

APPLYING TERRESTRIAL LANDSCAPE ECOLOGY PRINCIPLES TO THE
DESIGN AND MANAGEMENT OF MARINE PROTECTED AREAS IN CORAL
REEF ECOSYSTEMS

By

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by

Linda Erica “Rikki” Grober-Dunsmore

This dissertation is dedicated to my bedstefar, Jacob Nielsen and grandfather, Hyman Grober. You shared your passion for and intrigue with life and knowledge; and are my models of hard work, integrity, and compassion.

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Marine protected areas (MPAs) represent a popular, but often controversial, management option for the conservation of dwindling reef fish populations worldwide. Questions concerning appropriate design criteria for MPAs lie at the center of the controversy, and reflect a need to better understand the influence of landscape structure of coral reef ecosystems (e.g., size, shape, context of habitat patches) on reef fish assemblage structure. I explored the utility of various landscape metrics in predicting reef fish assemblage structure and found that reef context explained considerable variation in the several reef fish parameters. Specifically, I found that particular groups of fishes were associated with particular types of habitat. Based on these results, I designed a new study in the US Virgin Islands to determine whether functional habitat linkages between reef and seagrass habitat patches were detectable at a landscape-scale. Consistent with predictions, entire assemblage level parameters and abundances and species richness of mobile invertebrate feeders, haemulids, lutjanids, and

epinephelids were each significantly greater at reefs with seagrass within 1 kilometer of the study reef patch. The generality of reef context as a predictor of reef fish assemblage structure was then tested in the Florida Keys National Marine Sanctuary. Though reef context was significant in both systems, the particular habitat type responsible for the reef fish – habitat relationships differed between the coral reef landscapes. Seagrass was a strong predictor of abundances and species richness of mobile invertebrate feeders, haemulids, and lutjanids in the US Virgin Islands, but was not a predictor of these same fishes in Florida. Thus, the processes that structure reef fish communities appear to respond to variation in the landscape structure of these coral reef environments. These results are relevant to marine protected areas design, since they suggest that general design rules do not necessarily apply across systems. Rather, comparative studies are critical for developing the universal design principles to locate marine protected areas that meet their conservation and/or fisheries objectives.

CHAPTER 1 INTRODUCTION

Coral reef ecosystems are degrading worldwide with losses of biodiversity, declines in coral cover, and decreases in the average size and abundances of many coral reef fishes (Wilkinson 2000), and marine protected areas (MPAs) are gaining in popularity as the best management option for dealing with these concerns (Allison et al. 1998, Murray et al. 1999). Coral reef ecosystems are heterogeneous landscapes, comprising topographically-complex, calcium carbonate skeletal structures in which stony corals provide the major framework (Hallock 1997). Coral reefs are embedded in a mosaic of different habitat patches (e.g., reef, seagrass, open water, and mangrove forest) that are connected to one another through the movements of energy, material (e.g., fecal or detrital matter) and marine organisms (Ogden 1997) such as reef fishes.

Coral reef fishes are recreationally and commercially important components of coral reef ecosystems. Reef fish communities exist as spatially divided populations that reside in this mosaic. Connections among local subpopulations are maintained by the export and import of larvae from other subpopulations; or through the movement of fishes during ontogeny, foraging, or spawning (Sale 2002). Distribution of reef fish communities is likely governed by multiple biological and environmental processes that operate at a variety of spatial and temporal scales including biological processes such as predation (Hixon and Beets 1989, Hixon 1991), competition (Smith and Tyler 1973), recruitment limitation (Sale et al. 1984, Doherty and Fowler 1994), and priority effects (Almany 2003). While studies conducted at a small spatial scale associate various fish

parameters (e.g., fish density and biomass) with reef substratum complexity (Luckhurst and Luckhurst 1978, Gladfelter et al. 1980, Hixon and Beets 1989) and reef surface area (Molles 1978, Gladfelter et al. 1980), little research has explored whether these relationships scale up (but see Ault and Johnson 1998a, Acosta and Roberston 2002, Christensen et al. 2003, Jeffrey 2004).

Without an understanding of the distribution of reef fish communities at large spatial scales (> 10's of meters), scientists are ill-equipped to advise resource managers on decisions that require a large-scale examination (e.g., marine protected areas). Marine protected areas (MPAs), one of the most highly advocated forms of ecosystem-based management, can provide a spatial escape for intensely exploited species (Allison et al. 1998, Murray et al. 1999). MPAs constitute a broad spectrum of areas that are afforded some level of protection for the purpose of managing resources for sustainable use, and safeguarding ecosystem function and biodiversity (Plan Development Team 1990). Their potential has been demonstrated both theoretically (Plan Development Team 1990, Roberts and Polunin 1991, Carr and Reed 1993, Allison et al. 1998) and empirically (Rakitin and Kramer 1996). They can increase average size, abundance, and biomass of exploited organisms (see reviews by Rowley 1994, Halpern 2003); and networks of MPAs can insulate habitats and communities from extractive activities that lead to losses in biodiversity and changes in species interactions (Tegner and Dayton 2000, Murray et al. 1999). Because decisions about the placement of reserves are largely political, scientists have had few opportunities to understand the biological implications of reserve design (Allison et al. 1998). Moreover, the design of MPAs has typically focused on single habitats, neglecting associated habitats that may benefit reef fishes during various

stages of their life history (Ogden and Ehrlich 1977, Helfman et al. 1982) and failed to consider potentially-important functional habitat linkages between various habitat patches. At present, few quantitative rules exist for design and management of MPAs. In fact, criteria are broad (e.g., representation, replication). Decisions about the siting, location, size, and composition of MPAs are sorely needed in many places, yet it is currently difficult, if not impossible, to predict how alternative spatial arrangements influence the ability of an MPA to meet its stated conservation and/or fisheries objectives. Various landscape elements (e.g., the amount of edge habitat, corridor placement, and landscape connectedness) have considerable influence on the distribution of terrestrial organisms (Turner et al. 2001). Therefore it is crucial to explore the relevance of landscape elements in structuring coral reef fish communities as a prerequisite for designing effective MPAs. Because improperly designed refuges may provide a false sense of protection, and thereby endanger a fishery (Carr and Reed 1993), identifying simple metrics useful in predicting reef fish assemblage structure would be extremely valuable to resource managers. Combining the disciplines of landscape and coral reef ecology provides a logical starting point for addressing important management questions relevant to habitat-based conservation of reef fishes.

The discipline of landscape ecology deals with interactions and exchanges across large areas, relating the structure of an area to its function (Forman and Godron 1986). By using geo-referenced maps of vegetation, soils, and elevation, terrestrial landscape ecologists have quantified aspects of spatial patterning using a number of metrics, including (but not limited to) patch size and shape, and total area of critical habitats (Turner 1989, Forman 1995). These metrics, calculated statistics of landscape pattern

(Frohn 1998), can be used to predict the outcomes of ecological processes such as dispersal success (Gustafson and Gardner 1996, Schumaker 1996) and population dynamics such as density (McGarigal and McComb 1995), distribution (With and Crist 1995), community structure (Noss 1983), and survival probability (Fahrig 1997). In fact, large-scale metrics of habitat diversity have been successfully used to predict total species richness and abundance of birds, butterflies, and reptiles (Rafe et al. 1985, Rosenzweig 1995, Ricklefs and Lovette 1999). The challenge for scientists is to identify those landscape-scale metrics that may serve as proxies for resource managers of areas with high species diversity and abundance in the coral reef landscape.

Particular habitats such as seagrass communities may play a key role in structuring reef fish communities. Seagrass communities serve as refuge habitat for small fishes and benthic invertebrates, and may be beneficial to the settlement, survivorship, and growth for a variety of fishes and invertebrates that spend their adult life on the reef (Parrish 1989, Baelde 1990, Ogden 1997, Nagelkerken et al. 2000). Seagrass beds are some of the most productive ecosystems of the world (Zieman and Wetzel 1980, Duarte and Chiscano 1999), often forming a dense and extensive below-ground network of roots and rhizomes that support a structurally-complex system of short shoots. A diverse epibiont community attaches to the seagrass blades (Fong et al. 2000), and infaunal organisms live in the sediment of the seagrass, acting to enrich or stabilize the substrate (Suchanek 1983, Peterson and Heck 1999). Many organisms live in seagrass patches including mollusks (Irlandi et al. 1999), crustaceans (Arrivillaga and Baltz 1999), and fishes (Ogden 1997). High densities and biomass of economically-important reef fishes (such as snappers, grunts, and groupers) have been attributed to the availability of food resources in

surrounding seagrass habitat (Randall 1963), perhaps due to movement patterns of these exploited fish (Tulevech and Recksieck 1994, Burke 1995). No studies, however, have quantified the benefits of potentially critical habitat linkages between reef and seagrass (exception: Wolff 1996) or applied recently developed technologies such as geographic information systems, to determine whether the influences of such habitat linkages are detectable at a landscape-scale. If benefits of such habitat linkages can be detected at a large spatial scale (100's of meters), identifying and then subsequently protecting these habitat linkages (which has proven extremely valuable in terrestrial conservation) (Noss 1983, Forman 1995, Turner et al. 2001) may be feasible for delineating boundaries of MPAs in coral reef ecosystems.

Experience applying a landscape ecology approach in terrestrial systems provides a framework for addressing a number of relevant resource management questions that may prove valuable in marine systems.

- What are the relationships among coral reef landscape structure and reef fish assemblage structure?;
- Can functional habitat linkages be identified at a landscape-scale, and is it possible to measure and quantify the potential consequences of these habitat linkages?;
- What is the appropriate spatial scale for addressing these questions?;
- Can faunal-habitat relationships detected in one coral reef landscape be generalized to another?

To address these questions, a hypothetico-deductive study (Platt 1964, Peters 1991) was designed to explore the utility of terrestrial landscape ecology principles in the US Virgin Islands and the Florida Key National Marine Sanctuary (FKNMS) coral reef landscapes. Because little prior research had been conducted at large spatial scales in coral reef systems (exceptions: Appeldoorn et al. 2003, Kendall et al. 2003, Christensen

et al. 2003, Jeffrey 2004), it was necessary to start by exploring relationships of coral reef landscape structure with reef fish assemblage structure (Chapter 2). In the inductive stage of my study, data were collected from the US Virgin Islands, analyzed statistically, interpreted without having a prior specific hypothesis (although generally I expected landscape structure would be correlated with reef fish assemblage structure), and results were used to generate hypotheses tested later. Specifically, I explored those measures of landscape structure that have proven valuable in terrestrial ecosystems for predicting areas of high abundance and species richness.

The preceding exploratory approach, however, does not eliminate the risk of detecting patterns that are not biologically relevant or the risk of missing significant relationships that are (Bissonette and Storch 2003). Because organisms with different habitat requirements, feeding behaviors, and mobility can respond to the landscape differently (Turner et al. 2001, Sisk et al. 1997), analyses must be conducted with consideration for the natural history and ecology of the organisms of interest (Bissonette and Storch 2003). Therefore, while the entire shallow-water reef fish community was of interest to me in this study, this diverse assemblage of fishes (140 different taxa) was subdivided into groups of species that share a common set of life-history traits, morphological or behavioral attributes, or ecological functions. The response of these functional fish groups (trophic and mobility guilds, taxonomic groups, and by life history stage) to landscape features were examined later.

Because pattern exists at every spatial scale (Wiens 1989), it is necessary to link the organisms, species, or the processes being considered to the scales appropriate to the specific questions of interest (Bissonette and Storch 2003). The process for finding the

relevant scale is not well understood (Bissonette and Storch 2003), but generally researchers recommend analyzing data at multiple spatial extents to identify concordance with response variables using spatial statistics and multiple regression procedures (Pearson 1993, Pearson et al. 1995, Pedlar et al. 1997). Particularly in spatially heterogeneous systems, where little to no work has been conducted at a landscape-scale, faunal–habitat relationships should be explored at multiple spatial extents. Therefore, four spatial extents (100 m, 250 m, 500 m, and 1 km) were explored in all subsequent chapters of this dissertation.

It is also valuable to understand whether the distribution of organisms at a given location is explained by characteristics of the immediate locale (fine-scale within patch characteristics) or by the attributes of the surrounding landscape (landscape characteristics), so resource managers can evaluate the trade-offs of collecting patch-level or landscape-level information. For example, Pearson (1993) found that some birds responded only to characteristics of the local habitat (vegetation characteristics such as height, density, and species composition), while other bird species responded only to landscape context (amount of each habitat surrounding study areas). Thus, detailed within-patch surveys may be required to predict the presence of some species, whereas remotely-sensed surveys may be sufficient to detect the presence of others. In coral reef ecosystems, various within-patch measures of coral reef patch quality have been shown to influence reef fish abundance and diversity. These patch-level measures include coral cover (Bell and Galzin 1984) and topographic complexity (Luckhurst and Luckhurst 1978, Hixon and Beets 1989, Friedlander and Parrish 1998), therefore, the fine-scale measure of rugosity (Luckhurst and Luckhurst 1978) and various landscape-scale metrics

of habitat were evaluated to determine their relative influence in structuring reef fish communities for all analyses.

As progress in science is ideally made by the sequential development of hypotheses and the execution of experiments designed to test these hypotheses (Platt 1964, Quinn and Dunham 1983), ecologically-meaningful, and significant findings from the exploratory analyses were used to derive testable hypotheses for further study (Chapter 3). Of particular promise were metrics of reef context, which quantify the spatial arrangement and composition of surrounding habitat patches. A landscape patch, by definition, is bounded by something else, and these adjacent or proximal habitat patches can strongly influence organisms within that patch (Turner et al. 2001).

Correspondingly, scientists increasingly recognize that continental reserves are not islands surrounded by a neutral sea (Janzen 1986); rather isolating a reserve can lead to ecosystem degeneration and the extent and rapidity of this degeneration can depend upon the ecological condition of adjacent habitat patches (e.g., Kushlan 1979). Consequently, I examined how reef context influenced reef fish community structure. Specifically, I tested hypotheses that entire assemblage level parameters, and abundances and species richness within trophic and taxonomic groupings, would be higher at reefs with seagrass within 1 kilometer of the study reef patch.

Although considerable attention has been dedicated to the temporal variability inherent to natural communities, surprisingly little research has addressed the temporal consistency of faunal–habitat relationships, particularly those that occur at a landscape scale (Turner et al. 2001, Bissonette and Storch 2003). Many landscape studies have been discrete sampling events, and have failed to consider temporal variation in resources

or reproductive opportunities (Turner et al. 2001). Coral reef fish communities are notoriously dynamic, both spatially and temporally (Sale et al. 1984, Sale 2002), therefore, their temporal dynamics represent an important ecological dimension. Temporal variations in fish abundance may be induced by reproductive movements (Colin et al. 1997), ontogenetic shifts (Appeldoorn et al. 1997), feeding migrations (Ogden and Zieman 1977, Ogden and Quinn 1984), spatially segregated foraging and resting locations (Meyer et al. 2000), and spatial heterogeneity within and among habitat patches. If landscape metrics of the coral reef landscape are to prove valuable in understanding the distribution and abundance of coral reef fishes, a more thorough understanding of the temporal consistency of reef fish–habitat relationships is critical. To begin to meet this need, a portion of this study (Chapter 3) was conducted over 2 years.

Detection of faunal–habitat relationships in one system does not necessarily imply that resource managers can expect organisms in another system to respond to analogous landscape features in the same manner. Because each landscape is unique, the size and distribution of habitat differs, and may putatively exert different landscape-specific constraints (Bissonette and Storch 2003) on species richness, abundance, community structure, recruitment, and movement. If the constraints of each landscape result in qualitatively different responses of the reef fishes without apparent thresholds, then we may have no hope of developing a predictive theory for forecasting the fish assemblage structure of a given reef patch. Thus, in order to determine the generality of reef fish–habitat relationships detected in the insular US Virgin Islands to other Caribbean coral reef ecosystems, the study was replicated (Chapter 4) spatially in the Florida Keys National Marine Sanctuary.

The approach selected in this study is beneficial in that it addressed many of the short-comings of terrestrial landscape studies (Turner et al. 2001) by replicating the study both in time and space. In addition, multiple aspects of this research remain consistent throughout the dissertation, allowing insight into the generality and reliability of various measures in other systems and over time. For example, each chapter examines the influence of landscape pattern to the entire reef fish community, and then focuses on trophic and mobility guilds and taxonomic groupings of fishes. Furthermore, because there is no single correct spatial scale to describe a system (Levin 1992), a multi-scalar approach was adopted. Every study analysed relationships at multiple spatial scales including the fine-scale within-patch characteristics and explored the strength of relationships at various landscape scales (100 m – 1 km). While as a discipline, terrestrial landscape ecology has progressed from purely non-quantitative descriptive studies (Wiens 1992) to increasing emphasis on spatial statistics, modeling, and experimental design (Hobbs and Norton 1996), this dissertation also progresses from the exploratory to the testing of specific hypotheses. These hypotheses are tested over time and space in a robust study design, thus insights derived from this dissertation provide a foundation for applying the principles of landscape ecology to tropical marine systems, and improve our understanding of the relationships of reef fish communities to large-scale habitat features.

CHAPTER 2 INFLUENCE OF LANDSCAPE STRUCTURE ON REEF FISH ASSEMBLAGES

Marine protected areas represent a popular, but often controversial management option for the conservation of dwindling reef fish populations worldwide. Questions concerning appropriate design criteria for marine protected areas lie at the center of the controversy, and reflect a need to better understand the influence of landscape structure of coral reef ecosystems (e.g., size, shape, and context of habitat patches) on reef fish assemblage structure. Herein, I investigated the relationships between landscape structure and reef fish assemblage structure at 20 study reefs around the island of St. John, US Virgin Islands. Various measures of landscape structure were calculated and transformed into a reduced set of composite indices using principal component analyses (PCA) to synthesize data on the spatial patterning of the study reefs. However, composite indices (i.e. measures of habitat diversity) were not particularly informative for predicting reef fish assemblage structure. Rather, relationships were interpreted more easily when functional groups of fishes were related to individual habitat features. In particular, reef context was strongly associated with multiple reef fish parameters (e.g., abundances within trophic guilds and taxonomic groups). Fishes responded to benthic structure at multiple spatial scales, with each fish group correlated to a unique suite of variables. Accordingly, future experiments should be designed to test functional relationships based on the ecology of the organisms of interest. My study illustrates promise in applying a landscape ecology approach to coral reef ecosystems, and provides

an empirical basis to further test the influence of specific habitat features in structuring reef fish communities.

Introduction

The management of tropical marine environments calls for interdisciplinary studies and innovative methodologies that consider processes occurring over broad spatial scales (Allison et al. 1998). Landscape ecology is interdisciplinary by nature, with an appropriate focus on broad-scale patterns and ecological processes (Forman and Godron 1986). A landscape generally refers to a heterogeneous area composed of local interacting ecosystems (Forman 1995) made up of homogenous units, called habitat patches. Landscape structure describes the composition and spatial arrangement of habitat patches (Forman and Godron 1986), and has been quantified using a number of metrics (O'Neill et al. 1988) including composite indices (e.g., habitat diversity, principal components), measures of configuration (e.g., patch size), and measures of context (composition of surrounding habitat patches) (Turner 1989). The use of such metrics, derived largely from island biogeography theory (MacArthur and Wilson 1967), metapopulation theory (Hanski 1999), and patch dynamics (Pickett and White 1985) has improved our understanding of how landscape features influence terrestrial communities (Turner 1989, Gardner and O'Neill 1991). Because of its focus on broad and multiple spatial scales and entire ecosystems, landscape ecology has proven extremely valuable in addressing management problems in terrestrial systems (e.g., reserve design) (Noss 1983, Forman 1995). A landscape ecology approach to the study of coral reef fishes, however, has received little attention, until recently (Kendall et al. 2003, 2004, Jeffrey 2004).

Our understanding of the dynamics of reef fish assemblages has been largely derived from studies conducted at fine spatial scales (1 m² plots) (Williams 1980, Sale et

al. 1994, Pittman and McAlpine 2003), limiting our ability to predict the effects of large-scale features on reef fishes (Sale 2002). Fine-scale measures of topographic complexity (Hixon and Beets 1989, Friedlander and Parrish 1998), hole size (Friedlander and Parrish 1998), and coral cover (Bell and Galzin 1984) can influence reef fish assemblage structure. The few existing large-scale studies have examined relatively gross characteristics such as latitudinal gradients (Ebeling and Hixon 1991) and coral reef zonation (Williams 1991); features that are not particularly useful for selecting specific reef areas as candidates for protection. Thus, it is unclear whether findings from fine-scale studies can be extrapolated to large-scale resource management concerns. Understanding functional relationships between landscape structure and reef fish distribution at a broad spatial scale may therefore be useful for delineating the boundaries of MPAs (Christensen et al. 2003), since coral reef ecosystems exist as a complex mosaic of habitat patches (i.e. reefs, seagrass patches, and mangrove stands), and are therefore ideally suited for a landscape ecology approach.

The purpose of my study was to determine whether commonly-used terrestrial metrics can be quantified for coral reef environments, and to determine whether these metrics might be used to predict reef fish assemblage structure. Toward this end, a suite of landscape metrics was explored using multivariate statistics. Through a variety of procedures to eliminate redundancy and autocorrelation, I developed composite indices to synthesize data on the spatial patterning of the reef study sites. I then examined the utility of these composite indices to predict reefs that have relatively high reef fish species diversity and abundance. In addition, I explored individual habitat features (reef configuration and reef context) separately, and examined the relative importance of fine-

and landscape-scale habitat measures on reef fish assemblage structure. Configuration was selected because measures of mean patch size, shape, and arrangement are frequently associated with species abundance and diversity (Robinson et al. 1995, Villard et al. 1999); and protected area configuration can influence organisms within and outside their boundaries (Diamond 1975, Sisk et al. 1997, Mazerolle and Villard 1999). Context was selected because of the increasing recognition of its role in sustaining species targeted for conservation in terrestrial systems (Mladenoff et al. 1995, Robinson et al. 1995, Sisk et al. 1997). The relative influence of fine-scale (rugosity) and landscape-scale habitat characteristics on fish assemblage structure was explored because knowing the importance of features at each spatial scale can save precious resources for resource managers (Mazerolle and Villard 1999).

Study Area

Coral reefs around the island of St. John, US Virgin Islands (Figure 2-1) were selected for study, because benthic habitat were readily available (Kendall et al. 2001). Habitat maps (digitized from aerial photographs taken at an altitude of 5000 feet in 1999), were classified by visual interpretation by NOAA, using 26 discrete and non-overlapping habitat classes, with a minimum mapping unit of 1 acre (Kendall et al. 2001). Most sampling sites were located on the lower fore reef of fringing and patch reefs, dominated by *Montastraea annularis* or mixed corals (8-30% living cover; pers. obs.), although several were dominated by old *Acropora palmata* framework (5-10 % living cover; pers. obs.). Study reefs occurred in water depths between 5 and 15 m.

Methods

Twenty reefs were sampled: 14 reefs in 1994 and 6 in 2001 (Figure 2-2). Reefs were selected from an existing fish database as representative locations that varied with

respect to landscape features, yet relatively similar depth, reef morphology, and coral cover. For exploratory analyses, the 1994 and 2001 datasets were combined. Reefs sampled in 2001 were included to expand gradients in several habitat parameters of interest. To investigate specific functional relationships (e.g., configuration, context), only the 1994 dataset was used to reduce potential temporal variability due to changes in fishing pressure and storm damage.

Reef fish Sampling

Fish sampling was conducted within reef habitat only. Reef-associated fishes were sampled over a 10-day period in July 1994 (Beets and Friedlander 1994), and over a 5-day period in July 2001. The number of fish point counts per reef were determined based on reef size following Monte Carlo simulation, and ranged from 8-20 point counts per reef (Figure 2-2). In 1994, a modified Bohnsack and Bannerot (1986) point count method (a reduction in the sample radius from 7.5 m to 5 m) was used, whereas the original point count method was used in 2001. Mean species richness refers to the mean number of species observed per point count per replicate reef, whereas cumulative richness refers to the total number of species observed during all point counts at a reef. Abundance refers to the mean number of reef-associated fishes observed per point count per replicate reef. Two species were eliminated from abundance analyses, since these tended to overwhelm abundance estimates and are difficult to count accurately--*Jenkinsia* spp. (herring) and *Coryphopterus personatus* (masked/glass goby). Randall (1967) and Fish Base (Froese and Pauly 2002) were used as references to classify all fishes by trophic guild: piscivore, herbivore, mobile invertebrate feeder (MIF), sessile invertebrate feeder (SIF), planktivore, or omnivore (Appendix A). To the degree that the ecology of each species is known, each fish was classified into mobility guilds: resident, mobile or

transient (Appendix A). Resident species are sedentary and site-attached, and do not typically move from their primary reef patch. Mobile species are those that have restricted movements and may roam from the primary reef patch. Transient species are vagile, and can range on the scale of kilometers. Taxonomic groups of commercially and ecologically-important fishes were analyzed separately (e.g., haemulids, lutjanids, and scarids). Fishes were further subdivided into juvenile and adult categories, based on length of maturity where possible (Froese and Pauly 2002), to examine the influence of life-history stage on functional relationships. This resulted in 30 reef fish assemblage parameters (Table 2-1).

Habitat Sampling

The fine-scale measure of rugosity was obtained by running an underwater tape measure as closely as possible over the contour of the substratum. For each reef, 10 rugosity samples were collected along 10-m transects. The resultant mean value was used for subsequent analyses. Because these reefs are natural habitat patches, microhabitat variation that was not quantified, likely exists.

The original map classification scheme (Kendall et al. 2001) was condensed from 26 to 9 distinct and non-overlapping habitat classes (i.e. mud, mangrove, sand, reef, pavement, bedrock, seagrass, macroalgae, and deep unknown). Deep unknown was typically a deep (> 16m) soft-bottom habitat (R. Grober-Dunsmore, unpubl. data). This reduced set of nine habitat classes was selected based on terrestrial studies (which frequently use 5-10 habitat classes for resource management purposes; Turner et al. 2001), and to simplify results for resource managers. Haphazard groundtruthing was conducted in each habitat polygon within 100 m of each study reef. Percent cover of benthic invertebrates and substrate types were estimated using 1m² quadrats.

Fourteen metrics, used to quantify various aspects of the configuration and context of the study reefs (Table 2-2), were calculated with ArcView 3.2 (ESRI 1996). A single value for each (reef) patch metric was calculated ($n = 3$). Each landscape metric was calculated at three spatial extents; 100 m, 250 m, and 500 m from the leading edge of each reef. These extents were selected to represent a range of potential importance based on the known natural history of reef fishes. Because the area of deep unknown increased considerably beyond 500 m, the 1 km spatial extent was not included, resulting in 36 metrics that were correlated to reef fish parameters (Table 2-3).

Most sample reefs were determined to be subsections of larger mapped polygons, thus each reef polygon was slightly modified in Arc View 3.2 (ESRI 1996) to reflect the standardized 25,000-m² subsections where fish data were collected. A separate heterogeneity study (Grober-Dunsmore et al. 2004) determined that for most fish parameters, no significant differences existed between these reef sections and the entire mapped polygons. These results, and the fact that slightly-modified polygons were used for all calculations, justify the use of these reefs for exploratory purposes.

Data Analysis

To reduce the 36 landscape metrics into a more parsimonious dataset of composite indices that capture the wealth of information contained within the original dataset, a combination of techniques was applied. (1) Pearson product-moment correlations (Ppmc) between each pair of metrics, and (2) principal component analysis (PCA) using a correlation matrix. Each spatial extent was examined separately and results were compared across extents. Ppmc was applied sequentially by examining significant pair-wise correlations (Sokal and Rohlf 1995) to reduce the number of variables to a 3:1 ratio (observations to variables), which is required for PCA (McGarigal

et al. 2000). The choice of an index within a group of redundant metrics was determined by selecting ecologically-meaningful metrics and eliminating variables that failed normality tests. Ppmc reduced the 14 metrics to 8, and PCA was subsequently applied to further synthesize these into a smaller set of linear combinations (components) of the original variables. Loadings on original variables were used for interpretation.

Principal component plots of these landscape metrics were used to organize the sampling entities (reefs) in multivariate space. Reefs were classified into one of three categories based on our pre-existing knowledge of the surrounding coral reef environments. PCA plots were then displayed at each spatial extent to determine whether characterization of study reefs using landscape metrics corresponded to our local knowledge and groundtruthing data, allowing us to assess the broad accuracy of remotely sensed benthic habitat maps.

To explore the strength and nature of the relationships between landscape structure and fish assemblage parameters, stepwise multiple regression analyses using significant principal components as the independent variables, for each of the thirty reef fish parameters, was conducted. To control family-wise error rate for multiple correlations, sequential Dunn-Sidak Bonferroni corrections were applied using the number of reef fish parameters ($n = 30$) tested (Sokal and Rohlf 1995) for all subsequent regressions.

Specific functional relationships were examined separately: 1) reef configuration, 2) reef context, and 3) the relative influence of fine and landscape-scale habitat parameters, using the 1994 reef fish dataset only ($n = 14$). Landscape variables were selected based on Ppmc results (Sokal and Rohlf 1995) though several variables that were

eliminated from PCA were included to verify their potential importance. Only those that met assumptions of statistical independence were tested in a given model. Reef configuration variables were perimeter to area ratio (P: A) of each reef, reef size, and the number of habitat patches within 100 m. Reef context variables were surrounding habitat diversity and the areal coverage of reef, bedrock, seagrass and deepwater within 100 m. Fine-scale and landscape-scale variables were rugosity and the areal coverage of deepwater, seagrass and reef within 100 m. To optimize model performance and reduce potential effects due to multicollinearity, a series of diagnostic tests were used:

1) Akaike's Information Criterion (Akaike 1974), 2) leverage effects plots, 3) Durbin-Watson statistic, and 4) condition number (Belsley et al. 1980) for every stepwise regression analysis. Simple linear regressions were created to determine the stability of models using residual plots and residual normality plots (Sokal and Rohlf 1995).

Where necessary, reef fish and habitat data were $\log_{10}(x + 1)$ transformed to improve normality and data were tested using Shapiro-Wilks statistic (Sokal and Rohlf 1995). All statistical analyses were conducted with JMP 8.01 (SAS 2003). Statistical significance was accepted at the $p \leq 0.05$, unless otherwise noted.

Results

Landscape Structure

Configuration and context of study reefs varied widely. Most metrics had coefficients of variation $> 50\%$ of the mean, indicating that gradients in many aspects of the landscape were represented (Table 2-3). Of fourteen initial landscape variables, Ppmc resulted in 8 remaining landscape metrics (Table 2-4). PCA results were consistent across spatial extents (i.e. 100 m, 250 m, 500 m). In fact, the variance explained, the eigenvalues and the distribution of loadings were remarkably comparable. However,

interpretation was easiest at the 100 m spatial extent since the proportion of area classified as deep unknown was minimized. Thus, a single spatial extent (100 m) was selected for further analyses, using the remaining 8 landscape variables: number of habitat patches, reef size, habitat diversity, area of deep unknown, pavement, reef, sand and seagrass habitat.

PCA of these 8 landscape metrics at 100 m revealed four dominant components of variation based on retention of eigenvalues greater than the average, i.e. $\lambda > 1$ (Jackson 1993). These components explained approximately 80 % of the total variance of the original landscape variables (Table 2-5). However, landscape structure was not adequately represented by a single or even a few gradients. Final communalities indicated that most of the residual configuration indices were well accounted for by the four components, with no notable exceptions.

Principal component plots using landscape metrics generally corresponded with my pre-existing knowledge and groundtruthing of the local environments of these study reefs (Figure 3), though there were several outliers. PCA plots were also in general concordance across spatial extents (100 m, 250 m, and 500 m), although the 100 spatial extent resulted in strongest clustering of reefs in concordance with my local knowledge. Thus, PCA plots illustrated that benthic habitat maps were capable of differentiating among reef types (Figure 2-3).

Reef Fish Assemblage Structure

A total of 57,002 fishes representing 171 different species were recorded during 341 censuses at the 20 study reefs.

Principal components proved to be useful in explaining only a limited number of reef fish assemblage parameters. Both measures of species richness (i.e. mean richness

and cumulative richness) were marginally correlated (21% and 26%) with PC4, a positive gradient of seagrass (Table 2-6). Fifty-three percent of the variation in herbivore abundance was explained by PC2 and PC3, positive gradients of sand and habitat diversity. Acanthurids (a major component of the herbivore guild) were also positively correlated to PC2 (Table 2-6). Forty-three percent of haemulid abundance was negatively correlated to PC1, and 46 % of lutjanid abundance was negatively correlated to PC1 and positively related to PC2 (Table 2-6).

Configuration was generally a poor predictor of reef fish assemblage structure. There were a few exceptions. Seventy-four percent of the variation in the abundance of transient fishes (e.g., jacks) was explained by P: A of each reef and the number of habitat patches (Table 2-7, Figure 2-4). Abundances of two other trophic guilds (piscivores and omnivores) and three taxonomic groups (pomacentrids, acanthurids, and pomacanthids) were marginally correlated to P: A (Table 2-7, Figure 2-4). Importantly, examination of regression plots revealed the influence of single points, and residual plots revealed that several relationships exhibited heteroscedascity, thus calling into question the stability of these relationships (Sokal and Rohlf 1995). No reef fish assemblage parameter was correlated with reef size.

