A multi-scale assessment of the benthic communities of Bermuda's shallow water platform focusing on existing MPA's & control sites to enhance local management practices

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PROGRAMME
BERMUDA BIODIVERSITY PROJECT
BERMUDA ZOOLOGICAL SOCIETY

Non-Technical Summary

In this report we describe the assessment of benthic ecological data collected across the reef platform as a first step, in order to determine areas of special ecological character that would benefit from additional protection under legislation. We also evaluated the effectiveness of Bermuda's existing MPA's in limiting damage to corals, through the use of comparative digital videography surveys, and highly appropriate recommendations which are of use to local resource managers. A second document reports the concurrent assessment of fish populations across the Bermuda Platform and within MPA versus control sites.

Principle Findings

Distinct differences were found between fringing reefs, lagoonal patch reef, rim reef and fore reef habitats Additionally, reefs within all types of habitat demonstrated high variability in most measures of coral reef condition and in coral and fish community structure.

Lagoonal patch reefs could be broadly categorized into three types based on dominant coral species. These three types were: (1) Madracis Reefs, (2) Montastraea Reefs, and (3) Dipoloria-Porites Reefs. Madracis and Montastraea reefs appear to represent particularly unusual habitat. Fortunately the areas in which these two reef types are found are already benefiting from two levels of legislative protection, in that all corals are protected in Bermuda, and these reef types are located within the Northern Coral Reef Preserve, where no collecting of any benthic organisms are permitted..

Rim reefs also can be sub-divided into types based on location on the platform, as well as geomorphology. Deeper passes that intersect the shallow rim reef flats are statistically significantly different in coral cover and community structure. Several of these passes are currently protected as MPA sites, but additional passes should be protected as well.

MPA sites did NOT differ from environmentally similar control sites in the cover of most benthic functional groups, especially coral cover, in that all sites were quite healthy. A lack of differences is probably due to the hardy nature of the corals that live in the rim habitat where the MPAs were located, as well as low levels of impact by divers or boaters.

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Chapter One: Introduction

Bermuda, a United Kingdom Overseas Territory, is located on a 5560-hectare chain of limestone islands located in the North Atlantic near 32°N 64°W (Figure 3.01). Although Bermuda is north of the tropics, prevailing warm oceanic conditions support a limited number of small mangrove forests, extensive seagrass beds and well-developed coral reefs. The Bermuda reef platform encompasses a wide range of habitat types, from small, enclosed bays and harbors to the broad lagoon, all of which are encircled by a well-developed rim reef and large, exposed fore-reef zones. Bermuda is host to a reduced suite of species of reef-building corals relative to more southern reefs of the Caribbean, with only 22 species of shallow-water hard coral recorded (Appendix 2.01; Sterrer 1998).

It appears that acroporid corals were not present in Bermuda over the past several hundred thousand years (Garrett et al. 1971). Repeated transplant experiments carried out in the early 1970s at a site on the northern rim reef confirmed that acroporid corals are currently prevented from establishment on Bermuda reefs by cold winter temperatures (R. N. Ginsburg and E. A. Shinn personal communication). Consequently, unlike most of the western Atlantic (Aronson and Precht 2001), Bermuda's reefs were not affected by the loss of staghorn and elkhorn corals that occurred in the 1980s to early 1990s. Instead, in most places the reef community appears to have changed little in the past 30 years when compared to the rest of the Caribbean, despite continued perturbation from overfishing (Butler et al. 1993), ship groundings (Smith 1992), sedimentation (Dodge and Vaisnys 1977), land reclamation (Flood et al. 2006), coral bleaching and coral disease (Cook et al. 1990). Coral cover in Bermuda has typically been cited as averaging 50–90% on the terrace reef (Logan 1988), 20–26% at rim reef sites (Dodge et al. 1982, CARICOMP 1997), 17% (with a range of 10–45%) on patch reefs (Dodge et al. 1982, Garrett et al. 1971; Murdoch et al. unpublished data) and 13% inside the breaker line on the South shore (Garrett et al. 1971) – although the surveys described in this report will show that most of these values are underestimates of average cover across most of these reef zones.

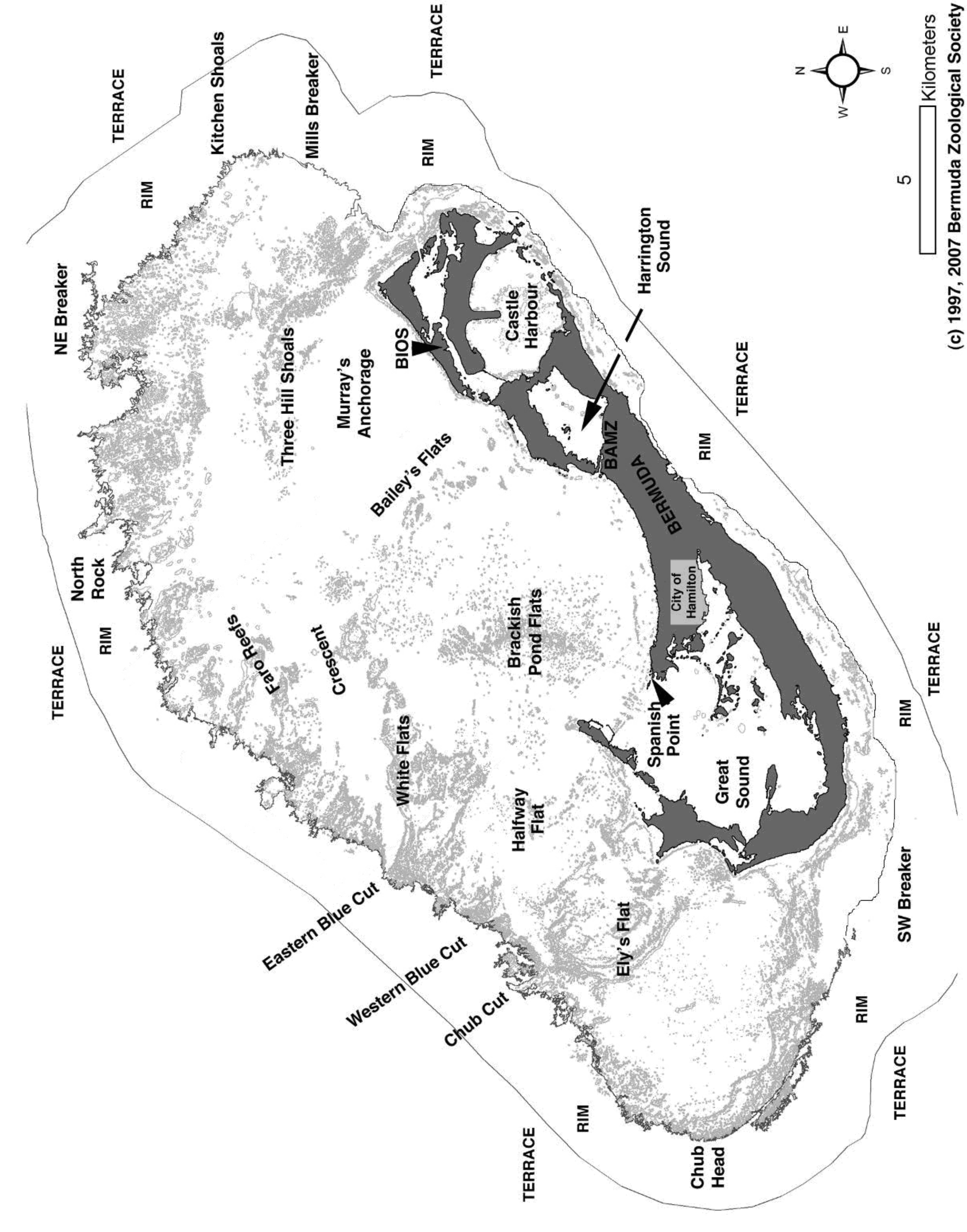
Figure 3.01. A photomosaic map of the Bermuda Islands and surrounding reef platform.

Study Area

Surveys were done across the lagoon, rim, and 30-ft forereef habitats. Platform margin (fore) reefs and lagoonal reefs have been historically classified into several different types, with some of the nomenclature specific to Bermuda (Figure 3.02; Garrett et al. 1971; Logan 1988; Logan and Thomas 1992). Within the lagoon, pinnacle reefs are characteristically steep-sided patch reefs measuring 10–150 m in width and 6–20 m in height, and are typically found in the outer lagoon. Ring-shaped patch reefs that are 50-m to 500-m wide are known as “mini-atolls”. Mini-atolls typically have a raised rim of coral and algae encircling a sediment-filled mini-lagoon containing only scattered coral knobs. When mini-atolls extend beyond 500 m in width they are referred to as “faro” reefs (Stoddart and Scoffin 1979; Logan 1988). In Bermuda faro reefs generally exhibit large central areas of shallow (~4-m depth) sandy seabed peppered with very sparse coral knobs, fringed by a ~10-m wide ridge of well-developed coral reef and surrounded by much deeper water (10 - 20-m depth).

The outer edge of the lagoon is ringed by a shallow rim reef, that does not shoal and therefore is not technically a reef crest. Just seaward of the rim around much of the reef platform are found algal-cup reefs built by crustose coralline algae and vermetiid gastropods that do shoal at low tide, and which are locally knows as “boilers”. The fore-reef forms a broad shelve from 8-m depth to 20-m, and thereafter slopes to depth at a steeper angle. Shallow water corals rarely grown below 75-m depth and little calcareous reef deposits occur below 200 m. Below 200-m depth the hard substrate is of volcanic origin, which continues down to the ocean floor at over 4000-m depth.

Figure 3.02. (below) An illustrated map of the islands and surrounding lagoonal patch reefs of Bermuda, with important geographic features labeled (produced by the author). The islands of Bermuda are clustered in a fishhook-like shape on the southeast side of the atoll. The reef platform extends 15 km to the northwest of the island. The rim reef reaches to within 2 m of the sea surface and encloses the north lagoon and the tens of thousands of patch and pinnacle reefs therein. The fore reef surrounds the island and platform and extends down to a continuous field of loose rubble rhodoliths that rings the platform at roughly 100-m depth. Below this field, the sides of the extinct volcano on which Bermuda rests continue down without coral growth to the Bermuda Rise, over 4000-m deep.


TERRACE
RIM
NE Breaker
North Rock
Kitchen Shoals
Mills Breaker
Three Hill Shoals
Murray's Anchorage
BIOS
Castle Harbour
Harrington Sound
BAMZ
BERMUDA
Bailey's Flats
Faro Reefs
Crescent
Brackish Pond Flats
City of Hamilton
Spanish Point
Great Sound
White Flats
Halfway Flat
Eastern Blue Cut
Western Blue Cut
Chub Cut
Ely's Flat
SW Breaker
Chub Head
N
E
S
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Kilometers
(c) 1997, 2007 Bermuda Zoological Society

Chapter 2: Mapping of Benthic Habitats

In order to aid in the scientific study of Bermuda's lagoonal reefs henceforth, we produced the first accurate, geo-referenced digital map of the entire suite of reefs. This map was produced by referencing a mosaic set of georeferenced aerial photographs of the islands and surrounding submerged platform that the Bermuda Zoological Society commissioned in 1997 (Figure 3.01).

The aerial photographs of the Bermuda Islands and surrounding reef platform were produced using a Zeiss Jena LMK photogrammetric survey camera with forward motion compensation, which was mounted onto a small aircraft. In 2003 a composite raster bitmap for the entire Bermuda platform was produced from the slides, with a final resolution of 50 cm per pixel and a geo-referenced error of less than 2 m (Bermuda Zoological Society 1997). A map of probable coral reef habitat was then created for the entire Bermuda platform from the digital mosaic with the GIS package ESRI ArcMap 9.1. To create this map, we manually digitized the boundaries of coral reef areas as continuous closed polygons at a scale of 1:2500, using color (light to dark reddish-brown) and the presence of sand halos around reefs as visual indicators of boundary edge. Spatial referencing of the digital photographs was accurate to 2 m and, combined with a pixel size of 50 cm, a spatial accuracy of about ±2.5 m was possible for visually mapped reef boundaries. Over 34,000 separate reefs were mapped across the extent of the lagoon. Once the boundaries of each patch reef within the lagoon was mapped to GIS, we then mapped the inner boundary of the rim reef. Boiler reefs and seagrass meadows were also mapped following the same procedures (Figure 1.02).

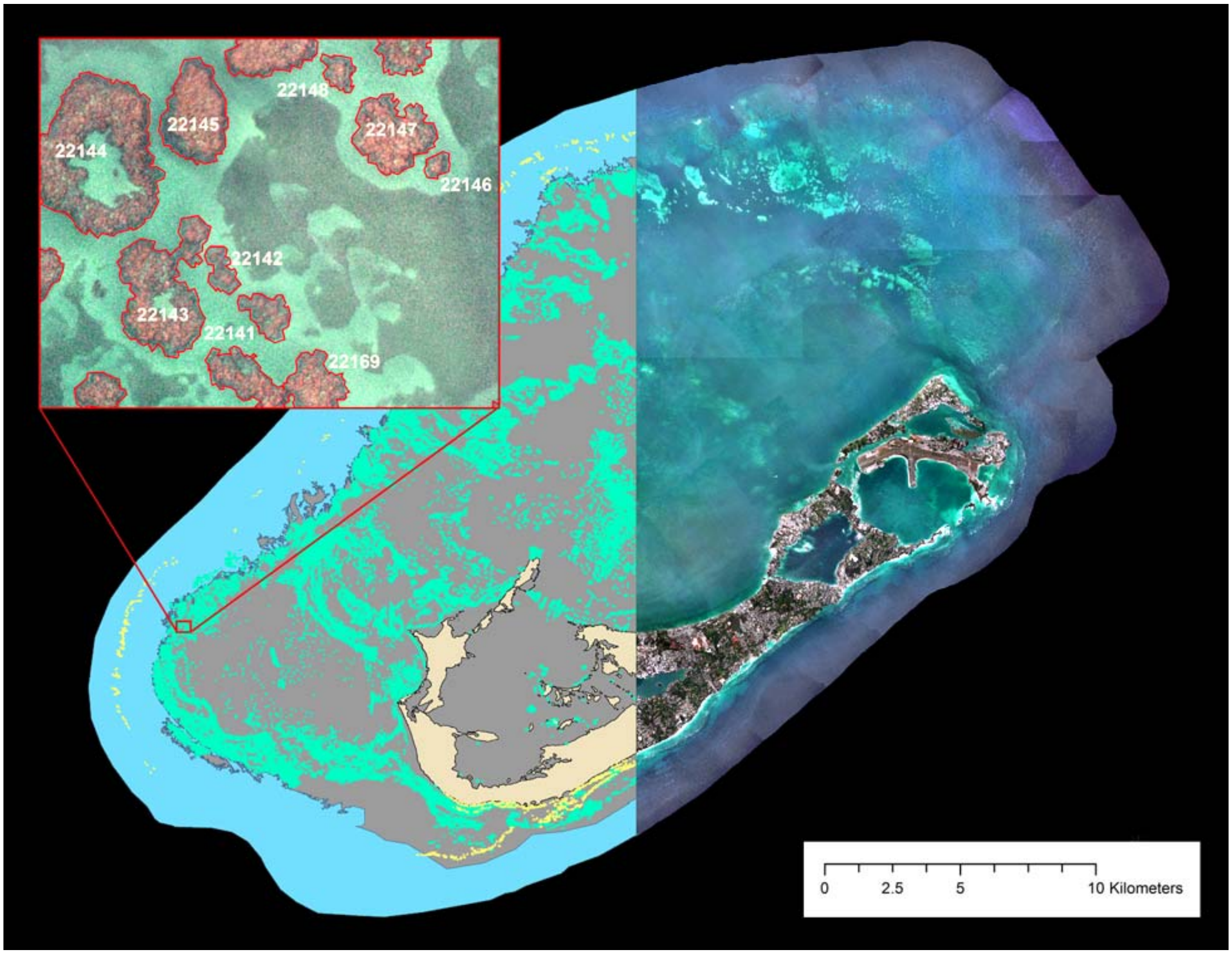


Fig. 1.01 The photomosaic of aerial images, shown on the right side) was used to generate a GIS map of all reef habitats across the Bermuda Platform, as shown on the left side of the image. The inset shows how GIS mapping allows for all ~35,000 patch reefs within the lagoon to be assigned their own unique identification number.

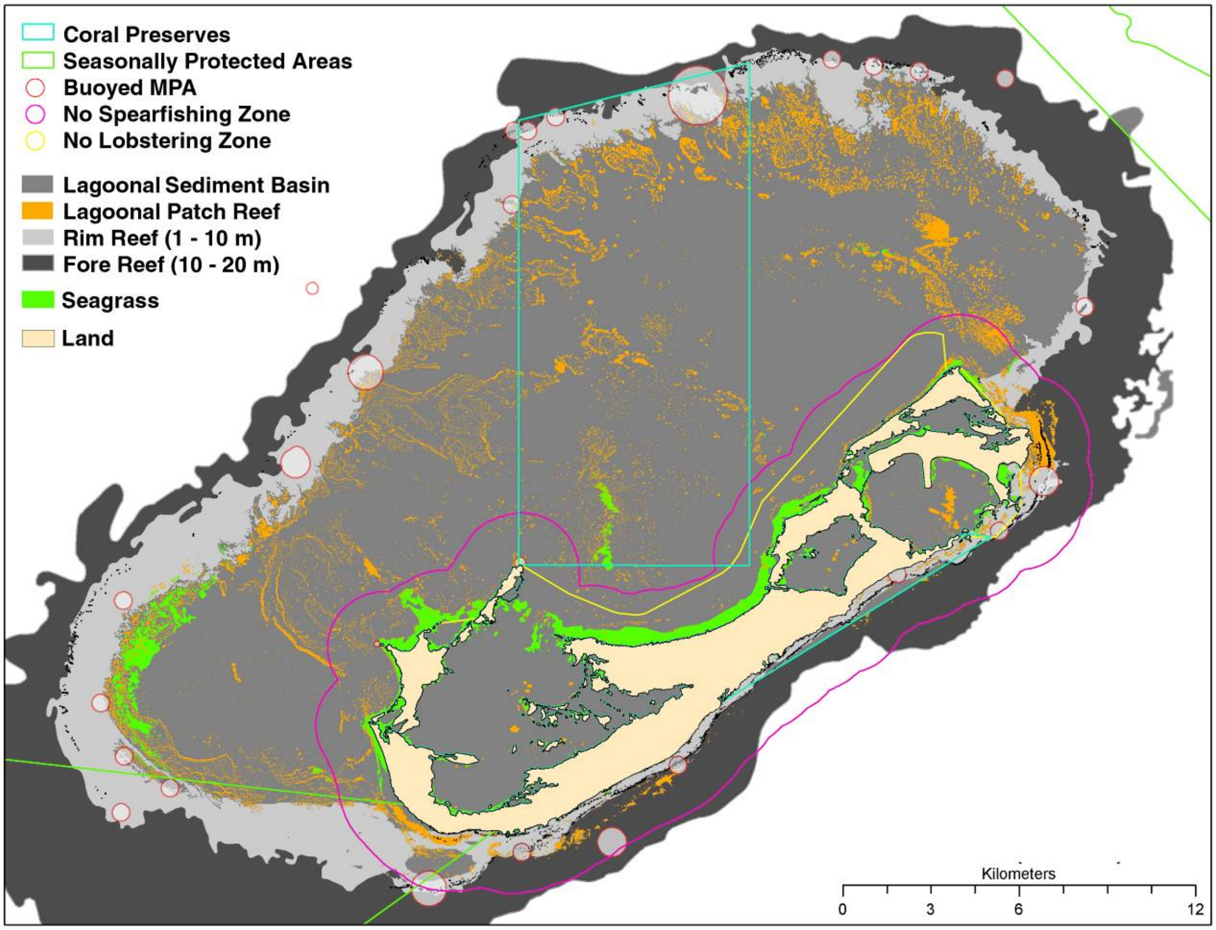


Fig. 1.02. Map of coral, seagrass and sediment habitats across the Bermuda reef platform, as well as the boundaries of the various kinds of marine protected areas.

Chapter 3: Assessing And Mapping The Distribution Of Ecological Characteristics Of Coral Reefs Across The Bermuda Platform, Including Key Life-History Stages Of Hard Corals

Introduction

The coral reefs of Bermuda have been the focus of interest for geologists and biologists for over 100 years (Heilprin 1889; Agassiz 1895; Verrill 1902). Recent research has focused on reefs within Castle Harbour (Dodge et al. 1982; Smith 1999; Flood et al. 2006; Jones et al. 2007), along the nearshore zones off North Shore (Smith et al. 1998; Jones et al. 2007), within the central lagoon at Three-Hill Shoals and Crescent Reef (e.g. Logan 1988; Smith et al. 2003; Jones et al. 2007), and on the northern and southern forereef terrace (Cook et al 1996; Jones et al. 2007). These previous surveys found that coral cover across the study area of the current project increases with distance from shore, with reefs near North Shore having the lowest cover (10-15 percent coral cover; Figure 3.02), lagoonal reefs at Crescent and Three Hill Shoals having higher cover (25-35 percent coral cover), and forereefs in the area around North Rock having the highest coral cover (35-45 percent coral cover; Jones et al. 2007). Nearshore sites were hypothesized to have lower cover due to the water quality of the area limiting growth and survivorship. Water quality was hypothesized to be poor nearshore due to the proximity to the reefs to areas of high population density and to the southern shipping channel, which is a source of increased sediment suspension (Jones et al. 2007).

Subsequent analysis by Murdoch 2007, refuted the previous results regarding a linear change in coral cover with distance from shore. By surveying sites at a finer scale, it was determined that coral cover and species actually peaked at over 50% at sites located roughly 3-km from shore in the central lagoon, and then declined to approximately 25% at backreef sites. These results indicate both the need for sampling more locations across the platform as well as the likelihood that the eastern and western ends of the lagoon may not exhibit the biological characteristics of the central lagoon.

The research described in this chapter represent the first attempt to assess coral condition across reefs located over the entire reef platform, both in the lagoon as well around the entire reef rim and over many forereef sites circling the platform at 10-m depth. Results indicate that coral cover varies in unpredictable ways across the lagoon. Additionally, statistical analysis indicates that rim reef sites are not all the same, but instead differ substantially from place to place in many ways, despite the apparent similarities in environment that they all experience. Forereef sites also exhibit high variability from place to place in many biological factors.

GOALS

- Determine areas within the lagoon, rim and forereef where the coral community would benefit from additional management protection in the form of a marine protected area.
- Determine degree of variability of sites within each habitat zone, in order to determine level of assessment needed and best location of sites for the accurate long-term monitoring of reef health across each zone.

