**yellowtail parrotfish**	**0.39**	**0.001**	**0.003**
	Haemulon aurolineatum	**tomtate**	**0.38**	**0.002**	**0.004**
	Caranx ruber	**bar jack**	**0.35**	**0.004**	**0.004**
	Paradiplogrammus bairdi	**lancer dragonet**	**0.33**	**0.006**	**0.006**
	Chromis scotti	purple reeffish	-0.33	0.007	0.006
	Microspathodon chrysurus	yellowtail damselfish	0.32	0.008	0.006
	Kyphosus sectatrix	Bermuda chub	0.32	0.008	0.006
	Microgobius carri	Seminole goby	0.32	0.009	0.006
	Equetus umbrosus	cubbyu	0.31	0.009	0.006
	Coryphopterus glaucofraenum	bridled goby	-0.31	0.010	0.006
	Hypoplectrus unicolor	butter hamlet	-0.31	0.010	0.006
	Lutjanus mahogoni	mahogany snapper	0.30	0.012	0.006
Eveness	***Centropomus undecimalis***	**common snook**	**0.41**	**0.001**	**0.003**
	Pomacanthus paru	**French angelfish**	**0.34**	**0.005**	**0.005**
	Chaetodon ocellatus	**spotfin butterflyfish**	**-0.38**	**0.002**	**0.004**
	Opistognathus aurifrons	yellowhead jawfish	-0.32	0.008	0.006

Table 5.4. Results from pair-wise correlation analysis between fish assemblage variables and the abundance of benthic habitats for 67 sites in the Florida Keys National Marine Sanctuary. Only correlations with $\rho \geq 0.30$ were considered for hypothesis testing. Coefficients *rho* (ρ) were significant ($p < \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ table-wise, Rice 1989). Variables are defined in Table 5.1 and were derived from 463 surveys conducted by divers of the Reef Environmental and Educational Foundation (REEF) between August 1993 and July 1997.

Benthic habitat abundance (m^2)	H_{sf}	GC_{sf}	P_{sf}	RA_{emg}
Platform margin reefs				
shallow spur and groove	0.34	-0.34		
drowned spur and groove		0.35	-0.30	0.30
Patch reefs - aggregated		-0.30		-0.30
Patchy seagrass				
moderate to dense with blowouts (S02)		-0.32		
predominantly sand or mud with small, scattered seagrass patches (<50%) (S03)		-0.40		-0.30

▒ Positive relationship
■ Negative relationship

Table 5.5. Spearman coefficients *rho* (ρ) computed for pair-wise correlations between sighting frequency of fish species ($\%_{sf}$) and the abundance of benthic habitats for 67 sites in the Florida Keys National Marine Sanctuary. Bold type indicates significant correlations ($\rho \geq 0.30$, $P \leq \alpha_i$); Asterisks indicate strong pair-wise relationships ($\rho \geq 0.50$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ table-wise, Rice 1989).

Habitat type	Common name	rho (ρ)	P
Platform margin reefs			
- shallow spur and groove	**longfin damselfish ***	**0.53**	**0.000**
	mahogany snapper *	**0.50**	**0.000**
	longspine squirrelfish	**0.43**	**0.000**
	white margate	**0.41**	**0.001**
	glassy sweeper	**0.39**	**0.001**
	black margate	**0.39**	**0.001**
	French angelfish	**0.39**	**0.001**
	peppermint basslet	**0.39**	**0.001**
	reef croaker	0.38	0.002
	Bermuda chub	0.37	0.002
	yellowtail parrotfish	0.37	0.002
	spotted drum	0.36	0.003
	red hind	0.36	0.003
	glasseye snapper	0.34	0.005
	jackknife-fish	0.33	0.006
	sand perch	0.33	0.006
	ocean triggerfish	0.33	0.007
	orangespotted filefish	0.32	0.009
	clown wrasse	0.30	0.013
	blue angelfish	**-0.42**	**0.000**
- drowned spur and groove	**blue chromis**	**0.45**	**0.000**
	foureye butterflyfish	**0.44**	**0.000**
	creole wrasse	**0.40**	**0.001**
	blue hamlet	**0.38**	**0.001**
	graysby	0.37	0.002
	rock beauty	0.33	0.007
	banded butterflyfish	0.33	0.007
	brown chromis	0.32	0.008
	dusky squirrelfish	0.32	0.008
	redtail parrotfish	0.31	0.011
	neon goby	-0.32	0.009
	blackear wrasse	-0.32	0.008
	slippery dick	-0.33	0.007
	red grouper	-0.33	0.006
	cocoa damselfish	-0.34	0.006
	tomtate	**-0.43**	**0.000**
- remnant low profile	beaugregory	0.35	0.003
- reef rubble	**cubbyu ***	**0.53**	**0.000**
	redlip blenny	0.36	0.002
	spotted trunkfish	0.32	0.009
	longfin damselfish	0.31	0.012
	butter hamlet	-0.32	0.009

Table 5.5 continued.