Reef context was correlated with thirteen of thirty possible reef fish assemblage parameters (Table 2-8). Species richness was positively correlated with the areal coverage of seagrass (Table 2-8). Several ecologically-relevant relationships between specific habitat types and abundances within trophic and taxonomic groups were also evident. Adult mobile invertebrate feeders (i.e. 64 species) were positively correlated with the areal coverage of seagrass ($R^2 = 0.33$) and adult piscivores were positively

correlated with the areal coverage of reef within 100 m ($R^2 = 0.51$) (Table 2-8, Figure 2-5). Several taxonomic groups were predicted, based on their life history, to be correlated with a particular habitat type, e.g., adult haemulids and lutjanids with seagrass and adult serranids with reef habitat. Simple linear regressions, based on stepwise results, were generally consistent with these predictions (Figure 2-5). Fifty-three percent of the observed variation in the mean abundance of adult haemulids, and 68 % of the variation in the mean abundance of adult lutjanids was explained by seagrass coverage (Figure 2-5). Juveniles of several groups of fishes were correlated with deep unknown habitat (Table 2-8). Subsequent examination of residuals plots and residual normality plots indicated that most relationships were stable; those that were not were eliminated from the results reported here.

Discussion

The coral reef landscape variables were successfully reduced into four principal components, thereby synthesizing the wealth of information contained within the benthic dataset (O'Neill et al. 1988, Riitters et al. 1995). When plotted, these components were able to differentiate between reefs of varying configuration and habitat composition, thus benthic habitat maps clearly appear useful in describing and quantifying coral reef landscapes. Clustering of reefs along PCA axes remained consistent across multiple spatial extents (100, 250, and 500 m), a result that represents an important contribution to the application of landscape ecology principle to coral reef ecosystems, since it is critical to determine the relevant scale of analyses for landscape studies (Gardner and O'Neill 1991). Because with increasing spatial extent, the total area of deep unknown increased, I recommend that the 100 m or 250 m spatial extent is the most informative characterization of the spatial patterning of the coral reef landscape, at least in this

system. Selection of scale is a defining challenge since different patterns emerge at different scale (Wiens 1989), and the appropriate spatial extent may depend on the benthic habitat maps available and the question of interest.

Ecologically-meaningful interpretation of the principal components proved difficult, because loadings were distributed across many variables, and no single component accounted for > 26 % of the variability contained in the original dataset. These findings differ from many terrestrial studies (McGarigal and McComb 1995, Riitters et al. 1995), where distinct elements of the landscape are often described by components that represent habitat complexity (Riitters et al. 1995), fragmentation (Andrén 1994), or patch shape (McGarigal and McComb 1995). This analysis suggests that complex composite indices are less informative than individual spatial features for characterizing the coral reef landscape at the individual reef scale.

In general, principal components were poor predictors of reef fish assemblage structure since most relationships were more easily interpreted using individual habitat features. For instance, species richness exhibited a marginal association with PC1 and PC4, which represented gradients in the areal coverage of reef and seagrass area, habitats considered critical for many reef fish species (Ogden and Zieman 1977, Sale 2002). Likewise, the association of herbivores with PC2 (a gradient of the areal coverage of shallow sand and seagrass habitat), may indicate the availability of shallow foraging habitat, where sufficient light is available for photosynthesis of their primary food source, algae. When testing new approaches in a new system, it is critical to determine the appropriate measures for understanding the spatial distribution of organisms (Turner 1989, Wiens 1992), thus this negative result may help guide future coral reef studies.

Several factors may explain the inability of principal components to predict reef fishes. These components may contain too much information to be germane to reef fishes since fish may not respond to multiple habitat parameters. Rather, interpretation suggests that specific fish groups respond to specific habitat features. Additionally, it appears that all species may not conform to the same landscape pattern, as in terrestrial systems (Mladenoff et al. 1995, Lindenmayer et al. 2003), but that each organism may respond to specific features at particular spatial scales.

The other composite index, habitat diversity, was also not a good predictor of reef fish diversity and abundance, which is contrary to predictions based on terrestrial research (Rafe et al. 1985, Ricklefs and Lovette 1999). These findings may indicate that this is not an appropriate measure of habitat diversity, since relationships can heavily depend upon the specific definition (e.g., elevation, vegetation structure) of habitat diversity (Rafe et al. 1985, Turner 1989). In Palau, another habitat diversity measure also failed to predict species diversity and species richness (Donaldson 2002) of reef fishes though Jeffrey (2004) found that measures of habitat richness and diversity were correlated (both positively and negatively) with several measures of trophic composition and occurrence of several species of fishes. I found frequent negative associations of individual reef fish parameters with habitat diversity, which may suggest that specific habitat types are likely to be better predictors of assemblage structure than habitat diversity *per se*. These findings lead us to concur with terrestrial studies that challenge the effectiveness of generic landscape indices (i.e., principal components and habitat diversity indices) to design protected areas (Lindenmayer et al. 2003) at the scale of individual reefs. Relationships in this study were better understood by examining

specific habitat features, therefore future studies may need to be designed to examine specific functional relationships between particular groups of fishes and specific habitat features.

Although useful in some terrestrial systems (Andrén 1994), but highly variable and weak in others (Trzcinski et al. 1999), configuration measures were generally not effective in predicting reef fish assemblage structure. These findings corroborate those of Pittman et al. (2004), which revealed that configuration explained less of the variation in the spatial distribution of fishes than habitat composition. There were a few potentially, ecologically-relevant relationships. The strong, positive association of reef P: A with abundances of transients (e.g., jacks, yellowtail snapper) may reflect their foraging behavior along reef edges. The negative association of reef P: A with adult piscivores was surprising. Perhaps larger transient predators prey on smaller piscivorous fishes along the edge, reducing their abundance. In addition, fish traps are typically set along reef edges in St. John, and other island locations, thus piscivores along reef edges may be more susceptible to fishing mortality, which may explain, in part, these findings.

Surprisingly, reef size was not positively correlated with any reef fish parameter. These findings contrast with terrestrial (Diamond 1975), small-scale patch reef (Molles 1978, Bohnsack and Talbot 1980, Sale et al. 1994) and seagrass studies (Irlandi et al. 1999, Hovel and Lipcius 2001), but may be a consequence of the limited gradient in reef size in this study (though the coefficient of variation was $> 67\%$ of the mean). It is possible that beyond a minimum reef size (which these reefs may exceed), the structure of reef fish communities may be mediated by other factors such as reef context (see below), physical disturbance (Syms 1998), larval supply (Sale et al. 1984, Doherty and

Fowler 1994), and/or predation (Hixon and Beets 1989). Such scale effects have been demonstrated in reef communities; e.g., the paradigm of locally-controlled recruitment from a superabundant pool of larval fish, developed at the scale of local populations (Smith and Tyler 1972) has been shown to be invalid at the scale of the whole reef population (Sale et al. 1984).

Reef context appears to be an important determinant of reef fish assemblage structure, corroborating findings involving multiple taxa in terrestrial (McGarigal and McComb 1995, Mazerolle and Villard 1999, Trzcinski et al. 1999), coral reef (Kendall et al. 2003) and seagrass systems (McAlpine et al. 2004). In particular, the areal coverage of seagrass, an important nursery and larval settlement habitat (Shulman and Ogden 1987, Ogden and Zieman 1977) and foraging area for some fishes (Randall 1967) was strongly associated with entire assemblage parameters (e.g., cumulative species richness). Seagrass habitat may contribute to higher species richness as a result of nutrient transfer and movement of invertebrates and energy from highly productive seagrass to adjacent reef habitat (Duarte 2000). For instance, Tektite and Yawzi reef, structurally complex reefs with the highest mean species richness values, are located within a bay with dense *Thalassia testudinum*. Higher species richness was also detected in mangroves adjacent to continuous seagrass in Australia (Pittman et al. 2004), and at reefs proximal to nursery habitats (i.e. seagrass) in Colombia using large-scale habitat maps habitats (Appeldoorn et al. 2003), although in coral reef systems researchers were not able to eliminate confounding factors of near shore-offshore effects nor separate independent contributions of other soft-bottom habitats.

Reef context was also strongly associated with abundances within specific trophic guilds and taxonomic groupings. As expected based on terrestrial (Turner 1989, Sisk 1997) and marine research (Pittman and McAlpine 2003, Pittman et al. 2004), relationships that met the model selection criteria were consistent with the ecology of each particular fish group. For example, the positive relationship of MIF abundances with seagrass is consistent with the foraging behavior of species in this trophic guild (e.g., taxa within mullidae, haemulidae, and lutjanidae). The relationship for haemulids and seagrass was even stronger, which is expected since some haemulids forage off-reef in seagrass nocturnally (Ogden and Quinn 1984). Common piscivorous fishes, which may forage preferentially in reef habitat, such as *Aulostomus maculatus*, *Carynx* sp., *Scomberomorus regalis*, *Synodus intermedius* were more abundant where there were large areas of reef habitat (e.g., Eagle Shoals and Tektite). The positive association of juvenile omnivores with deep water habitat is consistent with the functional role of deep water as a source of ichthyoplankton. Several species of omnivores (e.g., apogonids, blenniids) are fairly non-mobile as larvae, and are thought to recruit directly to reef substrate from the plankton. A direct test of this hypothesis, however, would be required to determine whether deep water enhances planktonic larval delivery at the reef scale. These findings suggest that a landscape ecology approach can be valuable for identifying functional linkages between organisms and their coral reef habitats at a scale appropriate for resource management decisions.

The fine-scale measure of rugosity was of limited value in predicting reef fish assemblage structure. The exception was for highly site-attached fishes, e.g., omnivores which were primarily blenniids, gobiids, and pomacentrids. The inability of rugosity to

predict reef fish assemblage structure, though contrary to previous small-scale research (Hixon and Beets 1989), may indicate the ineffectiveness of this measure to characterize topographic complexity within a single habitat at the scale of whole reefs. Most previous studies that detected rugosity relationships were conducted across multiple habitats (Friedlander and Parrish 1998) or used manipulated patch reefs to maximize the gradient of rugosity (Hixon and Beets 1989).

Some reef fishes respond to habitat features at fine spatial scales, while other reef fishes respond to features at landscape scales. For several fish groups, the combination of fine and landscape-scale features provided the best predictive model, findings that support, in part, small-scale reef research (Walsh 1985). Thus, scale has profound effects on resultant patterns (Wiens 1989) with fine-scale measures often better predictors of one group of organisms, and landscape measures predictors of others (Mitchell et al. 2001, Mazerolle and Villard 1999). This organism-based perspective appears to be true for coral reef fishes (Pittman et al. 2004), consequently future studies should acknowledge that species perceive the landscape in different ways. The relevant scale of investigation may depend on life history attributes of individual fish species (Hovel and Lipcius 2003, Pittman et al. 2004), or biological processes such as foraging behavior (Shulman and Ogden 1987), and predation (Hixon and Beets 1989). While these results, using a single fine-scale measure of rugosity, suggest that landscape-scale measures are more valuable in predicting most reef fish parameters, fishes appear to respond to benthic structure at multiple spatial scales, with each species responding to a unique suite of variables. Future studies will require an organism-based perspective that explores multiple spatial scales.

These results should be interpreted within the scope and limitations of this purely correlative study, and although a range in the values of different metrics was represented, I had little control on experimental units. These reefs are natural habitat patches, therefore considerable microhabitat variation exists, which is neither measure nor controlled. Reefs also do not represent a perfect gradient in landscape scale habitat features since sample units were selected from the naturally available set of reefs; rather they vary across multiple gradients. Additionally, while considerable groundtruthing was conducted, the benthic habitat maps were accepted without major modification. Since each decision in the mapping process effects the determination and analyses of spatial structure, it also effects our results of relationships between this structure and ecological pattern. Finally, the reef fish populations of the Virgin Islands have been heavily exploited (Beets and Rogers 2001), therefore future studies should examine reef fish distributions in less fished areas.

Conclusions

This exploratory analysis allowed me to investigate relationships between landscape structure and reef fish assemblage structure at 20 reefs to develop hypotheses and guide future coral reef landscape studies. Landscape-scale metrics proved valuable in characterizing and quantifying the landscape structure of the coral reef environment (e.g., size, shape and context). Principal components of these metrics, however, were correlated with few reef fish assemblage parameters. Interpretation of the few reef fish–principal component relationships led to the conclusion that individual habitat features are better measures of the influence of the spatial patterning of the coral reef landscape to reef fish species diversity and abundance. Specifically, reef context was associated with reef fish diversity and abundance for many groups of reef fishes. Because results

revealed that species responded to different scales depending on their life history attributes and habitat requirements, future studies will examine specific functional relationships (e.g., seagrass and grunts) based on the ecological requirements of the particular fish groups of interest. If the results detected in this exploratory study are replicable across systems and scales, combining the disciplines of landscape ecology and reef fish ecology offers promise in addressing important management questions relevant to habitat-based conservation of reef fishes.

Table 2-1. Reef fish assemblage parameters (n = 30) used as dependent variables in statistical analyses

Entire assemblage level parameters	Trophic guilds	Mobility guilds	Taxonomic groupings
Cumulative species richness	Herbivores (J & A)	Resident	Acanthurids (J & A)
Mean species richness	Mobile invertebrate feeders (J & A)	Mobile	Serranids (J & A)
Total abundance	Omnivores (J & A)	Transient	Haemulids (J & A)
	Piscivores (J & A)		Lutjanids (J & A)
	Planktivores		Scarids (J & A)
	Sessile invertebrate feeders		Chaetodontids
			Holocentrids
			Labrids
			Pomacanthids

Note: Fish groups are not always mutually exclusive. *Hypoplectrus* species were not included in Serranid grouping. For each trophic guild and taxonomic grouping, reef fish parameters were further subdivided into juvenile and adult components, where indicated (J = juvenile, A = adult).

Table 2-2. Fourteen metrics used to quantify the landscape structure of the 20 study reefs sampled in 1994 and 2001 in St. John, USVI.

Patch metric	Definition	Formula
Patch Size (reef) ^P	Size of individual habitat patches.	Area (m ²)
Polygon Size (reef) ^P	Size of individual patch	Area (m ²)
P:A of a Patch ^P	Sum of the patch edge divided by patch area for patch of interest.	$\Sigma P : A$ for particular patches
Habitat Richness ^L	Number of different habitat types present in an extent.	Number of different habitat types
Patch Richness ^L	Number of patches of each habitat type in extent of interest.	Number of patches
Habitat Area	Amount of each habitat type in landscape.	Area (m ²) in each habitat type
bedrock ^L		
deep ^L		
algal plain ^L		
pavement ^L		
reef ^L		
sand ^L		
seagrass ^L		
Patch Diversity ^L	Total abundance and type of different patches (p_i is the proportion of habitat for every individual patch)	- $\Sigma p_i \ln p_i$ p_i = proportion of area in (m ²) of patch i for all patches
Habitat Diversity ^L	Same as patch diversity but boundaries of similar habitat patches (by habitat class) are dissolved so that number of patches does not influence index. p_i for habitat diversity is proportion of habitat for all patches.	- $\Sigma p_i \ln p_i$ p_i = proportion of area in (m ²) of habitat type i for all habitat types

Note: For each patch metric^P, a single value was calculated for every reef. Each landscape metric^L was calculated at three spatial extents (100 m, 250 m, and 500 m) resulting in a total of 36 metrics for each study reef.

Table 2-3. Summary statistics on reef configuration, context and rugosity and for select reef fish assemblage parameters (entire assemblage level, trophic level and mobility guilds) for 20 study reefs sampled in 1994 and 2001, St. John, USVI for metrics at the 100 m spatial extent with coefficient of variation for landscape parameters and standard error for reef fish parameters.

Habitat parameter	Measure	Transform	Min	Max	Mean	CV
Total area	Ha	None	6.53	18.3	13.02	24.89
H' Patch diversity	Index	None	1.13	2.45	1.63	20.54
H' diversity	Index	None	0.54	1.57	1.17	24.32
Habitat richness	# habitat types	None	2.00	6.00	4.15	27.39
Patch richness	# patches	Log ₁₀ (x + 1)	5.00	19.00	8.50	43.09
Size of reef	Ha	None	0.54	15.74	6.59	67.62
P:A reef	ratio	None	0.03	0.09	0.05	34.33
Reef	Ha	Log ₁₀ (x + 1)	0.83	17.89	4.18	91.42
Seagrass	Ha	Log ₁₀ (x + 1)	0.00	7.80	1.32	166.26
Bedrock	Ha	Log ₁₀ (x + 1)	0.00	3.56	0.80	142.92
Pavement	Ha	Log ₁₀ (x + 1)	0.00	11.33	2.72	105.72
Deep water	Ha	Log ₁₀ (x+1)	0.00	7.30	2.18	120.10
Algal plain	Ha	Log ₁₀ (x + 1)	0.00	4.02	0.58	222.76
Sand	Ha	Log ₁₀ (x + 1)	0.00	6.03	1.17	160.39
Rugosity	Index	None	1.38	2.82	2.00	19.48
Reef fish Parameter	Units	Transform	Min	Max	Mean	SE
Mean spp richness	Number	Log ₁₀ (x + 1)	19.67	32.14	23.43	0.67
Cum spp richness	Number	Log ₁₀ (x + 1)	51.00	88.00	67.85	2.25
Total Abundance	Number	Log ₁₀ (x + 1)	24.12	88.13	55.23	0.02
A Herbivore	Number	Log ₁₀ (x + 1)	4.89	25.92	10.22	0.04
J Herbivore	Number	Log ₁₀ (x + 1)	14.14	73.13	41.66	0.04
A MIF	Number	Log ₁₀ (x + 1)	1.04	18.95	4.37	0.05
J MIF	Number	Log ₁₀ (x + 1)	7.71	32.11	16.38	0.03
A PISCI	Number	Log ₁₀ (x + 1)	0.05	1.75	0.45	0.02
J PISCI	Number	Log ₁₀ (x + 1)	0.58	3.27	1.63	0.03
PLANK	Number	Log ₁₀ (x + 1)	3.17	950.21	36.15	0.08
A OMNI	Number	Log ₁₀ (x + 1)	0.00	1.19	0.26	0.02
J OMNI	Number	Log ₁₀ (x + 1)	1.57	34.48	8.55	0.08
SIF	Number	Log ₁₀ x + 1)	1.69	34.48	9.23	0.03
Resident A	Number	Log ₁₀ (x + 1)	32.88	103.7	65.07	0.05
Mobile A	Number	Log ₁₀ x + 1)	0.48	11.59	1.95	0.03
Transient A	Number	Log ₁₀ (x + 1)	24.12	88.13	55.23	0.04

Note: All parameters for mean abundance, except where indicated. All data are backtransformed. CV = coefficient of variation, SE = standard error.

Table 2-4. Pearson product moment correlation matrix of the 14 landscape-scale habitat variables, with the resultant 9 remaining significant variables, at the 100 m spatial extent for the 20 reef sites sampled in 1994 and 2001 in St. John, USVI.

	P:A reef	# Patch	Habitat richness	Reef size	Focal reef	Patch diversity	Habitat diversity	Bed rock	Deep	Algal plain	Pave-ment	Reef	Sand	Seagrass
P:A reef	1.0	-0.03	0.03	-0.47	-0.76	-0.23	-0.03	-0.31	0.50	-0.02	0.17	-0.44	-0.32	-0.24
# patches	-0.03	1.00	0.44	0.43	0.33	0.84	0.29	-0.08	-0.05	0.02	0.20	0.36	0.09	-0.04
Habitat richness	0.03	0.44	1.00	0.41	0.23	0.63	0.87	0.45	0.17	0.41	-0.30	-0.19	0.25	0.04
Reef size	-0.47	0.43	0.41	1.00	0.40	0.44	0.43	0.29	-0.15	0.36	-0.003	0.24	0.25	-0.28
Focal reef	-0.76	0.33	0.23	0.40	1.00	0.46	0.09	0.40	-0.55	-0.01	-0.24	0.46	0.23	0.38
Patch diversity	-0.23	0.84	0.63	0.44	0.46	1.00	0.58	0.17	-0.10	0.17	-0.05	0.31	0.25	0.06
Habitat diversity	-0.03	0.29	0.87	0.43	0.09	0.58	1.00	0.46	0.22	0.45	-0.16	-0.14	0.30	-0.09
Bedrock	-0.31	-0.08	0.45	0.29	0.40	0.17	0.46	1.00	-0.20	0.21	-0.76	0.05	0.25	0.26
Deep	0.50	-0.05	0.17	-0.15	-0.55	-0.10	0.22	-0.20	1.00	0.30	0.12	-0.23	-0.43	-0.41
Algal plain	-0.02	0.02	0.41	0.36	-0.01	0.17	0.45	0.21	0.30	1.00	-0.08	-0.02	-0.05	-0.27
Pavement	0.17	0.20	-0.30	0.003	-0.24	-0.05	-0.16	-0.76	0.12	-0.08	1.00	0.30	-0.23	-0.44
Reef	-0.44	0.36	-0.20	0.24	0.46	0.31	-0.14	0.05	-0.23	-0.02	0.30	1.00	-0.12	-0.20
Sand	-0.32	0.09	0.25	0.25	0.23	0.25	0.30	0.25	-0.43	-0.05	-0.23	-0.12	1.00	-0.14
Seagrass	-0.24	-0.04	0.04	-0.28	0.38	0.06	-0.09	0.26	-0.41	-0.27	-0.44	-0.20	-0.14	1.00

Note: Values in bold represent those with significant pair-wise correlations. Those in shadow represent variables that were excluded based on significant pair-wise correlations. These 14 variables were thereby reduced to the remaining 8 variables (those not in shadow), which were used in subsequent principal component analyses.

Table 2-5. Principal component analyses on the correlation matrix of the 8 residual landscape-scale habitat variables at the 100 m spatial extent for the 20 study reefs sampled in 1994 and 2001 in St. John, USVI.

	PC1	PC2	PC3	PC4
Eigenvalue	2.10	1.82	1.49	1.01
Percent	26.33	22.76	18.65	12.61
Cum Percent	26.33	49.09	67.74	80.35
# Patches	0.488	0.013	-0.149	0.470
Reef Size	0.549	0.173	0.033	0.049
Habitat Diversity	0.359	0.258	0.493	0.243
Deep	-0.029	-0.422	0.607	0.216
Pavement	0.211	-0.537	-0.163	-0.192
Reef	0.333	-0.227	-0.516	0.084
Sand	0.234	0.490	0.043	-0.570
Seagrass	-0.347	0.381	-0.265	0.550

Note: Loadings in bold represent the top three variables that contribute the most to individual components.

Table 2-6. Stepwise regression results to determine the influence of principal components on reef fish assemblage structure at the 20 study reefs sampled in 1994 and 2001 in St. John, USVI at the 100 m spatial extent

Fish parameter	Model R ²	PC1			PC2			PC3			PC4		
		b1	R ²	p	b2	R ²	p	b3	R ²	p	b4	R ²	p
Mean richness	21%										1.38	0.21	0.040
Cumulative richness	26%										5.17	0.27	0.020
Herbivores	53%				0.05	0.22	0.01	-0.06	0.31	0.004			
Omnivores	21%							0.14	0.21	0.044			
Haemulids	43%	-0.14	0.43	0.002									
Epinephelids	23%							-0.05	0.23	0.030			
Acanthurids	35%				0.09	0.18	0.05	-0.10	0.17	0.040			
Lutjanids	46%	-0.07	0.32	0.006				0.05	0.14	0.050			
Mobile	28%				0.05	0.28	0.02						

Note: Each of the 30 reef fish parameters were used as dependent variables. Linear models: $\log \text{abundance} = b_0 + b_1 (\text{PC})$. Data represented are mean and cumulative species richness values and mean abundances within each guild derived from a minimum of 16 samples per reef. See table 4 for definitions of individual principal components. The suite of 30 fish parameters were analyzed, however, only those reef fish parameters with statistically significant relationships are reported. P-values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons ($n = 30$). Only those relationships with $p < 0.05$ are presented.

Table 2-7. Stepwise multiple regression results of the influence of reef configuration on reef fish assemblage structure for the 1994 (N = 14) study reefs in St. John, USVI.

Reef fish parameter	Habitat parameter	Model R ²	Partial R ²	p-value
A Piscivores	P:A reef (-)	0.32	0.32	0.0500
A Omnivores	P:A reef	0.40	0.40	0.0100
J Haemulids	# patches (-)	0.39	0.39	0.0200
A Acanthurids	P:A reef	0.33	0.33	0.0300
Pomacanthids	P:A reef	0.37	0.37	0.0200
J Lutjanids	# patches (-)	0.36	0.36	0.0300
Transients	P:A	0.74	0.62	0.0002
	# patches		0.12	

Note: Independent variables were: P:A of each reef, the number of patches and reef size. Results for 1994 reefs (n=14), with model R² and partial regression values for each variable with p < 0.05 level. P-values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons. Model effects are all positive, except where indicated (-). The suite of 30 fish parameters were analyzed, however, only those reef fish parameters with statistically significant relationships are reported. For all other reef fish parameters, there are no significant relationships. A = adult, J = juvenile.

Table 2-8. Stepwise multiple regression results of the influence of reef context on reef fish assemblage structure for the 1994 (N = 14) study reefs in St. John, USVI

Fish parameter	R ²	Partial R ²	p-value	Habitat parameter
Mean species richness	0.28	0.28	0.04	Seagrass
J Herbivores	0.30	0.30	0.04	Bedrock
A MIFs	0.33	0.33	0.03	Seagrass
J Omnivores	0.48	0.48	<0.01	Deepwater
A Piscivores	0.51	0.51	<0.01	Reef
J Piscivores	0.47	0.24	0.03	Deepwater
		0.23	0.05	Seagrass
SIFs	0.63	0.39	<0.01	Bedrock (-)
		0.27	<0.01	Deepwater
A Haemulids	0.53	0.53	<0.01	Seagrass
A Epinephelids	0.52	0.28	<0.01	Reef
		0.24	0.04	Seagrass
J Acanthurids	0.67	0.42	<0.01	Deepwater (-)
		0.25	0.01	H' (-)
A Lutjanids	0.68	0.50	<0.01	Seagrass
J Lutjanids	0.46	0.46	<0.01	Bedrock
Mobile	0.39	0.39	0.02	H'

Note: Independent variables were: H' and areal extent of reef, bedrock, seagrass and deep unknown within 100 m. Model R² and partial regression values for each variable with p < 0.05 level. P-values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons. The suite of 30 fish parameters were analyzed, however, only those reef fish parameters with statistically significant relationships are reported. Model effects are positive except where indicated by (-). A = adult, J = juvenile.

Table 2-9. Stepwise multiple regression results of the relative influence of landscape and fine-scale habitat measures on reef fish assemblage structure on the 1994 (N = 14) study reefs on St. John, USVI.

Fish parameter	R ²	Partial R ²	p-value	Habitat parameter
Mean species richness	0.68	0.38	0.0040	Seagrass
		0.30	0.0008	Rugosity
A MIFs	0.53	0.33	0.0100	Seagrass
		0.20	0.0500	Rugosity
J Omnivores	0.76	0.60	0.0079	Rugosity
		0.16	0.0200	Reef
A Piscivores	0.53	0.53	0.0090	Reef
J Piscivores	0.71	0.36	0.0030	Rugosity
		0.35	0.0070	Seagrass
A Haemulids	0.71	0.55	0.0006	Seagrass
		0.16	0.0300	Rugosity
A Epinephelids	0.54	0.38	0.0090	Reef
		0.16	0.0400	Seagrass
J Acanthurids	0.46	0.46	0.0100	Deepwater
A Lutjanids	0.44	0.44	0.0050	Seagrass

Note: Independent variables are rugosity and the areal coverage of deep unknown, seagrass and reef within 100 m. Results for the 14 reefs sampled in 1994, with model R² and partial regression values for each variable significant at the p = 0.05 level. P-values are Sequential Dunn-Sidak Bonferroni-corrected for the total number of comparisons. Relationships in bold are those that rugosity contributed to explanatory power. The 30 fish parameters were analyzed. Only fish parameters with significant relationships are reported. A= adult, J = juvenile.

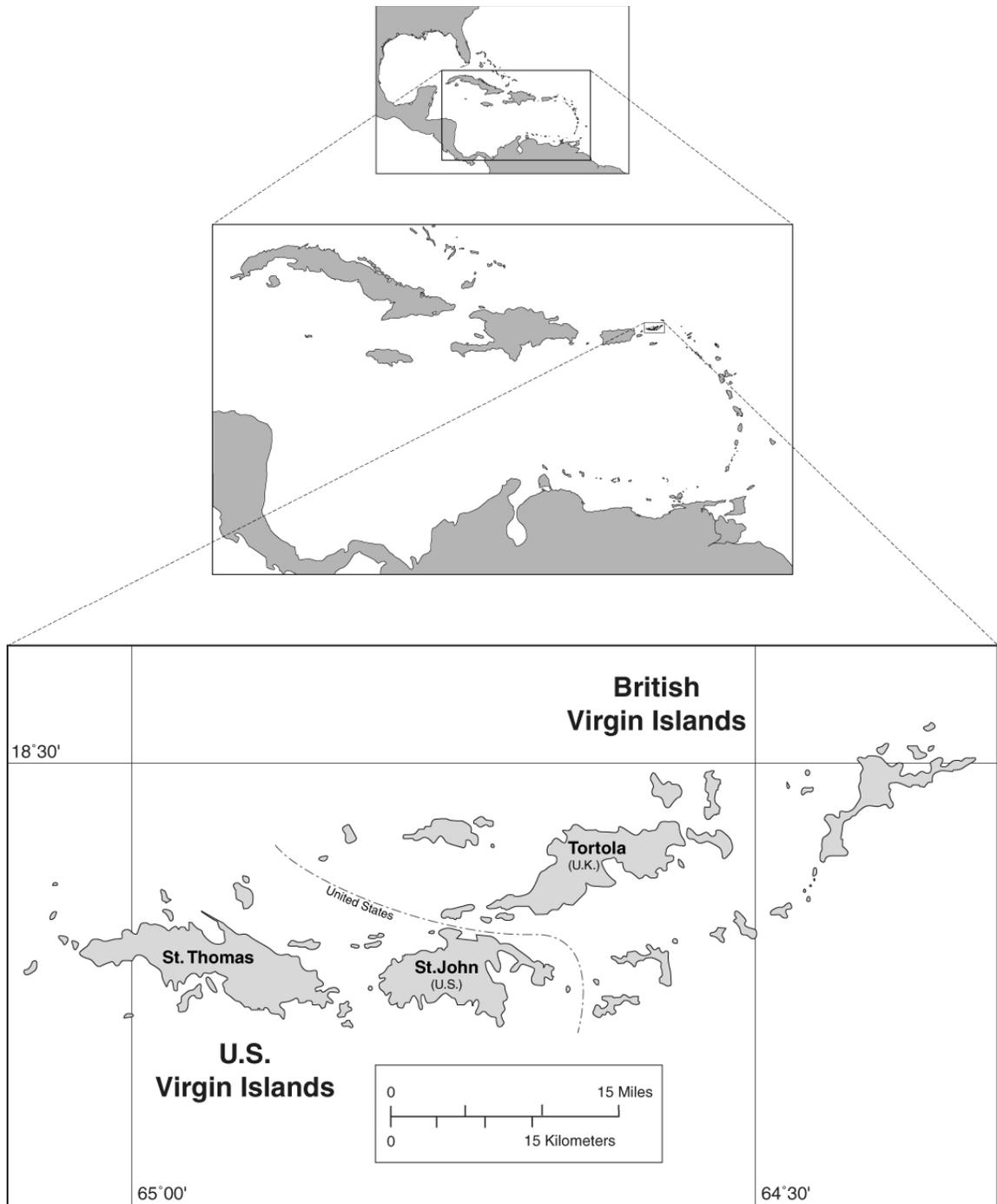


Figure 2-1. Location of St. John, US Virgin Islands in the Caribbean basin.

