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UNIVERSITY OF MIAMI

MULTI-SCALE PATCH DYNAMICS OF CORAL COMMUNITIES: A CROSS-CARIBBEAN INVESTIGATION USING A LANDSCAPE ECOLOGY APPROACH

By

Brittany Huntington

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

December 2011

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Brittany E. Huntington

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HUNTINGTON, BRITTANY E. (Ph.D., Marine Biology and Fisheries)
Multi-Scale Patch Dynamics of Coral Communities: A Cross-Caribbean Investigation Using a Landscape Ecology Approach (December 2011)

Abstract of a dissertation at the University of Miami.

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The overarching objective of this dissertation was to improve our knowledge of the relationship between seascape heterogeneity and diversity of stony coral assemblages across spatial scales. Coral communities on patch reefs in three regions of the Caribbean were used as a model system to investigating this relationship because patch reef heterogeneity could be readily quantified within the seascape using remote sensing and image analysis techniques. I began with a theoretical approach, exploring the origins of observed species diversity among coral communities at increasing spatial scales. Hierarchical sampling and null models revealed that coral diversity was governed by non-random processes at local- (10s of meters) and meso- (100s of m) scales. Spatial autocorrelation and reef heterogeneity were then investigated as potential mechanistic drivers of these non-random diversity patterns. I found limited support for spatial drivers. However, beta diversity was significantly correlated to metrics of reef heterogeneity (measured as reef size, spatial configuration, and complexity), indicating that differences in reef heterogeneity were making a disproportionate contribution to the overall coral community diversity. The relationship between corals and reef heterogeneity was found to be both scale-dependent and region dependent. This theoretical approach was followed

by a manipulative approach using an existing artificial patch reef array to experimentally test the influence of reef spatial configuration and topographical complexity on local diversity. Corals were most sensitive to reef size and secondarily reef configuration within the seascape. Unlike reef fishes, reef complexity did not emerge as a strong predictor of the coral community composition in either the observational data or the experimental manipulation. These observational and experimental explorations of the relationship between corals and habitat reveal that intra-habitat variability (i.e. differences between patch reefs) can influence the diversity and abundance of corals. I then focused on applying this improved theoretical understanding towards improving coral management efforts. I present a new methodology to assess the efficacy of marine reserve effects by controlling for natural seascape variation within and beyond the reserve boundary, and I quantified the bias of underestimating coral diversity by using conventional reef monitoring protocols that ignore differences in reef size. In conclusion, I demonstrate empirically that seascape attributes of reef heterogeneity can contribute to coral diversity at relatively small spatial scales (<1km) and can affect corals with different life history traits in different ways. Hence, management and conservation efforts must consider the role of these meso-scale spatial metrics to influence the structure of the coral assemblage at the local scale.

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A huge and heartfelt thanks goes to my honorary labmate, out-loud-brainstorming-partner and dive buddy extraordinaire, Mandy Karnauskas (a.k.a. Fish Girl). You are the sole reason I had the opportunity to work at Glover's Atoll, published a paper with Tim McClanahan, and enjoyed my degree so much. Our field work together in Glover's is the highlight of my 4 years at RSMAS and I have learned that collaboration in science is not only more fun, but more productive when you can work with stellar people like Mandy. I am excited to be working in close proximity to Mandy next year and hope we can form a "whirling dervish" of young, engaging, collaborative scientists that will continue to work together for the years to come.

I am grateful to past and present members of the Lirman Lab, for providing an entertaining and humorous work environment that continually exemplified the concept of working hard *and* playing hard. Especially to Ford, Rolando, Stephanie, and Travis, I am grateful for your help in field, willingness to talk science with me, and your encouragement over the past 4 years!

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: Introduction

The objective of this dissertation is to explore how landscape-scale measures of reef composition and spatial configuration influence the abundance, diversity, and distribution of stony coral within patch reef communities. Caribbean corals have declined significantly over recent decades (Gardner et al. 2003), resulting in smaller, 'flattened' reef structures fragmented across the seascape (Alvarez-Filip et al. 2009). It is unclear how these changes to reef size, spacing, and structural complexity influence the present ability of Caribbean reefs to support robust, diverse coral communities. Moreover, we know little about how these large-scale, spatial attributes of the reef impact trajectories of coral community recovery over time.

Repeatedly, 'reef heterogeneity' (defined in this dissertation as variation in reef size, spatial configuration, and structural complexity) has been ignored in coral reef studies that assume all reef habitats behave identically. However, the terrestrial literature lends strong evidence to the contrary. Terrestrial studies reveal that habitat heterogeneity, operating at the landscape scale, can drive local community dynamics (MacArthur & Wilson 1967; Kruess & Tscharntke 1994; Tews et al. 2004). In marine systems, there are numerous studies exploring the influence of landscape variation in of autogenically engineered habitats such as segrass, mangroves, and coral reefs (Simberloff, 1976; Hovel & Lipcius 2001; Grober-Dunsmore et al. 2007; Mellin et al. 2009). However, the vast majority of these existing studies investigate the influence of landscape habitat heterogeneity on organisms occupying the engineered habitat, not on the engineers themselves. Here, I am not focused on the occupying organisms within the reef habitat (e.g. Sandin et al. 2008; Mellin et al. 2010), but the coral species themselves.

My dissertation research is therefore the first investigation to adopt and adapt techniques from terrestrial landscape ecology to investigate how reef heterogeneity, within and between coral reef habitats, influences local coral dynamics. In the Caribbean, coral communities have been declining in health, complexity, and spatial extent since the 1970s (Gardner et al. 2003). Understanding the role of reef heterogeneity on coral community dynamics provides important insights into: 1) the recovery rates of reef types from disturbances (resilience), 2) the response of reef types to future disturbances (resistance), and 3) the design of marine reserves and artificial reef habitats to maximize resistance and resilience.

Patch reefs as a model system

Coral reef communities are complex systems not readily amenable to manipulation, except at very small scales. This difficulty in manipulating reef structure and spatial configuration has hindered our understanding of the underlying relationship between corals and reef habitat. Existing studies that have investigated the influence of reef size and spatial isolation on the biotic reef community have focused largely on fishes and frequently employed small artificial structures (Bohnsack et al. 1994; Belmaker et al. 2005), thereby limiting extrapolation to large, natural reefs. Furthermore, several observed relationships between marine organisms and their habitat from these previous investigations have contradicted theoretical predictions of island biogeography and species-area relationships (Table 1; Walsh 1985; Friedlander & Parrish 1998; Belmaker et al. 2005). Lastly, corals are ecosystem engineers that create structural heterogeneity in the reef environment as well as respond to existing heterogeneity, unlike reef fishes that do not build the reef structure. Hence, we cannot easily predict the relationship between coral communities and reef heterogeneity from these previous studies of reef occupants rather than reef builders. Rather, I focused my dissertation to explicitly explore the relationship between coral communities and reef heterogeneity using patch reefs, a geomorphic reef type, as a model system. Patch reefs were selected for this research because patch reefs are small in size with discrete spatial boundaries that facilitate easily quantifying metrics of reef heterogeneity. As such, these patch reefs were a logical starting point for untangling the relationship between the coral community and reef heterogeneity.

Landscape ecology considers both the size and configuration of habitat patches across the landscape (Turner et al. 2001). To adapt this landscape ecology framework to patch reefs, I capitalized on advances in marine remote sensing to gather high resolution satellite imagery, and image analysis techniques to create benthic habitat maps of the seascape. The discrete character of patch reefs, commonly surrounded by a sand or seagrass matrix inhospitable to corals, enabled spatial metrics of patch composition and configuration to be readily quantified through spatial analyses (Fig. 1.1). Patch reefs are not homogeneous; they can vary widely in shape, size, and boundary characteristics from one patch to the next (Forman & Godron 1986). Furthermore, patch reef complexes are also spatially variable in their configuration, exhibiting variation in their proximity to key geologic features in the seascape (Fig. 1.2) and variation in their spatial isolation from neighboring patches (Fig 1.3).

Research significance

Given the current degradation of coral reefs from bioerosion, disease, habitat fragmentation, and climate change (Knowlton 2001; Brown-Saracino et al. 2007; Bruno et al. 2007), there is a need to elucidate the importance of reef heterogeneity to coral community dynamics. Several recent studies have considered spatial heterogeneity in structuring marine communities (Irlandi et al. 1995; Bell et al. 2006; Grober-Dunsmore et al. 2008). Fewer have used hierarchical sampling designs to relate species diversity to spatial heterogeneity at appropriate scales for the system of study (Pittman et al. 2004; Cornell et al. 2007). None have employed a hierarchical landscape approach to evaluate community dynamics of stony corals in relation to spatial heterogeneity of the reef habitat. Quantifying patterns of coral diversity and abundance at increasing spatial scales and then relating these patterns to key metrics of reef heterogeneity not only furthers our theoretical understanding of coral biogeography, but aids coral reef management by determining the appropriate spatial scales needed to conserve coral reefs, informing reserve design and evaluation, and predicting future changes to corals that may result from increased habitat loss and bioerosion.

Chapter Objectives

The first objective of this dissertation was to investigate whether coral species on patch reefs were randomly distributed across space (Chapter 2). I began by documenting patterns in coral diversity across hierarchical scales ranging from ‘within’ a single patch reef to ‘among’ reefs, and comparing these patterns to null model predictions based on a model of random distribution of corals. I then compared these patterns of coral community diversity among three regions that encompass a latitudinal gradient of species richness. Patch reef complexes in Bermuda, the Florida Keys, and Glover's Atoll, Belize, were selected due to their variations in regional species richness following a latitudinal gradient of coral diversity. The relationship between coral diversity partitioned across hierarchical spatial scales and among regions was used to determine whether local diversity was constrained by local processes (e.g. aggregation, competition) or randomly distributed, and whether these patterns are consistent among regions that differ in coral species pools.

The second objective was to analyze the spatial heterogeneity of patch reef habitats within the three regions to evaluate the relative importance of reef heterogeneity to influence the coral communities (Chapter 3). I quantified three metrics of the reef heterogeneity: (1) reef size, (2) spatial isolation, and (3) topographic complexity. Again, I took a scale-dependent approach to evaluate the relationship between organism and habitat, quantifying diversity 'within' and 'among' patch reefs, and using metrics of seascape heterogeneity that varied in spatial resolution.

The first two data chapters of this dissertation described patterns of coral diversity across scale and space, and correlated these patterns to seascape influences in the three study regions. Chapter 4 complements these correlative approaches with a pseudo-manipulative study to test predictions of habitat selection theory An existing, artificial patch-reef array in the Florida Keys served as a novel proxy for experimental manipulation to determine the relative importance of patch reef size, spatial isolation, and topographic complexity in shaping coral communities. Unique features of this artificial habitat include: numerous patches of varying size, distinct spatial configuration of the patches, and contrasting topographic morphologies, yet a common disturbance history, construction material, and starting condition. Hence, the resultant coral communities that established on these artificial reefs were evaluated to determine to relative importance of seascape heterogeneity on coral community composition, without the addition of many confounding factors that affect natural reefs.

The final three chapters of this dissertation underscore the importance of considering natural seascape variability among reef habitats when undertaking coral reef management and monitoring activities. Chapter 5 both empirically shows that seascape variability can mask our ability to discern the effects of marine reserve protection, and puts forth a novel approach using advances in habitat mapping and spatial analysis to control for seascape heterogeneity during reserve assessments. The results of this chapter were the first to show that spatial variation within a single habitat type (*intra*-habitat) can significantly confound assessments of reserve performance. Hence, the application of this new landscape approach to reserve assessment can be used in future efforts to better evaluate marine reserve performance and guide the placement of future marine reserves.

The ability of reserves to replenish fish stocks is relatively well documented, but the evidence of their ability to induce positive effects on benthic communities remains inconclusive. In Chapter 6, I tested whether 10 years of reserve designation have translated into positive effects on coral communities in Glover’s Reef, Belize. Surveys of 87 patch reefs inside and outside the reserve revealed no clear indication of reserve implementation benefitting coral cover, coral colony size, or abundance of juvenile corals. No difference in herbivorous fish abundances or macroalgal cover between reserve and fished sites were detected, providing a potential explanation for the lack of cascading positive effects on the coral community. The results from Chapter 6 suggest that regional stressors are overwhelming local management efforts, and that additional strategies are required to improve local coral condition.

Chapter 7 of this dissertation addresses the bias that can arise when applying a popular sampling method (i.e. fixed number of belt-transects) to census coral community richness when the size of the reef and the regional species pools vary. Based on surveys of 148 patch reefs among the 3 sampling regions in the Western Atlantic, I showed that a fixed sub-sampling approach underestimated, albeit slightly, the true richness of the reef as reef size increased. Furthermore, this underestimation was found to increase in regions that were more diverse. Increasing sampling effort per reef was not effective in correcting for this underestimation. Rather, these results suggest that coral species in diverse regions are distributed in accordance with the variety of spatially structured microhabitats present on a reef, rather than distributing randomly across the reef surface. As such, sampling protocols should consider the size of the reef to be surveyed as well as the regional species pool to ensure accurate estimates of coral diversity.

Table 1.1 Existing studies in marine habitat evaluating the influence of reef size, spatial isolation, topographic complexity, and size + spatial isolation on community diversity. Also given are the organism of interest, the study results, resultant publications, and whether the results support established ecological theory.

Habitat variable	Organism	Result	Publications	Supports theory?
Size	Reef fish	Greater area → greater diversity	Gladfelter et al. 1980; Sale & Douglas 1984; Clarke 1988; Ault & Johnson 1998; Chittaro 2002; Jordan et al. 2005	Yes
		Greater area → no change in diversity	Grober-Dunsmore et al. 2008	No
	Intertidal inverts.	Greater area→ greater diversity	McGuinness 1984; Matias et al. 2010	Yes
Isolation	Reef fish	Greater isolation → greater diversity	Walsh 1985; Belmaker et al. 2004; Jordan et al. 2005	No
	Inverts. & reef fish	Greater isolation → greater abundance	Frazer and Lindberg, 1994	No
Topographic complexity	Reef fish	Greater complexity → greater diversity	Risk 1972; Gladfelter et al. 1980; Carpenter et al. 1981; Clarke 1988; Caley & St.John 1996; McLain &Pratt 1999; Gratwicke & Speight 2005	Yes
		Greater complexity → no change in diversity	Sale & Douglas, 1984; Roberts & Ormond 1987; Ault & Johnson 1998; Walsh 1985	No
	Intertidal inverts.	Greater complexity → variable diversity	McGuinness & Underwood, 1986; Matias et al. 2010	No
Size + Isolation	Reef fish	Large & less isolated →more diversity	Molles 1978; Sandin et al. 2008; Mellin et al. 2010	Yes

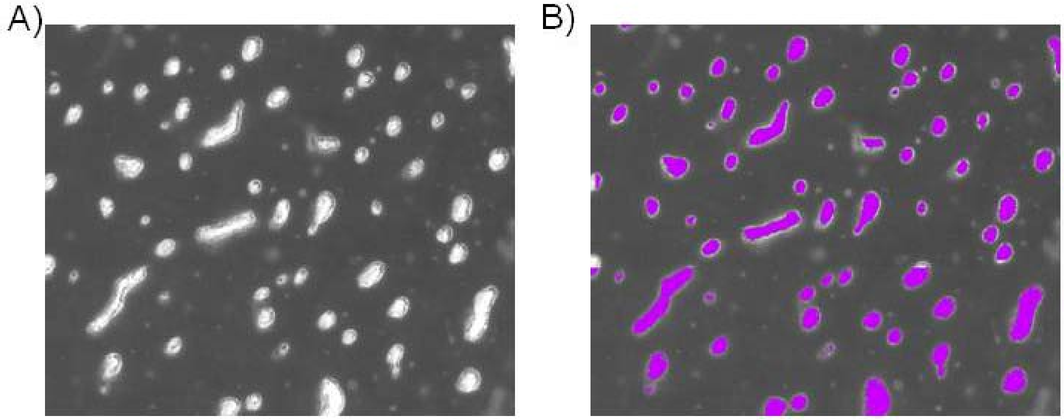


Fig. 1.1 High resolution satellite imagery of patch reefs amid a dark seagrass mosaic (A), and the same image analyzed to denote patch reefs as purple polygons (B) to quantify reef size and spatial configuration.

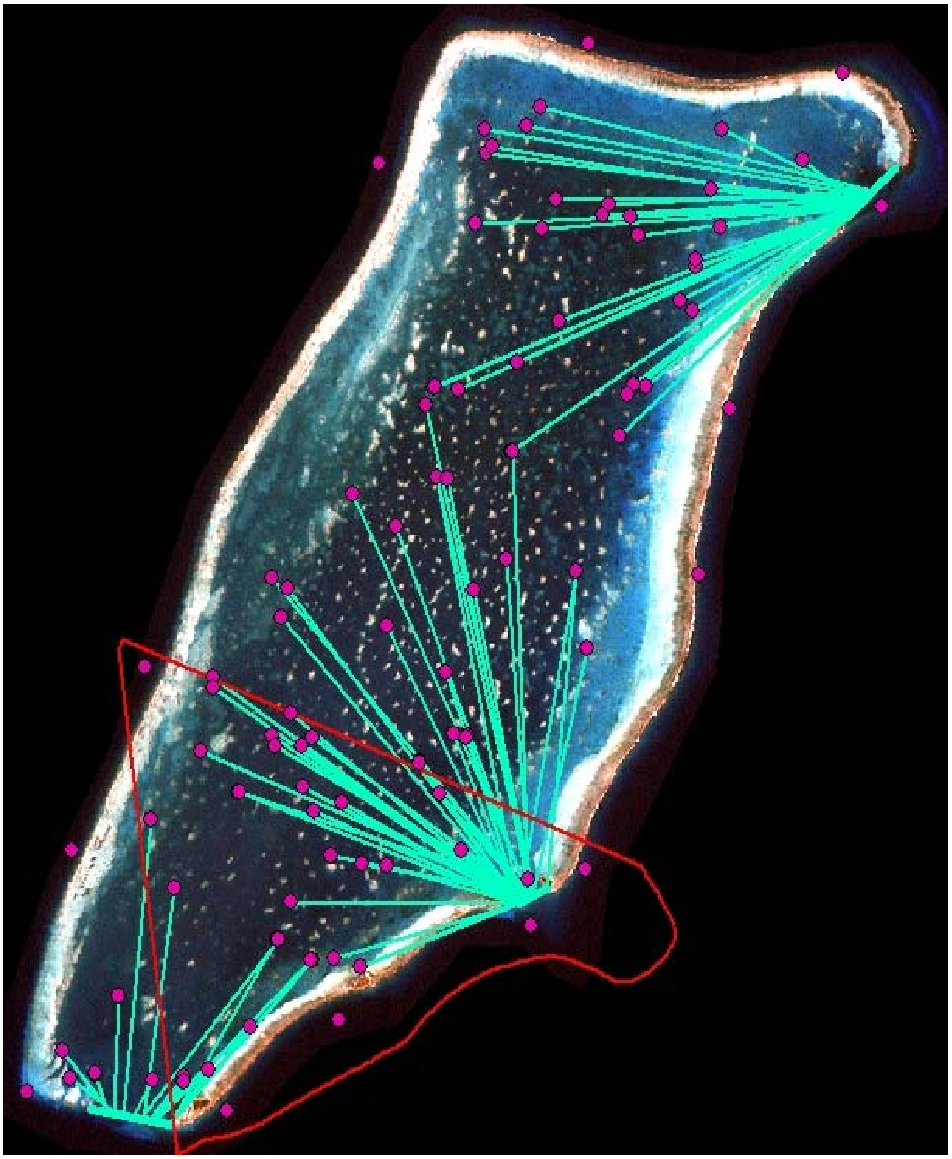


Fig. 1.2 Satellite color image of Glover's Atoll, Belize depicting a metric of reef configuration: reef proximity to key geologic spatial features. The distance of each reef to the nearest of one of three channel openings in the Atoll rim are shown as green lines originating from patch reef study sites (pink circles). The marine reserve boundary is shown as a red polygon.

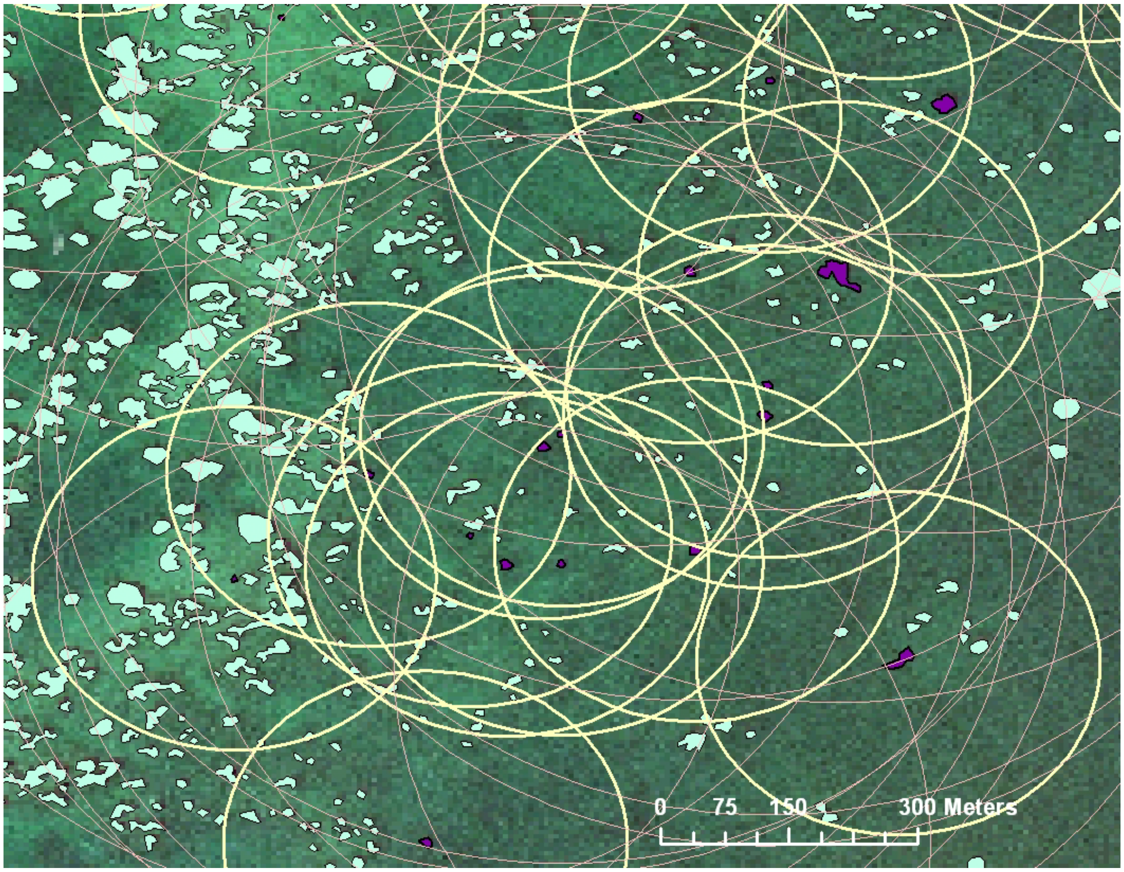


Fig 1.3 Satellite color image of Bermuda patch reefs depicting a metric of reef configuration: amount of surrounding reef habitat. Study reefs are shown as purple polygons and all other patch reefs as blue polygons. A 200m (yellow circle) and 500m (pink circle) buffer was overlaid around each study reef to calculate the amount of surrounding reef habitat.

CHAPTER 2: Local versus regional richness patterns

BACKGROUND

Identifying and explaining patterns of species distributions in space and time is a long-standing objective in ecology (Ricklefs 2004), and tropical marine ecology in particular (Karlson et al. 2004). More recently, elucidating diversity patterns has been viewed as a benefit for conservation science, in which quantifying scale-dependent patterns of diversity helps guide conservation measures and management plans aimed at preserving biodiversity (Summerville et al. 2003). Most resource management and conservation problems are dealt with at large spatial scales. This pattern holds in tropical coral reef systems where marine reserve networks and management plans operate beyond the local scale. By exploring patterns of species diversity among multiple scales in the reef seascape, we move closer to resolving the conflict between the large spatial scale of management and the fine scales at which most reef ecological studies occur (e.g. Syms & Jones 2000). Given the unique dispersal and connectivity properties of the marine environment (Jones et al. 2009), relationships between local and regional scales in tropical coral reef ecosystems may differ from those described in terrestrial systems. Hence, for coral reef systems, identifying patterns of diversity across spatial scales is not only a crucial step towards indentify the processes that support these patterns, but also determining the appropriate scales at which to structure conservation efforts that aim to preserve diversity in these threatened habitats (Semmens et al. 2010).

Spatial patterns of species diversity change over multiple spatial scales, such that the pattern found within a local community might be very different from those found over broader areas like a seascape. Whittaker (1960) partitioned species diversity into alpha, beta, and gamma components to explore the relationship between diversity and scale. Local, within- sample (α) diversity and between-sample (β) diversity together determine regional (γ) diversity. As both α and β diversity components are expressed in the same units, they can be related additively as: $\alpha + \beta = \gamma$ (Lande 1996). Using this additive partitioning approach with a hierarchical sampling scheme enables determining the specific contribution of each hierarchical level relative to the overall diversity (Gering & Crist 2002; Veech et al. 2002; Crist et al. 2003). While the use of additive partitioning to investigate patterns of diversity at multiple spatial scales is gaining traction in the terrestrial literature (Crist et al. 2003; Gering et al. 2003), its application in marine systems is still rare.

In this study, we focused on the stony coral assemblage of patch reefs in three regions of the Western Atlantic (Bermuda, Florida and Belize) that possess increasingly diverse species pools of corals (Appendix A). Our major objective was to identify if coral species diversity exhibited nonrandom patterns, and if so, at what spatial scales. This will enable us to highlight to appropriate spatial scales for studying what mechanisms might be driving these patterns. Our study was designed to additively partition coral diversity at multiple spatial scales using a randomization approach (Crist et al. 2003). To do this, we employed a hierarchical sampling design, maintaining a constant sampling unit (i.e. 10m belt transects) while conducting analyses of transects grouped within patch reefs, between patch reefs, and biogeographic regions. This design allows the sample grain (transect-scale) to remain constant while focal scale (area of inference) was increased (Chandy et al. 2006; Whittaker 2010). We then quantified how the relationship between diversity components changed with increasing spatial scales and increasing regional diversity. Specifically, we evaluated the null hypotheses that: (1) that partitioned diversity values would remain constant across a latitudinal gradient of species richness, and that (2) coral species are randomly distributed across increasing spatial scales. Lastly, we asked whether under-dispersion (observed diversity values lower than predicted by chance alone) was common for Caribbean corals.

METHODS

Coral surveys

The hierarchical sampling design was the same in all regions, although the total number of patch reefs surveyed did vary by region. A total of 36 reefs in Bermuda, 42 reefs in Florida, and 70 reefs in Belize were sampled between May 2008 and May 2010. Surveys were conducted within a single habitat type, shallow (<6m) patch reefs, in all regions to minimize difference in terms of reef structure, depth and other confounding environmental factors (Porter 1972; Arias-González et al. 2008). At each patch reef, 5 replicate, non-overlapping 10 x 1m belt-transects were haphazardly laid across the reef surface between depths of 2-5m to encompass the within-reef spatial heterogeneity (Belmaker et al. 2008). The species richness of all corals encountered within the transect was recorded. In addition, a census of all coral species found on a focal reef was assessed during a ‘roving diver’ 10-min visual search to generate patch-scale measures of coral richness.

To determine local abundance of coral species, coral cover was assessed from non-overlapping digital photographs taken 0.5m above the substrate along the long and short axis of the reef area (Huntington et al. 2010). Twenty images were randomly selected for point-intercept analysis, with 50 random points scored per image using CPCe software, v3 (Kohler & Gill 2006). Coral colonies >3cm diameter were identifiable to species from the digital photographs. Scoring colonies of <3cm diameter to species was not possible and marked as unknown.

Validating diversity estimates

Local-to-regional diversity relationships have been subject to numerous concerns regarding psuedosaturation resulting from underestimating local richness or over-representing regional richness (Hillebrand & Blenckner 2002; Hillebrand 2005). Underestimation is a concern in species-rich regions but unlikely in this study given the limited coral species pool and our ability to readily count rare species in the transect samples. The 10m belt-transect was used as the smallest sampling unit to ensure local diversity values were not artificially constrained by sampling exceedingly small spatial scales where the number of individuals within the plot dictate the upper limit on richness ('neighborhood effect', Cornell & Karlson 2000). Hence, we estimated local coral species richness (α_{obs}) from the 10m belt-transects with minimal concern of sampling bias. Regional diversity (γ_{obs}) was conservatively estimated by summing only those coral species observed on study reefs over the course of the study (Cornell & Lawton 1992; Freestone & Osman 2011). Using the observed regional richness, rather than the standard regional pool, guarded against any potentially confounding effects of psuedosaturation resulting from over-representing regional richness (Cornell et al. 2008; Freestone & Osman 2011).

Regional estimates of diversity were evaluated for undersampling using species accumulation curves and Chao 2 estimators (Colwell & Coddington 1994). Curves were constructed from all available transect data for each region and inspected for a leveling trend as transect number increased, indicating that sampling was sufficient to characterize the regional richness. Chao 2-estimates of regional richness were calculated to both compensate for potential undersampling of the observed regional richness and account for unequal sampling within each region. Chao 2 estimates the asymptote of a species accumulation curve by taking into account the effect of rare species on the total richness. Chao 2 richness is calculated as:

$$S = S_{obs} + (T_1)^2 / 2(T_2)$$

where S_{obs} is the number of species observed in the transect samples, T_1 is the number of species occurring in one transect, and T_2 is the number of species occurring in two transects. Curves were created in Primer v6.0 over 999 permutations, in which different sample orders are taken and the resultant curve is averaged (Clarke & Gorley 2006).

Latitudinal variation in local to regional richness

To test the latitudinal variation in the extent of regional influence on local species richness, the ratio of mean local richness to the observed regional diversity (i.e. alpha/gamma) was regressed against latitude (Witman et al. 2004; Freestone & Osman 2011). We calculated this ratio of local : regional richness at two different spatial scales using both the mean transect richness for a given region as well as the mean patch-scale richness (e.g. roving diver survey data). If regional influence on local diversity is equal irrespective of latitude, then we would expect local : regional richness ratio to be constant across the latitudinal gradient.

Species accumulation curves, calculated as proportion of the regional diversity to facilitate comparison, were also examined to determine if the rate of species accumulation varied with latitude. Null predictions of constant regional influence on local diversity across latitude would generate species accumulation curves that are comparable among regions. However, if the regional influence on local diversity is greater at higher latitude (as predicted by theory), then we would expect steeper slopes (i.e. faster rates of species accumulation) at higher latitudes. Lower latitude sites, where local interspecific interactions are purported to be stronger, would exhibit suppressed slopes for their species accumulation curves.

Partitioning of diversity

We employed the additive partitioning model described by Lande (1996) and Crist and Veech (2006). Additive partitioning allows diversity to be partitioned across multiple spatial scales while maintaining α, β, and γ diversity in the same units to foster comparison across regional gradients when α and β are expressed as proportions of γ (Gering et al. 2003). Since we used a nested sampling design (Fig. 2.1), samples at one scale are themselves composed of samples at a smaller scale. Alpha diversity (α) is defined here as the average coral richness within transects, β_1 is the average coral richness among transects within a patch reef, β_2 is the average coral richness among patch reefs within a given regional species pool (γ). Therefore, the coral diversity within each region was partitioned as: $\alpha + \beta_1 + \beta_2 = \gamma$ (Crist et al. 2003).