Habitat type		rho (ρ)	P
Hardbottom with seagrass < 50%	**jackknife-fish**	**0.40**	**0.001**
	blue tang	-0.30	0.012
Patch reefs			
- individual	**Townsend angelfish ***	**0.60**	**0.000**
	hybrid hamlet	**0.41**	**0.000**
	bluelip parrotfish	0.35	0.004
	yellowprow goby	0.31	0.011
	spotfin hogfish	0.30	0.012
	banded jawfish	0.30	0.012
- aggregated	**Silversides, herrings, and anchovies ***	**0.55**	**0.000**
	queen angelfish	0.36	0.002
	midnight parrotfish	0.33	0.006
	banded jawfish	0.32	0.008
	mutton snapper	0.31	0.010
	red hind	0.30	0.012
	rosy razorfish	0.30	0.013
	banded butterflyfish	-0.31	0.010
	redtail parrotfish	-0.33	0.007
Continuous seagrass	**yellowprow goby**	**0.43**	**0.000**
- moderate to dense (S01)	**red grouper**	**0.42**	**0.000**
	townsend angelfish	**0.40**	**0.001**
	knobbed porgy	0.31	0.011
	blue chromis	-0.30	0.013
	blue parrotfish	-0.31	0.012
	midnight parrotfish	-0.31	0.012
	bar jack	-0.31	0.011
	foureye butterflyfish	-0.32	0.007
	Bermuda chub	-0.33	0.006
	brown chromis	-0.35	0.003
Patchy seagrass			
- moderate to dense with blowouts (S02)	**tomtate**	**0.45**	**0.000**
	redband parrotfish	0.32	0.009
	bluestriped grunt	0.30	0.012
	slippery dick	0.30	0.014
	bridled goby	**-0.41**	**0.001**
- predominantly sand or mud with small, scattered seagrass patches (<50%) (S03)	**Silversides, herrings, and anchovies ***	**0.45**	**0.000**
	orange filefish	**0.40**	**0.001**
	Seminole goby	**0.39**	**0.001**
	rosy razorfish	**0.39**	**0.001**
	ocean triggerfish	0.36	0.003
	bar jack	0.35	0.004
	midnight parrotfish	0.33	0.007
	puddingwife	0.32	0.007
	mutton snapper	0.32	0.009
	red grouper	0.30	0.012
	spotted trunkfish	0.30	0.013
	atlantic spadefish	0.30	0.014
	banded butterflyfish	-0.33	0.006
Bare substrate (sand)	redlip blenny	0.33	0.007
	queen angelfish	-0.34	0.005

Table 5.6. Summary of significantly positive (+) and negative (-) relationships between benthic habitat measures (richness, evenness, and abundance) and the occurrence of fishes (guilds and species) that occurred in the Florida Keys National Marine Sanctuary. Significant relationships were those for which $P \leq \alpha_i$. Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ table-wise, Rice 1989). Habitat types are defined in defined in Figure 5.2.

Species and species groups	Habitat		Habitat abundance								
	Richness	Evenness	H01	H03	H05	H07	H08	H10	S01	S02	S03
grouper relative abundance				+		-					-
generalized carnivores	-	-		+		-		-		-	-
herbivores	+							+			
piscivores	+	+		-							
Atlantic spadefish											
banded butterflyfish											
banded jawfish											
bar jack	+										
beaugregory											
Bermuda chub											
black margate								+			
blackear wrasse											
blue angelfish								-			
blue chromis				+							
blue hamlet				+							
blue parrotfish											
blue tang											
bluelip parrotfish											
bluestriped grunt											
bridled goby										-	
brown chromis											
butter hamlet											
clown wrasse											
cocoa damselfish											
common snook		+									
creole wrasse				+							
cubbyu						+					
dusky squirrelfish											
foureye butterflyfish				+							
French angelfish	+	+						+			
glasseye snapper											
glassy sweeper								+			
graysby											
green razorfish	+										
hybrid hamlet							+				

Table 5.6 continued.

	Habitat		Abundance								
	Richness	Evenness	H01	H03	H05	H07	H08	H10	S01	S02	S03
jackknife-fish			+								
knobbed porgy											
lancer dragonet	+										
longfin damselfish											
longfin damselfish								+			
longspine squirrelfish								+			
mahogany snapper								+			
midnight parrotfish											
mutton snapper											
neon goby											
ocean triggerfish											
orange filefish											+
orangespotted filefish											
peppermint basslet								+			
puddingwife											
queen angelfish											
red grouper									+		
red hind											
redband parrotfish											
redlip blenny											
redtail parrotfish											
reef croaker											
rock beauty											
rosy razorfish											+
sand perch											
Seminole goby											+
silversides, herrings, anchovies					+						+
slippery dick											
spotfin butterflyfish		-									
spotfin hogfish											
spotted drum											
spotted trunkfish											
tomtate	+			-						+	
Townsend angelfish							+		+		
white margate								+			
yellowprow goby									+		
yellowtail parrotfish	+										

FIGURES

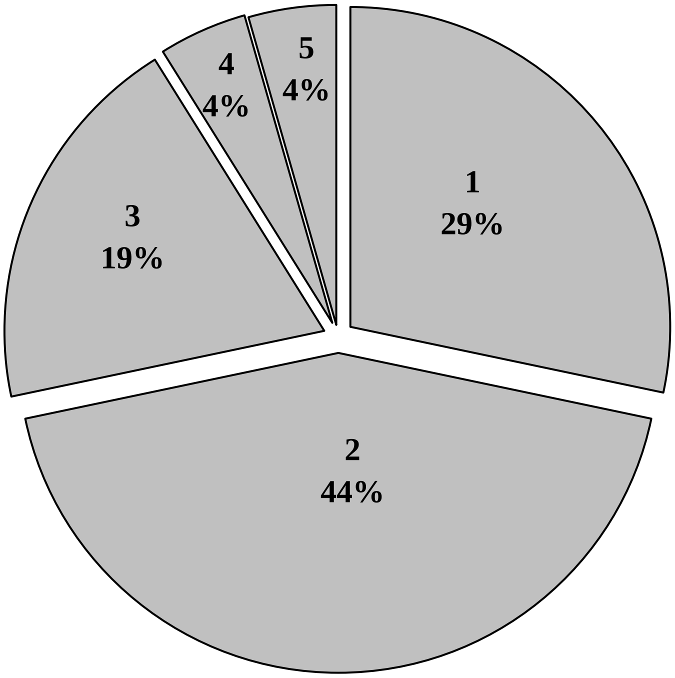


Figure 5.1. Richness of mapped benthic habitats (S_{bh}) occurring at 67 fish survey sites in the Florida Keys National Marine sanctuary. Sites were sampled with a 40000 m^2 virtual quadrat. Integers are values of S_{bh} - the number of mapped benthic habitat types observed within each quadrat. Percentages are the proportion of sites for each value of S_{bh}. Maximum possible value of $S_{bh} = 22$.

