

Higher Coral Cover and Diversity in a Marine Protected Area compared to nearby
Unregulated Reef in the Mesoamerican Barrier Reef System.

by

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Submitted in partial fulfillment of the requirements for the
degree of Honours Bachelor of Science in Biology

at

Dalhousie University
Halifax, Nova Scotia
April, 2010

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I would like to dedicate this to:

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Abstract

The Mesoamerican coral reefs are suffering from numerous anthropogenic stresses that threaten the long-term survival of this biologically, economically and culturally important ecosystem. A major method used to conserve these reefs is the establishment of marine protected areas (MPAs), which limit fishing and human development in coral sites. Despite their extensive use, it is uncertain how effective marine protective areas are at conserving Mesoamerican coral reefs. Utila and Cayos Cochinos are two islands in the Mesoamerican reef system that provide an excellent opportunity to study the effects of establishing a MPA on Mesoamerican reefs. Cayos Cochinos has been enforced as a primarily no-take MPA since 2003, and Utila is a nearby dive centre with largely unregulated fishing and coastal development. Cayos Cochinos and Utila were analyzed for coral cover, macroalgae cover, benthic taxa composition and diversity to compare the coral reef health on both islands. The Cayos Cochinos MPA has increased soft and scleractinian cover and decreased algae cover compared to Utila. Cayos Cochinos reefs also have increased coral diversity compared to the Utila reefs. This supports the theory that establishing a MPA can increase the health of the coral reefs in the protected area. Three other sites in the Mesoamerican reef, Puerto Morelos, Banco Chinchorro and Xcalak, were also analyzed for coral cover, species diversity and species composition to determine if the reef communities in other areas of the Mesoamerican reefs are similar to Cayos Cochinos and Utila. This provides a good estimate as to the extent that the results from Cayos Cochinos and Utila can be extrapolated to the rest of the Mesoamerican reef.

List of Abbreviations and Symbols

ANOSIM:	analysis of similarity
ANOVA:	analysis of variance
ArcGIS	Arc Geographic Information System
BC:	Banco Chinchorro
CC:	Cayos Cochinos
CPCe:	Coral Point Count excel edition
DF:	degrees of freedom
F:	Fisher-Snedecor distribution
MANOVA:	multivariate analysis of variance
MBRS:	Mesoamerican Barrier Reef System
MDS:	multidimensional scaling
MPA:	marine protected area
MS:	mean squares
P:	probability value
PM:	Puerto Morelos
PRIMERe:	Plymouth routines in multivariate ecological research
R:	analysis of similarities statistic R
SS:	sum of squares
Ut:	Utila
X:	Xcalak

Acknowledgements

I would like to thank Dr. Alan Pinder for his help and guidance throughout this study, Darren ___ for the parrotfish data, Allison Schmidt for her advice on statistical analyses, Camilo Mora for his help determining the protection and environmental risk indices and my lab mate Zabrina Prescott for her continual support.

INTRODUCTION

The Caribbean coral reefs are experiencing drastic declines in coral cover due to numerous anthropogenic stressors (Gardner *et al.* 2003, Bellwood *et al.* 2004). Coral reefs are of major ecological, economic and cultural importance, which makes their conservation a priority (Hughes *et al.* 2003). The establishment of marine protected areas is a major tool employed to halt the collapse of coral reef ecosystems (Game *et al.* 2008, Selig and Bruno 2010). Coral reefs in the Caribbean are experiencing degradation for numerous reasons. Multiple bleaching events are reducing growth and increasing coral mortality (Dunn *et al.* 2007), over-fishing is degrading the reef ecosystem (Pandolfi *et al.* 2003), disease is threatening coral resilience (Harvell *et al.* 2003), and coastal development and ocean acidification are all contributing to coral decline (Bellwood *et al.*, 2004, Weis and Allemand 2009).