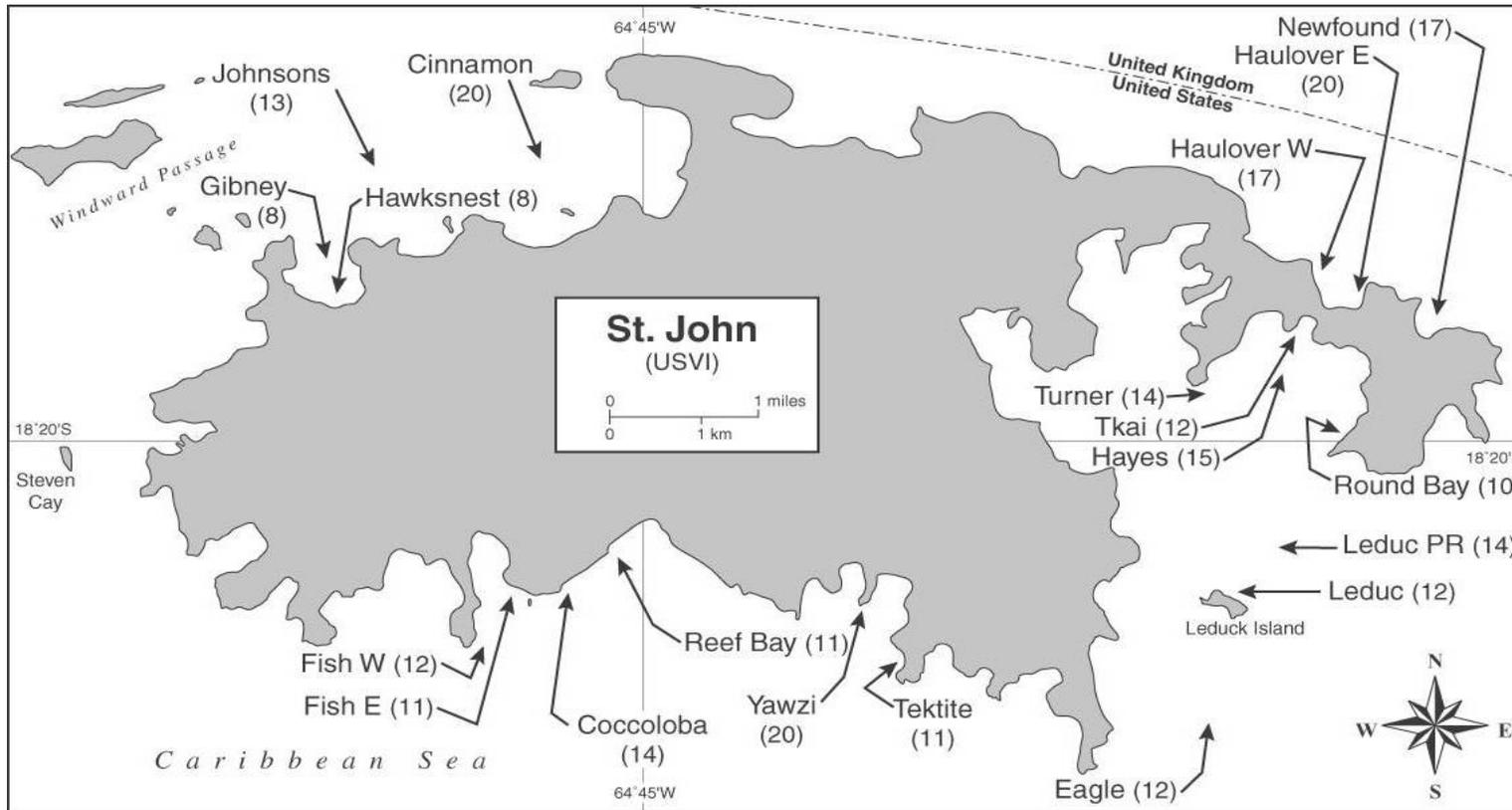


Figure 2-2. Distribution of the 20 study reefs around the island of St. John, USVI. Below the name of each reef is the number of fish point counts per reef.

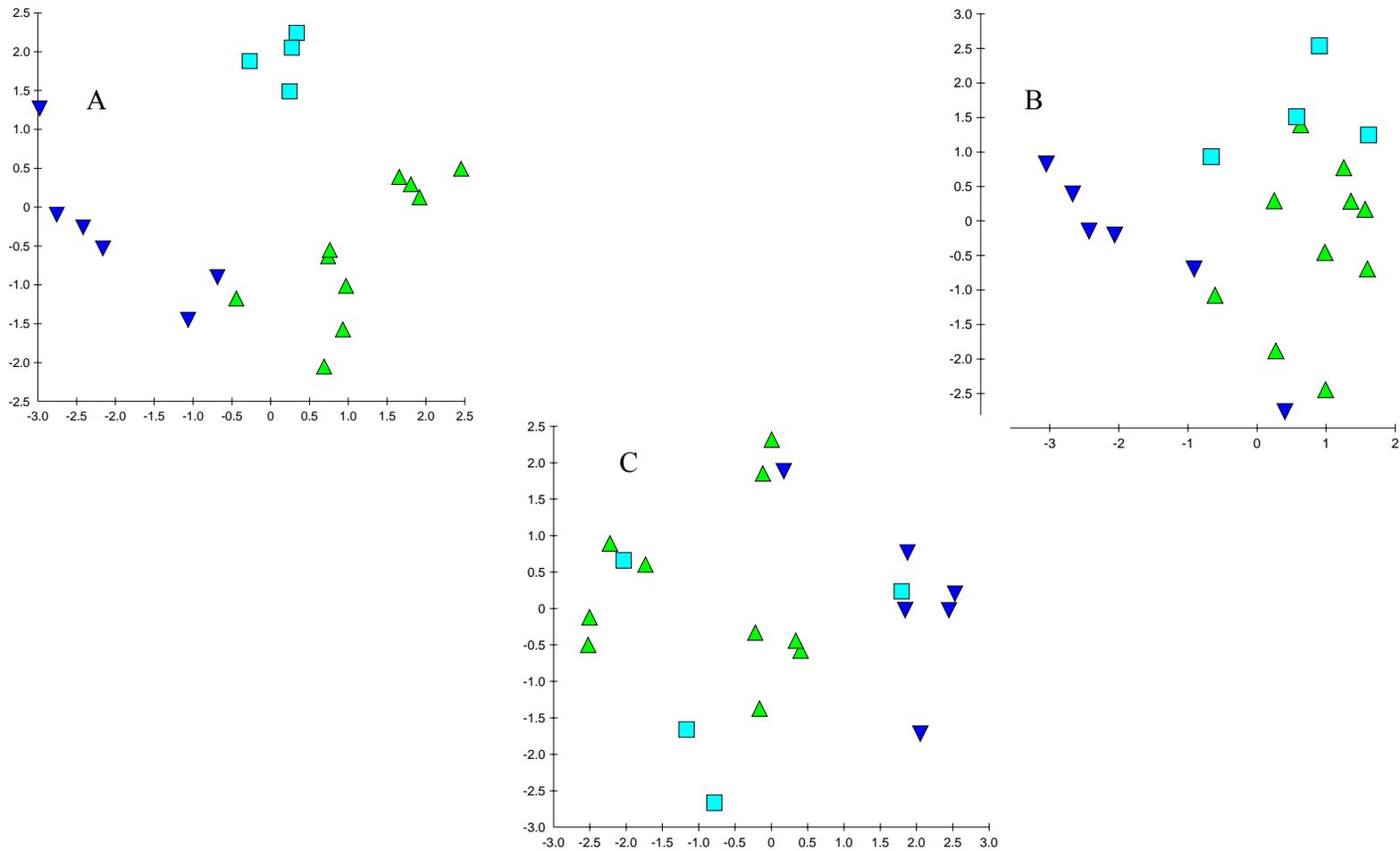


Figure 2-3. PCA plots of the landscape structure of the coral reef environments of the 20 study reefs sampled in 1994 and 2001 in St. John, USVI at the A) 100 m, B) 250 m and C) 500 m spatial extent. The x-axis is PC 1 and y-axis is PC 2. Symbols refer to different types of reefs based on pre-existing knowledge of the coral reef landscapes, irrespective of the benthic habitat maps. Triangles refer to shallow reefs with surrounding pavement habitat, squares refer to reefs with seagrass nearby, and upside down triangles refer to isolated patches of reef with large areas of deep water nearby.

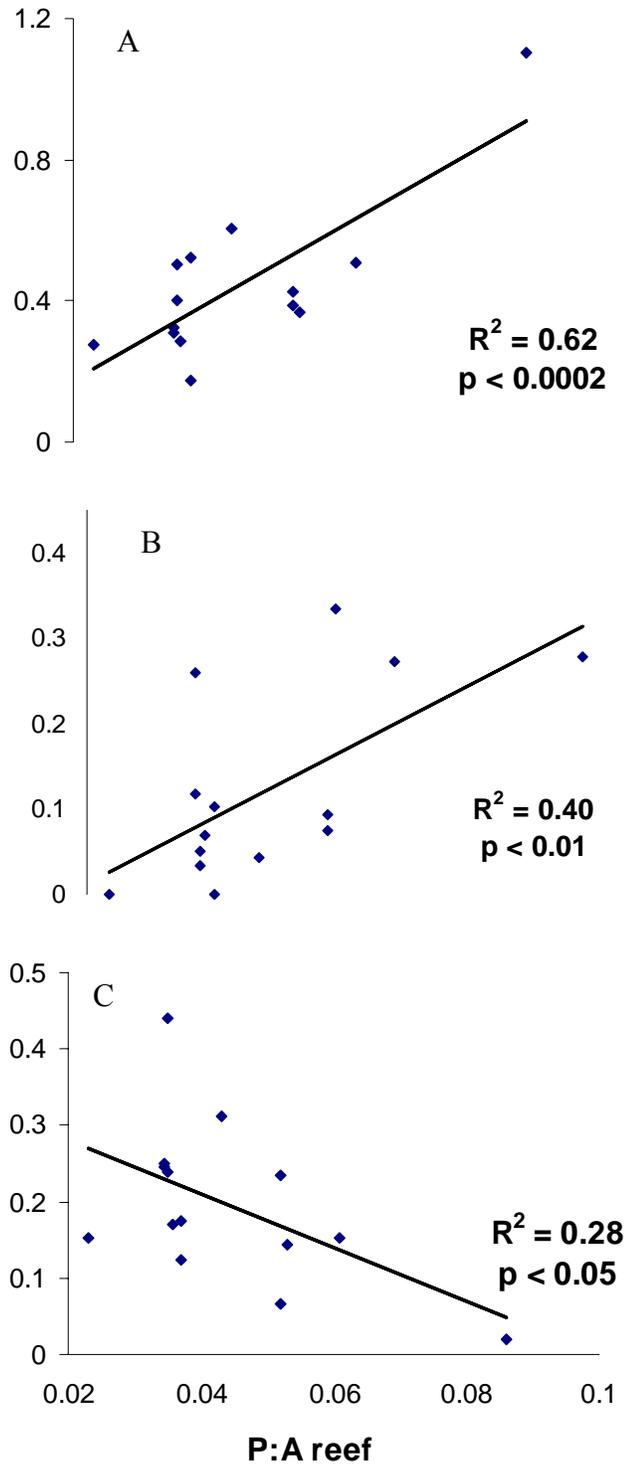


Figure 2-4. Effects of reef configuration on mean fish abundances of A) transient fishes, B) adult omnivores, and C) adult piscivores for the 1994 (N =14) study reefs in St. John, USVI.

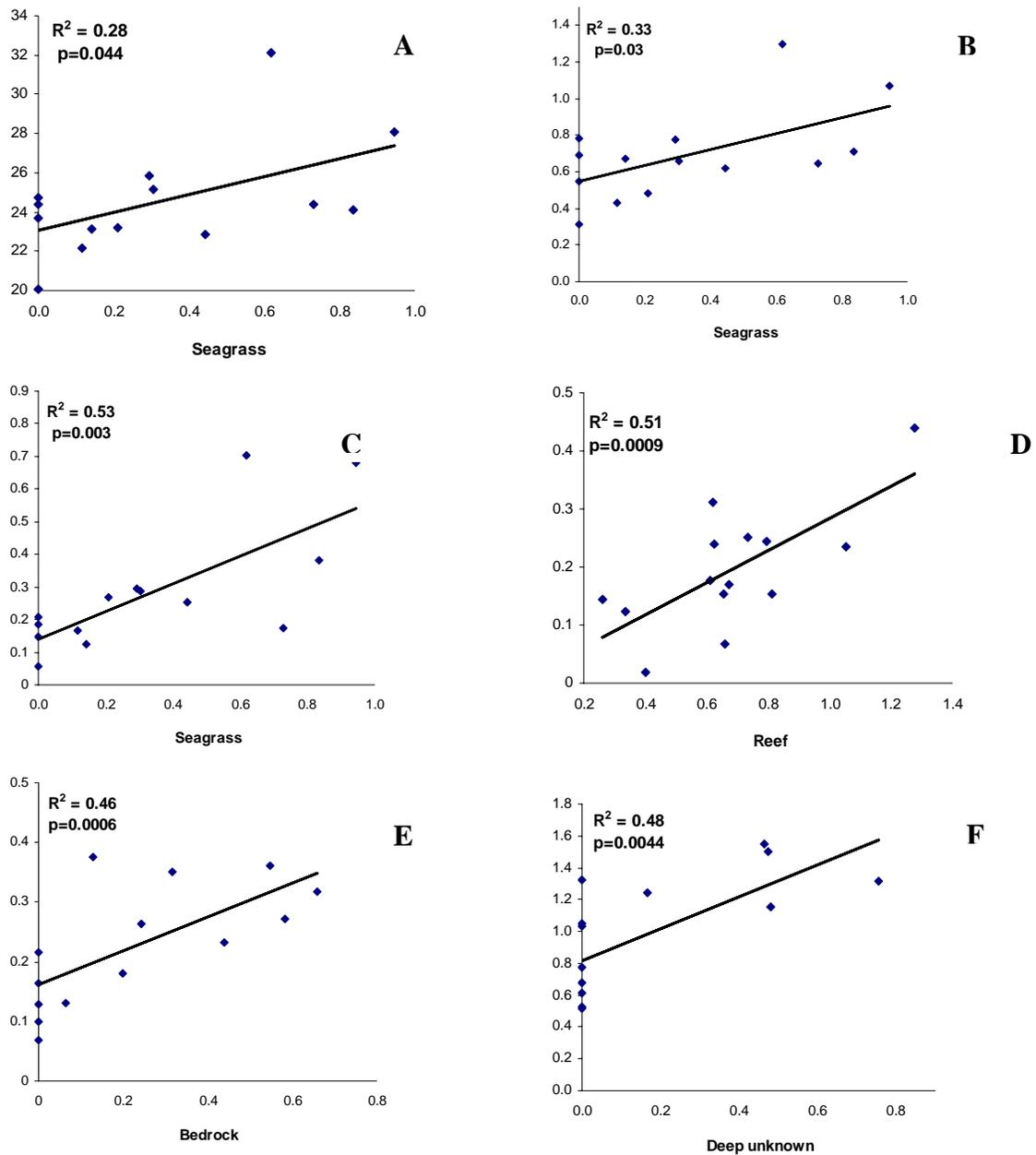


Figure 2-5. Effects of reef context on mean abundance of particular fish groups for the 1994 (N =14) study reefs in St. John, USVI. A) Mean species richness and areal extent of seagrass 100 m, B) mean abundance of MIFs and areal extent of seagrass 100 m, C) mean abundance of haemulids and areal extent of seagrass 100 m, D) mean abundance of piscivores and areal extent of reef 100 m, E) mean abundance of juvenile lutjanids and areal extent of bedrock 100 m, and F) mean abundance of juvenile omnivores and areal extent of deep unknown 100m. Independent variables are each $\log_{10} X + 1$ in hectares. MIFs refer to mobile invertebrate feeders. A = adult, J = juvenile.

CHAPTER 3 EVIDENCE OF FUNCTIONAL CONNECTIVITY IN A CORAL REEF ECOSYSTEM

Coral reef ecosystems are deteriorating worldwide, with symptoms including loss of hard corals, declines in abundances of exploited reef fishes and reduced biological diversity. Marine protected areas (MPAs) represent an important management tool for reducing this degradation; however, their effectiveness is contingent on our understanding of key ecological patterns and processes at appropriate spatial scales. MPA effectiveness may also be dependent upon maintaining critical linkages between essential habitat patches (e.g., seagrass and reef). Exploratory analyses of the relationship of reef fish assemblage structure with coral reef landscape structure in the U.S. Virgin Islands- one of the first studies that applied a landscape ecology approach to coral reef ecosystems- provided the foundation for developing specific hypotheses (i.e. reef context influences reef fish assemblage structure at the scale of individual reefs). These hypotheses were then tested in this new study at 22 independent reefs. As expected, reef context influenced the structure of reef fish assemblages, and specific relationships were functionally consistent with the ecology of the fishes of interest. Consistent with predictions, reefs with neighboring seagrass had the highest total fish abundance, and highest abundances of fishes within the mobile invertebrate feeding guild, and within the exploited families of haemulidae (grunts) and lutjanidae (snappers). Species richness for the entire fish community and within particular fish groups were also strongly associated with the areal coverage of seagrass neighboring study reefs, suggesting the importance of habitat linkages to a diversity of species. Potential habitat

linkages were detected as far away as 1 kilometer, which may indicate that reef fishes perceive the landscape at this spatial scale. These findings infer that functional habitat connectivity/juxtaposition between essential habitat patches is important in structuring reef fish assemblages, and further suggests that landscape measures of this habitat connectivity may be useful to managers in the design of MPAs.

Introduction

A landscape generally refers to a heterogeneous area composed of local interacting ecosystems (Forman 1995) made up of homogenous units, called habitat patches, and the sizes and spatial arrangement of these patches can exert a strong influence on the diversity, abundance, distribution, and movement patterns of organisms (Wiens 1989). Movements and flows of energy, nutrients or organisms between ecosystems can be either be facilitated or inhibited by the spatial arrangement of these habitat patches (Forman 1995, Turner et al. 2001). The degree to which this exchange occurs can depend upon the boundary (the zone composed of the edges of adjacent ecosystems), context (adjacency, neighborhood, and location within a landscape), or connectivity (how connected or spatially continuous a corridor or matrix is) of habitat patches within the landscape mosaic (Forman 1995). As we strive to manage entire ecosystems, maintaining functional habitat linkages within this landscape mosaic may be crucial to the effectiveness of protected areas (Noss 1983; Forman 1995, Robinson et al. 1995, Turner et al. 2001, Lindenmayer et al. 2002), since a failure to consider spatial elements such as edges, movement corridors, and landscape context in the design of protected areas is likely to result in undesirable changes in community characteristics and possibly the loss of key species (Noss 1983, McGarigal & McComb 1995).

Though these principles were largely derived in terrestrial systems, they likely apply to tropical marine systems (Grober-Dunsmore et al. 2004, Kendall et al. 2003, 2004, Pittman et al. 2004, Jeffrey 2004), and may be essential for designing functional marine protected areas (MPAs) in coral reef landscapes, particularly as coral reef landscapes exist as a complex mosaic of interacting habitat patches (i.e., seagrass, reef, and mangrove). Maintaining important habitat linkages among habitat patches should be considered in the design of MPAs, which are increasingly being considered as a primary ecosystem-based tool for improving fisheries management and protecting biodiversity (Carr & Reed 1993, Allison et al. 1998). Unfortunately, there is little information on how to best design MPAs (Ballentine 1997, Sale 2005), particularly for the conservation of the complex of fishes that constitute the reef fish community.

Historically, coral reef fishes have been difficult to manage, in part, because different species often have different habitat requirements (Sale 2002). Moreover, these habitat requirements frequently change with ontogeny (Lindeman et al. 2000, Appeldoorn et al. 2003). Though generally considered site-attached following settlement (Sale 1991), many regularly move hundreds and even thousands of meters from their primary resting and foraging locations (Plan Development Team 1990, Corless et al. 1997). These movement patterns are often species and life history stage-specific and occur across multiple spatial scales (Randall 1962, Lindeman et al. 2000, Appeldoorn et al. 2003). Some migrate daily to forage (Stark & Davis 1966, Ogden & Zieman 1977, Helfman et al. 1983, Holland et al. 1993, Tulevech & Recksiek 1994), others migrate annually to spawning aggregations (Colin et al. 1997) and several exhibit multiple ontogenetic shifts in habitat (Randall 1962, Appeldoorn et al. 1997). To date, the overwhelming majority of

reef fish studies have been conducted at small spatial scales (e.g., 1 m plots) (see Sale 2002), limiting our ability to understand important habitat linkages across larger spatial scales.

Recent landscape-scale (hundreds of meters to kilometers) research however, provides correlative evidence that cross-shelf location (Christensen et al. 2003), reef context (Appeldoorn et al. 2003, Kendall et al. 2003, 2004, Grober-Dunsmore et al. 2004a, 2004b, Pittman and McAlpine 2003, Mumby et al. 2004, Pittman et al. 2004) and landscape connectivity (Ault & Johnson 1998, Jeffrey 2004) influences reef fish community structure. This study builds on previous research by assessing the generality of my correlative models from the U.S. Virgin Islands (Grober-Dunsmore et al. 2004b) at an independent set of smaller candidate reefs (<1 hectare) and explicitly testing hypotheses of the importance of functional habitat linkages between two habitat types, reef and seagrass, in structuring reef fish communities. The following predictions were made (1) each reef fish parameter of interest (i.e. entire assemblage level parameters and abundances and species richness within mobile invertebrate feeders (MIFs), grunts, (Haemulidae), snappers (Lutjanidae), and groupers (Epinephelinae)) will be greater at reefs proximal to seagrass, (2) abundance and species richness of mobile fishes will be greater at reefs proximal to seagrass, but resident and transient guilds will not, (3) relationships of reef fish parameters and the areal coverage of seagrass will be similar in nature and strength between years and (4) the fine-scale measure of rugosity and landscape-scale measures of seagrass will both be included in the best predictive models of fish assemblage structure. These particular fish families were selected because they are important components of the subsistence fishery in the Caribbean region, and because

they rely on a variety of habitats (i.e. seagrass) for foraging and settlement (Lindeman et al. 2000). Consequently, they are more likely to demonstrate effects of habitat linkages between reef and seagrass.

Study Area

This study was conducted in the shallow waters around the island of St. John, USVI, located in the Northern Antilles approximately 88 km east of Puerto Rico (Figure 2-1). St. John is part of the Puerto Rico Bank, a submerged plateau defined by the 183 m depth contour extending from eastern Puerto Rico to the island of Anegada. Study reefs (n = 22) were selected around St. John (Figure 3-1) to maximize the variation of the particular landscape parameter of interest (i.e. the areal coverage of seagrass habitat), while reducing variation due to within-reef characteristics (e.g., coral cover). Each study reef was ~ 1-2 hectares in total area, within 1 km of the shoreline and occurred at depths of 3 to 10 m.

All reefs were dominated by *Montastraea annularis* with *Agaricia agaricites*, *Porites porites*, *P. astreaoides*, *Siderastraea siderea* and *S. radians* contributing to total living coral cover, estimated at approximately 5-15 % for each reef. The background matrices of study reef patches were typically hard-bottom or sand with large colonies of *M. annularis* providing the major structural components. In general, the neighboring seagrass communities were quite similar (e.g., typically dominated by *Thalassia testudinum*, in shallow areas with contributions from *Syringodium filiforme* and varying densities of rhizophytic algae).

Methods

Reef fish Sampling

Reef fishes were censused using a standardized visual point count census method (Bohnsack & Bannerot 1986), where all reef fishes were identified within a 5 minute sampling period, and enumerated during the following 10 minute period within a sampling radius of 7.5 m². Total lengths of fishes were estimated to the nearest centimeter. Sampling effort was standardized to reef size (one census per 1500 m²) following Monte Carlo simulation in Grober-Dunsmore et al. (2004a). A single observer (RGD) conducted all reef fish censuses to eliminate observer variability.

A suite of fish parameters was estimated from the visual point count data (see Table 3-1 and Grober-Dunsmore et al. 2004 for more details). Randall (1967) and Froese and Pauly (2002) were used as references to classify all fishes by trophic guild: piscivore, herbivore, mobile invertebrate feeder (MIF), sessile invertebrate feeder (SIF), planktivore or omnivore. A 'seagrass-associated' category of fishes was also created using Lindeman et al. (1998), Lindeman et al. (2000), Appeldoorn et al. (2003) and personal observations (for *Epinephelus striatus* and *Cephalopholis cruentatus*), and includes these grunt, grouper and snapper with explicit associations with seagrass: *Lutjanus apodus*, *L. analis*, *L. griseus*, *L. jocu*, *L. mahogoni*, *Ocyurus chrysurus*, *Haemulon plumieri*, *H. sciurus*, *H. flavolineatum*, *E. striatus* and *C. cruentatus*. Commercially-important families of grunts, snappers, and groupers were examined separately. Given the known natural history, each species was also into mobility guilds. Resident species are site-attached, and do not typically move from their primary reef patch. Mobile species have restricted movements among adjacent habitat patches, and may roam from the primary reef patch during foraging. Transient species are vagile, ranging on the scale of kilometers. Fishes were

also subdivided into juvenile and adult categories, based on average size at maturity (Froese & Pauly 2002), where possible. Using minimum estimated length, a fish was placed in the juvenile category if it was below the average estimated size at maturity, and placed in the adult category if it was at or above this estimate. Mean abundance values based on replicate censuses at each reef were calculated and used in subsequent analyses for all groups.

Temporal Sampling

In August 2003, reef fishes at a subset ($n = 8$) of the original 22 (2002) reefs were recensused (Figure 3-1, reefs in bold) to assess the temporally consistency of detected relationships. These reefs were selected as they represented a near maximal gradient in seagrass areal coverage, and had similar benthic community structure and depth, reducing effects of among-reef variability. Sampling effort was increased to improve the accuracy of the estimate of the mean value for each reef fish parameter, thus a minimum of 10 censuses per reef were conducted, regardless of reef size.

Habitat Sampling

Landscape metrics of reef context were calculated with ArcView 3.2 software (ESRI 1996), using digital benthic habitat maps. Maps were created from aerial photographs flown at an altitude of 5000 feet in 1999 and were classified by visual interpretation, using 26 discrete and non-overlapping habitat classes, with a minimum mapping unit of 1 acre (Kendall et al. 2001). The original map classification scheme was condensed from 26 to 7 distinct, non-overlapping habitat classes (pavement, sand, reef, bedrock, seagrass, macroalgae and deep unknown), so results would be more broadly applicable to resource managers and to reduce potential classification errors. Reefs served as focal units for all analyses because MPAs are frequently designed around

individual reefs (e.g., Florida Keys National Marine Sanctuary). Landscape metrics were calculated at the 100 m, 250 m, 500 m and 1 km spatial extent, to explore the appropriate scale for each response variable. Rugosity was measured in situ along ten 10 m transects at each reef fish census location, using methods described by Luckhurst and Luckhurst (1978). A mean was calculated for each reef.

Statistical Analyses

All data were checked for normality using Shapiro-Wilks tests ($p < 0.01$) (Zar 1984), and transformed where appropriate (Table 3-1). If assumptions were met, analyses were conducted using parametric statistics, and non-parametric statistics if not. For all analyses, each reef fish parameter was used as the dependent variable and the landscape and/or rugosity measure was used as the independent variable. Residual plots were examined to assess stability of regression models (Sokal & Rohlf 1995).

Because predictions were derived at different study reefs, analyses were conducted to verify the importance of reef context at these independent reefs using stepwise multiple regression methods as in Grober-Dunsmore et al. (2004b) for all reef fish parameters. Model II linear regression analysis (Sokal & Rohlf 1995) was used to test the prediction: 1) abundances of MIFs, grunts, snappers, groupers, mobile reef fishes, seagrass-associated taxa and species richness values within these fish groups are higher at reefs proximal to seagrass. Model II linear regression was also used to test the prediction: 2) mobile taxa will be influenced by reef context (measured by the areal coverage of seagrass), whereas resident and transient taxa will not. Non-parametric Spearman Rho correlations (Sokal and Rohlf 1995) were calculated for the subset of 8 reefs (2003), sampled in 2002 and 2003 to test the prediction: 3) relationships between reef fish parameters and reef context will be similar in nature (e.g., direction) and

strength between years. Statistical comparisons of the abundances of reef fishes, using raw census data ($n = 130$), were conducted using the non-parametric Kruskal-Wallis to test for differences in abundance between years. Stepwise multiple regression analyses was used to test the prediction: 4) reef fishes will be structured by both landscape-scale and fine-scale measures of habitat.

Results

A total of 107 fish censuses were conducted at 22 reefs during July and August 2002. One hundred eighteen species were identified and a total of 14,389 individuals recorded. In August 2003, 97 reef fish censuses were conducted at the subset of 8 reefs, with one hundred twenty two species identified and a total of 14,239 individuals recorded. The ten most abundant taxa in each fish group are listed in Table 3-1.

The configuration and composition of the study landscapes varied widely among reefs, with coefficients of variation for most landscape metrics $> 50\%$ of the mean (Table 3-2). Gradients in the areal coverage of seagrass were represented adequately to test hypotheses concerning reef-seagrass habitat linkages (Table 3-2). Rugosity also varied, although to a small degree than seagrass (Table 3-2).

Exploratory stepwise regression analyses confirmed that reef context was the best predictor of reef fish assemblage structure, allowing me to test specific hypotheses concerning the importance of seagrass in particular. For all subsequent analyses, I verified that reefs were not consistently higher for other reef fish parameters to refute the possibility that some unmeasured factor did not result in high values for all fish parameters.

Entire Assemblage Level Parameters

The areal coverage of seagrass was a positive predictor of all entire assemblage level parameters for every spatial extent (Table 3-3), with 48-58 % of the variation in cumulative species richness explained by seagrass (Table 3-3, Fig. 3-2). Higher cumulative richness at reefs with seagrass nearby can be partially attributed to the presence of several species with specific dependencies on seagrass (e.g., *Aetobatus narinari*, *Xyrichtys splendens*, *Sparisoma radians*, *Holocentrus rufus*). Reefs surrounded by seagrass had the highest total number of species.

Abundances within Reef Fish Groups

The areal coverage of seagrass was a positive predictor of abundances of grunts ($R^2 = 0.52-0.57$), seagrass-associated taxa ($R^2 = 0.33-0.50$), snappers ($R^2 = 0.34-0.40$), and MIFs ($R^2 = 0.27-0.41$), though groupers were marginally associated ($R^2 = 0.13-0.17$) with seagrass (Table 3-4, Fig. 3-3). Reefs with large expanses of adjacent seagrass had the highest abundances of MIFs, grunts and seagrass-associated taxa were Donkey, Hansens and Marys.

Abundances within Life History Stages

Juvenile grunts were strongly ($R^2 = 0.52-0.56$), whereas adults were weakly associated with the areal coverage of seagrass ($R^2 = 0.16-0.21$) (Table 3-5), and the juvenile component of the seagrass-associated taxa also exhibited a stronger relationship than the adult (Table 3-5). The only reefs without juvenile yellow-tail snapper (*Ocyurus chrysurus*) were those without seagrass within 1 km (e.g., Peter Bay, PeterOne), and juvenile schoolmaster (*Lutjanus apodus*) and mahogany snapper (*L. mahogoni*) were only present at reefs with extensive shallow back-reef seagrass (e.g., Saba E, Mary's, Rendezvous).

Species Richness

The areal coverage of seagrass was also a positive predictor of species richness within MIFs ($R^2 = 0.63-0.72$), grunts ($R^2 = 0.56-0.71$), snappers ($R^2 = 0.24-0.41$) and groupers ($R^2 = 0.23-0.33$) (Table 3-6, Figure 3-4). Increased species richness values were frequently attributed to the presence of those particular species associated with seagrass. For example, species richness of MIFs was increased by the presence of species that reside or forage in seagrass (e.g., *Aetobatus narinari*, *Holocentrus marianus*, and *Calamus pennatula*), and species richness of snapper was increased by the presence of small schools of juvenile schoolmaster, grey snapper and lane snapper. Grunt species richness was enhanced by the presence of *H. plumieri*, *H. carbonarium*, *H. chysargyreum*, and *H. macrostomum*; while *H. plumieri* is a known seagrass-specialist, seagrass dependencies of the other taxa are not understood. Residual analysis suggested that caution is warranted in interpreting the relationship for snappers and groupers.

Mobility

The areal coverage of seagrass was a positive predictor of abundances ($R^2 = 0.19-0.21$) and species richness ($R^2 = 0.55-0.69$) of mobile taxa, but not for resident (except at the 250 m extent) and transient species (Table 3-4, Table 3-6). Abundances of transient taxa violated normality tests, and may have contributed to my inability to detect relationships. Species richness was enhanced at reefs with neighboring seagrass by the presence of more mobile species such as: *Acanthurus chirugus*, *Balistes vetula*, *Calamus calamus*, *Gerres cinereus* and *Holocentrus rufus*, species that likely to migrate into neighboring foraging patches (Kramer & Chapman 1999).

Spatial Extent

Although the R^2 and p-values were comparable across all spatial extents for most reef fish parameters and/or groups, the strength of relationships for the adult life history stages was often greatest at the 500 m spatial extent, and generally occurred at the 100 m or 250 m spatial extent for the juvenile life history stages (Table 3-5). For species richness, the strength of associations was strongest at the 100 m (grunts, MIFs) and 250 m (snappers, groupers, and mobile taxa) spatial extents (Table 3-6).

Temporal Consistency

Twelve of sixteen reef fish–habitat associations were similar between years in 2002 and 2003 (Table 3-7, Figure 3-5). Of these twelve, seven relationships (cumulative richness, mean richness, total abundance, juvenile grunt abundance, juvenile grouper abundance, species richness of MIFs, and species richness of groupers) were positively correlated to the areal coverage of seagrass in 2002 and 2003 at the 8 reefs (Figure 3-5). Five were consistent in that they were not correlated with seagrass in either year (adult and juvenile MIF abundance, adult and juvenile snapper abundance, and species richness of snappers). Several relationships from the 2002 dataset of 22 reefs were not evident when analysis was constrained to the subset of 8 reefs. The reduction in sample size from 22 to 8 clearly resulted in a loss of statistical power (Sokal and Rohlf 1995), and abundances of three fish groups (MIFs, adult grunts, and adult snappers) were statistically lower in 2002 compared to 2003 (Table 3-7).

Relative Influence of Fine and Landscape-scale Measures

The fine-scale measure of rugosity was of limited value in predicting reef fish assemblage structure; rather, landscape-scale measures of seagrass areal coverage were better predictors of most fish assemblage parameters, though there were a few exceptions

(Table 3-8). Collinearity diagnostics suggested that although weak relationships exist between the independent variables, all model condition indices were less than 10, well below the recommended value of 30 (Belsley et al. 1980).