Methods

Coral reef habitats were assessed at 105 sites across the Bermuda platform using a version of the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol #4.0, modified to suit the ecology of Bermuda (Figure 2.01). Reefs surveyed with AGRRA were chosen based on the criteria that they cover at least 75 m^2 (i.e. be of sufficient area to distribute the 6 transects appropriately), and that the reefs were as close as possible to the intersection points of a 3-km grid which spanned the reef platform.. Sites were not located on a grid because the intention was to use the collected data to produce map models of the density of the measured variables, and sites surveyed across regular points produce more accurate maps than do those distributed across random points. Reef surveys were completed between May and December from 2004-2007. All or most of the reef sites in each zone being surveyed within a single year to limit temporal confounds within zones.

At each site, AGRRA assessments of coral, algae and other benthic biota were made by two SCUBA divers along six transects. Briefly, 10-m transect lines were laid on the reef surface from a haphazardly determined starting point. The following data were then recorded for any stony coral colonies underlying the transect that were of 10 cm length or greater in any dimension:

i) Species of coral

ii) Length of coral colony under the line,

iii) Maximum length,

iv) Perpendicular width

v) Height of coral colony

vi) Coral Health (disease, bleaching, damselfish bites, parrotfish bites)

vii) Partial Mortality of Colony: percentage of live tissue cover of the entire colony, as seen from a planar view (measured to the nearest cm for corals <100 cm and to the nearest 5 cm for corals ≥100 cm), Supplemental data were collected at five points at 2-m intervals per each transect, starting at the 1-m mark and using a 25 x 25 cm quadrat. These data included substrate type, heights and coverage of fleshy and calcareous algae, dominant algal species, and number and species of stony coral recruits per quadrat. *Diadema* and damselfish territory presence along the transects were also recorded (AGRRA, 2005).

Concurrent with coral and algae assessments, fish assemblages were assessed with AGRRA surveys. Fish were enumerated by two SCUBA divers, conducting a total of ten 30 m belt transects per site. Transects were laid haphazardly and away from other divers to minimize any bias related to diver-activity. While surveying, divers swam slowly in one direction while an attached spool of transect line unraveled to signal completion of the transect. Any fish encountered within a lane bounded one meter on either side of the transect and upwards to the surface was counted and assigned to one of six visually-estimated total length categories (<5cm, 10-20cm, 20-30cm, 30-40cm, and >40cm; AGRRA, 2005).

To ensure coverage of less abundant fish species that may not have been recorded on diver transects, the REEF Roving-Diver Technique was also employed by two divers during surveys. This protocol involved a timed period of swimming observation for over 30 minutes, where all fish species seen were recorded. Species were then categorized by abundance and recorded as "Single" (1 fish), "Few" (2-10 fish), "Many" (11-100 fish) or "Abundant" (>100 fish; REEF, 2007).

Data Analysis

Univariate analysis of coral cover data was used to assess the variability between sties within zones. While it is generally assumed that the patch and pinnacle reefs in the lagoon exhibit considerable variation in coral cover and other biological factors, historically the rim and fore-reef has been considered to possess very low variability at a scale greater than 1-km. For this reason only a very small number of rim reef sites have historically been monitored though time, as it is generally believed that the few sites monitored are representative of all rim and forereef sites.

Maps of measured variables, and multivariate analysis were used to investigate how the coral community differs within and between zones and to detect groups of sites that possess unusual assemblages of corals that may benefit from additional protection through the implementation of marine protected areas or other management instruments.

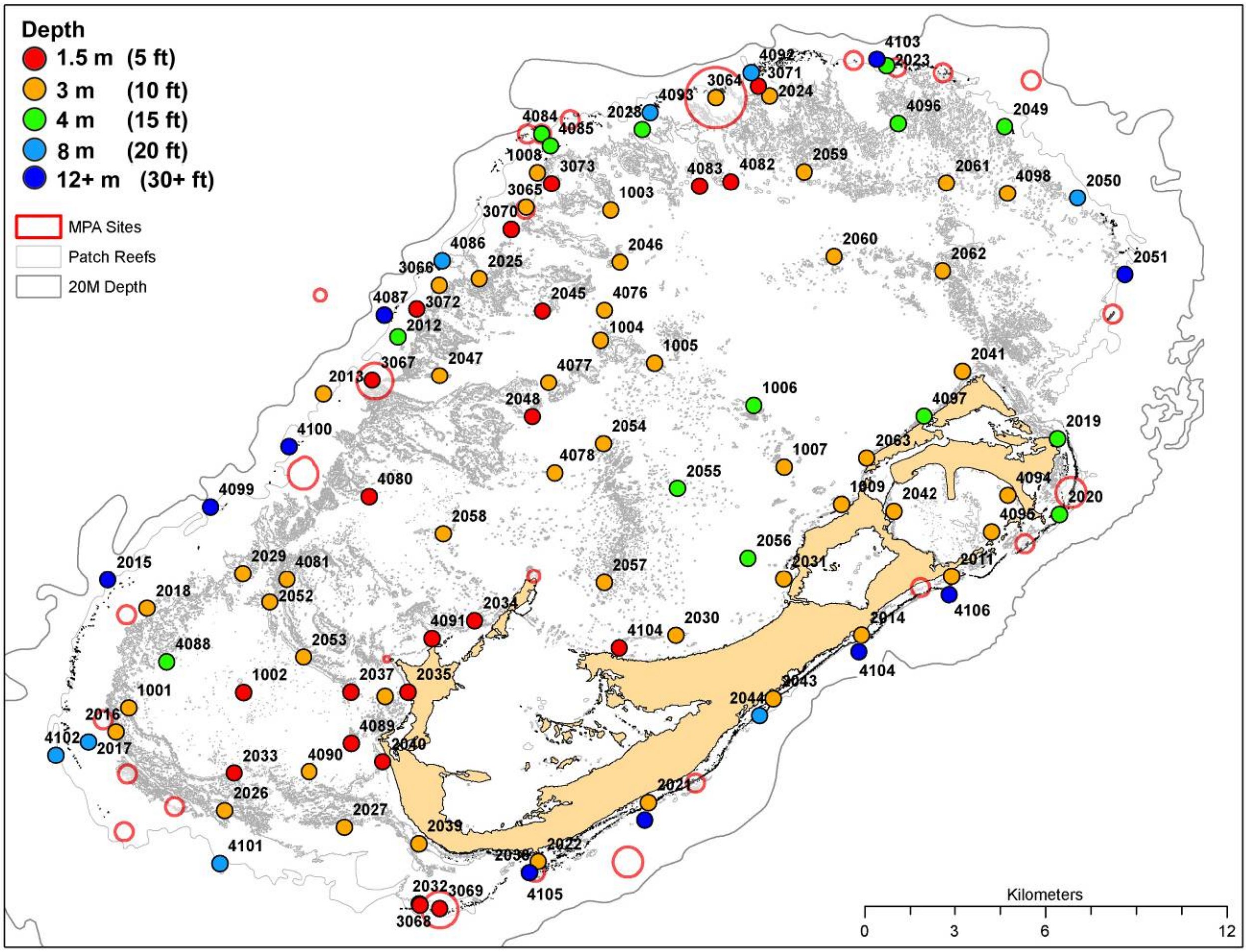


Figure 3.01. Location of the 104 AGRRA and REEF benthic survey sites completed across the Bermuda Reef Platform from 2004 to 2007. Fish and benthic community structure was assessed at each point. Sites are color coded by the average depth on the top of the reef surveyed.

Results

Univariate Analysis per Zone

Lagoon

Percent coral cover varied across the lagoon in an unpredictable manner (Figure 3.02), with a maximum of 42% cover and a minimum of 14% cover at the sites surveyed. Coral cover was more variable at nearshore sites, with extreames of high and low cover exhibited, while offshore sites appeared more consistent in cover. Nested analysis of variance confirmed that differences between zones were not significant, while within zone variability was highly significant (Table 3.01).

Rim Reef

Percent cover was compared between sites within four zones around the rim, based on location (Figure 3.03). Average percent cover varied highly from site to site across all zonesThe highest and lowest values were observed in the SE zone, with less than 10% cover measured on a rim reef near St. David's Head, and over 40% cover assessed on a rim reef near Sinky Bay, Southampton. The SE zone is located next to the south shore of the island and is therefore blocked from exposure with lagoonal water. The other three zones, alternatively, are exposed to lagoonal water due to tidal exchange between the reef platform and the open ocean. These three zones exhibited less variability in coral cover but still showed a range of over 15% across sites. Nested analysis of variance determined that inter-zone variability was highly significant (table 3.02), while zone-to-zone differences were not significant. These results indicate that it is invalid to assume that a few sites are adequate to represent the condition of the rim reef habitat around the island, as other researchers have done in the past.

10-m Fore Reef

Fourteen fore reef sites have been surveyed, with five sites located in the southern zone which is near the South Shore of the island, and the other nine sites distributed around the rest of the platform (where lagoonal water may affect the reef, even at 10-m depth). Sites varied from reef to reef in an unpredictable manner, with the lowest level of cover being 17% at a site near a reef pass at NE Breaker, and the highest cover, of over 70%, observed on the southern side of the platform near Sinky Bay, Southampton (Figure 3.04). Nested analysis of variance again found highly significant variation in coral cover between reefs within zones (Table 3.03). The north and south zones were marginally insignificantly different. The pattern previously described by researchers in which coral cover is low nearshore and increases with distance from shore was not observed in this substantially more comprehensive assessment.

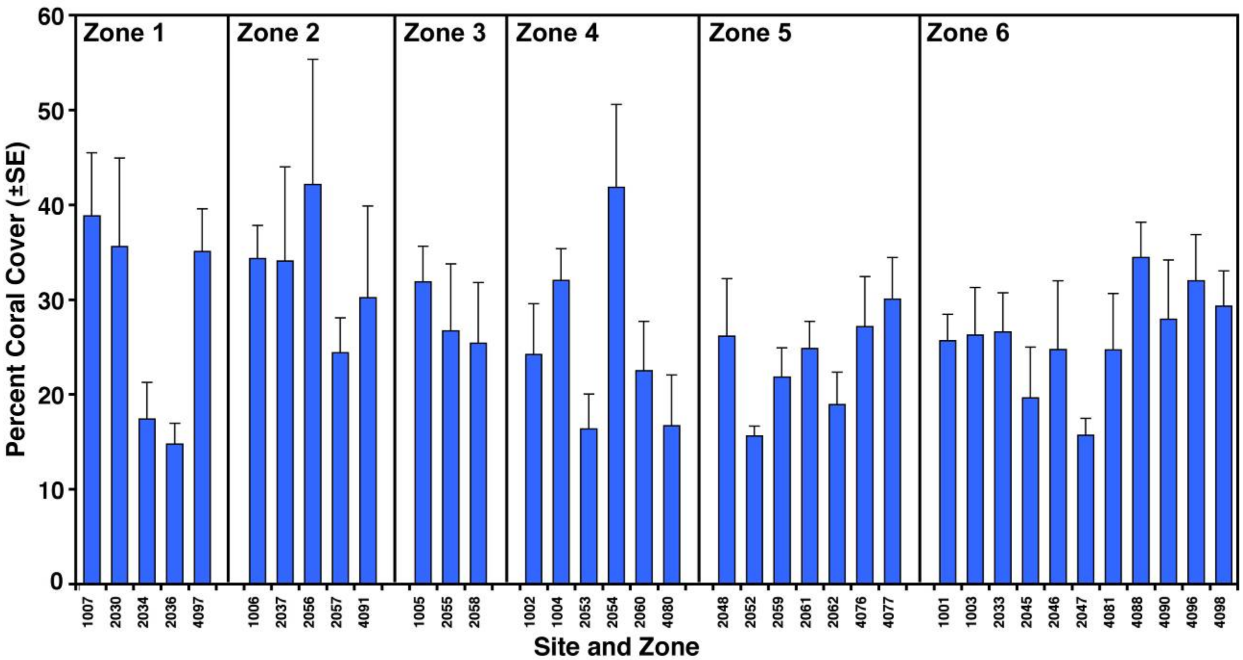


Figure 3.02. Average percent cover (±SE) across the six zones surveyed across the lagoon.

Table 3.01. Nested analysis of variance of coral cover at sites across six zones within the lagoon.

Source	**DF**	**SS**	**MS**	**F ratio**	**P value**
Zone	5	0.11376	0.02275	0.5474	0.7390
Site[Zone]	31	1.28837	0.04156	1.7841	0.0104
Error	185	4.30945	0.02329		
Total	221	5.71157			

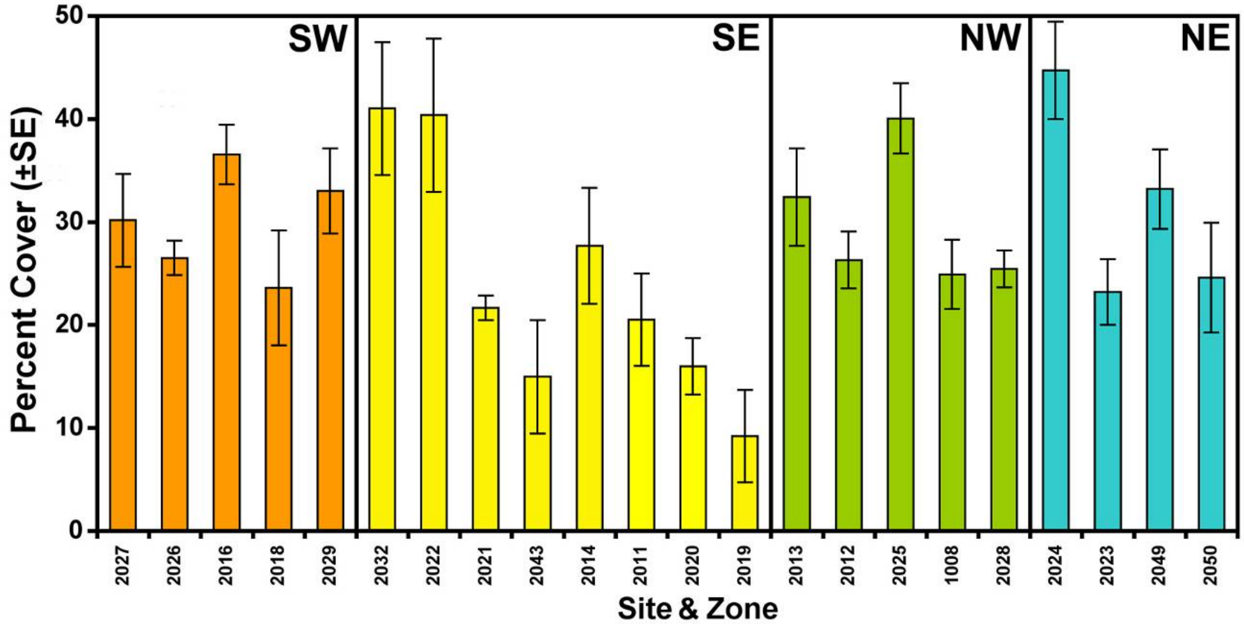


Figure 3.03. Average percent cover (±SE) at rim reef sites across the four zones. Sites are separated by ~ 4 km.

Table 3.02. Nested analysis of variance of coral cover at sites across four sectors across the rim.

Source	**DF**	**SS**	**MS**	**F ratio**	**P value**
Sector	3	0.51491	0.17164	2.5536	0.0877
Site[Sector]	18	1.20984	0.06721	3.5738	<0.0001
Error	110	2.06879	0.01881		
Total	131	3.79353			

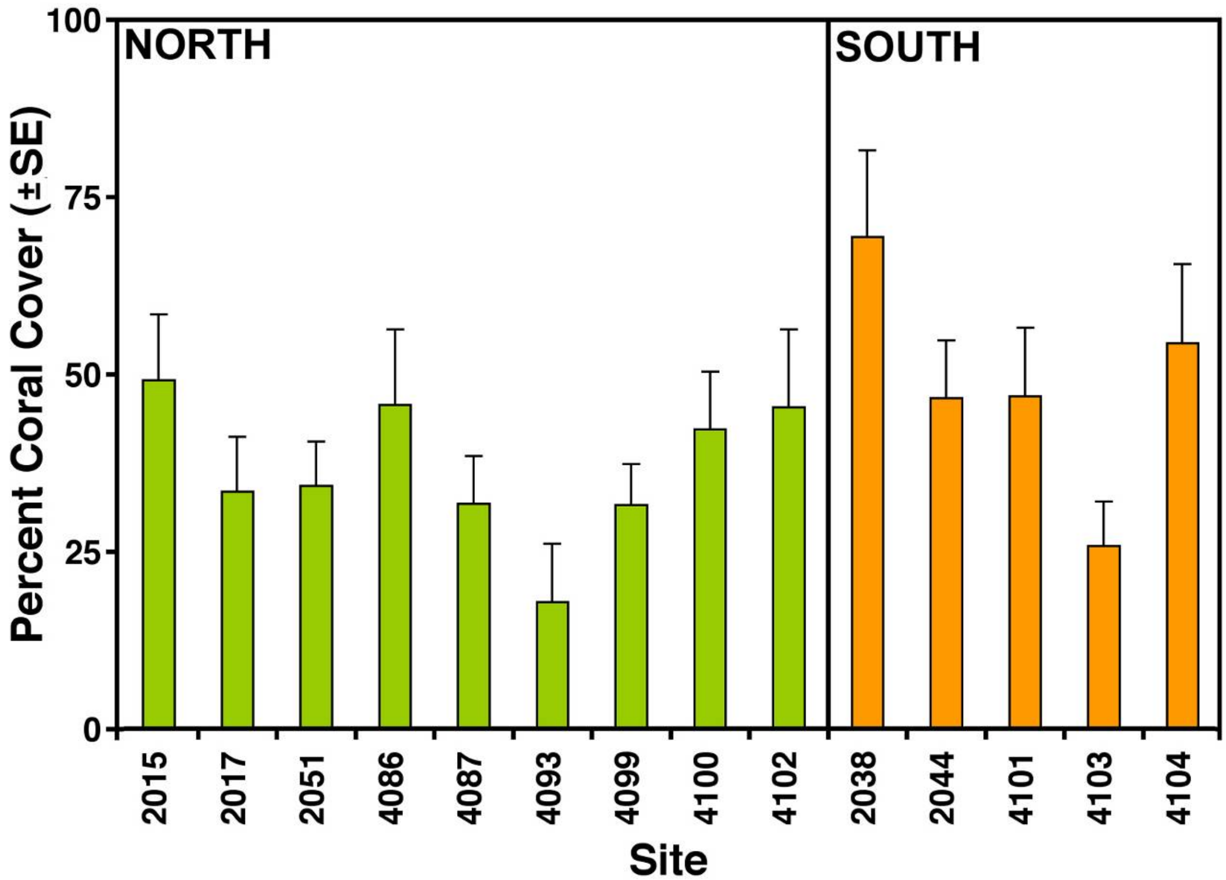


Figure 3.04. Average percent coral cover (±SE) at thirteen forereef sites.

Table 3.03. Analysis of variance for coral cover at thirteen sites across the forereef.

Source	**DF**	**SS**	**MS**	**F ratio**	**P value**
Sector	1	0.36357	0.36357	4.2382	0.0594
Site[Sector]	13	1.18539	0.09118	4.6718	<0.0001
Error	55	1.1934	0.0213		
Total	69	2.5730			

Multivariate Analysis

Percent coral cover data for each site was square-root transformed and the similarity in coral community among sites were compared using Bray Curtis analysis with the PRIMER v6.1 statistical package and the results plotted onto a multidimensional scaling (MSD) diagram. Sites from each habitat zone were indicated with icons of different shapes and colors, and sites that were more similar were bounded by borders of differing similarity values. Reefs clustered in two different ways. Sites from the same habitat zone (i.e. lagoonal patch reefs or rim reefs) tended to occur together, with rim reef sites clustering between patch and fore reef clusters. ANOSIM analysis of similarity (Table 3.04) confirm these impressions, with all zones being highly significantly different in cluster distribution.

Additionally two other clusters formed that were not part of the *a priori* zonal classification schemes. Five lagoonal patch reefs and one fringing reef formed a distinct cluster (on the left hand side of Figure 3.05), and five reefs from a range of zones clustered separately from the main cluster (at the top of the Figure 3.05 below). SIMPER analysis (Table 3.05) and plotting species cover for each site in the MDS diagram as a bubble plot (Figure 3.06) showed that the cluster on the left of the MDS diagram was different in that the branching corals of the genera *Madracis* and the species *Millepora alcicornis* dominated these lagoonal reefs. The other cluster at the top of the MDS diagram possessed a higher proportion of the head coral *Diploria labyrinthiformis*.

Other subtle patterns could also be discerned. Rim reef sites tended to have the highest proportion of the head coral *Diploria strigosa,* while lagoonal reefs possessed more of the massive coral *Montastrea frankesi* and *Montastrea cavernosa*. Forereef sites had higher cover of most species relative to patch and rim reefs. The deeper fore reef sites also exhibited a smaller proportion of the brooding head coral *Porites astreoides*, whose distribution tends to be strongly negatively depth dependant (T. Murdoch unpublished data).

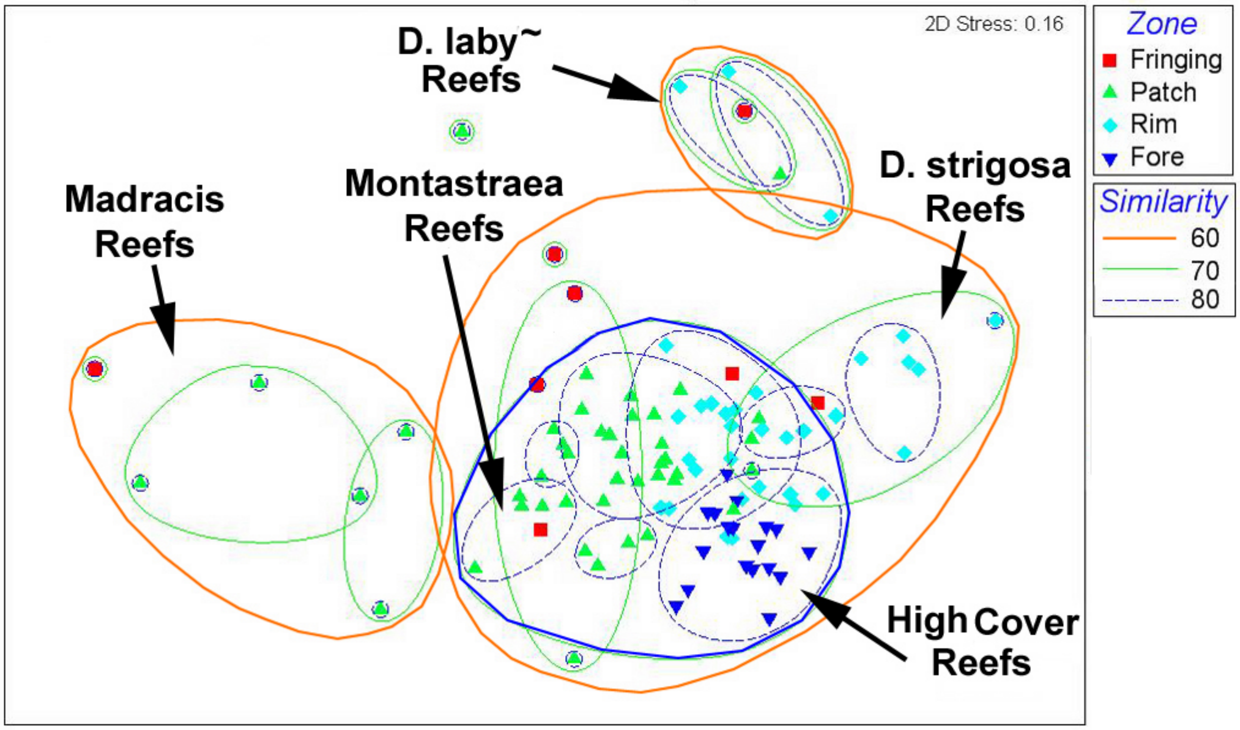


Figure 3.05. MDS plot of all sites surveyed across the Bermuda Platform, with different icons representing each habitat zone. Sites with similar coral assemblage structure are grouped together, with isopleths indicating boundaries of equal similarity. Reefs cluster by zone as well as by five sub-zonal groups, named for the coral species or genera that dominates each sub-zone.