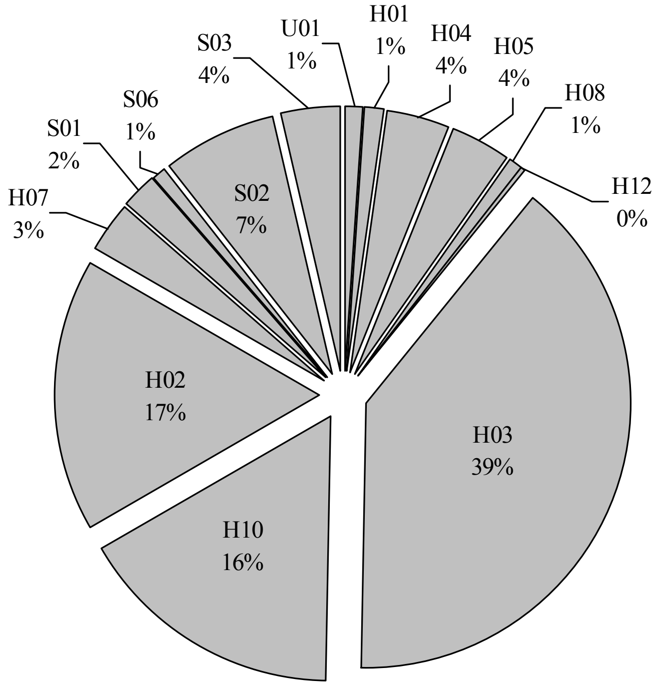


Figure 5.2. Coverage of mapped benthic habitats occurring at fish survey sites in the Florida Keys National Marine sanctuary. Sites were sampled with a 40000 m^2 virtual quadrat. H01: hardbottom - perceptible seagrass (<50%); H02: Platform margin reefs - remnant - low profile; H03: platform margin reefs - drowned spur and groove; H04: patch reefs - coral or rock patches with bare sand; H05: patch reefs - aggregated; H07: platform margin reefs - reef rubble; H08: patch reefs - individual; H09: patch reefs - aggregated with halo; H10: platform margin reefs - shallow spur and groove; H12: platform margin reefs - back reef; S01: continuous seagrass - moderate to dense; S02: patchy seagrass - moderate to dense with blowouts; S03: patchy seagrass - predominantly sand and-or mud with small, scattered seagrass patches (<50%); S06: continuous seagrass - sparse; U01: bare substrate - carbonate sand.

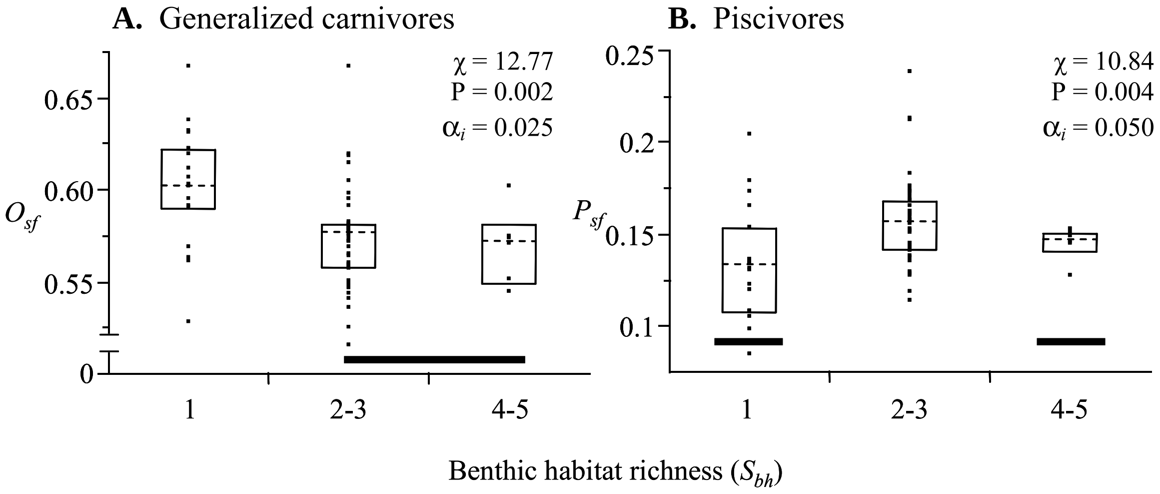


Figure 5.3. Box plots of sighting frequency of generalized carnivores (GC_{sf}) and piscivores (P_{sf}) plotted against benthic habitat richness (S_{bh}). Boxes show the interquartile range (25th - 75th percentile); dashed lines within boxes are medians. The results of Kruskal-Wallis nonparametric tests are shown on each graph. Solid horizontal solid lines join medians that are not significantly different from each other ($P \leq \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).