The Mesoamerican Barrier Reef System (MBRS) is the second largest barrier reef in the world and runs from Cancun, on the northeastern corner of Yucatan, along the coast of Belize and Guatemala to the Bay Islands off Honduras. The southern MBRS experienced a general degradation of coral after Hurricane Mitch hit in 1998 (Andérouët *et al.* 2002), after the *Diadema* urchin population collapsed (Steiner and Williams 2006) and two severe bleaching events occurred in the 1990s (Brown-Saracino *et al.* 2007). In the absence of human impacts corals that are exposed to environmental disturbances, such as hurricanes, are able to recover. Currently, however, reefs are not recovering from disturbances but are shifting to an alternate state (Ledlie *et al.* 2007, Scheffer *et al.* 2001). Degraded coral reefs typically shift to a state dominated by fleshy algae, but other forms or alternative states have been identified (Bellwood *et al.* 2004).

Marine protected areas (MPA) usually function by restricting fishing and have been relatively successful at restoring populations of reef fish and invertebrates (Halpern 2003). There have been few studies done on the impact of marine protected areas on coral, but it seems that establishing MPAs tends to slow coral declines on reefs (Selig and Bruno 2010).

The establishment of the Cayos Cochinos marine protected area off the northern mainland coast of Honduras in 2003 provided an opportunity to examine the effects of a marine protected area on coral reefs in the MBRS. Cayos Cochinos is an island archipelago located close to Utila, which is an unprotected island. Both Cayos Cochinos and Utila are surrounded by fringing reefs and have relatively similar environmental histories. Cayos Cochinos is a well enforced MPA that only allows a small amount of subsistence fishing on the reefs, and Utila is a major dive center with growing tourism-related development and largely unregulated fishing (Saunders *et al.* 2008). These two locations are good study sites because they allow for a localized comparison of the effects of establishing a MPA on the health and diversity of the coral reef.

This study compared the coral community, coral cover, algae cover and coral reef diversity between Cayos Cochinos and Utila to determine if the MPA increases coral cover as predicted. The coral communities of three other study sites in the Mesoamerican Barrier Reef System, Puerto Morelos, Banco Chinchorro and Xcalak, were also examined to determine how similar the Cayos Cochinos and Utila study sites are to the rest of the Mesoamerican reef. This will provide a measure of the generality of conclusions from Cayos Cochinos and Utila.

MATERIALS AND METHODS

Study sites

The five Mesoamerican reef locations selected for this study were Cayos Cochinos, Utila, Xcalak, Banco Chinchorro and Puerto Morelos (Figure 1). Study sites along the coral reef were chosen in each of these locations. Nine sites were chosen in Cayos Cochinos, six sites in Puerto Morelos, twelve sites in Utila, ten sites in Banco Chinchorro and seven sites in Xcalak (Figure 2). The Cayos Cochinos islands are located 18 km off the coast of Honduras, and make up the southern end of the MBRS (Saunders *et al.* 2008). The islands are located within a 489 km² MPA and are surrounded by fringing reefs that run along the edge of the continental shelf (Bronzo and Woods 2007). The MPA consists of the two main islands, Cayo Mayor which is 1.8 km wide and 1.7 km long and Cayo Menor which is 1 km wide and 1.3 km long, and 13 small cays (Saunders *et al.* 2008). The reefs extend to 30 m depth and tend to be more developed on the north side of the islands (Saunders *et al.* 2008). Cayo Major is populated by a small artisan fishing community, several private homes and a small hotel, but the rest of the archipelago is largely uninhabited apart from one small fishing community (Saunders *et al.* 2008). The establishment of the Cayos Cochinos reserve in 1993 made commercial fishing illegal, regulated fishing gear and established no-take zones throughout the archipelago (Clifton and Clifton 1998). These regulations are effectively enforced by regular patrol boats of the Honduran army (Clifton and Clifton 1998).

Utila is the smallest of the Bay Islands of Honduras and is located 29 km off the coast of Honduras (Harm *et al.* 2008). The study location consists of the main Utila island, which is 45 km², and 13 coral cays (Harm *et al.* 2008). Utila is primarily

composed of mangroves (66 % coverage) and is surrounded by fringing reefs (Harm *et al.* 2008). The reefs on the north side of Utila are more developed than the reefs on the southern leeward side which do not extend beyond 25 meters (Saunders *et al.* 2008). Utila has a population of around 7000 people and is experiencing growing coastal development, especially on the southern side (Saunders *et al.* 2008).