Figure 3.06 (next page). Bubble plots of relative species cover across sites, as plotted in the MDS map as above. Each bubble plot represents a different hard coral species, and illustrates how each zone and sub-zone is composed of unique proportions of the regional species pool.

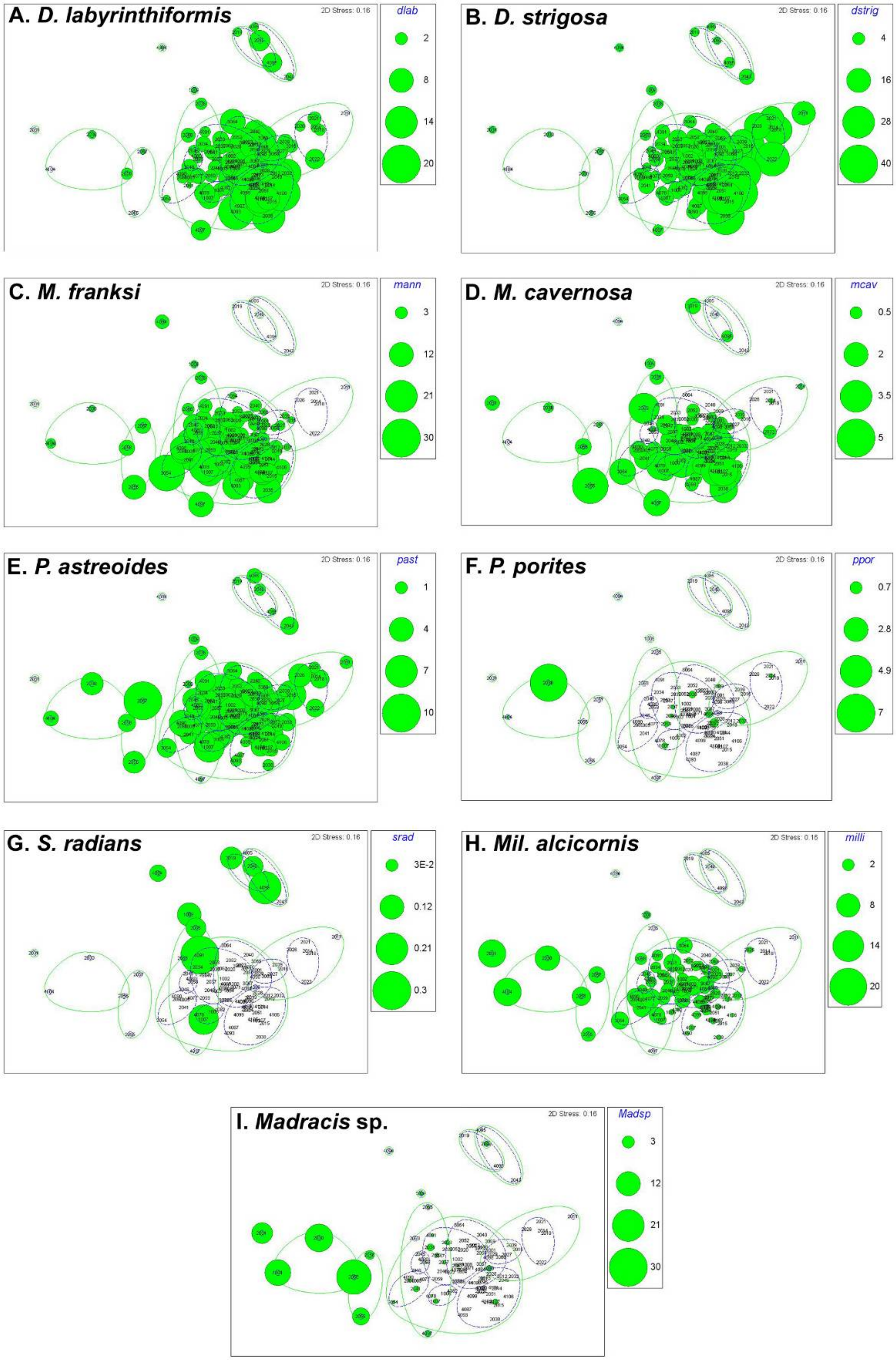

A. D. labyrinthiformis
2D Stress: 0.16
dlab
2
8
14
20
B. D. strigosa
2D Stress: 0.16
dstrig
4
16
28
40
C. M. franksi
2D Stress: 0.16
mann
3
12
21
30
D. M. cavernosa
2D Stress: 0.16
mcav
0.5
2
3.5
5
E. P. astreoides
2D Stress: 0.16
past
1
4
7
10
F. P. porites
2D Stress: 0.16
ppor
0.7
2.8
4.9
7
G. S. radians
2D Stress: 0.16
srad
3E-2
0.12
0.21
0.3
H. Mil. alcicornis
2D Stress: 0.16
milli
2
8
14
20
I. Madracis sp.
2D Stress: 0.16
Madsp
3
12
21
30

Table 3.04. Analysis of similarity (ANOSIM) of reef zones.

Global Test
Sample statistic (Global R): 0.3
Significance level of sample statistic: 0.1%
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Pairwise Tests

Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
Patch, Rim	0.285	0.1	Very large	999	0
Patch, Fringing	0.398	0.3	636763050	999	2
Patch, Fore	0.306	0.1	Very large	999	0
Rim, Fringing	0.454	0.2	95548245	999	1
Rim, Fore	0.150	1.4	Very large	999	13
Fringing, Fore	0.809	0.1	1562275	999	0

Table 3.05. SIMPER (Similarity Percentage) analysis of the coral species by site matrix, which allows the determination of how coral composition varies across zones. Tabulated average abundances represent square root of average percent cover.

SIMPER
Similarity Percentages - species contributions

One-Way Analysis

Group Fringing Zone
Average similarity: 55.62

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
D. strigosa	2.10	18.26	3.97	32.82	32.82
D. labyrinthiformis	1.41	10.54	1.16	18.96	51.78
P. astreoides	0.94	8.05	1.53	14.48	66.26
M. frankesi	1.27	7.73	1.00	13.89	80.16
M. cavernosa	0.73	4.12	1.00	7.41	87.57
Mi. alcicornis	0.98	2.87	0.49	5.16	92.73

Group Patch Zone
Average similarity: 70.31

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
M. frankesi	2.65	18.90	2.55	26.89	26.89
D. strigosa	2.40	16.62	2.21	23.64	50.53
P. astreoides	1.67	12.34	2.81	17.55	68.08
D. labyrinthiformis	1.48	10.53	2.17	14.98	83.06
Mi. alcicornis	1.29	7.63	1.55	10.85	93.91

Group Rim Zone
Average similarity: 72.00

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
D. strigosa	3.68	30.72	3.42	42.67	42.67
D. labyrinthiformis	2.33	16.91	2.56	23.49	66.16
Past	1.47	12.85	3.67	17.84	84.00
M. frankesi	1.20	5.89	0.97	8.18	92.18

Group Fore Zone
Average similarity: 84.57

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
D. strigosa	4.38	27.50	5.41	32.51	32.51
D. labyrinthiformis	3.39	22.62	7.76	26.74	59.25
M. frankesi	2.93	19.19	5.26	22.69	81.95
P. astreoides	1.15	6.86	3.59	8.12	90.06

Visually Interpretation of Maps of Data

Species Density

Species density is the count of species per transect. This measure tends to underestimate species richness at a site, but has the benefit of being a standard measure across sites of varying geomorphology. Figure 3.07 illustrates the average species density across the 105 survey sites, with large purple circles representing the sites containing the most species. There is a clear pattern in which species density is highest in the lagoon, along the northern shore of the island, with roughly half the species occurring on the wave-swept rim and fore reef.

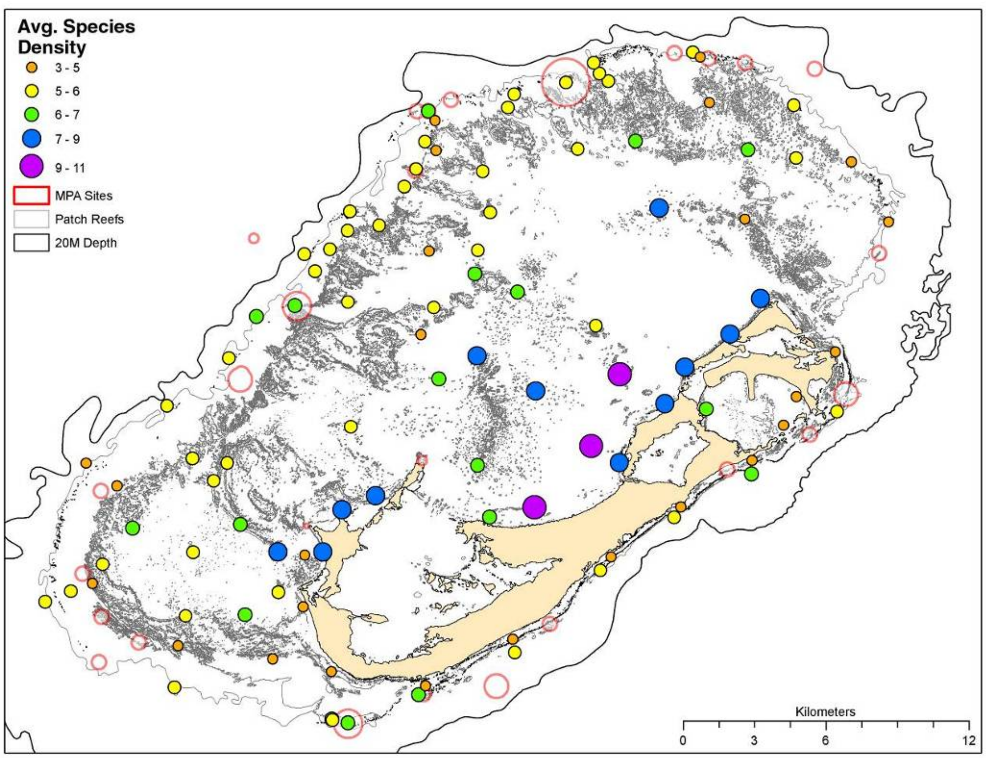


Figure 3.07. Average species density of hard coral colonies within the six 10-m transects at each site, regardless of species.

Coral Colony Abundance

Figure 3.08 illustrates the pattern of coral colony counts, or abundance, across the Bermuda Platform. Small red dots represent the sites with the fewest colonies, while large blue dots represent the sites with the most coral colonies across the 6 transects comprising a site. Coral abundance was found to be highest on the 30-ft fore reef sites located along the south shore of the island. Rim reef sites around the island also had moderately high counts of coral colonies. Coral abundance declined towards the center of the lagoon, with the lowest measures observed within Castle Harbour and near Shelly Bay, Hamilton Parish.

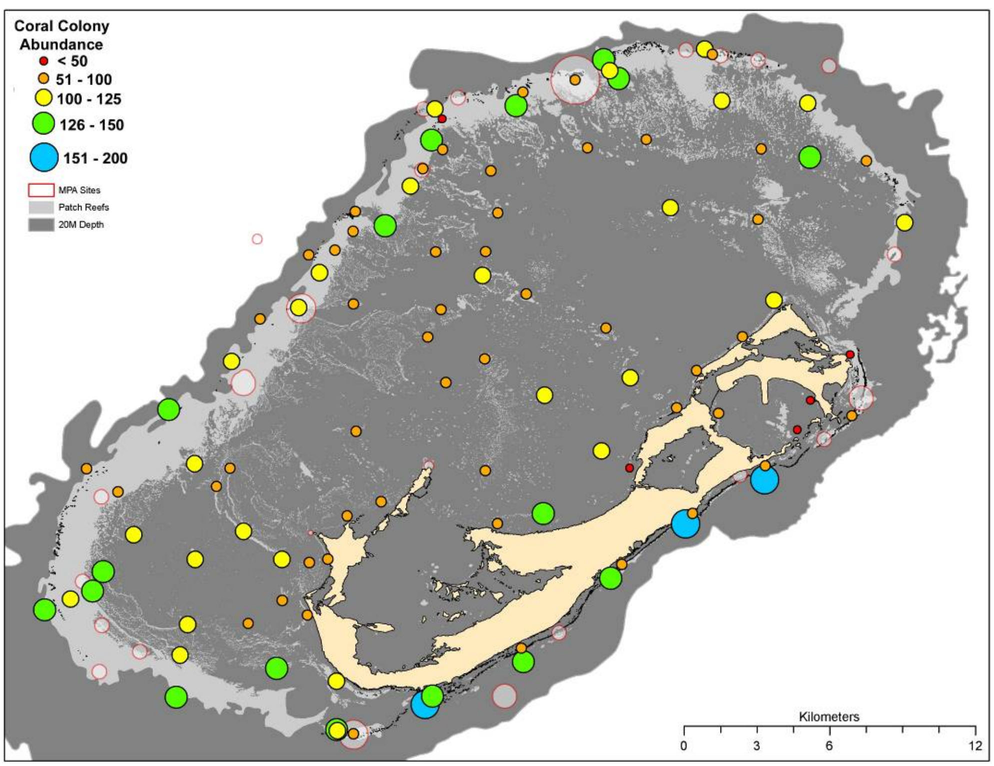


Figure 3.08. Average abundance of hard coral colonies within the six 10-m transects at each site, regardless of species.

Coral Recruit Density (All Corals)

The average density of coral recruits, regardless of species, is plotted in the map in Figure 3.09. The density of coral recruits per species is described below. High coral recruitment was observed to occur primarily around the reef rim at some, but not all sites, as well as in the central lagoon. Recruitment was poor west of Sandy's Parish and north of St. George's Parish, at either end of the island, as well as at some of the shallow wave-swept rim sites along South Shore.

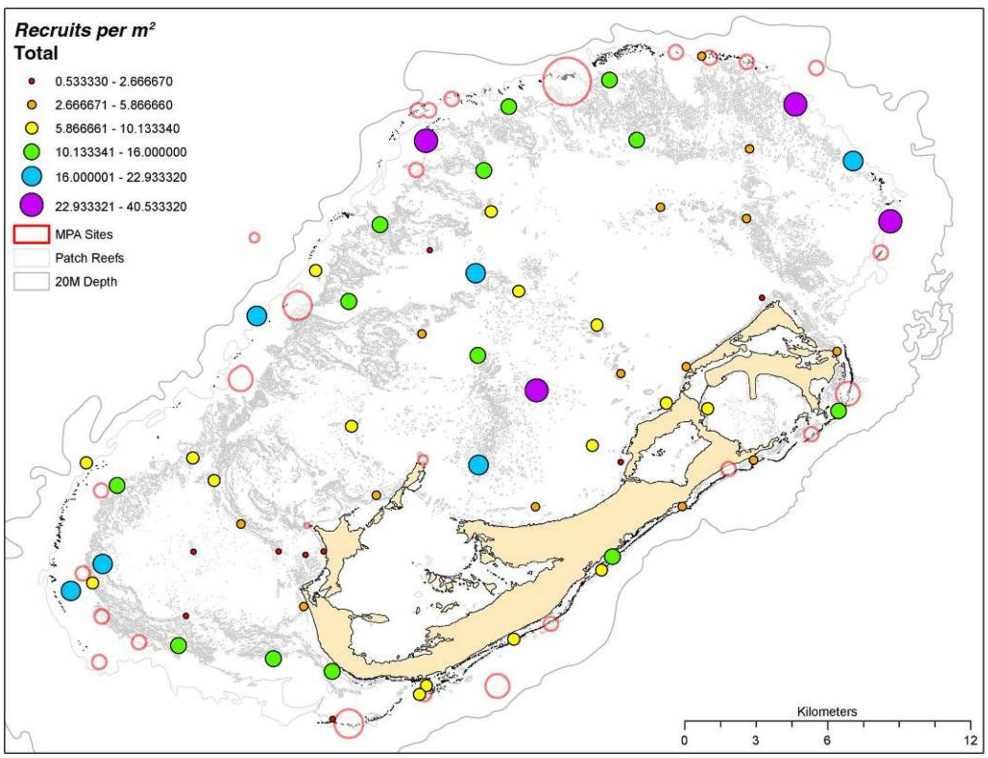


Figure 3.09. The average density of coral recruits of all species.

Coral Cover

The average percent coral cover at each of the 105 sites is plotted in the map below (Figure 3.10). Highest coral cover was consistently observed at the 30-ft fore reef sites that were surveyed along the South Shore of the island. Moderately high coral cover was also observed in the northern-most part of the lagoon and rim, as well as in a cluster in the center of the lagoon. A band of low-cover can be seen in the map running from west of the west end of the island and along the large flats found on the north-west side of the lagoon (e,g Ely's Flat, Halfway Flat, White Flat, Devil's Flat) and also at Three Hill Shoals. Analysis of fish distributions in the following chapter will show that these reefs are also characterized by exceptionally high densities of damselfish. It is probable that these fish, which kill coral so they can grow algae, are causing the low coral cover on these otherwise healthy reefs.

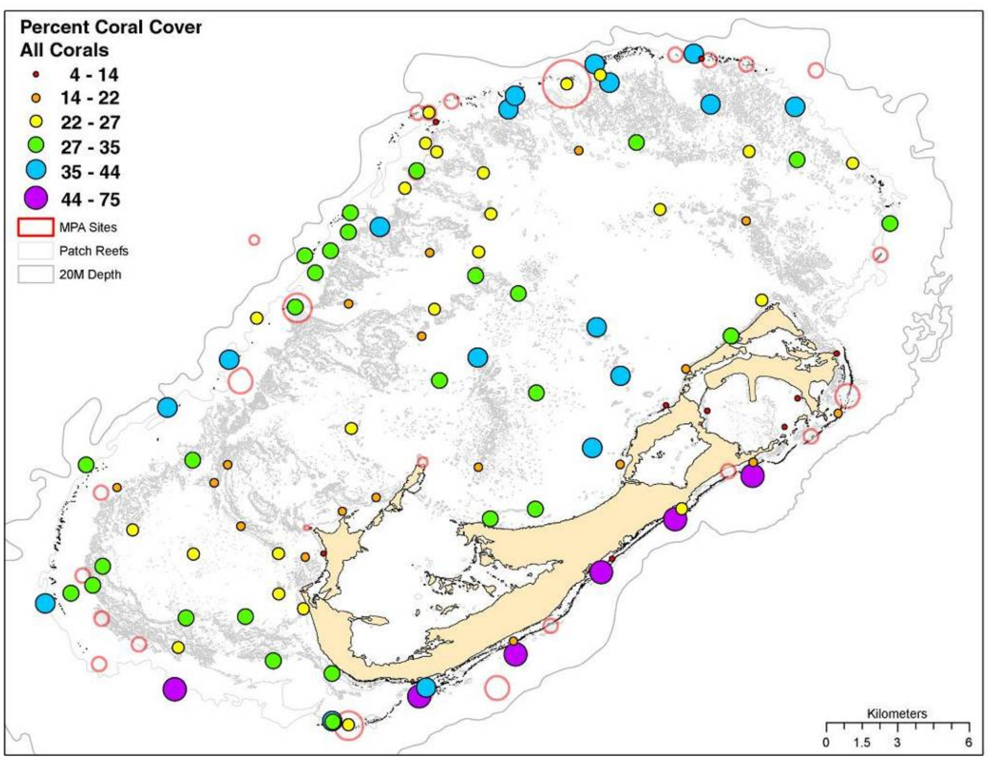


Figure 3.10 A map of the average percent coral cover for all hard corals at each AGRRA site.

Distribution of coral recruits and adults by species

Diploria labyrithiformis

Relative to most coral species in Bermuda, *Diploria labyrinthiformis* recruits fairly well. Recruits were found mainly at rim and back reef sites on the outer edge of the lagoon, with no very few sites exhibiting recruits in the central or inner lagoon (Figure 3.11A). Some rim reef sites also did not have many recruits of this species, although the causes for patchy recruitment between rim reef sites is not known at this time.

Adult D. labyrinthiformis colonies showed the highest cover around the outer edge of the lagoon, with high values at both the northern-most and southern-most reefs (Figure 3.11B). Rim and back reef sites along the northwest side of the lagoon also exhibited high cover of D. labyrinthiformis. The patterns of recruits and adults did not match exactly. Long-term sampling and the analysis of size-frequency data would be needed in order to determine whether this species does occasionally recruit to lagoonal reefs and whether adult colonies in the lagoon are from some previous recruitment event in the past.

Diploria strigosa

The head coral *Diploria strigosa* is a common recruit in Bermuda, relative to most coral species. Figure 3.12A illustrates the distribution of *D. strigosa* recruits across the platform. Recruitment was highest along the northern rim and back reef, with moderate levels also detected along the southwest rim and at the rim sites along the South Shore of the island. Recruitment was low on the 30-ft fore-reef as well as in the central lagoon, although slightly higher along Ely's Flat in the western lagoon.

Diploria strigosa is the most abundant coral in Bermuda and contributes the most to overall coral cover across the region. This is apparent in Figure 3.12B, where cover values over 20% can be seen around the rim and outer lagoon, and particularly at 30-ft along the South Shore. The cover of this head coral is substantially reduced in the center of the lagoon, as well as in Castle Harbour.

The most noticeable difference between the patterns of recruits versus adult *D. strigosa* corals can be seen at the 30-ft fore reef sites along South Shore. Recruitment was not high, but cover is, indicating the colonies are capable of surviving for long periods despite rare additions to the population. Such a pattern highlights the susceptibility of this coral to damage to the adult population, since recruitment may not be enough to allow the recovery of what are now dense populations of adult corals should disease or bleaching or another form of disturbance occur.