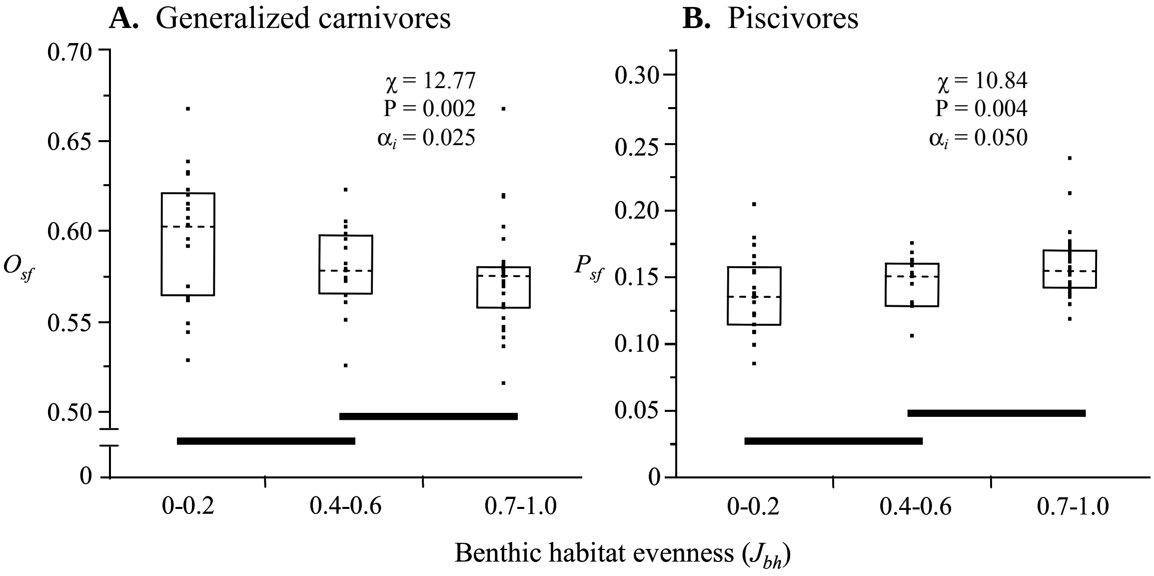
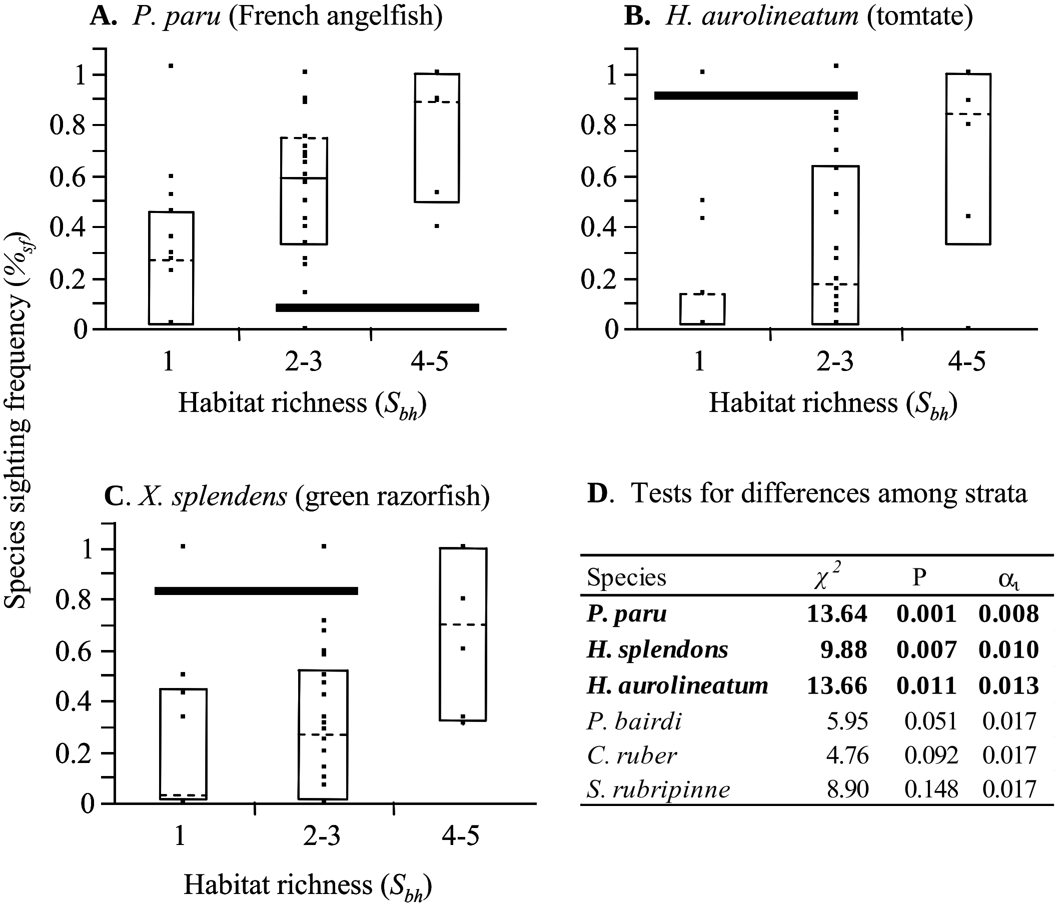