Discussion

As predicted, landscape-scale measures of the areal coverage of seagrass calculated with simple GIS tools and habitat maps were useful surrogates for reefs with high entire assemblage level parameters (e.g., cumulative species richness). These findings are relevant because earlier marine ecologists alluded to the importance of reef context (Ogden & Zieman 1977, Parrish 1989) and high fish diversity has been attributed to the presence of seagrass in the Florida Keys (Robblee & Zeiman 1984), the Virgin Islands (Quinn & Ogden 1984, Grober-Dunsmore et al. 2004a), the Red Sea (Khalaf & Kochzius 2002) and the Australia (Pittman et al. 2004) and with other habitats such as algal beds (Rossier & Kulbicki 2000) and mangroves (Birkeland 1985, Thollot 1992) in post-hoc correlative analyses, but these results contribute to the growing body of evidence that suggests that resource managers may be able to use landscape-scale measures of reef context to detect areas with high fish abundance and diversity (Appeldoorn et al. 2003, Kendall et al. 2003, Pittman and McAlpine 2003, Jeffrey 2004).

Abundances and species richness of predicted reef fish groups (grunts, seagrass-associated taxa, snappers and MIFs) were higher at reefs with neighboring seagrass, and observed patterns of distribution were remarkably consistent with the foraging ecology of each fish group. For example, haemulids exhibited the strongest association to seagrass; several taxa are known to regularly move from reefs into adjacent seagrass patches (Burke 1995, Appeldoorn et al. 1997, Beets et al. 2003), sheltering on or near the reef by day and feeding on crustacean fauna in surrounding seagrass by night (Ogden & Quinn

1984, Robblee & Zieman 1984, Burke 1995, Appeldoorn et al. 1997, Beets et al. 2003). Abundances of seagrass-associated taxa were also strongly associated with seagrass, which is expected since this guild is comprised exclusively of species that complete part of their life history in seagrass. Because many MIF and snapper species have generalist foraging requirements (Sale 2002), it is not unexpected that relationships with seagrass-though still robust are less than that observed for grunts. Remarkably, the strength of associations for abundances and species richness of the different fish groups corresponded quite strongly with their known natural history, with the strength of relationships generally following this rank order; grunts, seagrass-associated, snappers, MIFs, and groupers.

This study design does allow inferences concerning the mechanisms that might explain the higher species richness and abundances of reef fishes at reefs proximal to seagrass. (1) Settlement and survivorship of some juvenile fishes may be higher in seagrass (Nagelkerken et al. 2000, 2002, Appeldoorn et al. 2003) due to its high plant diversity (e.g., epiphytes, algae, and phytoplankton) (Bell & Pollard 1989), which may facilitate coexistence of species that would otherwise compete (Keller 1983). Settlement (of individuals and different species) may be higher if seagrass intercepts larval fish more effectively than other habitat patches (Parrish 1989). (2) The structural complexity of seagrass can provide shelter from predation (Parrish 1989, Robertson & Blaber 1992), thereby increasing survivorship of fishes in seagrass communities, which then may migrate to neighboring reef patches as they mature. (3) Reef fish movement may occur more readily in highly-connected marine landscapes (Noss 1983), therefore patches that have habitat linkages to other essential habitat patches may support more fishes. (4)

Energy, nutrients and organic matter generated within seagrass communities (Duarte 2000) may flow to nearby reefs through direct animal movement (Meyer et al. 1983, Meyer & Schultz 1985), predation, or outwelling of dissolved and particulate organic matter (Sogard 1989, Beck et al. 2001), providing important resources for reef fishes. While the mechanisms responsible for increased richness and abundances of fishes at reefs proximal to seagrass remains to be identified, some combination of these factors appears beneficial for recruitment, settlement, survivorship and/or coexistence of large numbers of fishes.

Contrary to predictions, groupers were weakly associated with seagrass, although detecting relationships at this spatial scale may be inhibited by their low population densities (0-0.2 fishes per sample) and species composition. Historically, high densities of groupers at several reefs in the U.S. Virgin Islands have been attributed to surrounding seagrass communities (Randall 1962). Over time, grouper species dominance has shifted to smaller, potentially less mobile, taxa; *E. guttatus*, *Cephalopholis cruentatus* and *C. fulvus* are relatively more abundant than *E. striatus*, *E. morio*, and *Mycteroperca tigris*. These latter groupers likely ranged over comparatively large areas; *E. striatus* made daily movements of 400 m (Carter et al. 1994). In contrast, presently-dominant taxa (e.g., *E. guttatus*) demonstrated high short-term fidelity at small patch reefs in Bermuda (Bardach 1958) and the U.S. Virgin Islands (Randall 1962, Beets et al. 2003). Habitat requirements may be less stringent, abundances may be severely depressed (thereby limiting our ability to detect relationships; Osenberg et al. 2002), or shifts in the species composition may favor more site-attached species, such that detecting habitat linkages for groupers is difficult in this system.

The juvenile component of the fish assemblage generally exhibited a stronger seagrass association compared to adults, perhaps due to nursery benefits (Nagelkerken et al. 2002) such as increased recruitment, increased habitat-mediated post-settlement survivorship (Beukers & Jones 1997), and/or direct (Meyer et al. 1983, Meyer & Schultz 1985) or indirect transfer (Duarte 2000) of nutrients and energy from adjacent seagrass. The strongest evidence that seagrass provides a nursery benefit is provided by the relationships for juvenile grunts and juvenile seagrass-associated fishes with seagrass, which was also demonstrated by Kendall et al. 2003 in St. Croix for juvenile *Haemulon flavolineatum*. These two groups are comprised of those taxa with the greatest dependencies on seagrass (Lindeman et al. 2000), and as expected these relationships were relatively strong ($R^2 = 0.56$, $R^2 = 0.46$), respectively.

Fishing pressure and within-reef heterogeneity may also explain why the adult component of the reef fish assemblage generally exhibited weaker seagrass associations compared to juveniles. Reef fish populations of the U. S. Virgin Islands appear heavily over-fished (Rogers & Beets 2001), and densities of exploitable-sized fishes were typically low in this study. In addition, adult grunts and snappers feed on benthic invertebrates (Randall 1967, Rooker 1995, Nagelkerken et al. 2000) that typically reside in soft-bottom patches (Gillanders et al. 2003). Such soft bottom patches contribute to within-reef heterogeneity, and these patches may not be detectable at the resolution of these habitat maps (Kendall et al. 2001). Consequently habitat linkages are expected to be more evident in less-fished systems and for juveniles (which was the case) and habitat specialists.

Consistent with predictions and terrestrial research (Sisk et al. 1997, Mitchell et al. 2001, Turner et al. 2001), the mobility (vagility) of fishes influenced how fishes relate to the coral reef landscape. Resident taxa are more likely associated with finer-scaled features (Hixon & Beets 1989, Sale 1998), as evidenced by the positive correlation between rugosity and abundances of resident fishes, and the lack of an association with this landscape measure of seagrass. The absence of a relationship for transient taxa is consistent with their habitat utilization patterns, (e.g., *Carynx* spp. are likely to transit indiscriminately over sand, reef, and seagrass habitats), as they respond to features at larger spatial scales (i.e. 100's to 1000's of meters). These findings are a strong imperative to focus on the scales that are appropriate to the organism, and indicate that these scales can often be predicted by considering the ecology of the particular species.

Reef fish–seagrass associations were evident up to 1 km spatial extent from study reefs, suggesting that functional habitat linkages may operate at least at this spatial scale. Again, the appropriate spatial scale appeared remarkably consistent with the ecology of fishes; particularly with their life history stage. For example, juvenile relationships were most strong at close distances (100 m and 250 m), whereas adults were strongest at 500 m and 1 kilometer. Given the high risk of mortality for juvenile fishes, reefs that have seagrass in closer proximity may reduce predation risks, which would explain in part the strong association at closer distances. Many adult fishes travel greater distances. For example, several tagging studies revealed transit distances of 100 m - 400 m for adult *H. plumieri* (Tulevech & Recksiek 1994), *H. sciurus* (Beets et al. 2003) and lutjanids (Chapman & Kramer 2000). These results are relevant for determining the geographic

boundaries of MPAs, since failure to include habitat patches at least 1 kilometer away may result in mortality as fishes move outside MPA boundaries.

While several recent studies provide evidence of the importance of reef context to reef fish assemblage structure (Nagelkerken et al. 2000, 2002, Appeldoorn et al. 2003, Kendall et al. 2003, 2004, Dorenbosch et al. 2004, Jeffrey 2004, Mumby et al. 2004), this study builds on existing research in several important ways. 1) This study presents data on abundance, rather than simple presence or absence of fishes. This distinction is important since marine resource managers are frequently interested in determining the location of reefs with high numbers of individuals and species. 2) This study differentiates between soft-bottom (e.g., seagrass, sand) and hardbottom (e.g., reef, pavement), which has often been difficult. 3) Measures of each habitat were quantified using geo-referenced, digital habitat maps and GIS, which has historically not been feasible. 4) Confounding effects of previous studies (i.e. reef size, location and other habitat types) were minimized, though not eliminated. 5) Relationships were examined for the entire fish community (e.g., within trophic and taxonomic groups), thereby providing a comprehensive functional perspective of the response of fish parameters to reef context. Previous studies have often been restricted to a subset of the reef fish community (Nagelkerken et al. 2000, 2002, Kendall et al. 2003). 6) Explicitly-stated *a priori* hypotheses were tested in this study, and study reefs were selected to test these hypotheses. Future studies that apply landscape ecology principles to marine systems should adopt a rigorous hypothetico- deductive approach.

To investigate the generality of new findings, it is ideal to determine the temporal and spatial consistency of results (Sale et al. 1994), thus it is relevant that many reef fish–

seagrass relationships were similar between 2002 and 2003. For those relationships that were not similar, a loss of statistical power (caused by the reduction in sample size) and low fish densities may have lessened the ability to detect associations (e.g., Eggleston et al. 1998). Reef fish communities display stochastic variability in community structure at small spatial and temporal scales, and it is unclear from this limited temporal analysis whether the absence of several expected relationships in 2002 is an indication that results are not reliable. Clearly, future research is necessary to determine the influence of the complex spatial and temporal variability of reef fish communities in predicting reef fish habitat associations. While multiple sources of temporal variability induced by larval recruitment (Doherty and Fowler 1994), post-settlement mortality (Hixon 1991), fishing pressure and food availability (Williams 1980) exist, habitat relationships appeared remarkably consistent over time, providing added confidence that this evidence of strong habitat linkages is not a fluke consequence from a single sampling event.

Contrary to predictions and smaller-scale studies (e.g., Luckhurst and Luckhurst 1978, Hixon and Beets 1989, Friedlander and Parrish 1998), the fine-scale measure of rugosity was not a predictor of most reef fish parameters, which may have important consequences for MPA design. Landscape parameters are increasingly easy to measure (Green et al. 2000, Kendall et al. 2001) conversely; rugosity is a time-consuming in-water measure. If such high quality benthic maps as those produced today can now accurately identify topographically complex reef habitat (Kendall et al. 2001), landscape measures may be superior to fine-scale for designing effective spatial management schemes. The failure of this measure of rugosity to predict remaining fish parameters may be because rugosity is only a positive predictor of fish assemblage structure when sampling across a

larger range of topographic complexity (among distinct habitats). Sampling was constrained within a single high relief habitat for this study, thus the range in rugosity was lower than others (e.g., Friedlander and Parrish 1998). In addition, other measures of structural complexity (e.g., hole size) may be better predictors of fish assemblage structure (Friedlander & Parrish 1998). This multi-scalar analysis confirms that there is clearly no correct scale that can be universally applied to all organisms (Bissonette 2003), and corroborates terrestrial (Graham and Blake 2001) and marine studies (Grober-Dunsmore et al. 2004b) that habitat–faunal relationships are inextricably scale-dependent. Clearly, scale has profound effects on resultant patterns (Wiens 1989) with fine-scale measures often better predictors of one group of organisms, and landscape measures predictors of others (Mitchell et al. 2001, Mazerolle and Villard 1999). This organism-based perspective appears to be true for coral reef fishes (Pittman and McAlpine 2003, Pittman et al. 2004); consequently future studies should acknowledge that species perceive the landscape in different ways.

Conclusions

Landscape measures of coral reef context appear to be valuable predictors of coral reef fish assemblage structure, which may have important implications for MPA design. Specifically, the areal coverage of seagrass may be used to successfully predict which reefs have diverse reef fish assemblages and high abundances of commercially and recreationally important species. Although this study cannot identify the processes driving relationships, it provides strong evidence that functionally-linked marine landscapes contribute to increased species richness and abundance of many fish groups. Admittedly, MPA design requires an understanding of numerous factors (i.e. location, distribution and amount of various habitats necessary for spawning, recruitment, larval

export, settlement, growth, foraging and reproduction). However, given the urgency of MPA design decisions, the selection of areas for conservation should also consider their contribution to the whole system and how well the location of a patch relates or links to other patches within the landscape.

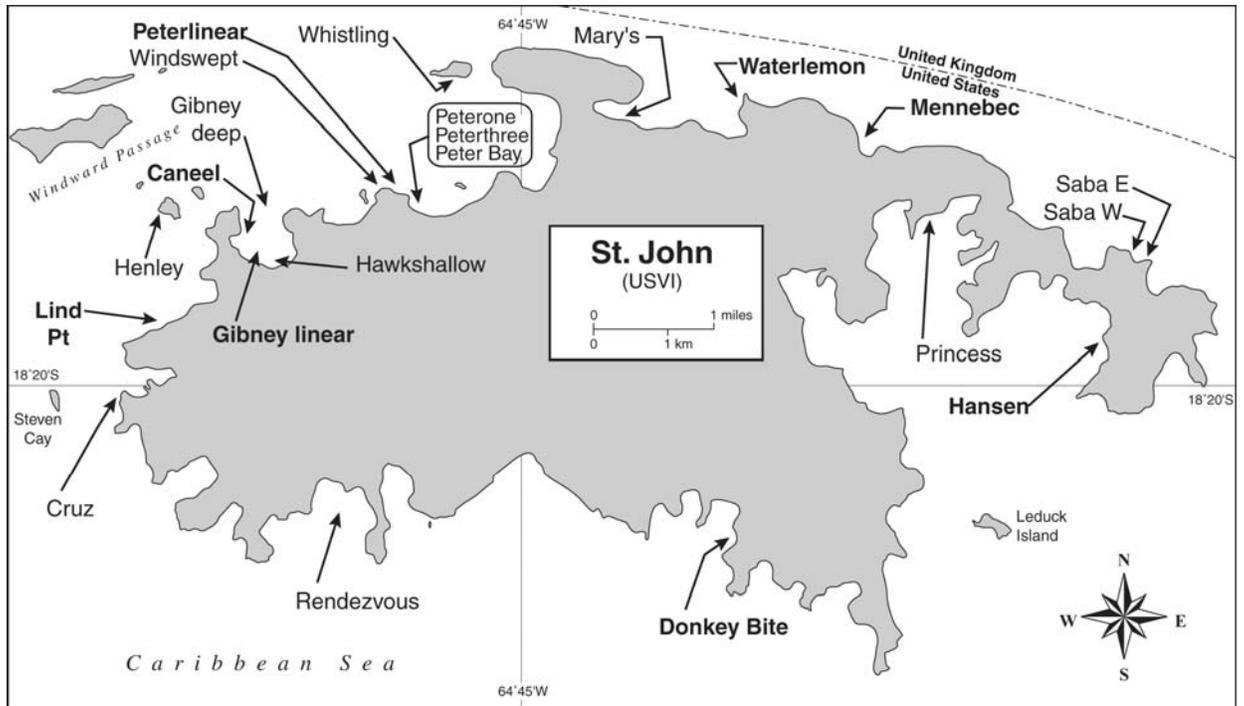


Figure 3-1. Location of the 22 study reefs around the island of St. John, US Virgin Islands sampled in 2002, with the eight study reefs re-sampled in 2003 indicated in bold.

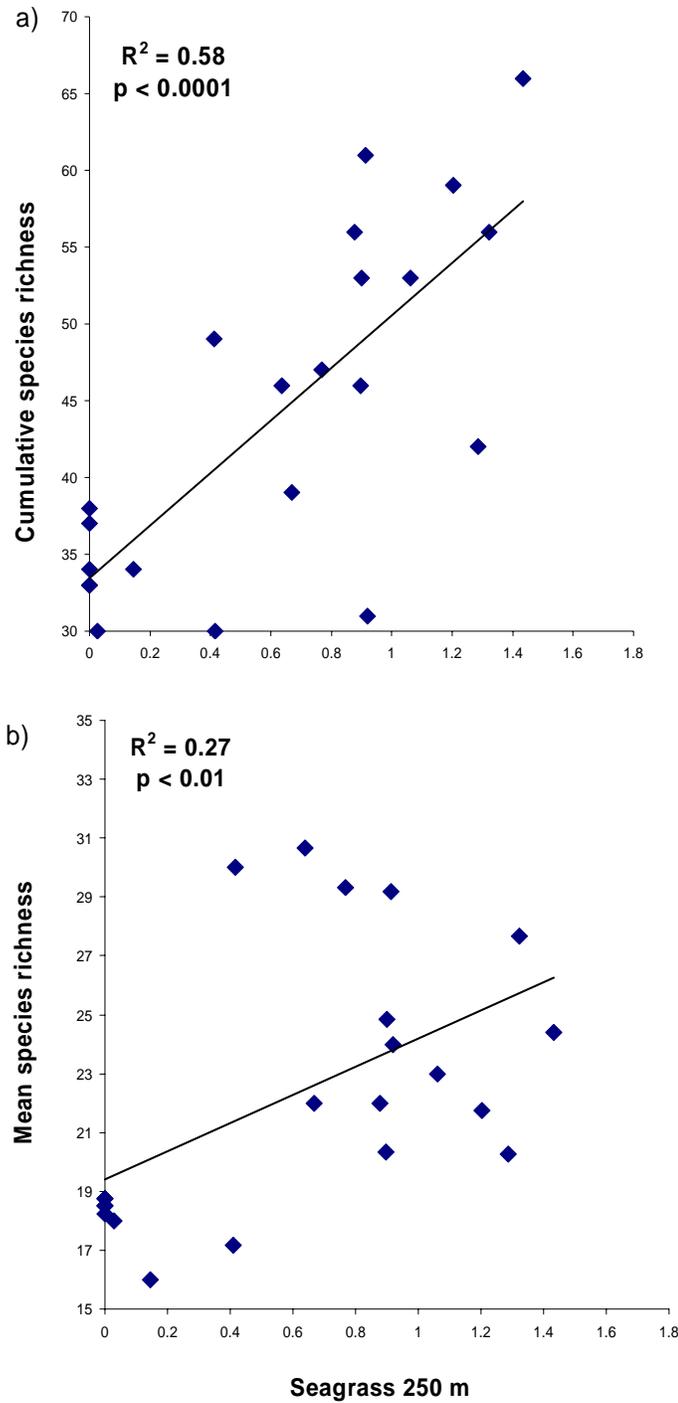


Figure 3-2. The relationship of a) cumulative richness and b) mean species richness with the areal coverage of seagrass (hectares) at 250 m for the 22 study reefs sampled in 2002 in St. John, U.S. Virgin Islands. The x-axis is $\log_{10}(x+1)$ transformed.

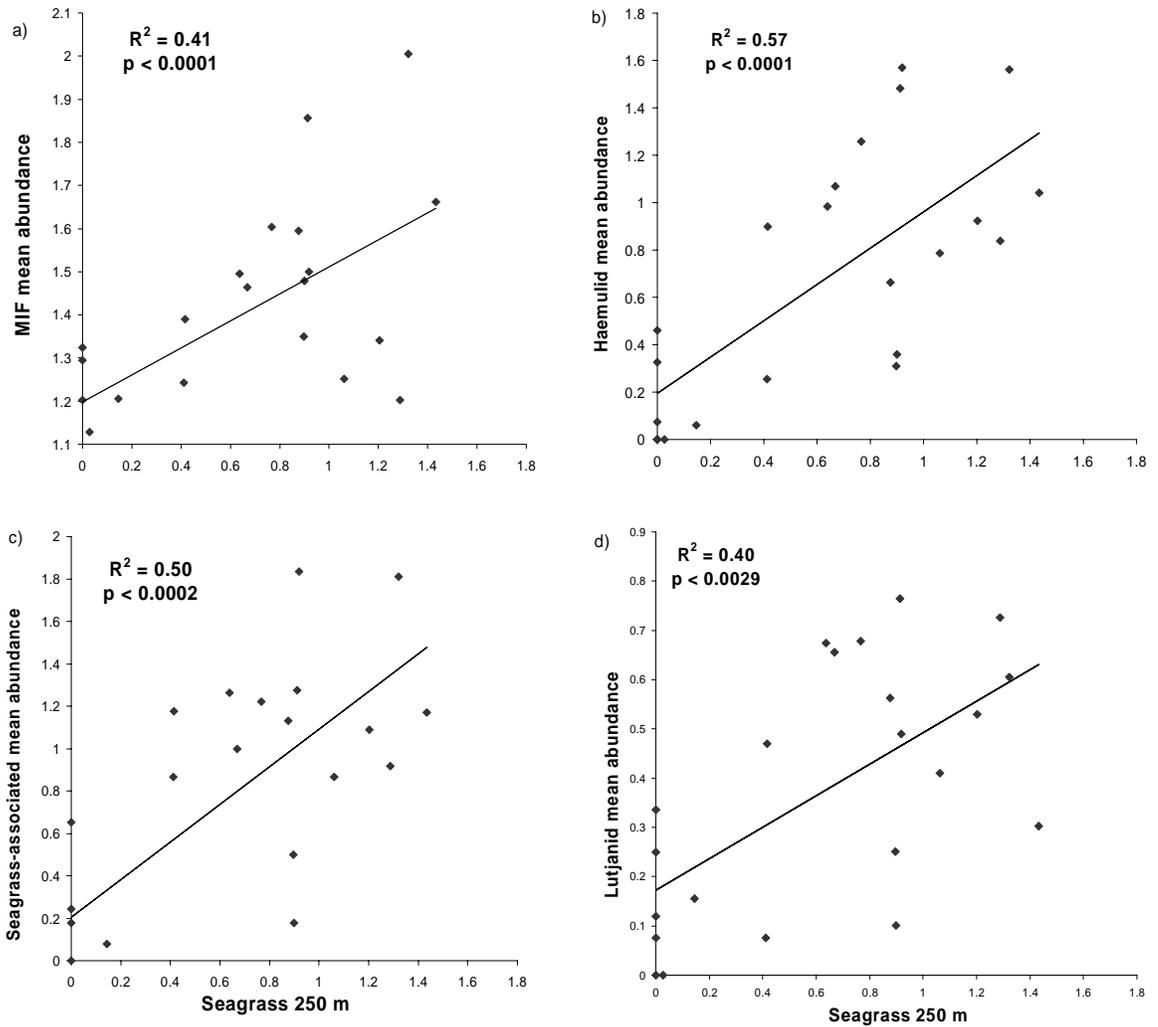


Figure 3-3. The relationship of mean abundances of a) MIFs, b) haemulids, c) seagrass-associated taxa and d) lutjanids with the areal coverage of seagrass (hectares) within 250 m of the 22 study reefs in St. John, U.S. Virgin Islands sampled in 2002. Mean abundances and the areal coverage of seagrass are $\log_{10}(x + 1)$ transformed.

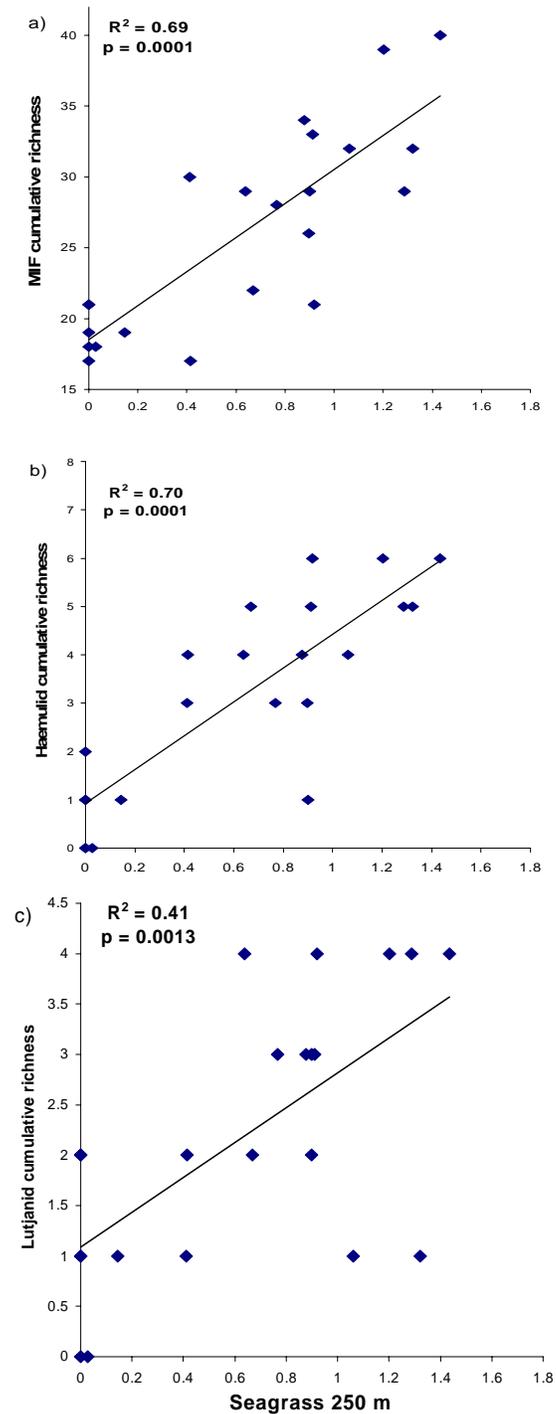


Figure 3-4. The relationship of cumulative species richness of a) MIFs, b) haemulids and c) lutjanids with the areal coverage of seagrass (hectares) within 250 m for 22 study reefs in St. John, U.S. Virgin Islands sampled in 2002. The y-axis is $\log_{10}(x+1)$ transformed.

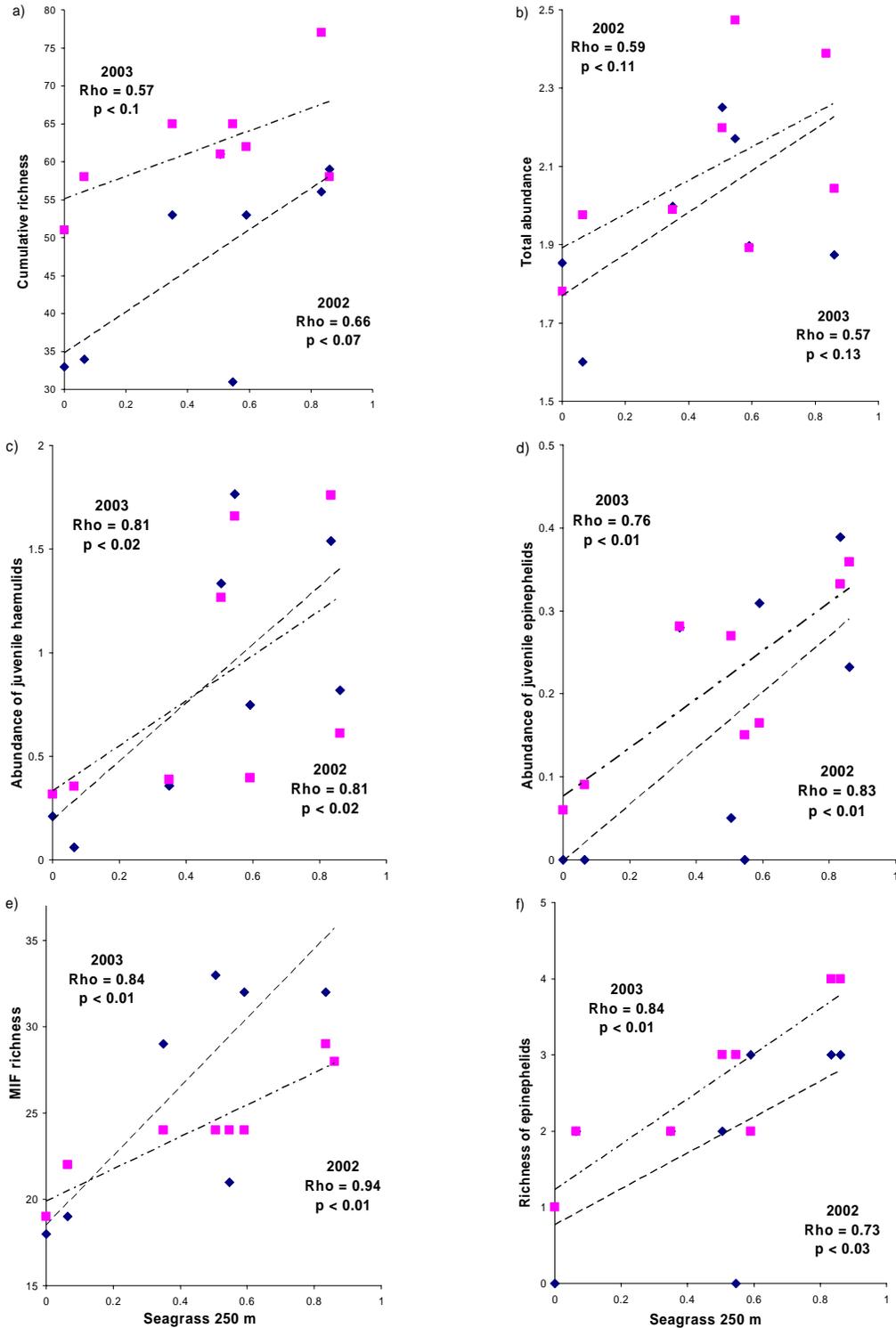


Figure 3-5. Spearman rank correlations for those reef fish parameters that demonstrated a consistent relationship with the areal coverage of seagrass habitat between 2002 (- - -) and 2003 (- · - · -) at the subset of 8 study reefs in St. John, U.S. Virgin Islands

Table 3-1. Most abundant taxa in each reef fish group for the 22 study reefs sampled in 2002 in St. John, U.S. Virgin Islands.

Reef fish parameter	Dominant taxa
Total abundance	<i>Thalassoma bifasciatum</i> , <i>Acanthurus coeruleus</i> , <i>Haemulon aurolineatum</i> , <i>Scarus</i> spp. (unidentified juveniles), <i>H. flavolineatum</i> , <i>Stegastes planifrons</i> , <i>A. bahianus</i> , <i>Halichoeres garnoti</i> , <i>S. leucostictus</i> , and <i>Caranx ruber</i>
MIFs*	<i>H. flavolineatum</i> , <i>H. aurolineatum</i> , <i>H. garnoti</i> , <i>Abedufduf saxtalis</i> , <i>Halichoeres bivittatus</i> , <i>Ocyurus chrysurus</i> , <i>Holocentrus rufus</i> , <i>Halichoeres maculapinna</i> , <i>Hypoplectrus puella</i> , and <i>Mulloides martinicus</i>
Haemulids (grunts)	<i>Haemulon aurolineatum</i> , <i>H. flavolineatum</i> , <i>H. juvenile</i> , <i>H. sciurus</i> , <i>H. plumieri</i> , <i>H. parrai</i> , <i>H. carbonarium</i> , <i>H. macrostomum</i> , and <i>H. chysargyreum</i>
Lutjanids (snappers)	<i>Ocyurus chrysurus</i> , <i>Lutjanus apodus</i> , <i>L. synagris</i> , <i>L. mahogani</i> , <i>L. jocu</i> , <i>L. griseus</i> , and <i>L. analis</i>
Epinephelins (groupers)	<i>Epinephelus guttatus</i> , <i>Cephalopholis cruentatus</i> , <i>C. fulvus</i> , <i>E. striatus</i> , and <i>E. adscensionis</i>
Mobile taxa	<i>Acanthurus coeruleus</i> , <i>Haemulon aurolineatum</i> , <i>Scarus</i> spp. (unidentified juveniles) <i>Haemulon flavolineatum</i> , <i>Halichoeres garnoti</i> , <i>Haemulon</i> spp. (unidentified juveniles), <i>Thalassoma bifasciatum</i> , <i>Halichoeres bivittatus</i> , and <i>Sparisoma aurofrenatum</i>
Resident taxa	<i>Stegastes planifrons</i> , <i>S. leucostictus</i> , <i>S. partitus</i> , <i>Abedufduf saxtalis</i> , <i>Chromis cyanea</i> , <i>C. multilineatum</i> , <i>Hypoplectrus puella</i> , and <i>S. variabilis</i>
Transient taxa	<i>Carynx ruber</i> , <i>Ocyurus chrysurus</i> , <i>Inermia vittata</i> , <i>Scomberomorus regalis</i> , and <i>Dasyatis americana</i>

* Mobile invertebrate feeders

Table 3-2. Variable names, transformations, minimum, maximum and mean values for each reef fish parameter and landscape metric, with the standard error for fish parameters and the coefficient of variation for habitat measures for the 22 study reefs sampled in 2002 in St. John, US Virgin Islands.