Madracis mirabilis

The branching coral *Madracis mirabilis* recruits rarely and instead often reproduces asexually through fragmentation of adult colonies. Recruits of this species were not observed across most sites in the lagoon, rim or fore-reef (Figure 3.12A). Some recruitment was, however, observed in the central lagoon.

Adult *Madracis mirabilis* was not observed on the majority of fore reef or rim sites, nor in much of the lagoon (Figure 3.12B). There was, however, a cluster of reefs in the central lagoon near the middle of the island in which this species exhibited high coral cover, often dominating 10-m+ areas of reef.

Montastraea cavernosa

The mound-shaped coral *Montastraea cavernosa* can be found as recruits in Bermuda, but typically in relatively low numbers compared to some species. Recruits were observed haphazardly distributed across the lagoon (Figure 3.14A) , as well as at a couple of sites on the northeast and southwest rim. High numbers of recruits at one fore reef site on South Shore hints that perhaps this species recruits patchily in pulses in Bermuda.

As an adult coral, *Montastraea cavernosa* is fairly common can be expected to be found on almost any reef, although generally in low abundance. As can be seen in Figure 3.14B, the species was observed across the lagoon and in rim and fore reef sites. There appears to be particularly abundant in a cluster of reefs in the central lagoon , as well as occasionally showing small peaks in cover around the rim or on fore reef sites.

Montastraea frankesi

Montastraea frankesi, as well as it's sister species Montastraea annularis and Montastraea faveolata are reknowed for exhibiting poor levels of recruitment across the Caribbean, and the data shown here for Bermuda (Figure 3.15A) matches the ocean-wide trend. Recruitment was confirmed in two locations however, although no obvious environmental cause could be inferred since one location was on a marginal reef located near North Shore, while the other site was located on the rim reef in the south west side of the lagoon,

Adult Montastraea frankesi corals constitute one of the primary reef builders though out the Caribbean, and in Bermuda as well. This species peaks in cover on the sides of patch reefs instead of on their tops, where the AGRRA surveys are focused, so its contribution to overall cover across the Bermuda sites should be seen in that light. Percent cover values can be seen to peak in a group of reefs in the middle of the lagoon (Figure 3.14B), as well as on scattered fore-reef sites across the rest of the platform. Shallow, wave-swept rim reef sites tended to have very low cover of *Montastraea frankesi*.

Porites astreoides

Porites astreoides, in comparison to Montastaea frankesi, is known for consistently high levels of recruitment throughout the Caribbean. Our surveys confirm this for the Bermuda region, with very high recruitment densities found on some reef sites (Figure 3.16A). Areas of particularly high recruitment of this brooding coral were located along the outer edge of the lagoon on rim and backreef sites, as well as occasionally within the central lagoon. Nearshore reefs and those within Castle Harbour were characterized by very low to no recruits, presumably due to high levels of sediment occurring on surfaces on reefs in these areas.

The average percent cover of adult *Porites astreoides* peaked along the patch reefs found on the outer edge of the western lagoon, was well as along the reefs of Bailey’s Flats, with one reef in Brackish Pond Flats exhibiting the highest cover. Low cover was seen in Castle harbour and on the fore-reef sites. The distribution of adult *P. astreoides* did not seem to match the distribution of recruits, again implying populations across the platform are sustained by pulses of recruitment across years.

Other species

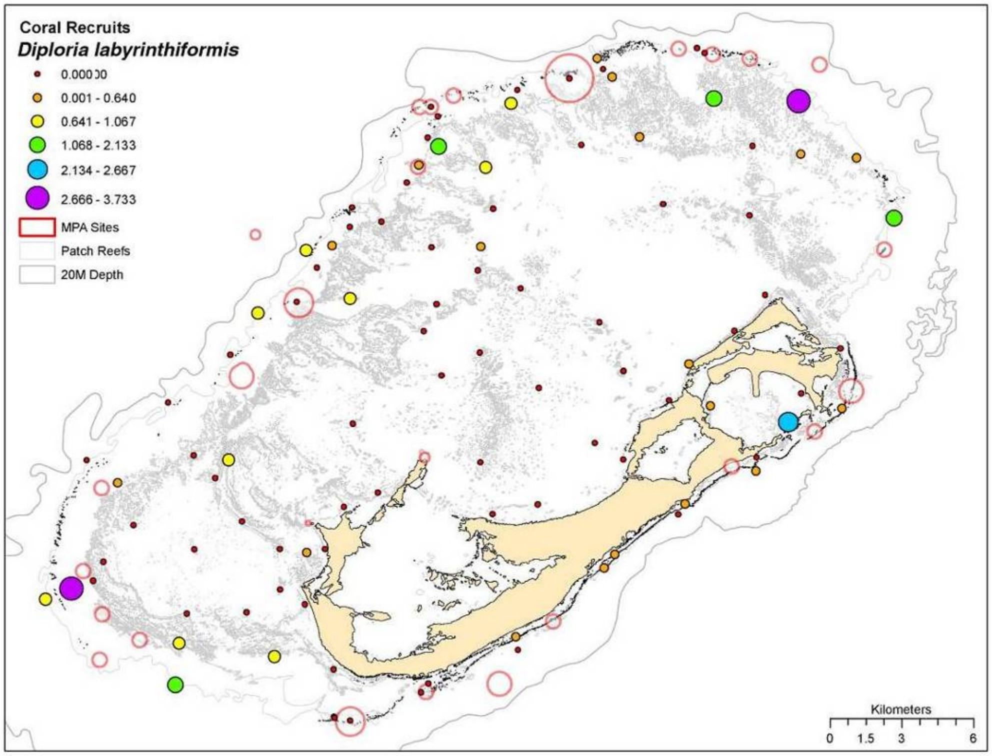
An additional 16 species of coral exist in Bermuda, but either are rare or so small as to as to not contribute to patterns of overall coral reef development. The distributions of these species were mapped across the 105 sites as well, but not presented as no consistent meaningful patterns were apparent.

Discussion

Univariate and multivariate analysis indicates that there exists three basic kinds of reef within the lagoon, with rim and 10-m fore reef zones also differing in coral composition and structure. Most importantly, there are two group of reefs in the central lagoon that are very different from the rest of the platform reefs (Figure 3.17). Considering Bermuda's extreme location these groups of reefs are also probably unique in the world and therefore should be considered of special scientific interest. One group of reefs occurs between Dockyard and Shelly Bay, and are dominated by the branching corals of the genera Madracis, Oculina and Millipora. The second group of reefs merges with the first group, and consists of reefs with higher than average cover of the same branching corals, but also are dominated by the massive coral Montastraea frankesi, with higher than average cover of Montastraea cavernosa as well. Fortunately, all hard and soft corals are protected within the Exclusive Economic Zone of Bermuda. Additionally, both the Madracis Reefs and Montastraea Reefs are mostly located within the North Coral Reef Preserve, where collection of all benthic organisms including corals has be restricted since 1966 (Coral Reef Preserve Act 1966).

Reef to reef variations in coral cover, recruitment and other factors are high within each of the habitat zones considered. This result is contrary to how researchers from another institution have assumed the reef to be, and indicates that a small number of sites is not enough to encompass the range of conditions characterizing Bermuda's reefs. Similarly, coral cover does not increase from nearshore across the lagoon to the rim, as has previously been thought to be true, based on a small number of surveys. These results show the strength in assessing a broad suite of sites across the entire platform if the condition of the entire ecosystem is to be understood. It also shows that environmental and biological factors are not affecting reef condition in the form of simple gradients, and that monitoring of these factors will have to also be done across a large number of sites across reef habitats for their disparate roles to be understood.

A.



B.

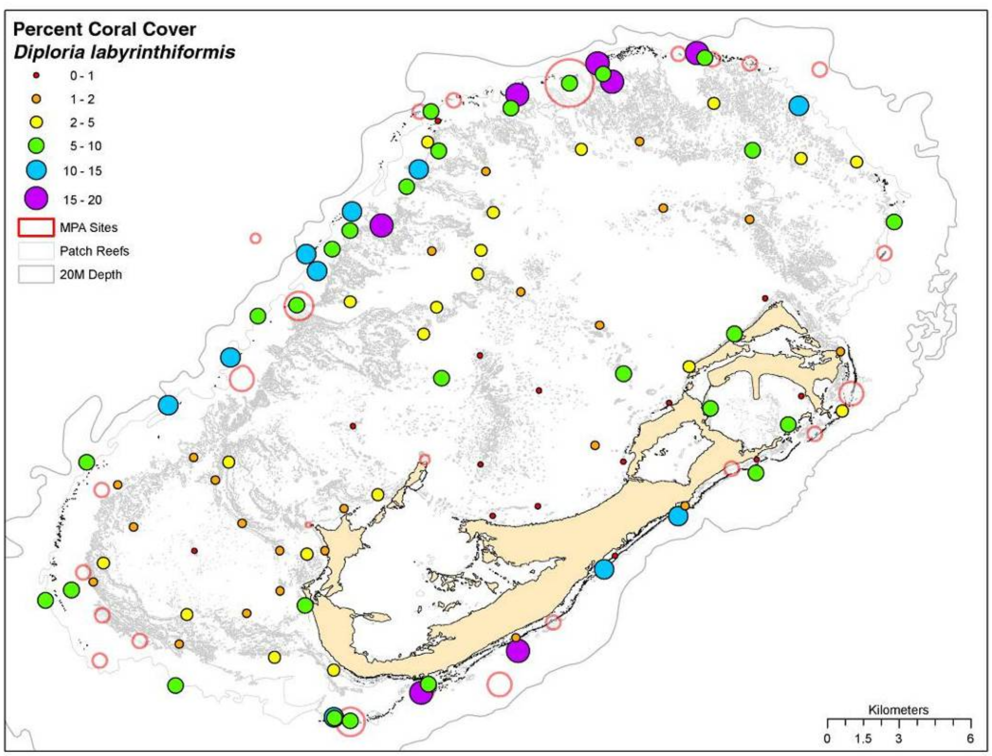
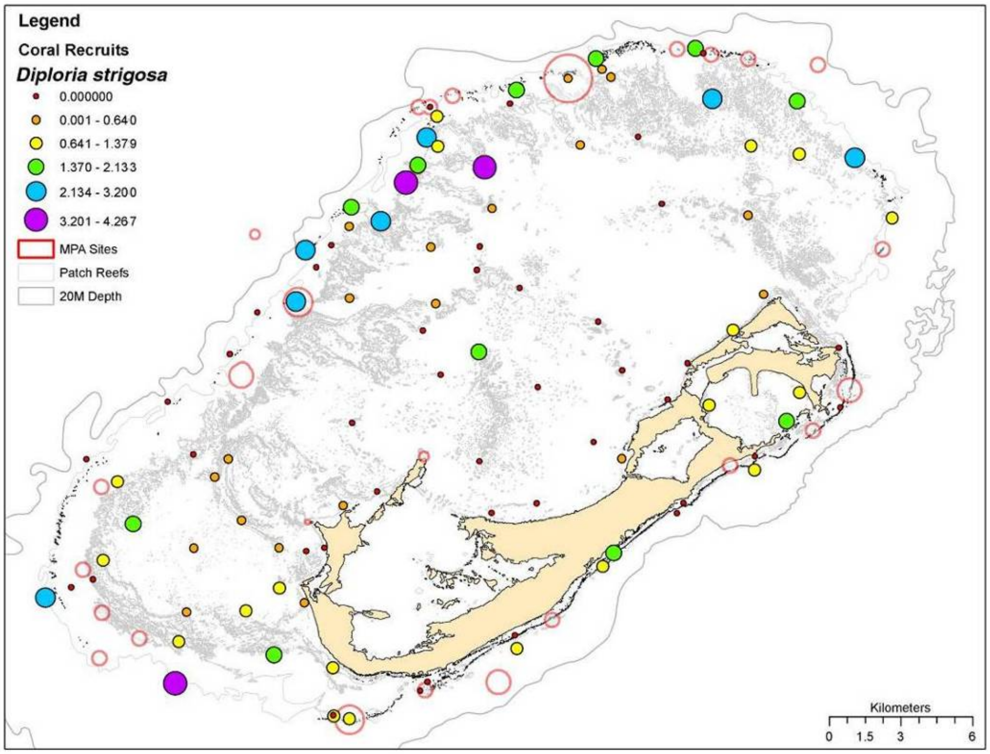


Figure 3.11. (A) Average number of recruits per m^2 and (B) average percent coral cover for the hard coral *Diploria labyrinthiformis*.

A.



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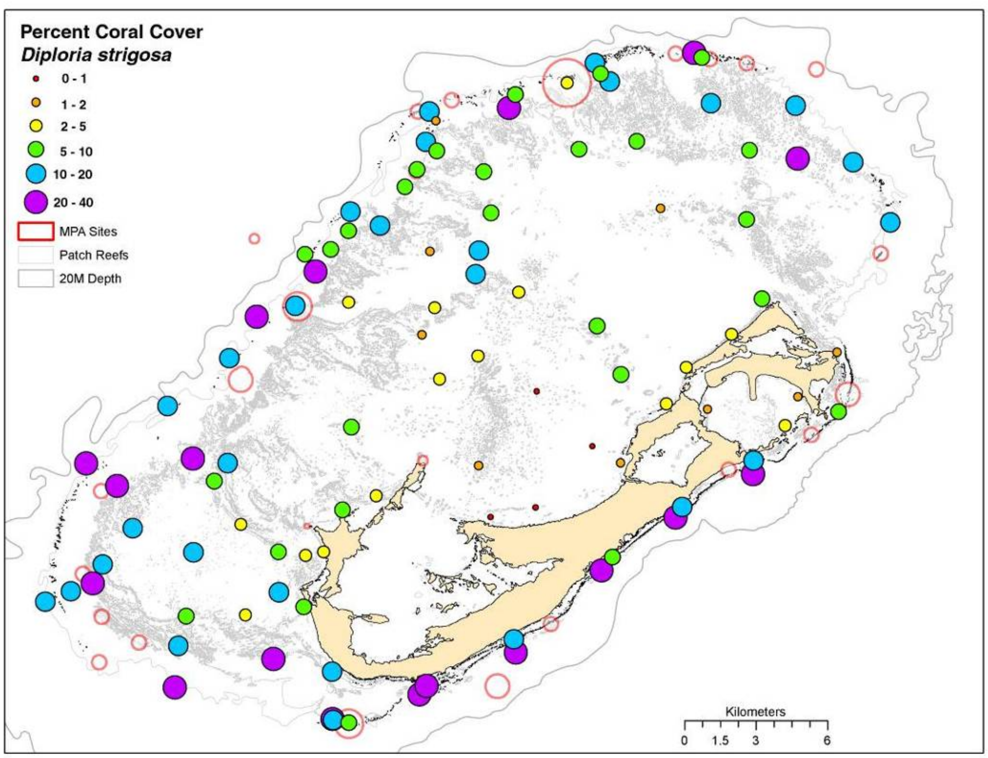
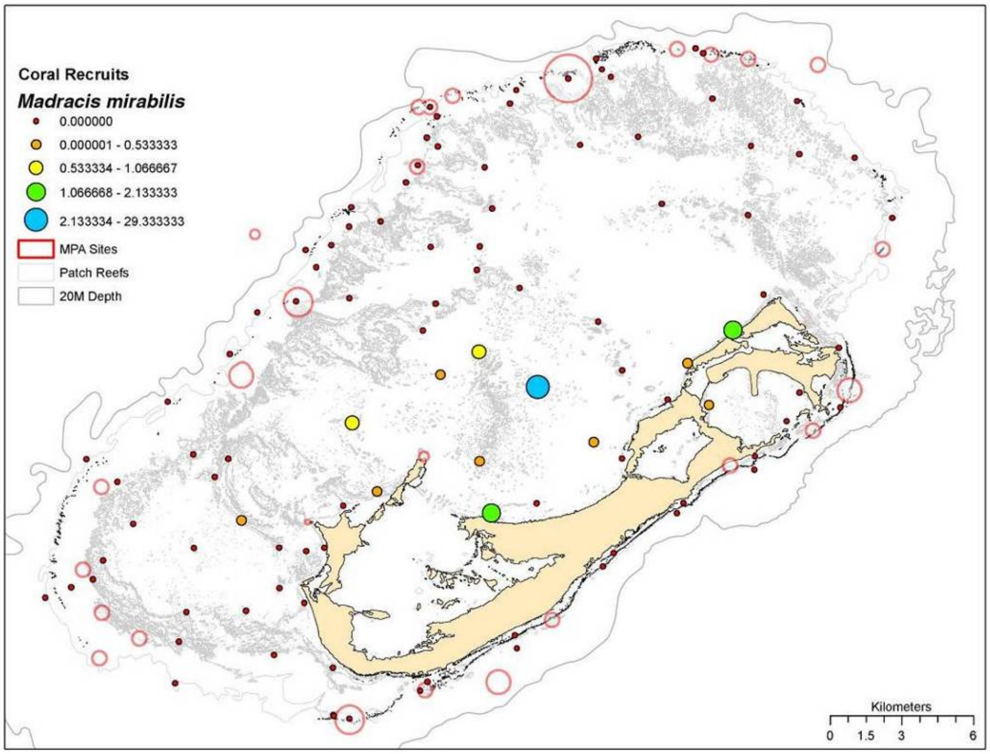


Figure 3.12. (A) Average number of recruits per m^2 and (B) average percent coral cover for the hard coral *Diploria strigosa*.

A.



B.

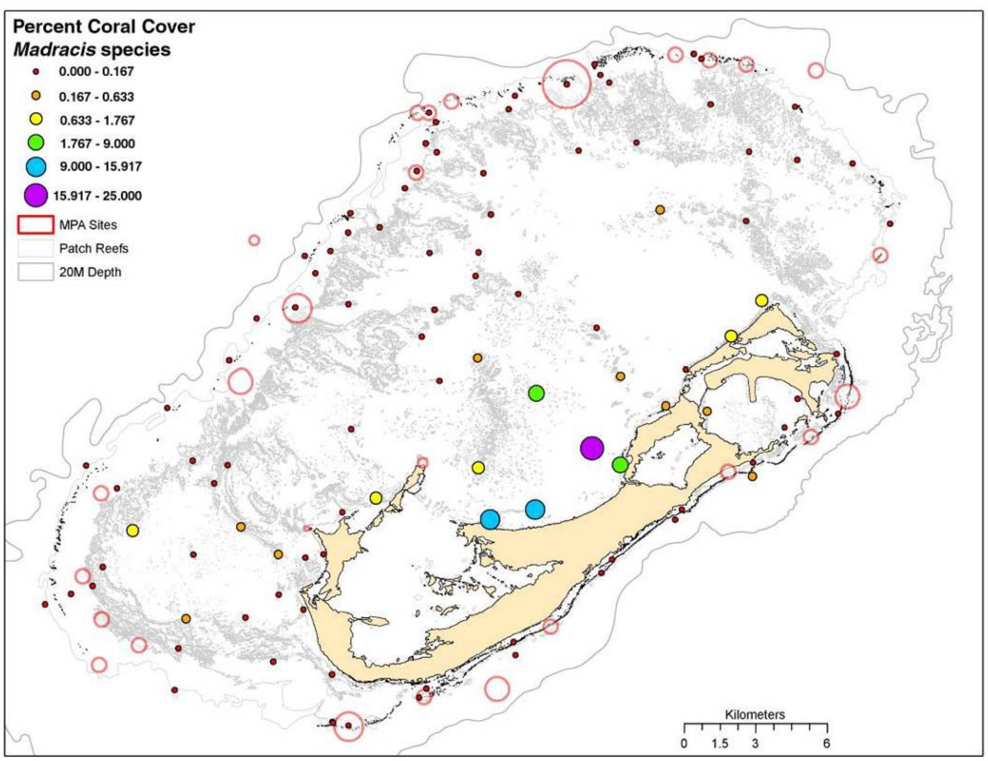
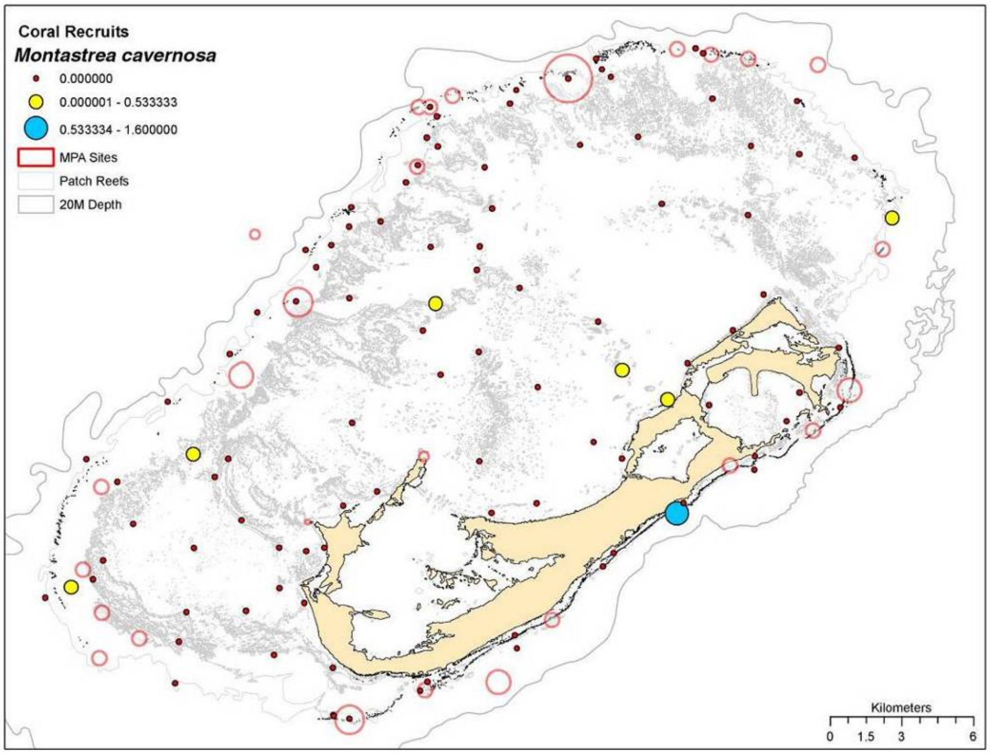


Figure 3.13. (A) Average number of recruits per m^2 and (B) average percent coral cover for the hard corals of the genus *Madracis*.

A.



B.