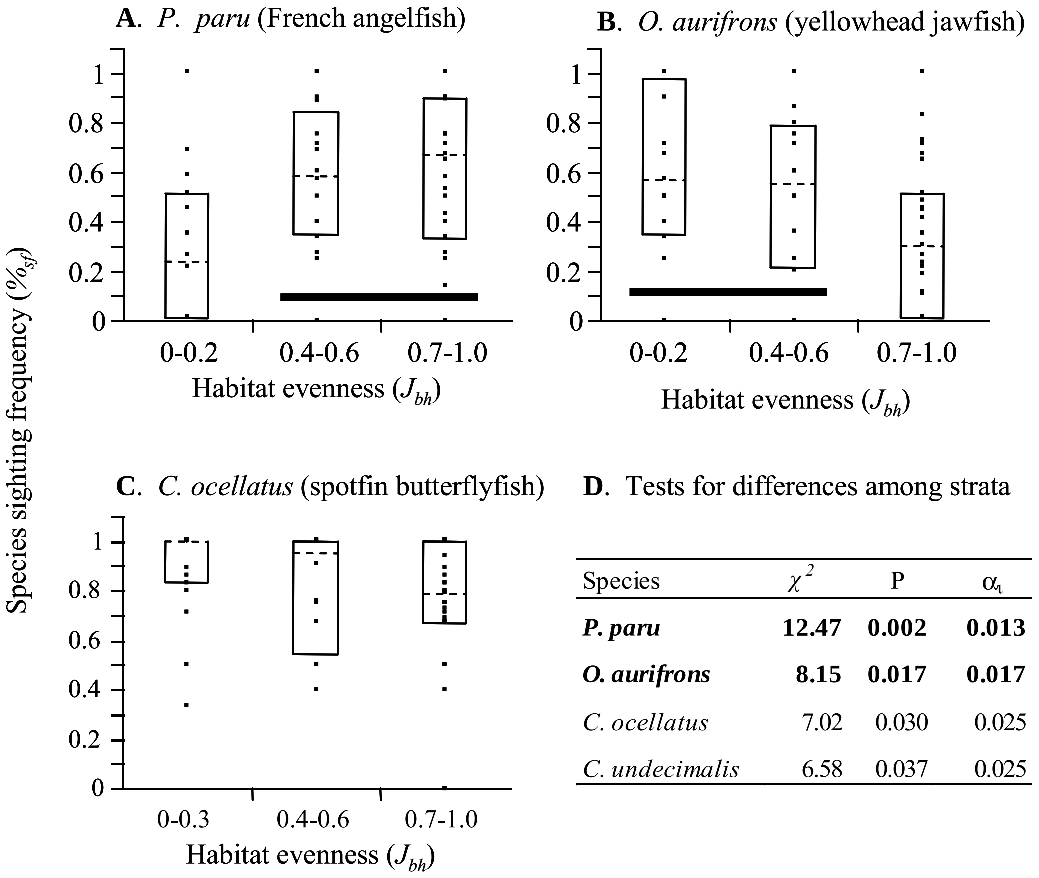
Figure 5.4. Box plots of sighting frequency of A: generalized carnivores (GC_{sf}) and B: piscivores (P_{sf}) plotted against three levels of benthic habitat diversity (J_{bh}). Boxes show the interquartile range (25th -75th percentile); dashed lines within boxes are medians. The results of Kruskal-Wallis nonparametric tests are shown on each graph. Solid horizontal solid lines join medians that are not significantly different from each other ($P \leq \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).



D. Tests for differences among strata

Species	χ^2	P	α_i
P. paru	**13.64**	**0.001**	**0.008**
H. splendons	**9.88**	**0.007**	**0.010**
H. aurolineatum	**13.66**	**0.011**	**0.013**
P. bairdi	5.95	0.051	0.017
C. ruber	4.76	0.092	0.017
S. rubripinne	8.90	0.148	0.017

Figure 5.5. Box plots of species sighting frequency for three species plotted against benthic habitat richness (S_{bh}). Rectangles show interquartile ranges (25^{th} - 75^{th} percentile); dashed lines within rectangles are medians. Solid horizontal lines join medians that are not significantly different from each other ($P > \alpha_i$). The table shows results of Kruskal-Wallis nonparametric tests for significant differences in median $\%_{sf}$ of fish species S_{bh} levels (df = 2). Bold type indicates species that showed significant differences among site strata based on species richness ($P \leq \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).



D. Tests for differences among strata

Species	χ^2	P	α_i
P. paru	**12.47**	**0.002**	**0.013**
O. aurifrons	**8.15**	**0.017**	**0.017**
C. ocellatus	7.02	0.030	0.025
C. undecimalis	6.58	0.037	0.025

Figure 5.6. Box plots of sighting frequency for three species plotted against benthic habitat evenness (J_{bh}). Rectangles show interquartile ranges (25th - 75th percentile); dashed lines within rectangles are medians. Solid horizontal lines join medians that are not significantly different from each other ($P > \alpha_i$). The table shows results of Kruskal-Wallis and nonparametric tests for significant differences in median $\%_{sf}$ of fish species among J_{bh} levels (df = 2). Bold type indicates species that showed significant differences among strata based on J_{bh} ($P \leq \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).