Null models of the expected diversity were then generated to determine the probability that observed values of α, β_1, and β_2 diversity could be obtained by chance alone. Separate null models were constructed for each region according to two distinct null randomization approaches: individual-based randomization and sample-based randomization (Crist et al. 2003). Individual-based randomization (IBR) models assume that presence of a species is random within the smallest sampling level, independent of the presence or absence of other corals or locality. For instance, if conspecifics aggregate at local scales or within specific habitats, then diversity would be lower at within-habitat scales and greater at among-habitat scales than expected by chance. Likewise, if conditions at the local scale attracted greater numbers of individual species, or facilitation exists between coral species, then local diversity could be greater than expected by chance alone. To construct the IBR null models, the richness of all species found at the transect scale were combined to create a single species pool. Individual species were then randomly assigned to transect samples to generate a new number of taxa. The randomized samples were then partitioned to provide diversity at each scale (α_1, β_1, and β_2) the same way as the observed data. Restricted IBR null models were generated for comparison to unconstrained models. In the restricted model, randomization of species richness censused in transect samples was restricted to the patch reef from which they were sampled.

For sample-based randomization (SBR) models, entire samples at the transect level were randomly assigned to any sample at the patch level within a given region. Hence, the transect samples themselves (not the presence of individual coral species) were randomized, maintaining the integrity of samples at each hierarchical level. SBR models are useful in testing whether nonrandom groups of species explain the observed patterns of diversity (Crist et al. 2003). We use SBR models here to determine whether the observed diversity at the patch scale could have been obtained by a random distribution of samples at the transect level within each region.

The program PARTITION (Veech & Crist 2009) was used to partition diversity for each of the 3 regions and construct all null models. For all null models, the randomization procedure was repeated 1000 times to obtain distributions of expected α, β_1, and β_2 diversity. The observed values were then compared against expected values for each sampling scale (α_1, β_1, and β_2). The proportion of null values greater than or less than the observed values was used to assess statistical significance. The probabilities obtained from the randomization test were interpreted as *P*-values as in traditional parametric statistical tests. Significant deviations of observed values from null expectations indicated a non-random spatial distribution of coral species.

Abundance-occupancy relationship

For each region, the relationship between patch occupancy and local abundance was explored by plotting the proportion of patch reefs occupied (from roving-diver patch richness data) against local abundance (mean coral cover (%) within a region) for each observed species (Freckleton et al. 2005). These relationships were then evaluated by fitting linear and non-linear regressions. Non-linear fits were accepted if the variance explained (R^2) was >5% compared to linear models (Chandy et al. 2006). Patterns of occupancy and spatial variance in abundance are likely to be linked to particular ecological strategies (e.g. species with low dispersal abilities will tend to have lower occupancy; Gaston 1994). Hence, separate regression analyses were also conducted for brooding coral species versus broadcasting coral species, as these two distinct reproductive strategies are associated with differing dispersal abilities (Nishikawa et al. 2003).

RESULTS

A total of 42 coral species were observed in this study; 16 species in Bermuda, 35 in Florida, and 36 in Belize (Appendix A). As anticipated, diversity was highest in Belize, followed by Florida and then Bermuda. Belize also supported the highest number of 'unique' coral species (i.e., species that only occurred on <5% of the patch reefs surveyed in a given region), regardless whether we examined the transect richness data or the reef-scale richness data (Table 2.1). Bermuda, on the other hand, did not support any unique coral species at either the transect- or reef-scale. Total coral cover for each region increased with increasing latitude, such that Belize, the region nearest the equator, had the lowest average coral cover (5.8 ± 0.4%), followed by Florida (8.4 ± 0.8%), and Bermuda (26.5 ±1.5 %). The species accumulation curves for all three regions showed a strong leveling trend as transect number increased, indicating that sampling was sufficient to characterize the regional species pool (Fig. 2.2a). As Chao 2 estimates of regional richness yielded very similar results to observed values (Fig. 2.2a), γ_{obs} was used to represent regional diversity.

Local to regional diversity

The rate of coral species accumulation did differ among the regions, such that species accumulated occurred more quickly in regions of higher latitude (Fig. 2.2b). Bermuda, the highest latitude region that is also defined by the smallest species pool, was characterized by a faster rate of species accumulation than either Belize or Florida. Correlative results of latitudinal variation in the local : regional richness ratios are also consistent with the alternative hypothesis that higher latitudes may be more regionally enriched (Fig.2. 3). The local : regional ratios (measured as both $\alpha_{transect}/\gamma_{obs}$ and $\alpha_{patch}/\gamma_{obs}$) increased from low to high latitudes. This relationship was not statistically significant when the transect scale was considered separately from the patch scale, due to limited sample size of 3 regions. However, considering both scales simultaneously did generate a significant linear fit with local to regional species richness increasing as a function of latitude ($R^2 = 0.86$, $p= 0.008$, $n= 6$; $y = 0.182 + 0.0172x$).

Diversity partitioning across spatial scales

Absolute local richness (α_1) of corals was remarkably consistent among the 3 regions despite the differences in the diversity of the regional pools (Table 2.2), suggesting that species richness at local scales may be saturated irrespective of the regional pool. However, when viewed as a proportion of the regional diversity (γ), local richness constituted a greater proportion of the regional diversity at regions of higher latitude with depauperate species pools (Fig. 2.4). Local alpha (α) diversity in Bermuda contributed the greatest amount to the observed diversity ($\alpha = 56\%$), and correspondingly smaller amounts in Florida and Belize which have larger species pools. As the contribution of α_1 to the observed diversity declined with increasing regional richness, the contribution of 'between reef diversity' (β_2) increased from 20% in Bermuda, to 58% in Belize (Fig. 2.4). Hence, we reject the null hypothesis that partitioned diversity values would remain constant across a latitudinal gradient of species richness.

Similarly, corals were not randomly distributed at any of the spatial scales explored, rejecting our second null hypothesis. Observed values of diversity differed significantly from expected values generated from individual-based randomizations (IBR) under the assumption that corals within the region settle independently of locality and independently of the presence or absences of other corals. Both unconstrained and restricted individual-based null models generated statistically identical patterns between observed and expected partitioned diversity (Table 2.2). Hence, we focus our results on the more defined unconstrained models. Observed diversity was significantly greater than null expectations between reefs (β_2) and at the local scale (α_1; Fig. 2.4). Conversely, the observed diversity between transects (β_1) was significantly lower than expected values (Fig. 2.4). By applying the partitioning approach and null model separately for each region, we were able to examine how observed and expected diversity components varied along a regional gradient of species richness. Among all 3 regions, the patterns between observed and expected components of diversity were consistent across spatial scales.

Expected values from sample-based randomization (SBR) models mirrored patterns found in the IBR models; namely, that observed β_2 component (between reefs) of diversity was significantly greater than expected, and the observed β_1 component (between transects) was significantly lower than expected. No comparisons can be made of the alpha diversity as no randomization occurs within the transect-scale, the smallest sampling unit, using a SBR approach.

Abundance-occupancy relationships

We examined abundance-occupancy plots by reproductive mode in corals and found no clear distinction in the shape of the curve, nor different patterns in amount of patches occupied by reproductive mode. Hence, results are presented for the entire coral community per region. The most abundant species were also the most widespread among the sampled patch reefs in all regions (Fig. 2.5). The relationships between the proportion of reefs occupied and local mean cover was best fit by a non-linear regression for species-rich regions of Florida and Belize, such that patch occupancy increased rapidly with small gains in cover, but became saturating at higher cover.

DISCUSSION

Patterns of species diversity across space are often scale-dependent, and stony corals are no exception. In the Western Atlantic, we have shown that coral diversity at each of three hierarchical spatial scales differed from null expectations based on a random distribution of species. These patterns in observed versus null values of α and β diversity were remarkably consistent among our three study regions, despite large differences in the regional (γ) diversity. Under-dispersion of coral diversity (i.e. observed diversity values lower than predicted by chance alone) was evident among the patch reef coral communities, though only at the intermediate, ‘between transects’ scale (i.e. $50m^2$ scale). At the smallest scale (‘within transects’: $10m^2$) and the largest scale (‘between reefs’: 100s of m^2), diversity was significantly higher than null expectations. These deviations from random suggest that neutral forcing (Hubbell 2001), such as demographic stochasticity, is insufficient to explain the observed patterns of coral diversity (Zvuloni et al. 2010). Rather, processes that are both non-random and scale-dependent are disproportionately influencing spatial patterns of coral diversity.

The difference between observed and expected alpha and beta values of coral diversity suggest ecological trade-offs exist among corals. When trade-offs are primarily at the local scale, alpha diversity is predicted to be relatively high (Kneital and Chase, 2003). Conversely, beta diversity is expected to be low because there is little turnover in species composition because coexistence is primarily at the local scale. We have some experimental evidence of local scale coexistence among corals. Idjadi and Karlson (2007) demonstrated empirically that spatial aggregation in corals at small spatial scales (<1m) contributes to the persistence of weakly competitive species and species coexistence among corals (Idjadi & Karlson 2007). Movement of species between spatial units is also predicted to reduce β diversity and increasing α diversity as immigration homogenizes species compositions at the local scale (Loreau & Mouquet 1999). For corals, movement is limited to the larval dispersal stage. As beta diversity was lower than expected between transects, yet higher than expected between reefs, homogenization of coral diversity appears to be restricted to within a reef. The recent dominance of brooding coral species in the Caribbean (Precht & Miller 2006; Green et al. 2008) may account for lower than expected β diversity within a reef. Brooding corals (those that release fertilized larvae capable of immediate settlement to the reef substrate), have been shown to preferentially recruit near adult conspecifics at local (1-10m) scales (Vermeij et al. 2007; Huntington et al, in review). . Additionally, asexual coral reproduction via fragmentation may contribute to under-dispersion of diversity between transects. Shallow reef habitats, such as patch reefs, are subject to higher levels of physical disturbance from storms and hurricanes than deeper reefs, inducing fragmentation and promoting a recovery process that often leads to within-patch aggregations of species (Jackson, 1986). Larval recruitment is low in the Caribbean, while the survival of asexually produced fragments within a given patch reef may be higher, leading to greater localized clustering of species via fragmentation rather than larger-scale dispersal via larval spawning which can cross inhospitable matrixes of sand that separate the patch reefs. Hence, we postulate mechanistically that local asexual propagation and local sexual recruitment together may exceed sexual recruitment from neighboring patches, resulting in community homogenization within a patch reef and greater dissimilarity in the coral community between patches.

The importance of the regional species pool on local diversity shifted with latitude. Although absolute coral richness (α) was fairly constant among regions (8-10 species), this local diversity comprised a smaller proportion of the regional pool γ at lower latitudes. In other words, high-latitude Bermuda had a larger number of widespread, regionally dominant coral species evident at both the patch and within patch scales, supporting the idea that regional enrichment and co-existence is greater at higher latitudes. In contrast, low-latitude Belize supported larger numbers of unique coral species (i.e., species that only occurred on <5% of reefs) and slower rates of species accumulation. Accordingly, dissimilarity, or beta diversity, between Belizean reefs was greater than their high latitude neighbors. These results are consistent with the hypothesis that the relative importance local interactions and regional enrichment shifts with latitude in marine communities (Witman et al. 2004; Freestone & Osman 2011). Greater than expected dissimilarity, increasing at lower latitudes, suggests that local processes are swamping regional enrichment. As interspecific competition among corals is limited (Van Woesik 2002), dispersal-limitation and differential survival among patch reefs in response to environmental gradients are more likely large-scale mechanisms supporting beta diversity in corals.

A main concern of biodiversity conservation is to predict the number of habitats a given species occupies at any one time and whether that number is being reduced by human influence. Hence, documenting spatial patterns in coral species richness has important implications for conservation strategies aimed at protecting coral diversity (see Zvuloni et al. 2010). Our results suggest that, within the Western Atlantic, preservation of coral diversity will require larger areas than predicted by models that assume random distribution, as communities among reefs are more different than expected. Hence, for conservation strategies to maximize the coral richness encompassed in protected areas, greater numbers of reefs must be protected, especially among regions that have larger species pools (γ). For example, the number of unique coral species in Belize is 10 times greater than in Florida and Bermuda. Combined with a slower accumulation of species and lower coral cover, these patterns suggest that Belize would benefit from larger tracts of protected reefs compared to their northern counterparts to conserve the same proportion of diversity.

As coral reefs continue to decline globally, understanding of the scaling of diversity is particularly urgent to inform effective conservation practices. Management strategies focused on conserving biodiversity in corals should be centered at the spatial scale where species richness is high. Very few studies have quantified the spatial dispersion of corals at large scales (but see Karlson et al. 2007), and none based in the Western Atlantic. To our knowledge, this is only the second study to use additive partitioning to study the spatial patterns of stony-coral diversity (see Zvuloni et al. 2010), and the first to do so across a latitudinal gradient defining reef sites by their natural boundaries (i.e. the extent of hard substrate comprising existing patch reefs). Our approach has shown that there are non-random processes influencing the observed coral diversity in the Western Atlantic. Within each of the three regions we surveyed, beta diversity exceeds random expectations. Based on these results, marine reserves aimed at preserving coral diversity within a region will need to be larger than if based on models assuming random distribution of corals among patch reefs. While we did not explicitly attempt to indentify which non-random processes are at play, out findings do identify the spatial scales and direction in which these processes are forcing diversity patterns in corals. These findings inspire further investigation into the role of coral dispersal mechanisms (i.e. brooders versus broadcasters) and differences in the seascape environmental gradients (i.e. reef size, spatial isolation, or structural complexity) between reefs to drive these patterns. We encourage further research into not only establishing patterns of diversity across spatial scales, but also the mechanisms and processes that create these patterns.

Table 2.1 Inter-region comparisons showing the total number of coral species found within each region at the transect-scale (pooled transect) and the patch reef scale (roving diver survey). The number in parentheses is the number of 'unique' species (i.e., species only occurring on <5% of the patch reefs surveyed in a given region).

Region	Transect	Patch reef
Bermuda	15 (0)	16 (1)
Florida	33 (1)	35 (1)
Belize	33 (10)	36 (7)

Table 2.2 Observed and expected additive partitioning values of diversity for the coral community in three regions at 3 spatial scales. Unconstrained individual-based (UIB) randomization null model results are shown in the top panel, followed by individual-based restricted (IBR) randomization null models. IRB are undefined at largest spatial scale (β_2) and hence cannot be calculated. In all cases, pairs of observed and expected values are significantly different from each other ($P < 0.001$). All values are absolute.

	Bermuda		Florida		Belize	
Partition	Observed	Expected	Observed	Expected	Observed	Expected
UIB model						
β_2	3.06	2.75	14.90	13.54	19.30	18.20
β_1	3.51	6.11	8.34	11.82	5.60	8.64
α	8.43	6.14	9.76	7.64	8.10	6.16
IBR model						
β_2	3.06	--	14.90	--	19.30	--
β_1	3.51	5.60	8.34	10.42	5.60	7.45
α	8.43	6.34	9.76	7.68	8.10	6.25
SBR model						
β_2	3.06	2.92	14.90	14.32	19.30	19.05
β_1	3.51	3.65	8.34	8.92	5.60	5.85
α	8.43	--	9.76	--	8.10	--

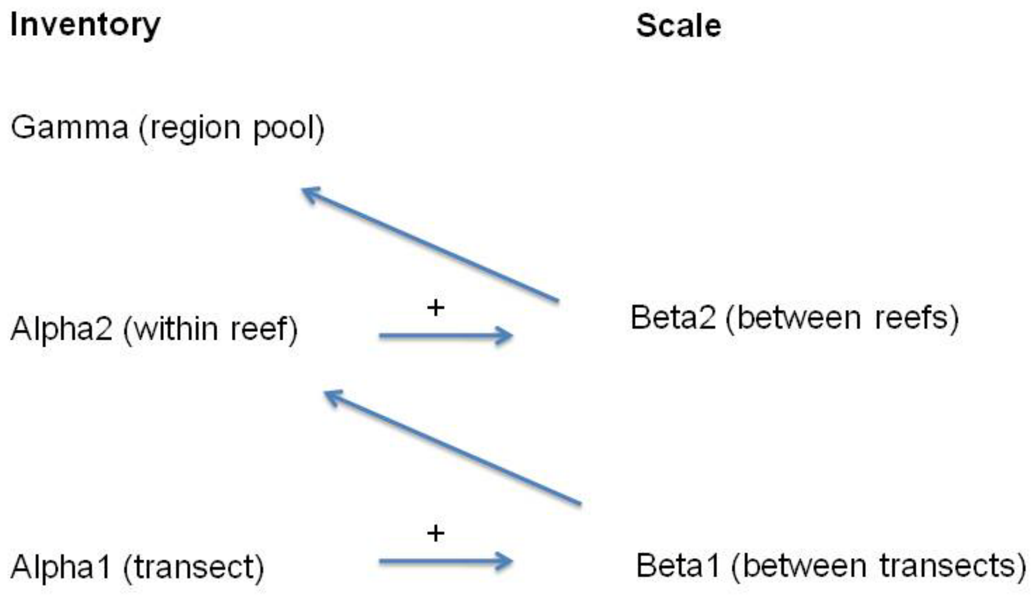


Fig. 2.1 Schematic representation of the difference hierarchical scales studies among Caribbean patch reefs. The α scale is the within- and the β scale the between-level component using additive partitioning. Each lower level of α and β add to create the next hierarchical level α diversity.

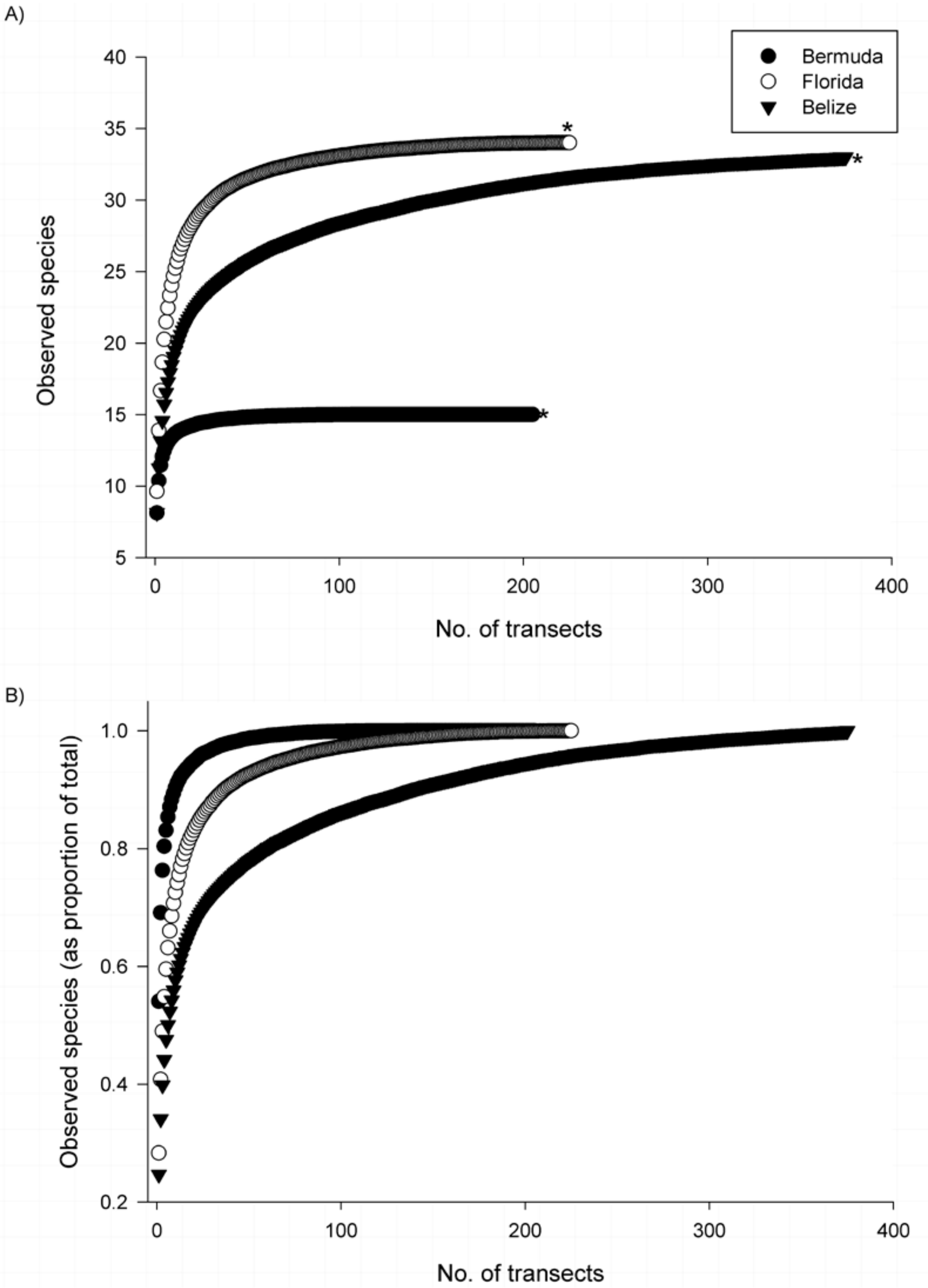


Fig. 2.2 Species-accumulation curves for the 3 survey regions (a) as absolute values of species richness and (b) as a proportion of the regional species pool to facilitate comparisons among regions. * Chao 2 estimates of total regional richness are shown on the top panel.

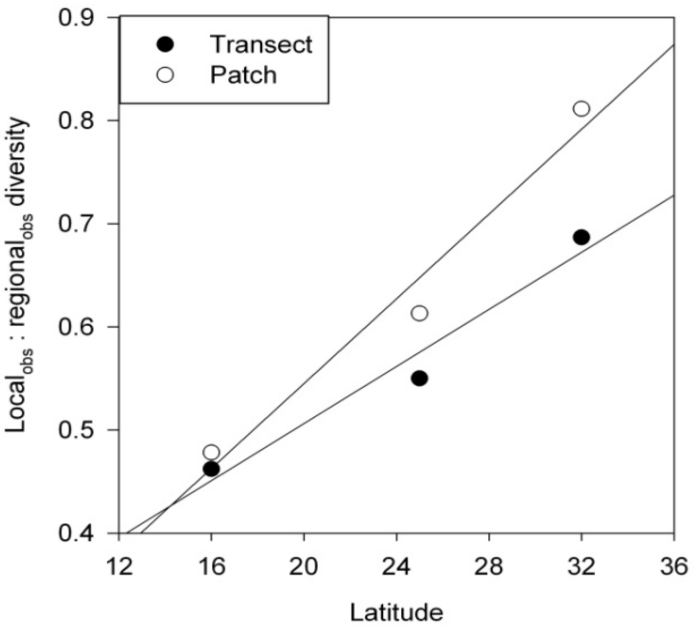


Fig. 2.3 Relationships between the ratio of local to regional diversity and latitude for local transect diversity (dark circles) and local patch reef diversity (open circles).

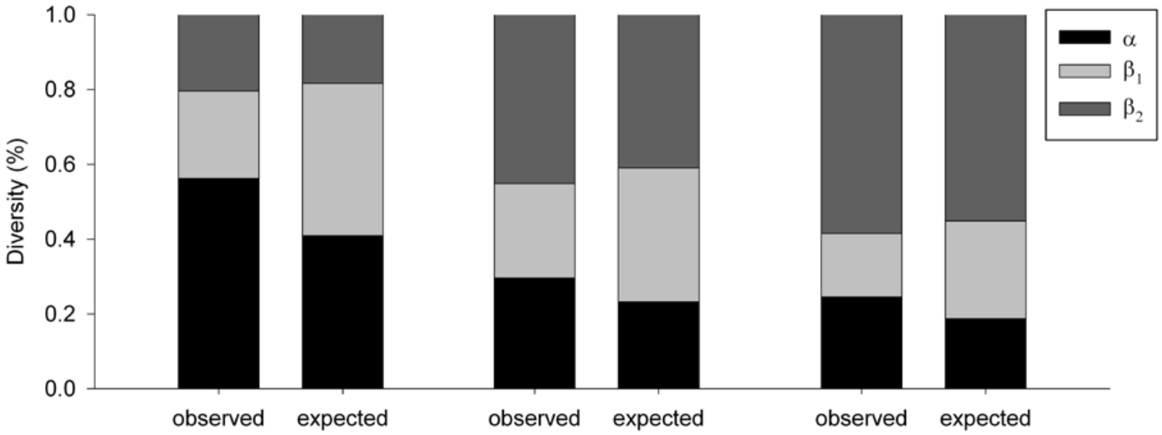
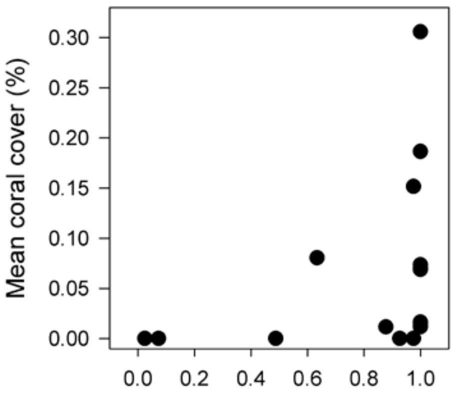
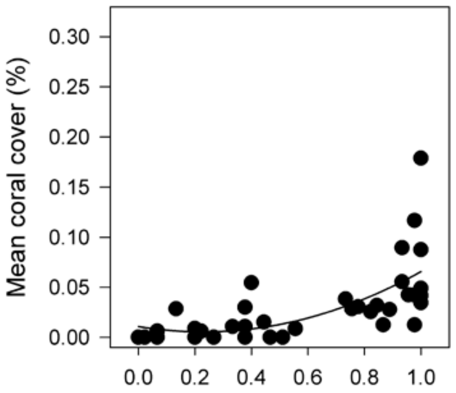


Fig. 2.4 Observed and expected additive partitioning of diversity at three hierarchical scales. Diversity values are presented as a proportion of the total (γ) diversity to facilitate comparison across the 3 regions that have differing region species pools.

a) Bermuda



b) Florida



c) Belize

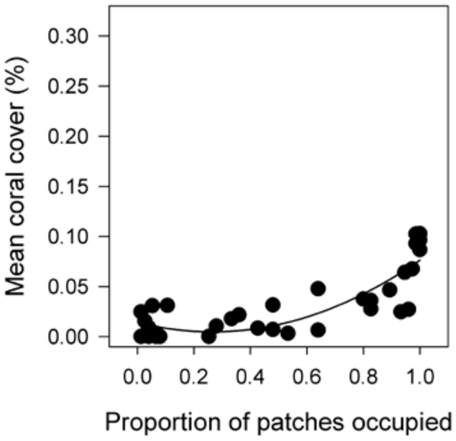


Fig. 2.5 Relationship between the average coral cover (%) when present, and the frequency of occurrence (no. of reef occupied) of species in a) Bermuda, b) Florida, and c) Belize. Each dot represents a single species. Significant quadratic polynomial regression lines are shown for Florida ($R^2 = 0.42$, F= 12.19, $p < 0.001$) and Belize ($R^2 = 0.72$, F = 43.33, $p < 0.001$).

Chapter 3: Determining the cause of variation in coral community composition (β diversity) across space

BACKGROUND

Whittaker (1960) partitioned species diversity into alpha (α), beta (β), and gamma (γ) components to characterize diversity in relation to spatial scale. The diversity of the regional species pool is γ, while the local diversity of a given sampling unit or site is α. The variation in species compositions among sites is β diversity (Whittaker 1960). At large spatial scales, biogeographic, historical, phylogenetic, and climatic processes are thought to regulate regional species pools (γ). At local spatial scales, α diversity is thought to be regulated by biotic interactions. In between these two spatial extremes, the physical characteristics of the habitat can strongly influence the diversity of species among sites (β). Beta diversity increases as the similarity in species compositions among sites decreases; therefore, it is a measure of the extent by which species diversity differs between sites.

Ecosystem management requires that we understand the processes by which β diversity is created and maintained, as well as the spatial scales at which these processes operate, in order to generate predictive relationships and inform management (Chandy et al. 2006; Winberg et al. 2007; Zvuloni et al. 2010). Within coral reef ecosystems, a central need for managers is to identify the dominant mechanistic drivers of coral-reef diversity within their study region and the spatial scale at which these drivers operate. However, much of our understanding of coral biodiversity has been conducted at the local scale (i.e. within a reef; Connell 1978) or at the regional scale (i.e. across broad geographic expanses of reefs; Karlson & Cornell 1998; Karlson et al. 2004). Variation in species diversity at the landscape scale (β) is a subject of only recent investigation, often encompassing several geomorphic reef types within a single analysis (Cornell et al. 2007; Arias-González et al. 2008). While still an informative approach, it is perhaps intuitive that coral species composition, comprised of corals known to have various depth, physical and environmental preferences (Jackson 1991), differ among environmentally distinct reef types. Here, we are interested in exploring the drivers of beta diversity within a single reef type to allow for a more detailed analysis of the factors that influence the variation in coral composition.

The origins of beta diversity can be categorized into 3 hypotheses (Legendre et al. 2005). The first hypothesis (often considered the null model), is that species are uniformly distributed across space. Hence, β diversity among habitats is small. From a management angle, under this hypothesis reserves can be located anywhere within the ecosystem because all parts of the ecosystem are equivalent. The second hypothesis predicts that species composition will fluctuate in a random, autocorrelated way. Founded in neutral theory, this hypothesis emphasizes dispersal differences among organisms to drive β diversity. Under this model, different parts of the ecosystem may possess similar species compositions (e.g. autocorrelation) as a result of spatial dispersal-limitation. Management under this model necessitates large reserves to support different parts of the ecosystem with differing communities. The third hypothesis predicts that species composition vary in accordance to variable environmental conditions. Landscapes are viewed as mosaics, where variations in habitat structure, configuration, and condition result in variations in species composition. Hypothesis 3 implies that all parts of an ecosystem are not equivalent; hence, reserve placement needs to target specific environmental conditions, and reserve sizes should be large to ensure different types of habitats are adequately protected.

Using these three hypotheses as a theoretical guide, we were interested in determining the origins of community variation in corals (β diversity) across space. In Chapter 1, we determined that β diversity at the reef scale is larger than expected if coral species were randomly distributed. Therefore, we reject the first hypothesis outlined by Legendre et al. (2005) and focus this analysis on non-random spatial and/or environmental drivers that may be contributing to the greater β diversity in corals. Nonrandom patterns of species distributions are particularly common among insular systems where species number is positively correlated with patch size (Schoener & Schoener 1983; Simberloff & Levin 1985). However, we do not detect significant species area relationships for corals on patch reefs in the Western Atlantic (Huntington & Lirman, in review; Ch. 7). Precisely because these larger patch reefs are not necessarily more diverse, we ask what other spatial or environmental factors are influencing the diversity of corals between patch reefs.

We focused on reef heterogeneity as our environmental variable of interest. Here, we define reef heterogeneity as landscape-scale variations in reef size, reef density, and reef spatial isolation, in tandem with local-scale variations in topographic complexity (Grober-Dunsmore et al. 2008). We already know that different reef types support different coral assemblages (Arias-González et al. 2008). We know much less about the roles of reef size, spatial configuration, and benthic complexity to support differences in coral communities. Habitat heterogeneity has been shown to have important influences on community composition in both terrestrial ecosystems (Rosenzweig 1995; Ellingsen &

Gray 2002) and marine ecosystems (Hewitt et al. 2005; Balata et al. 2007), though the nature of this organism-habitat relationships is often scale-dependent (Hurlbert & Haskell 2003). Likewise, measures of habitat heterogeneity can be quantified at various spatial scales, ranging from the local to the landscape (Irlandi et al. 1995; Hovel & Lipcius 2001; Hewitt et al. 2005). To reach general conclusions about the relationship between reef heterogeneity and beta diversity in corals, we needed to assess the relationship at increasing spatial scales, treating reef heterogeneity as a multi-facetted variable, characterized by both local- and landscape-scale variations (e.g. Grober-Dunsmore et al. 2008). Using *in situ* monitoring, we then specifically evaluated the influence of local and landscape-scale reef heterogeneity on coral community composition (β diversity), also measured at two spatial scales: 'within-patch' and 'among-patch'.