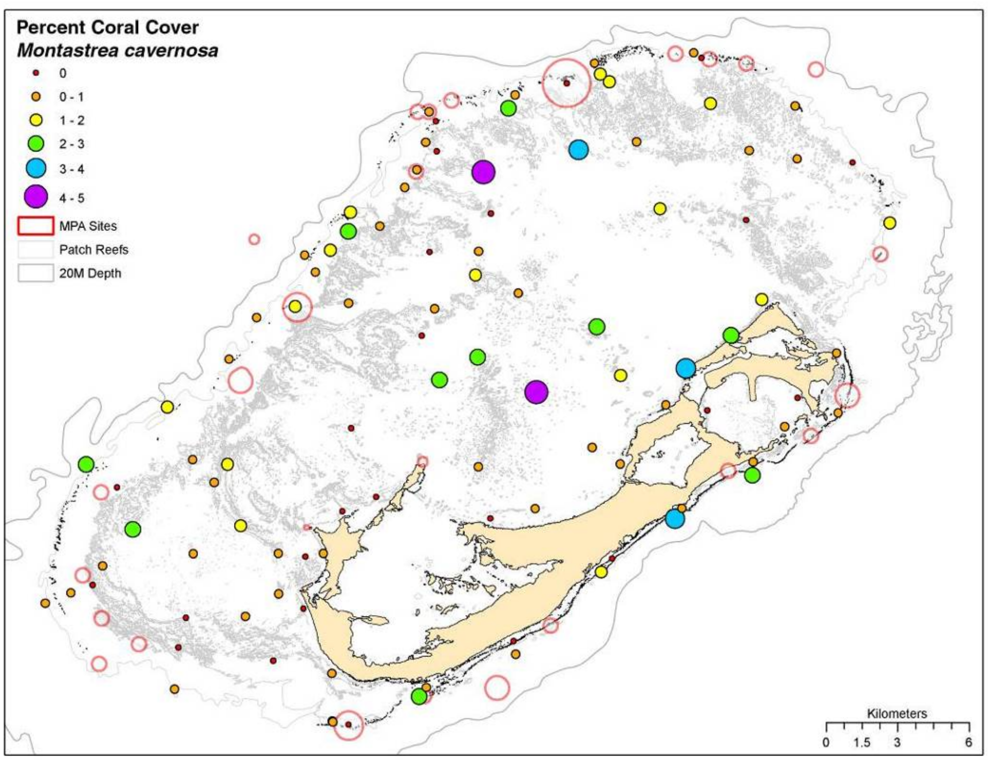
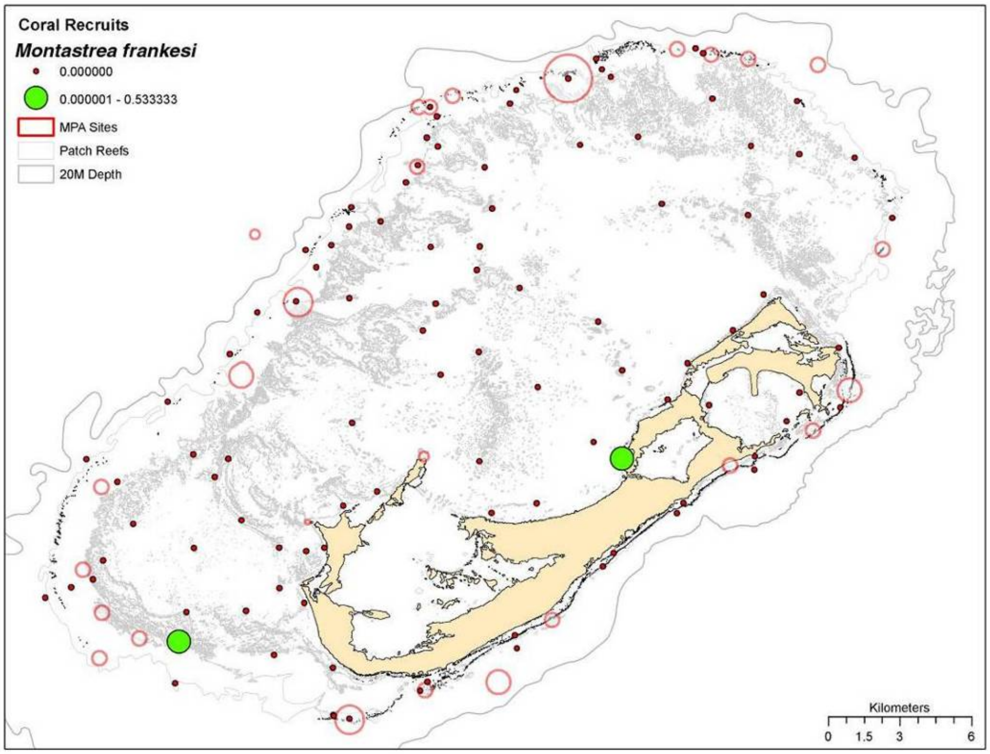


Figure 3.14. (A) Average number of recruits per m^2 and (B) average percent coral cover for the hard coral *Montastraea cavernosa*.

A.



B.

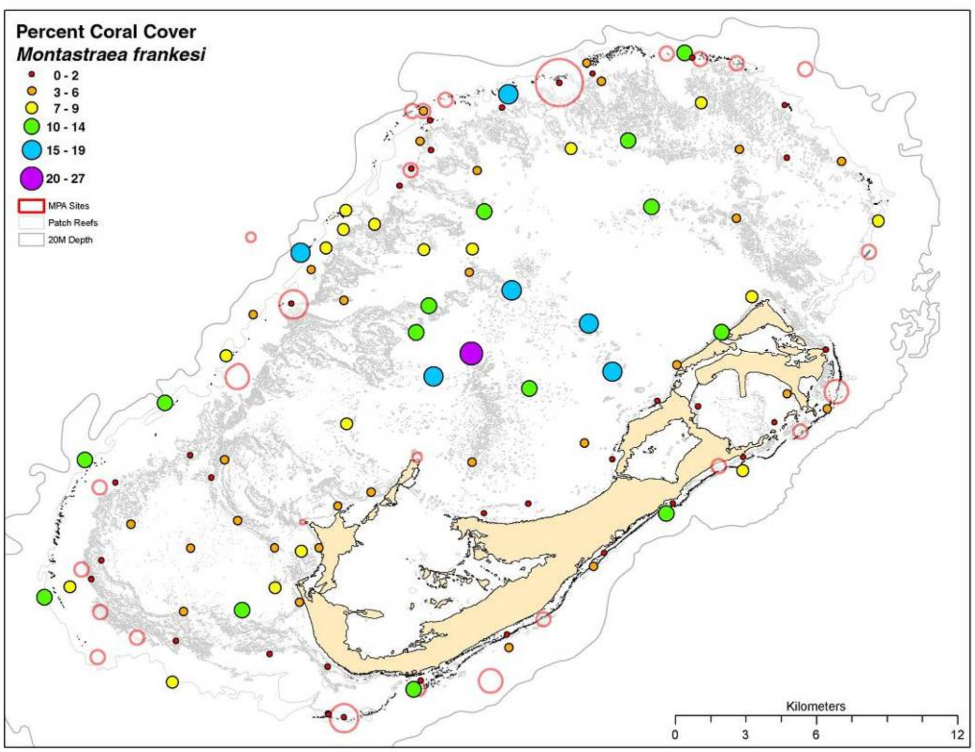
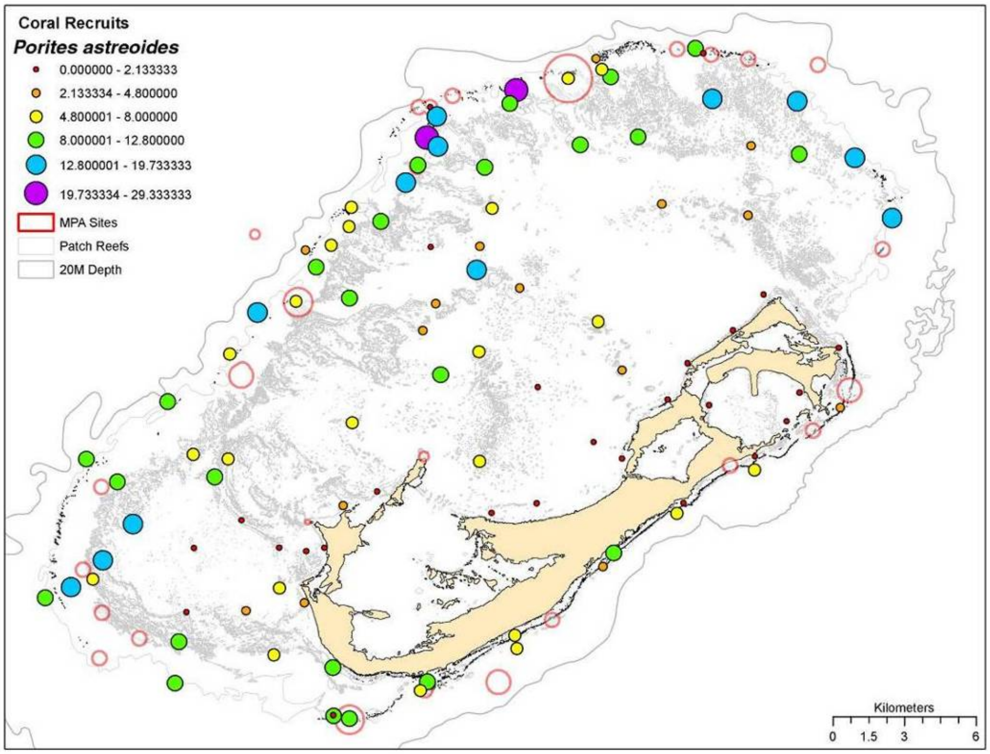


Figure 3.15. (A) Average number of recruits per m^2 and (B) average percent coral cover for the hard coral *Montastraea frankesi*.

A.



B.

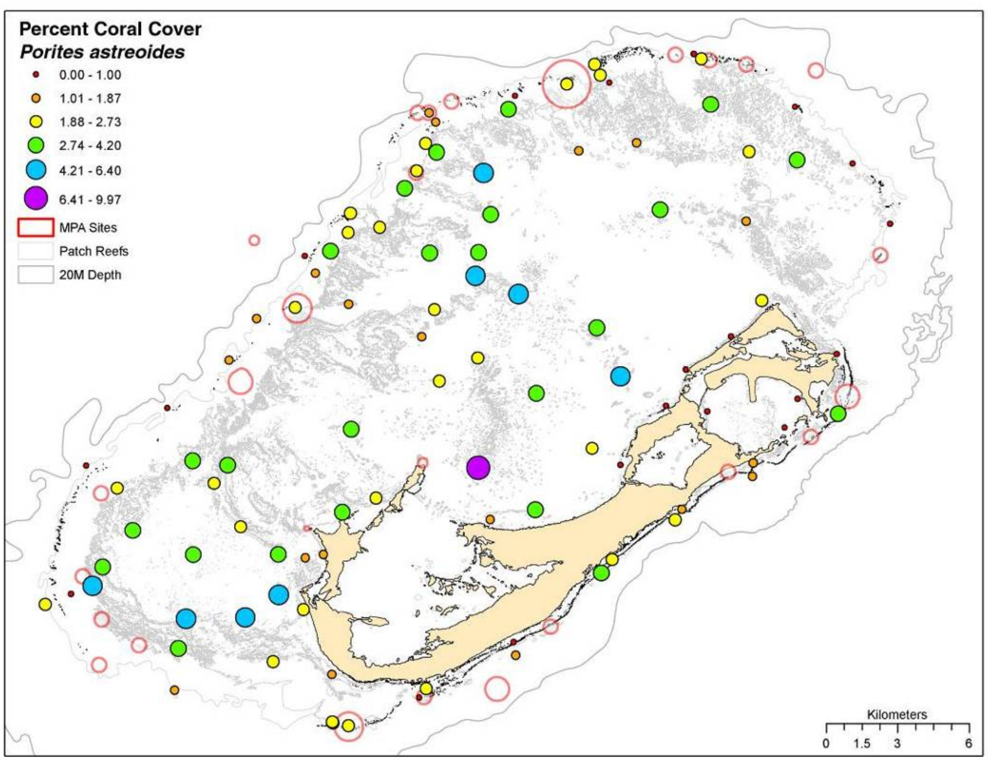


Figure 3.16. (A) Average number of recruits per m^2 and (B) average percent coral cover for the hard coral *Porites astreoides*.

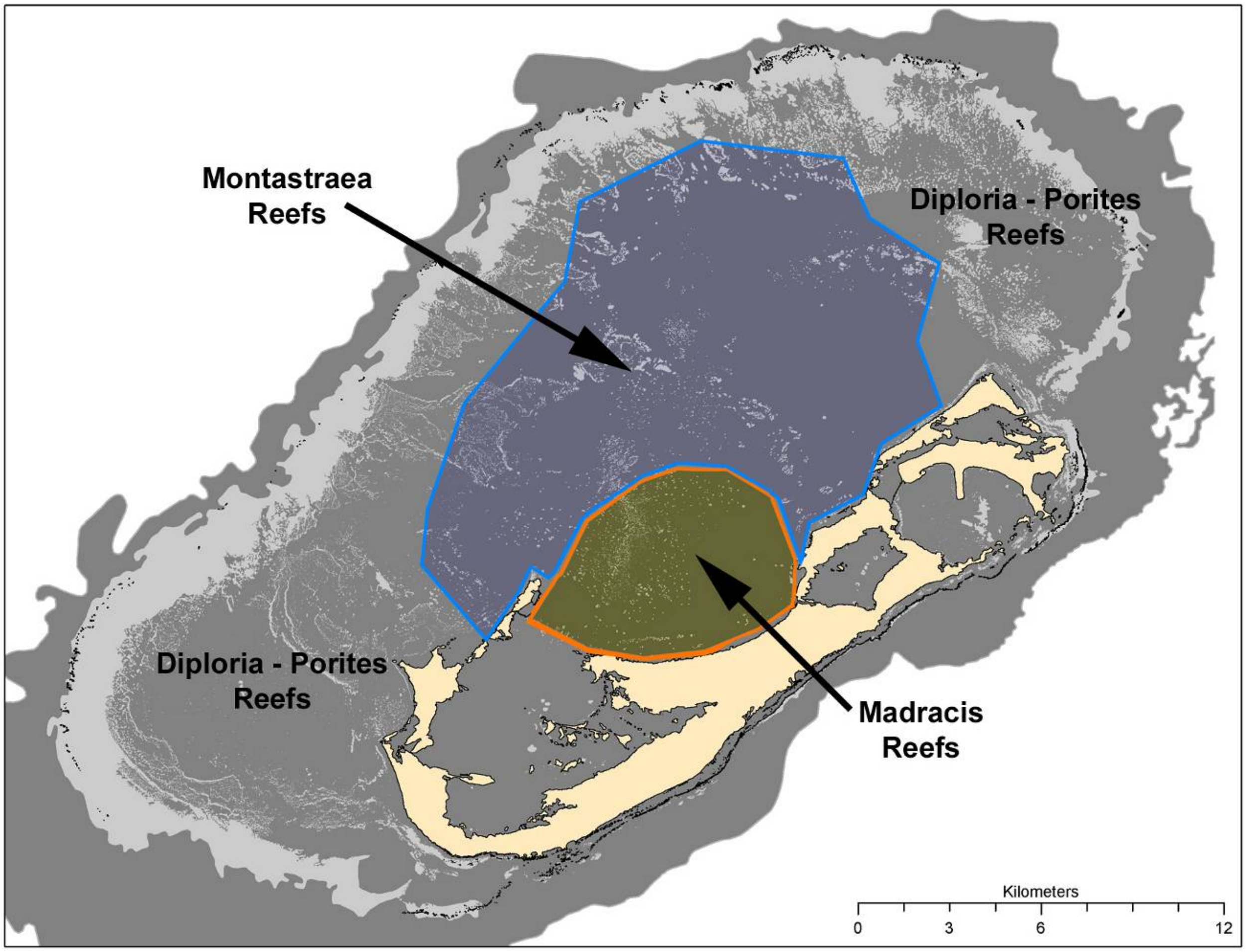


Figure 3.17. Distribution of Madracis, Montastraea and Diploria-Porites reef types in the lagoon.

Chapter 4. An Assessment Of Diver And Anchor Damage In Permanently Buoyed, Protected Dive Sites.

Introduction

Located in the North Atlantic at 32°20'N and 64°50'W, Bermuda supports the most northerly coral reef system in the world. With a land mass of just 55 km^2, surrounded by a total reef platform area of approximately 750 km^2, the northerly extension of subtropical systems to this latitude is a direct result of the transport of warm waters by the Gulf Stream. Hence the majority of the species represented are derived from Caribbean reefs (Thomas and Logan, 1992). However, perhaps due to the absence of the temperature-sensitive acroporids, whilst these 'neighbouring' reefs have suffered dramatic declines in their live coral coverage, Bermuda's reefs remain relatively healthy (Wilkinson, 2000).

Despite this connectivity, local management practices treat the marine ecosystem as a highly stressed, self-sustaining entity, and as such, are generally recognized to be extremely conservative. Since the 1966 enactment of the Coral Reef Preserves Act, there has been complete protection of all attached animals and plants within two substantial areas of Bermuda's shallow waters. Further, in 1978 a protected species order was passed under the Fisheries Act that completely banned the harvest of any coral, stony or soft. With this action Bermuda became, in effect, a national coral preserve.

Bermuda's fish stocks have suffered a different fate. With steady harvesting pressure over 500 years, it is evident from historic accounts that Bermuda's fisheries are now severely depleted

(Lefroy, 1877); certain species are economically extinct, whilst others have been locally extirpated (Butler et al, 1993). In 1990, after it had become apparent that groupers could not support the heavy fishing pressure being exerted (despite a series of increasingly restrictive management tactics), and with fears that health of the entire coral community was being jeopardized along with the increase in landings of the previously ignored herbivorous fish, the trap fishery was closed.

In addition to the ban of trap fishing , three seasonally protected areas were created to protect red hind spawning grounds in 1977. Two of the three areas were re-shaped and combined into a smaller, but more focused special protected area in 2005, in order to encompass black grouper spawning aggregations which were found to also be in the general area. Unfortunately it is generally known that local fishermen continue to fish both protected and undisclosed open black grouper spawning aggregations, despite fairly substantial fines for fishing within the protected areas or for landing more than 1 black grouper per day.

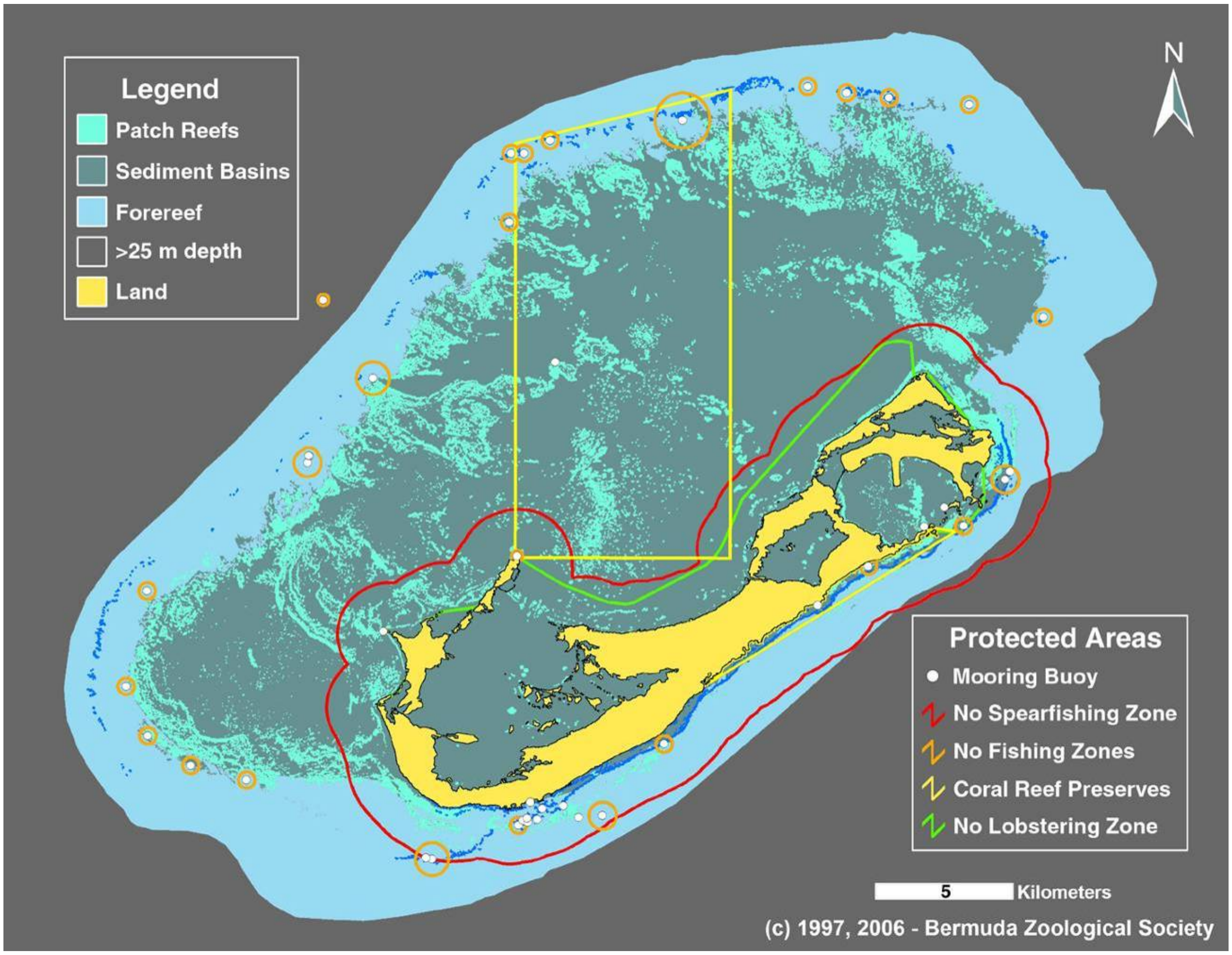


Figure 4.01. A map of the Bermuda Reef Platform showing the locations of different management areas. The orange No Fishing Zones were the focus of this project. The locations of the offshore Grouper Spawning Aggregation Protection Zones are not shown. Additionally, the entire reef platform is a protected area for all hard and soft corals, as well as most herbivorous and many predatory fish.

An unpublished user-survey carried out in 1988 by the Bermuda Divers Association effectively proved that SCUBA divers were becoming one of the most significant user groups, a series of permanent moorings was established in the mid-1980s at the most frequently visited dive sites, each surrounded by a ‘No Fishing’ radius of between 300 and 1000 meters. These moorings were established to reduce user conflicts by separating SCUBA divers and fishermen, as well as to minimize anchor damage from dive boats. However, there is some skepticism within the community that these sites serve as a magnet to the dive community and therefore concentrate higher levels of diver-related damage as well.

These small, disconnected sites constitute the only officially designated permanent Marine Protected Areas currently established. However, the newly enacted Protected Species Act 2003 opens the possibility of creating networks of larger protected areas. Specifically the Act mandates the development of recovery plans for critical habitats, including those used by threatened marine species.