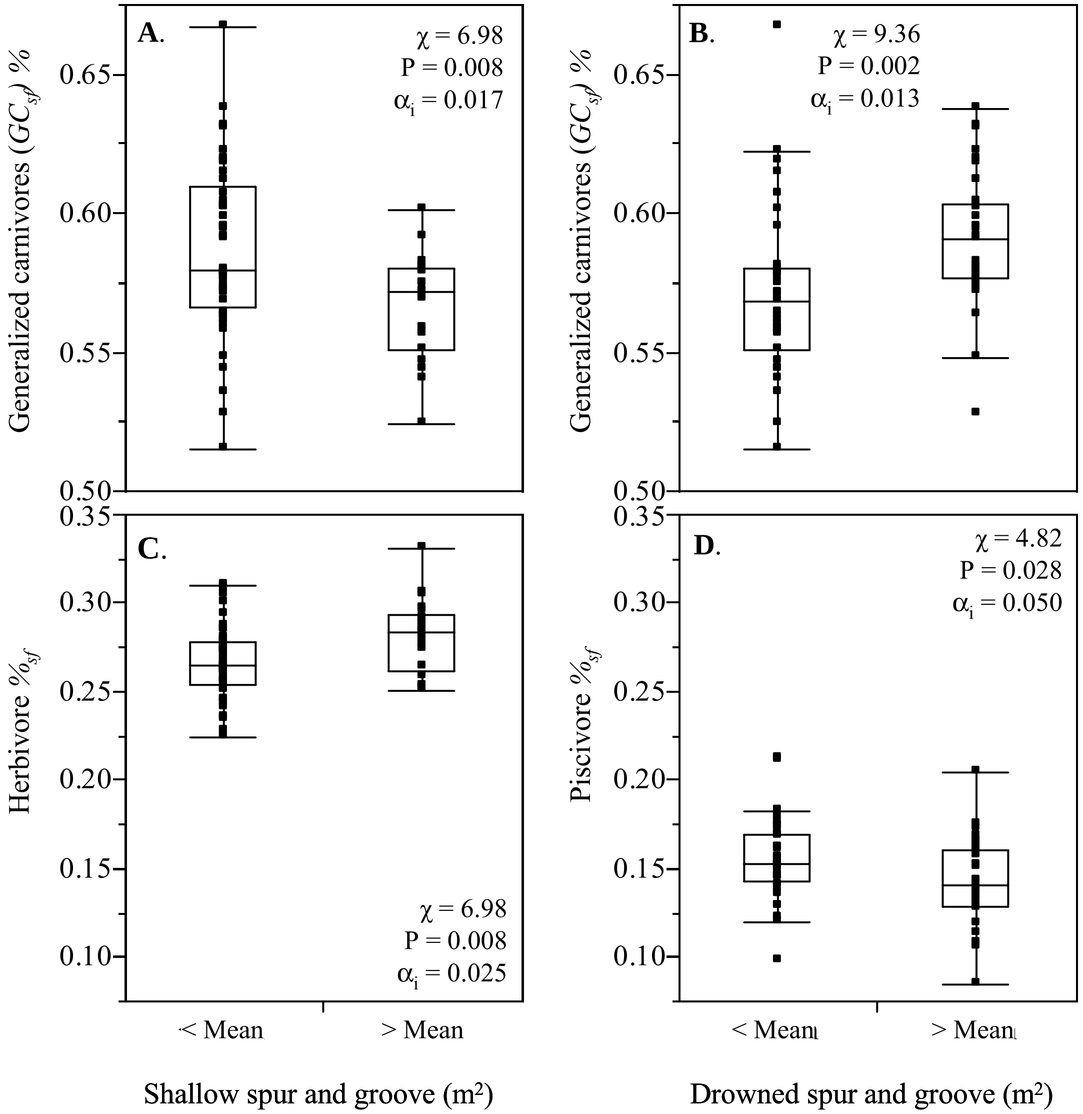


Figure 5.7. Box plots of trophic sighting frequency plotted against the abundance of two habitats. Rectangles show interquartile ranges (25th - 75th percentile); lines within rectangles are medians. The results of Kruskal-Wallis nonparametric tests are shown in each graph. Medians are significantly different between abundance strata ($P \leq \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).