We expected metrics of reef heterogeneity to significantly influence the community composition of corals and vary with spatial scale. Within a given patch reef, we expected β diversity among transect samples to be more strongly correlated with the local-scale metric of topographic complexity. Conversely, we expect β diversity among patch reefs to be correlated with landscape-scale metrics of reef spatial isolation and configuration. Lastly, we explored the role of the regional species pool (γ) and coral reproductive mode (i.e. broadcasting spawners versus brooding spawners) to influence the patterns between organism and habitat.

METHODS

To minimize additional environmental, anthropogenic, and geomorphologic differences among our sampling units, we restricted our analyses to patch reefs, among comparable depths (<6m) within the Western Atlantic. Surveys were conducted in Bermuda, the Florida Keys, and Belize. These regions were selected to represent regions of low, intermediate, and high coral richness, respectively, across a latitudinal diversity gradient. A total of 36 reefs in Bermuda, 42 reefs in Florida, and 70 reefs in Belize were sampled between May 2008 and May 2010.

Sampling design, variables

The coral community was censused at each patch reef using 5 replicate, non-overlapping 10 x 1m belt transects laid haphazardly across the reef surface between depths of 2-5m. The species richness of all corals encountered within the transect were recorded. Local-scale heterogeneity (i.e. within a given reef) was measured as topographic complexity, as previous studies suggest that coral larvae (the only mobile phase of a coral's life), exhibit species-specific settlement preferences for various orientations of the reef surface (Edmunds et al. 2004). Topographic complexity was quantified using the rugosity-chain method, using a 1.5cm link chain, for 5 replicate, 10-m transects per reef (Risk 1972).

Landscape-scale heterogeneity was quantified as the reef area, isolation, and configuration within the seascape. Patch reef area (m^2) and perimeter (m) were quantified using ArcMap from high-resolution, multi-band IKONOS satellite imagery of the reef arrays in each region. Reef isolation was measured as the Euclidean distance to the nearest neighboring reef. Area-based spatial configuration was measured the amount of 'surrounding reef habitat' (m^2) within circular buffers of 200-m, 500-m, and 1-km radii for each focal reef (Moilanen & Nieminen 2002; Huntington et al. 2010). Spatial measures of reef geographic position were collected as latitude-longitude coordinates and converted into projected coordinates (m) prior to analysis. Raw values for each environmental and spatial metric are given in Appendix B.

For each region, correlation coefficients were examined between all reef heterogeneity metrics to explore colinearity (Table 3.1). Reef perimeter and area were closely correlated; hence, reef area was chosen to be the more informative metric. Similarly, strong correlations were detected between buffer distances, so that 1km buffers were retained for further data analysis as they yielded the strongest correlation to β diversity measures for each region. Measures of reef heterogeneity were log-transformed or square root transformed as if they failed to pass tests of normality (Table 3.1; Shapiro-Wilk test, $p < 0.05$). Descriptive statistics for the final set of environment metrics are given in Table 3.2. Values were comparable among all three regions.

Quantifying beta diversity

We defined β diversity as variation, or the dissimilarity between two samples, rather than as species turnover along an environmental or spatial gradient (Whittaker 1960). β diversity can be calculated in a number of ways; see Anderson et al. (2011) and Koleff et al. (2003) for an overview and assessment. Here, we measured β diversity in two ways: (1) a classic, univariate measure calculated by comparing the number of species found in small area (α) to the number of species in a larger area (γ) using additive partitioning (Lande 1996), and (2) a multivariate measure using a coral community composition data table based on species presence-absence (Legendre et al. 2005).

Our hierarchical sampling design enables us to calculate β diversity using additive partitioning at two difference spatial scales: 'within-patch' and 'among-patch' (Veech et al. 2002; Crist et al. 2003). β diversity should be compared among equally sized areas (Koleff et al. 2003), hence coral species composition for each patch was determined from 5, 10-m belt transects per reef. At the 'within-patch' scale, $\beta_{\mathrm{transect}}$ was determined as the mean transect diversity ($\alpha_{\mathrm{transect}}$) subtracted from the total transect richness ($\gamma_{\mathrm{transect}}$) for that reef (Fig. 3.1). At the 'among-patch' scale, β_{patch} was determined as the total regional diversity ($\gamma_{\mathrm{regional}}$) – the number of species observed on a given patch reef (α_{patch}). Due to the hierarchical nature of this analysis, $\alpha_{\mathrm{patch}} = \gamma_{\mathrm{transect}}$ (Fig. 3.1). To facilitate comparisons among regions that differ in the size of their species pools (γ) (Koleff et al. 2003), the values for β-diversity at both scales were converted into proportions of the regional pool (γ).

Our second measure of β diversity was based on a community composition data table at the patch scale. We were interested in explaining the origins of beta diversity; hence, tests of significance must be carried out on the original (or transformed) community composition data rather than dissimilarity coefficients such as Jaccard or Sorensen (Legendre et al. 2005; Tuomisto & Ruokolainen 2006). The Hellinger transformation was performed on each species composition data table, which converts presence-absence data into relative values per site and is recommended prior to canonical analyses when zeros are common in the species data table (Legendre & Gallagher 2001).

Data analysis

A one-way ANOVA was conducted on both $\beta_{transect}$ and β_{patch} (as proportions of the regional species pool) to determine if β diversity varied by region. To investigate scale-dependent patterns in the habitat-diversity relationship, multiple ordinary least squares regression was performed for both $\beta_{transect}$ and β_{patch} and measure of reef heterogeneity for each region. The squared terms of each independent reef heterogeneity factor (reef area, nearest neighbor, surrounding reef habitat, and topographic complexity) were included in initial models to allow for non-linear responses of β-diversity to the metrics of habitat heterogeneity, however, squared terms did not result in improved model fits hence, model result presented include only the original factors.

We used redundancy analysis (RDA), a direct gradient analysis method in which species are presumed to have linear relationships to environmental gradients. Hellinger-transformed community composition was the response data table, whereas reef heterogeneity variables and spatial variables formed the explanatory table. This raw-data approach (in which community composition is the response variable) allows us to determine how much of the observed overall β diversity in a region can be explained by environmental factors, by spatial coordinates, or remains unexplained (Tuomisto & Ruokolainen 2006). The statistical significance of each selected variable was determined by a Monte Carlo permutation test (499 permutations) on the residuals from the reduced model. We are limited to explaining the observed β diversity within each of the three regions, but not analyzing variations in β diversity among the regions. This additional analysis requires a distance approach to partition the variation in β diversity among our 3 regions (Legendre et al. 2005), and is beyond the scope if this initial analysis.

RESULTS

β diversity, measured from diversity partitioning, varied with spatial scale such that ‘within-patch’ β diversity ($\beta_{transect}$) comprised a smaller proportion of the total diversity (γ) than ‘among-patch’ diversity (β_{patch}). β diversity at both scales differed significantly between the three regions (single factor ANOVA; Table 3.3). β diversity was lowest in Bermuda, the northern most region with the smallest regional species pool indicating that differences in coral species richness among sampling units (i.e. transect or patch) was low in this regions. β diversity was significantly higher in both Florida and Belize indicating a greater dissimilarity in coral species richness among sampling units.

The relationships between β diversity and reef heterogeneity varied with the spatial scale at which β diversity was measured (i.e. transect or patch). Overall, model fits for β_{patch} were higher than $\beta_{transect}$, indicating a stronger relationship between patch reef coral community composition and metrics of reef heterogeneity (Table 3.4; based on model R^2 values). As predicted, more variance in β_{patch} could be explained by landscape-scale metrics of spatial configuration within the seascape, than the local-scale metric of topographic complexity. Conversely, the metrics of spatial configuration (i.e. nearest neighbor and amount of surrounding reef habitat) were not important correlates of $\beta_{transect}$ (Table 3.4A). Regression models also differed by region. The best model fits were found in Bermuda, the region with the smaller regions species pool (γ). Reef geographic position of latitude and longitude were not important correlates of β_{patch} in any region; rejecting the hypothesis of spatial autocorrelation as a mechanistic driver of variation in the coral assemblage at the reef scale (latitude and longitude were not evaluated at the transect scale as all transects on a given reef all possess the same geographic position).

Multivariate analyses comparing variation in community composition at the patch scale to spatial and environmental variables also revealed that environmental measures of reef heterogeneity were better predictors of β diversity than spatial metrics. Reef geographic position of latitude and longitude were not selected in any of the final models for Bermuda, Florida, or Belize (Table 3.5). However, the majority of variation in coral community composition remained unexplained by either spatial variables or habitat heterogeneity variables. Final RDA models did differ by region, and, as with the multiple regression models, the models explaining the greatest amount of variance were in Bermuda (variance explained = 0.17), while this proportion declined with decreasing latitude and corresponding increasing γ (variance explained in Florida = 0.08; Belize = 0.03).

Redundancy analysis (RDA) was also conducted on a subset of the total coral community to consider broadcast spawners separately from brooding spawners. Broadcasters release separate egg and sperm gametes that must fertilize in the water column before settlement to the reef, while brooding spawners release larvae capable of immediate settlement. A greater proportion of the total variance for brooders could be explained by reef heterogeneity variables than for broadcasting communities, though coral communities in Belize were poorly predicted in all cases (Table 3.5). Model fits again declined with increasing regional diversity, such 33% of the variance in brooder β diversity was explained in Bermuda, 11% in Florida, and only 3% in Belize.

The influence of reef geographic position (i.e. latitude and longitude) was not a strong determinant of multivariate β diversity. Only β diversity of brooding coral communities in Bermuda were significantly correlated to reef latitude (Table 3.5), suggesting some degree of spatial autocorrelation across the 3km gradient of latitude encompassed by the study reefs. However, caution must be used when linking correlation to causation from this result, as other, unmeasured environmental gradients exists along the latitudinal axes of our sampling region in Bermuda. For example, in this region a decrease in latitude also corresponds to a spatial location closer to a large shipping channel and the mainland of Bermuda. Hence, gradients in water quality, turbidity and other factors of disturbance likely co-vary with latitude in this region.

DISCUSSION

Our analyses of coral β diversity support the concept that even seemingly homogeneous habitat types can possess sufficient degrees of intra-habitat variation to drive significant differences in community structure of reef organisms (Huntington et al. 2010; Yeager et al. 2011). We found no clear evidence of spatial-autocorrelation in coral community composition among patch reefs. Rather, we identified both local-scale and landscape-scale metrics of reef heterogeneity as important predictors of the coral community. This organism-habitat relationship was found to be both scale-dependent and life-history dependent. The relationship between coral species composition and reef heterogeneity was strongest at the reef scale. In general, local-scale metrics of topographic complexity and the patch size were more important correlates of variation in coral richness among transects within a patch, while landscape-scale metrics of reef spatial configuration in the larger seascape were more important correlates of variation in richness between patches. Furthermore, the importance of reef size, isolation, and topographic complexity to significantly explain variation in coral community composition was strongest for brooding corals.

This study explored reef heterogeneity across the seascape and spatial drivers of coral β diversity. The majority of current studies using partitioning of diversity in coral communities (Cornell et al. 2007; Zvuloni et al. 2010) enforcing spatial sampling scales on to tracts of continuous reef habitat. Hence, the underlying spatial heterogeneity and discrete boundaries of the reefs within the seascape are largely ignored as mechanistic drivers that could influence diversity patterns. To the best of our knowledge this is the first study in a coral reef system to mix hierarchical scales of diversity sampling and hierarchical measures of naturally occurring reef heterogeneity. Our results show limited evidence (only among brooding corals) that coral species compositions fluctuate in a random, autocorrelated way (Hypothesis 2; Legendre et al. 2005). While brooding corals that are thought to exhibit spatially limited dispersal (Nishikawa et al. 2003), the model identifying reef latitude as a significant component also included two metrics of reef heterogeneity suggesting that species distributions are also related to environmental condition.

Previous studies on reef fishes have identified metrics of reef size and spatial isolation within the seascape as important drivers of not only fish community structure (Gladfelter et al. 1980; Walsh 1985; Chittaro 2002; Belmaker et al. 2004), but also, stability over time (Mellin et al. 2010). However, the majority of these investigations are limited to a single study region. Here, we explored similar metrics of reef heterogeneity in corals while also evaluating the consistency of such organism-habitat relationships across regions. Regional differences prevent us from identifying clear patterns between β diversity and reef heterogeneity that were consistent among all three regions in the Western Atlantic. Rather, the relationship between beta diversity and reef heterogeneity varies with latitude and the size of the regional species pool (γ), such that the organism-habitat relationship is stronger at higher latitudes where γ is reduced.

While reef heterogeneity explained a larger component of beta diversity than spatial variables, the majority of beta diversity remains unexplained by either the spatial or environmental factors investigated here. Arias-Gonzalez et al. (2008) also found environmental variation to be a stronger correlate of beta diversity in Caribbean corals than spatial variables. Their study considered environmental variables of total coral cover, depth, complexity, reef rugosity, area, and benthic assemblage rather than the metrics of spatial reef heterogeneity, yet the explanatory power of their models within a reef type were also low ($R_a^2 = 0.083$-0.371). In contrast, a similar analysis of beta diversity in soft sediment marine habitats returned models with explanatory power of $R^2 = 0.65$ and 0.58 when considering habitat size, density, and mean particle size as predictor environmental variables (Hewitt et al. 2005). Perhaps the complex and interactive processes common on coral reef systems, more so than soft bottom habitats, make indentifying the mechanistic drivers of the majority of coral β diversity more challenging to quantify. Patch productivity (Chase & Leibold, 2002), free settlement space, benthic substrate composition (Diaz-Pulido & McCook, 2004; Kuffner et al. 2006), or larval retention and hydrodynamic connectivity (Jones et al. 2004) may be other meaningful environmental variables to consider in future investigations of beta diversity drivers in corals.

Conclusions

Recently, ecologists have begun to recognize the relevance of intra-habitat variability within marine habitats that were formerly considered homogeneous (Kraan et al. 2009; Huntington et al. 2010). Here, we show that this intra-habitat heterogeneity of patch reefs can be influential on the community composition of corals across space. To mechanistically link these metrics of reef heterogeneity to coral diversity, experimental manipulations of the focal patch and the surrounding seascape is necessary. This scale of manipulation is logistically prohibitive for natural reef systems; however, artificial reefs offer an alternative option that may facilitate such experimentation. In the following chapter, we present results from one such artificial reef area, in which the size, spatial isolation, and the topographic complexity of the focal patch were artificially constructed and the structure of the ensuing coral community explored.

The existence of 'bottom-up' linkages between reef heterogeneity and coral community composition has important bearing to reef conservation (Jones et al. 2004) in an era where 'top-down' closure of fishery activities garners more attention. Firstly, understanding the origins of beta diversity is important for marine reserve placement in reef systems (Legendre et al. 2005; Zvuloni et al. 2010). Our results support a hypothesis that beta diversity is corals related to environmental conditions, rather than uniformly, randomly, or spatially autocorrelated. For the patch reef systems studies here, marine reserves should, therefore, be large enough to represent the different types of patch reef habitats at sufficient quantities to be sustainable (Legendre et al. 2005). Secondly, by considering differences in community composition and the metrics of landscape heterogeneity and increasing spatial scales, we are working at spatial scales (km's) relevant to resource management. Land-use changes, coastal development, and loss of live coral cover have the potential to alter the landscape characteristics of nearshore reef systems (Pandolfi et al. 2003; Alvarez-Filip et al. 2009). By understanding the scales and extent to which corals depend on these landscape features, we can better predict the consequences of these ongoing changes to the landscape heterogeneity of coral reefs.

Table 3.1 Correlation matrices for metrics of reef heterogeneity for each region. Transformations to improve normality are shown for each metric. NN= nearest neighbor; 200m, 500m, 1km = amount of surrounding reef habitat within the given radius buffer; complexity = topographic complexity.

A) Belize	log(area)	perimeter	sqrt(NN)	log(200m)	log(500m)	log(1km)
log(area)						
perimeter	0.943					
sqrt(NN)	0.341	0.205				
Log(200m)	0.073	0.200	-0.373			
log(500m)	-0.187	-0.113	-0.331	0.551		
log(1km)	-0.214	-0.102	-0.342	0.478	0.840	
rugosity	-0.309	-0.223	-0.257	0.134	0.180	0.288

B) Florida	log(area)	perimeter	log(NN)	log(200m)	log(500m)	log(1km)
log(area)						
perimeter	0.852					
log(NN)	0.302	0.216				
log(200m)	0.339	0.275	-0.378			
log(500m)	0.335	0.228	-0.031	0.804		
log(1km)	0.247	0.057	-0.006	0.668	0.890	
rugosity	-0.179	-0.033	0.188	0.059	0.094	0.093

C) Bermuda	log(area)	perimeter	sqrt(NN)	log(200m)	log(500m)	sqrt(1km)
log(area)						
perimeter	0.9486					
sqrt(NN)	0.2974	0.1791				
log(200m)	0.2048	0.2265	-0.3411			
log(500m)	0.1744	0.1593	-0.3417	0.9302		
sqrt(1km)	0.0999	0.1549	-0.4891	0.8579	0.8595	
rugosity	0.0351	-0.0523	-0.0267	-0.0684	0.0373	-0.0794

Table 3.2 Descriptive statistics for the final set of environment metrics for each region. Values reported are for untransformed data. Rugosity index was calculated as linear length(m)/chain length (m), such that a flat reef would receive an index score of 1. This score would increase with increasing rugosity.

A) Reef area (m^2)	Mean	SE	min.	max.
Bermuda	278	44	42	924
Florida	1152	204	55	5570
Belize	3735	419	100	12169

B) Nearest neighbor (m)	Mean	SE	min.	max.
Bermuda	44.8	5.5	13.4	215.8
Florida	82.7	7.2	26.5	228.5
Belize	115.0	9.4	5.2	328.8

C) 1km buffer (m^2)	Mean	SE	min.	max.
Bermuda	324378	9268	168537	412265
Florida	249460	21588	46131	598798
Belize	288822	29705	49456	1412634

D) rugosity index	Mean	SE	min.	max.
Bermuda	1.74	0.04	1.36	2.22
Florida	1.59	0.02	1.30	2.03
Belize	1.49	0.02	1.18	2.00

Table 3.3 Result of one-way ANOVA on the regional differences in A) $\beta_{transect}$ and B) β_{patch}. Beta-diversity means and standard errors (SE) are given as a proportion of the regional richness. * indicates a region that is statistically difference from all other regions based on Tukey's post-hoc analysis.

Dependent variable	Mean (SE)	df	F	p
A) β-transect		2, 145	133.4	<0.001
Bermuda	18.6 (1.3)*			
Florida	45.1 (1.2)*			
Belize	39.3 (0.9)*			
B) β-patch				
Bermuda	30.6 (1.4)*	2,145	137.6	<0.001
Florida	45.7 (1.3)*			
Belize	59.4 (1.0)*			

Table 3.4 Results of multiple regression analysis of beta diversity additively partitioned at the (A) transect- scale and (B) patch-scale with habitat heterogeneity characteristics among the three regions.

A) β-transect

Region	df	SS	F	Est.	p
Bermuda, $R^2 = 0.12$					
Model	1	221.4	4.7		0.038
Error	34	1610.9			
Intercept				4.36	0.518
area				6.67	0.038
Florida, $R^2 = 0.16$					
Model	1	209.7	7.8		0.008
Error	40	1074.1			
Intercept				22.42	0.009
rugosity				14.35	0.008
Belize, $R^2 = 0.14$					
Model	1	710.4	11		0.002
Error	68	4433.8			
Intercept				21.14	<0.001
area				5.52	0.002

B) β-patch

Region	df	SS	F	Est.	p
Bermuda, $R^2 = 0.32$					
Model	2	721.9	7.8		0.002
Error	33	1533.7			
Intercept				48.61	<0.001
area				-11.14	<0.001
near neigh.				1.11	0.089
Florida, $R^2 = 0.26$					
Model	2	209.7	7.8		0.008
Error	39	1074.1			
Intercept				-28.38	0.297
near neigh.				-1.20	0.045
1km buffer				15.89	0.003
Belize, $R^2 = 0.15$					
Model	2	671.8	5.9		0.004
Error	68	3814.8			
Intercept				68.38	<0.001
area				2.67	0.109
rugosity				-11.91	0.020

Table 3.5 RDA model outcomes for each region. Separate RDAs were run for species compositions of brooding species and broadcasting species given the different dispersal modes of these two reproductive strategies in corals. Only significant variables (based on Monte Carlo permutations) are shown with the corresponding f ratio, and p value. The cumulative variance explained by the model for each additional variable is also presented.

Region	Species pool	Model variables	F	p	variance explained
Bermuda	all	area	4.01	0.002	0.11
		rugosity	2.69	0.012	0.17
	broadcasters	area	4.18	0.006	0.11
		rugosity	4.04	0.01	0.21
	brooders	area	4.09	0.002	0.11
		1km buffer	2.55	0.038	0.17
		latitude	4.01	0.004	0.26
		rugosity	2.83	0.034	0.33
Florida	all	1km buffer	1.83	0.014	0.04
		rugosity	1.62	0.044	0.08
	broadcasters	1km buffer	2.18	0.012	0.05
		complexity	1.82	0.048	0.09
	brooders	area	2.72	0.01	0.06
		nearest neigh.	1.98	0.026	0.11
Belize	all	area	2.23	0.006	0.03
	broadcasters	area	2.13	0.034	0.03
	brooders	area	2.25	0.014	0.03

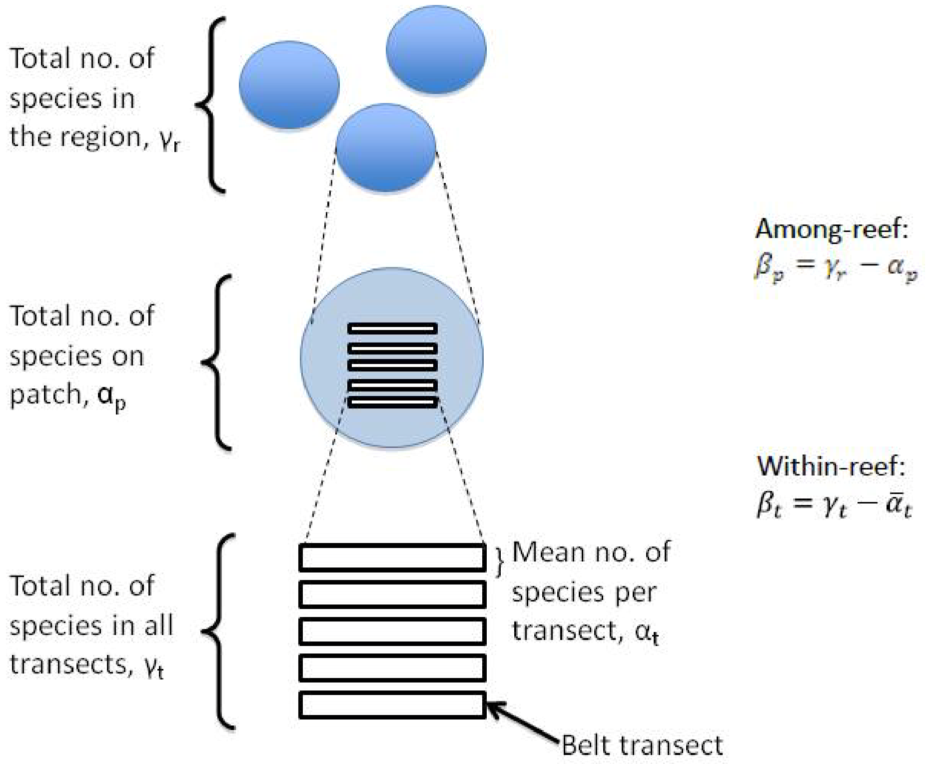


Fig. 3.1 Schematic of the hierarchical sampling scheme used to additively partition beta diversity at the within-reef (transect) and among-reef (patch) scales.

CHAPTER 4: Evaluating the influence of reef size, spatial isolation, and complexity on stony coral assemblages in a heterogeneous seascape

BACKGROUND

The mechanisms underlying patterns of species diversity across space are a fundamental ecological concern. While much of community ecology has traditionally focused on the influence of habitat quality on local species diversity (Lennon et al. 2000; Chase & Leibold 2002; Eriksson et al. 2006), there is a growing body of work founded in biogeography theory exploring the role of spatial factors to influence diversity (Leibold et al. 2004). Recently, models that combine both spatial biogeography and habitat heterogeneity have received strong support (Cottenie 2005; Kalmar & Currie 2006; Kallimanis et al. 2008; Huth & Possingham 2011), underscoring that these two mechanistic categories are not mutually exclusive, but may act in tandem to determine patterns of species diversity across space. Here, we adopt this approach to explore the fundamental relationship between coral diversity and the reef seascape, considering both the spatial biogeography and complexity of reef habitats.

How organisms perceive and respond to spatial and habitat heterogeneity has conservation implications in light of ecosystem degradation. Coral mortality, reef fragmentation, and bioerosion are causing reef habitats to become not only smaller and more isolated, but also less complex (Bellwood et al. 2004; Alvarez-Filip et al. 2009; Hughes et al. 2010). Yet, the effects of reef fragmentation and degradation on corals have not been quantified, largely because of difficulties in manipulating reef configuration and composition at relevant spatial scales. Here, we address this limitation by using an artificial reef array that served as a proxy for habitat manipulation at meso-scales (100s of m). Determining the influence of reef area, spatial isolation, and complexity on coral diversity and abundance will help predict how future shifts to reef habitats will impact the coral community.

The first step of this study was to test the null hypothesis that there was no positive correlation between reef area and number of species (along with several of its mathematical variants; Connor & McCoy 1979; Anderson 1999). Next, we considered the mechanisms that may cause larger reefs to be more diverse by testing four hypotheses that have been proposed to explain species-area relationships (SARs) but never explicitly tested in corals (Table 4.1). These mechanisms are not mutually exclusive, but rather represent increasingly levels of complexity. The first hypothesis of "random placement" predicts that larger patches contain greater number of individuals that represent more species (Arrhenius 1921; Coleman 1981). Under this model, sampling equal areas, regardless of the total size of the habitat patch, should result in the same average number of species (Simberloff 1976; Anderson 1999). Random placement is not a biological phenomenon, but a sampling artifact. Therefore, random placement should be considered the null hypothesis underlying an observed SAR and empirically rejected before considering alternative hypotheses (Connor & McCoy 1979).

An alternative to the random placement is the "target area hypothesis," that predicts the greater diversity observed on larger habitat patches is due to a positive correlation for immigration rate as patch size increases (Gilpin & Diamond 1976). Larger habitats are thought to be both better targets for active immigrants and more likely to intercept passive immigrants, resulting in greater numbers of individuals per unit area compared to smaller habitats (Simberloff 1976). The greater number of individuals per unit area corresponds to greater species richness per area due to sampling effects.

Thirdly, we consider the “habitat-diversity hypothesis,” which predicts that larger areas enclose more habitat types, thus fostering greater diversity (Williams 1943). This hypothesis assumes area is correlated with the number of different habitats and that these habitats are associated with different sets of species. In this case, we use the topographic complexity of the reef surface (i.e. rugosity) as a measure of habitat diversity as corals settle directly on to the reef surface. Lastly, we evaluated predictions of the "equilibrium theory of island biogeography", which incorporates the spatial configuration of habitats across the landscape relative to a source population, in addition to habitat size (MacArthur & Wilson 1967). Reduced extinction and greater immigration rates are predicted for larger habitats that are less isolated from neighboring habitats, leading to greater species richness. In contrast, smaller and more isolated habitats are expected to have fewer species than their larger, better-connected counterparts.

Most investigations simultaneously considering spatial and environmental mechanisms have been conducted in terrestrial systems (Thomas et al. 2001; Kalmar & Currie 2006; Kallimanis et al. 2008). Yet, recent studies suggest this approach may have traction in marine tropical reef systems as well (Sandin et al. 2008; Matias et al. 2010). By testing these 4 hypotheses within coral communities, we can begin to untangle the influence of reef size, spatial isolation, and topographic complexity and their roles in supporting diverse and abundant coral communities.

METHODS

Study site

The configuration and composition of reef habitats are next to impossible to manipulate at the meso-scale (100s of m) and would require maintaining these manipulations for several decades to allow corals to colonize naturally. As a proxy for manipulation, we sampled reefs from an artificial reef array in the Florida Keys National Marine Sanctuary (80°49’44.9 W, 24°43’52.4 N) consisting of >100 distinct reefs at 7m of depth. This unique system allowed us to distinguish effects of reef area, isolation, and complexity from other confounding factors as the artificial reefs are of comparable depth, disturbance history, distance to shore, and of identical age. All reefs are constructed of the same concrete material but with varying levels of benthic complexity and spatial isolation across the seascape. Lastly, the array is ~25 years old, allowing sufficient time for natural colonization by the regional species pool. We used high-resolution satellite imagery to view the entire extent of the array and then haphazardly selected 31 reefs for *in situ* sampling of varying area, isolation, and complexity (Fig. 4.1).

Reef area, isolation, and complexity

The area of the 31 patch reefs was quantified using ArcMap and ranged from 31 to 608 m^2. Reef isolation was measured in two ways: a distance-based and an area-based measure (Moilanen and Nieminen 2002). Area-based isolation measured the amount of ‘surrounding reef habitat’ (m^2) within circular buffers of 50m, 100m, and 200m radii for each focal reef (Moilanen & Nieminen 2002; Huntington et al. 2010). Additionally, ‘nearest neighbor,’ measured the shortest distance to a neighboring reef. Nearest neighbor was not correlated to the surrounding reef habitat at 50m, 100m, or 200m scales. The area-based metrics of reef isolation, however, were correlated; therefore, we focused on the 100m radius as it contributed the most to the first axis of a principle component analysis, and was not correlated significantly to other predictor variables.

Reef topographic complexity was quantified at two different scales: (1) fine-scale resolution, using the rugosity index for 5 haphazardly placed, 10-m transects with 1.5cm link chain per patch (Risk 1972); and (2) coarse-scale resolution, using an topographic complexity score ranging from 0 to 3 assigned during towed snorkel surveys in which 0 indicated no vertical relief (flat concrete slab), while reefs with high complexity were given a rating of 3 (Wilson et al. 2007). Both metrics of complexity were positively correlated (r = 0.802, n = 31), therefore the rugosity index was retained over the coarse-scale topographic score as the most ecologically interpretable metric. All reef parameters and correlation coefficients are presented in the Table 4.2 and Table 4.3.

Coral community surveys

Coral percent cover and community composition were assessed from non-overlapping digital photographs taken 0.5m above the substrate along the long and short axis of the reef. Twenty images were randomly selected for point-intercept analysis, with 50 random points scored per image using CPCe software, v3.5 (Kohler & Gill 2006). Coral colonies >3cm in diameter were identified to species, while corals between 1-3cm in diameter were classified as unknown coral species. Corals <1cm in diameter were not consistently identifiable in the digital images and were not scored.

Coral species richness per unit area, colony density, and colony size were quantified at each reef from 2, haphazardly placed 10 x 1m belt transects. Each coral colony whose center point lay within the transect was identified to species. Maximum diameter along the long and short axis of the colony and colony height were measured to the nearest cm. The coral colonies present showed no evidence of partial mortality or fragmentation; hence, demography measurements accurately reflect total colony size. Species richness and number of individuals were pooled from both transects to provide transect richness and colony density (indiv. m^{-2}) values per reef. In addition, comprehensive coral species checklists were recorded for each focal reef during a 10-min visual search to generate total reef richness.

Colony size serves as a proxy for colony age, assuming that growth environment has remained relatively constant in the ~25 years since establishment. Colony size was calculated as the surface area of the colony using the approximation for a dome shape, as only mounding corals were measured. Colony sizes were standardized to the largest observed individual for a given species among all reefs, $\log_{10}$-transformed to improve normality of the size frequency distributions. Following standardization, colony sizes we then pooled across all species. Mean colony size per reef was then calculated on the standardized, $\log_{10}$- transformed data.