The other locations along MBRS are along the coast of Mexico. Puerto Morelos is a fringing reef lagoon about 4 km long (Coronado *et al.* 2007). It is located on the Yucatan Peninsula in Mexico, which is on the northern part of the MBRS (Coronada *et al.* 2006). Puerto Morelos was damaged by hurricane Wilma in 2004 (Rodríguez-Martínez 2008) and has been recently threatened by pollution and development for tourism infrastructure, largely from the spread of Cancun which is 25 km north (Coronada *et al.* 2006). The sites in the Xcalak study location are within the Xcalak national park which is a relatively undeveloped area just north of the border with Belize. Banco Chinchorro is an uninhabited coral reef complex located 30 km off the south coast of Quintana Roo, Mexico (Aguilar-Perera and Aguilar-Dávila 1993).



Figure 1: Map of the five Mesoamerican Barrier Reef locations, Puerto Morelos, Xcalak, Banco Chinchorro, Utila and Cayos Cochinos.

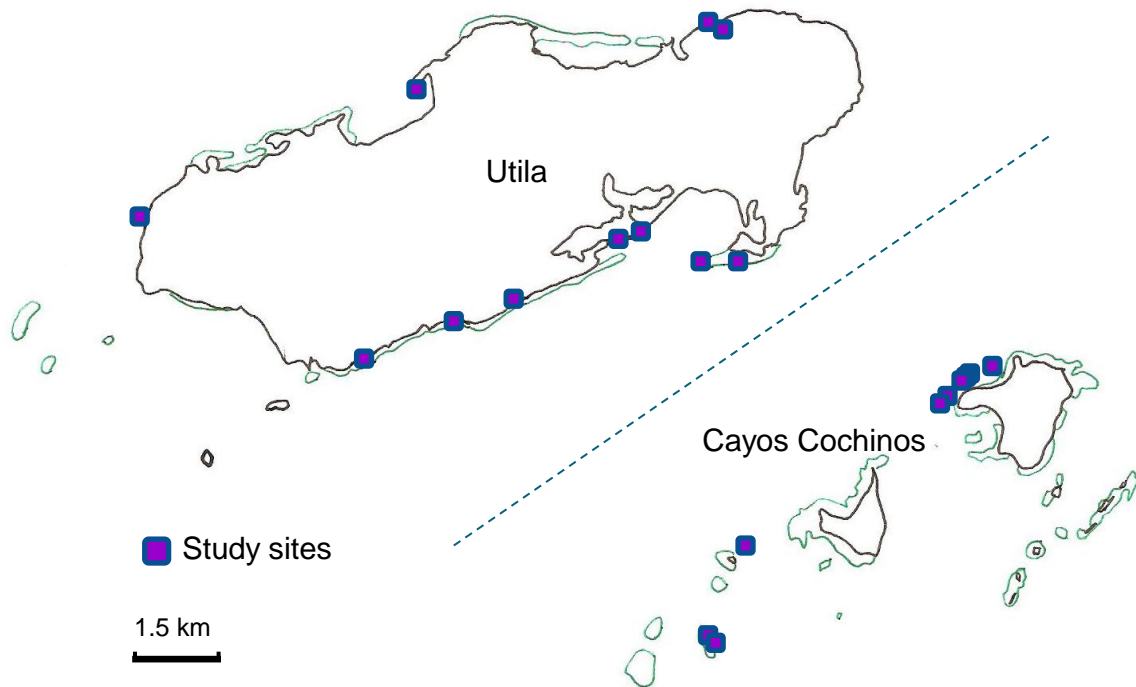


Figure 2: Map of Cayos Cochinos and Utila islands showing study sites.