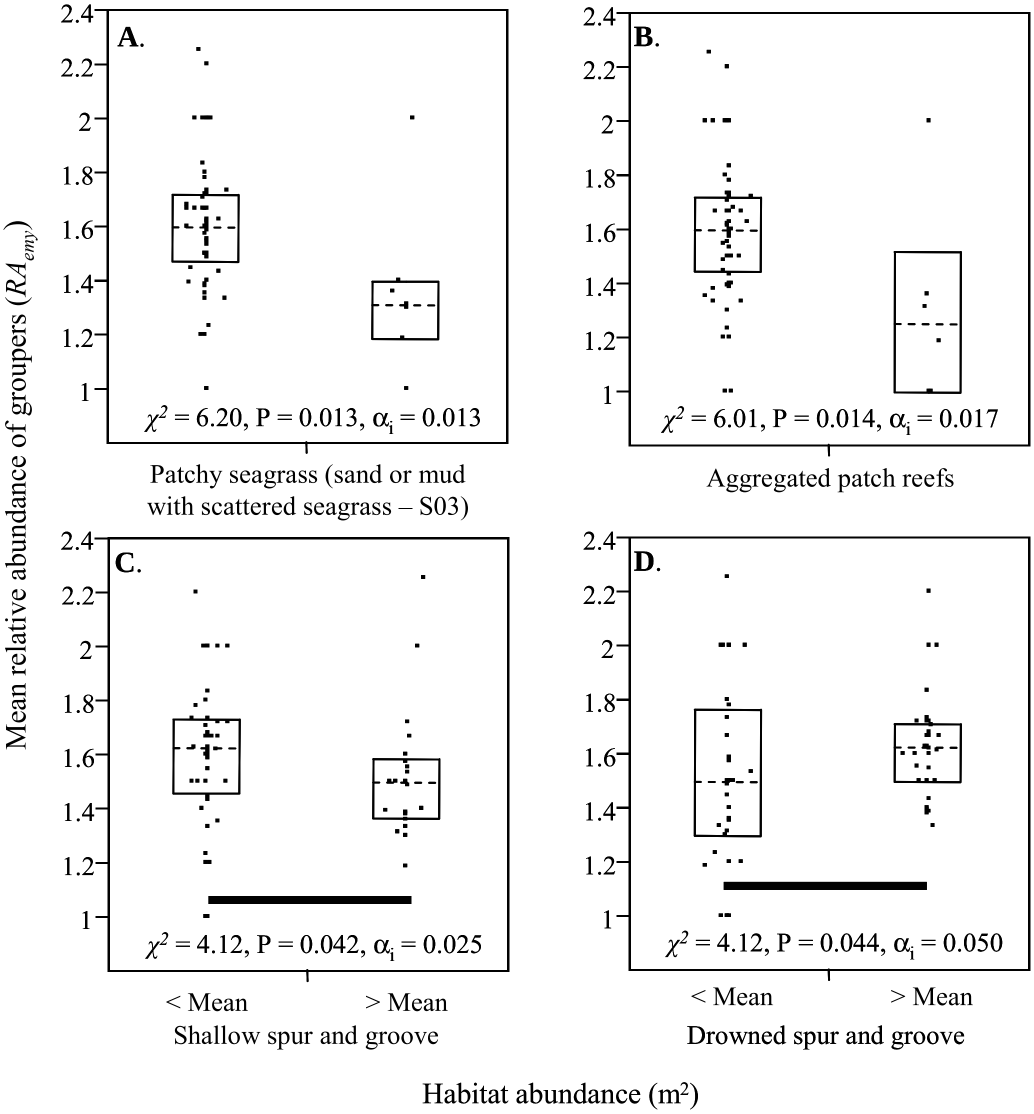


Figure 5.8. Box plots of mean relative abundance of commercially important groupers plotted against abundance of four benthic habitats. Rectangles show interquartile ranges (25th - 75th percentile); dashed lines within rectangles are medians. The results of Kruskal-Wallis tests are shown in each graph. Solid lines join medians that are not significantly different between abundance strata ($P > \alpha_i$). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).

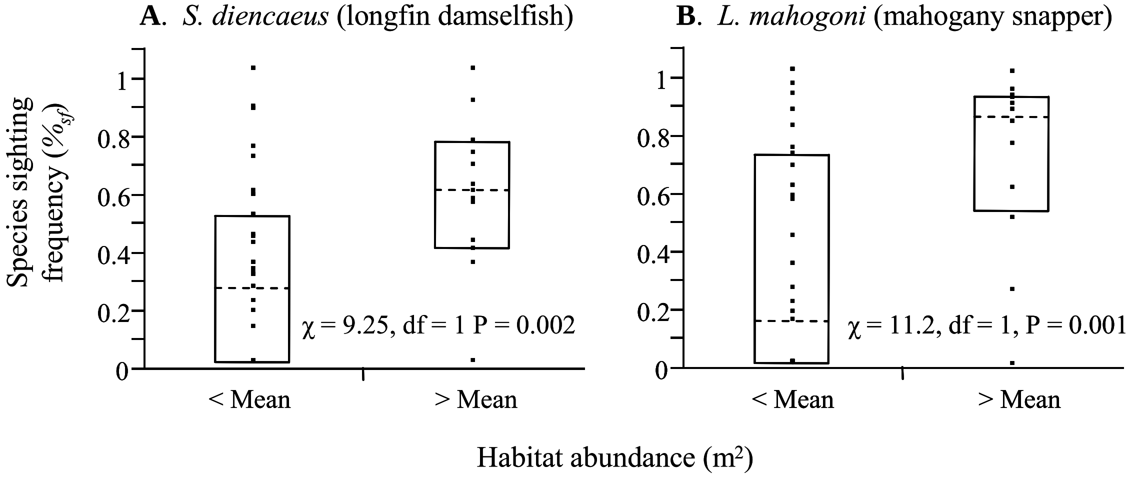


Figure 5.9. Box plots of species sighting frequency plotted against two abundance levels of Platform margin reef – shallow spur and groove. Rectangles show interquartile ranges (25th - 75th percentile); dashed lines within rectangles are medians, which are significantly different among abundance strata ($P \leq \alpha_i$). The results of Kruskal-Wallis nonparametric tests are shown in each graph. Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).