Data analysis

The importance of reef area, isolation, and complexity on the coral community were assessed through regression-based approaches. All coral response variables (richness, density, percent cover, and mean colony size) satisfied assumptions of normality. The presence of a SAR was tested by correlating: (1) untransformed area and total number species, (2) $\log_{10}$-area and the number of species, (3) $\log_{10}$-area and $\log_{10}$-number of species, and (4) area and $\log_{10}$-number of species. The model that yielded the greatest coefficient of determination was deemed the best fit, as suggested by Connor and McCoy (1979). The null hypothesis of random placement (hypothesis 1) was tested by examining whether species per unit area (from pooled transects) remained constant among reefs of increasing area. Target area effects (hypothesis 2), in which larger reefs support greater numbers of individuals per unit area, were tested by comparing colony density across reefs of increasing size. Hypotheses 3 and 4 (habitat diversity and island biogeography) were tested using multiple linear regressions with $\log_{10}$-reef area, nearest neighbor, surrounding reef habitat, and reef complexity as independent factors. All possible models were run. Variance inflation factors (VIF) for the global model were evaluated to ensure that colinearity among the predictor variables was not influencing model outputs (indicated by VIF factors <3.0). Models were then judged for fit from model AIC_c (corrected Akaike Information Criterion), Cp (Mallows' Cp), and R^2 (Burnham & Anderson 2004), as well as whether additional predictor variables significantly improved the model (p-values < 0.05). AIC_c (AIC corrected for finite sample sizes) is recommended when *n* is small and imposes extra penalties for increasing the number of estimated parameters. The preferred model is one with the minimum AIC_c value. Mallows' Cp is another tool for model selection that addresses the issue of overfitting and therefore is used a stopping rule for various forms of stepwise regression. The preferred model is one where Cp = the number of estimated parameters including the intercept.

RESULTS

In accordance with SAR predictions, the number of coral species per reef increased with reef area (Table 4.4). The best fitting model, a power curve plotted on a log-log scale, returned a slope (*z*-value) of 0.17 and intercept of 0.79 ($p < 0.001$, $R^2 = 0.54$). Coral richness per reef averaged 15.1 ± 0.5 (SE) species, with a minimum of 9 species and a maximum of 20. Individual coral colonies were relatively small (mean colony surface area = 133.5 ± 3.1cm^2, SE, among all reefs). Hence, ample space for coral colonization and growth remain, avoiding the ‘neighborhood’ or species-packing effect which can limit species richness due to space-restrictions over small scales (Cornell & Karlson 2000).

Species richness per unit area (from pooled transects) also increased with reef area (Fig. 4.2a; $p < 0.001$, $R^2 = 0.37$). As species richness was not constant among equal areas sub-sampled from reefs of varying total size, the null hypothesis of random placement (hypothesis 1) is rejected as the null mechanism explaining the observed species-area relationship.

Reef size affected the density of coral colonies (hypothesis 2: target area). A positive correlation was found between the number of colonies per unit area and reef size (Fig. 4.2b; $p = 0.002$, $R^2 = 0.28$). This greater colony density, in turn, supported greater coral richness per unit area ($p = 0.002$, $R^2 = 0.28$), rejecting the null hypothesis of no difference in number of individuals per unit area among habitats of varying size (supporting hypothesis 2).

When considering all predictor variables of reef size, isolation, and topographic complexity simultaneously, coral species richness at both the transect-scale and the reef-scale was best explained by a single variable: reef size (Table 4.5). Topographic complexity did not predict the number of species at either scale (rejecting hypothesis 3). Likewise, there was no additive effect of reef size and spatial isolation, measured as either nearest neighbor or amount of surrounding reef habitat, to explain species richness, rejecting predictions of island biogeography (hypothesis 4).

Unlike species richness, coral colony density was significantly predicted by metrics of both reef size and decreasing reef isolation (model adjusted $R^2 = 0.30$; Table 4.5). Including the amount of surrounding reef habitat into the model along with reef area improved the overall model fit (Appendix C). We then distinguished coral species by their reproductive mode, as brooding species release well-developed larvae competent to settle immediately and are thought to have shorter dispersal distances than broadcasting species that release egg and sperm into the water column and require external fertilization prior to settlement (Nishikawa et al. 2003). The colony density of brooding species was explained by reef area and the amount of surrounding reef habitat (multiple linear regression model, $p < 0.001$, $R^2_{adj.} = 0.36$), while no significant model was generated for broadcasting species.

Patterns of coral cover and mean colony size were not significantly related to any of the spatial or environmental metrics measured here (Appendix C).

DISCUSSION

In this study, we capitalized on the unique spatial and structural features of an artificial reef array to experimentally test the influence of reef size, isolation, and complexity on the coral community. The coral assemblages that established on these reefs adhered to species-area relationships (SARs). The coral SAR, fit by a power function, corroborates with observed species-area patterns in Caribbean reef fish investigated on small ($<64m^2$) patch reefs (Chittaro 2002). The slope for the SAR model documented here for corals (z = 0.17) was smaller than that reported by Chittaro (2002) for reef fish and for independent (non-nested) sampling schemes from a range of terrestrial and marine systems (mean z = 0.24; Drakare et al. 2006). Smaller z-values are expected when the geographic ranges of the species are much larger than the spatial extent of the analysis (Rosenzweig 1995). The extent of this study was ~1km, an admittedly small scale compared to natural reef tracts. Hence, we anticipate steeper slopes for coral communities assessed over larger spatial scales (Drakare et al. 2006). Ultimately, documented SARs for corals, where the actual size of the reef habitat is quantified, are exceedingly rare in the literature (Neigel 2003), limiting our ability to meaningfully compare these data to other regions.

Coral species richness increased with reef size at both the transect-scale and the reef-scale, enabling us to reject sampling artifacts as the cause of the observed SAR in favor of biological mechanisms. In accord with the target area hypothesis, larger reefs were not only more species-rich, but also possessed greater colony densities. These greater densities, in turn, supported greater species richness per unit area. Interestingly, this pattern of higher densities of corals on larger artificial reefs contrasts with those of reef fishes from artificial reef in the Florida Keys (Bohnsack et al. 1994), and natural patch reefs in Belize (Acosta & Robertson 2002), where smaller reefs, not larger, supported greater densities of reef fish. A positive correlation between reef size and colony density could results from reduced extinction rates ("area-per-se hypothesis", MacArthur & Wilson 1967). However, given the young age of these reefs and absence of dead coral colonies, we speculate that greater colonization is the more likely process. Greater colonization includes survival and establishment as well as immigration. Teasing apart these dynamic processes will require further investigations that directly measure immigration and survival of coral larvae.

We found no support for the habitat diversity hypothesis (measuring "habitat diversity" for corals as the topographic complexity of the reef substrate) despite the wide range of topographic complexity values encompassed by this study (rugosity index range = 0.02 -0.45; mean = 0.28 ± 0.02 SE). Corals contribute dramatically to the structural complexity of the reef framework, forming the habitat upon which many reef inhabitants depend. Yet, from our results, these ecosystem engineers (organisms that create, maintain, or destroy habitat for other species) appear to not require high complexity substrates to support a diverse and abundant coral community. Again, corals are showing opposite patterns to reef fishes, who repeatedly exhibit greater diversity among higher complexity reefs (Risk 1972; Gladfelter et al. 1980; Gratwicke & Speight 2005). The contribution of habitat diversity may become more important across larger scales or among older reefs given that community dynamics during early succession are often dispersal-dominated due to the high availability of free-space (Palmer & White 1994).

Colony density adhered to predictions of island biogeography theory, however, not all coral species responded similarly. Greater density of short-dispersing, brooding colonies were observed as reef isolation decreased, yet broadcasting species were unaffected. Recruitment of brooding corals is known to be enhanced by substrate availability and presence of adult conspecifics at local spatial scales (<1m^2; Vermeij

2005), but this the first study to demonstrate the local density of brooding corals is sensitive to spatial configuration of reef habitat at much larger spatial scales (100s of m). In terrestrial systems, species with shorter dispersal distances are thought to contribute to nested distributions across patchy landscapes reflecting greater local recruitment (Kadmon 1995). Our findings suggest that this pattern also holds at meso-scales (<1km) for brooding corals where greater amounts of nearby reef habitat can lead to greater densities of brooding species reflecting greater local recruitment.

Our best-fitting models explained slightly more than half of the observed coral richness, indicating that other factors not measured here influence coral diversity. Rather, we selected reef size, isolation, and complexity based on theoretical mechanisms that underlie species-area patterns. Capitalizing on the unique attributes of the artificial reef array, we were able to control for successional differences and substrate types that confound coral richness (Brock et al. 2008). However, we were constrained by the extent of the array such that the range of reef sizes and isolation are limited. Still, significant differences in these metrics were detected among the patches in the array and created a foundation for isolating the effects of each of these factors on the coral community. Hence, this artificial reef array remains a unique and useful system from which to address the mechanistic drivers of coral diversity.

Contrasting with species-area predictions, several marine studies found smaller habitat attracting more immigrants, supporting higher survival rates, and having greater diversity than larger patches (Eggleston et al. 1998; Hovel & Lipcius 2001; Acosta & Robertson 2002). Corals, however, appear to adhere to the species-area relationship such that reefs of larger area are more diverse. Identifying these patterns across space is a major first step in indentifying the causal processes driving these distributions. Our results support both target area and island biogeography hypotheses as key drivers influencing the diversity and abundance of corals, and reveal that differences in dispersal mode lead to differences in how the spatial configuration influences coral diversity.

Caribbean reefs continue to decline resulting in alterations to the complexity, position, and extent of reef habitat available (Hughes et al. 2003; Pandolfi et al. 2005; Alvarez-Filip et al. 2009). Understanding how these attributes of reef configuration and complexity influence coral assemblages will help us predict coral responses to future change. As the first study investigating these spatial and habitat influences in corals, the patch-scale is a logical starting point. We conclude that habitat fragmentation, resulting in smaller, more isolated reefs can be a driver of coral community structures that is presently not being considered in tropical reef systems. Further exploring these spatial drivers across increasing scales will aid our understanding of how future changes to reef configuration and composition will alter the diversity of these ecosystems.

Table 4.1 Hypothesized processes that can generate a relationship between species and area. Mechanism, hypothesis, and tests of reef area, isolation, and structural complexity on the coral community response variables.

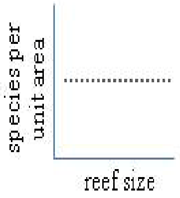
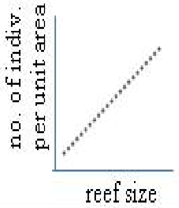
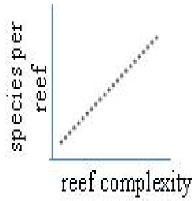
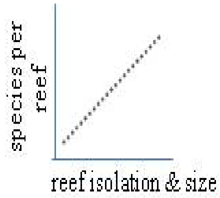
Model and hypothesis	Null hypothesis	Expected relationship
(1) Random placement: as area sampled increases, numbers of individuals increases and consequently species sampled		
H_1: Samples of equal area, taken from reefs of different overall areas, yield the same number of species	H_o: Samples of equal area vary in species richness	
(2) Target area: larger habitats support greater number of individuals per unit area due to greater immigration rates		
H_2: Positive relationship between number of individuals per unit area and reef size	H_o: No relationship between number of individuals per unit area and reef size	
(3) Habitat diversity: habitats of greater structural complexity have greater coral richness		
H_3: Positive relationship between reef richness and complexity	H_o: No relationship between richness and complexity	
(4) Island biogeography: larger and less isolated habitats support greater richness and numbers of individuals		
H_4: Greater in richness and colony density on reef of larger area and less isolation	H_o: No difference in richness and density among reefs of different size and isolation	

Table 4.2 Seascape parameters for patch reefs. Rugosity index = linear length (m) /chain length (m) such that a flat reef receives a score of 1. Surrounding reef habitat (a metric of area-based isolation) is calculated using a circular buffer of designated radius (m) around a focal patch reef.

Patch #	Area	Rugosity index	Rugosity score	Nearest neighbor (m)	Surrounding reef habitat (m^2) - 200m	Surrounding reef habitat (m^2) - 100m	Surrounding reef habitat (m^2) - 50m
23	31	0.24	0	15.2	2692	818	252
28	35	0.02	0	16.1	5295	3255	931
27	41	0.03	0	10.8	5553	2954	1077
29	45	0.08	0	10.8	5817	2392	1096
18	66	0.21	1	19.9	3453	1747	769
13	73	0.22	1	29.1	2964	2281	1189
17	76	0.39	1	17.5	3453	1724	757
15	87	0.39	1	13.2	2012	1536	1103
19	89	0.28	2	8.1	2440	1536	872
30	101	0.2	1	36.5	5501	2765	1471
26	110	0.06	0	16.9	4251	3535	1479
31	112	0.21	1	17.5	5501	3379	1866
20	128	0.35	3	13.4	3490	2202	686
22	138	0.31	2	9.8	2518	1536	733
24	180	0.31	1	10.2	2318	1536	933
25	190	0.18	1	22.9	5335	2435	1160
14	267	0.45	3	60.5	2564	1490	267
4	312	0.37	2	20.2	3665	3665	2041
3	335	0.34	3	31.8	3665	2007	1020
2	343	0.27	2	48.6	2574	1924	609
11	349	0.37	3	37.3	2564	2231	888
9	359	0.33	2	35.3	4252	3127	1158
5	367	0.29	2	17.4	3675	3195	1128
6	373	0.3	2	33.5	3665	3314	1768
8	380	0.33	2	49.4	3453	1288	525
16	381	0.35	2	41.9	4583	1225	572
21	381	0.3	2	28.1	2466	1536	1304
12	396	0.45	3	57.3	2564	1983	796
10	453	0.34	3	14.7	3886	2103	484
7	480	0.33	2	24.9	4755	2958	1282
1	608	0.33	2	37	2262	2254	1126

Table 4.3 Pearson's correlation coefficient among all seascape parameters.

	Log(area)	Rugosity index	Rugosity score	Nearest neighbor (m)	Surrounding reef habitat (m^2) - 200m	Surrounding reef habitat (m^2) - 100m	Surrounding reef habitat (m^2) - 50m
Log(area)	1.000						
Rugosity index	0.643*	1.000					
Rugosity score	0.786*	0.802*	1.000				
Nearest neighbor	0.575*	0.459*	0.509*	1.000			
SRH-200m	-0.280	-0.642	-0.442	-0.205	1.000		
SRH-100m	0.041	-0.416	-0.184	-0.159	0.582*	1.000	
SRH-50m	0.073	-0.257	-0.209	-0.207	0.364*	0.775*	1.000

*statistically significant correlations ($r_{crit\ (0.01,\ d.f.\ =29)} \geq |0.456|$)

Table 4.4 Summary of linear regression models of species-area relationships (n=31). All regressions were significant at $P < 0.001$. A: reef area; Sp: species richness.

	A-Sp	Log(A)-Sp	Log(A)-Log(Sp)	A-(Log)Sp
R^2	0.39	0.53	0.54	0.40

Table 4.5 Final model results relating coral community variables to spatial and environmental metrics.

Coral variable	Model	Estimate	SE	p	R_a^2	AICc	Cp
Transect richness				<0.001	0.36	125.04	1.39
	intercept	4.07	1.84	0.035	0.36	125.04	1.39
	RA	3.4	0.81	<0.001			
Reef richness				<0.001	0.52	134.67	2.21
	intercept	3.08	2.13	0.16			
	RA	5.39	0.94	<0.001			
Colony density				0.003	0.3	173.15	1.31
	intercept	-2.67	4.23	5.34			
	RA	5.1	1.7	0.006			
	SRH	0.002	0.001	0.027			
Brooders density				<0.001	0.36	160.72	1.18
	intercept	-4.71	3.46	0.18			
	RA	5.13	1.39	0.001			
	SRH	0.001	<0.001	0.04			
Broadcaster density	No solution						
Colony size	No solution						
Coral cover	No solution						

RA, $\log_{10}$–reef area (m^2); SRH, surrounding reef habitat (m^2)

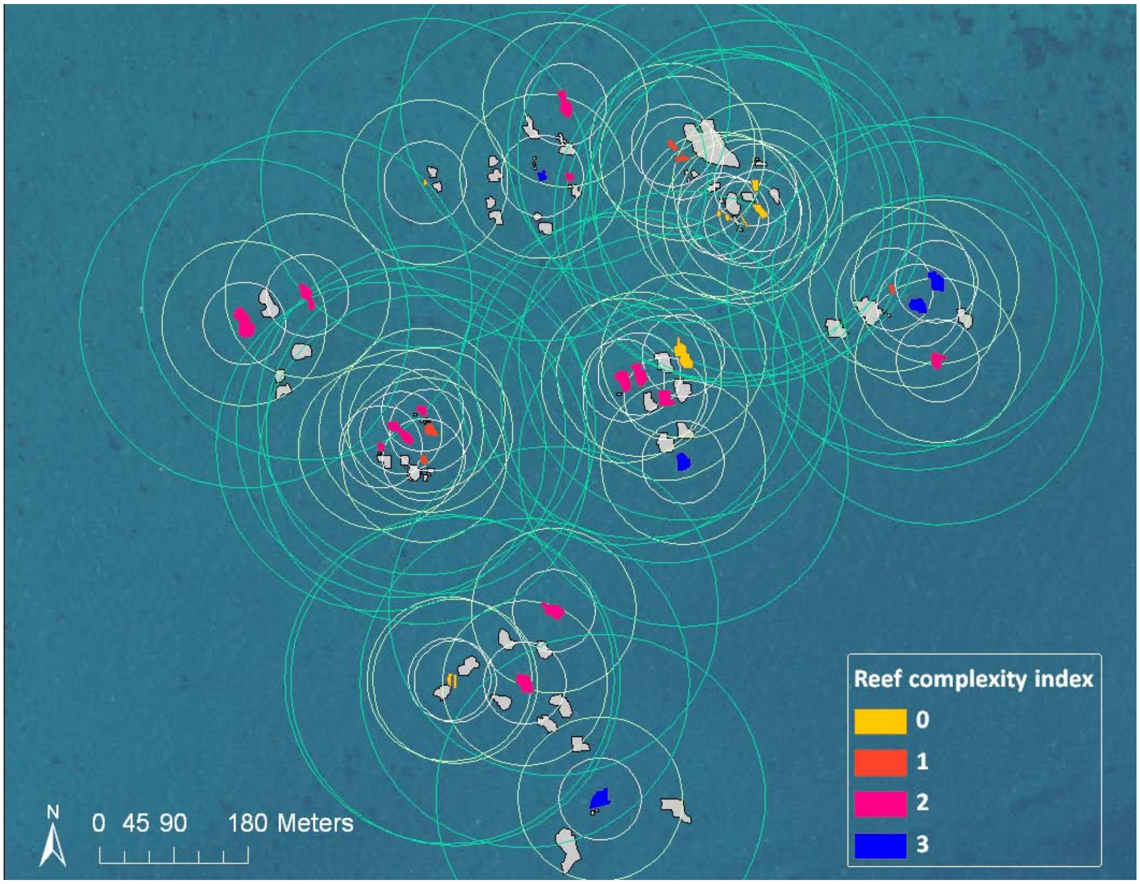


Fig. 4.1 Habitat map constructed from satellite imagery of the artificial reef array. Reef boundaries are demarcated by polygons. Colors indicate benthic complexity index values. Grey polygons were not sampled. Concentric rings demarcate the 50m, 100m, and 200m radii buffers around each focal reef used to calculate surrounding reef habitat.

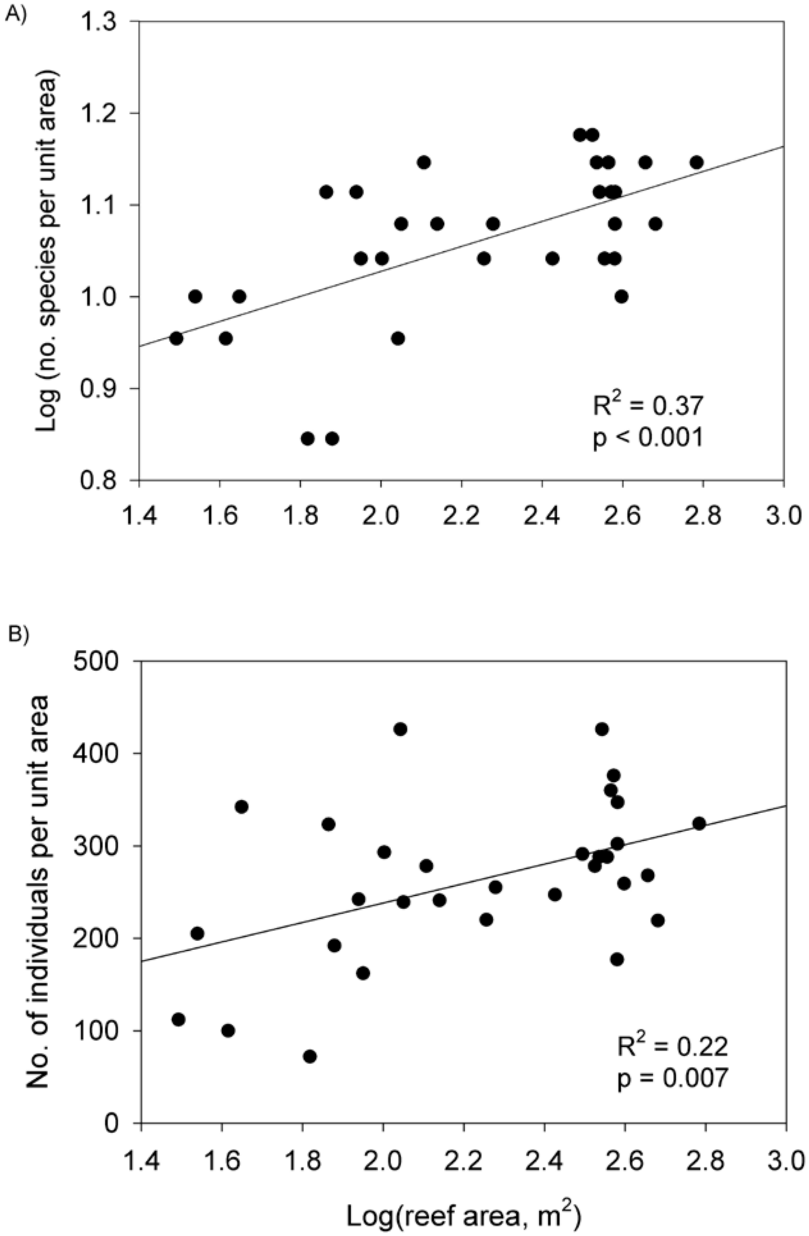


Fig. 4.2 Relationship between A) the number of species per unit area and reef area and B) the number of individuals per unit area and reef area. Linear regression lines and their significance are shown. Note log scale used for reef area and y axis for top panel.

CHAPTER 5: Untangling natural seascape variation from marine reserve effects using landscape approach.

BACKGROUND

No-take marine reserves have been increasingly promoted as a management tool to conserve biodiversity and prevent over-exploitation of marine communities (Halpern 2003; Lubchenco et al. 2003). Assessing whether reserves meet these objectives relies upon sampling designs that can evaluate management impacts on the communities targeted by reserve designation while controlling for the confounding spatial and temporal effects that could influence the assessment (García Charton et al. 2000). Yet, the most commonly used analyses for reserve assessment leave results open to interpretation, stressing the need for improved designs to document reserve effects (García Charton et al. 2000; Willis et al. 2003). Existing reserve assessments have been consistently criticized for a myriad of insufficiencies, including limited sample replication (Halpern 2003), non-random reserve placement (Russ 2002), and inadequate controls for temporal and spatial variability in the systems being protected (Osenberg et al. 2006; Pande & Gardner 2009). The Before-After-Control-Impact (BACI) assessment and its relatives (e.g., BACIPS, Beyond BACI) were developed in response to these criticisms as sampling designs capable of controlling for natural temporal changes [8, 9]. However, all BACI approaches rely on 'Before' data collected at the reserve inception; data that are not available for the vast majority of marine reserves (Halpern 2003).

Given the paucity of baseline data, Control-Impact (CI) comparisons are the most commonly used marine reserve assessment methodology, in which control sites outside of the reserve are compared to impact sites within (Micheli et al. 2004). CI comparisons putatively attribute observed differences to a reserve effect; however, this methodology cannot distinguish between management effects and intrinsic seascape heterogeneity between control and impact sites (García Charton et al. 2000; Osenberg et al. 2006). Even in well-replicated studies with high numbers of control sites, separating the effects of spatial seascape variation from those of protection can be difficult given that a procedural framework is lacking for selecting appropriate control sites within a heterogeneous seascape (Fraschetti et al. 2002). To date, no sampling designs have explicitly quantified and controlled for seascape heterogeneity, defined as habitat configuration and composition, when conducting CI assessments. In a literature review of 68 studies assessing the prevalence of BACI and CI approaches from 2004-2009, only 10 studies (15%) employed a BACI approach. The remaining studies relied on CI assessments. Of these, only 4 (7%) quantified any spatial metric pertaining to seascape measures of habitat configuration or composition when selecting control sites for reserve evaluation.

In both terrestrial and aquatic systems, the response of organisms to heterogeneity in a landscape varies across spatial scales (Turner et al. 2001; Cushman & McGarigal 2004; Tews et al. 2004). Coral reef habitats are no exception. Reef systems are heterogeneous, composed of patches that vary in size, shape and spatial arrangement across the seascape. This spatial context of a patch of reef habitat within the surrounding seascape can exert a strong influence on abundance and distributions of reef-associated organisms, including reef fishes that are commonly targeted for reserve protection (Ault & Johnson 1998b; Mumby et al. 2004; Grober-Dunsmore et al. 2007). Hence, marine reserves that span heterogeneous seascapes should take into account this variability when assessing the efficacy of marine reserves to protect reef fish and other marine organisms.

In comparison to the numerous terrestrial-based landscape studies, a landscape ecology approach in marine systems is still in its infancy (Mellin et al. 2009). Advances in remote sensing and mapping technology have recently enabled marine scientists to quantify submersed seascapes and apply terrestrial landscape metrics to investigate ecological patterns and relationships on spatial scales relevant to marine organisms (Pittman et al. 2004; Bell et al. 2006; Friedlander et al. 2007). We continue in that vein by applying a multi-scale landscape approach to distinguish between the effects of natural seascape variation and management actions when assessing the impacts of marine reserve designation. This approach is centered on determining the importance of specific seascape configuration and composition metrics on communities targeted for reserve protection. For this investigation, two target communities, reef fish and corals, were identified in our study site of Glover's Reef Marine Reserve, Belize. We examined reserve efficacy to increase biodiversity and biomass of fishes, as well as enhance diversity and cover of the coral community through cascading effects that reduce macroalgal cover, a major coral competitor (Mumby et al. 2007a). We describe steps to: (1) quantify seascape spatial heterogeneity of patch reef sites; (2) identify key spatial, compositional, and structural seascape characteristics of patch reefs that correlate to observed variability in both reef fish and coral communities; (3) classify patch reef sites into groups sharing similar seascape attributes; and (4) evaluate reserve efficacy with and without site groupings to compare our ability to discern reserve effects when controlling for seascape variability.

METHODS

Study Area

Glover's Reef Atoll (87 ° 48' W, 16 ° 50' N) is located 30km offshore of Belize, Central America, and comprises an area of 560km^2 (Fig. 5.1A). The atoll perimeter consists of emergent crest reef interrupted by three channel passes. The interior lagoon slopes gently to a depth of 6-18m and is dotted with approximately 850 patch reefs varying in size from 20m^2 to 10,000m^2. These patches are primarily elliptical in shape and rise from the lagoon floor to within 0-3m of the surface. A no-take marine reserve, enforced by wardens since 1998, is located in the southern section of the atoll.

Patch reefs served as the focal habitat for this analysis. Several features of the patch-reef array at Glover's Atoll make this reserve an ideal model system to test the applicability of landscape ecology approach to marine reserve evaluation. First, patch-reef complexes are pervasive, often containing hundreds of individual patches enabling ample replication within the reef system. Second, the discrete boundaries of patch reefs, often surrounded by sand or seagrass, enables spatial metrics of patch composition and configuration to be readily quantified through remote sensing and spatial analyses. Third, due to the geographic isolation and deep waters (>400m) surrounding the atoll (Wallace 1975), the confounding influence of fish immigration and emigration to and from the atoll are likely limited (Kramer & Chapman 1999; Starr et al. 2007). Fourth, the size of the atoll limits the maximum distance between reserve and control sites to less than 10km, suggesting that dispersal ranges of our sampled populations are not limiting (Almany et al. 2009).

Sampling fish and corals

We assessed the fish and benthic communities at 87 submerged patch reefs in 2008-09 using a spatially explicit stratified random sampling design in which the entire lagoon area was divided into 23, equally sized blocks. A random point generator in ArcGIS was used to select a minimum of 3 patch reef sites within each block. A total of 56 non-reserve sites and 31 reserve sites were sampled in three field efforts: May 2008, February 2009 and April 2009. To investigate possible temporal changes over the 10-month sampling period, fish and coral surveys were repeated at 15 randomly selected patches from the total 87. No significant differences in coral cover, coral diversity, fish abundance or fish diversity were detected in this subset from 2008 sampling to 2009, and we therefore pooled the two years of data. Fish abundances were determined using the stationary point-survey method (Bohnsack & Bannerot 1986) for all observed fishes over 5cm within a 5m-diameter cylinder. A total of 5 surveys, positioned at the 3m depth contour on N, E, S and W patch edges and patch center, were completed for each patch reef surveyed using SCUBA. Species, number of individuals, and length were estimated for all observed fish. Fish-length estimates (fork length, cm) were calibrated before each sampling period by estimating lengths of fish-shaped objects until estimates were within 10% of true lengths. Fish lengths were converted to biomass for each cylinder using allometric coefficients from Bohnsack and Harper (Bohnsack & Harper 1988) and were averaged per patch. Fish communities were summarized at each patch reef with the following metrics: (1) species richness, defined as the total number of fish species observed within the 5 cylinders per patch reef; (2) total fish biomass, defined as the sum biomass of all species averaged across the 5 cylinders, and (3) commercial fish biomass, defined as sum biomass of all species observed in the fishery catches (Table 5.1) averaged across the 5 cylinders.

The benthic composition of each patch reef was determined through the use of digital photography. Photographs of the benthos encompassing a reef area of approximately 0.25m^2 were taken every 2m from 0.5m above the substrate along transects running the long and short reef axes. Depending on the total patch size, 25-100 images were generated per patch. Images were analyzed to species for scleractinian corals (>2cm min. diameter), to functional group for benthic biota or to substrate class for non-biotic substrates. Using point-intercept methods, 100 random points were scored per image, on 20 randomly selected images per patch using CPCe v3.5 software (Kohler & Gill 2006). From this analysis, we calculated an average per patch for (1) coral cover and (2) coral : macroalgal ratio (not including turfs or crustose coralline algae). The species richness of stony corals per patch was determined by noting species presence/absence during a 10-minute search interval.

Quantifying seascape heterogeneity

A comprehensive approach to quantifying spatial heterogeneity in the seascape combined remote sensing, image analysis and *in situ* classifications across multiple spatial scales. Seascape metrics were selected based on previous studies linking specific features of seascape and habitat variability to fish and/or coral community structure (Ault & Johnson 1998b; Overholtzer-McLeod 2006; Grober-Dunsmore et al. 2009; Table 5.2). Metrics were assessed at increasing hierarchical spatial scales when possible to explore the most appropriate spatial extent to our diverse target communities (Pittman et al.

2004). Metrics of patch composition included measures of area and volume to account for the 3-dimensional nature of the aquatic environment (Balasubramanian & Foster 2007). Patch area, perimeter, and edge: area ratio were calculated using Hawth's Analysis Tools for ArcGIS (freely available from www.spatialecology.com/htools) on polygons drawn around the patch boundaries using multi-band, high-resolution (4 x 4m ground resolution) IKONOS imagery. An adjusted patch area was also calculated using the percentage of sand and seagrass to account for differences in hard substrate on each patch. Patch volumes were obtained from bathymetric maps generated in ENVI v4.7 based on depth and GPS data collected throughout the atoll at 183 points (Fig. 5.1B).