Dependent Variable	Transform	Min	Max	Mean	SE
Cumulative richness	Log (x +1)	30.00	66.00	44.20	2.37
Mean species richness	Log (x +1)	16.00	0.66	22.42	0.97
Total abundance	Log (x +1)	322.00	38.81	99.00	0.05
MIF abundance	Log (x +1)	10.22	99.00	25.92	0.06
Grunt abundance ^a	Log (x +1)	0.00	59.26	3.89	0.12
Snapper abundance ^a	Log (x +1)	0.00	22.99	1.69	0.07
Grouper abundance ^a	Log (x +1)	0.00	2.09	0.78	0.03
Seagrass asso. abundance ^a	Log (x +1) ^b	0.50	68.50	13.2	3.92
Mobile abundance	Log (x +1)	26.54	193.98	59.26	0.05
Residents abundance	Log (x +1)	8.77	101.33	25.92	0.06
Transients abundances	Log (x +1) ^b	0.00	17.20	2.31	0.08
Richness MIFs	None	9.00	30.00	17.36	1.52
Richness haemulids	None	0.00	6.00	3.13	0.44
Richness lutjanids	None	0.00	4.00	2.18	0.28
Richness epinephelids	None ^b	0.00	6.00	3.59	0.23
Richness mobile	None	17.00	40.00	26.10	1.53
Richness residents	None	8.00	24.00	15.68	0.86
Richness transients	None	0.00	4.00	2.18	0.23
Independent Variable	Transform	Min	Max	Mean	CV
Area (ha) seagrass 100 m	Log (x +1)	0.00	11.59	1.21	97.96
Area (ha) seagrass 250 m	Log (x +1)	0.00	25.92	3.27	78.36
Area (ha) seagrass 500 m	Log (x +1) ^b	0.00	41.36	6.76	65.23
Area (ha) seagrass 1 km	Log (x +1)	1.01	76.62	13.79	38.97
Rugosity	None	1.18	2.28	1.56	15.70

^a Divided into adult and juvenile components, also. ^b Those parameters that failed Shapiro-Wilks normality tests, using $p < 0.01$.

Table 3-3. Simple linear regression for entire assemblage level parameters of reef fish communities with the areal coverage of seagrass within 1 km of each study reef as the independent variable at the 22 study reefs, sampled in 2002 in St. John, U.S. Virgin Islands*.

Dependent variable	Independent Variable	F ratio	Model R2 (x 100)	p-value
Mean Species Richness	Seagrass 100m (+)	6.21	23.68	0.0200
	Seagrass 250 m (+)	7.42	27.02	0.0100
Cumulative Species Richness	Seagrass 500 m (+)	10.95	35.38	0.0035
	Seagrass 1 km (+)	7.82	29.16	0.0015
	Seagrass 100 m (+)	17.62	47.84	0.0004
	Seagrass 250 m (+)	27.29	57.77	0.0001
Mean Abundance	Seagrass 500 m (+)	24.02	54.57	0.0001
	Seagrass 1 km (+)	19.59	50.77	0.0003
	Seagrass 100 m (+)	4.22	17.44	0.0500
	Seagrass 250 m (+)	6.21	23.60	0.0200
	Seagrass 500 m (+)	9.38	31.94	0.0060
	Seagrass 1km (+)	8.98	32.09	0.0070

*For each relationship, the dependent and independent variables are presented with corresponding F-ratio, entire model R2 and p-value for the final model. Relationships in bold represent the spatial extent with the strongest relationship, for the given fish parameter. All relationships are positive (+).

Table 3-4. Simple linear regression of abundances of mobile invertebrate feeders, grunts, snappers, groupers, and seagrass-associated taxa and within mobility guilds with the areal coverage of seagrass within 1 km of each study reef at the 22 study reefs, sampled in 2002 in St. John, U.S. Virgin Islands*.

Dependent variable	Independent Variable	F-ratio	Model R ² (x 100)	p-value
Adult Haemulids	Seagrass 100 m (+)	3.82	16.06	0.064*
	Seagrass 250 m (+)	4.85	19.50	0.0390
	Seagrass 500 m (+)	5.34	21.08	0.0300
	Seagrass 1 km (+)	5.03	20.92	0.0370
Juvenile Haemulids	Seagrass 100 m (+)	21.38	54.29	0.0002
	Seagrass 250 m (+)	23.36	56.48	0.0001
	Seagrass 500 m (+)	19.84	52.43	0.0003
	Seagrass 1 km (+)	21.27	55.59	0.0002
Adult Lutjanids	Seagrass 100 m (+)	3.52	16.37	0.076*
	Seagrass 250 m (+)	5.29	22.72	0.0330
	Seagrass 500 m (+)	6.06	25.20	0.0240
	Seagrass 1 km (+)	5.56	22.63	0.0290
Juvenile Lutjanids	Seagrass 100 m (+)	5.34	21.08	0.0300
	Seagrass 250 m (+)	4.48	18.65	0.0400
	Seagrass 500 m (+)	3.20	13.81	0.080*
	Seagrass 1 km (+)	---	---	NS
Adult Epinephelids	Seagrass 100 m (+)	---	---	NS
	Seagrass 250 m (+)	3.10	14.70	0.090*
	Seagrass 500 m (+)	4.73	20.81	0.0400
	Seagrass 1 km (+)	---	---	NS
Juvenile Epinephelids	Seagrass 100 m (+)	---	---	NS
	Seagrass 250 m (+)	---	---	NS
	Seagrass 500 m (+)	---	---	NS
	Seagrass 1 km (+)	---	---	NS
Adult seagrass-associated taxa	Seagrass 100 m (+)	3.42	14.59	0.079*
	Seagrass 250 m (+)	5.63	21.96	0.0280
	Seagrass 500 m (+)	7.14	26.30	0.0150
	Seagrass 1 km (+)			
Juvenile seagrass-associated taxa	Seagrass 100 m (+)	17.26	46.32	0.0005
	Seagrass 250 m (+)	13.87	40.05	0.0013
	Seagrass 500 m (+)	9.92	33.14	0.0051
	Seagrass 1 km (+)			

*Models with p-values less than 0.15 are shown. a $p > 0.05$ level. NS means not significant at the $p < 0.15$. b Bold represents the spatial extent with the strongest relationship.

Table 3-5. Simple linear regression of abundances of the adult and juvenile components for grunts, snappers, groupers, and seagrass-associated taxa with the areal coverage of seagrass within 1 km of each study reef at the 22 study reefs, sampled in 2002 in St. John, U.S. Virgin Islands.

Dependent variable	Independent Variable	F ratio	Model R ² (x100)	p-value
MIFs	Seagrass 100m (+)	9.50	32.23	0.0058
	Seagrass 250 m (+) ^b	11.13	41.25	0.0033
	Seagrass 500 m (+)	10.01	33.36	0.0049
	Seagrass 1 km (+)	6.88	26.60	0.0160
Grunts (Haemulids)	Seagrass 100 m (+)	20.38	53.10	0.0003
	Seagrass 250 m (+)	23.47	56.59	0.0001
	Seagrass 500 m (+)	19.27	51.66	0.0001
	Seagrass 1 km (+) ^b	22.84	57.32	0.0002
Snappers (Lutjanids)	Seagrass 100 m (+)	10.26	36.29	0.0049
	Seagrass 250 m (+) ^b	11.82	39.64	0.0029
	Seagrass 500 m (+)	9.42	34.35	0.0066
	Seagrass 1 km (+)	8.83	34.17	0.0086
Groupers (Epinephelines)	Seagrass 100 m (+)	2.57	12.51	0.120 ^a
	Seagrass 250 m (+)	3.71	17.09	0.070 ^a
	Seagrass 500 m (+)	2.67	12.93	0.120 ^a
	Seagrass 1 km (+) ^b	3.57	17.36	0.070^a
Seagrass- associated taxa	Seagrass 100 m (+)	16.05	44.52	0.0007
	Seagrass 250 m (+) ^b	14.93	50.12	0.0002
	Seagrass 500 m (+)	11.21	35.01	0.0032
	Seagrass 1 km (+)	10.35	33.42	0.0030
Resident taxa	Seagrass 100 m (+)	----	----	NS
	Seagrass 250 m (+)	5.76	22.36	0.0260
	Seagrass 500 m (+)	----	----	NS
	Seagrass 1 km (+)	----	----	NS
Mobile taxa	Seagrass 100 m (+)	4.79	20.00	0.0406
	Seagrass 250 m (+) ^b	4.86	20.34	0.0390
	Seagrass 500 m (+)	----	----	NS
	Seagrass 1 km (+)	4.47	19.07	0.0478
Transient taxa	Seagrass 100 m (+)	----	----	NS
	Seagrass 250 m (+)	----	----	NS
	Seagrass 500 m (+)	----	----	NS
	Seagrass 1 km (+)	----	----	NS

* Models with p-values less than 0.15 are shown. a $p > 0.05$ level. NS means not significant at the $p < 0.15$. b Bold represents the spatial extent with the strongest relationship.

Table 3-6. Simple linear regression analyses of cumulative species richness of MIFs, haemulids, epinephelids, lutjanids and within resident, mobile and transient mobility guilds the areal coverage of seagrass within 1 km of each study reef as the independent variable at the 22 study reefs, sampled in 2002 in St.

Dependent variable	Independent Variable	F ratio	Model R ² (x 100)	p-value
Cumulative species richness of MIFs	Seagrass 100m (+)	46.47	72.29	0.0001
	Seagrass 250 m (+)	63.59	68.59	0.0001
	Seagrass 500 m (+)	45.84	71.81	0.0001
	Seagrass 1 km (+)	28.83	62.91	0.0001
Cumulative species richness of Haemulids	Seagrass 100 m (+)	49.89	71.38	0.0001
	Seagrass 250 m (+)	45.46	69.44	0.0001
	Seagrass 500 m (+)	25.36	55.91	0.0001
	Seagrass 1 km (+)	28.59	60.07	0.0001
Cumulative species richness of Lutjanids	Seagrass 100 m (+)	12.63	38.73	0.0020
	Seagrass 250 m (+)	14.09	41.33	0.0013
	Seagrass 500 m (+)	8.22	29.12	0.0095
	Seagrass 1 km (+)	6.06	24.19	0.0235
Cumulative species richness of Epinephelids	Seagrass 100 m (+)	8.77	32.76	0.0084
	Seagrass 250 m (+)	9.06	33.49	0.0075
	Seagrass 500 m (+)	7.19	28.57	0.0152
	Seagrass 1 km (+)	5.08	23.00	0.0377
Cumulative species richness of Resident Taxa	Seagrass 100 m (+)	---	---	NS
	Seagrass 250 m (+)	---	---	NS
	Seagrass 500 m (+)	---	---	NS
	Seagrass 1 km (+)	---	---	NS
Cumulative species richness of Mobile Taxa	Seagrass 100 m (+)	29.79	59.83	0.0001
	Seagrass 250 m (+)	43.68	68.59	0.0001
	Seagrass 500 m (+)	34.31	63.17	0.0001
	Seagrass 1 km (+)	23.51	55.30	0.0001
Cumulative species richness of Transient Taxa	Seagrass 100 m (+)	---	---	NS
	Seagrass 250 m (+)	---	---	NS
	Seagrass 500 m (+)	6.21	25.65	0.0220
	Seagrass 1 km (+)	---	---	NS
Cumulative species richness of Transient Taxa	Seagrass 100 m (+)	---	---	NS
	Seagrass 250 m (+)	---	---	NS
	Seagrass 500 m (+)	6.21	25.65	0.0220
	Seagrass 1 km (+)	---	---	NS

John, US Virgin Islands.

* Models with p-values less than 0.15 are shown. ^a p > 0.05 level. NS means not significant at the p < 0.15. ^b Bold represents the spatial extent with the strongest relationship.

Table 3-7. Spearman rank correlations of relationships of each fish parameter and the areal coverage of seagrass at the 250 m spatial extent for the 8 study reefs in St. John, sampled in 2002 and 2003. For each relationship, the Spearman Rho correlation, and probability < Rho are presented by year. Kruskal-Wallis tests for significant differences in abundance using raw census data for 2002 (n = 43) and 2003 (n = 87) between years are presented, with direction of change indicating an increase (+) or decrease (-) in abundance. Relationships in bold are those that are consistent between years. All p-values < 0.20 are presented.

Reef fish parameter	2002 Rho	Prob Rho	2003 Rho	Prob Rho	Kruskal- Wallis	Direction of change
Cumulative richness	66.21	0.07	56.63	0.100		
Mean species richness	59.21	0.11	57.14	0.130		
Total abundance	59.21	0.11	57.14	0.130	0.186	
Abundances of MIFs	61.23	0.09	---	NS	0.016	-
Abundances of adult MIFs	52.78	0.18	---	NS	0.137	
Abundances of juvenile MIFs	52.78	0.18	---	NS	0.386	
Abundances of adult haemulids	---	---	---	NS	0.022	-
Abundances of juvenile haemulids	88.35	0.004	80.95	0.015	0.690	
Abundances of adult epinephelids	68.45	0.06	---	NS	0.268	
Abundances of juvenile epinephelids	82.47	0.01	76.19	0.009	0.292	
Abundances of adult lutjanids	---	---	---	NS	0.012	-
Abundances of juvenile lutjanids	50.36	0.20	---	NS	0.847	
Cumulative richness MIFs	84.09	0.001	93.86	0.001		
Cumulative richness haemulids	75.16	0.03	---	NS		
Cumulative richness lutjanids	---	---	---	NS		
Cumulative richness epinephelids	73.03	0.03	84.01	0.001		

Table 3-8. Influence of fine-scale (rugosity) and landscape-scale (seagrass) features in predicting reef fish parameters for the 22 study reefs sampled in 2002.

Dependent variable	Independent Variable	Partial R ²	Model R ²	p-value
Cumulative richness	Seagrass 250 m Rugosity	71.76 ---	71.76	< 0.0001
Mean species richness	Seagrass 250 m Rugosity	35.67 ---	35.67	0.0054
Total abundance	Seagrass 250 m Rugosity	9.60 33.10	42.70	0.0033
Abundances of MIFs	Seagrass 250 m Rugosity	40.36 ---	40.36	0.0026
Abundances of Haemulids	Seagrass 250 m Rugosity	56.59 ---	56.59	< 0.0001
Abundances of Epinephelids	Seagrass 250 m Rugosity	17.09 ---	17.09	0.070*
Abundances of Lutjanids	Seagrass 250 m Rugosity	39.64 ---	39.64	0.0029
Abundances of Resident taxa	Seagrass 250 m Rugosity	--- 28.92	28.92	0.0200
Abundances of Mobile taxa	Seagrass 250 m Rugosity	33.79 12.89	46.58	0.0072
Species richness of MIFs	Seagrass 250 m Rugosity	69.35 ---	69.35	< 0.0001
Species richness of Haemulids	Seagrass 250 m Rugosity	69.98 ---	69.98	< 0.0001
Species richness of Epinephelids	Seagrass 250 m Rugosity	19.97 ---	19.97	0.0400
Species richness of Lutjanids	Seagrass 250 m Rugosity	41.34	41.34	0.0013
Species richness of Resident taxa	Seagrass 250 m Rugosity	25.41 ---	25.41	0.0200
Species richness of Mobile taxa	Seagrass 250 m Rugosity	69.37 ---	69.37	< 0.0001

Models with p-values less than 0.15 are shown. An asterisks (*) designates where $p > 0.05$ level. NS means not significant at the $p < 0.15$. Relationships in bold indicate where rugosity was a significant predictor variable in the final model.

CHAPTER 4 REEF FISHES RESPOND TO VARIATION IN LANDSCAPE STRUCTURE

Reef context explained a significant amount of the variability in reef fish assemblage structure in the Florida Keys National Marine Sanctuary (FKNMS) and the US Virgin Islands. Although reef context was significant in both systems, the specific measure of context varied. Rather, the particular habitat type (e.g., seagrass, pavement) responsible for the reef fish–habitat relationships differed between systems. Although the areal coverage of seagrass positively predicted abundances and species richness of mobile invertebrate feeders, haemulids, and lutjanids in the US Virgin Islands, seagrass did not explain a significant amount of the variation of these same fishes when analyses was limited to the FKNMS only. Instead, the amount of pavement and reef habitats were positively associated with several reef fish parameters in Florida. Differences in the landscape structure of the two systems may explain this disparity. In the US Virgin Islands, seagrass comprises a relatively small proportion of the essential fish habitat. However in Florida, seagrass is the dominant habitat type, whereas pavement, which was common in the US Virgin Islands, comprises a smaller proportion of the essential fish habitat. Thus, the processes that structure reef fish communities appear to respond to variation in the landscape structure of these coral reef environments. The shape of reef fish–seagrass curves for pooled data including the FKNMS and US Virgin Islands suggest that there may be critical threshold of seagrass habitat. Once this critical threshold of seagrass is exceeded, seagrass may become less important in structuring reef fish communities than other habitat types. These results are relevant to marine protected

areas design, since they suggest that general design rules do not necessarily apply across systems. Comparative studies such as this are critical for developing the universal design principles required to establish marine protected areas that meet their conservation and/or fisheries objectives.

Introduction

Landscape-scale metrics, traditionally employed in the study of terrestrial systems, have been applied recently to the study of coral reef ecosystems to better understand fish–habitat relationships (Grober-Dunsmore et al. 2004a, 2004b, 2004c and Kendall et al. 2003 in the US Virgin Islands; Christensen et al. 2003 in Puerto Rico, Appeldoorn et al. 2003 in Columbia, Jeffrey 2004 in the Florida Keys). Coral reef ecosystems, like most terrestrial ecosystems, can be described quantitatively by the spatial pattern or arrangement of landscape elements (Forman 1995, Dramstad et al. 1996), including patches of habitat and corridors of movement. Ault and Johnson (1998a, 1998b), Appeldoorn et al. (2003), Kendall et al. (2003) and Grober-Dunsmore et al. (2004a, 2004b, 2004c) have all used a landscape-scale approach to demonstrate significant fish–habitat relationships, and generally conclude that the context of individual habitat patches may be a critical factor determining reef fish community structure. In the latter case, simple measures of reef context (calculated with GIS software) were used to predict reef locations with high reef fish abundances and reef fish diversity in the US Virgin Islands (Grober-Dunsmore et al. 2004a, 2004b). Mean abundance and species richness of several groups of exploited reef fishes, in particular, showed strong positive correlations with those reefs in close proximity to seagrass habitat (Grober-Dunsmore et al. 2004c). The generality of these findings, however, have not yet been tested.

To assist in the development of an emerging, coherent landscape-scale theory that explains the structure of reef fish communities, it is essential to critically examine observed patterns of reef fish abundance, distribution, species richness and diversity, and determine which landscape elements, if any, best describe these patterns. Furthermore, it is necessary to explore how reliably these landscape elements predict assemblage structure in other systems, and under differing environmental conditions. Studies of landscape structure effects on fauna in terrestrial habitats (Paton 1994, Trzcinski et al. 1999, Villard et al. 1999) often yield markedly different results, and, as a consequence, generalizations regarding these relationships have been slow to evolve. Inconsistencies in relational patterns can occur due to discrepancies in the scale of observation (Hewitt et al. 1998, Wiens and Milne 1989), the natural heterogeneity of ecosystems (Kolasa and Pickett 1991), disparity in the metrics used to measure spatial patterning (Frohn 1998), differences in sampling techniques and in the spatial resolution and grain of the benthic habitat maps. In the pursuit of identifying general operational guidelines for MPA design, it will be mandatory to replicate experiments in time and space (Sale 2002), to understand how variation in the structure of underlying habitats may influence the composition, structure and distribution of reef fish communities.

Faunal abundance and survivorship of specific organisms in marine systems has been associated with landscape configuration (Robbins and Bell 1994, Irlandi et al. 1999, Hovel and Lipcius 2001), landscape context (Bell et al. 2001, Appeldoorn et al. 2003, Grober-Dunsmore et al. 2004a, 2004b, 2004c), and reef connectivity (Ault and Johnson 1998), although few of these studies have been replicated in space, limiting our ability to draw general conclusions. The present study was carried out in the Florida Keys

National Marine Sanctuary (FKNMS), and was designed to test the generality of reef fish–habitat relationships previously detected in the US Virgin Islands (Grober-Dunsmore et al. 2004c). FKNMS represents one of the few other Caribbean locations with digitally-referenced benthic habitat maps, and was therefore amenable to applying the same landscape approach and methods as that used in the previous study. FKNMS was selected for several reasons. First, the FKNMS habitat maps were created jointly by Florida Marine Research Institute (FMRI) and National Oceanographic and Atmospheric Association (NOAA). Because the habitat maps for the US Virgin Islands were also created by NOAA, I assumed some consistency in methods throughout the classification and interpretation process. Furthermore, the grain, which is the smallest resolvable unit of study (King 1991) and the extent, which is the area over which observations are made (Morrison and Hall 2001) were comparable between studies. This is important to my comparisons, since interpretation of how ecological systems are structured often depends on the spatial and temporal scale at which a study is conducted. In fact, results of studies conducted at different scales may not be comparable (Osenberg et al. 1999). Second, because reef fish populations in the US Virgin Islands are heavily exploited and several targeted fish groups (e.g., groupers) exhibit low population densities (Rogers and Beets 2001), many reef fish–habitat relationships were hypothesized to be stronger in less-fished systems, such as no take areas where abundances of reef fish populations are expected to be higher. The designation of a network of special protected areas (SPA) in the FKNMS afforded the opportunity to sample inside no fishing areas (where reef fish populations were expected to be less fished than the US Virgin Islands) and to compare reef fish–habitat relationships inside and outside of no-take areas. Finally, it is

preferential to test the generality of landscape relationships in systems where the habitat patches are arranged differently, to determine the robustness of landscape variables as predictors among locations (Bissonette and Storch 2003). The US Virgin Islands is an insular fringing reef system with a highly variable distribution of habitat patches comprised of seagrass, reef, sand, and pavement interspersed in no particular pattern from shore. In comparison, the FKNMS is a continental bank reef system with a more homogeneous distribution of habitat patches. For example, the continuous bank system of shallow spur and groove reef is 6-10 kilometers offshore, and separated from the coast by large expanses of seagrass habitat, interspersed with patch reefs. If reef fish–habitat relationships are similar and robust across these two disparate ecosystems, i.e. the US Virgin Islands and FKNMS, patterns might be expected to hold across other Caribbean coral reef systems.

The objective of this study was to determine how robust reef fish–habitat relationships are to variation in landscape structure, since the expectation that relationships will be similar across systems assumes that the processes that gave rise to these relationships are not modified by variation in landscape structure. The primary predictions, based on my findings in the US Virgin Islands, were that reef fish assemblage structure would not be correlated with reef configuration (e.g., reef size, shape), complex landscape-scale (e.g., habitat diversity) or fine-scale (rugosity) metrics of habitat heterogeneity, yet reef fishes would be positively correlated with reef context, i.e. the spatial arrangement and composition of surrounding habitat patches. Specifically, I predicted that species richness and abundances of targeted fishes (i.e. mobile invertebrate feeders, haemulids, lutjanids, and serranids) would be higher at reefs

proximal to seagrass. If these reef fish assemblage parameters were not higher at reefs proximal to seagrass habitat, I expected that variation in the landscape structure of the coral reef environments of the US Virgin Islands and FKNMS would explain differences in the response of reef fishes to landscape structure. In addition, relationships were also explored across the largest landscape gradient possible, by pooling data from the US Virgin Islands and FKNMS. Furthermore, I expected that reef fish assemblage structure would be associated with landscape-scale measures of landscape structure to a greater extent than with the fine-scale measure of rugosity. I also tested whether there were significant differences in abundance of targeted reef fishes within protected and unprotected reference sites to assess whether reef fish–habitat relationships were stronger at those sites with higher reef fish abundances.

Methods

Study Areas

This study was conducted in the FKNMS in May 2003, and results from the FKNMS were compared to those from a previous study in St. John, U.S. Virgin Islands (Grober-Dunsmore et al. 2004c). The FKNMS (980,000 ha), designated in 1990 to protect nationally significant biological and cultural marine resources, including critical coral reef habitats, seagrass beds, hard-bottom communities, and mangrove shorelines, encompasses all but the northernmost extent of the Florida Reef Tract (Department of Commerce 1997). A network of 24 fully protected zones, which cover approximately 6% of the Sanctuary, but protect 65% of shallow bank reef habitats and 10% of coral resources overall, were implemented in 1997 and in 2001 to preserve specific areas more completely (NOAA et al. 2002). Inside these special protected areas (SPA), most fishing activities are prohibited. In contrast, the island of St. John has 56% of the marine portion

of its near shore waters under the jurisdiction of Virgin Islands National Park (VINP). The VINP was established in 1956 with marine portions totaling 2,287 ha added in 1962. Most types of fishing are allowed within VINP, and effects of intensive fishing are evident (Rogers and Beets 2001). While spear fishing is banned, rod and reel, line traps and fish traps are still allowed within VINP and the territorial waters of the US Virgin Islands.

Study reefs in Florida were selected to facilitate comparisons between systems by reducing variability in reef type and inshore-offshore effects and to include the maximum number of SPA and reference pairs. Therefore, all SPAs (which were all spur and groove habitat), and their approximate reference (fished) reefs were sampled (Figure 4-1). To the extent feasible, I selected the reference monitoring sites used by Bohnsack et al. (1999). Following ground-truthing, only four SPA-reference pairs were used as comparative reef pairs to reduce variability based on within-reef characteristics such as coral cover and topographic complexity. Thus, all study reefs in the FKNMS were relatively shallow (2–3 m) and comprised of an eroding submerged reef framework, with living coral cover estimated between 2 and 20 % (Miller et al. 2000). Dominant corals were *Montastraea annularis* with *Porites astreoides*, *P. porites*, *Diploria labyrinthiformes*, *D. strigosa*, *Siderastraea siderea* and *S. radians* making lesser contributions to living coral cover. The background matrix consisted of sand channels in deeper areas (5-13 m) and an eroding calcium carbonate framework in shallower areas (1-5 m).

In comparison, the 22 study reefs sampled in 2002 in the US Virgin Islands (shallow (1–13 m) fringing and patch reefs; Grober-Dunsmore et al. 2004c) were selected

as the primary comparative reefs so that the dominant shallow water reef types for each system were used for comparisons. Several were contained in a sand matrix with large boulders of coral, primarily *M. annularis*, providing the major topographic relief. Other reefs had more distinct zonation with edge and platform (hard-bottom) zones. Total living coral cover in the US Virgin Islands, estimated at 5–20 %, was dominated by *M. annularis*, with lesser contributions by *Porites astreoides*, *S. siderea*, *S. radians*, *D. labyrinthiformes* and *D. strigosa*.

Habitat Sampling

Aerial photographs of the FKNMS were taken in December 1991-March 1992 and were interpreted by FMRI and NOAA personnel in 1998 (Florida Marine Research Institute et al. 1998). Habitat types were classified as one of four major categories, i.e. corals, seagrasses, hard-bottom and bare substrate, and these four broad categories were further refined to represent 24 subcategories at a nominal scale of 1:48,000 (see Florida Marine Research Institute et al. 1998 for details). Benthic habitat maps of the US Virgin Islands were created in 2001, from aerial imagery acquired in 1999 (Kendall et al. 2001). For the FKNMS benthic maps, the minimum area delineated was 0.5 ha, which contrasts slightly with the minimum area of 0.4 ha for the US Virgin Islands. The maps were created approximately 5-9 years apart, with the US Virgin Islands being more recent.

To the extent possible, landscape metrics in the FKNMS were calculated the same as in the 2002 study in the US Virgin Islands (Grober-Dunsmore et al. 2004a, 2004b, 2004c). To facilitate comparisons between systems, the 24 habitat classes in the FKNMS were reduced to the same number of classes ($n = 7$) as in the US Virgin Islands. Habitat classes in the FKNMS were: inland water, pavement, reef, patch reef, sand, seagrass, and unknown, although only five of these habitat classes occurred within 500 m of my study

reefs. These habitat classes contrast slightly with those in the US Virgin Islands, i.e. pavement, reef, bedrock, sand, seagrass, deep unknown, and macro algal plain. The classification schemes were created to be as similar as possible, given differences between the systems (e.g., bedrock was not classified in Florida, and thus was not included; patch reefs were classified separately in Florida to keep the total number of habitats as equitable as possible). However, there were slight differences in the definitions for unknown habitat. In the US Virgin Islands, deep unknown represents habitat that could not be identified from aerial photos, typically due to depths in excess of 20 m (pers. obs.). Groundtruthing revealed, however, that much of this was soft-bottom and to a lesser extent hard-bottom. In the Florida Keys, turbid water in the inshore areas precluded accurate classification of large portions of Hawks Channel, and was classified as unknown (FMRI 1998). Groundtruthing revealed that much of this was seagrass habitat (pers. obs.).

Comparisons of the coral reef landscape structure of the FKNMS and US Virgin Islands were conducted at reef and ecosystem-scales. Comparisons at the reef-scale were conducted at 100 m, 250 m and 500 m from study reefs, because spatial extent should be two to five times larger than the spatial features of the habitat patches in the landscape (O'Neill et al. 1996). To account for minor differences in the size of study reefs, I also calculated the proportion of area of each habitat type per unit area of sample reef. At the ecosystem-scale, the area of each habitat within the entire mapped spatial extent (e.g., Carysfort to Sand Key in the FKNMS; see Figure 4-1) was calculated for each system.

Reef Fish Sampling

Fish sampling was conducted using the point count method described by Bohnsack and Bannerot (1986). Sampling effort in the US Virgin Islands was determined based on

reef size to achieve a minimum of 1 point count per 1500 m² following a sample size optimization procedure using pre-existing data (Grober-Dunsmore et al. 2004a).

Sampling effort was increased in FKNMS so that a minimum of 12 point counts per reef were conducted, regardless of reef size (Table 4-2) in an attempt to improve accuracy of reef fish parameter estimates within each reef. Comparisons of the mean values for reef fish parameter estimates in the FKNMS were conducted between the two levels of sampling effort. In general, there were not differences in mean abundance estimates with increased sampling, though species richness obviously increased with increased sampling. Point counts were randomly-generated in each reef polygon using a script in Arc View 3.2 (ESRI 1996). Corresponding GPS coordinates were used to approximate the location of point counts using waterproof site maps, GPS coordinates, and ranging techniques in the water. Reef fish census data were used to calculate a suite of reef fish parameters, which are the same as those in Grober-Dunsmore et al. 2004b (Table 4-1).

Statistical Analyses

Predictions of the relationships of reef fish assemblage structure to various landscape structure parameters were derived based on my findings from study reefs in the US Virgin Islands. To confirm that findings in the FKNMS were similar to those in the US Virgin Islands, the same stepwise multiple regression analyses were conducted in both studies. Every reef fish parameter was tested and used as the dependent variable (Table 4-1), and landscape variables were, in general, the same as those in Grober-Dunsmore et al. 2002b. The only differences were that reef context measures differed slightly between the US Virgin Islands and FKNMS, due to differences in classification (see above). In the FKNMS, reef context measures were: the areal coverage (ha) of reef, patch reef, pavement, seagrass and sand habitats. The areal coverage of reef, seagrass,

pavement, bedrock and sand habitats were used for the US Virgin Islands. The strength and nature of reef fish–habitat relationships were explored at the 100-meter, 250-meter and 500-meter spatial extents; these spatial scales were selected based on the known ecology of the majority of the focal organisms (Kotliar and Wiens 1990), the reef fish community as a whole. To further explore the generality of findings across systems, relationships were regressed using the FKNMS ($n = 17$) and USVI ($n = 22$) reefs for a total of 39 reefs, thereby maximizing the gradient for several landscape variables.

For all regressions, a p-value of 0.05 was set for variables to enter the model, to reduce Type I errors (Zar 1984). Model selection was improved using Mallows p (Mallows 1973), leverage effects plots (Sall 1990) and Akaike's Information Criterion (AIC) (Akaike 1974). Because it is not appropriate to simply select the model with the lowest AIC value, each alternative model was evaluated by determining the difference between model AIC and the minimum AIC; $\Delta_i < 2$ was used as an acceptable value (Burnham and Anderson 1998). In addition, sequential Bonferroni Dunn-Sidak corrections were applied, using the total number of comparisons ($n = 30$) (Zar 1984). For every significant multiple regression, a simple linear regression was conducted to graphically display data and perform residual analyses (Sokal and Rohlf 1995).

To determine whether reef fish–habitat relationships were stronger where abundances of reef fishes were higher, mean abundance within each fish group was compared between SPA and reference reef pairs ($n = 4$) in the FKNMS. Paired t-tests assuming equal variance were conducted, after it was verified that for most reef fish parameters, variance was not significantly different between no-take and reference sites (Zar 1984). Simple linear regressions were developed separately for SPA and reference

reefs. Then, variance ratio tests (Zar 1984) were used to test whether the strengths of relationships were stronger where (SPA or reference sites) reef fish abundances were highest. In the US Virgin Islands, mean abundance of each fish group was compared between MPA ($n = 15$) and reference reefs ($n = 7$) using t-tests assuming equal variance, after it also was determined that variance was not significantly different for most reef fish parameters between reefs inside and outside VINP.