Consideration of the location, size and connectivity of potential site(s) appropriate for further MPA designation is precluded at present due to the vacuum in the data available on the benthic community structure across the entire Bermuda Platform. To date, research has focused on small-scale patterns observed on a few individual reefs. However, high variability has been demonstrated in hierarchical analyses of coral assemblages from other jurisdictions such as the Florida Reef Tract (Murdoch and Aronson, 1999), which suggests that the current data available for Bermuda cannot necessarily be used to extrapolate to the entire 1000 km^2 Platform. Similarly, established fish census programs have concentrated on a few selected reef sites, and provide limited data on critical nursery habitats. This report addresses this vacuum.

Methods

Site Selection

The effectiveness of permanent MPA's as refugia from destructive human impacts was assessed by comparing coral indicators of reef health at existing MPA's with those from adjacent reefs. 29 buoyed permanent marine protected areas are in place around the Bermuda Platform (Fig 4.01). Of these nine were created in 1990 as an amendment of the 1972 Fisheries Act, with an additional 20 added in 2000,.. Four of the MPA sites that were created in 1990 were chosen for analysis, based on their popularity as dive sites (Figure 4.02; Table 4.01). These four MPA sites were each compared to two control sites of comparable depth and geophysiology. Photographic and AGRAA methods described coral and fish indicators. Meanwhile, the efficacy of MPA's in alleviating user conflict was also examined with user group surveys.

Table 4.01 A list of the reef sites surveyed and their location, depth and protection status.

Site Name	Latitude	Longitude	Depth (m)	Status
North Rock	32.4740	-64.7686	4	MPA
Conch Rock	32.4774	-64.7535	4	Control
Skull Rock	32.4674	-64.7863	5	Control
Snake Pit	32.4411	-64.8355	3	MPA
Mini Snake Pit	32.4345	-64.8409	3	Control
Snapper Point	32.4482	-64.8267	3	Control
Eastern Blue Cut	32.3894	-64.8897	4	MPA
Angelfish Pass	32.4108	-64.874	4	Control
Creole Canyon	32.4178	-64.8661	4	Control
SW Breaker	32.2313	-64.8657	4	MPA
Diadema Plateau	32.2324	-64.8727	4	Control
Elusive Reef	32.2326	-64.8599	6	Control

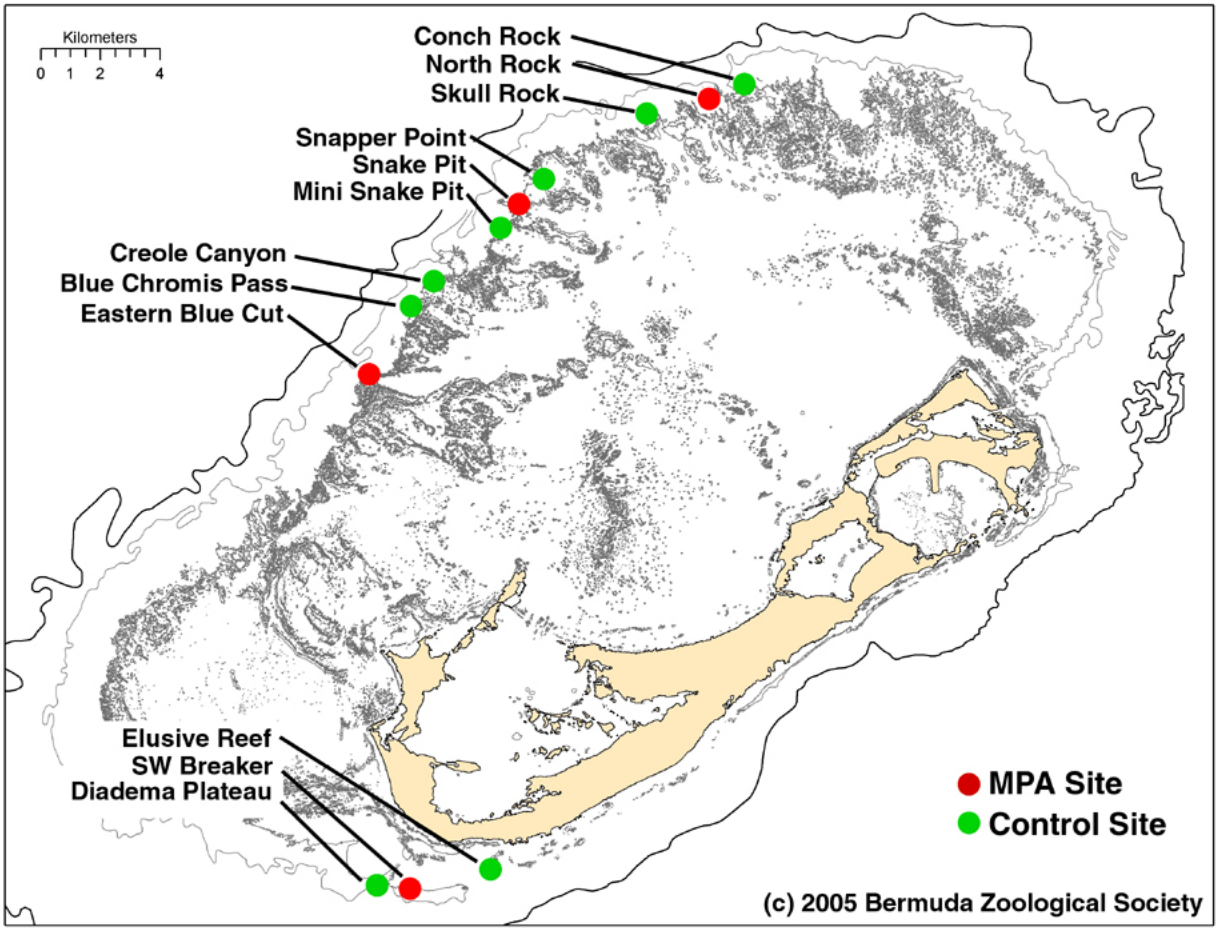


Figure 4.02. Locations and conservation status of the 12 sites surveyed for MPA effect.

Data collection and analysis

Photographic and species presence-absence data sets were collected during the months of July through November of 2006. Four MPA sites and eight control sites were surveyed, with each set of one MPA and 2 controls representing a separate comparative analysis. All sites were between 2- and 8-m depth. Transects were digitally photographed and analyzed following a modified version of methodology described in Aronson et al. (1994; Appendix I). One or two divers stretched 25-m long waterproof tape measures across the top of the reef under study. Transects were generally placed in parallel and 3–10 m apart. The area photographically surveyed at each site encompassed approximately 25m x 100m of reef. Care was taken to avoid placing the transect lines over sand or down the steep sides of the reefs. Once each transect line was in place, another diver slowly swam down its length, photographing 50 non-overlapping frames at every 50-cm mark along the transect line, with each photographed frame encompassing an area of 44 cm by 60 cm, with a resolution of 4.4 pixels per mm. Photography was accomplished with a Canon Powershot S70, 7 Mb digital still camera that was enclosed in a underwater housing. Since all transects were in shallow water < 10m depth, photographs were taken without a flash and instead digitally enhanced in the laboratory. A 65-cm long aluminum bar projected forward from the camera housing. This bar was used as a guide so the diver could maintain a set distance (of 67 cm) between the camera lens and the reef surface. The end of the bar was bent at a 90º angle and positioned to appear within the field of view of the video camera. The part of the bar perpendicular to the camera lens functioned as a scale bar in the photographed images, with a width of 25 mm. During photography the underwater camera was held perpendicular to the overall slope of the reef, with the end of the aluminum bar suspended less than 2 cm from the reef surface. This camera position ensured that the photographed images were of the reef in plan view.

Statistical analysis

Coral species density data and percent cover for each benthic category were analyzed by a one-way ANOVA to test for differences between each MPA and either control site. The assumption of a normal distribution of the data was tested by the Shapiro-Wilk W-test, while assumption of homogeneity of variances was examined with Levene's test. Where possible, non-normal distributions were transformed to conform to a normal distribution using either a log-transformation or an arc-sin transformation of the percentage date converted to proportional data. In cases of heterogeneity of variances, a Welch ANOVA, assuming unequal standard deviations, was employed. Significant differences among group means were distinguished by comparing all pairs with Tukey-Kramer HSD *post-hoc* tests. To assess the capacity of each ANOVA test to detect statistical differences, each one-way ANOVA was accompanied by a power analysis. All statistical procedures used JMP 5.1 (SAS Inc., 2005).

Results

Variation in coral cover among MPA's and control sites:

Mean percent coral cover at MPA's did not consistently exceed coral cover at their associated control sites (Fig. 4.03). For example, while ANOVA and *post-hoc* tests did reveal significant differences in mean coral cover between control sites and the MPA's at North Rock, Eastern Blue Cut, and Southwest Breaker (Table 4.02), the direction of these differences was not constant. In the North Rock grouping, mean coral cover at Skull Rock (25.25 ± 0.99%) significantly exceeded that at both the other control site (Conch Rock; 18.53 ± 1.42%) and the MPA (North Rock; 14.11 ± 1.52%). A similar pattern existed in the Southwest Breaker grouping, where a higher mean coral cover at the control, Elusive Reef (44.85 ± 1.88%), differed significantly from both the other control (Diadema Plateau; 19.84 ± 1.48%) and the MPA site (Southwest Breaker; 21.62 ± 1.85%). The low mean coral cover at North Rock and Southwest Breaker MPA's, however, contrasts with differences found in the Eastern Blue Cut grouping. Here, mean coral cover at the MPA (Eastern Blue Cut; 23.80 ± 1.49%) was greater than means at both control sites (22.78 ± 1.24 and 18.27 ± 1.06% for Creole Canyon and Angelfish Pass, respectively); a difference that proved significant for Angelfish Pass. The Snakepit grouping appeared to follow a similar trend with Snakepit MPA mean coral cover (22.26 ± 1.25%) exceeding means at the control sites, Mini-Snakepit and Snapper Point (19.75 ± 1.29 and 19.62 ± 0.93%, respectively), though these differences were not statistically significant.

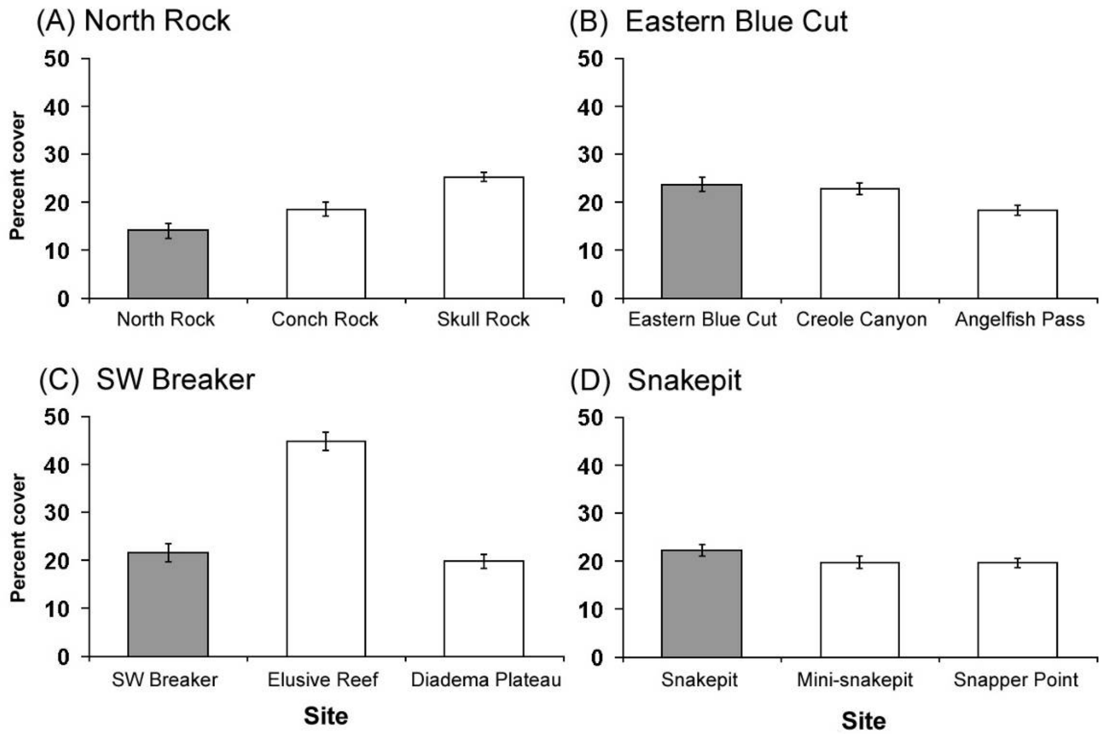


Figure 4.03. Comparison of mean percent coral cover at MPA's to their two associated control sites for the regions (A) North Rock, (B) Eastern Blue Cut, (C) Southwest Breaker, and (D) Snakepit. MPA sites appear as gray bars, control sites as white. Data are means ± standard error.

Table 4.02. Outputs of four one-way ANOVA; each comparing percent coral cover in an MPA with its two control sites. Significant *p*-values highlighted in bold.

Site	**Source**	**df**	**Sum of Squares**	**Mean Square**	**F Ratio**	***p***
North Rock	Site	2	0.06296529	0.031483	17.7106	**<.0001**
	Error	27	0.04799555	0.001778		
	C. Total	29	0.11096085			
Eastern Blue Cut	Site	2	0.01732166	0.008661	5.3356	**0.0111**
	Error	27	0.04382646	0.001623		
	C. Total	29	0.06114812			
Southwest Breaker	Site	2	0.38954115	0.194771	63.9457	**<.0001**
	Error	27	0.08223862	0.003046		
	C. Total	29	0.47177977			
Snakepit	Site	2	0.00441731	0.002209	1.6117	0.2182
	Error	27	0.03700105	0.001370		
	C. Total	29	0.04141836			

Variation in coral species diversity among MPA's and control sites:

Mean coral species diversity, as measured by the Shannon-Weiner diversity index, peaked at the MPA in three out of four groupings (Figure 4.04). At Eastern Blue Cut, the MPA mean (1.23 ± 0.07) exceed that at Creole Canyon (1.16 ± 0.04) and Angelfish Pass (1.12 ± 0.09), where Eastern Blue Cut MPA differed significantly from Angelfish Pass (Table 4.03). Mean diversity at Southwest Breaker MPA (1.04 ± 0.07) similarly exceeded both control sites (Elusive Reef and Diadema Plateau; 1.00 ± 0.08 and 1.00 ± 0.09, respectively), though this relationship was not statistically significant. In the Snakepit grouping, the MPA and Mini-Snakepit had equal means (1.27 ± 0.09 and 1.27 ± 0.07, respectively), while the other control site, Snapper Point, displayed a lower and significantly different mean (1.16 ± 0.07) from both Snakepit and Mini-Snakepit. The opposite trend existed in the North Rock grouping, where the MPA had the lowest mean diversity (0.92 ± 0.12), which also differed significantly from the control sites, Conch Rock (1.09 ± 0.04) and Skull Rock (1.05 ± 0.09).

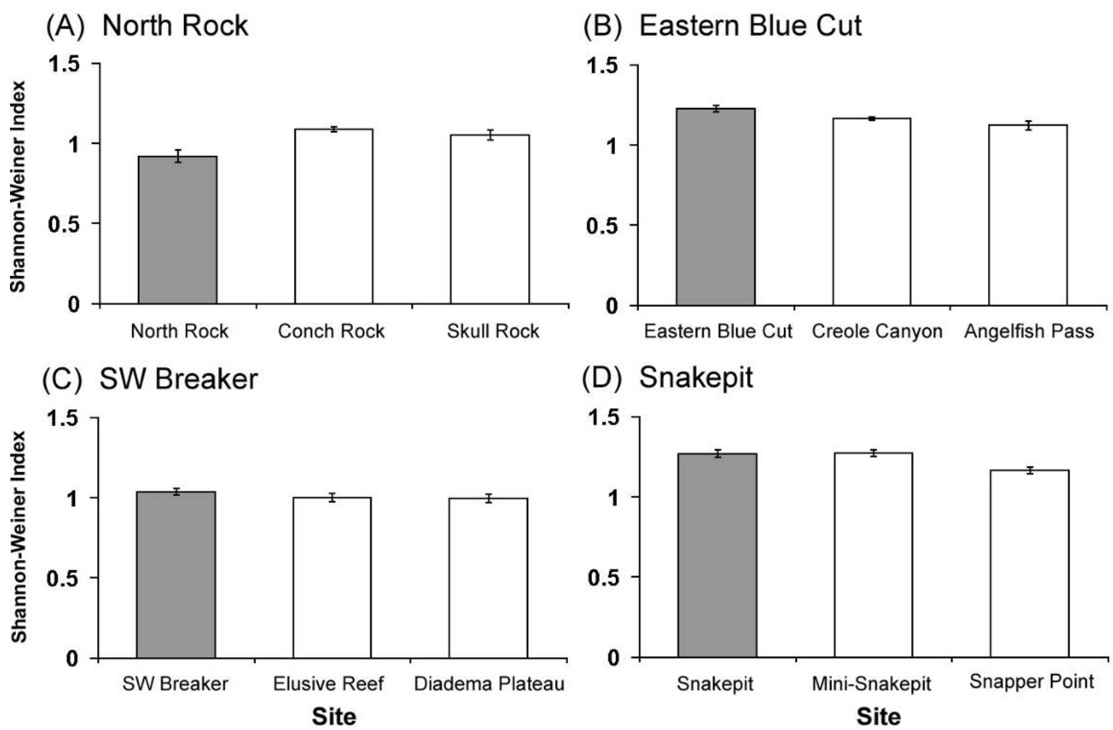


Figure 4.04 Comparison of mean coral species diversity, as measured by the Shannon-Weiner Index, at MPA's to their two associated control sites for the regions (A) North Rock, (B) Eastern Blue Cut, (C) Southwest Breaker, and (D) Snakepit. MPA sites appear as gray bars, control sites as white. Data are means ± standard error.

Table 3.03 Outputs of four one-way ANOVA; each comparing coral species diversity, as measured by the Shannon-Weiner Index, in an MPA with its two control sites. Signficant p-values highlighted in bold.

Site	Source	df	Sum of Squares	Mean Square	F Ratio	p
North Rock	Site	2	0.15385228	0.076926	9.8606	**0.0006**
	Error	27	0.21063712	0.007801		
	C. Total	29	0.36448940			
Eastern Blue Cut	Site	2	0.05621731	0.028109	5.27	**0.0174***
	Error	27	0.12037901	0.004458		
	C. Total	29	0.17659633			
Southwest Breaker	Site	2	0.00951957	0.004760	0.7885	0.4647
	Error	27	0.16299404	0.006037		
	C. Total	29	0.17251361			
Snakepit	Site	2	0.07840550	0.039203	7.0638	**0.0034**
	Error	27	0.14984416	0.005550		
	C. Total	29	0.22824966			

* As variances proved heterogeneous, Eastern Blue Cut Shannon-Weiner diversity index data were tested with a Welch ANOVA that assumed unequal standard deviations.

Variation in coral species density among MPA's and control sites:

Coral species density remained remarkably constant between MPA's and their control sites and also among regions (Figure 4.05). In only one grouping did any statistically significant differences exist (Table 4.04). Here, Southwest Breaker MPA displayed a greater mean species density (6.3 ± 0.2) than at Diadema Plateau (5.7 ± 0.3) and Elusive Reef (5.5 ± 0.2). The difference between the MPA and Elusive Reef proved marginally significant, though this difference may be approached conservatively as species density data could not be normalized. Means from all other sites were comparable to those in the Southwest Breaker grouping and ranged from 5.3 to 6.3.

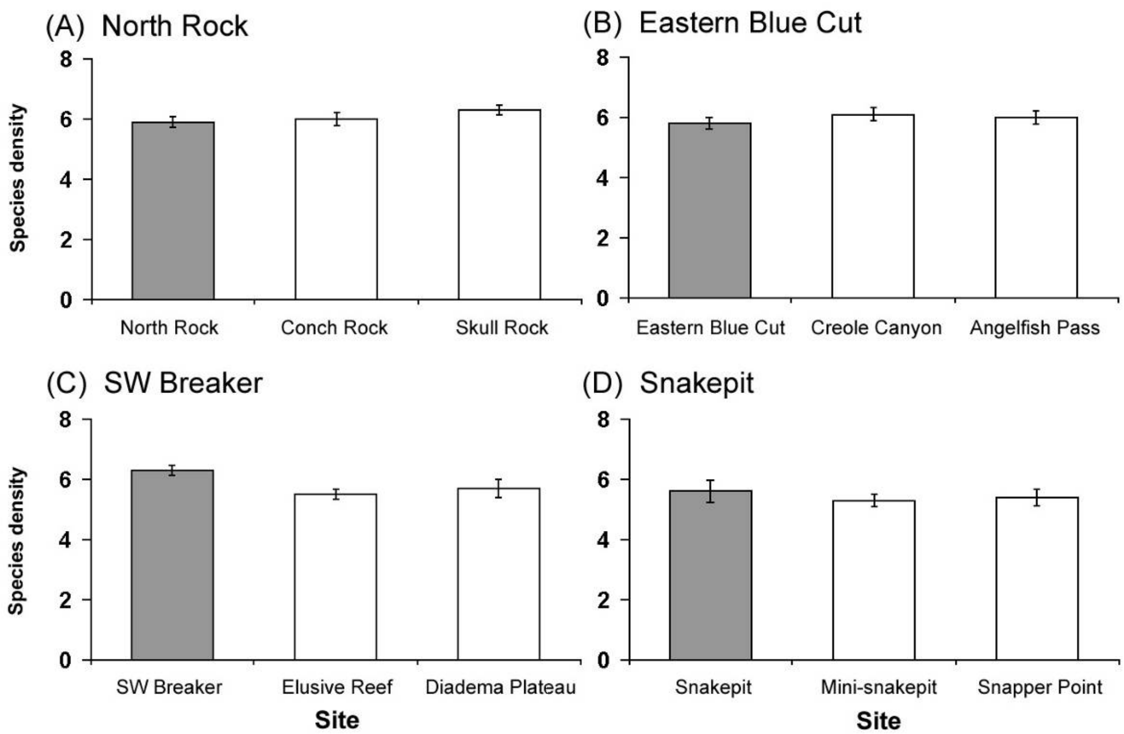


Figure 4.05. Comparison of mean coral species density, measured as the total species counted per transect, at MPA's to their two associated control sites for the regions (A) North Rock, (B) Eastern Blue Cut, (C) Southwest Breaker, and (D) Snakepit. MPA sites appear as gray bars, control sites as white. Data are means ± standard error.