To generate metrics of the spatial distribution of patch reefs across seascape, a benthic habitat map of the lagoon was made using a supervised spectral classification in ERDAS Image Analysis™ for ArcGIS v9.2 (Fig. 5.1C). Classes delineating patch-reef habitats were merged into a single layer and compared for accuracy to hand-drawn polygons for each patch. Landscape metrics quantifying the amount of surrounding reef habitat (m^2) around a focal reefs were calculated using 200m, 500m, and 1km buffers around each reef to explore appropriate spatial extent for fish and coral communities (Fig. 5.1D). Nearest neighbor distances were determined by creating a center point within each patch reef polygon and calculating the minimum distance between points. Distance-to-habitat features, including mangrove habitats and the two large channel openings were quantified as potential landscape metrics influencing fish community.

Topographic complexity of each patch reef was assessed a three different resolution scales. At the reef scale, an *in situ* score of topographic complexity was determined based on a ordinal scaling in which 0 indicated no vertical relief, while reefs with exceptionally high complexity were given a rating of 3 (Wilson et al. 2007). Coarse-scale topographic complexity was estimated by calculating the maximum patch length and width in ArcMap and assessing the change in depth between consecutive 4 x 4m grid cells from the bathymetric maps over the entire length of both diameters. Fine-scale topographic complexity measures were taken *in situ* along 5 haphazardly-placed, 10m transects using a 2cm-link chain closely draped over the benthic contours (Risk, 1979).

Statistical analysis

To investigate which seascape metrics explained the greatest amount of variation in fish and coral community parameters, canonical correspondence analysis (CCA) was used. In CCA, regression analysis is used to find the best possible relationship between multiple environmental variables and multivariate community response data, assuming key environmental variables have been measured and the community response is unimodal in relation to these variables. Multicollinearity between seascape metrics was explored through correlation matrices. When evident ($r > 0.2$), a principle component analysis was conducted on the co-linear metrics and the first principal component was used in subsequent analyses as an independent explanatory variable (Graham 2003). Separate CCAs were conducted to describe the relationships among seascape metrics and (1) fish composition (i.e., fish species richness, total biomass, and commercial biomass as defined above), and (2) coral composition (i.e., coral species richness, % cover, and coral : macroalgal ratio). Seascape metrics and community response parameters were log10-transformed (or arcsine square-root transformed for % cover data) as needed before analyses to normalize data and ensure homogeneity of variance. Akaike’s information criterion was used to select the simplest multivariate regression model that explained the maximum amount of variation for each community (McCune & Grace 2002; Burnham & Anderson 2004). Significance of the selected model was tested using Monte Carlo Permutation tests.

Separate hierarchical clustering analyses were preformed for coral and fish to classify patches together into 'seascape groups' sharing similar attributes of the significant seascape metrics identified for fish and for corals in the CCAs. Reserve effects were then evaluated using a modified Control-Impact design, in which reserve effects were only tested among patch reefs sharing the same seascape grouping for fish and corals, respectively. Comparisons of the fish assemblage (e.g. species richness, biomass, and commercially-valued biomass) and coral assemblage (e.g. richness, cover, and coral : macroalgal ratio) between management zones were conducted using one-way analysis of variance (ANOVA). We then repeated our analyses for each response variable using a traditional Control-Impact methodology with all 87 patch reef sites. Reserve effects were then compared between the two Control-Impact assessments.

Following detection of reserve effects, additional analyses were conducted to determine which organisms were influenced by reserve protection. Community similarity within coral and fish communities with respect to reserve protection and patch type were calculated in multidimensional space using a two-way crossed analysis of similarity (ANOSIM). Community similarity matrices were calculated using a Bray-Curtis index on 4th root-transformed abundance data in order to reduce the contribution of common species (Clarke & Warwick 2001). To determine if specific functional groups or trophic levels were more responsive to reserve protection than others, the fish community was classified by target/non-target species, diet, and trophic level. Analyses between reserve effects and fish class or species were then conducted within a given patch reef grouping to identify which organisms were responding to both seascape heterogeneity and reserve protection.

RESULTS

Identifying key seascape metrics

Three seascape-level metrics of spatial configuration were identified in CCAs as explaining the greatest amount of variation in the fish community: distance from channel, patch reef area within a 500m buffer, and nearest neighbor distance (Table 5.3). Using these seascape configuration metrics, patch reefs were clustered into two groups (hereafter called Fish Type I and Fish Type II for simplicity), which was sufficient to generate significant differences between groups for each seascape metric (Fig. 5.2A; ANOVA; $P < 0.05$) and enabled maximum sample sizes within a group for subsequent analyses of reserve effects. Type I patches are located further from channels, surrounded by less patch reef habitat within a 500m buffer, and are more isolated. Type II patches are closer to the channels, have more surrounding patch reef habitat within 500m, and are less isolated.

CCA was used to identify 3 seascape level metrics that explained the greatest amount of variation in the coral community: distance from channel, ‘patch size’, and structural complexity of the patch (Table 5.3). ‘Patch size’ was generated using a PCA on 6 multicollinear metrics pertaining to the patch area and using first principal component as a seascape metric (PC1 = 98.4% of total variance; Table 5.2). Using these three metrics, patch reefs were clustered into two groups (Coral Type I and Coral Type II). Type I patches are further from the channels, larger, and consist of a dome-shaped morphology. Type II patch reefs are closer to the channels, smaller, and have a complex morphology. As was the case for the Fish patches, Coral Type I and Type II patches show significant differences in all three seascape metrics between groups (Fig. 5.2B; ANOVA; $p < 0.05$).

Evaluating reserve effects

We assessed differences in fish species richness, total biomass, and commercially important biomass inside and outside of reserve using two different site grouping approaches. No significant reserve effects were detected for any fish community response variable when seascape differences among patch-reef sites were disregarded (Table 5.4). However, grouping sites based on key seascape metrics identified using multivariate ordination models made it possible to detect significant reserve effects (Fig. 5.3 and Table 5.4). Commercial fish biomass was approximately 75% greater inside the reserve than outside for Type II patches (one-way ANOVA, $F_{1,43} = 8.05$, $p = 0.007$). A similar significant increase of 50% was seen in total fish biomass from outside the reserve to inside ($F_{1,43} = 7.479$, $p = 0.009$). There was no difference in fish species richness inside versus outside reserve for either site grouping approach (Table 5.5).

As with the fish community, no significant differences between reserve and non-reserve sites were detected in coral community parameters when all patch reef sites were pooled (Table 5.4; Table 5.5). However, grouping sites that shared similar attributes of relevant seascape metrics to the coral community revealed significant reserve effects in all three community parameters (Fig. 5.3). Coral Type II patch reefs responded positively to reserve protection, with greater coral cover and coral : macroalgal ratios for reserve sites compared to fished sites. Coral cover in Type II patches was 68% higher inside versus outside the reserve ($F_{1,27} = 8.24$, $p = 0.008$). Similarly, coral : macroalgal ratio was 80% larger for Type II sites within the reserve versus outside ($F_{1,27} = 14.22$, $p < 0.001$).

Yet, reserve effects were not uniform across or within site grouping for either the fish or coral communities (Table 5.4). Results for Coral Type I patches showed negative reserve responses for 2 of the 3 response variables. For this patch group, coral cover and coral : macroalgal ratio was lower inside the reserve (coral cover: one-way ANOVA, $F_{1,56} = 9.037$, $p = 0.004$; coral : macroalgal: one-way ANOVA, $F_{1,56} = 5.362$, $p = 0.024$). Similarly, Fish Type II patches showed positive responses, while Type I patches showed no differences between reserve and non-reserve sites (Table 5.4). Coral Type II reefs, despite responding positively in coral cover and coral : macroalgal ratio to reserve protection, did show a small but significant decline in mean coral species richness from 17.4 (± 0.61) species outside the reserve to 14.9 (± 0.84) species inside the reserve (Fig. 5.3).

Analysis of similarity (ANOSIM) results revealed that coral communities were statistically indistinguishable between both Type I and Type II patches and across the reserve boundary ($p > 0.05$). ANOSIM of the fish community revealed significant differences by patch type and reserve protection, but only Type II reefs showed marginal separation of community composition across the reserve boundary ($p = 0.001$, global $R = 0.35$). Non-commercial fish species showed no significant response to reserve protection within either Type I or Type II patch reefs (one-way ANOVA, $p > 0.05$), suggesting that the positive reserve effect detected among Type II patch reef was driven by commercially important fish species sensitive to seascape heterogeneity and reserve management. Further investigation of the differences in commercial fish species composition on Type II patches showed no significant difference across the reserve boundary based on fish diet or trophic level (one-way ANOVA, $p > 0.05$). Species-specific responses within Type II patches revealed significantly greater biomass within the reserve for 3 species; two snappers (*Lutjanus griseus* and *L. synagris*) and the hogfish (*Lachnolaimus maximus*; Figure 4.4; one-way ANOVA, $p < 0.05$). In contrast, Type I patches revealed significant reserve responses for the grey angelfish (*Pomacanthus arcuatus*) and the grey snapper (*Lutjanus griseus*); *L. griseus* was more abundant outside the reserve boundary while *P. arcuatus* was more abundant within the reserve on Type I patches (Figure 4.4; one-way ANOVA, $p < 0.05$).

DISCUSSION

Coral reef ecosystems are complex, three-dimensional seascapes that exhibit multi-scaled structural heterogeneity. We hypothesized that this seascape heterogeneity would confound our ability to detect reserve effects using existing Control-Impact assessment strategies. This was found to be the case at Glover’s Atoll Marine Reserve, Belize, where we have shown that it is possible to detect significant differences between reserve and non-reserve sites by separating out key aspects of the spatial variability in the system. Our findings agree with those from terrestrial (Cushman & McGarigal 2004; Davis et al. 2007) and marine (Pittman et al. 2004; Grober-Dunsmore et al. 2008) investigations, in which specific landscape features, quantified over spatial scales exceeding the local scale, were associated with particular group of organisms.

It is not surprising to report that reserve effects vary across the seascape. What is surprising is that current methods for assessing reserve impacts, in the absence of baseline data, do not account for this variability. The composition and placement of individual patch reefs within the seascape has been shown to exert a strong influence on the assemblage structure of reef fishes (Ault & Johnson 1998b; Acosta & Robertson 2002; Grober-Dunsmore et al. 2008). We are not aware of any studies investigating the response of coral assemblages to landscape-scale metrics prior to our investigation, but it is reasonable to presume that corals would also be responsive to seascape-level heterogeneity. Therefore, to accurately assess the efficacy of marine reserves targeting organisms such as fish and coral communities, a methodology that integrates habitat variability at the appropriate ecological scales is necessary (Friedlander et al. 2007). Our approach sets forth a new protocol for controlling for seascape differences that can be both readily assessed and used to pair reserve site to appropriate control sites for Control-Impact assessment.

Our results corroborate those of Friedlander et al. (Friedlander et al. 2007) who concluded that habitat type was an important predictor of the effectiveness of marine reserves in Hawaii. Similarly, Harborne et al. (2008) found that robust reserve effects for a Caribbean coral reef reserve were restricted to a specific habitat type, presumably in response to fish habitat preferences. A recent study by Hamilton et al. (2010) acknowledged the role of seascape variability at large spatial scales over which marine networks may operate. Similarly to our goals for this study, they grouped reserve and control sites into biogeographic zones based on differences in fish community assemblages across the marine network driven by large-scale abiotic gradients. While both Harborne et al. (2008) and Hamilton et al. (2010) demonstrate the ability of inter-habitat variability to influence the spatial distribution of organisms and thereby potentially confound reserve evaluation, ours is the first study to evaluate the potential of intra-habitat variability, within a single habitat ‘type’ of coral reef, to influence organism distributions and mask reserve effects. This suggests that seascape heterogeneity can be subtle but still informative to guide the selection of appropriate reference sites when estimating reserve effects. Conducting this analysis within the single reef type of shallow-water patch reefs does prevent extrapolating the specific seascape metrics and reserve responses detected in this case study to other reef systems. However, the landscape approach used to identify these seascape metrics and control for them during reserve assessment can be readily applied in a diverse array of marine habitats.

Inferring ecological processes of community assembly based on landscape-scale patterns is not the objective of the approach we have presented in this study. The seascape variables identified for the patch reef grouping in our Glover’s Reef case study are not necessarily drivers for the variations observed in the coral and fish communities. Rather seascape metrics, like all metrics of spatial heterogeneity in a landscape framework, serve directly as a means to quantifying variability across the system and indirectly as a proxy for underlying ecological processes (Turner et al. 2001). Further analyses can offer a step forward to understanding the mechanistic processes regulating the community composition in this shallow lagoon system. Our analyses suggest that commercial fish species, rather than a particular functional group or trophic level, are driving the positive effects of reserve protection detected on Type II patches. Of these, 3 species, hogfish (*Lachnolaimus maximus*), grey snapper (*Lutjanus griseus*) and lane snapper (*Lutjanus synagris*) appear to drive not only a positive response to reserve protection, but also a response that is sensitive to seascape heterogeneity. While these species showed strong reserve responses (biomass within reserve > biomass outside reserve), this response varied according to patch type.

Fish and coral assemblages showed different relationships to seascape metrics operating at varying spatial scales, suggesting an organismal perspective is important. Habitat area and morphology at the patch-scale were a significant factor explaining the observed variation in the diversity and abundance for corals. In contrast, meso-scale (100s-1000s of m) factors of nearest neighbor and reef area within a 500m buffer were significant factors explaining composition of fishes. Interestingly, topographic complexity of the patch reefs (i.e. rugosity) at the fine or medium grain scale was not found to be an important predictor for fish or coral assemblage parameters. This suggests that when patterns of community composition are assessed and constrained to a single, topographically complex habitat type, landscape level parameters may be better predictors of marine assemblage structure.

For the large number of marine reserves lacking baseline data, augmenting the traditional Control-Impact reserve assessment with the seascape approach can improve reserve evaluation by controlling for influential aspects of seascape variability that affect target populations. While applied here to shallow water patch reef environments, this approach is repeatable in other marine systems given the increased access to high-resolution benthic habitat maps and GIS technology (Bell et al. 2006). Coupling existing habitat maps and free-source satellite imagery with simple image analysis techniques can prove a viable means to creating inexpensive seascape metrics for a diverse array of marine reserve habitats. Additionally, this method can be applied *ex post facto* to existing reserve assessment data to generate seascape metrics that be used to ensure that appropriate control sites are compared to impact sites to determine reserve efficacy. Lastly, this approach can be tailored to specific organisms targeted by reserve mandates, providing a more exact analysis of reserve effects to the species in question. In summary, this landscape approach provides a cost-effective, improved assessment of management efforts and ultimately, improved conservation for a variety of marine ecosystems.

We stress the need to control for spatial heterogeneity in the evaluation of marine reserves, but application of these landscape ecology principles may improve criteria for reserve placement and design (Fraschetti et al. 2002; Friedlander et al. 2007). Reserve effects at Glover's Atoll were not uniform across groups of patch reefs; positive reserve effects were detected in some patch reefs types and negative (or neutral) effects in others. These differential reserve responses correlated with variations in seascape heterogeneity, indicating that reserve placement would benefit from a more nuanced classification of marine habitat types across the seascape. For example, greater meso-scale connectivity between patches, measured as reef area within a specified buffer and nearest neighbor distance, was important to supporting more diverse and abundant fish community parameters in this shallow patch reef system. Hence, reserve expansion at Glover's Atoll should target patch reefs arrays that share these spatial configuration attributes, if the management goal is to increase fish diversity and biomass. We see the future of marine reserve design guided by spatial explicit management schemes that incorporate structure, connectivity, and reef context to ensure that protected habitats respond favorably to reserve management.

The establishment of marine reserves as a conservation tool has increased rapidly over the past decade. Yet the absence of baseline data, even within relatively well-replicated studies, makes it challenging to separate management effects from natural variability in populations driven by seascape differences. A weak assessment design that fails to capture reserve effects when they are present can generate false conclusions about reserve efficacy, seriously crippling management efforts to expand the use of marine reserves as a conservation tool. The burden of proof rests on managers and scientists to clarify how marine reserves can function as viable strategies for conservation and population replenishment. Therefore, we need a better understanding of the effects of reserves, which can be positive, negative, or mixed. The use of a robust assessment methodology should be implemented to ensure that, when present, positive or negative effects can be properly ascertained. We suggest that the seascape approach applied in this study is one such method, and will serve as a powerful tool to improve our ability to distinguish management effects from natural system variation in future assessments of reserve efficacy.

Table 5.1 Commercially important fish species observed during sampling for Glover's Atoll.

Scientific name	Common Name
Balistes vetula	Queen triggerfish
Calamus calamus	Saucereye porgy
Canthidermis sufflamen	Ocean triggerfish
Caranx ruber	Bar jack
Cephalopholis fulva	Coney
Epinephelus cruentatus	Graysby
Epinephelus guttatus	Red hind
Epinephelus morio	Red grouper
Epinephelus striatus	Nassau grouper
Gerres cinereus	Yellowfin mojarra
Holacanthus ciliaris	Queen angelfish
Lachnolaimus maximus	Hogfish
Lutjanus analis	Mutton snapper
Lutjanus apodus	Schoolmaster snapper
Lutjanus griseus	Gray snapper
Lutjanus mahagoni	Mahogany snapper
Lutjanus synagris	Lane snapper
Mycteroperca bonaci	Black grouper
Ocyurus chrysurus	Yellowtail snapper
Pomacanthus arcuatus	Gray angelfish
Pomacanthus paru	French angelfish
Pseudupeneus maculatus	Spotted goatfish
Scarus vetula	Queen parrotfish
Scomberomorus regalis	Cero mackerel
Sparisoma aurofrenatum	Redband parrotfish
Sparisoma chrysopterum	Redtail parrotfish
Sparisoma viride	Stoplight parrotfish
Sphyraena barracuda	Barracuda

Table 5.2 Summary statistics for seascape metrics and patch structure variables. All metrics and variables were quantified for each sampling site (n = 87).

Seascape category	Variable	Units	Trans-formation	Min.	Max.	Mean	CV
Config-uration	Distance from channel	km	Log_{10}	1	13	7	43.8
	Distance to mangroves	km	Log_{10}	0.1	17	7	68.0
	Nearest neighbor	m	Log_{10}	4	342	117	75.7
	Reef area in 1km buffer	m^2	Log_{10}	49456	1412634	311542	81.3
	Reef area in 500m buffer	m^2	Log_{10}	10832	310756	67834	78.8
	Reef area in 200m buffer	m^2	Log_{10}	95	47177	10509	91.8
Comp-osition	Area*	m^2	Log_{10}	17	17660	4020	104.2
	Area of hard substrate *	m^2	Log_{10}	16	12856	2906	98.4
	Perimeter (m)*	m	Log_{10}	17	696	217	64.0
	Edge: area ratio*	ratio	Box cox	1	36	14	59.5
	Est. volume*†	m^3	None	26	33342	6022	110.8
	Volume* Δ	m^3	Box cox	10584	387969	112978	88.5
	Surface areaΔ	m^2	None	654	71073	10992	111.1
Patch structure	Rugosity chain index	index	None	1.2	2.1	1.5	13.4
	Coarse-scale topographic complexityΔ	index	None	1.0	1.6	1.1	3.3
	Topographic complexity score	index	None	1.0	3.0	1.7	54

[*] metrics included in PCA of ‘patch size’ due to multicollinearity

[†] calculated as area * mean fine-scale rugosity

[Δ] estimated from ENVI bathymetric habitat maps

Table 5.3 Summary of best fit model from CCA. Models selected using AIC value to examine the relationship between seascape metrics and fish community and coral community on study patch reefs (n = 87). Statistical significance of each model is reported using Monte Carlo simulations (999 permutations) to generate an F-statistic and p-value. * 1st principal component using multicollinear patch size metrics.

Comm-unity	Dependent variables	Significant seascape metrics	Variance explained by 1st axis	AIC	F	p-value
Fish	Richness	distance from channel				
	Total biomass	reef area in 500m buffer				
	Commercial biomass	nearest neighbor	0.11	-148.4	3.57	0.008
Coral	Richness	distance from channel				
	% cover	patch size*				
	Coral : macroalgae	Topographic complexity score	0.11	-205.6	3.12	0.014

Table 5.4 Reserve effects using different site classification scenarios. Proportional difference for each fish and coral response variable under varying clustering scenarios between reserve and non-reserve sites. Only significant results are shown. Positive values are greater inside reserve versus outside; negative values are lower inside reserve versus outside.

Community	Response variable	Pooled (n = 87)	Type I (n = 58)	Type II (n = 29)
Fish	Species richness	--	--	--
	Total biomass	--	--	+50%**
	Commercial biomass	--	--	+74%**

		Pooled (n = 87)	Type I (n = 42)	Type II (n = 45)
Coral	Species richness	--	--	-17%*
	% cover	--	-65%**	+68%**
	Coral : macroalgal	--	-57%*	+80%**

*p < 0. 05 and ** p < 0.01 as determined using one-way ANOVA comparing reserve and non-reserve sites.

Table 5.5 ANOVA results of reserve effects on fish and coral response variables using varying site classification scenarios.

Community	Site classification	Response	df (effect,error)	F	p
Fish	Pooled	richness	1, 85	0.040	NS
	(n =87)	total biomass	1, 85	2.039	NS
		commercial biomass	1, 85	1.718	NS
	Type I	richness	1, 40	0.3621	NS
	(n = 58)	total biomass	1, 40	0.342	NS
		commercial biomass	1, 40	0.996	NS
	Type II	richness	1, 43	0.179	NS
	(n = 29)	total biomass	1, 43	7.479	0.009*
		commercial biomass	1, 43	8.050	0.007*
Coral	Pooled	richness	1, 85	0.04	NS
	(n = 87)	% cover	1, 85	0.135	NS
		coral : macroalgae	1, 85	0.003	NS
	Type I	richness	1, 56	0.846	NS
	(n = 42)	% cover	1, 56	9.037	0.004*
		coral : macroalgae	1, 56	5.362	0.024
	Type II	richness	1, 27	5.171	0.031
	(n =45)	% cover	1, 27	8.243	0.008*
		coral : macroalgae	1, 27	14.222	0.001*

* denotes highly significant p values ($p < 0.01$)

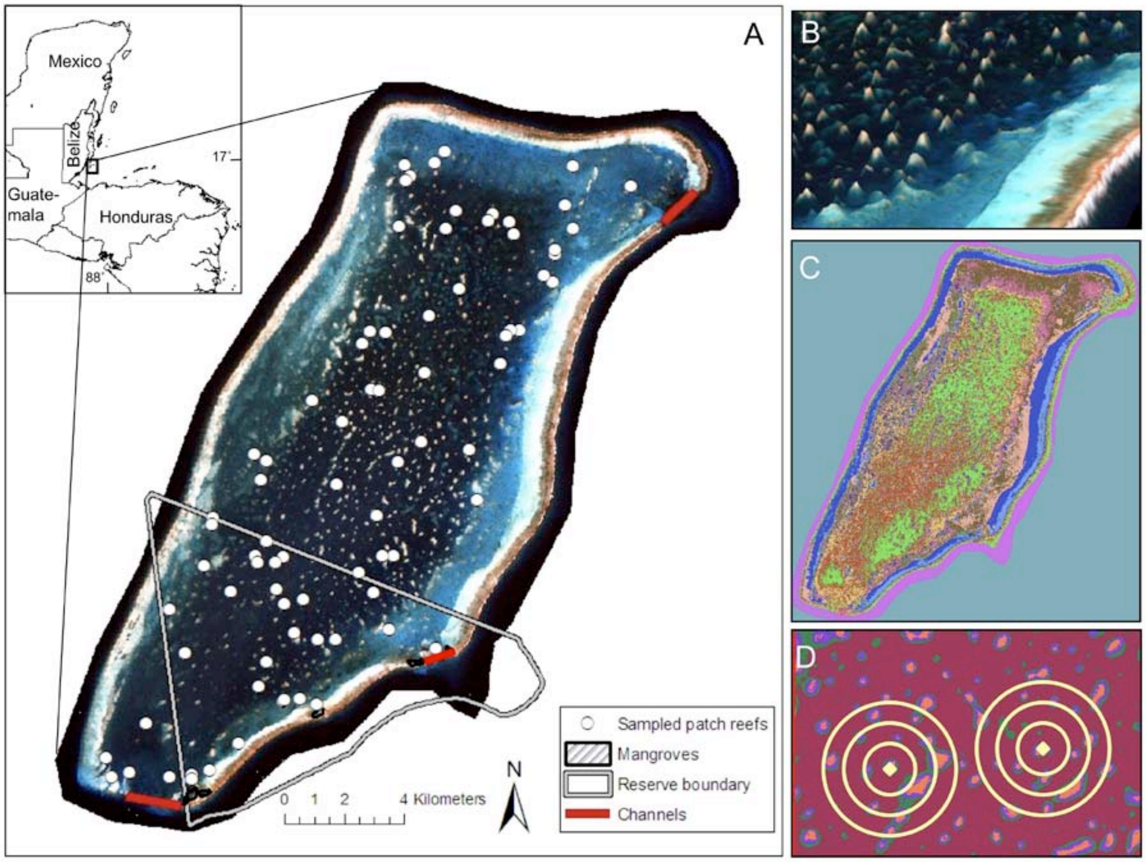


Fig 5.1 Remote sensing imagery of sampling locations and benthic habitats for Glover's Atoll, Belize. (A) IKONOS satellite imagery of Glover's Atoll showing patch reef study site (white circles). (B) ENVI bathymetric map of NE section of lagoon. (C) Habitat classification map featuring 12 benthic habitat classes. (D) Delineation of 200m, 500m, and 1km buffers around patch reef sites to generate metrics of surround reef area.

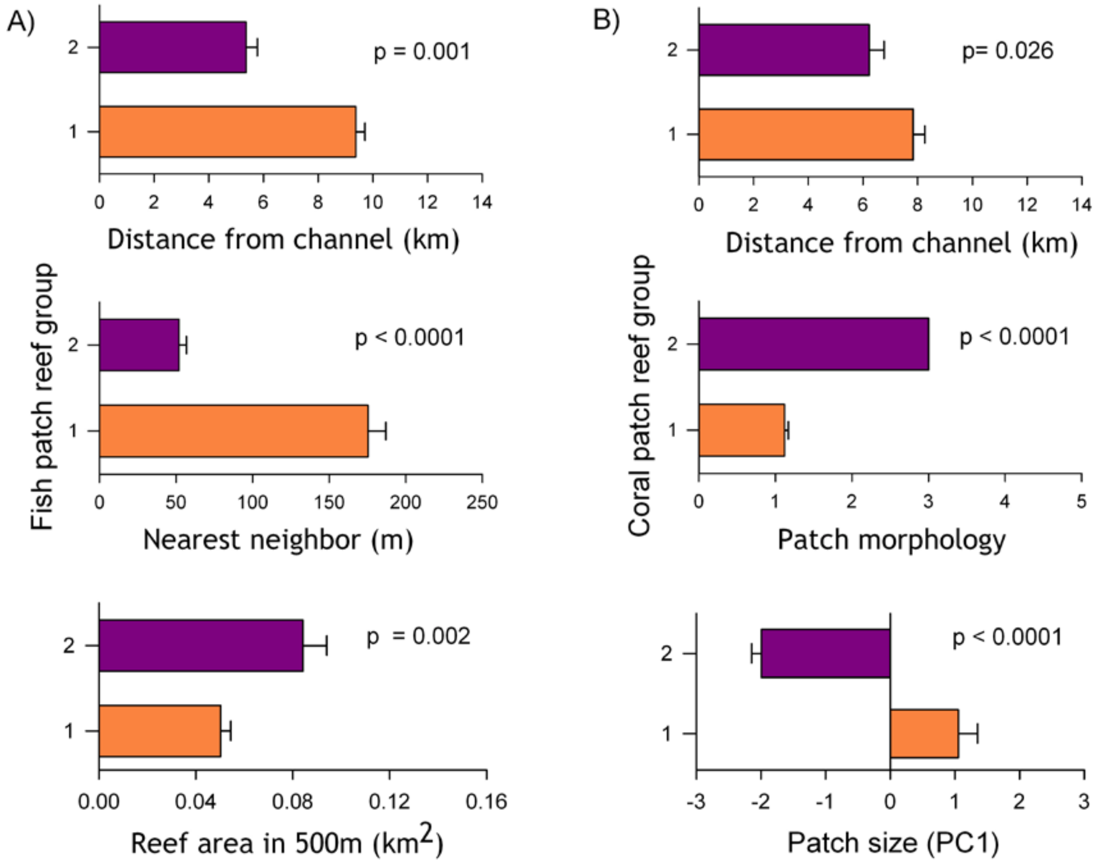


Fig. 5.2 Seascape attributes by patch reef groups. Attributes of (A) fish and (B) coral site groups for each key seascape metric. Group 1 attributes are in purple; group 2 in orange. One-factor ANOVA significance values for each metric are shown.

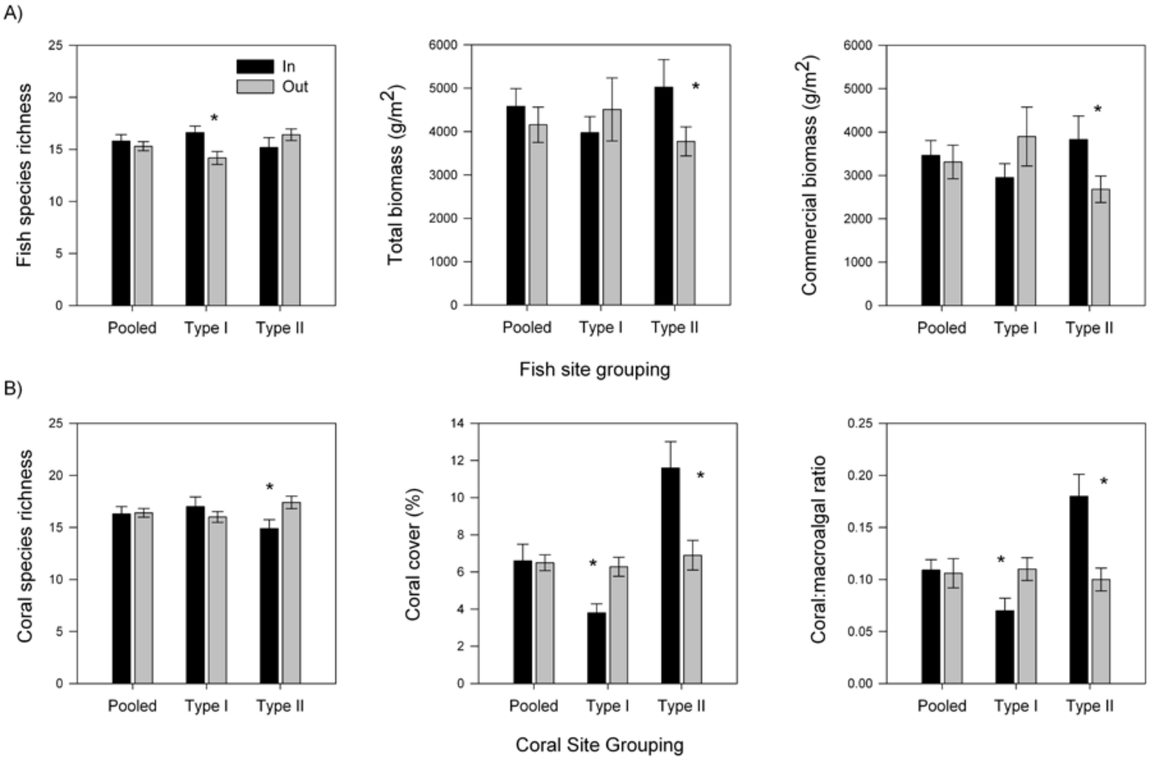


Fig. 5.3 Reserve responses for pooled versus grouped sites. Fish response variables (A) shown in top panels and coral response variables (B) on bottom panels. Significant differences ($p < 0.05$) between in (dark bars) and outside reserve (light bars) are denoted with an *.