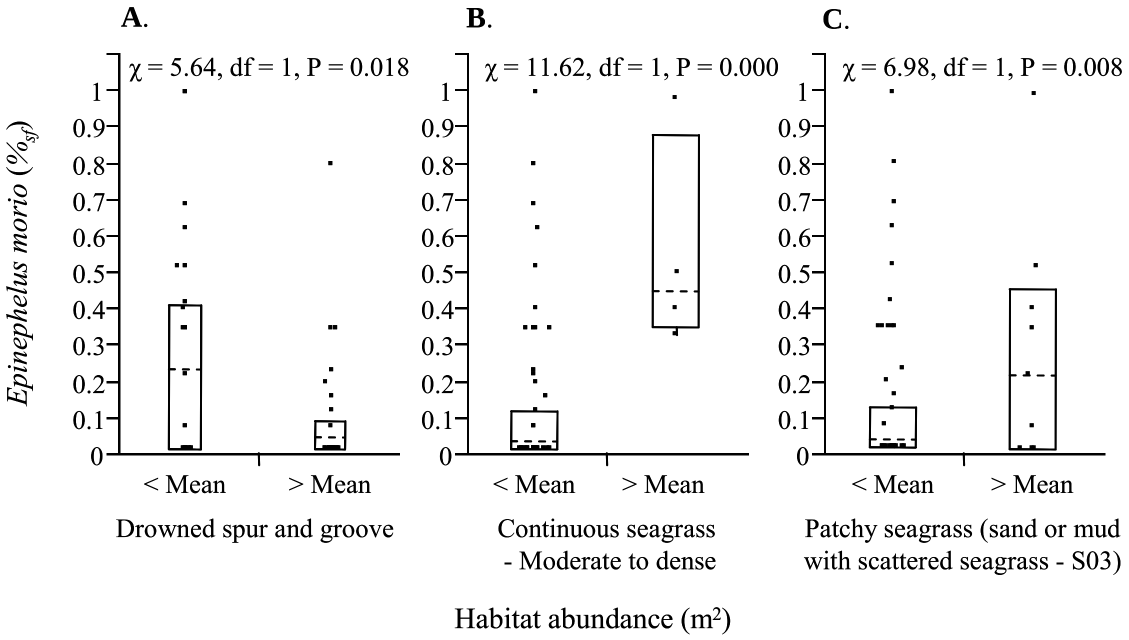


Figure 5.10. Box plots of species sighting frequency of *Epinephelus morio* (red grouper) plotted against two level of abundance for three habitats. Rectangles show interquartile ranges (25th - 75th percentile); dashed lines within rectangles are medians, which are significantly different between abundance strata ($P \leq \alpha_i$,). Levels of α_i were calculated using the sequential Bonferroni technique ($\alpha = 0.05$ Figure-wise, Rice 1989).

CHAPTER 6

GENERAL CONCLUSION

In summary, studies were conducted on 1) the distribution of coral reef fishes in the Florida Keys National Marine Sanctuary (FKNMS); 2) the effectiveness of volunteers as assessors of coral reef fishes; 3) spatial patterns in the occurrence and abundance of benthic habitats in the FKNMS; and 4) the influence of habitats on coral reef fishes. Based on fish data obtained from the Reef Environmental Education Foundation (REEF) and habitat data derived from benthic maps of the FKNMS, the following conclusions are apparent:

1. Distinct regional patterns in fish assemblage structure and composition occurred in the Florida Keys. Measures of species richness were highest in the Upper Keys and lowest in the Dry Tortugas. Comparisons of data on fish species sighting frequency among the Upper Keys, the Middle Keys, the Lower Keys, and the Dry Tortugas indicate that the Dry Tortugas contains a unique assemblage of fishes. Six species were observed more frequently in the Tortugas (barred, blue and butter hamlets; cocoa damselfish; blue angelfish; and neon goby) than in other regions of the FKNMS. Five other species were less frequently encountered in the Dry Tortugas (bluestriped grunt, yellowtail damselfish, sergeant major, porkfish, and foureye butterflyfish). Regional differences in habitat richness, evenness, and abundance and in oceanographic processes such as current circulation patterns and water flow exchange may be responsible for these patterns in fish assemblages.

2. Multiple linear regressions consistently showed that three factors – volunteer divers, survey locations, and dive time – explained about 95% of the variation in fish species richness measures at individual reefs and in the FKNMS as a whole. Data from inexperienced REEF divers, broadly defined as those who had conducted fewer than 35 surveys, allowed greater detection of among-site differences in

species richness, probably because the large number of such divers increased statistical power. However, data from inexperienced divers but were more variable and may be more unreliable than data from experienced REEF divers. A better measure of diver ability is needed because current methods of categorizing the level of diver experience as novices versus experts account for less than 5% of the variability associated with both inexperienced and experienced REEF divers. Accounting for observer-related variation in analyses of REFF's data could increase the probability of differentiating between the effects of FKNMS management on the structure and composition of fish assemblages and those due to natural variation or observer-related variation.

3. Identifiable patterns occurred in the distribution of habitats among regions and between protected and unprotected areas of the FKNMS. Seagrass habitats dominated the Upper and the Lower Keys, whereas hardbottom habitats dominated the Dry Tortugas and the Middle Keys. The FKNMS comprise a mosaic of hardbottom habitat patches interspersed in a matrix of seagrass habitats. Protected areas had fewer habitat types but greater habitat diversity relative to unprotected areas, and could house a greater variety of fish and invertebrate species than non-protected areas. Quantification of the spatial patterns in seascape structure may provide the spatial framework needed to assess the effects of habitats on fish assemblage structure and to evaluate the effects of marine protected areas on fish populations in the FKNMS.

4. Significant but weak linear correlations exist between fishes and benthic habitats occurring in the FKNMS. The trophic structure of fish assemblages was most affected by habitat composition and abundance. Omnivores occur less frequently, whereas piscivores and herbivores occur more frequently at sites with higher habitat richness and evenness. The sighting frequency and relative abundance of some fishes such as mahogany snapper, longfin damselfish, epinepheline and mycteropercine groupers, and small pelagic species are influenced by the abundance of seagrass and hardbottom habitats, but vary in the direction of the relationship with some being positive and others negative. Fish-habitat correlations demonstrate the influence of habitats on the structure and

composition of fish assemblages. Benthic habitat maps 1) can be used to identify similarities and differences in benthic structure among areas, and 2) facilitate direct comparisons of fish assemblages among sites with different habitats.

Successful stewardship of coral reefs as they rapidly change to alternate states requires an understanding of broad-scale spatial patterns and interactions among ecosystem components. In addition, sustaining the long-term ability of coral reef ecosystems to provide ecosystem goods and services such as fisheries, coastal protection, and tourism, necessitates management approaches that are science-based, involve input from resource users, and have public support. Through their monitoring activities, effective volunteer-based programs (e.g., REEF) provide a wealth of information on species' occurrence, educate users about resource issues and conflicts, and engender public support for better resource stewardship. When coupled with geographic information systems based on accurate environmental maps, species-occurrence data from volunteer-monitoring programs could help identify important linkages between ecosystem components that are crucial to the successful implementation and management of marine protected areas.