Table 4.04. Outputs of four one-way ANOVA; each comparing coral species density, measured as the total species counted per transect, in an MPA with its two control sites. Signficant p-values highlighted in bold.

Site	Source	df	Sum of Squares	Mean Square	F Ratio	p
North Rock	Site	2	0.8666667	0.433333	1.3000	0.2890*
	Error	27	9.0000000	0.333333		
	C. Total	29	9.8666667			
Eastern Blue Cut	Site	2	0.466667	0.233333	0.5040	0.6097*
	Error	27	12.500000	0.462963		
	C. Total	29	12.966667			
Southwest Breaker	Site	2	3.466667	1.73333	3.6850	**0.0385***
	Error	27	12.700000	0.47037		
	C. Total	29	16.166667			
Snakepit	Site	2	0.466667	0.233333	0.2751	0.7616*
	Error	27	22.900000	0.848148		
	C. Total	29	23.366667			

* As coral species density data did not conform to a normal distribution, untransformed data were tested.

Variation in macroalgal cover among MPA's and control sites:

In common with coral cover, percent macroalgal cover showed either no or significant but contrasting differences between MPA's and their associated controls sites (Figure 4.06, Table 4.05). For instance, mean percent cover was highly similar for Snakepit MPA (15.87 ± 0.84%) and its control sites (Mini-snakepit and Snapper Point; 16.51 ± 0.56 and 18.27 ± 0.78%, respectively). Similarly, Southwest Breaker MPA and the control sites, Elusive Reef and Diadema Plateau, shared almost identical means (10.22 ± 1.24, 9.46 ±1.21, and 10.81 ± 0.64%, respectively). Significant differences did exist between MPA's and control sites in the North Rock and Eastern Blue Cut groupings, but showed contrasting trends. Mean macroalgal cover at Eastern Blue Cut MPA (25.87 ± 1.51%), for example, differed significantly from the lower means at both Creole Canyon (18.57 ± 1.21%) and Angelfish Pass (12.27 ± 0.84%). In contrast, mean macroalgal cover at North Rock MPA (11.27 ± 0.90%) as well as at the control site, Skull Rock (12.04 ± 0.85%), was lower and significantly different from the second control, Conch Rock (20.68 ± 1.34%).

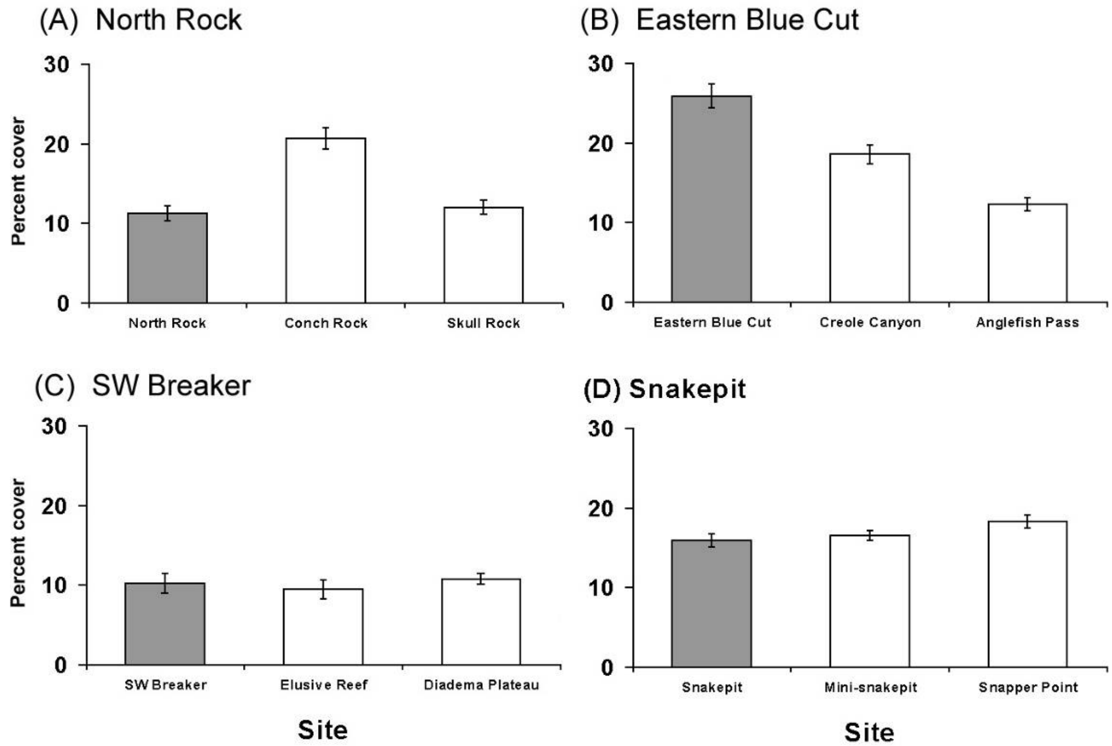


Figure 4.06. Comparison of mean percent macroalgal cover at MPA's to their two associated control sites for the regions (A) North Rock, (B) Eastern Blue Cut, (C) Southwest Breaker, and (D) Snakepit. MPA sites appear as gray bars, control sites as white. Data are means ± standard error.

Table 4.05. Outputs of four one-way ANOVA; each comparing percent macroalgal cover in an MPA with its two control sites. Signficant p-values highlighted in bold.

Site	Source	df	Sum of Squares	Mean Square	F Ratio	p
North	Name	2	0.05454009	0.027270	24.5940	**<.0001**
Rock	Error	27	0.02993779	0.001109		
	C. Total	29	0.08447789			
Eastern	Site	2	0.09269741	0.046349	31.3215	**<.0001**
Blue Cut	Error	27	0.03995383	0.001480		
	C. Total	29	0.13265124			
Southwest	Site	2	0.00092036	0.000460	0.4064	0.6701
Breaker	Error	27	0.03057474	0.001132		
	C. Total	29	0.03149510			
Snakepit	Site	2	0.00311803	0.001559	2.9032	0.0721
	Error	27	0.01449879	0.000537		
	C. Total	29	0.01761682			

Variation in gorgonian (soft coral) cover among MPA's and control sites:

In three out of the four MPA and control site comparisons, mean percent cover of gorgonians in MPA's exceeded means at both control sites (Figure 4.07). Furthermore, in all three of these comparisons, MPA means differed significantly from at least one control site (Table 4.06). After $\log_{10}$-transformation, mean cover at Eastern Blue Cut MPA (5.61 ± 0.58%) differed significantly from both control sites, Creole Canyon (4.79 ± 0.49%) and Angelfish Pass (3.64 ± 0.48%). In the Southwest Breaker grouping, significant differences occurred between Southwest Breaker MPA (5.12 ± 0.56%) and the control site, Elusive Reef (1.36 ± 0.25%), as well as among the control sites, Elusive Reef and Diadema Plateau (1.36 ± 0.25 and 4.17 ± 0.39%, respectively). Mean gorgonian cover at Snakepit (6.10 ± 0.58%) also exceeded and differed significantly from the two control sites, Mini-snakepit (3.93 ± 0.55%) and Snapper Point (3.29 ± 0.34%). In the only grouping where gorgonian cover was not highest in the MPA, mean cover at Conch Rock (3.35 ± 0.20 %) differed significantly from both the other control site (Skull Rock; 2.18 ± 0.48%) and North Rock MPA (2.17 ± 0.26%).

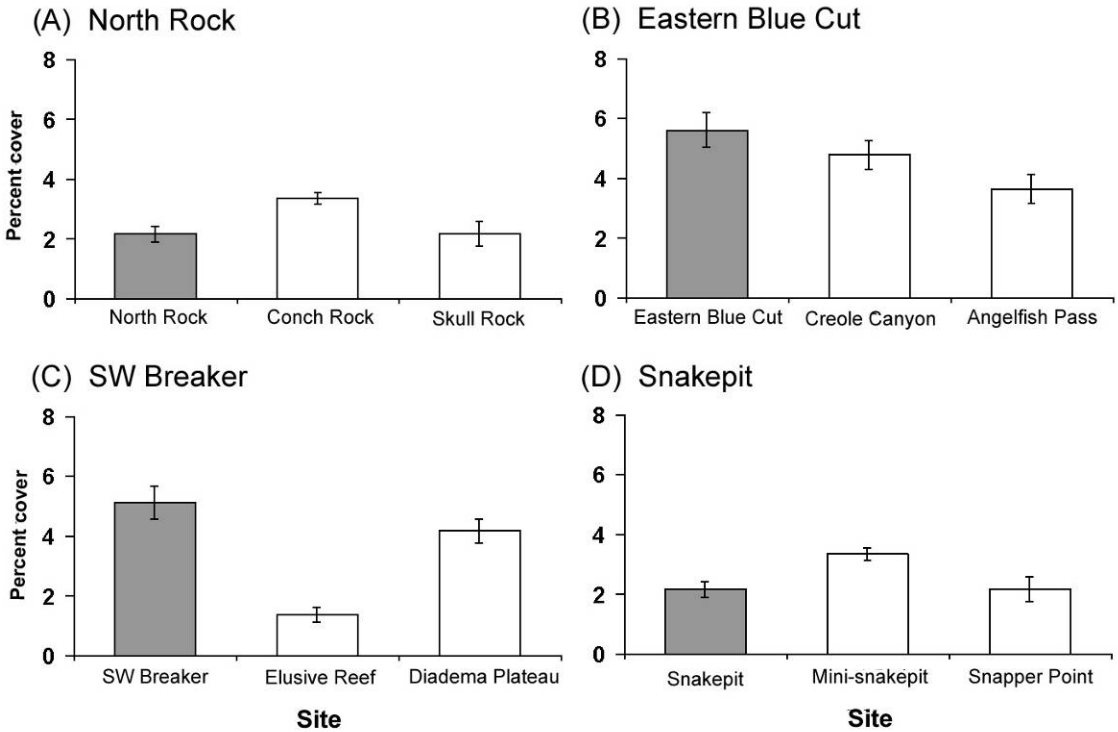


Figure 4.07. Comparison of mean percent gorgonian cover at MPA's to their two associated control sites for the regions (A) North Rock, (B) Eastern Blue Cut, (C) Southwest Breaker, and (D) Snakepit. MPA sites appear as gray bars, control sites as white. Data are means ± standard error.

Table 4.06. Outputs of four one-way ANOVA; each comparing percent gorgonian cover in an MPA with its two control sites. Signficant p-values highlighted in bold.

Site	**Source**	**df**	**Sum of Squares**	**Mean Square**	**F Ratio**	**p**
North Rock	Name	2	0.00093116	0.000466	4.9661	**0.0146**
	Error	27	0.00253130	0.000094		
	C. Total	29	0.00346247			
Eastern Blue Cut	Site	2	0.21784905	0.108925	4.1155	**0.0275***
	Error	27	0.71459984	0.026467		
	C. Total	29	0.93244889			
Southwest Breaker	Site	2	0.00762695	0.003813	21.7475	**<.0001**
	Error	27	0.00473451	0.000175		
	C. Total	29	0.01236145			
Snakepit	Site	2	0.00434854	0.002174	8.6416	**0.0013**
	Error	27	0.00679334	0.000252		
	C. Total	29	0.01114189			

*Data from Eastern Blue Cut was $\log_{10}$-transformed prior to analysis.

Variation in crustose coralline algae, turf and bare (CTB) cover among MPA's and control sites: Like macroalgae and coral cover, there was no consistent pattern of relationships between MPA's and their control sites for CTB percent cover (Figure 4.08, Table 4.07). Mean percent cover at Eastern Blue Cut MPA (44.06 ± 2.11%) was lower and differed significantly from the two control means (Creole Canyon and Angelfish Pass; 52.83 ± 0.98 and 60.21 ± 1.16%, respectively). This trend also existed for the Snakepit grouping, where Snakepit MPA exhibited the lowest mean CTB cover and differed significantly from one control site, Snapper Point (55.55 ± 0.85%). In the Southwest Breaker grouping, the control site, Elusive Reef had the lowest mean cover (44.07 ± 1.25%), which differed significantly from the other control site (Diadema Plateau; 64.59 ± 1.57%) and Southwest Breaker MPA (62.14 ± 1.75%). Finally, in the North Rock grouping, North Rock MPA displayed the highest mean CTB cover (69.39 ± 1.91%) and differed significantly from the control sites, Skull Rock (58.86 ± 1.41%) and Conch Rock (56.94 ± 0.94%). ANOVA results for the North Rock trio, however, must be interpreted conservatively as data analyzed did not conform to a normal distribution.

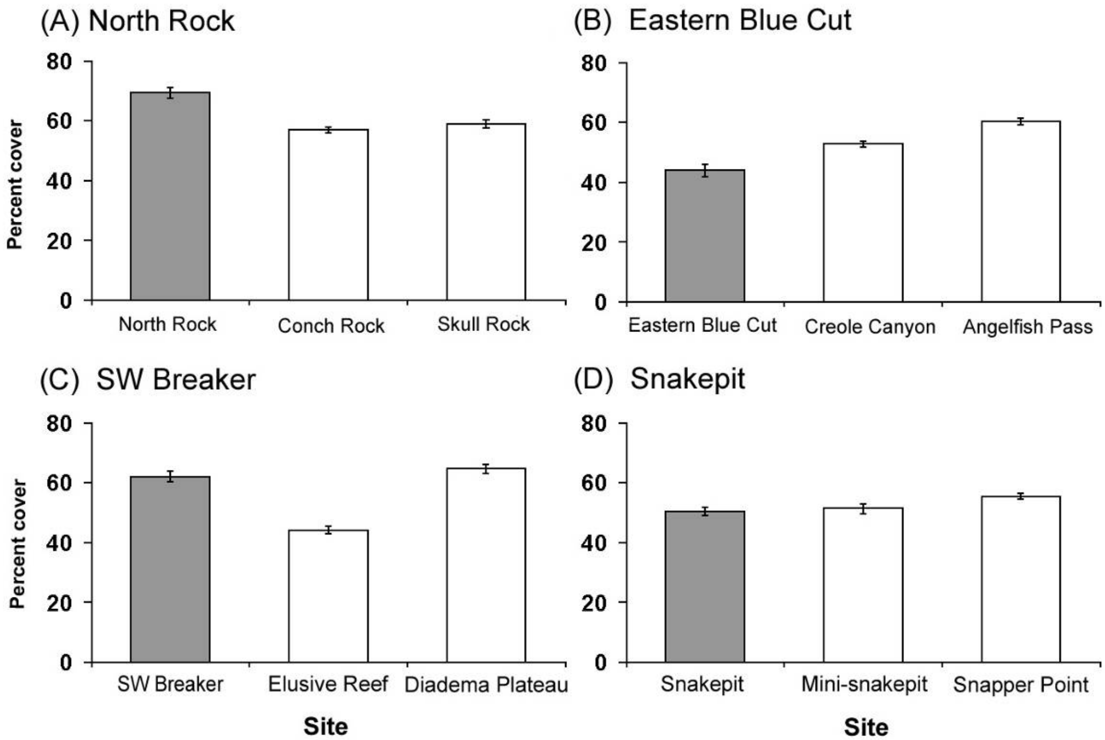


Figure 4.08. Comparison of mean percent crustose, coralline algae, turf and bare (CTB) cover at MPA's to their two associated control sites for the regions (A) North Rock, (B) Eastern Blue Cut, (C) Southwest Breaker, and (D) Snakepit. MPA sites appear as gray bars, control sites as white. Data are means ± standard error

Table 4.07. Outputs of four one-way ANOVA; each comparing percent CTB cover in an MPA with its two control sites. Signficant p-values highlighted in bold.

Site	**Source**	**df**	**Sum of Squares**	**Mean Square**	**F Ratio**	**p**
North Rock	Name	2	0.04161391	0.020807	20.3825	**<.0001***
	Error	27	0.02756220	0.001021		
	C. Total	29	0.06917611			
Eastern Blue Cut	Site	2	0.13078692	0.065393	28.9816	**<.0001****
	Error	27	0.06092228	0.002256		
	C. Total	29	0.19170921			
Southwest Breaker	Site	2	0.25128925	0.125645	53.2080	**<.0001**
	Error	27	0.06375742	0.002361		
	C. Total	29	0.31504667			
Snakepit	Site	2	0.01359808	0.006799	5.1125	**0.0131**
	Error	27	0.03590693	0.001330		
	C. Total	29	0.04950502			

* As North Rock CTB data could not be normalized, untransformed data were tested.
** As variances proved heterogeneous, Eastern Blue Cut CTB data were tested with a Welch ANOVA that assumed unequal standard deviations.

Statistical power of one way ANOVA:

Power analysis of all one-way ANOVA showed generally high statistical power, with a mean power of 0.68 ± 0.06 when tests for all benthic cover types and coral species diversity measures were combined. When power was examined according to the different variables tested, large differences in power were evident among data types (Figure 3.11). Species density displayed by far the lowest power with a group mean of 0.27 ± 0.12. Mean powers of other groups were consistently high with CTB ANOVA demonstrating the greatest power with a mean of 0.94 ± 0.06. Coral and gorgonian mean powers were similar (0.78 ± 0.16 and 0.85 ± 0.08, respectively) and intermediate to CTB power values.

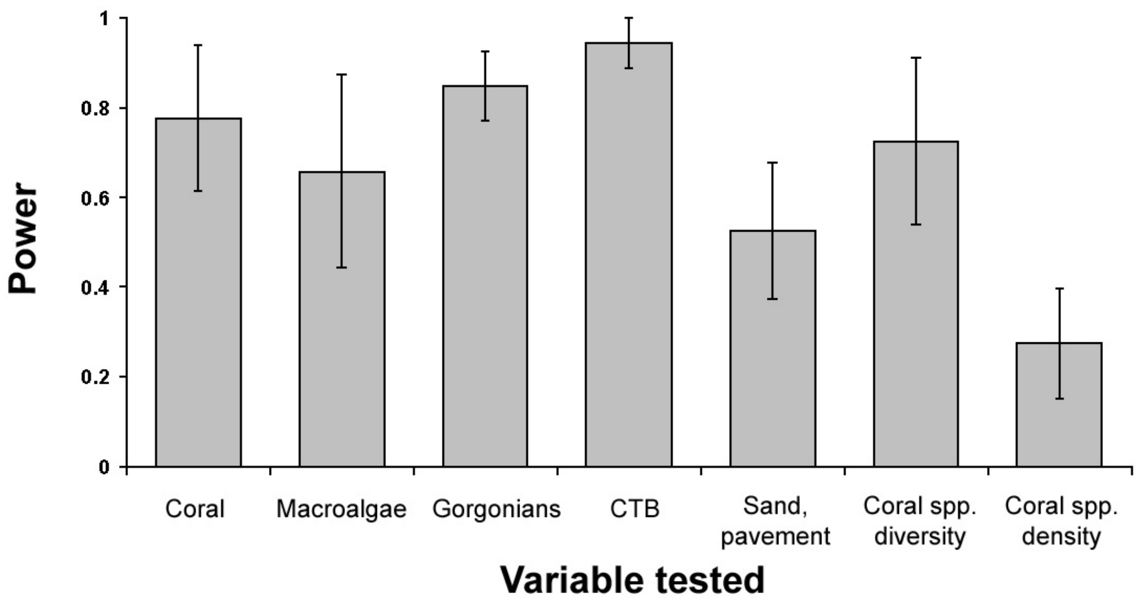


Figure 4.09. Mean statistical power of one-way ANOVA comparing MPA's to their control sites for major benthic cover types and coral species diversity (n = 4 per variable tested).

Discussion

Statistical analysis of the percent cover of corals, macroalgae and the other benthic functional groups indicated no consistent differences between currently buoyed MPA dive sites and control sites that were similar in geomorphology. Some buoyed sites had more coral cover, while other buoyed sites had less cover, relative to controls, but diver impacts did not seem to be a factor in the site by site differences in coral quality on reefs.

The four buoyed dive sites surveyed are all located in rim reef habitat, as that is where most permanently buoyed dive sites are located. The rim habitat is by nature composed of a coral community that can tolerate high levels of physical disturbance, as the rim on all sides of Bermuda is exposed to large storm waves from either hurricanes in the summer or northeasters during the winter. Both kinds of storms generate winds in excess of 60-kts, along with predicted ocean waves in excess of 8-m height. Relative to these formidable natural events it seems likely that diver impacts are relatively limited. Dive shop operators educate the diver clients on how to minimize damage to corals on reefs, and are careful to not anchor on the reefs where they take tours, and these behaviors probably also substantially limit the amount of diver damage occurring at the buoyed dive sites.

Chapter 5. Comparison Of Reef Passes To Reef Flats In The Northern Rim Reef Zone.

Introduction

The buoyed marine protected areas along the northern rim of the Bermuda platform tend to be located in either areas of natural interest or where a ship wreck has occurred. In general the natural MPA sites are all located where a natural pass intersects the rim, connecting the lagoon to the forereef. These sites are interesting to divers as they are deeper than the surrounding rim reef and usually possess “swim-throughs” or other features of natural beauty. Chapter 4, above, also demonstrated that there are enhanced fish diversity and abundance at the passes relative to the nearby reef flats in the same rim zone.

In this section we examined whether reef passes are also different from reef flats in coral cover and in coral community composition (a multivariate measure). Percent cover data collected using the modified AGRRA protocol was used. It may be expected that passes have higher percent cover and more species of coral than reef flats, since divers seem to prefer passes as dive sites. Conversely, passes may be expected to have poorer coral health, since passes are locations in which lagoonal water is funneled out to the forereef, and lagoonal water is generally more turbid and more thermally variable than offshore water (Barnes and Bodungen 1977).

Analysis indicates that percent cover is slightly lower in passes than the neighbouring reef flats. The passes also exhibit a significantly different coral community compared to the reef flats. Sites across both habitats exhibited high variability, however. This indicates that rim reef habitat can vary substantially in the condition of the coral community from place to place regardless of the presence of a pass.

Methods

Coral cover data for each species and for hard corals overall were calculated using the modified AGRRA protocol. Six transects were assessed at each site. The species membership and length under the 10-m long transect was measured for every coral of 10-cm maximum length or greater, and summed by species for each transect. Nested analysis of variance (ANOVA) was done to compare percent cover across sites within each habitat type (reef pass or reef flat) designated by expert coral reef scientists. Note that sites were randomly selected from an large population of possible survey locations for both habitat types.

Locations that share environmental conditions should tend to affect the membership of coral species in a similar manner, while locations that differ in environmental character should tend to possess discrete coral communities. In order to examine the degree of similarity in the distribution of sites across both habitat types, we calculated an Analysis of Similarity (ANOSIM;) on the summed percent cover data of the 11 most abundant species across the 17 sites transects. Bray Curtis similarities between square-root transformed cover data for all species were calculated and similarity trees and non-metric multidimensional-scaled diagrams produced for visually comparison against the hypothetical patterns.