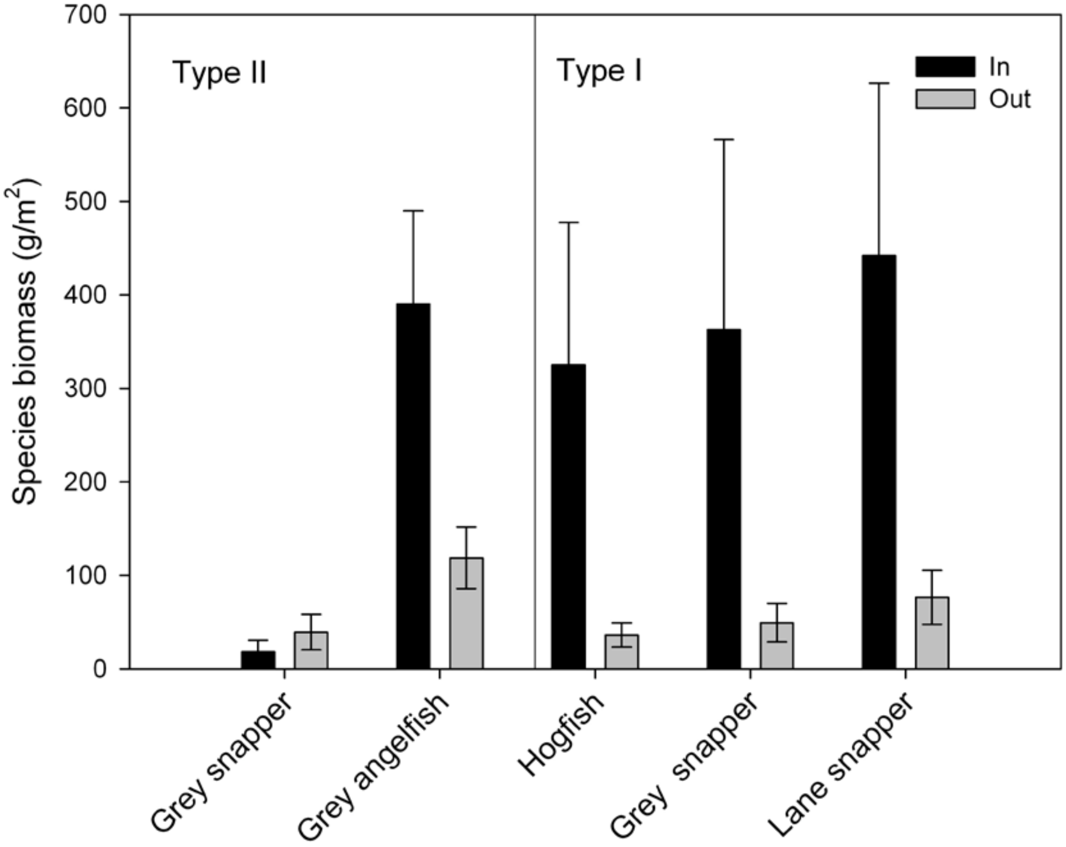


Fig. 5.4 Species-specific fish reserve response by patch reef seascape grouping. Only species showing statistically significant ($P < 0.05$) differences between in (dark bars) and non-reserve (light bars) sites within a patch reef type are shown. The left panel shows fish species from Patch Type II; the right panel shows fish species from Patch Type I.

CHAPTER 6: Corals fail to recover at a Caribbean marine reserve despite ten years of reserve designation

BACKGROUND

Marine reserve protection, a common conservation tool for rebuilding diminished fish and invertebrate communities, has recently been shown in one Caribbean marine reserve to enhance the recovery of coral communities (Mumby et al. 2007a; Mumby & Harborne 2010). These results have timely management implications for beleaguered Caribbean corals (Gardner et al. 2003; Schutte et al. 2010), as recent subtle shifts in coral composition and abundance are eroding the health of Caribbean coral communities. Currently, Caribbean reefs are experiencing: 1) declines of massive coral *Montastraea spp.*(Edmunds & Elahi 2007; Alvarado-Chacón & Acosta 2009; Precht et al. 2010); 2) increased dominance of small, opportunistic brooding species such as *Porites astreoides* and *Agaricia spp.*(Aronson & Precht 2001; Green et al. 2008); 3) sexual recruitment failure limiting the establishment of new corals (Hughes & Tanner 2000); and 4) a shift to smaller colony sizes resulting from habitat degradation (Bak & Meesters 1999). A key question remains as to whether marine reserve protection will confer benefits to Caribbean corals in the face of these regional pressures on coral communities, such that coral communities within reserves will fare better than their unprotected counterparts.

Reserve protection is hypothesized to facilitate coral recovery through indirect cascades that shift the balance between macroalgae and corals (Mumby et al. 2007a). Under this scenario, fishing closures allow depleted stocks of herbivorous fish such as parrotfishes (*Scaridae)* and surgeonfishes (*Acanthuridae)* to rebound. Increased abundance and diversity of these grazing fishes leads to greater consumption pressure on their food supply: namely fleshy and turf algae that have been shown to directly (McCook et al. 2001; Burkepile & Hay 2008; Rasher & Hay 2010) and indirectly (Smith et al. 2006; Rasher & Hay 2010) inhibit a variety of coral life-stages including settlement (Diaz-Pulido et al. 2010) and recruitment (Kuffner et al. 2006). Moreover, reserve protection can directly benefit corals by reducing direct physical damage to corals from fishing gear (Mangi & Roberts 2006; McClanahan et al. 2009). Regardless of the hypothesized mechanistic pathway, there is limited empirical evidence linking reserves protection to positive effects in the coral community (but see Mumby et al. 2007a; Mumby & Harborne 2010). Furthermore, not all reserve studies reporting significant increases in fish biomass and abundance have found commensurate cascading positive effects on corals (Kramer & Heck 2007).

We assessed whether no-take reserve designation induced positive effects on the patch reef coral communities at Glover's Reef Marine Reserve (GRMR) following 10 years of reserve designation by the Belizean Fishery Department (Garaway & Esteban 2002). By contrasting reserve sites to fished sites across Glover's Atoll, we tested whether reserve protection has: 1) prevented or mitigated the coral loss patterns observed elsewhere in the Caribbean, 2) prevented shifts in coral community composition; and 3) enhanced juvenile recruitment. Patch reefs at Glover's Atoll have been the subject of numerous scientific studies dating back to the 1970s (Wallace 1975; McClanahan & Muthiga 1998; Thoney 2001). These studies provide context for assessing how patch-reef coral communities of Glover's Atoll have fared since reserve designation. Lastly, to address potential mechanisms driving the observed changes to the coral community, temporal changes in the herbivorous fish population were evaluated across the reserve boundary.

METHODS

Site selection

Glovers Reef (87 ° 48’W, 16 ° 50’ N) is a large atoll (260km^2) located 45km offshore of Belize, Central America. The interior lagoon contains approximately 850 patch reefs varying in size from 25m^2 to several thousand m^2 (Fig. 6.1, Wallace 1975). Patch reef sites were selected using a stratified random design to facilitate sampling the entire lagoon while re-sampling as many of the patch reefs sampled in 1998-99 as possible (Thoney 2001; dataset available at: http://projects.exeter.ac.uk/msel/glovers/index.html). Of the 87 patch reefs selected in 2008-09, 51 were re–sampled reefs from the 1998-99 survey.

Fish and coral surveys

In 1998-1999, the benthic cover of each patch reef was determined using the line-intercept transect method. Four, 10m transects per reef were laid along the N-S and E-W reef axes at depths of 2-4m (Thoney 2001). In 2008-2009, sampling efficiency was improved through the use of benthic digital photography (Dumas et al. 2008). While sampling methods to assess benthic cover differed between the 1998-99 surveys and 2008-9, photo quadrat point intercept methods have been shown to be comparable to the line intercept transect method for abundant (>10%) substrate categories (Leujak & Ormond 2007). Along the same N-S and E-W reef axes used in 1998-99, a minimum of

50 photographs was taken at 2m intervals from 0.5m above the substrate. From these 50+ images, 20 were randomly selected for point-intercept analysis. Fifty random points were scored per image (CPCe software, v3.5; Kohler and Gill 2006). To match benthic scoring categories used in 1998-99, hard corals were identified to species with no distinction made between *Montastraea annularis*, *M. faveolata*, and *M. franksii*. All other substrates were classified as: fleshy macroalgae, turf algae, crustose coralline algae, sponge, seagrass, soft coral, mobile invertebrate, sand, or rubble.

Population size-structure data were collected by laying a 10m belt transect between 2-4m depth and measuring the maximum diameter along the long and short axis of the colony and colony height to the nearest cm for all boulder corals with any portion of the colony in the transect (Kramer & Lang 2003) and corrected for sampling bias according to Zvuloni et al. (2008). Branching corals were excluded from population structure measurements due to lack of standardized methods to accurately measure branching morphologies. Two belt transects were completed per patch reef. To distinguish partial mortality or fragmentation from juvenile corals with the same amount of live tissue, colony size was measured as continuous coral skeleton material and the number of discrete tissue isolates or percent partial mortality recorded (McClanahan et al. 2008).

In addition to benthic data, fish abundance and diversity were assessed at each patch reef, using identical methods in both sampling periods. Fish abundances were determined using the stationary point-survey method of Bohnsack and Bannerot (1986). The species, number of individuals, and fork length were estimated for all fish >5cm swimming through an estimated 5m radius cylinder extending from the ocean floor to the surface of the water over a 5 min interval. A total of 5 surveys, positioned at the 3m depth contour on N, E, S, and W edges of the patch reef as well as the center, were completed for each patch reef surveyed.

Data Analyses

Spatial differences in the benthic coral and algal community on patch reefs inside the reserve were compared to fished reefs using a one-factor ANOVA (factor: reserve). Percent cover data of benthic substrate groups were arcsine-square-root-transformed prior to analysis to achieve normality and homoscedasticity. However, patch reefs at Glover's Atoll are not identical. These patch reefs are heterogeneous in reef size, shape, and configuration in within the atoll, which can lead to differences in the benthic communities that reflect spatial seascape differences among reefs rather than reserve protection (Huntington et al. 2010). To control for these between-patch differences, we wanted to evaluate reserve effects at the same patch reefs over time following a Before-After-Control-Impact (BACI) analysis to improve our ability to discern true reserve effects (Green 1979). Hence, we analyzed temporal changes in cover of coral species and reproductive groups (brooders versus broadcasters) on the same individual patch reefs over time using matched-pairs analyses, grouped by reserve status. While benthic sampling methods differed from 1998-99 to 2008-09, contrasting the absolute temporal change in the coral community composition between reserve sites and fished sites should still be useful because the error introduced by different sampling methodologies should be the same among all patch reef sites from a given dataset, regardless of reserve protection.

Metrics of colony size were quantified to assess reserve effects beyond the traditional metric of coral cover. Due to their clonal growth, corals may respond relatively quickly to changes in environmental conditions by subtle alterations to their population structure (Vermeij et al. 2007; Green et al. 2008). Hence, changes in the metrics defining the population (i.e. mean colony size, maximum colony size) for specific species or functional groups of corals may reveal reserve effects not observed in conventional percent coral cover measures. As colony-size data were collected only in 2008-09, differences among population structure metrics were limited to comparisons between reserve and fished sites. Population metrics were generated from the size frequency distributions (SFDs) for the most abundant coral species and for pooled brooding and broadcasting species groups (McClanahan et al. 2008). While log-transformation improved normality of the SFDs, the data failed to meet normality assumptions and non-parametric Mann-Whitney *U* and Kolmogorov-Smirnov tests were used to evaluate differences in mean colony size and size frequency distributions, respectively.

To assess whether reserve protection increased the recruitment and survival of young corals, the abundance of juvenile coral colonies was approximated from the colony-size data collected in 2008-09. The size (cm^2) of a juvenile ‘5 year-old coral’ was estimated from species-specific minimum growth rates to conservatively approximate the size of corals established post-reserve designation (Table 6.1). All colonies smaller than the species-specific ‘5-year old coral’ were considered juveniles. The abundance of juveniles (indiv. m^{-2}) pooled across species was determined for each reef, log-transformed, and then compared between reserve and control sites using a single factor ANOVA.

To explore the potential for grazing fish abundances to drive the observed changes in benthic community, the abundance of Acanthurids (surgeonfishes) and Scarids (parrotfishes) were compared between 1998-99 and 2008-09 using a matched-pairs analysis grouped by reserve protection for the 51 replicate sites. Fish abundance data were log (x + 0.01) transformed prior to analyses to improve normality and homoscedasticity. Queen, midnight, and blue parrotfishes, which had mean abundance values of zero for the 2008-09 sampling period, were compared using a non-parametric binomial presence-absence test.

RESULTS

Contrasting reserve versus fished reefs

Following 10 years of reserve designation, we detected no differences in coral % cover between reserve sites and fished sites in 2008-09 (ANOVA, df = 86, $p > 0.05$). Likewise, considering algal turfs, fleshy macroalgae, and crustose coralline algae separately, as well as pooled as 'total algae', yielded no significant differences between reserve and fished patch reef sites.

Temporal changes in coral & macroalgal cover

Across the lagoon, the mean absolute coral cover of ~80% documented by Wallace in the 1970's declined to 7% by 2008-09 (Fig. 6.2), though the absolute loss over the past decade is small (8.36% ± 0.41 SE in 1998-99 to 6.50% ± 0.42 SE in 2008-09).

Coral cover in both reserve sites and fished sites declined at a comparable rate during this time period; with no evidence of coral cover recovery in the reserve (Fig 6.2). Similarly, macroalgal cover has remained relatively constant over the past 15 years since documented by McClanahan and Muthiga (1998) in the mid-1990s (Fig. 6.2). Mean macroalgal cover was higher in fished sites, but this pattern was present in both 1998-99 and 2008-09, and is therefore representative of higher initial macroalgal abundances among fished reefs compared to reserve reefs at the time of reserve designation (Fig. 6.2). Macroalgal abundances inside the reserve remained constant from1998-99 to 2008-09 indicating that reserve designation had little effect on the macroalgal cover over the past decade (32.3% ± 2.6 SE in 1998-99 to 32.4% ± 2.6 SE in 2008-09).

Among the same reefs sampled in 1998-99 and again in 2008-09, the percent cover of broadcasting coral species declined from 5.08% in 1998-99 to 3.06% in 2008-09 (matched-pair analysis, df = 50, t = -3.84, p < 0.001). Brooding species, in contrast, changed only slightly from 2.96% to 2.40% over the same time span. While differences in sampling methodologies in 1998-99 and 2008-09 confounded our ability to reliably interpret this loss of broadcasters across the entire atoll due to the small % cover values of corals (<10%), contrasting the degree of temporal change between reserve and fished sites grouping lends more convincing results. Grouping patch-reef sites by reserve revealed distinct differences between reserve and fished sites; reserve sites lost significantly more cover of broadcasting corals over time compared to fished sites (Fig. 6.3; group effect: reserve, F = 4.91, p = 0.03). In contrast, reserve and fished sites showed no change in brooding coral species over the past decade.

Of the 6 most common coral species found in 1998-99, 4 declined by 2008-09. Only *Agaricia agaricites* and *Porites astreoides*, both opportunistic brooding species, showed slight increases in mean % cover (Fig. 6.3). The broadcasting, massive coral species *M. annularis* was the only taxon to decline significantly over the past decade (Fig. 6.3, matched-pairs analysis, df = 50, t = -3.63, $p < 0.001$). While the losses of *M. annularis* inside the reserve were twice as great as those outside the reserve, this trend was not significant (group effect: reserve, F = 3.21, p = 0.08).

Coral population structure

Mean colony sizes pooled for all species were significantly smaller in the reserve than in the fished area (Table 6.2). Broadcasting taxa appear to be driving this pattern, exhibiting significantly smaller colony sizes within the reserve, while brooding taxa did not. At the species level, mean colony size was significantly smaller in the reserve for the two broadcasting species, *M. annularis* and *Siderastrea siderea*, while *P. astreoides*, a brooder, reached a significantly greater mean size inside the reserve (Mann-Whitney *U;* $p < 0.017$). SFDs between reserve and fished sites matched patterns in mean colony size; broadcasting species were smaller across all size classes in the reserve while *P. astreoides* was larger (Kolmogorov-Smirnov comparisons, $p < 0.05$).

Estimated juvenile densities (indiv. m^{-2}) revealed no difference by reserve (reserve density = 0.63 ± 0.08, mean ± SE; fished recruit density = 0.64 ± 0.08, mean ± SE; non-parametric Kruskal-Wallis test, n =81).

Reserve effects on the grazing fish community

Across the entire atoll, scarid densities declined significantly over time (matched-pairs analysis, df = 50, t = -2.13, p = 0.038) with significantly greater declines within the reserve than in the fished area (group effect: reserve, F = 6.26, p = 0.016; Fig. 6.4). Acanthurid densities did not differ significantly over time, however reserve sites did differ from fished sites such that abundances were significantly greater among fished reefs compared to reserve reefs (group effect: reserve, F = 4.88, p = 0.032; Fig. 6.4). At the species level, temporal declines were significant for the stoplight parrotfish *Sparisoma viride* (matched pairs analysis, df = 50, t = 5.75, p < 0.001), blue tang *Acanthurus coeruleus* (matched pairs analysis, df = 50, t = 5.34, p < 0.001), and queen parrotfish *Scarus vetula* (binomial test, p <0.05; Fig. 6.5), through temporal responses for these species did not vary between reserve and fished sites. The redband parrotfish (*Sparisoma aurofrenatum)* exhibited no significant temporal or reserve effects.

DISCUSSION

Regional patterns of coral decline are also evident among the patch reef communities within Glover's Atoll. Unfortunately, we found no evidence that no-take reserve within the southern section of the atoll ameliorated these declines since its establishment. Coral cover within the reserve was comparable to fished sites despite 10 years of reserve designation. Algal community cover (i.e. turf, fleshy macroalgae, and crustose coralline algae) and estimated densities of juvenile corals also did not differ between reserve and fished sites. Significant shifts to the coral community composition have occurred over this time period, led by significant losses of the massive broadcasting coral species within the reserve contrasted to fished sites. Lastly, colonies of broadcasting species were observed to be smaller within the reserve, reflecting either greater mortality or fragmentation of larger colonies, not the influx of recruits as estimated densities of juvenile corals were not greater in the reserve.

Historically, *M. annularis* dominated the coral community in the southern region of the lagoon (Wallace, 1975); the same region now encompassed in the no-take marine reserve. We observed declines of *M. annularis* over the past decade to be more pronounced in the marine reserve where M. *annularis* was more abundant in mid-1990s compared to the fished reefs in the mid-northern lagoon (McClanahan and Muthiga 1998). This greater loss of *M. annularis* in the reserve may reflect reserve sites having greater 'initial' abundances of *M. annularis* and thus, more to lose. Yet, reserve designation did little to stem or prevent this loss. Declines of *M. annularis* are not unique to Glover's lagoon but are reported with increased frequency across the Caribbean (Edmunds & Elahi 2007; Carpenter et al. 2008). Likewise, for Glover's lagoon and the broader Caribbean, small brooding species are surviving better over time as larger species decline (Precht & Miller 2006; Green et al. 2008). Dominance of Caribbean reefs by small to medium-sized brooders is unprecedented in the geologic record (Precht and Miller 2006). However, current environmental shifts in the Caribbean appear to not favor massive, slow-growing, broadcasting coral taxa. Rather, the opportunist, 'weedy' brooding species characterized by high recruitment, fast growth, and smaller colony sizes are exhibiting a competitive advantage in today's Caribbean reefs (Knowlton 2001; Green et al. 2008; Edmunds 2010).

Less macroalgae was detected in reserve sites versus fished sites in the 2008-09 surveys. However, considering that macroalgal cover did not change from 1998-99 to 2008-09 within the reserve, this pattern is an artifact of reserve reefs having lower macroalgal cover than fished reefs at the time of reserve designation, rather than a positive effect of reserve protection. Notably, the macroalgae cover at Glover's Atoll (~40%) is twice the average for the Mesoamerican region (Schutte et al. 2010). Since macroalgal cover within the reserve has remained constant over the past decade and is exceptionally high for the region, reserve designation is unlikely to generate positive cascading effects on the coral community for Glover's lagoon. Rather, this system may be pushed far beyond a coral dominated state such that feedback mechanisms maintain high algal cover. In such a system, extreme forcing through increased grazing pressure is required to move the system towards a trajectory of greater coral cover (Mumby et al. 2007b).

Well-enforced no-take marine protected areas, when placed in areas with depleted fish assemblages, typically lead to strong responses of fish populations in units of biomass and abundance. The simplest hypothesis for why grazing fishes have not rebounded with the GRMR might be the lack of sufficient enforcement of no-take laws. The GRMR does possess several of practices known to favor strong enforcement, including: clear reserve boundaries demarcated with buoys, daily armed patrols of the reserve, a surveillance tower, and government funding through the Belizean Fisheries Department to staff multiple enforcement officers on-site (Byers & Noonburg 2007; Samoilys et al. 2007; Guidetti et al. 2008; Sethi & Hilborn 2008). However, some of these practices were initiated only recently (e.g. the watch tower was constructed 2 years ago) and “illegal fishing remains a continuous problem” according to the Glover’s Reef Marine Reserve Management Plan (Gibson 2007). Indeed, poaching of the large-bodied stoplight parrotfish (*S. viridae*) was documented in October 2009 at Glover’s Atoll, despite national legislation fully protecting parrotfish is Belizean waters, though whether this event occurred with the no-take reserve is unclear. We found larger parrotfish species, those coveted by fisherman, to have declined across the atoll over the past decade while the smaller-bodied redband (*Sparisoma aurofrenatum*) have not, suggesting that the commercially-valuable larger parrotfish species are under greater poaching pressure across the entire atoll.

While poaching may have some effect on changes in parrotfish abundances across the atoll, it doesn't explain why temporal parrotfish declines inside the reserve are more severe than in the fished areas. Furthermore, fork lengths of both *Scarus vetula* and *Sparisoma viride* observed in 2008-09 sampling were significantly larger in the reserve compared to fished sites, and this trend would not be expected if severe poaching were occurring (M. Karnauskas, unpub. data). An alternative hypothesis for the lack of increase in herbivorous fishes and coral cover within the reserve lies with trophic level. The GRMR has been effective in increasing abundances of certain fish species over the same ten-year period examined here (Karnauskas et al. 2011), including the commercially important hogfish (*Lachnolaimus maximus*), black grouper (*Mycteroperca bonaci*), and lane snapper (*Lutjanus synagris*), as well as increasing the abundance of conch and lobster populations (Gibson & Hoare 2006). These results indicate that reserve protection has performed well for some, but not all, species within Glover’s Atoll.

The increased abundance of higher trophic level fish species within GRMR reserve could exert greater predation pressure on lower trophic level, herbivorous fishes limiting their abundance. In support of this hypothesis, we found abundances of the smallest parrotfish species (*Sparisoma aurofrenatum*) surveyed here to increase over the past decade outside the reserve where predation pressure is hypothesized to be lower.

Lastly, reserves are unlikely to be successful if they are located in stressed, degraded or frequently disturbed habitats (Jameson et al. 2002), or not enough time has passed since reserve establishment (Claudet et al. 2008). In corals, reserve protection has been shown to insufficiently compensate for environmental stress (Epstein et al. 2005). The GRMR's placement in a low-flow environment within the atoll (McClanahan & Karnauskas 2011), may limit corals' ability to recover from the high macroalgal dominance at Glover's Atoll, especially among broadcasting species sensitive to 'marginal' habitats (Vermeij et al. 2007; McClanahan et al. 2011). The addition of frequent hurricanes and warm-water anomalies act as acute stressors causing coral fragmentation and bleaching within the Glover's Atoll (Goreau et al. 2000) and thereby preventing positive reserve effects from gaining traction over longer temporal scales. Finally, the time needed for cascading positive effects to be realized in the GRMR may exceed the 10 years elapsed since the reserve was designated. These hypotheses may not be mutually exclusive but act simultaneously to prevent reserve effects from cascading to the benthos. While we are unable to rigorously support or refute these competing hypotheses using this data, it is note-worthy to challenge the assumption that marine reserve protection will favor coral recovery. We encourage further study as to why reserves perform well in some regions and poorly in others.

For coral reef systems, no-take marine reserves are a commonly used conservation tool (Mora et al. 2006), yet the efficacy of this tool to build coral resilience in the face of regional stressors remains uncertain. Here, we document the limitations of reserve protection to increase the resilience of the coral community within Glover's Atoll. Based on their studies of a single Bahamian reserve in the eastern Caribbean, Mumby et al. (2007a; 2010) suggest that cascading reserve effects can be realized over fairly short time scales. We did not find similar results at GRMR. The few other marine reserve studies that assessed coral populations over time yielded results similar to those observed here. These studies reported no effect of reserve protection in abating declines in coral cover (Jones et al. 2004; McClanahan et al. 2008). We conclude that reserve performance can vary considerably across the Caribbean, reflecting local differences in reef community composition, reserve placement and no-take enforcement. The issue of whether well-managed reserves can protect coral communities must await further examination of additional reserves where reserve enforcement, reserve placement, and herbivory are simultaneously evaluated.

Table 6.1 Minimum, maximum, and calculated average growth rates (mm/yr) by coral species, as reported in Edmunds 2007, Edmunds and Elahi 2007, and Huston 1985.

Species	Growth	rate (mm/yr)
Diploria labyrinthiformis	min	3.5
	max	7
	ave	5.25
D. strigosa	min	3.5
	max	7
	ave	5.25
Montastraea cavernosa	min	2.8
	max	12.2
	ave	7.5
Porites astreoides	min	3.25
	max	5.8
	ave	4.5
Siderastrea siderea	min	3
	max	7
	ave	5
M. annularis	min	7
	max	9
	ave	8
Agaricia agaricites	min	2.2
	max	5.2
	ave	3.7

Table 6.2 Colony population structure metrics for the 4 dominant non-branching coral taxa across management zone (values are untransformed). * indicates pooled colony size data, standardized by species. Non-parametric Mann-Whitney *U* and Kolmogorov-Smirnov test and were used to identify significant difference in mean colony size and size frequency distributions on log-transformed values, respectively.

Taxa	Zone	Population metrics			Mann-Whitney *U*		Kolmogorov-Smirnov	
		Median colony size (cm^2)	25th Quantile	n	Chi-square	p-value	*Z*	p-value
A. agaricites	Reserve	58.2	20.4	604	0.23	NS	0.092	NS
	Fished	58.2	16.5	777				
M. annularis	Reserve	160.2	58.1	685	6.79	0.009	1.551	0.016
	Fished	216.8	75.4	759				
P. astreoides	Reserve	103.7	35.3	343	5.69	0.017	1.685	0.007
	Fished	81.7	25.9	817				
S. siderea	Reserve	235.6	58.1	521	11.77	<0.001	1.746	0.005
	Fished	306.3	92.7	656				
Brooders	Reserve	0.012*	0.0042	947	0.23	NS	1.010	NS
	Fished	0.014*	0.0043	1594				
Broadcasters	Reserve	0.0043*	0.0011	1205	19.4	<0.001	2.250	<0.001
	Fished	0.0046*	0.0015	1415				
Total	Reserve	0.0078*	0.0021	2152	28.42	<0.001	2.802	<0.001
	Fished	0.0082*	0.0028	3009				

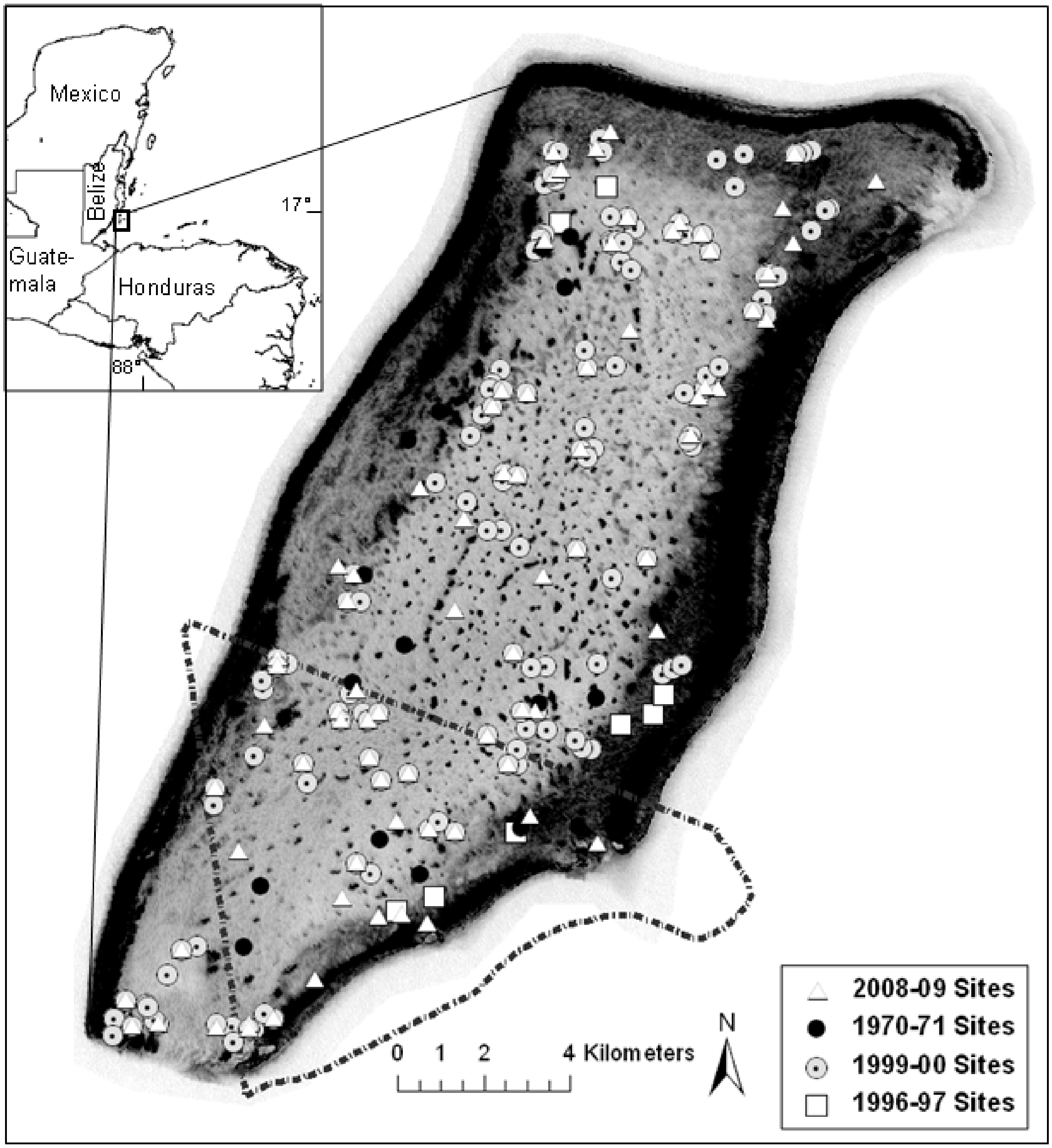


Fig. 6.1 Map of Glover's Atoll, Belize. Polygon in the southern portion of the atoll denotes location of no-take reserve enforced in 1998. Patch reef sites representing 4 different research efforts are shown: 1970-71 (black circles, n=16, Wallace 1975); 1996-7 (white squares, n=20, McClanhan and Muthiga 1998); 1998-99 (white circles with center dot, n=150, Thoney 2001); 2008-9 (white triangles, n=87, present study).