A variety of multivariate methods available in PRIMER software (Clarke and Warwick 2001) were employed to analyze differences in the reef fish communities among individual reefs and among different reef systems (FKNMS and US Virgin Islands). For reef fish community analyses, I calculated Bray-Curtis similarity on \log_{10} -transformed abundances (a satisfactory coefficient for biological data on community structure; Clarke and Warwick 2001) at the trophic and family levels, and conducted analysis of similarities (ANOSIM) to test for differences in reef fish community structure between the FKNMS and US Virgin Islands. ANOSIM calculates a global R statistic that reflects the differences in variability between groups, compared to within groups (so R values are proportional to differences between the groups) and checks for significance of R using permutation tests (Clarke and Warwick 2001). To quantify the relative contribution of trophic and family categories to dissimilarities, I conducted a similarity breakdown using the SIMPER procedure, which provides similarity percentages with respect to contribution to average similarity within a group and average dissimilarity between groups (Clarke and Warwick 2001). Non-metric multi-dimensional scaling (MDS) was used to further analyze reef fish community structure and the landscape structure in both the FKNMS and US Virgin Islands. MDS can be used to generate plots

in which the distance between points is proportional to their degree of dissimilarity, so closer points are more similar than points farther away (Clarke and Warwick 2001). MDS plots were calculated using mean abundances for reef fish community structure, and measures of rugosity, reef size and the areal coverage of the habitat types common to the FKNMS and US Virgin Islands for every reef were used for comparing landscape structure between systems. In MDS plots, reefs were classified in two manners. First, reefs were classified according to location (1 = USVI, 2 = FKNMS) to examine differences between systems. Second, reefs were classified according to the amount (hectares) of seagrass (1 = 0–0.5 ha, 2 = 0.5–1.2 ha, 3 = \geq 1.2 ha) within 500 meters of each study reef. This classification was also used for each of the other habitat types common to both systems, to verify that other habitat types did not result in a similar spatial patterning of reefs for trophic and family structure, as that found using seagrass.

Results

A total of 59,239 individual fishes representing 152 species were recorded during 316 point counts at the 17 study reefs in the Florida Keys National Marine Sanctuary, which compares to the 14,389 individual fishes recorded representing 118 species during 107 point counts at 22 study reefs in the US Virgin Islands during July and August 2002.

As expected based on my findings in the US Virgin Islands, reef configuration was not a good predictor of fish assemblage structure in FKNMS. In fact, configuration was weakly associated with only 5 of 30 fish parameters in the FKNMS, and explained $< 30\%$ of the variation of any single fish parameter (Table 4-3). Though reef size was marginally correlated with total fish abundance ($R^2 = 0.22$), abundances of mobile fishes ($R^2 = 0.26$), serranids ($R^2 = 0.27$) and lutjanids ($R^2 = 0.24$) (Table 4-3) in FKNMS, examination of Mallows C_p and AIC revealed that these model estimates were fairly

unstable (e.g., total abundance $C_p = 3.84$, $\Delta_i = 4.3$). Pooled datasets for the FKNMS and USVI confirmed these findings. Likewise, rugosity was a poor predictor of reef fish assemblage structure, as no fish parameter was significantly correlated with rugosity. The coefficient of variation for rugosity was rather low, although no relationship was detected after datasets of the FKNMS and US Virgin Islands were pooled to maximize the gradient of rugosity.

As in the US Virgin Islands, reef context explained the greatest amount of the variation in reef fish assemblage structure, as 16 of 30 possible fish parameters were strongly associated with measures of reef context in FKNMS (Table 4-4). However, the particular measure of reef context associated with the majority of fish parameters differed between systems (Table 4-4). Contrary to my expectations, seagrass cover was not the best predictor of reef fishes in the FKNMS; rather the amount of pavement and reef habitat was strongly associated with several reef fish parameters (Table 4-4, Figure 4-2A-F). Within trophic guilds, abundances of herbivores ($R^2 = 0.52$) and piscivores ($R^2 = 0.33$) were associated with pavement (Table 4-4, Figure 4-2B-C). Within mobility guilds, resident fishes were correlated ($R^2 = 0.53$) with reef habitat (Figure 4-2D), whereas mobile fishes were strongly correlated ($R^2 = 0.70$) with reef, pavement and seagrass habitats (Table 4-4). Within taxonomic groupings, abundances of chaetodontids ($R^2 = 0.31$), acanthurids ($R^2 = 0.31$), and pomacentrids ($R^2 = 0.48$) were positively associated with reef habitat (Table 4-4, Figure 4-2E-F).

The landscape-scale measure of habitat patch diversity was a predictor of one reef fish parameter only; piscivore abundance was positively associated with patch diversity at the 250 m spatial extent only in the FKNMS ($R^2 = 0.35$) and the US Virgin Islands (R^2

= 0.51) (Figure 4-3). Model selection techniques confirmed the stability of these relationships (e.g., $C_p = 2$, and $\Delta_i < 2$), yet this was the only one that remained consistent across systems.

Differences in reef fish community structure were not likely to account for the lack of consistency in reef fish–habitat relationships across systems. In fact, reef fish community structure was quite similar in the US Virgin Islands and FKNMS at the entire assemblage level (cumulative species richness per reef in USVI = 44.23, FKNMS = 68.53; mean species richness per point count in USVI = 22.42, FKNMS = 22.06; mean number of fishes per point count in USVI = 96.72, FKNMS = 179.46). Higher mean abundances of reef fishes in the FKNMS can be attributed to the tendency of several species (e.g., *Abududuf saxtalis*) to aggregate around divers, possibly as a result of fish feeding. Reef fish community structure was significantly different between the US Virgin Islands and FKNMS at the trophic (one-way ANOSIM, global $r = 0.16$, $p < 0.02$) and family level (one-way ANOSIM, global $r = 0.22$, $p < 0.01$), though these differences were minor. These minor differences in reef fish community structure can be attributed to a 30 % difference in mean planktivore abundance and 26 % difference in herbivore abundance, with the means higher in the FKNMS for both parameters (Table 4-5). In addition, there was a 19 % difference in mean abundance of haemulids between sites (Table 4-5), with a slightly higher mean in the FKNMS compared to the USVI. In general, though, these differences were minor, thus fundamental differences in community structure do not preclude comparisons of reef fish–habitat relationships between systems.

The spatial arrangement and composition of habitat patches differed between the FKNMS and US Virgin Islands. There were significant differences ($df = 37, p < 0.0001$) in the mean areal coverage of seagrass within 500 m of focal reefs (FKNMS = 12.10 ha; US Virgin Islands = 6.76 ha), with a higher coefficient of variation of seagrass at 500 m in the US Virgin Islands (65.0) compared to the FKNMS (12.10). Furthermore, in the FKNMS, seagrass comprises 41 % of the habitat within 500 m of study reefs, which contrasts with 19 % in the US Virgin Islands (Figure 4-4). At the scale of the entire system, 69 % of the mapped extent of the FKNMS consists of seagrass, whereas 26 % is hardbottom (which includes pavement, reef, and patch reef). Differences in the amount of pavement and reef within 500 m of the study reefs were less clear, as the absolute percentages of pavement habitat are quite similar between study systems (20 % versus 17 %, Figure 4-4). However, the relative amount of pavement (17 %) and reef (30 %) in the FKNMS was low relative to the amount of seagrass (41%) in the FKNMS (Figure 4-4). In addition, the mean amount (ha) of pavement at 500 m in FKNMS was significantly less (2.3 ha) than the US Virgin Islands (12.2 ha). The coefficient of variation for pavement was comparable between systems, except at the 250-meter scale, in which case, the FKNMS was slightly higher than the US Virgin Islands. Finally, the proportion of potentially “essential” fish habitat (seagrass, reef and pavement habitats within 500 m of study reefs) was higher in the FKNMS (96 %) than the USVI (55 %) (Figure 4-4).

Comparisons of the landscape structure of the entire mapped systems revealed important differences between the FKNMS and US Virgin Islands. In general, the landscape structure of the FKNMS is more homogeneous (Figure 4-6C), as there is a distinct pattern of inshore seagrass that extends 6–10 km offshore, at which point spur

and groove reef development typically occurs. MDS plots revealed that reefs in the FKNMS clustered together, with less variability in landscape structure than the USVI (Figure 4-6C), although there were three outlier reefs (Figure 4-6C). Conversely, reefs in the US Virgin Islands exhibited greater variability in landscape structure (Figure 4-6C), with reefs dispersed across the MDS plots (Figure 4-6C). Likewise, there is a less distinct zonation of reef formation in the US Virgin Islands compared to the FKNMS. The stress value of 0.07 for the MDS plot of landscape structure corresponds to a good ordination with no real prospect of misinterpretation (Clarke and Warwick 2001).

Although there were not significant differences in fish community structure among systems (USVI and FKNMS), at the individual reef level, there was greater variation in reef fish assemblage structure in the US Virgin Islands compared to the FKNMS (Figure 4-6A-B). For example, in the FKNMS, both at the trophic and taxonomic levels, reefs were clustered tightly together in MDS plots (Figure 4-6A-B). Conversely, in the US Virgin Islands, there was greater variability at the trophic and taxonomic level, in reef fish assemblage structure (Figure 4-6A-B). There was also considerably more variability in landscape parameters in the US Virgin Islands, compared to the FKNMS (Figure 4-6C). Thus, variability in reef fish community structure appears greater in the more heterogeneous coral reef landscape of the USVI (Figure 4-6C), and lowest at reefs in the more homogeneous FKNMS coral reef landscape (Figure 4-6A-C). Stress values for the MDS plots of reef fish community structure were < 0.2 for trophic structure, which gives a potentially useful 2-dimensional picture and < 0.1 for family structure, which corresponds to a good ordination (Figure 4-6A-B).

Reef fish community structure for individual reefs corresponded to differences in the presence or absence of seagrass (Figure 7A-B). Both at the trophic and family level, there was clear segregation between reefs with and without seagrass nearby (Figure 7A-B). Reefs with high to medium amounts of seagrass clustered together, regardless of location (US Virgin Islands or FKNMS), although reefs with moderate amounts (class = 2) of seagrass were less distinguishable from one another (Figure 4-7A-B). There was a tendency for reefs with moderate amounts of seagrass to be located closer to reefs with high amounts of seagrass (Figure 4-7A-B). Notably, when this classification was applied to the other common habitat types (e.g., pavement), there was no spatial pattern evident.

There were few differences in reef fish assemblage structure inside SPAs and MPAs compared to fished reference reefs in either FKNMS or the US Virgin Islands (Table 4-6). Importantly, the abundances of targeted reef fishes (e.g., haemulids, lutjanids) were not higher inside protected areas. Actually, for several fish parameters, abundances were greater at the fished reference reefs (Table 4-6). The lack of significant differences in reef fish abundance for most parameters of interest inhibited our ability to test whether reef fish–habitat relationships are higher where reef fish abundances are higher. Variance ratio tests revealed no significant differences in the strength of associations at reefs with higher abundances compared to those with lower fish abundances.

The models that best explained the relationships of various reef fish parameters and seagrass area for the pooled data (FKNMS and US Virgin Islands) were curvilinear (Figure 4-5A-D). Forty-five percent of the variation in haemulid abundance, and 30 % of the variation in lutjanid abundance was explained by a quadratic relationship with

seagrass (Figure 4-5A-D). For most relationships, the quadratic reaches an asymptote, at which point additional seagrass does not further increase each fish parameter (Figure 4-5A-D).

Discussion

Reef configuration measures explained little of the variation in reef fish assemblage structure in either the FKNMS or the US Virgin Islands. These findings contrast with reef fish research conducted at a small spatial scale (1–100 meters), where reef size (Molles 1978, Bohnsack et al. 1994), reef patchiness (Acosta and Robertson 2002), reef connectivity (contiguous versus patch reefs; Ault and Johnson 1998a, 1998b) and reef shape (Shulman 1984, Eristhee and Oxenford 2001) measures were shown to strongly influence reef fish assemblage structure (e.g., total abundance, species richness). A plausible explanation for the inability of configuration to predict fish assemblage structure in the FKNMS and US Virgin Islands is that the scale of analyses (10s to 100s of meters) is above the minimum scale where configuration effects are germane to reef fishes, and therefore these effects were not detectable.

In terrestrial systems, configuration effects are only detectable and/or operable below some minimum size threshold (McGarigal and McComb 1995, Fahrig 1997, 1998, Trzcinski et al. 1999). For example, Fahrig (1997, 1998) found that when the percentage of habitat in a landscape exceeded 20%, species persistence was virtually assured, regardless of configuration. Likewise, Andrén (1994) showed that patch isolation only becomes important when the percentage of critical habitat decreases below a 20–30% threshold. I hypothesize that my study reefs are above the minimum size (0.2–17 ha) where configuration effects are easily detectable, and that below some minimum size, which my reefs exceed, the influence of reef size and shape may become more important.

While the species–area relationships detected for insular habitats (Preston 1962, MacArthur and Wilson 1967) provides a firm basis for predicting that fish abundance and species richness will be greater on large reef patches compared to smaller reef patches, reef size explained little of the variation in reef fish assemblage structure in the FKNMS. Conversely, reef size was a strong predictor of cumulative species richness ($R^2 = 0.43$, $p < 0.001$) in the US Virgin Islands. These contradictory findings support terrestrial researchers who concluded that species–area relationships were too ambiguous to indicate whether two reserves, each half the size of a larger reserve, will contain more species than the single one (Simberloff and Abele 1976, Diamond 1975). The contentious SLOSS (single large or several small) reserve design debate (Quinn and Harrison 1988), asks whether a single large reserve or several small reserves of equal total area contain more species? While there are convincing management arguments for single large reserves (Terborgh 1976), my study suggests that small reefs may provide conservation benefits comparable to a single large reef, at this spatial scale. Furthermore, some of the smallest, yet most heterogeneous reefs had the highest values for several reef fish parameters (e.g., North North Dry Rocks had highest species richness), which may indicate the importance of microhabitat influences on species assemblages (Gilpin and Diamond 1980). The issue of SLOSS may not have a simple, clear solution, and may be a function of many factors including habitat heterogeneity.

Neither the fine-scale measures of habitat heterogeneity (rugosity) nor landscape-scale measures of habitat diversity were useful in explaining variation in reef fish assemblage structure, which contradicts ecological theory that predicts species diversity increases with habitat diversity (Ricklefs 1973, Roughgarden 1996), yet supports my

earlier findings in the US Virgin Islands (Grober-Dunsmore et al. 2004a, 2004b, 2004c). The only exception was patch diversity, which was positively associated with piscivore abundance; a relationship that may be facilitated by the piscivore behavior of searching the reef edge for prey (Sweatman and Robertson 1994). The inability of habitat diversity to explain reef fish assemblage structure is also contrary to findings from a number of fine-scale coral reef studies (1–10s of meters), which demonstrated a positive relationship with reef fish diversity and abundance and habitat heterogeneity, measured by parameters such as spatial complexity (Hixon and Beets 1989), living coral (Reese 1981), coral reef zonation (Friedlander and Parrish 1998), and reef surface area (Gladfelter et al. 1980). Contrary to recent experimental evidence (Armbrecht et al. 2004), it does not appear that diversity per se at one level creates conditions that promote diversity at another level in coral reef systems, therefore one key finding is that habitat diversity may not scale up at the landscape level (i.e. 100s of meters scale) as a predictor of reef fish assemblage structure.

Habitat diversity (at fine or landscape spatial scales) may fail to explain reef fish assemblage structure for several reasons. At the landscape scale, individual habitat types appear more important than diversity per se, as revealed in this and previous studies (Wiens 2002, Grober-Dunsmore et al. 2004a, 2004b, 2004c, Lindenmayer and Hobbs 2004, Jeffrey 2004, though see Cushman and McGarigal 2003). The fine-scale measure of rugosity may not have been capable of predicting reef fish community structure in this study because sampling was constrained to reef habitat only. Historically, rugosity was a good predictor of fish assemblage structure because it indicated topographically-complex habitat (Friedlander and Parrish 1998, Luckhurst and Luckhurst 1978), however, benthic

habitat maps are likely to be capable of assuming this function. Because rugosity is a costly in-water measure, it will be important to explore remotely-obtained measures of rugosity (e.g., LIDAR, side-scan sonar) that may be readily available for measuring within-reef heterogeneity at a scale appropriate for marine resource managers. Therefore, landscape-scale measures of habitat diversity may not prove useful in discerning the value of individual reefs as candidates for protection.

Context clearly exerts a strong influence on reef fish assemblage structure. Reef context–reef fish relationships that passed model selection criterion were consistent with our knowledge of the ecology of each particular fish group, as was recently demonstrated in the US Virgin Islands (Kendall et al. 2003, Grober-Dunsmore et al. 2004c), Puerto Rico (Christensen et al. 2003), Belize (Mumby 2004), Colombia (Appeldoorn et al. 2003) and the Florida Keys (Jeffrey 2004). For example, total fish abundance was associated with the areal coverage of pavement, perhaps because the dominant fish in the assemblage (labrids) tend to roam across this low relief habitat. Similarly, grazers (herbivores) were also associated with pavement, where they often forage. Not surprising is the fact that identified resident reef species were strongly associated with the areal coverage of reef habitat. Thus, different fish groups do not appear to perceive the landscape the same, thus it will be necessary to focus on organisms (Wiens 1989, Pearson 1993) or functional groups (as in this study) in the future to understand how landscape structure affects marine systems. This study contributes to a growing body of work that points to the importance of reef context (Appeldoorn et al. 2003, Christensen et al. 2003, Kendall et al. 2003, Mumby et al. 2004), and builds on recent research by replicating the study spatially, demonstrating the effects of reef context to the entire reef fish community

(not just select parameters), and providing quantified measures of reef context, rather than simple presence or absence for multiple habitat types.

The processes that structure reef fish communities appear modified by variation in landscape structure. While measures of reef context consistently explained the greatest variation in reef fish assemblage structure in both study systems, the individual habitat types driving the relationships varied. For example, seagrass was strongly associated with many fish parameters in the US Virgin Islands (e.g., abundances within MIFs, grunts, snappers), yet pavement and reef habitats were associated with the majority of reef fish parameters in the FKNMS. Differences in the landscape structure of the two study systems may help explain this disparity in findings. The distribution of seagrass habitat is highly variable in the US Virgin Islands; seagrass is the background matrix of several embayments, yet absent completely in others. In this landscape, seagrass is a strong predictor of many commercially and recreationally-important reef fishes in the US Virgin Islands. Conversely, the distribution of seagrass is less variable, and the dominant habitat type around study reefs in the FKNMS, but not a predictor of these same commercially and recreationally-important fishes. Thus, seagrass could be used as a reliable predictor of these fish groups only in the landscape where seagrass was less available. These findings have important consequences for MPA design, suggesting that habitat estimates for predicting reef fishes derived from one system, may not be broadly applicable in another (Lindenmayer et al. 2003). It appears that applying a particular metric (e.g., areal coverage of seagrass) simplistically may be dangerous, if the regional ecology and specific landscape is not considered explicitly (Noss 1983). Rather, MPA

design may be more complicated, and require intimate knowledge of the spatial arrangement and composition of the habitat patches in each system.

Perhaps there is some critical threshold of habitat, at which point other habitat types structure reef fish communities. Combined reef fish datasets (FKNMS and US Virgin Islands) revealed a significant curvilinear relationship; with increasing seagrass, several reef fish parameters increased until an asymptote was reached. While the critical threshold hypothesis purports that a nonlinear decrease in richness or abundance occurs below some level of habitat loss (Summerville and Crist 2001), perhaps at some threshold of seagrass habitat gain, seagrass no longer has pronounced (or detectable) influence on the reef fish community. If such a critical threshold exists, it appears to occur between 20-30 % of the total area of habitat, since at this amount of seagrass, reefs in the FKNMS and US Virgin Islands converged in simple linear regression models and became difficult to distinguish from other. The inability to detect a relationship with seagrass within the FKNMS system on its own, may be explained by the abundance of seagrass immediately beyond the 250-meter spatial scale.

The critical threshold hypothesis is further supported by the MDS plots of reef fish community structure at the trophic and family level, which reveal a clear spatial segregation of reefs (FKNMS and US Virgin Islands) with and without seagrass. Regardless of location, i.e. USVI or FKNMS, reefs with large amounts of seagrass were more similar to one another. Reefs with moderate amounts of seagrass most resembled reefs with large amounts of seagrass, suggesting that modest amounts of seagrass may yield considerable influence on reef fish community structure. The absence of a spatial pattern when reefs were classified by other habitat types confirmed the importance of

seagrass in particular, and eliminated the possibility that other habitat types were responsible for observed spatial patterns. Such thresholds in the response of organisms to landscape characteristics is widely recognized in terrestrial systems (Wiens 2002), and can be useful in forecasting threshold points (e.g., habitat loss or fragmentation) given precise rules for movement and dispersal (With and Crist 1995). While much remains to be learned about the importance of possible habitat thresholds in coral reef systems, combining datasets from the US Virgin Islands and FKNMS (though problematic for some purposes), allowed a potentially valuable insight that would not have been possible with data only from an individual system.

The relative amount of an individual habitat type within a given system may be as important as the absolute amount in structuring reef fish communities. In the USVI, pavement and reef habitats were common, but were poor predictors of most fish parameters. In the FKNMS these same habitat types were relatively less common, but explained significantly more of the observed variation in the reef fish parameters of interest. These findings are congruent with those from an experimental shelter manipulation where groupers responded to shelter limitation when reefs were surrounded by sand, but failed to do so when reefs were surrounded by pavement habitat (Hart 2002). Thus, my initial assumption (stated earlier in the text) that the processes that gave rise to the relationships in the US Virgin Islands are not modified by variation in the landscape structure, appears incorrect. Rather, the critical element driving differences in community structure in one landscape may depend upon the specific landscape attributes of that landscape.

For instance, the relative heterogeneity or homogeneity of a particular coral reef landscape may determine the importance of landscape attributes in structuring communities. Reef fish community structure was more variable in the more heterogeneous landscape of the US Virgin Islands, whereas fish community structure was less variable in the more homogeneous landscape of the FKNMS. The FKNMS reef tract (totaling 591,422 ha) has a consistent pattern of 6–10 kilometers of inshore seagrass, interspersed with small patch reefs, until reaching the offshore drowned spur and groove zone to the east. This pattern extends the 285-kilometer length of FKNMS. Perhaps the relative homogeneity of the FKNMS coral reef landscape inhibited our ability to evaluate the importance of landscape structure on reef associated fishes in the FKNMS. The US Virgin Islands systems is smaller, and extends from the shoreline of St. John to the British Virgin Islands to the north, and to deep water to the south; totaling 49,588 ha. The spatial patterning of habitat patches in the US Virgin Islands is more heterogeneous, with patches of reef and seagrass interspersed among other habitat patches that are similar in areal coverage. Some areas of the island have distinct enclosed embayments, whereas other areas are more exposed. Thus, the range of variability in landscape parameters may be greater within the US Virgin Islands system, and as a consequence of this landscape heterogeneity, the reef fish community structure may be more variable. In spite of the greater variability of reefs (with regard to fish community structure at the trophic and family levels), the overall fish community structure between systems was remarkably similar as demonstrated by ANOSIM. Such consistency in structure has been found across regions and reef types (Bohnsack and Talbot 1980, Bohnsack et al. 1999),

yet served as a control by eliminating the possibility that differences in reef fish community structure precluded the ability to make comparisons across systems.

Reef fish abundances of family and trophic fish groups were not higher inside protected areas relative to reference (fished) areas, which greatly inhibited the ability to test whether reef fish–habitat relationships are stronger where fish densities are high. In fact, the abundances of several fish groups were higher at open access reference reefs. While abundances of select target species (e.g., *Ocyrus chyrseyus*) may be increasing inside SPAs in the FKNMS (see Ault et al. 1998, Bohnsack et al. 1999), protection measures may be too recent to produce positive community-level effects. The limited time since establishment of FKNMS SPAs (six years) may partially explain the absence of protection effects, since Looe Key, which has the longest protection history (> 20 years), had the highest mean abundance of adult and juvenile groupers, adult grunts, and adult snappers. Our findings suggest that the effects of protecting heavily-exploited fishes may only become apparent after six or more years of no-take status and enforcement. In fact, some have suggested it may take as long as 50 years (Russ and Alcala 2004). With regard to the VINP, it is not surprising that reef fish abundances were not higher inside park boundaries, since the primary fishing gear (trap fishing) is still allowed. Reef fish populations may continue to decline in the US Virgin Islands, unless strict fishing regulations are instituted and enforced (Rogers and Beets 2001). Studies to determine whether reef fish density influences our ability to detect relationships with landscape features remain to be conducted.

Conclusions

This study provides considerable insight into the generalities of applying landscape ecology principles to coral reef ecosystems. Most importantly, reef context clearly

influences reef fish assemblage structure, and I recommend that selection of reef patches for conservation should be based on how well a patch relates or links to other patches in the landscape. However, extrapolation of patterns observed in local studies may not hold regionally (Flather and Sauer 1996) or across systems. Furthermore, considerable risk is often associated with broad application of conservation strategies (Kareiva 1987), and as a consequence, conservation policies must consider the natural variation in landscape structure, since overlooking system differences may lead to errors arising from simple landscape perceptions of patterns (Kotliar and Wiens 1990). It is clear from our findings that the same landscape can be perceived quite differently by different species (Lindenmayer et al. 2003, Westphal et al. 2003). Thus, a functional MPA design must consider the autecology of those species targeted for management. Finally, while this inductive approach is less conclusive than the hypothetico-deductive method based on experimental manipulations (Underwood 1997), it may be the only practical means to ascertain the influence of factors acting at large spatial scales.

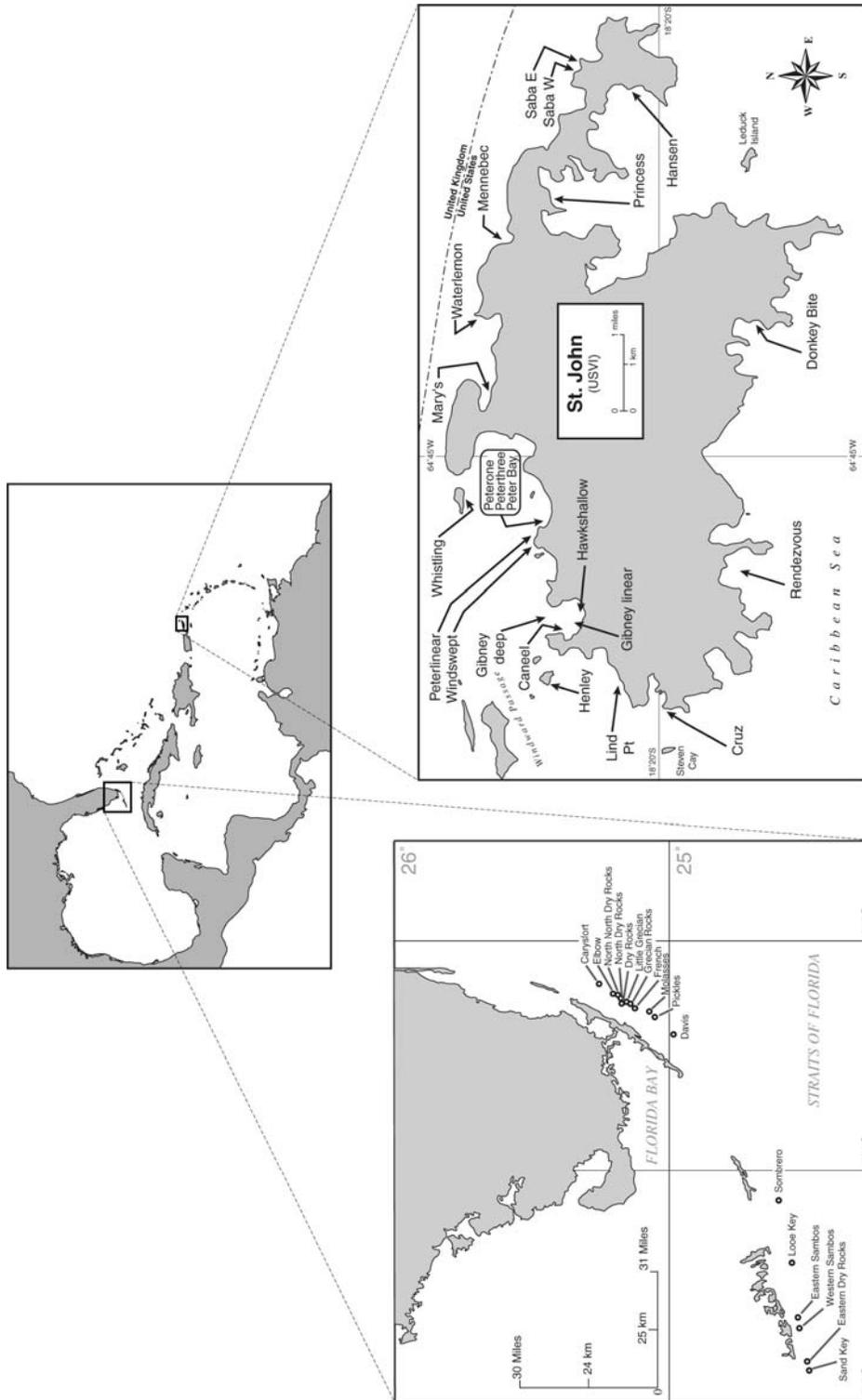


Figure 4-1. Location of the 17 study reefs sampled in 2003 in the Florida Keys National Marine Sanctuary and the 22 study reefs sampled in 2002 in St. John, U.S. Virgin Islands.

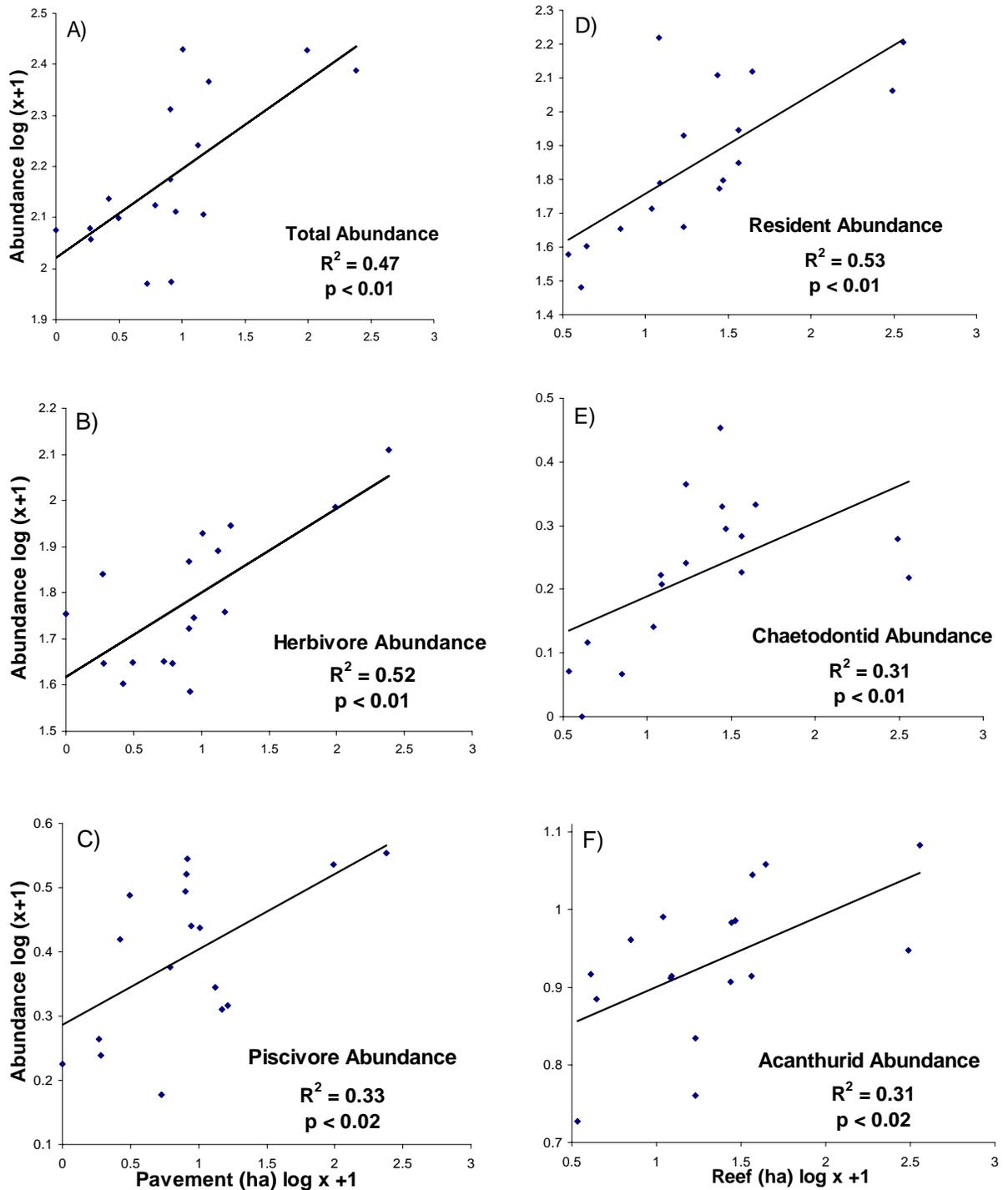


Figure 4-2. Simple linear regression results of the effects of reef context (the areal coverage of pavement and reef habitat $\log_{10}(x+1)$) at the 100-meter spatial scale on mean abundance of various reef fish parameters at the 17 study reefs sampled in 2003 in the FKNMS.