Results

Sites on reef flats tended to have higher coral cover, but lower species density relative to sites at reef passes, although differences between sites within each habitat category were high. Figure 5.01 illustrates the average percent cover of corals at the 9 reef flat sites and 8 reef pass sites surveyed along the northern rim of the Bermuda Reef Platform. Nested analysis of variance of the coverage data (Table 5.01) confirmed that within-category variance from reef to reef was high, and that differences between habitat categories were not significantly different, although only marginally so.

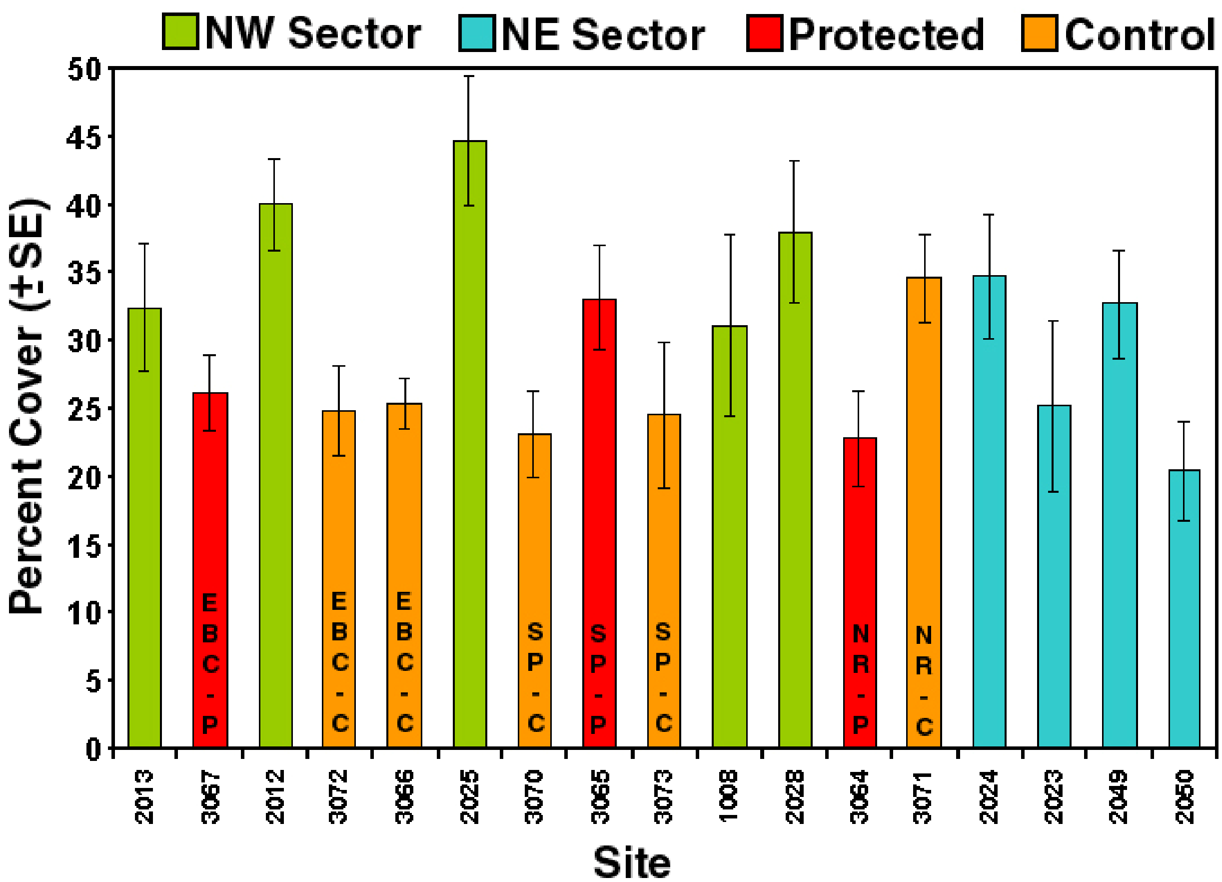


Figure 5.01. A graph of average percent coral cover (±SE) at reef flat (green or blue) and reef pass (red or orange) locations along the NW and NE rim of the Bermuda lagoon. Sites are presented in order of location, from west to east.

Table 5.01. A nested ANOVA examining whether 2 habitats (Reef Passes & Reef Flats) exhibited significant differences in percent cover of hard corals. Six transects were assessed at each site. Proportional data was arcsine square-root transformed before analysis.

Source	**df**	**SS**	**MS**	**F ratio**	***p* value**
Habitat	1	0.11090	0.11090	3.8080	0.0699
Site[Habitat]	15	0.43686	0.02912	2.1284	**0.0157**
Error	85	1.16311	0.01368		
Total	101	1.71087			

Sites were plotted into a multidimensional scaling diagram in order to see how reefs of the two different geomporphologies compared in coral composition (Figure 5.02). Sites on reef flats and sites on reef passes form two distinct clusters with few sites clustering with the wrong category. Multivariate analysis of the differences in coral community structure between reef flats and reef passes using PRIMER techniques determined that most sites on reef flats were highly significantly similar to each other, as were sites on reef passes, but reef flats and reef passes differed in community composition (Table 5.02). SIMPER analysis (Table 5.03) determined that reef flats tended to have higher cover of the head corals *D. strigosa*, *D. labyrinthiformis*, *M. frankesi* and *M. cavernosa*, while reef passes tended to have higher cover of the more weedy corals *P. astreoides* and *M. alcicornis*.

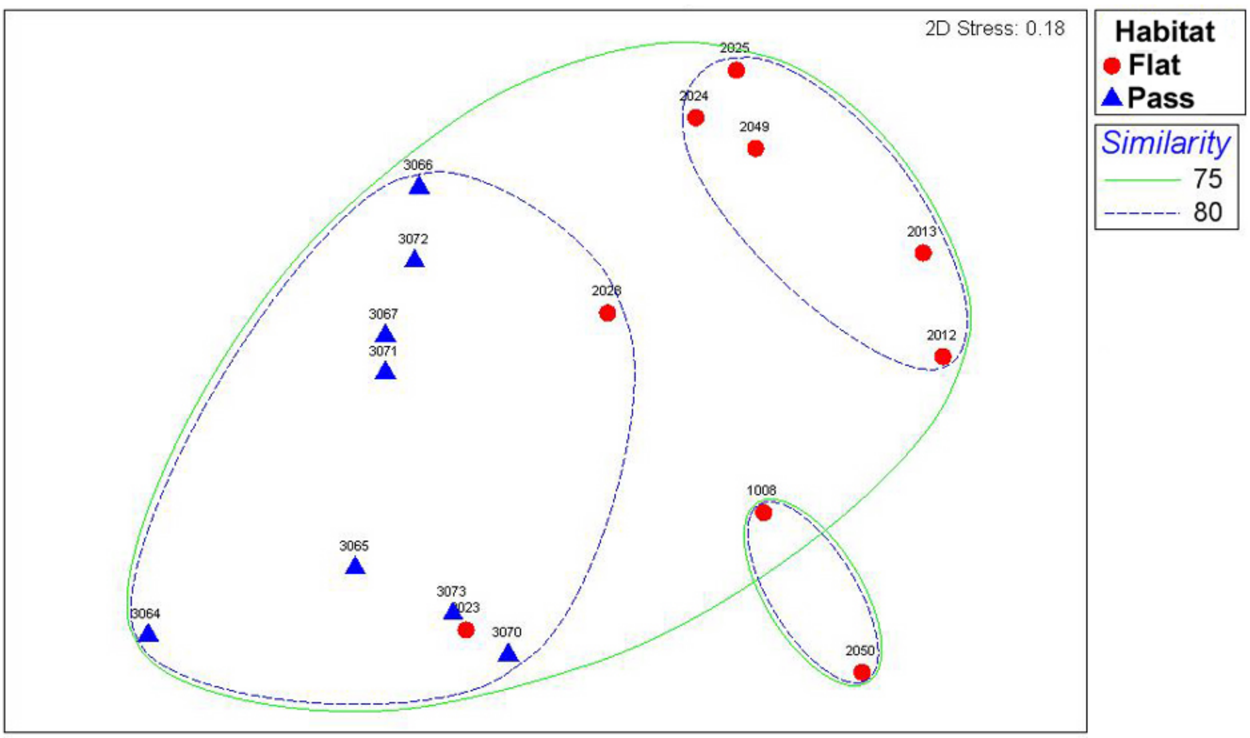


Figure 5.02. MDS showing the differences in coral community composition between survey sites located on reef flats versus reef passes.

Table 5.02. Analysis of Similarities (ANOSIM) comparing the likelihood that coral communities at reef passes are the same as from those at reef flats.

Global Test
Sample statistic (Global R): 0.393
Significance level of sample statistic: 0.9%
Number of permutations: 999 (Random sample from 24310)
Number of permuted statistics greater than or equal to Global R: 8

Table 5.03. SIMPER analysis revealing which coral species contribute to the differences between sites located at reef flats versus those at reef passes. Abundances are square-root percentage data.

SIMPER
Similarity Percentages

One-Way Analysis

Group Reef Flat
Average similarity: 83.01

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Dstrig	3.99	30.17	11.02	36.34	36.34
Dlab	3.03	21.09	5.43	25.40	61.74
Mann	2.02	14.17	5.03	17.07	78.81
Past	1.29	8.97	4.52	10.81	89.62
Mi. alc	0.93	5.63	3.05	6.78	96.40

Group Reef Pass
Average similarity: 85.56

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Dlab	2.93	24.88	10.83	29.08	29.08
Dstrig	2.88	23.43	8.25	27.39	56.47
Past	1.65	13.86	9.28	16.20	72.67
Mann	1.59	10.59	4.18	12.38	85.05
Mi. alc	1.41	9.74	2.68	11.39	96.43

Groups Flat & Pass
Average dissimilarity = 19.33

	Group Flat	Group Pass				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Dstrig	3.99	2.88	4.92	1.77	25.46	25.46
Mann	2.02	1.59	3.44	1.56	17.81	43.27
Dlab	3.03	2.93	3.10	1.84	16.03	59.30
Mi. alc	0.93	1.41	2.89	1.40	14.94	74.24
Mcav	0.74	0.73	2.82	1.35	14.61	88.85
Past	1.29	1.65	1.88	1.33	9.71	98.56

Flats have more D. strig, D. lab and M. frankesi.
Passes have more Mi. alcicornispora and P. astreoides.

Discussion

Univariate and multivariate analysis determined that reef flats had higher coral cover than reef passes, and that the coral communities were significantly different between habitat types. Differences in geomorphology probably cause reef flats and reef passes to experience differences in wave stress, tidal current flow, and exposure to lagoonal water (Figure 5.03). Lagoonal water tends to be more turbid and more thermally variable than offshore water. Lagoonal water may also possess different nutrient concentrations and different plankton than offshore oceanic water, and these physical, chemical and biological differences may be presumed to cause the differences in coral assemblage structure between the two habitat types.

Analysis of fish community structure, described in a separate section of this project, also determined that more species of fish and a greater biomass of fish tend to be found at passes relative to reef flats at the rim, presumably because of the same environmental differences between reef passes and flats. In particular, large predatory fish tended to be more common at reef passes than reef flats and these kinds of fish have been subject to overfishing for the past 50 years at least. Reef passes are easily distinguishable from reef flats both by boaters on the water and in visual inspection of aerial maps of the reef platform. As there are less than 40 reef passes of noticeable size across the western and northern rim of the Bermuda platform, it would seem reasonable to attempt to make the majority of these geomorphological features Marine Protected Areas. Divers prefer reef passes to reef flats, and the presence of sand within the passes generally means permanent moorings can be installed in sand instead of into the reef matrix.

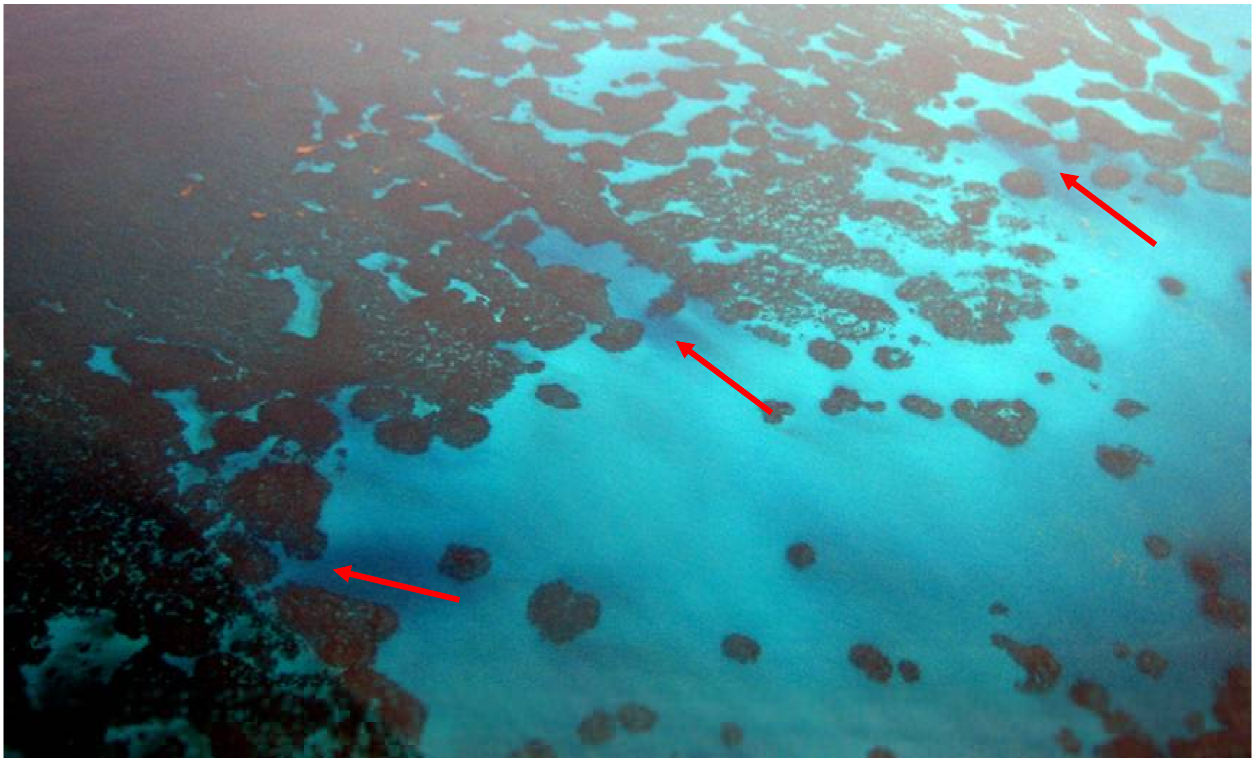


Figure 5.03 Aerial photograph of the North Rim of the Bermuda lagoon, showing the geomorphology of three passes (marked with red arrows) through the platform rim. Reef flat habitat is found between the passes.

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Appendix 1: A list of coral species observed in Bermuda

Branched Oviparous

1. *Oculina diffusa*
2. *Oculina robusta*

Branched Viviparous

1. *Madracis decactis*
2. *Madracis formosa*
3. *Madracis mirabilis*
4. *Porites furcata* (New record: T.J.T. Murdoch: unpublished confirmation)
5. *Porites porites*

Massive Viviparous

1. *Dichocoenia stokesii*
2. *Favia fragum*
3. *Isophyllia sinuosa*
4. *Meandrina meandrites*
5. *Porites astreoides*
6. *Siderastrea radians*

Massive Oviparous

1. *Diploria labyrinthiformis*
2. *Diploria strigosa*
3. *Montastraea cavernosa*
4. *Montastraea faveolata*
5. *Montastraea franksi*
6. ~~*Siderastrea siderea*~~ (T.J.T. Murdoch, S. du Putron: possibly regionally extinct?)
7. *Stephanocoenia intersepta*

Foliose, Plating and Solitary

1. *Agaricia fragilis*
2. *Scolymia cubensis* (W. Sterrer: potentially more than one species)

Appendix 2. Summary of MPA ANOVA, nested models and power analyses of % cover data at MPA's and control sites

One-way Anova:

Sites	Cover type	Normal?	Homogeneity of variance?	Normal after transformation?	Test statistics	Differing means
NR	Coral	Y	Y	-	F=17.71 P<0.0001	SR ≠ NR SR ≠ CR
	Gorg.	Y	Y	-	F=4.97 P=0.0146	CR ≠ SR CR ≠ NR
	CTB	N	Y	Arcsin – no Sqrt – no Log(10) – no Box-Cox - no	F=20.30 P<0.0001	NR≠SR NR≠CR
	Macroalg.	Y	Y	-	F=24.59 P<0.0001	CR ≠ SR CR ≠ NR
	SPR	N	N	Log(10) – no Sqrt – no Arcsin - no Box-Cox - no	F=3.89* P=0.047*	-
	Shannon-Weiner	Y	Y	-	F=9.86 P=0.0006	NR≠SR NR≠CR
	Species density	N	Y	No	F=1.30 P=0.2890	-
SNP	Coral	Y	Y	-	F=1.61 P=0.2182	-
	Gorg.	Y	Y	-	F=8.64 P=0.0013	SNP≠MS SNP≠SP
	CTB	Y	Y	-	F=5.11 P=0.0131	SP≠SNP
	Macroalg.	Y	Y	-	F=2.90 P=0.0721	-
	SPR	Y	Y	-	F=3.58 P=0.0418	MS≠SP
	Shannon-Weiner	Y	Y	-	F=7.06 P=0.0034	SP≠MS SP≠SNP
	Species density	N	Y	No	F=0.28 P=0.7616	
EBC	Coral	Y	Y	-	F=5.34 P=0.0111	AP≠CC AP≠EBC

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Sites	Cover type	Normal?	Homogeneity of variance?	Normal after transformation?	Test statistics	Differing means
	CTB*	Y	N*	-	F=28.98* P<0.001*	AP≠EBC AP≠CC CC≠EBC
	Gorg.	N	Y	Log(10) - yes	F=4.12 P=0.0275	AP≠EBC
	Macroalg.	Y	Y	-	F=31.32 P<0.0001	EBC≠CC EBC≠AP CC≠AP
	SPR	N	N	Log(10) – no Sqrt – no Arcsin – no Box-Cox - no	F=4.619* P=0.028*	AP≠EBC AP≠CC
	Shannon-Weiner	Y	N	-	F=5.27* P=0.017*	EBC≠AP
	Species density	N	Y	No	F=0.50 P=0.6097	-
SWB	Coral	Y	Y	-	F=63.95 P<0.0001	ER≠SWB ER≠DP
	Gorg.	Y	Y	-	F=21.75 P<0.0001	ER≠SWB ER≠DP
	CTB	Y	Y	-	F=53.21 P<0.0001	ER≠SWB ER≠DP
	Macroalg.	Y	Y	-	F=0.41 P=0.6701	-
	SPR	N	Y	Log(10) – no Sqrt – no Arcsin – no Box-Cox -no	F=1.45 P=0.2520	-
	Shannon-Weiner	Y	Y	-	F=0.79 P=0.4647	-
	Species density	N	Y	No	F=3.69 P=0.0385	SWB≠ER

* Homogeneity of variances not satisfied for Anova of CTB from EBC and control sites. Alternative test statistics of Welch Anova (allowing that standard deviations not equal) are as follows: F=24.80 P<0.0001. Test statistics of other heterogeneous Anova reported in table above.

Power analysis:

Site	Cover Type	Anova power	Least Significant Number
NR	Coral	1.000	8.846
	Gorg	0.764	21.392
	CTB	1.000	8.172
	Macroalg	1.000	7.563
Continued on next page			
Site	**Cover Type**	**Anova power**	**Least Significant Number**
	Sand, pavement, rubble	0.2890	63.554
	Shannon-Weiner	0.9714	12.638
	Species density	0.2570	72.213
SNP	Coral	0.311	58.863
	Gorg	0.950	13.873
	CTB	0.777	20.881
	Macroalg	0.520	34.135
	SPR	0.6137	28.325
	Shannon-Weiner	0.8989	16.124
	Species density	0.0890	329.692
EBC	Coral	0.795	20.158
	Gorg	0.679	25.086
	CTB	1.000	7.072
	Macroalg	1.000	6.867
	SPR	0.9153	15.442
	Shannon-Weiner	0.8610	17.620
	Species density	0.1241	181.35
SWB	Coral	1.000	5.577
	Gorg	1.000	7.992
	CTB	1.000	5.830
	Macroalg	0.109	224.177
	SPR	0.2829	65.027
	Shannon-Weiner	0.1702	117.032
	Species density	0.6271	27.612

Note: Data normality tested by Shapiro-Wilk test. Homogeneity of variances tested by Levene's test. In cases of significant Anova's, differences among group means were distinguished by comparing all pairs with Tukey-Kramer HSD post-hoc test. All procedures done with JMP v.7.

Simple nested model:

Cover type	**Normal? (By region)**	**Effect test type**	**Test statistics**	**Differences**
Coral	Y	Overall	F=107.62 P<0.0001	
		Treatment within region	F=3.40 P=0.0133	
		Region	F=246.59 P<0.0001	NR≠SNP NR≠SWB NR≠EBC EBC≠SNP SWB≠SNP
Cover type	**Normal? (By region)**	**Effect test type**	**Test statistics**	**Differences**
Macroalgae	Y	Overall	F=173.90 P<0.0001	
		Treatment within region	F=24.55 P<0.0001	
		Region	F=373.04 P<0.0001	EBC≠NR EBC≠SNP NR≠SWB SWB≠SNP
Gorgonians	Y	Overall	F=57.85 P<0.0001	
		Treatment within region	F=8.17 P<0.0001	
		Region	F=124.07 P<0.0001	SWB≠NR SWB≠SNP SNP≠NR NR≠EBC EBC≠SNP
CTB	Y	Overall	F=973.25 P<0.0001	
		Treatment within region	F=20.08 P<0.0001	
		Region	F=2244.13 P<0.0001	EBC≠NR EBC≠SNP NR≠SNP NR≠SWB SWB≠SNP NR≠SWB
SPR	N	Overall	F=8.95 P<0.0001	
		Treatment within region	F=2.12	

			P=0.0867	
		Region	F=18.06 P<0.0001	EBC≠SNP NR≠SNP SNP≠SWB
Shannon-Weiner Index	Y	Overall	F=31.02 P<0.0001	
		Treatment within region	F=7.49 P<0.0001	
		Region	F=62.39 P<0.0001	EBC≠NR EBC≠SNP EBC≠SWB NR≠SNP SNP≠SWB

Note: Normality tested on groups as regions rather than sites. Homogeneity of variances not tested, but assumed equal at the level of region. Simple nested model constructed on JMP v.7: JMP Starter>Model>Fit Model. Nested notation used as standard for JMP as follows: Treatment [Region] as in "Treatment within region" and the additional added effect of "Region" alone.