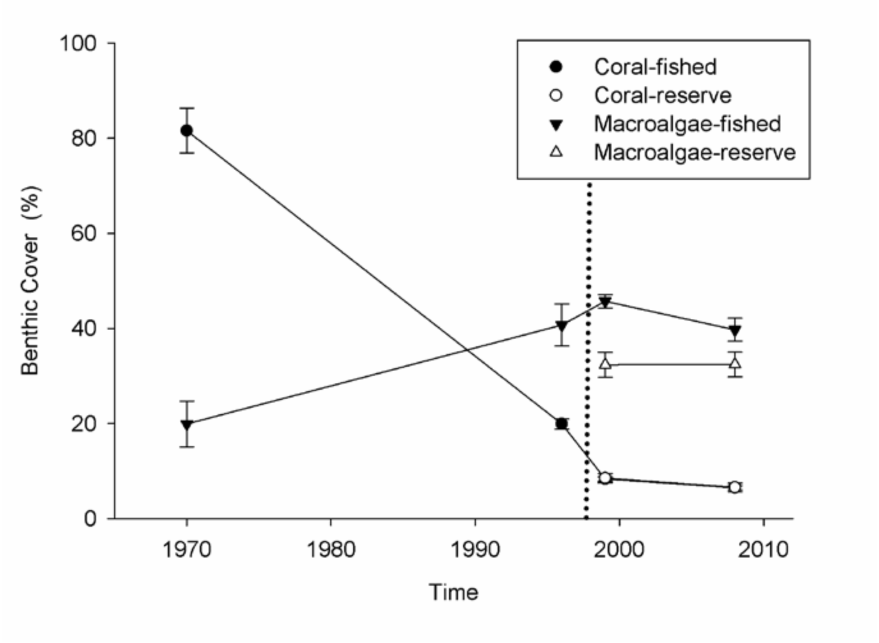


Fig. 6.2 Mean coral cover (circles) and macroalgal cover (triangle) between 1970-1 and 2008-9 (adapted from McClanahan and Muthida, 1998). Mean cover was estimated from patch reef surveys with bars representing standard errors: 1970-1 (n=16), 1996-7 (n=20), 1998-99 (n=150), and 2008-9 (n = 87). Following the enforcement of the no-take zone (dashed line), white symbols are reserve sites and black symbols are fished sites. Note: coral values between reserve and fished sites are similar and therefore overlap on the figure.

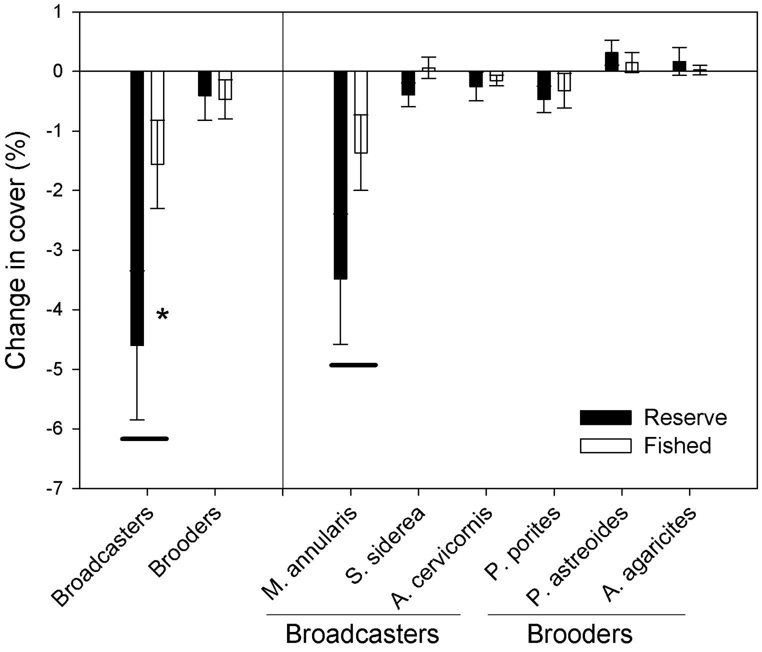


Figure 6.3 Change in % coral cover from 1998-99 to 2008-9 by reproductive mode and by species (n =51). Pooled spawning taxa and brooding taxa (left); 3 most abundant broadcasting and brooding species (right). Dark bars show mean change in coral cover (± SE) for reserve sites; light bars show means (± SE) for fished sites. Bold bars indicate significant change in coral cover over time, irrespective of management zone ($P < 0.05$; matched pairs analysis); * indicate significant difference in change in coral cover over time between reserve and fished sites ($P < 0.05$; matched pairs analysis, grouped by reserve).

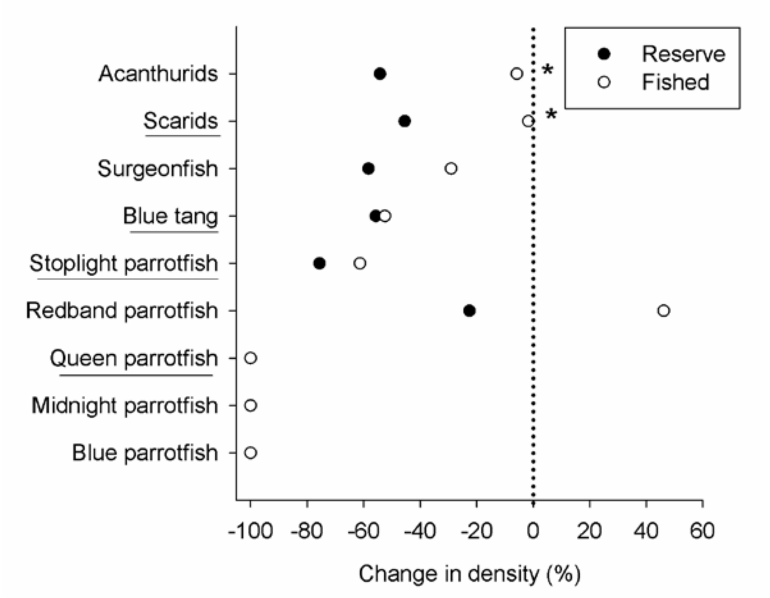


Figure 6.4 Percent change in grazing fish abundance from 1998-99 to 2008-09. Reserve sites are dark circles and fished sites are open circles. Species underlined on the y-axis exhibited significant temporal declines from 1998-99 to 2008-09. * indicate a significant difference in temporal change between reserve and fished sites.

CHAPTER 7: Coral species richness estimates are sensitive to differences in reef size and regional diversity

BACKGROUND

The size of habitat patches can vary widely (Forman & Godron 1986), highlighting the need to understand how this variability influences the diversity of organisms occupying a habitat patch, and our ability to accurately census that diversity. As patch size increases, the amount of spatially structured microhabitats (e.g. patch edge, cores) change in relation to the total available area. Resource differences between these microhabitats can drive differences in species richness, such that edge species, interior species, and generalists differ in their spatial partitioning within the patch. Hence, sampling all patches identically, without adjusting for patch size or the location of the sampling units within the patch, may significantly influence estimates of species richness (Anderson 1999).

While edge effects are often studied in terrestrial systems (reviewed by Ries et al. 2004; Laurance et al. 2007), we know less about their tropical marine analogs. This is especially true for corals, where survey protocols are rarely adjusted to accommodate differences in habitat size or shape (but see Huntington et al. 2010). Yet, spatial variations in coral species' distributions across the reef surface do exist, even within a single reef type, as shown for Florida patch reefs over geologic time scales (Brock et al. 2008). Repeatedly, variations in reef size have been ignored in monitoring studies that assume all reefs of a given type, regardless of size or shape, are structured similarly. Large-scale reef survey protocols, such as the Atlantic and Gulf Rapid Reef Assessment (AGRRA; Kramer & Lang 2003), the Florida Reef Resilience Program, and the

Caribbean Coastal Marine Productivity Program (CARICOMP), all rely on sample-based assessments using a set number of haphazardly-placed transects to census reef diversity, irrespective of reef size.

If coral species exhibit preferences for spatially-structured microhabitats, coral richness per unit area would be underestimated in larger habitats. For example, let us suppose that coral richness is estimated from five, randomly selected non-overlapping transects per reef, regardless of reef size. On smaller reefs, those five transects sample a greater percentage of the total surface, compared to larger reefs (Fig. 7.1A). Let us further assume that coral species are not randomly distributed across the reef surface, but are partitioned in the reef according to specific microhabitats (Knowlton & Jackson 1994). Sampling protocols with a fixed sampling effort would therefore have a greater probability of encompassing a greater variety of these habitats on small reefs compared to larger reefs. Hence, the estimated richness on larger reefs may be depressed by a sampling protocol insensitive to reef size.

Here, we evaluate the accuracy of reef survey methods that rely on a fixed sampling effort, regardless of reef size. We first vary the number of replicate transects sampled on patch reefs of increasing size. We then evaluate how the relationship between estimated coral richness and reef size varies across a regional gradient of species diversity by comparing patch reefs from Bermuda, Florida, and Belize. This study benefits from the discrete character of patch reefs, enabling reef size to be easily quantified through remote sensing (Lirman & Fong 2007; Huntington et al. 2010). As such, patch reef arrays are ideal for investigating the importance of scaling sampling effort to the extent of the habitat patch. We first hypothesize that as reef size increases, so will the likelihood of underestimating coral species richness. Our second hypothesis is that this relationship will be more pronounced (e.g. steeper slope) in speciose regions where larger species pool may lead to greater habitat partitioning (Knowlton & Jackson 1994; Tilman 1994; Fig. 7A). If the size and regional location of a reef significantly influence the estimated species richness captured using conventional sub-sampling methodologies, then these spatial metrics need to be considered to reduce the risk of underestimating species richness by adjusting sampling protocols as needed.

METHODS

Data collection

Patch reef complexes in Bermuda; Biscayne National Park, Florida; and Glover's Reef, Belize were selected for sampling due to their different regional species pools following a latitudinal gradient. Bermuda's species pool consists of 19 species of scleractinian corals (Murdoch et al. 2008), 16 of which were observed on patch reefs in this study. Species pools for reef habitat in Florida and Belize consist of 43 and 51 coral species, respectively (Miloslavich et al. 2010; NOAA), though only 35 species in Florida and 36 species in Belize were observed on study patch reefs (Table 7.1). A total of 36 reefs in Bermuda, 42 reefs in Florida, and 70 reefs in Belize were sampled between May 2008 and May 2010. Sampling was conducted at depths between 2-5m on a single reef type (patch reefs) based on geomorphologic features to restrict the potential influence of depth and reef type on coral richness (Porter 1972).

Coral richness for each reef was subsampled using five, replicate 10 x 1m belt transects placed haphazardly across the reef surface. All coral species with any portion of the colony inside the transect were recorded. In total, 740 transects were censused among all regions. 'True' reef richness was determined by combining species observed during the transect surveys with those species encountered during a roving free-swim conducted by all divers (2-4 divers) over the entire reef for a minimum of 10 min. Larger reefs required greater search intervals to ensure all sections of the reef were inspected. At the conclusion of the search interval, cumulative species lists were compiled among observers as an estimated measure of total species richness. Given the relatively small size of the patch reefs surveyed in the study (Table 7.1) dive teams of 2-4 divers were able to reliably assess the species richness of the entire patch reef within a 50 min dive.

Reef size, defined as the two-dimensional reef area, was measured from high-resolution (50cm) multiband satellite imagery for each patch reef (Huntington et al. 2010). Areas were log-transformed to achieve normality.

Data analyses

We determined species richness per sampling effort using a rarification approach (randomized species-accumulation curves). In this approach, we repeatedly re-sampled the pool of 5, non-overlapping transects at random, corresponding to a sampling effort of 1, 2, 3, 4, or 5 transects. This re-sampling was conducted with replacement, for each sampled patch reef. The number of unique species for a given sampling effort was tallied for each draw (i.e. species were counted only once). Random draws were repeated 100 times for each sampling effort (1-5 transects) and averaged. Thus, this approach generated the expected number of species in a small collection of n transect samples drawn at random from the larger pool of N samples (Simberloff 1978; Grotteli and

Cowell 2001). The relationship between mean transect richness for a given sampling effort and the estimated total reef richness was represented as the percentage of the total reef richness captured by the transect subsamples (transect richness/total richness *100). This proportional approach allowed comparison of 'transect-to-reef richness', for each sampling effort, across reefs of varying size.

Regional differences in the ratio of transect-to- reef richness were analyzed using ANCOVA, with reef size as a continuous covariate and sampling effort (no. of transects) as a categorical variable. Transect-to-reef richness values met assumptions of normality and homogeneity of variance. To evaluate whether regional differences were present, a second ANCOVA was performed using region as a categorical variable. Bermuda's patch reefs were smaller than those sampled in either Florida or Belize (Table 7.1). Therefore, to ensure that the reefs between regions were comparable, the data from Florida and Belize were restricted to reef sizes representative in the Bermuda data (~50-1000m^2) and reanalyzed.

ASSESSMENT

Consistent with our first hypothesis, the transect-to-reef richness ratio varied significantly as reefs increased in size, such that larger reefs had lower transect-to-reef richness values (Table 7.2A; Fig. 7.2). This decline was consistent among sampling efforts (ANCOVA, no interaction effect), resulting in an underestimation of reef richness by 6.1% with each ten-fold increase in reef size (slope = -6.1, log-scaled x-axis). Sampling effort was a significant factor in determining the transect-to-reef richness, with greater numbers of transects resulting in a higher proportion of the total reef richness censused (Fig. 7.3). Yet, transect-to-reef richness did not increase indefinitely with sampling effort. No significant difference in the transect-to-reef richness was detectable between 4 and 5 transects, indicating that sampling >4 transects conferred no improvement to estimates of coral richness (Fig. 7.3; Tukey's post hoc analysis). At this sampling effort (4 or 5 transects), 70% ± 0.6 (mean ± SE) of the total reef richness was censused. Repeating this analysis with the truncated dataset (n = 440) generated results statistically similar to the full dataset (Table 7.2B).

The prediction that the regression relationship between transect-to-reef richness and reef area will have a steeper slope in speciose regions (hypothesis 2) was supported by the full set of patch reef data. Raw species richness counts (or in this case the ratio between transect : reef richness) can only be validly compared when the richness sampling curves have reached an asymptote (Grotelli and Colwell 2001). Hence, we compared richness estimates among regions using a sampling effort of 5 transects, as this level of sampling reflected an asymptote in our transect-to-reef richness values (Fig. 7.3). The slope of the regression varied among the three regions (Fig. 7.4A). Bermuda, the most species poor region, showed no relationship of transect-to-reef richness and reef size, while Florida and Belize showed steeper slopes resulting in a marginal underestimation of reef richness with increasing reef size (simple linear regression, $p < 0.01$, slope = -5.0 and -5.6, respectively). The size-restricted analysis revealed similar results to the full dataset, although the severity of the underestimation changed by region (Table 7.3). Among reefs of 55-1000m^2, Belize, the most species-rich region, was the only region to show significant underestimation of richness with increasing reef size (Fig. 7.4B; estimated slope = -15.1).

While we determined a greater risk of underestimating coral richness among larger patch reefs in species-rich regions, this pattern is not the result of larger reefs simply being more diverse, and therefore requiring greater sampling effort. Indeed, the larger patch reefs in this study were not the most diverse. We were unable to fit power or exponential curves to the relationship between reef size and total reef richness for any of the three regions. As such, these reefs do not conform to the typical species-area relationship common in many terrestrial and marine systems (Connor and McCoy 1979; Rozenweig 1995; Niegel, 2003).

DISCUSSION

This study empirically tests whether variation in patch reef size and the available species pool influences the accuracy of conventional methodologies for assessing coral diversity. By surveying coral communities on 148 patch reefs across a regional diversity gradient in the Western Atlantic, we show that fixed survey protocols underestimate richness as reefs increase in size, though the magnitude of this bias is relatively small: a 6% underestimation for each 10-fold increase in reef size. Risk of underestimation was greatest within regions that supported greater species pools of corals. Our results agree with other marine studies, where differences between habitat edges and cores have revealed differences in sub-sampled diversity as habitat size increased (Benedetti-Cecchi & Cinelli 1993; Anderson 1999).

Underestimation of patch reef coral richness increased with the size of the species pool. Early studies of corals dismissed niche partitioning as a likely mechanism for maintaining coral diversity in favor of random placement within a reef (Connell 1978).

More recently, this generalist view was replaced with a more specialized view (Jackson 1991; Knowlton & Jackson 1994), in which coral species have distinct preferences for specific substrata (Morse et al. 1988). While our investigation did not directly evaluate random versus specialized distributions of corals within patches, we found evidence that coral diversity is spatially structured across the reef surface in species-rich regions. This spatial structuring of coral species is not likely the result of interspecific competition leading to niche partitioning (Tanner et al. 1996; Van Woesik 2002). Rather, a more parsimonious explanation is that larger species pools are more likely to contain species that fulfill their resource requirements within specific microhabitats or can tolerate edge habitats, which are frequently harsher than the interior. Our study and hence results are limited to patch reef communities in the Western Atlantic. While untested, a similar, more significant pattern of underestimation may be expected among discretely bounded reefs in the Indo-Pacific were species pools are much larger than the Caribbean. A comparable evaluation of estimates of coral richness among reefs of increasing size in the Indo-Pacific region would, therefore, be prudent.

Underestimation of coral species richness was greatest among small patch reefs ranging from 55-1000m^2 in Belize, the most speciose region surveyed in this study. We speculate that greater underestimation of richness among small reef patches may be the result of both the small size of the species pool and steep drop in the reef area surveyed within transects. The depauperate species pool of the Caribbean prevents a continuous increase in the number of species that can establish on reefs of increasing size. Potentially, species-area effects are no longer relevant on Caribbean reefs beyond the ~1000m^2 reef size. Additionally, as reefs increased in size from 55-1,000m^2, the percentage of the reef surface sampled within 5 transects dropped from 91% to 5%. However, as reef size further increased from 1,000-10,000m^2, the area of reef sampled only changed from 5 to 0.5%, perhaps obscuring significance differences in diversity estimates among these larger reefs. As such, the potential of significantly underestimating coral richness on larger, continuous reef forms (e.g. forereefs and fringing reefs) would be low as these reefs are likely to easily exceed 10,000m^2. Furthermore, large tracts of reefs are commonly sampled at multiple sampling "sites" resulting in a sampling scheme outside of the hypotheses we investigated here.

Comments and recommendations

Maximizing species richness is often a goal of conservation studies (May 1988), yet accurately quantifying richness among spatially variable habitats with limited resources is challenging (Molloy et al. 2010). Within patch reef habitats, our results suggest that reef managers and scientists should consider the risk of bias when estimating coral species richness using fixed sub-sampling methods, especially when sampling among small reef patches habitats in speciose regions. Several countries within the Caribbean possess arrays of small patch reefs with larger species pools, including Belize, the Virgin Islands, Panama, the Cayman Islands, Nicaragua, Turks and Caicos, the Bahamas, Venezuela, Antigua, Guadeloupe, and Aruba. These small reefs (<1000m^2) in speciose regions may benefit from a stratified random sampling design across the reef surface to ensure spatially-structured microhabitats are equally sampled across reefs of varying size. In the Western Atlantic, reefs ranging in size from 55–10,000 m^2 exhibited highly variable transect-to-reef richness values, of which differences in reef size could only account for a small portion of this variability (10%). Therefore, targeting more reef sites rather than more transects per reef, will reduce variance in coral diversity estimates. Additionally, we suggest that coral richness estimates from patch reefs in the Caribbean region should be based on four replicate belt transects to maximize sampling efficiency, regardless of reef size, as greater sampling effort did not ameliorate richness underestimation nor lead to greater richness estimates. These recommendations agree with those of Smith et al. (2011), who propose that increasing the number of reefs sampled, as opposed to increasing the number of transects, will lead to a higher sampling accuracy within a region.

Table 7.1 Descriptive statistics for (A) reef area and (B) coral richness by region.

A) Reef area

Region	n	Mean	SE	Min.	Max.
Bermuda	36	279.5	43.4	59	924
Florida	42	1151.9	203.7	55	5570
Belize	70	3734.7	419.1	100	12169

B) Coral richness

Region	n	Mean	SE	Min.	Max.
Bermuda	36	12.9	0.17	10	15
Florida	42	21.6	0.40	16	27
Belize	70	17.11	0.39	11	24

Table 7.2 ANCOVA results evaluating transect: reef richness values across varying sampling effort (no. of transects), with reef area as a continuous covariate. The top panel (A) are ANCOVA results for the full data set (Bermuda = 36 reefs, Florida = 42 reefs, Belize = 70 reefs); the bottom panel (B) are results for a subset of the reefs sampled to control for differences in reef size among regions (Bermuda = 36 reefs, Florida = 30 reefs, Belize = 24 reefs).

A) Full data set

Source	df	SS	F	p
Log(area)	1	3058.1	34.1	<0.001
No. of Transects	4	46133.0	128.7	<0.001
Log(area)*no. of transects	4	108.5	0.3	0.876

B) Size-restricted data set

Log(area)	1	492.0	7.1	0.008
No. of Transects	4	25544.8	92.1	<0.001
Log(area)* no. of transects	4	37.4	0.1	0.969

Table 7.3 ANCOVA results evaluating transect: reef richness values across the three regions, with reef area as a continuous covariate. Transect: reef richess was based on a sampling effort of 5 transects for this analysis. The top panel (A) are ANCOVA results for the full data set (Bermuda = 36 reefs, Florida = 42 reefs, Belize = 70 reefs); the bottom panel (B) are results for a subset of the reefs sampled to control for differences in reef size among regions (Bermuda = 36 reefs, Florida = 30 reefs, Belize = 24 reefs).

A) Full data set

Source	df	SS	F	p
Log(area)	1	1070.4	7.4	0.007
Region	2	4953.6	17.1	<0.001
Log(area)*region	2	1571.2	5.4	0.005

B) Size-restricted data set

Source	df	SS	F	p
Log(area)	1	989.4	8.7	0.003
Region	2	3714.9	16.4	<0.001
Log(area)*region	2	2769.0	12.2	<0.001

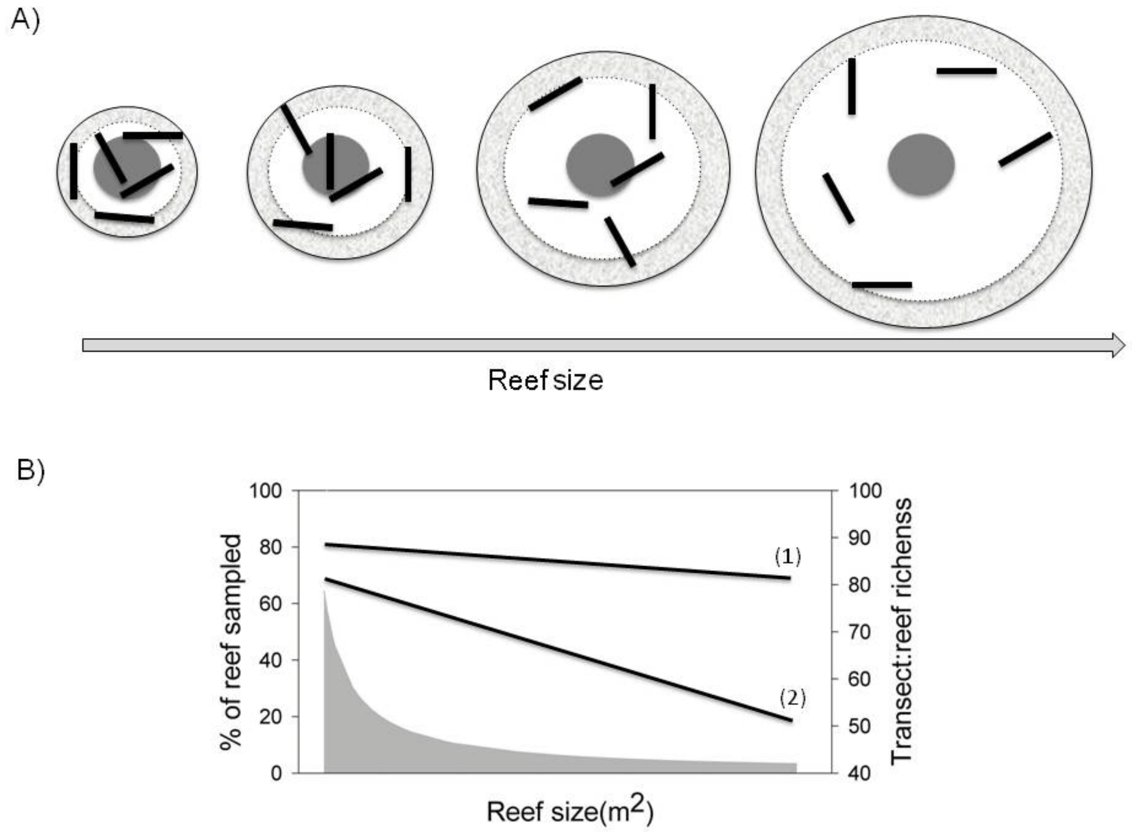


Fig. 7.1 A) Schematic depicting how 5, non-overlapping belt transects (black bars) randomly positioned across the reef surface have a lower probability of encompassing spatially structured features of the reef, such as reef edges (light grey region) and reef cores (dark gray region) as reefs increase in size. B) The qualitative predicted relationship between reef size, the % of reef surface sampled by 5 transects (shaded region), and the proportion of the total reef richness captured in 5 transect (solid lines). Line (1) is the predicted relationship for a species-poor region, while line (2) reflects a species-rich region where the likelihood of habitat partitioning is greater.

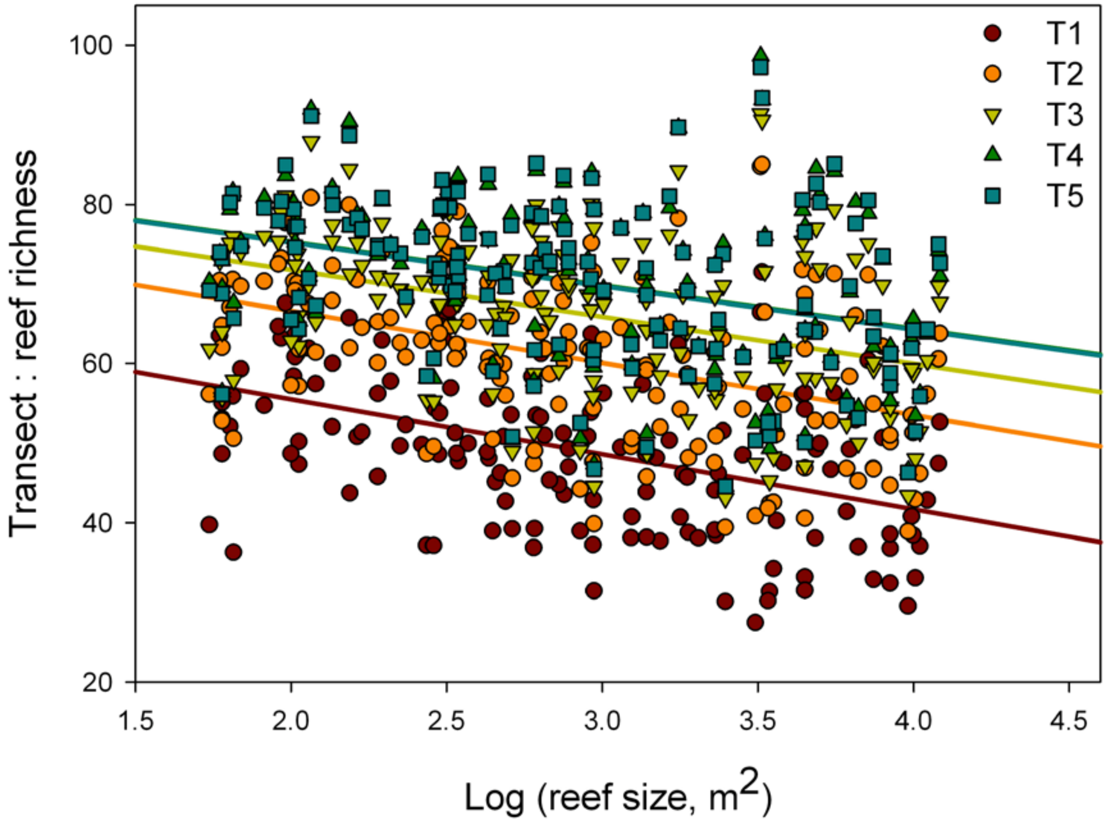


Fig. 7.2 Decline in the proportion of the total reef richness censused in transect subsamples (transect: reef richness) as reef size increases. Transect subsamples were generated for each sampling effort (no. of transects) using a random re-sampling simulation. Sampling effort from 1 to 5 transects are shown in difference colors and fitted with a linear regression. Regression lines for 4 and 5 transect are overlapping on the figure.

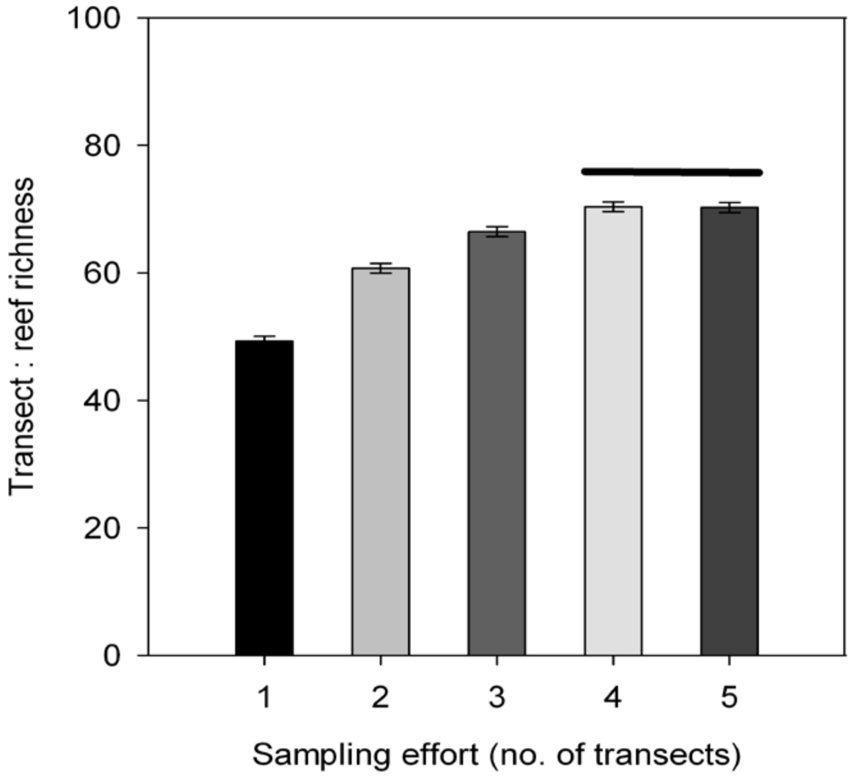


Fig. 7.3 The mean proportion of total reef richness (as least squares means) captured by increasing numbers of transects based on a random re-sampling simulation of transects. Error bars are standard error. The horizontal bar indicates no significant difference between sampling efforts (Tukey's post-hoc test).