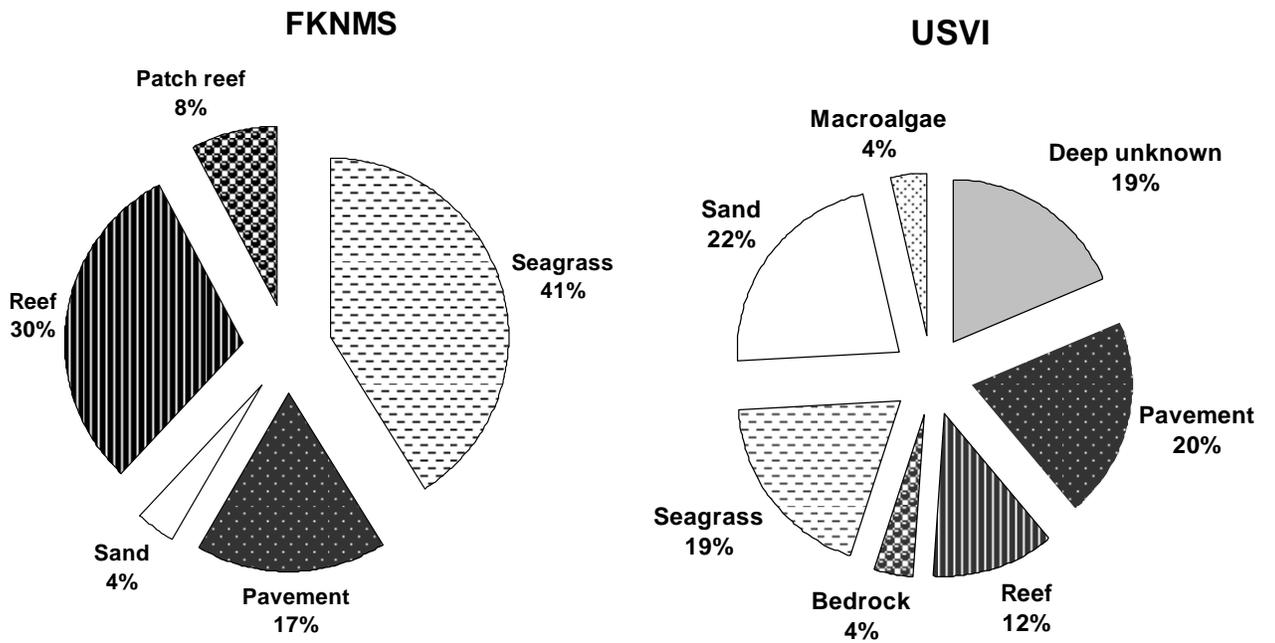


Figure 4-4. Comparison of the relative proportion of mapped habitat classes within 500 m of the study reefs in the FKNMS and US Virgin Islands.

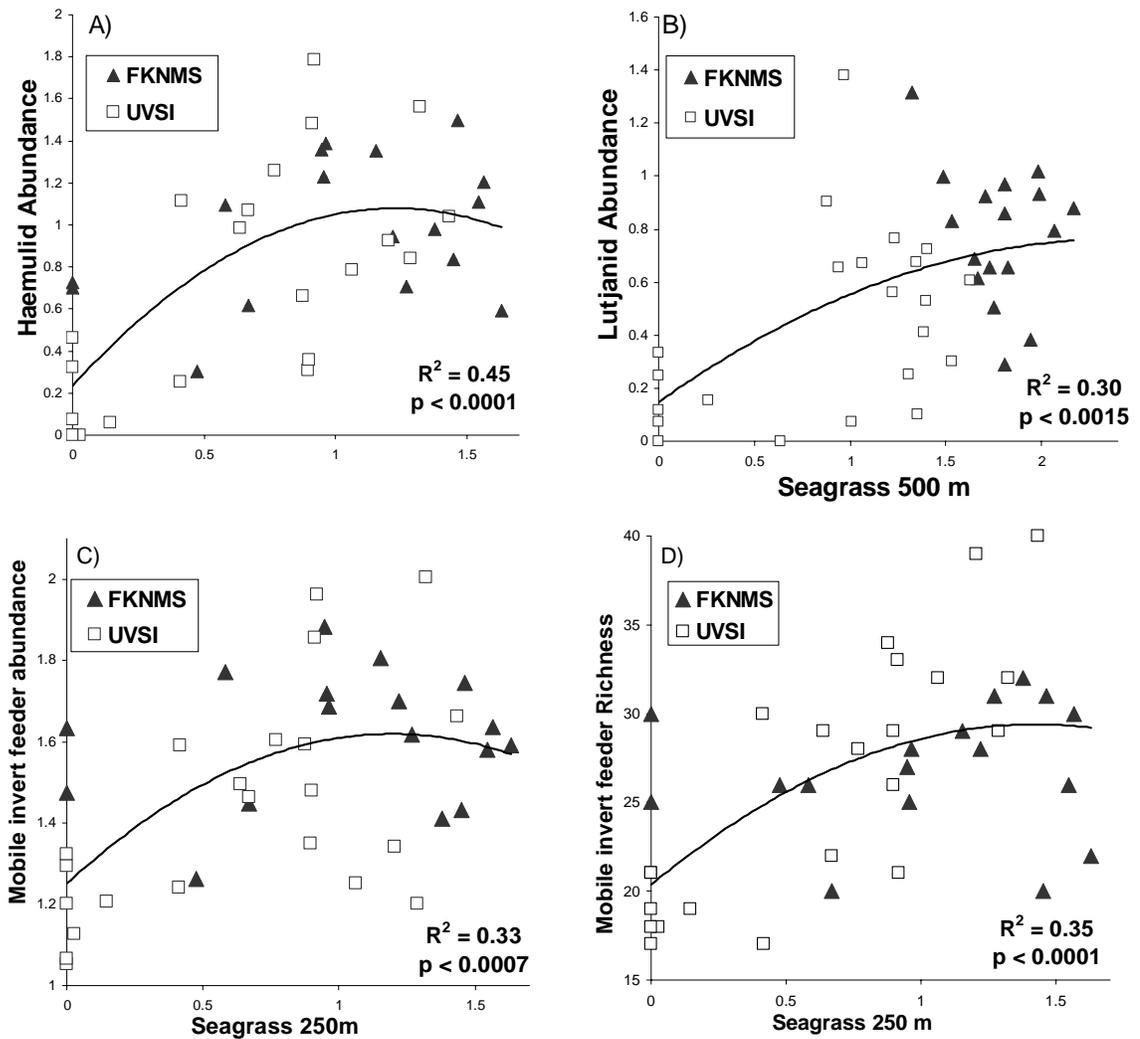


Figure 4-5. Reef fish abundance–seagrass relationships for the US Virgin Islands and the FKNMS ($n = 39$). The amount of seagrass (ha) $\log_{10}x + 1$ is on the x-axis. The spatial extent (250 m and 500 m) with the strongest relationship is shown for each fish parameter. Mean abundance values were $\log_{10}x + 1$ -transformed.

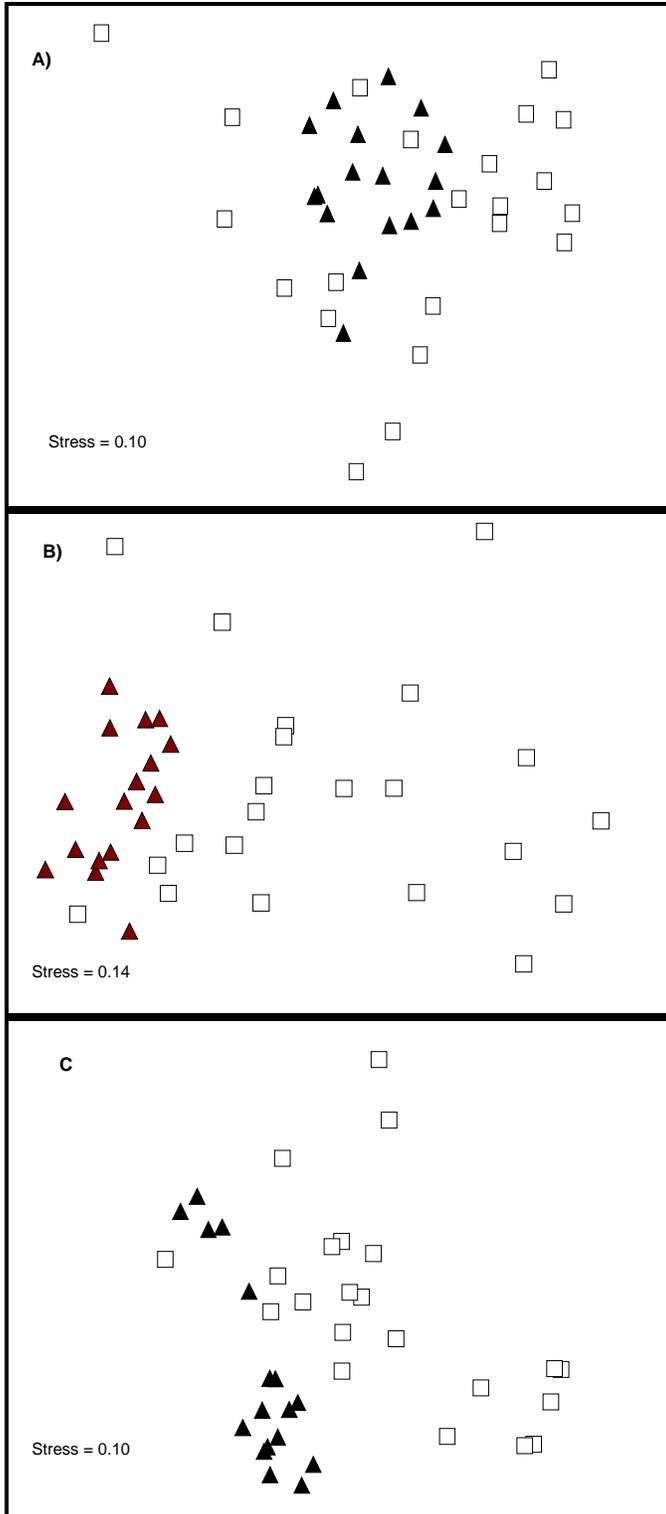


Figure 4-6. Multidimensional scaling plots of the (A) trophic and (B) family structure of reef fish communities and the (C) landscape structure of the US Virgin Islands (squares) and FKNMS (triangles).

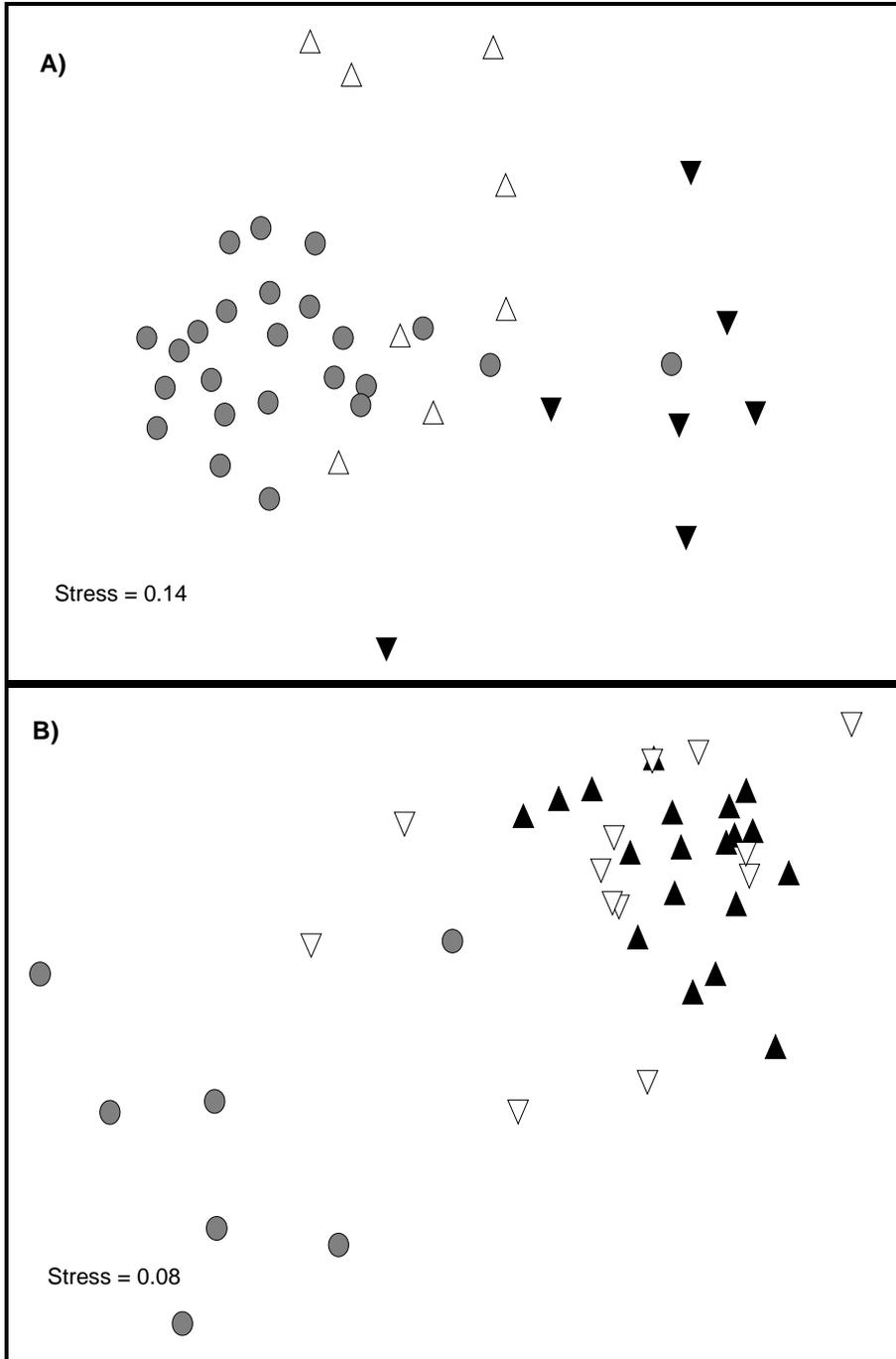


Figure 4-7. MDS plots of the (A) trophic and (B) family level reef fish community structure for reefs in the US Virgin Islands and FKNMS, with reefs classified according to high (circles), moderate (open triangles) and low seagrass (upside down closed triangles) areal coverages.

Table 4-1. Reef fish assemblage parameters (n = 30) used as dependent variables in statistical analyses

Entire assemblage level parameters	Trophic guilds	Mobility guilds	Taxonomic groupings
Cumulative species richness	Herbivores (J & A)	Resident	Acanthurid (J & A)
Mean species richness	Mobile invertebrate feeders (J & A)	Mobile	Serranid (J & A)
Total abundance	Omnivores (J & A) Piscivores (J & A) Planktivores Sessile invertebrate feeders	Transient	Haemulid (J & A) Lutjanid (J & A) Pomacanthid Scarid (J & A) Holocentrid Labrid Chaetodontid

Note: Fish groups are not always mutually exclusive. *Hypoplectrus* species were not included in Serranid grouping. For each trophic guild and taxonomic grouping, reef fish parameters were further subdivided into juvenile and adult components, where indicated (J = juvenile, A = adult).

Table 4-2. Study reef name, protection status and reef fish sampling effort for FKNMS (May 2003) and St John, USVI (July-August 2002).

FKNMS (n = 17)	Protection status	No. of samples	USVI (n = 22)	Protection status	No. of samples
Carysfort	SPA	18	Caneel	MPA	6
Davis	SPA	16	Cruz1	MPA	4
Dry Rocks	SPA	13	Donkey	MPA	6
E Dry Rocks	SPA	21	Gibneydeep	MPA	4
Eastern Sambo	SPA	12	Gibneylinear	MPA	8
Elbow	SPA	13	Hansen	Reference	6
French	SPA	22	Hawkshallow	MPA	6
Grecian Rocks	SPA	14	Henley	Reference	4
Little Grecian	Reference	14	LindPoint	MPA	6
Looe Key	SPA	31	Mary's	MPA	2
Molasses	SPA	20	Mennebec	MPA	5
North Dry Rocks	Reference	16	Peterbay	MPA	4
NN Dry Rocks	Reference	15	Peterlinear	MPA	4
Pickles	Reference	15	Peterone	MPA	4
Sand Key	SPA	17	Peterthree	MPA	4
Sombrero	SPA	14	Princess	Reference	4
Western Sambos	SPA	20	Rendezvous	Reference	10
			SabaE	Reference	4
			SabaW	Reference	2
			Waterlemon	MPA	8
			WhistlingCay	MPA	4
			Windswept	MPA	12

Note: In the FKNMS, SPA refers to special protected areas, which are no-take areas, and in the US Virgin Islands, MPA refers to reefs within the boundaries of Virgin Islands National Park, where fishing is permitted, except with spear guns. Reference reefs refer to areas outside the boundaries of SPAs in FKNMS and outside the boundaries of Virgin Islands National Park in the US Virgin Islands.

Table 4-3. Stepwise regression results indicating the relationship of landscape configuration and reef fish assemblage structure for the FKNMS and US Virgin Islands, with the R-square, associated p-value, and explanatory habitat variable.

Reef fish parameter	FKNMS R ²	FKNMS p-value	Habitat variable	USVI R ²	USVSI p-value	Habitat variable
Total Abundance	22%	0.06	Reef size	--	--	None
Mobile	26%	0.04	Reef size	--	--	None
Serranid	27%	0.03	Reef size	--	--	None
Pomacanthid	30%	0.02	No. of patches	--	--	None
Lutjanid	24%	0.03	Reef size	--	--	None

Notes: Relationships for the US Virgin Islands are presented, only if significant relationships were found in FKNMS, though all reef fish parameters were explored. Input habitat variables were reef size, number of habitat patches within 100 m and perimeter to area ratio of each study reef. The -- symbol indicates where no relationship was detected.

Table 4-4. Stepwise multiple regression results of the relationships of reef context and reef fish assemblage structure for FKNMS and US Virgin Islands, with the R-square, p-value, and explanatory variable by location.

Fish parameter	FKNMS R ²	FKNMS p-value	Habitat variable	USVI R ²	USVI p-value	Habitat variable
Entire						
Total abundance	47 %	0.0025	Pavement	17 %	0.0500	Seagrass
Total richness	---	---	---	47 %	0.0004	Seagrass
Mean richness	57 %	0.0013	Pavement	24 %	0.0200	Seagrass
		0.0220	Seagrass			
		0.0086	Reef			
Trophic						
Herbivore	52 %	0.0011	Pavement	---	---	---
A MIF	---	---	---	32 %	0.0050	Seagrass
J MIF	24 %	0.0400	Patch reef			
J Omnivore	32 %	0.0100	Seagrass	14 %	0.0300	Seagrass
Piscivore	33 %	0.0170	Pavement	16 %	0.0300	Reef
Planktivore	50 %	0.0017	Reef	---	---	---
SIF	56 %	0.0047	Patch reef	---	---	---
		0.0015	Reef	---	---	---
Mobility						
Resident	53 %	0.0009	Reef	---	---	---
Mobile	70 %	0.0004	Patch reef	20 %	0.0400	Seagrass
		0.0024	Pavement			
		0.0429	Seagrass			
Family						
Acanthurid	31 %	0.0200	Reef	---	---	---
Chaetodon	31 %	0.0210	Reef	---	---	---
Haemulid	---			48 %	0.0004	Seagrass
Holocentrid	---			20 %	0.0300	Seagrass
Labrid	51 %	0.0013	Pavement	---	---	---
Pomacentrid	48 %	0.0020	Reef	34 %	0.0400	Pavement
A Lutjanid	---	---	---	39 %	0.0052	Seagrass
						Reef
A Scarid	62 %	0.0003	Patch reef	---	---	---
J Scarid	70 %	0.0028	Pavement			
		0.0002	Seagrass			
		0.0067	Patch reef			

Note: Relationships that are significant ($p < 0.05$) following Sequential Dunn-Sidak Bonferroni-corrections are presented. The --- symbol indicates where no relationship was detected.

Table 4-5. Average dissimilarity in reef fish community structure at the trophic and family level in the FKNMS and US Virgin Islands, and the relative contribution of each trophic and family category to community dissimilarities using SIMPER analyses on standardized data.

Dissimilarity		Relative Contribution				
Trophic	Planktivore	Herbi	MIF	Omni	Pisci	SIF
29.19	30.79	26.06	21.63	12.38	6.29	1.06
Family	Haemulid	Scarid	Pomacentrid	Acanthurid	Labrid	Lutjanid
38.56	18.45	17.23	16.58	14.63	13.65	5.51

Note: Plankti = planktivore; Herbi = herbivore; MIF = mobile invertebrate feeders; Omni = omnivore; Pisci = piscivore; SIF = Sessile invertebrate feeders; Haem = Haemulid

Table 4-6. T-test comparison results to test for significant differences in abundance of the 30 reef fish parameters in the FKNMS (SPA and reference sites n = 8 reefs) and the US Virgin Islands (MPA and reference sites n = 22 reefs).

Fish parameter	FKNMS	USV Virgin Islands
Cumulative species richness	0.63	0.630
Mean species richness	0.29	(Ref) 0.001
Total abundance	0.44	(Ref) 0.06
J Herbivores	0.59	0.76
A Herbivores	(SPA) 0.01	(Ref) 0.06
J MIFs	0.37	0.31
A MIFs	0.61	(Ref) 0.01
J Omnivores	0.86	0.11
A Omnivores	0.58	(Ref) 0.07
J Piscivores	(Ref) 0.07	(Ref) 0.07
A Piscivores	(Ref) 0.09	(Ref) 0.07
Planktivores	0.60	(Ref) 0.07
SIFs	0.14	0.48
Resident	0.19	(Ref) 0.08
Mobile	0.27	(Ref) 0.06
Transient	0.28	(Ref) 0.07
J Acanthurids	0.96	0.32
A Acanthurids	0.11	0.13
J Serranids	0.26	(MPA) 0.05
A Serranids	0.35	0.21
J Haemulids	0.81	(Ref) 0.10
A Haemulids	0.79	(Ref) 0.008
J Lutjanids	0.58	0.19
A Lutjanids	0.34	0.15
Pomacanthids	0.59	0.48
J Scarids	0.29	0.99
A Scarids	0.20	(Ref) 0.08
Holocentrids	0.99	(Ref) 0.03
Labrids	0.75	(Ref) 0.01
Chaetodontids	0.26	0.35

Note: A = adult, J = juvenile

CHAPTER 5 SUMMARY

Maintenance of biodiversity (the abundance, variety, and genetic makeup of native animals and plants) requires a landscape perspective (Franklin 1993) that complements population, community, and ecosystem considerations. A landscape ecology perspective is compellingly distinct from an ecosystem approach since functional landscapes typically consist of multiple ecosystems that are spatially differentiated but still interact through energy flow and ecological processes (Bissonette and Storch 2003). While an ecosystem approach is an important advance over single species management (which has dominated fisheries management approaches for decades), loss of biodiversity and sustainable populations of targeted species will continue unless conservation of functioning landscapes and their associated spatial processes is addressed (Bissonette and Storch 2003). Conservation initiatives, such as marine protected areas design, that neglect the ecological and evolutionary context of a landscape and their component ecosystems and species are likely to fail (Bissonette and Storch 2003). Though these landscape principles were derived in terrestrial systems, it is reasonable to assume that they may similarly apply to marine systems.

Marine resource managers and scientists have recently recognized the need for large-scale, ecosystem-based approaches to enhance the conservation of marine biodiversity (Allison et al. 1998, Murray et al. 1999, Carr et al. 2003) and to manage sustainable fisheries (Pikitch et al. 2004). To address this need and because so little work has been previously conducted at a landscape-scale in marine systems, a hypothetico-

deductive study approach (Peters 1991) was developed as a starting point toward applying terrestrial landscape ecology principles in tropical marine systems. Coral reef ecosystems were used as the study system, as they exist as a mosaic of interacting habitat patches including reef, hardbottom, seagrass, and sand. The objectives of this dissertation study were to: 1) explore the ability of landscape metrics to quantify and characterize the spatial arrangement of habitat patches in coral reef ecosystems, 2) explore relationships between reef fish assemblage structure and these metrics of landscape structure to develop testable hypotheses, 3) design a new study to test these hypotheses to further understand the relationship of reef fish assemblage structure to landscape structure of coral reef environments, and 4) to test the generality of findings from previous studies by repeating the studies temporally and spatially. Three separate studies (Chapter 2, Chapter 3, and Chapter 4) were conducted over multiple years at two locations in the Caribbean (the US Virgin Islands and the Florida Keys National Marine Sanctuary). Empirical data of the reef fish community and landscape structures of 59 study reefs (representing reefs of varying depth, types, and locations) formed the basis of this dissertation.

To accomplish the first objective (Chapter 2), a suite of fourteen patch and landscape-level metrics (that have proven useful in describing terrestrial environments) were calculated using geographic information systems (GIS) tools and digitized benthic habitat maps for the study reef landscapes at four spatial extents (100 m, 250 m, 500 m, 1 km). The ability of these metrics to describe and distinguish between different coral reef landscapes was explored by examining simple summary statistics. Furthermore, Pearson-product moment correlations and principal component analyses were applied to reduce

the landscape metrics into a more parsimonious set of variables that represent the information in the original benthic datasets. Examination of principal component plots at the four spatial extents revealed that the 250 m and 500 m spatial extents were the most appropriate scales for describing individual reef landscapes, in large part because beyond this extent, the total area of deep unknown increased considerably. These complex indices, however, were difficult to interpret because loadings were distributed across multiple variables. Thus, I concluded that individual habitat features, which were divided into two logical categories (configuration and context) were most valuable in characterizing and quantifying the landscape structure of the coral reef environments (e.g., size, shape, and context).

Because the creation of new hypotheses is one of the most obscure and demanding aspects of science (Peters 1991), an existing dataset of the reef fish assemblage structure and landscape structure of 20 reefs from St. John, US Virgin Islands was used to accomplish objective two (to explore relationships to generate testable hypotheses). I found, contrary to findings from large-scale studies in terrestrial systems (Rafe et al. 1985, Rosenzweig 1995, Ricklefs and Lovette 1999) and coral reef fish studies conducted at a small (1- 10 m) spatial scale (Bell and Galzin 1984, Hixon and Beets 1989, Friedlander and Parrish 1998), that measures of habitat heterogeneity (e.g., habitat diversity) do not appear to explain much of the variation in reef fish assemblage structure (Grober-Dunsmore et al. 2004a). Furthermore, the complex principal components were similarly not useful in explaining variation in reef fish assemblage structure. These findings contrast with those from terrestrial systems, where composite measures such as habitat diversity and principal components have successfully predicted hotspots of

diversity and abundance (Rosenzweig 1995, Ricklefs and Lovette 1999, Turner et al. 2001). Interestingly, habitat diversity was often negatively associated with various fish assemblage parameters, thus I concluded that single habitat types may be valuable in explaining variation in reef fish assemblage structure.

In Chapter 2, I found that landscape-scale measures of the areal coverage of different habitat types played an important role in determining the distribution of reef fishes in the US Virgin Islands. Reef context, as measured by the areal coverage of individual habitats, clearly influenced patterns of abundance and species richness at the entire assemblage level (e.g., total fish abundance, species richness) as well as within trophic and mobility guilds and taxonomic groups of fishes. One habitat type in particular, seagrass, explained a large amount of the variation in abundances of several exploited reef fishes (e.g., haemulids, lutjanids). Given these results, I generated a set of the most biologically-relevant hypotheses. I then identified which hypotheses were robust using model selection techniques to ensure that insights into habitat associations do not continue to be ambiguous and have poor explanatory power (Bissonette and Storch 2003). Hypotheses that met model selection criteria were used to design a new experiment to accomplish objective 3.

Chapter 3 was specifically designed based on exploratory findings from the previous study to test the importance of seagrass habitat surrounding study reefs on reef fish assemblage structure parameters of interest to resource managers. The reef fish parameters of interest include entire assemblage level parameters (e.g., cumulative species richness) and abundance and species richness within trophic and mobility guilds and within taxonomic groups of fishes. As expected, landscape-scale habitat associations

for several reef fish groups were clearly evident. Consistent with predictions, entire assemblage level parameters and fish abundances and species richness within mobile invertebrate feeders, haemulids, lutjanids, and epinephelids were significantly higher at those reefs with seagrass habitat within 1 kilometer, and these fish parameters increased with increasing areal coverage of seagrass. Consequently, the areal coverage of seagrass habitat proximal to individual reef patches may be used to successfully predict which reefs have high abundances of commercially and recreationally-important species and diverse reef fish assemblages. Although the study design of Chapter 3 is not able to identify the processes driving relationships, it provides strong evidence that functionally-linked marine landscapes contribute to increased species richness and abundances of several important fish groups.

While several recent studies provide evidence of the importance of reef context (Nagelkerken et al. 2000, 2002, Appeldoorn et al. 2003, Kendall et al. 2003, Dorenbosch et al. 2004, Mumby et al. 2004), the study in Chapter 3 builds on existing research in several important ways, thereby contributing to our understanding of how landscape ecology principles apply in tropical marine environments. First, this study addresses the effects of reef context on fish density, rather than on simple absence or presence of individual species. Second, this study differentiates between soft-bottom (e.g., seagrass, sand) and hardbottom (reef, pavement) habitats. Third, measures of each habitat type were quantified using digital habitat maps and GIS, rather than using estimates derived using non-digital habitat maps and a planimeter. Fourth, considerable groundtruthing of the neighboring habitat patches was conducted to confirm habitat measures. Fifth, confounding effects of previous studies (i.e. reef size, location, and other habitat types)

were minimized. Sixth, relationships were examined at the community level, within trophic guilds, within taxonomic groups, and within mobility guilds, thereby providing a comprehensive functional perspective of the response of various dimensions of the fish community to reef context. Finally, no previous study to our knowledge was designed explicitly to test the influence of reef context (specifically seagrass habitat) to a number of reef fish parameters of importance to resource managers. Therefore, this work represents an important contribution to our understanding of how landscape features influence reef fishes.

Because extrapolation of patterns observed in one landscape may not hold regionally or across systems (Flather and Sauer 1996), and because the coral reefs of the US Virgin Islands have been exploited from fishing pressure and suffered hurricane damage (Rogers et al. 1991), I designed a separate study (Chapter 4, objective 4) in the Florida Keys National Marine Sanctuary (FKNMS) to determine the generality of reef fish–habitat relationships detected in the US Virgin Islands. Measures of reef context consistently explained the greatest amount of variation for most reef fish parameters compared to measures of reef configuration, complex indices (e.g., habitat diversity) and fine-scale measures of habitat (rugosity) in both the US Virgin Islands and the FKNMS. The individual habitat measure of reef context driving the relationships (e.g., areal extent of seagrass or reef), however, varied between the US Virgin Islands and FKNMS.

These findings suggest that the processes that structure reef fish communities appear modified by variation in landscape structure. For example, seagrass was strongly associated with many fish parameters in the US Virgin Islands (e.g., abundances of haemulids and lutjanids), yet pavement and reef habitats were associated with the

majority of reef fish parameters in the FKNMS. Differences in the landscape structure of the two study systems may help explain this disparity. The distribution of seagrass habitat is highly variable in the US Virgin Islands; seagrass is the background matrix of several embayments, yet it is absent completely in others. Seagrass also comprises a relatively small proportion of the total habitat within the landscape, yet seagrass is a strong predictor of many commercially and recreationally-important reef fishes. Conversely, around study reefs in the FKNMS, the distribution of seagrass is less variable, and it is the dominant habitat type, however, it is not a predictor of these same commercially and recreationally-important fishes. Thus, seagrass was a reliable predictor of these reef fishes only in the landscape where seagrass habitat was relatively less available. These findings have important consequences for MPA design, suggesting that habitat estimates for predicting reef fishes derived from one system may not be broadly applicable in another (Lindenmayer et al. 2003). It appears that applying a particular metric (e.g., areal coverage of seagrass) simplistically may be dangerous if the regional ecology and specific landscape is not considered explicitly (Noss 1983).

Perhaps there is some critical threshold of habitat at which point other habitat types structure reef fish communities. When datasets from the FKNMS and US Virgin Islands were combined, the best model fit was a curvilinear relationship; as seagrass increased, several reef fish parameters increased until an asymptote was reached. While the critical threshold hypothesis purports that a nonlinear decrease in richness or abundance occurs below some level of habitat loss (Summerville and Crist 2001), perhaps at some threshold of seagrass habitat gain, seagrass no longer has pronounced (or detectable) influence on the reef fish community. If such a critical threshold exists, it appears to occur between

20-30 % of the total area of habitat, since at this areal coverage of seagrass, reef fish parameters from the FKNMS and US Virgin Islands begin to converge for most fish groups. The inability to detect a relationship with seagrass within the FKNMS system when examined independently may be explained by the ubiquity of seagrass habitat immediately beyond the 250 m spatial scale. Beyond this spatial scale, these spur and groove reefs have vast expanses of back-reef seagrass, and seagrass becomes the dominant habitat type for most study reefs. The absence of significant relationships between reef fish parameters and seagrass under these conditions indicates that caution is warranted in applying broad design principles across systems, since the processes that structure fish communities appear to respond to variation in the landscape structure of each particular system. My findings generally concur with common terrestrial principles: when seeking specific predictive models, structuring mechanisms may always be local and empirically-based, making prediction difficult and perhaps impossible (Bissonette and Storch 2003).

Several findings in this dissertation remained consistent across the different study designs, therefore these may represent general principles for applying a landscape ecology approach to tropical marine systems. First, many landscape metrics were valuable in describing and quantifying the landscape structure of the coral reef environments. However, the challenge was to identify those appropriate to the objectives of the study and to organisms or processes of interest. In the US Virgin Islands and the FKNMS, individual habitat features appeared more valuable than complex indices (e.g., principal components) in characterizing the coral reef landscapes. Second, the assumption that all species conform to the same coral reef landscape pattern is rejected by

findings in this dissertation. Rather, the same landscape can be perceived quite differently by different species, as has been consistently reported in terrestrial findings (Lindenmayer et al. 2003, Westphal et al. 2003). Third, landscape relationships were generally consistent with the natural history of each reef fish group, since various life history stages and specific trophic and mobility guilds responded to different habitat features. These findings broadly concur with those from terrestrial systems, which reveal the importance of the natural history of each organism of interest (e.g., life history stage, mobility, dispersal, habitat generalist or specialist) (Stamps et al. 1987, Sisk et al. 1997, Mitchell et al. 2001). Clearly, the design of functional MPAs must consider the autoecology of the species of interest. Fourth, the appropriate spatial scale was also a function of the unique natural history of each reef fish group. For example, juveniles responded to spatial features at a smaller scale (meters to 250 meters) compared to adults (100 m-1 km). In addition, there were clear differences in the response of fishes to landscape characteristics based on mobility. In general, resident species were most closely associated with the fine-scale measure of rugosity within the reef patch, mobile species were strongly associated with landscape characteristics at the scale of 100 m – 1km, and transient species were typically not associated with either fine-scale or landscape scale characteristics. Clearly, there is no single scale that is universally appropriate to reef fishes, thus any landscape study warrants investigation at multiple spatial scales (Storch and Bissonette 2003). Fifth, reef context clearly matters. The context of individual reef patches can exert a strong influence on the assemblage structure of reef fishes, perhaps as much or more than the characteristics within a given patch. Selection of reef patches for MPA design should therefore consider how well a

patch relates or links to other patches in the landscape. Sixth, the processes structuring reef fish communities may be modified with variation in the structure of the landscape. Because seagrass habitat was only a valuable predictor of various reef fish groups in the landscape where seagrass was relatively limited (US Virgin Islands), and not a predictor of these same groups in the landscape where seagrass was relatively ubiquitous suggests that managers must consider the specific attributes of each coral reef landscape. Results from the FKNMS suggest that there may be strong limits and thresholds to the response of reef fishes to individual landscape features, which is the case in terrestrial systems (Wiens 2002). Lastly, landscape-scale habitat features appear more valuable than the fine-scale measure of rugosity in predicting most reef fish groups. These findings provide promise for resource managers, since landscape scale metrics are becoming more readily obtainable, and may save precious in-water resources if they can reliably predict reef fish abundance and diversity (Margules and Pressey 2000).

There were also consistent negative findings in this research, and though notoriously underreported in the scientific literature, negative results can provide valuable insights for future research. First, complex indices such as habitat diversity and principal components were not predictors of reef fish assemblage structure, findings that contradict several terrestrial studies (Rafe et al. 1985, Ricklefs and Lovette 1999). Second, neither reef size nor reef shape were predictors of reef fish assemblage structure, although both small-scale coral reef studies (Molles 1978, Bohnsack et al. 1994, Gladfelter et al. 1980) and terrestrial theory (MacArthur and Wilson 1967) and empirical studies (Helzer and Jelinski 1999) indicate otherwise. Third, at this spatial scale, the number of habitat patches or habitat richness (the number of different habitat patch types)

are not predictors of reef fish assemblage structure. Finally, the fine-scale measure of rugosity is not capable of predicting reef fish assemblage structure when sampling is limited to within topographically complex reef habitat. Consistency among these negative findings may eliminate particular landscape features as potential predictors of reef fish community structure, or help us to understand the conditions that these metrics do not apparently apply. Because sampling was conducted over a wide range of reef types and locations, and many reef fish parameters were investigated in every study, these negative results appear to be broadly consistent.

The findings reported in this dissertation must be interpreted with consideration for the natural spatial and temporal variability of this dynamic system. This is particularly important when interpreting results and applying models derived from this system to another. Understanding the organization of natural communities in spatially heterogeneous environments is difficult because of the inherent complexity of natural systems (Drake 1990), the high spatial and temporal variability of reef fish communities (Sale et al. 1994), and the multiple interactions and processes that occur across scales (Drake 1990). For example, local reef fish abundance may be determined by the relative magnitude of larval recruitment, juvenile settlement, emigration by adults, or by predation and/or competition for structural refuge (Hixon and Beets 1993). Each of these attributes may vary in space and time, potentially obscuring detection of patterns in community organization, and thus contribute to a lower than expected explanatory power for any particular landscape metric.

Reef fish community structure in the US Virgin Islands and the FKNMS implies that both systems are heavily overfished. Both systems are dominated by herbivores,

with piscivores contributing less than 5 % of the mean abundance of fishes within trophic guilds. The mean abundance of exploited reef fishes such as haemulids, lutjanids, and serranids was extremely low in both systems, particularly in the exploitable size class (adults). Low densities of exploited reef fishes may have impaired my ability to detect relationships of reef fishes with landscape-scale features, and thus results must be interpreted with some caution. Further experimentation in less-fished systems will be required to determine whether fish density influences the response of reef fishes to landscape structure. However, the absence of differences in reef fish community structure within and outside protected areas in both systems highlights that current protective measures (i.e. inadequacy of existing fishing regulations, enforcement) are not resulting in significantly different reef fish communities. These findings corroborate other studies in the US Virgin Islands (Rogers and Beets 2001) and FKNMS (Ault et al. 1998c), which conclude that reef fish populations are heavily-exploited due to fishing pressure from recreational and commercial-level fishing. These marine protected areas occur within the jurisdiction of the US federal government, arguably in two of the few locations in the Caribbean that have access to adequate resources for enforcement and education. The overfished status of reef fish communities within these MPAs does not bode well for the rest of the Caribbean region (Jackson et al. 2003).

Generalizations relevant to MPA design will be difficult, and may depend on the population structure of the target reef fish community, the degree of fishing within and outside the boundaries of an MPA, the degree of protection sought, recovery rates of the species of particular interest, and landscape features of the area being considered for protection. Some species invariably require very large areas to achieve reasonable

protection, however, findings from this study indicate that the sedentary nature of the majority of fishes may indicate that relative small (1-5 km diameter) MPAs may provide conservation benefits, at least for some species. Resident fishes appear most likely to be influenced by within-patch characteristics (e.g., coral cover), and do not respond to habitat features beyond 500 m from study reefs. Mobile fishes, however, were most influenced by habitat features from 10's of meter to at least 1 km away, and thus MPA should consider the home range sizes of species of interest. Finally, it should be recognized that transient fishes may not be easily conserved within MPAs. Admittedly, this study does not address two important mechanisms that likely influence the ability of a particular MPA to meet its objectives; larval dispersal and spillover. While spillover is not directly addressed in this study, findings imply that spillover benefits to surrounding areas may depend upon the spatial arrangement of the specific coral reef landscape. Larval dispersal was not measured, but further research is clearly needed to determine the extent to which reef fish populations are open or closed (Mora and Sale 2002). Larval dispersal and settlement are likely influenced by a number of factors, including the location, distribution and amount of various habitats necessary for spawning, recruitment, larval export, settlement, growth, foraging and reproduction.

I recommend several areas for future research to improve our understanding of how to apply terrestrial landscape ecology principles to tropical marine systems. First, Mechanistic studies that examine individual movements (e.g., sonic tagging) are needed to track the flow of materials and organisms between various habitat patches. Such studies should be designed to examine specific aspects of the landscape (e.g., isolation, corridors of movement) and specific species that vary in their life history strategies (e.g.,

fishes from different mobility guilds). Second, these results must be interpreted within the scope and limitations of this study, and require testing in different coral reef landscapes for results to be more generalizable. Future studies should test whether the processes that structure reef fish communities respond to variation in the landscape structure of individual reef landscapes. To do this, studies should be designed in landscapes that vary along a particular landscape gradient of interest to test whether critical thresholds of habitat exist, and if so to identify the threshold values. Finally, neutral landscape models, which represent real landscapes as null models, have proven extremely valuable in theoretical analyses of pattern-process relationships in terrestrial systems. The utility of neutral models should be explored in coral reef ecosystems, using a variety of reef fish species. Because terrestrial landscape ecology is only recently being applied to tropical marine systems (Appeldoorn et al. 2003, Christensen et al. 2003, Kendall et al. 2003, Jeffrey 2004), there is considerable research needed to improve our understanding of the landscape principles in marine systems. Although this area of research is in its infancy, clearly there is considerable promise in using terrestrial landscape ecology principles to help us better design and manage reef fishes in coral reef environments.

APPENDIX
REEF FISH DATABASE

Species code for every reef fish species encountered in the US Virgin Islands and FKNMS, with the genus, species, diet, trophic guild, size at maturity and mobility guild. Classification into trophic guilds determined using Randall 1965, 1967 and Froese and Pauly 2002. If a single food item comprised greater than 50 % of the diet of a species, the species was classified into that particular trophic guild. * indicates those taxa detected only in the Florida Keys.

Species	Genus & species	Diet	Trophic	Maturity	Mobility
ABSA	<i>Abudefduf saxatilis</i>	zoobenthos 44%, zooplankton 13%	mif	14.6	resident
ABTA	<i>Abudefduf taurus</i> *	plants 94%	herb	15.0	resident
ACBA	<i>Acanthurus bahianus</i>	plants 97%	herb	10.0	mobile
ACCH	<i>Acanthurus chirurgus</i>	plants 94%	herb	15.5	mobile
ACCO	<i>Acanthurus coeruleus</i>	plants 93%	herb	12.0	mobile
ACMA	<i>Acanthemblemaria a maria</i>	plankton	plank	2.2	resident
ACSP	<i>Acanthemblemaria</i> sp.	no data	plank	3.9	resident
AENA	<i>Aetobatus narinari</i>	zoobenthos 54%	mif	141.4	transient
ALSC	<i>Aluterus scriptus</i>	zoobenthos	sif	58.3	transient
AMPI	<i>Amblycirrhites pinos</i>	zooplankton 46%, zoobenthos	plank	6.7	resident
ANSU	<i>Anisotremus surinamensis</i> *	zoobenthos 99%, crabs, urchins, gastropods	mif	36.6	transient
ANVI	<i>Anisotremus virginicus</i>	zoobenthos 70%	mif	22.8	transient
APBI	<i>Apogon binotatus</i>	zooplankton	plank	8.8	resident
APMA	<i>Apogon maculatus</i>	shrimps 49%, crabs 24%, polychaetes 4%, crustaceans 13%	mif	7.7	resident
APSP	<i>Apogon</i> sp.	zooplankton	plank	5.0	resident
APTO	<i>Apogon townsendi</i>	no data	omni	4.8	resident

Species	Genus & species	Diet	Trophic	Maturity	Mobility
ARRH	<i>Archosargus rhomboidalis</i>	plants 45%	herb	8.0	transient
ATSP	<i>Atherinomorus</i> sp.	plankton	plank	7.0	transient
AUMA	<i>Aulostomus maculatus</i>	nekton 74%, zoobenthos 23%	pisci	53.5	resident
BAVE	<i>Balistes vetula</i>	echinoderm 73%, crabs 5%, shrimp 6%	mif	25.0	mobile
BOLU	<i>Bothus lunatus</i>	nekton 86%	pisci	27.0	mobile
BORU	<i>Bodianus rufus</i>	crabs 35%, echinoderms 34%, gastropods 10%	mif	23.8	mobile
CABA	<i>Caranx bartholomaei</i>	nekton 97%	pisci	31.0	transient
CACA	<i>Calamus calamus</i>	zoobenthos 98.5%, polychaetes, mollusks	sif	32.1	mobile
CALA	<i>Caranx latus</i>	nekton 100%	pisci	40.0	transient
CAMA	<i>Cantherhines macroceros</i>	zoobenthos 87%, sponges tunicates	sif	27.0	mobile
CAPE	<i>Calamus pennatula</i>	crabs 24%, echinoderms 14%, bivalve 12%, gastropod 8%	mif	22.3	mobile
CAPU	<i>Cantherhinus pullus</i>	plants 50%, zoobenthos 50%- crustaceans	omni	12.9	mobile
CARO	<i>Canthigaster rostrata</i>	plants 20%, sponges 17%, crabs 13%, polychaetes 12%, amphipods 10%, gastropods 10%	omni	8.2	resident
CARU	<i>Caranx ruber</i>	nekton, zooplankton	pisci	24.0	transient
CASP	<i>Calamus</i> sp.*	based on other species	mif	27.0	mobile
CASU	<i>Canthidermis sufflamen</i> *	echinoderms 30%, mollusks 24%, zooplankton 42%	omni	36.6	transient
CHAN	<i>Chilomycterus antillarum</i>	sessile benthic invertebrates	sif	18.5	mobile
CHCA	<i>Chaetodon capistratus</i>	zoobenthos 38% cnidarian, 31%	sif	9.0	mobile

Species	Genus & species	Diet	Trophic	Maturity	Mobility
CHCY	<i>Chromis cyanea</i>	zooplankton 52.4%, planktonic crustaceans	plank	10.0	resident
CHMU	<i>Chromis multilineatus</i>	zooplankton 88%	plank	12.9	resident
CHOC	<i>Chaetodon ocellatus</i>	zoobenthos 90%, worms 35%, cnidarians 53%	sif	13.6	mobile
CHSC	<i>Chromis scotti</i> *	no data	plank	7.0	resident
CHSE	<i>Chaetodon sedentarius</i>	detritus 40%, polychaetes 16%, shrimps 16%, zoobenthos	sif	10.0	mobile
CHST	<i>Chaetodon striatus</i>	zoobenthos 59%, polychaete worms 60%, cnidarians	sif	12.8	mobile
CLPA	<i>Clepticus parrai</i>	zooplankton 90%	plank	18.5	resident
CLSP	<i>Clupeidae</i>	zooplanktivorous	plank	10.0	transient
CODI	<i>Coryphopterus dicrus</i>	no data	omni	3.8	resident
COEI	<i>Coryphopterus eidolon</i>	no data	omni	4.5	resident
COGL	<i>Coryphopterus glaucofraenum</i>	plants 50%, ostracods 12%, benthic invertebrates 30%	herb	2.4	resident
COLI	<i>Coryphopterus lipernes</i>	no data	omni	2.4	resident
COPE	<i>Coryphopterus personatus</i>	no data	omni	3.1	resident
DAAM	<i>Dasyatis americana</i>	nekton 21.8%, crustaceans, worms	mif	98.8	transient
DEMA	<i>Decapterus macarellus</i>	zooplankton 97%	plank	23.8	transient
DEPU	<i>Decapterus punctatus</i>	zooplankton 66%, ostracods 12%	plank	11.0	transient
DIAR	<i>Diplodus argenteus</i>	no data	mif	18.0	mobile
DIHO	<i>Diodon holocanthus</i> *	mollusks, sea urchins, hermit crabs, 70%	mif	29.0	mobile
DIHY	<i>Diodon hystrix</i>	echinoderms, crustaceans, mollusks 99%	mif	49.31	mobile

Species	Genus & species	Diet	Trophic	Maturity	Mobility
ECNA	<i>Echeneis naucrates</i>	zooplankton, detritus, isopods, crustaceans	mif	58.3	mobile
ELBI	<i>Elagatis bipinnulata</i>	nekton and invertebrates	mif	90.0	transient
ELSA	<i>Elops saurus</i>	nekton 43%, crustaceans, crabs & shrimp	pisci	53.5	transient
EMAT	<i>Emmelichthyops atlanticus</i>	nekton and crustaceans	pisci	8.8	transient
EPAD	<i>Epinephelus adscensionis</i>	zoobenthos 82%, crust, mollusks, nekton 20%	mif	25.0	mobile
EPCR	<i>Epinephelus cruentatus</i>	nekton 67%, zoobenthos 17%	pisci	20.0	mobile
EPFU	<i>Epinephelus fulvus</i>	nekton 46%, benthic crustaceans 56%	pisci	16.0	mobile
EPGU	<i>Epinephelus guttatus</i>	zoobenthos 70% crabs 40%, stomatopods 21%, nekton 21%	mif	25.0	mobile
EPIT	<i>Epinephelus itajara</i> *	zoobenthos lobster 70%, nekton 13%	mif	120.0	mobile
EPMO	<i>Epinephelus morio</i>	zoobenthos-nekton	mif	40.0	mobile
EPST	<i>Epinephelus striatus</i>	nekton 59%, crustaceans	pisci	48.0	mobile
EQAC	<i>Equetus acuminatus</i> *	zoobenthos 74%	mif	14.6	mobile
EQPU	<i>Equetus punctatus</i>	zoobenthos 99%, crustaceans, urchins	mif	16.9	mobile
FITA	<i>Fistularia tabacaria</i>	nekton	pisci	98.8	mobile
GECI	<i>Gerres cinereus</i>	benthic crust, worms, mollusks	sif	18.0	mobile
GICI	<i>Ginglymostoma cirratum</i>	finfish 99%	pisci	227.0	mobile
GNTH	<i>Gnatholepis thompsoni</i>	plants 74%, copepods 18%	herb	5.9	resident
GOEV	<i>Gobiosoma evelynae</i>	ectoparasites	sif	3.1	resident
GOGI	<i>Gobiosoma genie</i>	ectoparasites	sif	3.5	resident

Species	Genus & species	Diet	Trophic	Maturity	Mobility
GOSA	<i>Gobiosoma saucrum</i>	Based on other species	sif	3.8	resident
GRLO	<i>Gramma loreto</i>	planktonic and benthic crustaceans	mif	3.29	resident
GYFU	<i>Gymnothorax funebris*</i>	nekton	pisci	120.4	mobile
GYMO	<i>Gymnothorax moringa</i>	nekton	pisci	62.9	mobile
GYVI	<i>Gymnothorax vicinus</i>	nekton 63%, zoobenthos 25%	pisci	63.9	mobile
HAAL	<i>Haemulon album*</i>	zoobenthos 28%, echinoderms, worms	mif	36.0	mobile
HAAU	<i>Haemulon aurolineatum</i>	zoobenthos 64%, zooplankton 35%	mif	13.0	mobile
HABI	<i>Halichoeres bivittatus</i>	crabs 25%, urchins 18.7%, polychaetes 18%, gastropods 12%	mif	14.1	mobile
HACA	<i>Haemulon carbonarium</i>	zoobenthos 99%, crabs 38%, gastropods 15%, urchins 10%, chitons 8%	mif	21.7	mobile
HACH	<i>Haemulon chrysargyreum</i>	zooplankton 40%, zoobenthos 40%	plank	14.6	mobile
HAFI	<i>Haemulon flavolineatum</i>	zoobenthos - worms, crustaceans	mif	16.0	mobile
HAGA	<i>Halichoeres garnoti</i>	zoobenthos, benthic crustacean	mif	12.5	mobile
HAJU	<i>Haemulon</i> sp. juvenile	zooplankton	plank	14.0	mobile
HAMA	<i>Halichoeres maculipinna</i>	worms 49%, planktonic and benthic crustaceans	mif	11.8	mobile
HAMC	<i>Haemulon macrostomum</i>	zoobenthos-benthic crustaceans	mif	25.4	mobile
HAME	<i>Haemulon melanurum*</i>	benthic crust	mif	19.0	mobile
HAPA	<i>Haemulon parrai</i>	benthic crust	mif	22.3	mobile
HAPI	<i>Halichoeres pictus</i>	zoobenthos	mif	8.8	mobile
HAPL	<i>Haemulon plumieri</i>	zoobenthos, benthic crustacean	mif	18.0	mobile

Species	Genus & species	Diet	Trophic	Maturity	Mobility
HAPO	<i>Halichoeres poeyi</i>	zoobenthos 100%	mif	12.9	mobile
HARA	<i>Halichoeres radiatus</i>	zoobenthos 100%	mif	25.5	mobile
HASC	<i>Haemulon sciurus</i>	zoobenthos 97%, nekton 3%	mif	13.0	mobile
HASP	<i>Haemulon</i> sp.	based on other species	mif	13.0	mobile
HESI	<i>Hemiemblemaria simulus</i> *	No data	sif	7.0	resident
HOAD	<i>Holocentrus adscensionis</i>	zoobenthos 100%, crabs, polychaetes, gastropods, isopods	mif	14.5	mobile
HOBE	<i>Holacanthus bermudensis</i> *	sponges, tunicates	sif	26.5	mobile
HO CI	<i>Holacanthus ciliaris</i>	sponges, tunicates	sif	23.0	mobile
HOCO	<i>Holocentrus coruscus</i>	zoobenthos, benthic crustacean	mif	10.0	resident
HOMA	<i>Holocentrus marianus</i>	zoobenthos, crabs, shrimp,	mif	11.8	resident
HORU	<i>Holocentrus rufus</i>	zoobenthos, mollusks, echinoderms	mif	13.5	mobile
HOTR	<i>Holacanthus tricolor</i>	zoobenthos 97%, crabs	sif	17.0	mobile
HYAB	<i>Hypoplectrus aberrans</i>	shrimps, prawns	mif	8.8	resident
HYCH	<i>Hypoplectrus chlorurus</i>	shrimp, prawns, fish, crabs	mif	8.6	resident
HYGU	<i>Hypoplectrus guttavarius</i>	based on other species	mif	8.8	resident
HYIN	<i>Hypoplectrus indigo</i>	based on other species	mif	9.6	resident
HYJU	<i>Hypoplectrus</i> sp.	No data	plank	8.5	resident
HYNI	<i>Hypoplectrus nigricans</i>	fish, inverts	mif	10.2	resident
HYP U	<i>Hypoplectrus puella</i>	shrimps, crabs, fish, mysids	mif	10.2	resident
HYSP	<i>Hypoplectrus species</i>	based on other species	mif	8.5	resident
HYUN	<i>Hypoplectrus unicolor</i>	benthic crustaceans, fish	mif	8.6	resident
INVI	<i>Inermia vitata</i>	zooplankton	plank	14.6	transient

Species	Genus & species	Diet	Trophic	Maturity	Mobility
JELA	<i>Jenkinsia lamprotaenia</i>	zooplankton	plank	2.9	transient
JESP	<i>Jenkinsia</i> sp.	based on other species	plank	2.9	transient
KYSE	<i>Kyphosus sectatrix</i>	plants 100%	herb	42.0	transient
LABI	<i>Lactophrys bicaudalis</i>	sponges, tunicates, echinoderms 20%, algae	sif	28.0	mobile
LAMA	<i>Lachnolaimus maximus</i>	mollusks, crabs, urchins, amphipods	mif	46.1	transient
LANU	<i>Labrisomus nuchipinnis</i>	crabs, gastropods, urchins, fish	mif	14.6	resident
LAPO	<i>Lactophrys polygonia</i>	shrimps, crabs, gastropods, sponges, tunicates	mif	29.0	mobile
LAQU	<i>Lactophrys quadricornis</i>	no data	mif	27.5	mobile
LATR	<i>Lactophrys triqueter</i>	worms, annelids, ascidians: 50%, crabs 12%, sponges and tunicates 12%	sif	27.5	mobile
LIRU	<i>Liopropoma rubre</i>	related to soap fishes feed on crabs, mantis, shrimps	mif	53.5	resident
LUAN	<i>Lutjanus analis</i>	crabs 44%, mollusks 13%, nekton 30%	mif	51.0	mobile
LUAP	<i>Lutjanus apodus</i>	Nekton 100% adults, zoobenthos juv	pisci	25.0	resident
LUCY	<i>Lutjanus cyanopterus</i>	nekton 100%	pisci	81.1	mobile
LUGR	<i>Lutjanus griseus</i>	zoobenthos 40%, fish 40%	mif	20.0	mobile
LUJO	<i>Lutjanus jocu</i>	zoobenthos, crab, shrimp, fish 65%-61%	pisci	45.0	mobile
LUMA	<i>Lutjanus mahogani</i>	finfish, zoobenthos, shrimps, crabs	mif	28.0	mobile

Species	Genus & species	Diet	Trophic	Maturity	Mobility
LUSY	<i>Lutjanus synagris</i>	zoobenthos-crabs, stomatopods, polychaetes,	mif	18.5	mobile
MABO	<i>Malacoctenus boehlkei</i>	no	omni	4.7	resident
MAMA	<i>Malacoctenus macropus</i>	based on other species	omni	4.1	resident
MAPL	<i>Malacanthus plumieri</i>	echin, crabs, stomatopods, polychaetes	mif	39.1	mobile
MASP	<i>Malacoctenus</i> sp.	based on other species	omni	4.1	resident
MATR	<i>Malacoctenus triangulates</i>	benthic crustaceans	miff	5.4	resident
MAVE	<i>Malacoctenus versicolor</i>	benthic algae, copepods, amphipods, eggs	omni	5.5	resident
MEAT	<i>Megalops atlanticus</i>	fish	pisci	110.0	transient
MENI	<i>Melichthys niger</i>	plants 76%, zoobenthos	herb	29.0	transient
MICH	<i>Microspathodon chrysurus</i>	plants 93%	herb	13.5	resident
MOTU	<i>Monacanthus tuckeri</i>	zooplankton 42%, detritus 42%, benthic crustaceans rest	omni	7.0	mobile
MUMA	<i>Mulloidichthys martinicus</i>	zooplankton 35%, zoobenthos 30%, bivalves 14%, polychaetes 19%, echinoderms 9%, chitons	mif	18.0	mobile
MUMI	<i>Muraena miliaris</i>	fish, crabs no relative abundance data	pisci	39.1	mobile
MYBO	<i>Mycteroperca bonaci</i> *	nekton 100%	pisci	61.5	mobile
MYIN	<i>Mycteroperca interstitialis</i>	nekton 100%	pisci	45.3	mobile
MYJA	<i>Myripristis jacobus</i>	zoobenthos 90%, crabs, stomatopods, mysids, shrimps	mif	15.7	resident

Species	Genus & species	Diet	Trophic	Maturity	Mobility
MYVE	<i>Mycteroperca venenosa</i>	nekton 96%	pisci	51.0	mobile
NIUS	<i>Nicholsina usta</i>	plants 100%	herb	18.5	mobile
OCCH	<i>Ocyurus chrysurus</i>	crabs, isopods	mif	24.0	transient
ODDE	<i>Odontoscion dentex</i>	isopods, crabs, fish	mif	18.5	
OPAT	<i>Ophioblennius atlanticus</i>	detritus, algae	omni	12.4	resident
OPAU	<i>Opistognathus aurifrons</i>	zooplankton 97%	plank	7.0	
OPOG	<i>Opisthonema oglinum</i>	zooplankton 70%	plank	13.0	
PESC	<i>Pempheris schomburgki</i>	congeneric amphipods and mysids	mif	.	resident
POAR	<i>Pomacanthus arcuatus</i>	zoobenthos sponges tunicates 81%	sif	24.0	mobile
POPA	<i>Pomacanthus paru</i>	zoobenthos 90%, tunicates, ascidians	sif	26.7	mobile
PRAR	<i>Priacanthus arenatus</i>	zooplankton 52%, worm 11%, shrimps 35%	plank	26.8	resident
PRCR	<i>Priacanthus cruentatus</i>	zooplankton 60%, shrimps 35%, polychaetes	plank	29.4	resident
PSMA	<i>Pseudupeneus maculatus</i>	crabs 31%, shrimps 22%, mysids	mif	18.0	mobile
RERE	<i>Remora remora</i> *	zooplankton 22%, isopods 20%, polychaetes 13.7%, detritus	plank	47.1	transient
RYSA	<i>Rypticus saponaceus</i>	nekton 48%, shrimps crabs rest, parasites	pisci	21.2	resident
SCCA	<i>Scomberomorus cavalla</i>	nekton 93%	pisci	79.0	transient
SCCL	<i>Scarus coelestinus</i> *	plants 98%	herb	42.5	mobile
SCCO	<i>Scarus coeruleus</i>	plants 100%	herb	30.5	mobile
SCCR	<i>Scarus croicensis</i>	plants 100%	herb	21.2	mobile

Species	Genus & species	Diet	Trophic	Maturity	Mobility
SCGU	<i>Scarus guacamaia</i> *	plants 100%	herb	62.0	mobile
SCJU	<i>Scarus</i> sp. juvenile	based on other species	herb	21.2	mobile
SCPL	<i>Scorpaena plumieri</i>	zooplankton 43%, crabs, shrimps, octopi 57%	plank	26.5	resident
SCRE	<i>Scomberomorus regalis</i>	nekton 100%	pisci	36.0	transient
SCSP	<i>Scarus</i> species	based on other species	herb		mobile
SCTA	<i>Scarus taeniopterus</i>	plants 82%	herb	21.2	mobile
SCVE	<i>Scarus vetula</i>	plants 94%	herb	30.6	mobile
SEBA	<i>Serranus baldwini</i> *	nekton and shrimp, zoobenthos	mif	8.2	resident
SETA	<i>Serranus tabacarius</i>	nekton 100%	pisci	14.1	resident
SETI	<i>Serranus tigrinus</i>	shrimps 72%	mif	17.9	resident
SETO	<i>Serranus tortugarum</i>	plankton 72%	plank	14.1	resident
SPAT	<i>Sparisoma atomarium</i>	no data	herb	15.7	resident
SPAU	<i>Sparisoma aurofrenatum</i>	plants 98%	herb	15.0	mobile
SPBA	<i>Sphyraena barracuda</i>	nekton 96%	pisci	66.0	mobile
SPCH	<i>Sparisoma chrysopterum</i>	plants 84%	herb	23.9	resident
SPJU	<i>Sparisoma</i> sp. juvenile	based on other species	herb	13.1	mobile
SPRA	<i>Sparisoma radians</i>	plants 88%	herb	12.9	resident
SPRU	<i>Sparisoma rubripinne</i>	plants 93%	herb	16.0	mobile

Species	Genus & species	Diet	Trophic	Maturity	Mobility
SPSP	<i>Sphoeroides spengleri</i>	bivalves 28, crabs 22%, plants 9%, amphipods 8%, polychaetes 8%, urchins 7%	omni	18.5	resident
SPVI	<i>Sparisoma viride</i>	plants 98%	herb	17.0	mobile
STDI	<i>Stegastes diencaeus</i>	algae, detritus	omni	8.5	resident
STDO	<i>Stegastes dorsopunicans</i>	plants 64%	herb	10.0	resident
STLE	<i>Stegastes leucostictus</i>	plants 28%, polychaete 15%, nekton 8%, cnidarians 8%	omni	7.0	resident
STPA	<i>Stegastes partitus</i>	benthic algae	herb	7.0	resident
STPL	<i>Stegastes planifrons</i>	detritus 27%, plants 24%, cnidarians 20%, zoobenthos 11%	omni	9.3	resident
STVA	<i>Stegastes variabilis</i>	plants 57%, worms, tunicates, isopods	herb	8.5	resident
SYFO	<i>Synodus foetens</i>	fish 100%	pisci	27.0	resident
SYIN	<i>Synodus intermedius</i>	fish 95%	pisci	27.0	resident
THBI	<i>Thalassoma bifasciatum</i>	zooplankton 51%, benthic inverts 32%, fish 9.4%, isopods,	plank	15.7	resident
TRFA	<i>Trachinotus falcatus</i>	fish	pisci	60.1	transient
TYCR	<i>Tylosurus crocodilus</i>	nekton 91%	pisci	76.7	transient
URJA	<i>Urolophus jamaicensis</i> *	bony fish, shrimps, bivalves, annelids	mif	42.0	transient
XYSP	<i>Xyrichtys splendens</i> *	zooplankton 72%, amphipods 12.5%, bivalves 3%, gastropods 5%	plank	11.5	resident

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BIOGRAPHICAL SKETCH

Linda Erica “Rikki” Grober-Dunsmore was born in Oslo, Norway, on October 15, 1964 and was raised in Ft. Pierce, Florida. She graduated from Florida State University (Tallahassee) in 1987, and completed her Master’s of Environmental Management at Duke University (Durham, NC) in 1992 in coastal resource ecology, with Dr. Orin Pilkey. There she was selected as a fellow for the Organization for Tropical Studies, to attend the tropical ecology and conservation program in Costa Rica.

Rikki worked for the World Wildlife Fund’s Biodiversity Support Program, for Dr. Ed Towle of the Island Resources Foundation in St. Kitts, British West Indies. She then worked as a marine ecologist for Virgin Islands National Park and Biosphere Reserve. There she conducted coral reef monitoring and research, under the direction of Dr. Caroline Rogers, of the US National Park Service, the National Biological Service and the US Geological Survey (USGS). In 1997, she worked with Dr. Doug Markle (at the University of Oregon in the Department of Fisheries and Wildlife) on endangered suckers in the Lower Klamath River Basin.

In 1999, she started with the Hawaii Coral Reef Initiative, Hawaii, where she edited the “Proceedings of the Hawaii Coral Reef Monitoring Workshop” with Dr. Jim Maragos and worked with Dr. Mark Ridgley at the University of Hawaii’s, Department of Geography to develop a strategic, multi-objective framework to integrate scientific knowledge with resource-use patterns to improve coral reef management. She worked

with Dr. Chip Fletcher at the Department of Coastal Geology and Geophysics, University of Hawaii, researching a book "Living with the Shores of Hawai'i".

Rikki matriculated to the University of Florida in fall 2000, to work with Dr. Tom Frazer under a Student Cooperative Education Program with the Biological Resources Division of the USGS, in the Coral Reef Ecology program headed by Dr. Nick Funicelli. Rikki spent several months a year in the US Virgin Islands, and conducted field research in the US Virgin Islands, and Turks and Caicos Islands, and the Florida Keys.

Rikki is also mother to Thatcher Kai Dunsmore, born August 4th 1997.