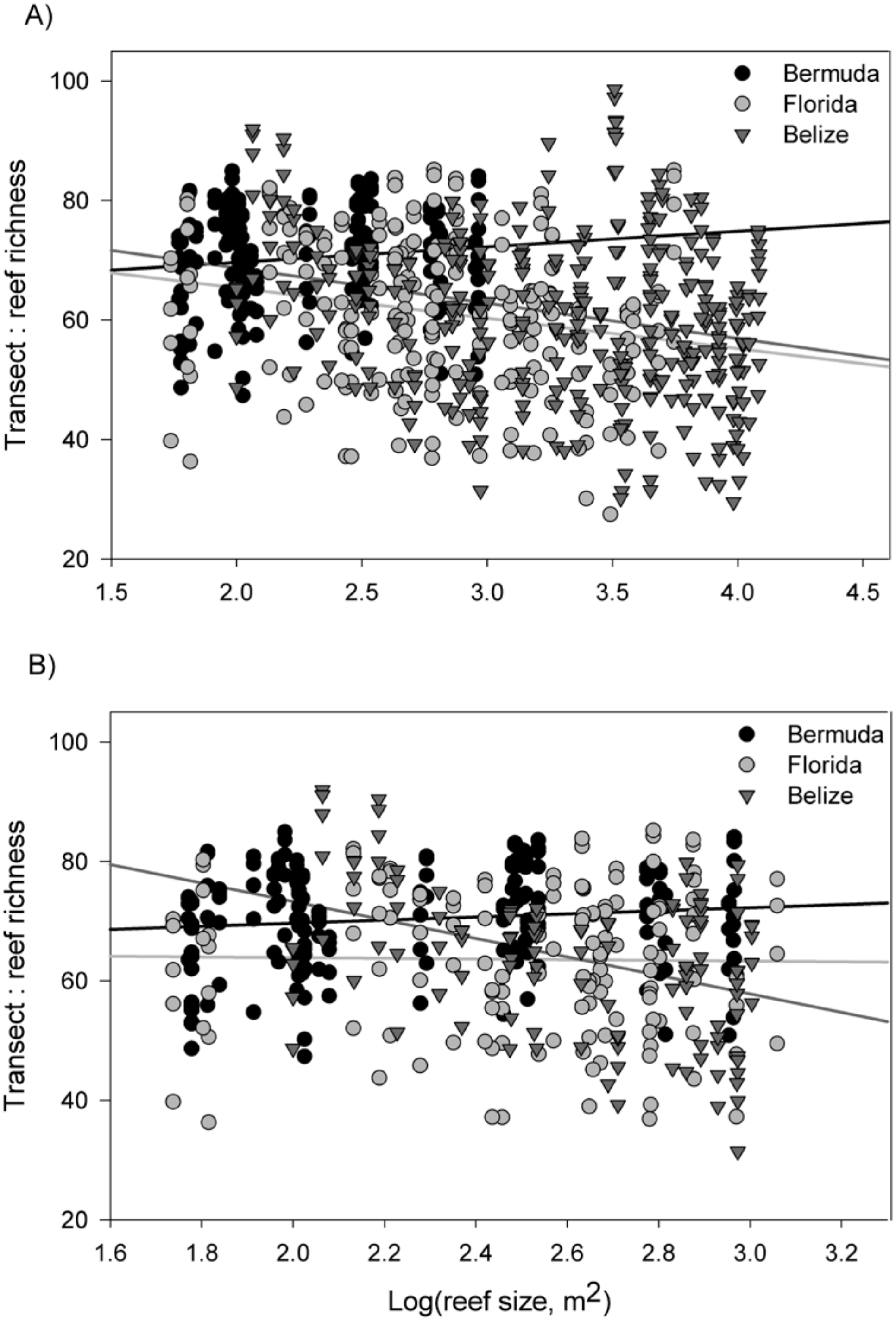


Fig. 7.4 Region-specific relationships between reef size and the proportion of reef richness censused in 5 transect. A) Full dataset (n=740). B) Truncated dataset to reef sizes of ~50-1000m^2 to facilitate regional comparisons (n=440).

CONCLUSIONS

Results Summary

The objectives of this dissertation were to explore the patterns of diversity in coral communities at increasing spatial scales and determine what factors influence these observed patterns. I was interested if coral species were randomly distributed across the reef surface, and if not, whether environmental or spatial factors were influencing coral species distributions. In particular, I sought to apply theoretical principles from the terrestrial-based theories of island-biogeography (MacArthur & Wilson 1967) and species-area relationships (Arrhenius 1921; Connor & McCoy 1979) to investigate the influence of seascape heterogeneity on coral community structure. To achieve this aim, I capitalized on recent advances in remote sensing and image analysis techniques to quantify the spatial configuration composition and composition of patch reefs within the seascape. I focused on the metrics of reef size, reef isolation (configuration), and reef complexity as potential environmental drivers of coral species richness patterns. These metrics of habitat heterogeneity have been identified as important habitat attributes in terrestrial diversity studies (MacArthur & Wilson 1967; Simberloff 1976; Rosenzweig 1995) as well as investigations of reef fish diversity (Gladfleder et al. 1980; Walsh 1985; Bohnsack et al. 1995; Chittaro 2002; Mellin et al 2011). Hence, these environmental metrics were selected as a logical starting point to investigate the role of seascape heterogeneity on corals.

To determine whether coral diversity was randomly distributed, I additively partitioned coral species richness at increasing hierarchical scales among patch reef communities. Coral diversity was partitioned as within-transect (α_1), among transect (β_1), and between reef (β_2) diversity, and compared across 3 regions spanning a 15,000-km latitudinal gradient in the Western Atlantic. Nonrandom patterns in coral species distributions were observed at each of these three hierarchical scales by comparing observed diversity patterns to null model predictions. Additionally, these non-random distributions were consistently observed in each of the three regions of the Western Atlantic, establishing a robust pattern. Hence, I was able to reject the null hypothesis that corals were randomly distributed across space and pursue analyses that explored the alternative hypotheses that (1) geographic position (i.e. spatial autocorrelation) and/or (2) environmental variability (i.e. reef heterogeneity) were making a disproportionate contribution to the overall regional diversity of corals (Legendre et al. 2005).

Coral communities were not found to be spatially autocorrelated among patch reefs, such that reefs in closer geographic proximity to one another shared more similar species compositions. Rather, I found evidence that spatial heterogeneity in the reef habitat correlated with observed coral diversity within a patch reef and between patches. My results indicate that *seascape* configuration and composition has an important role on ecological processes in coral communities. This result is analogous to an extensive body of work in terrestrial systems in which variation in *landscape* configuration and composition has been shown to influence the distribution of species (Thomas et al. 2001; Summerville et al. 2003; Tews et al. 2004).

My results from monitoring natural and artificial patch reefs indicate the importance the size of the reef and the amount of surrounding reef habitats to shape the diversity and abundance of corals on a focal patch. While the largest reefs were not necessarily the most diverse, reef area (m^2) was the foremost predictor of coral richness among the metrics tested, and larger reefs were found to support higher abundances of coral colonies per unit area, suggesting greater immigration rates on larger reefs. Unlike reef fishes, habitat complexity was not a strong predictor of coral diversity, despite the wide range of benthic complexity values sampled. Coral responses to metrics of reef size and spatial isolation did vary by coral reproductive mode, such that brooding species with shorter larval dispersal distances were more sensitive to variations in reef size and isolation than broadcasting species. I conclude that seascape attributes of reef size and configuration can contribute to coral diversity at relatively small spatial scales (<1km). While the significance of these attributes was found to be both scale- and region-specific, I have demonstrated that variability within a single reef type (intra-habitat variability) can play a significant role on organismal diversity in coral reef systems.

While the first chapters of this dissertation explored the importance of spatial variability within a single reef type to influence the coral community, I was also interested in linking this ecological understanding to management efforts. Hence, the two final chapters sought to provide methods to account for landscape heterogeneity when evaluating marine reserve performance and monitoring diversity. A key consideration when assessing the efficacy of reserves is to distinguish the effects of management from the effects of natural variability. I demonstrated how reef heterogeneity, defined as the spatial configuration, composition, and structure of coral reef habitats, can mask our ability to discern reserve effects on both fish and coral communities. I then developed and tested the application of a novel landscape approach to control for the influence of reef heterogeneity by ensuring that reserve sites and fished sites have comparable attributes of reef heterogeneity (Ch. 5). When the performance of the Glover's Reef

Marine Reserve, Belize was assessed without using this landscape approach, no reserve effects were detected in the diversity and abundance of fish and coral communities despite 10 years of management protection. Significant reserve effects for both fish and coral communities were revealed only when sites were classified based on landscape attributes to control for reef heterogeneity.

The final chapter exposed a sampling bias that arises during commonly used methods to census coral community richness when the size of the reef and the regional species pool vary (Ch. 6). I showed that a fixed sub-sampling approach underestimated the true richness of the patch reef as reef size increased. This bias was relatively minor for the entire region of the Western Atlantic on average; underestimation of true diversity was 6% for every 10-fold increase in reef size. However, the magnitude of this bias did increase with regional diversity (γ). Hence, in Belize, the most speciose sub-region sampled, coral richness was underestimated by 15% solely as a result of a ten-fold increase in reef size. Increasing sampling effort per reef was not able to correct for this underestimation, demonstrating that this sampling bias is not an artifact of larger reefs simply being more diverse and requiring greater sampling efforts. Rather, these results again suggest (as in Ch. 2) that coral species are not distributed randomly across the surface of the reef, but in accordance with the variety of spatially structured microhabitats. Furthermore, these patterns seem to be highly scale-dependent such that risk of underestimating coral species richness not only increases in more speciose regions, but also among smaller sized reefs.

Management recommendations and future directions

As coral reefs continue to decline globally, identifying patterns of diversity across spatial scales is a crucial step towards indentify the processes that support these patterns, and determining the appropriate scales to structure coral conservation efforts. My results indicate that, within the Western Atlantic, corals are not randomly distributed within or between patch reefs. Hence, preservation of coral biodiversity will require areas larger than predicted by models that assume random dispersion, especially among lower latitude sites that have larger regional pools.

Furthermore, the preceding chapters reveal that not all patch reefs are created equal. There is substantial variation in the size, spatial isolation, and configuration of patch reefs across the seascape. In this dissertation, I generated models relating coral species distributions to these spatial metrics of reef heterogeneity that were both scale-specific and region-specific. Testing the predictive power of these models will require independent datasets from those used here to generate the models (Hallgren et al. 1999). Hence, I advocate for future work to include expanded data collection of coral communities across reef varying in their attributes of reef heterogeneity and regional species pool (γ) to test the significance of the models presented here.

Given the significant relationships between coral diversity and intra-habitat reef heterogeneity, management plans aiming to protect the coral diversity will need to again be large to encompass intra-habitat variability and be tailored to region seascape features of importance. Likewise, assessments of marine reserve performance should be sensitive to differences among reef sites. My results suggest that not all reef habitats will respond identically to conservation measures. Therefore, when a reserve evaluation is restricted to a Control-Impact assessment, I recommend employing the landscape approach. The landscape classification approach vastly improved our ability to evaluate the efficacy of a marine reserve in the absence of baseline data. To date, this approach has been tested successfully at a single reserve. I advocate for expanded use of this approach in other Caribbean marine reserves to help managers untangle true reserve effects from variability caused differences in habitat.

With regards to monitoring coral reef diversity, I suggest that reef managers consider both the size of the reef to be surveyed as well as the size of the regional species pool (γ) to ensure accurate estimates of coral diversity. Commonly used reef monitoring protocols in the Caribbean (e.g. AGRRA, CARICOMP, NOAA reef assessments) rely on a fixed number of transects per survey site. Among small reefs ($<1000\ m^2$) in speciose regions, the risk of underestimating diversity increases. An alternative search method using a roving diver survey to estimate richness of the entire reef would lead to more accurate assessments of reef diversity in these cases.

The underestimation of coral species richness does suggest that coral species are recruiting non-randomly to specific habitats on the reef surface. To explore the extent of this potential ‘niche-based’ distribution in Caribbean corals, the video mosaic technique (Lirman et al. 2007) would be a major asset. By creating landscape mosaics of these small patch reefs, the spatial position of individual coral colonies, indentified to species, can be mapped across the reef surface. Comparing the spatial positioning of species in relation to patch scale features of the reef edge, the reef core, or specific microhabitats could provide insight into what species are spatially structured.

Significance of approach

The drivers of reef fish diversity have long been evaluated against the theoretical framework of the species-area relationship (Gladfelter et al. 1980; Sale & Douglas 1984; Clarke 1988; Ault & Johnson 1998; Chittaro 2002), the habitat diversity hypothesis (Risk 1972; Gladfelter et al. 1980; Carpenter et al. 1981; Clarke 1988; McLain &Pratt 1999; Caley & St.John 1996; Gratwicke & Speight 2005), and island biogeography (Sandin et al. 2008; Mellin et al. 2010). As a result, tropical marine ecologists are well-informed as to the influence of reef heterogeneity, measured at a variety of spatial scales, on reef fish diversity. In contrast, we know remarkably little about the roles of these same metrics on the coral organisms. Whether this discrepancy arises because coral organisms lack a commercially important fishery to fuel research, exhibit fewer intriguing behaviors to capture ecologist's fascination, or are difficult to experimentally manipulate, the result is a knowledge gap in defining spatial habitat quality from a coral's perspective.

There is an important ecological difference between the fish communities that were the subject of previous studies and the coral communities investigated here. Corals function as ecosystem engineers in the reef system, creating and maintaining reef habitat for other species. Reef fish are occupying fauna of this reef habitat. It is commonly accepted that increases habitat complexity introduced by ecosystem engineers results in an increase in diversity or abundance of the associated fauna (Bandano & Cavieres 2006). However, the influence of habitat complexity, spatial configuration, or size on the habitat-forming organisms themselves remains largely unstudied in terrestrial or marine systems. The unique nature of my dissertation study is that I investigated the influence of seascape heterogeneity on the community composition of the engineering species upon which so many other organisms depend, but that is often overlooked in studies of the relationships between organism-habitat in reef systems.

The community composition, demographics, and habitat structure of ecosystem engineers have been shown to be influenced by environmental gradients such as productivity (Cole & McQuaid, 2010) and temperature (Whittaker 1960). This is the first study in marine systems to explore naturally existing gradients in *intra*-habitat heterogeneity (defined as variations in patch size, spatial isolation, and topographic complexity of patch reefs) to influence coral diversity. Reef heterogeneity influenced the diversity and abundance of corals, yet the significance of this influence on coral communities differed among regions. These finding provide a new insight into the often-overlooked importance of seascape context within a reef type. My results show that existing variations in the size of the reef and its spatial isolation from neighboring reefs can influence coral density and diversity. In low diversity regions at higher latitudes, these effects of habitat heterogeneity may be more pronounced and therefore ecologically important. While at lower latitudes where diversity is greater, local interactions among species swamp meso-scale influences of habitat heterogeneity.

Until recently, community ecology has focused on local-scale phenomena, implicitly assuming that systems are closed and that spatial processes are unimportant. In this dissertation, I take a broader-scale approach to investigating spatial patterns in coral diversity, exploring the role of meso-scale aspects of reef heterogeneity to influence coral distributions.I am in the company of a handful of other reef ecologists using remotely-sensed satellite imagery and habitat mapping techniques to place reef sites in the context of the larger seascape (see Friedlander et al. 2007; Harborne et al. 2008; Mellin et al.

2010). These techniques allow for the generation of detailed benthic habitat maps upon which spatial heterogeneity of habitats within the seascape can be readily quantified. This spatial heterogeneity, and its underlying abiotic and biotic causes, is known to generate diversity in terrestrial communities and shapes species distributions (Legendre and Fortin 1989; Talley 2007). Hence, a landscape ecology approach, in which the relationships between spatial patterns and species composition across multiple scales are explored, is a promising area of study in shallow coral reef habitats to understanding the consequences of spatial heterogeneity in sustaining community diversity.

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APPENDICES

Appendix A. Latin names of the Caribbean corals known to occur within each region.

Bermuda	**Belize**	**Florida**
Agaricia fragilis	*Acropora cervicornis*	*Acropora cervicornis*
*Dichocoenia stokesii**	*Acropora palmata*	*Acropora palmata**
Diploria labyrinthiformis	*Acropora prolifera*	*Agaricia agaricites*
Diploria strigosa	*Agaricia agaricites*	*Agaricia fragilis*
Favia fragum	*Agaricia fragilis*	*Agaricia lamarcki*
Isophyllia sinuosa	*Agaricia lamarcki**	*Colpophyllia natans*
Madracis decactis	*Agaricia grahamae**	*Dendrogyra cylindrus*
*Madracis formosa**	*Agaricia tenuifolia*	*Dichocoenia stokesii*
Madracis mirabilis	*Colpophyllia natans*	*Diploria clivosa*
Meandrina meandrites	*Dendrogyra cylindrus*	*Diploria labyrinthiformis*
Montastraea cavernosa	*Dichocoenia stokesii*	*Diploria strigosa*
Montastraea franksi	*Diploria clivosa*	*Eusmilia fastigiata*
Oculina diffusa	*Diploria labyrinthiformis*	*Favia fragum*
Oculina robusta	*Diploria strigosa*	*Isophyllia sinuosa*
Porites astreoides	*Eusmilia fastigiata*	*Leptoseris cucullata*
Porites porites	*Favia fragum*	*Madracis decactis*
*Scolymia cubensis**	*Isophyllia sinuosa*	*Manicina areolata*
Siderastrea radians	*Isophyllastrea rigida*	*Meandrina meandrites*
Stephanocoenia intersepta	*Leptoseris cucullata*	*Montastraea annularis*
	*Madracis mirabilis **	*Montastraea cavernosa*
	*Madracis formosa**	*Montastraea faveloata*
	Madracis decactis	*Montastraea franksi*
	Manicina areolata	*Mycetophyllia aliciae*
	Montastraea annularis	*Mycetophyllia danaana*
	Montastraea cavernosa	*Mussa angulosa*
	Montastraea faveloata	*Oculina diffusa*
	Montastraea franksi	*Porites astreoides*
	Mycetophyllia aliciae	*Porites branneri*
	Mycetophyllia danaana	*Porites divaricata*
	*Mycetophyllia ferox**	*Porites furcata*
	Mycetophyllia lamarckiana	*Porites porites*
	*Mycetophyllia reesii**	*Scolymia cubensis*
	Mussa angulosa	*Siderastrea radians*
	*Oculina diffusa**	*Siderastrea siderea*
	Porites astreoides	*Solenastrea bournoni*
	Porites branneri	*Stephanocoenia intersepta*
	Porites divaricata	
	Porites furcata	
	Porites porites	
	Scolymia cubensis	
	Siderastrea radians	
	Siderastrea siderea	
	*Solenastrea bournoni**	
	Stephanocoenia intersepta	

* indicates a species that is regionally present but not observed in my samples

Appendix B. Environmental and spatial metrics for each sampled patch reef in A) Bermuda, B) Florida, and C) Belize. All values are raw, untransformed data.

A) Bermuda	site #	area (m^2)	Nearest neighbor (m)	1km buffer (km^2)	rugosity	latitude	longitude
	32	42	36	0.36	1.89	32.350	64.799
	24	59	28	0.29	1.91	32.337	64.800
	1	60	30	0.23	1.86	32.344	64.793
	2	60	49	0.28	1.85	32.343	64.795
	6	60	43	0.30	1.94	32.341	64.797
	5	65	38	0.35	1.57	32.350	64.798
	41	69	80	0.26	1.49	32.338	64.796
	3	82	35	0.31	1.42	32.349	64.795
	42	91	52	0.27	1.72	32.333	64.800
	13	93	27	0.32	1.44	32.345	64.797
	27	96	36	0.28	2.22	32.338	64.798
	12	102	67	0.41	1.64	32.359	64.805
	9	103	31	0.25	1.82	32.337	64.797
	25	103	37	0.28	1.97	32.339	64.797
	16	105	36	0.37	1.91	32.351	64.799
	17	106	50	0.32	1.55	32.348	64.796
	7	114	25	0.36	2.05	32.351	64.798
	4	120	61	0.29	1.36	32.348	64.794
	10	190	31	0.36	2.00	32.353	64.799
	8	196	36	0.35	1.59	32.354	64.798
	11	289	31	0.41	1.56	32.356	64.801
	43	302	25	0.36	1.55	32.348	64.798
	18	306	27	0.36	1.43	32.347	64.799
	15	308	13	0.37	2.06	32.352	64.799
	14	319	27	0.37	1.70	32.352	64.800
	38	323	33	0.31	1.83	32.343	64.798
	34	326	34	0.26	1.49	32.341	64.794
	45	344	65	0.33	1.61	32.358	64.796
	47	344	21	0.40	1.52	32.354	64.802
	19	595	37	0.33	1.65	32.343	64.799
	20	596	52	0.41	1.96	32.356	64.803
	39	635	28	0.26	1.71	32.339	64.795
	35	653	216	0.17	1.88	32.342	64.791
	21	899	39	0.36	1.78	32.347	64.800
	40	920	80	0.36	1.80	32.344	64.803
	22	924	58	0.36	1.81	32.346	64.801

B) Florida	site #	area (m^2)	nearest neighbor (m)	1km buffer (km^2)	rugosity	latitude	longitude
	25	55	52	0.18	2.03	25.453	80.158
	24	64	43	0.19	1.54	25.457	80.156
	20	65	55	0.24	1.90	25.464	80.152
	19	136	71	0.16	1.67	25.476	80.153
	22	155	44	0.31	1.72	25.460	80.151
	63	163	58	0.1	1.32	25.497	80.127
	66	190	65	0.2	1.66	25.520	80.132
	45	224	183	0.15	1.75	25.376	80.155
	23	263	103	0.09	1.50	25.466	80.159
	17	273	27	0.44	1.53	25.467	80.140
	64	287	45	0.2	1.68	25.503	80.128
	1	345	132	0.22	1.75	25.366	80.188
	27	372	74	0.07	1.57	25.439	80.163
	40	429	46	0.05	1.51	25.430	80.166
	18	432	133	0.11	1.49	25.483	80.153
	15	445	58	0.40	1.61	25.422	80.156
	48	454	60	0.10	1.48	25.405	80.146
	55	470	49	0.40	1.41	25.448	80.146
	47	482	101	0.16	1.48	25.391	80.151
	26	510	71	0.11	1.53	25.448	80.162
	2	603	26	0.27	1.42	25.363	80.167
	58	606	58	0.3	1.37	25.482	80.141
	37	614	68	0.29	1.70	25.383	80.175
	50	633	95	0.23	1.43	25.436	80.153
	34	751	98	0.09	1.60	25.384	80.182
	57	755	47	0.32	1.53	25.476	80.141
	14	934	195	0.44	1.59	25.396	80.168
	61	1147	72	0.1	1.66	25.402	80.149
	13	1238	59	0.22	1.72	25.485	80.149
	51	1246	44	0.35	1.48	25.447	80.151
	43	1494	82	0.23	1.45	25.425	80.161
	36	1535	133	0.30	1.71	25.377	80.175
	54	1644	106	0.20	1.57	25.427	80.139
	10	1783	228	0.40	1.52	25.397	80.158
	65	1816	61	0.2	1.40	25.514	80.136
	56	2322	55	0.40	1.30	25.453	80.140
	7	2486	48	0.59	1.56	25.389	80.163
	6	3104	63	0.60	1.80	25.388	80.163
	3	3633	159	0.43	1.58	25.364	80.176
	12	3825	85	0.19	1.69	25.496	80.143
	9	4828	160	0.41	1.92	25.397	80.159

	8	5570	64	0.05	1.51	25.444	80.176

C) Belize	site #	area (m^2)	nearest neighbor (m)	1km buffer (km^2)	rugosity	latitude	longitude
	14	100	69	1.02	1.56	16.731	87.837
	36	116	38	0.40	2	16.722	87.851
	54	136	51	0.28	1.54	16.905	87.777
	65	154	24	0.27	1.58	16.901	87.784
	52	169	37	0.07	1.39	16.870	87.740
	30	209	46	0.55	1.43	16.765	87.790
	41	234	185	0.22	1.58	16.819	87.765
	27	298	225	0.21	1.37	16.818	87.832
	35	300	21	0.92	1.94	16.723	87.846
	73	337	30	0.26	1.71	16.904	87.786
	53	341	56	0.17	1.38	16.879	87.739
	55	427	30	0.26	1.57	16.900	87.785
	62	489	16	0.51	1.99	16.726	87.878
	25	514	37	0.45	1.73	16.804	87.763
	22	677	27	0.14	1.58	16.878	87.739
	19	725	69	0.46	1.41	16.886	87.788
	42	726	76	0.42	1.49	16.771	87.859
	8	780	79	0.28	1.45	16.834	87.814
	43	780	79	0.14	1.34	16.776	87.839
	24	850	79	0.05	1.7	16.845	87.756
	7	936	5	1.41	1.72	16.760	87.776
	76	939	194	0.08	1.63	16.853	87.754
	10	940	107	0.73	1.58	16.784	87.848
	69	1009	167	0.40	1.55	16.798	87.845
	60	1350	202	0.13	1.38	16.890	87.758
	50	1382	158	0.17	1.46	16.854	87.791
	61	1387	207	0.14	1.2	16.888	87.760
	44	1388	72	0.14	1.22	16.859	87.778
	51	1758	120	0.09	1.33	16.855	87.753
	57	1877	70	0.14	1.27	16.800	87.794
	16	1894	158	0.11	1.56	16.758	87.854
	46	2035	72	0.19	1.34	16.837	87.796
	37	2295	152	0.38	1.5	16.762	87.807
	71	2299	165	0.10	1.18	16.787	87.832
	90	2362	44	0.25	1.47	16.885	87.773
	28	2443	39	0.24	1.5	16.816	87.788
	26	2833	164	0.23	1.7	16.828	87.805
	56	3223	226	0.12	1.56	16.773	87.823
	59	3261	81	0.09	1.57	16.884	87.752

40	3328	273	0.22	1.24	16.787	87.789
92	3408	125	0.19	1.18	16.837	87.794
1	3447	200	0.22	1.71	16.748	87.831
21	3554	303	0.36	1.47	16.886	87.734
39	4400	275	0.19	1.65	16.783	87.800
93	4475	189	0.22	1.45	16.821	87.780
98	4475	225	0.07	1.38	16.787	87.823
99	4477	161	0.07	1.23	16.785	87.826
87	4481	99	0.56	1.85	16.904	87.733
45	4863	153	0.17	1.36	16.842	87.779
63	4997	49	0.78	1.42	16.722	87.871
89	5433	235	0.14	1.47	16.891	87.770
29	6108	72	0.26	1.35	16.809	87.807
17	6232	52	0.17	1.78	16.867	87.769
38	6516	90	0.19	1.21	16.755	87.828
88	6649	15	0.09	1.38	16.888	87.754
70	7149	161	0.41	1.34	16.797	87.845
75	7431	50	0.07	1.52	16.871	87.742
49	7444	174	0.40	1.35	16.855	87.797
72	7963	54	0.25	1.25	16.816	87.829
94	8416	118	0.24	1.31	16.776	87.795
97	8418	167	0.08	1.41	16.785	87.831
96	8425	191	0.15	1.57	16.792	87.828
85	9608	61	0.28	1.65	16.762	87.812
83	9865	43	0.86	1.39	16.721	87.877
68	9977	103	0.20	1.46	16.788	87.792
86	10126	329	0.12	1.7	16.774	87.817
15	10489	73	0.17	1.71	16.764	87.819
100	11086	136	0.14	1.41	16.777	87.825
91	12048	16	0.44	1.35	16.851	87.799
67	12169	184	0.29	1.24	16.810	87.830

Appendix C. All possible models from Ch. 3 multi-predictor models linking seascape metrics to measures of the coral community. Models are ranked by small sample correction to Akaike's information criterion (AIC_c). Models with $\Delta AIC_c < 2$ have substantial support.

Coral variable	Model	R^2	Cp	AIC_c	ΔAIC_c
Transect Richness	RA	0.44	1.39	125.04	0.00
	C	0.38	2.42	125.76	0.72
	SRH	0.39	3.64	127.58	2.54
	NN	0.45	3.13	127.60	2.56
	RA + NN	0.44	3.39	127.90	2.86
	RA + SRH	0.38	4.37	128.35	3.31
	RA + C	0.40	5.53	130.32	5.28
	C + SRH	0.45	5.00	130.54	5.50
	RA + NN +SRH	0.25	10.43	134.17	9.13
	RA + C +NN	0.14	13.79	135.89	10.85
	RA + C + SRH	0.25	12.35	136.97	11.93
	C + NN +SRH	0.02	19.10	139.68	14.64
	RA + C + NN +SRH	0.02	19.20	139.76	14.71
Reef richness	RA	0.53	2.21	134.67	0.00
	RA + NN	0.56	2.32	135.24	0.57
	RA + C	0.55	3.38	136.42	1.75
	RA + C + NN	0.58	3.06	136.64	1.97
	RA + SRH	0.54	3.95	137.04	2.37
	RA + NN + SRH	0.57	3.61	137.29	2.62
	RA + C + SRH	0.55	5.38	139.28	4.61
	RA + C + NN +SRH	0.58	5.00	139.67	5.00
	C	0.31	16.04	146.68	12.01
	C + RSA	0.36	15.11	147.14	12.48
	C + NN +SRH	0.36	17.09	149.99	15.33
	NN	0.08	30.69	155.76	21.09
	SRH	0.00	35.42	158.21	23.54
Colony density	RA + SRH	0.35	1.31	173.15	0.00
	RA + C	0.30	3.47	175.59	2.45
	RA + C + SRH	0.35	3.06	175.71	2.56
	RA + NN + SRH	0.35	3.26	175.95	2.80
	RA	0.22	4.41	175.99	2.85
	NN + SRH	0.23	6.13	178.37	5.22
	RA + C + NN	0.30	5.47	178.45	5.31
	RA + NN	0.22	6.33	178.56	5.42
	RA + C + NN +SRH	0.36	5.00	178.74	5.60

	SRH	0.14	7.73	179.11	5.96
	C + NN +SRH	0.26	7.06	180.14	6.99
	NN	0.06	11.15	182.02	8.87
	C + NN +SRH	0.01	13.01	183.49	10.35
Brooder density	RA + SRH	0.40	1.18	160.72	0.00
	RA	0.30	3.54	162.85	2.13
	RA +NN + SRH	0.41	3.06	163.45	2.72
	RA + C + SRH	0.40	3.11	163.50	2.78
	RA +C	0.33	4.56	164.48	3.76
	RA + NN	0.30	5.53	165.48	4.76
	C + SRH	0.29	6.22	166.18	5.45
	RA + C + NN +SRH	0.41	5.00	166.47	5.75
	C + NN +SRH	0.33	6.54	167.32	6.60
	RA + C + NN	0.33	6.56	167.34	6.62
	SRH	0.11	11.87	170.33	9.60
	NN	0.09	12.90	171.14	10.42
	C	0.06	14.35	172.24	11.52
Broadcaster density	C	0.06	0.32	129.34	0.00
	SRH	0.04	1.02	130.12	0.78
	RA + C	0.11	1.01	130.46	1.13
	NN	0.00	2.10	131.30	1.96
	RA + C	0.00	2.18	131.38	2.04
	C + SRH	0.07	2.00	131.63	2.29
	C + NN	0.07	2.17	131.81	2.47
	NN + SRH	0.04	3.00	132.75	3.42
	RA + C + NN	0.11	3.00	133.32	3.98
	RA + C + SRH	0.11	3.01	133.32	3.98
	C + NN +SRH	0.08	3.87	134.33	4.99
	RA + NN + SRH	0.04	5.00	135.62	6.28
	RA + C + NN +SRH	0.11	5.00	136.41	7.08
% Coral Cover	RA	0.04	-0.28	178.95	0.00
	NN	0.02	0.21	179.52	0.56
	SRH	0.00	0.71	180.08	1.12
	C	0.00	0.72	180.09	1.14
	RA + C	0.06	1.20	180.99	2.03
	RA + NN	0.04	1.69	181.57	2.61
	RA + SRH	0.04	1.71	181.59	2.64
	C + NN	0.02	2.14	182.08	3.13
	RA + C + SRH	0.06	3.05	183.67	4.71
	RA + C + NN	0.06	3.12	183.76	4.80

	RA + NN + SRH	0.04	3.67	184.41	5.45
	C + NN +SRH	0.02	4.11	184.91	5.96
	RA + C + NN +SRH	0.06	5.00	186.71	7.76
Mean colony size	C	0.13	1.52	-127.58	0.00
	RA	0.11	1.90	-127.17	0.41
	RA + NN	0.16	2.47	-126.09	1.49
	C + NN	0.15	2.72	-125.82	1.76
	RA + C	0.15	2.85	-125.67	1.91
	C + SRH	0.14	3.08	-125.42	2.16
	RA + C + NN	0.20	3.01	-124.92	2.66
	RA + NN + SRH	0.17	4.11	-123.64	3.94
	C + NN +SRH	0.17	4.22	-123.51	4.07
	SRH	0.00	5.59	-123.45	4.13
	NN	0.00	5.62	-123.41	4.17
	RA + C + SRH	0.15	4.73	-122.94	4.64
	RA + C + NN +SRH	0.20	5.00	-121.84	5.74

RA, $\log_{10}$–reef area (m^2); C, benthic complexity; NN, nearest neighbor (m); SRH, surrounding reef habitat (m^2)