Data collection

All data were collected in 2009 between the months of March and July. At each study site non-overlapping photographic transects were taken, each approximately 20 meters long and consisting of about 20 photographs. All photographs were roughly 0.25 m² with 10 megapixel resolution. All sites within a study location were treated as independent samples. Some moorings in Cayos Cochinos were used for two sites because there were not enough mooring locations available, so these sites were closer to each other than the other Cayos Cochinos sites. Usually two transects were taken at each site, which totaled 17 transects at Cayos Cochinos, 24 transects from Utila, 14 transects from Puerto Morelos, 20 transects from Xcalak and 10 transects from Banco Chinchorro. Transects at Cayos Cochinos and Utila were chosen to be at 6 to 8 meters depth, while transects from Puerto Morelos, Xcalak and Banco Chinchorro varied from 7 to 20 meters

depth because they were opportunistically taken on dive charters. Areas of sand were not included in photographic transects.

Surveys were also taken at Cayos Cochinos and Utila to count the number of parrotfish (*Scaridae*) and sea urchins (*Echinometra spp.*, *Diadema spp.* and *Eucidaris spp.*) present at each site. Sea urchin abundance was determined through actively searching the site for 10 minutes by two divers and identifying, counting, and estimating the sizes of the urchins present. The parrotfish abundance was determined by a single observer counting the number of fish within a 5 m radius for 10 minutes, and recording the species and the size to the nearest 5 cm.

Data Analysis

The photographs from the photograph transects were inputted into Coral Point Count with Excel Extensions (CPCe) (Kholer and Gill 2006). Each photograph was overlaid with 15 randomly stratified points using CPCe, and the live benthic taxon under each overlaid point was identified to species (scleractinians), genus (macroalgae and gorgonians) or to higher taxa (sponge, turf algae and coralline algae). The identification key consisted of 52 taxa of hard coral (scleractinians), 11 taxa of soft coral (gorgonians), 13 taxa of macroalgae, one sponge category, turf category and coralline algae category (appendix h). The identifications for each photograph were summed over the entire transect, and the percent cover was calculated for each identified taxon. A Shannon Weiner index of diversity was calculated for macroalgae, scleractinians and gorgonians in each transect. Analyses of variance (ANOVA) were performed to compare the percent cover of scleractinian, gorgonians, macroalgae, turf algae, sponge and coralline algae between Cayos Cochinos and Utila. The diversity indices of algae, scleractinian and

gorgonians on Cayos Cochinos and Utila were also compared using ANOVAs. The normality of the data distribution was verified using normal probability plots, and results that were greater than 1.5 standard deviations from the mean were designated outliers.

Multidimensional scaling (MDS) and ordination were used to detect patterns in the coral communities in all MBRS locations using PRIMER software program (Clarke and Ainsworth 1993). The benthic cover data were square-root transformed to meet assumptions for MDS analysis. A one-way analysis of similarity or an ANOSIM was performed to evaluate differences in the coral community between Cayos Cochinos and Utila. An ANOSIM uses Bray-Curtis similarities to calculate the statistic R, which is a measure of observed differences between replicates. An R value close to 1 or -1 indicates that the communities are different and an R value close to zero indicates that the communities are similar. The difference between the Utila and Cayos Cochinos sites and the sites in the three locations in Mexico was illustrated by a cluster dendrogram using Bray-Curtis Similarity. This analysis determined the percent similarity between each location. The sites were at different depths so a nested multivariate analysis of variance (MANOVA) was performed to determine the effect of depth on algae, sponge, scleractinian and gorgonian cover in the five locations.

All five study locations have some measure of environmental protection in place. The effectiveness of the protection for each site was determined using an index developed by Mora *et al.* (2006) which incorporates the level of assigned protection, the enforcement of the protection and the amount of risk in the area of interest. Mora *et al.* (2004) calculated the effectiveness of the protection for Cayos Cochinos, Xcalak, Banco Chinchorro and Puerto Morelos as part of a worldwide evaluation of MPAs. Since Utila

was omitted from the analysis due to its lack of formal protection, it was assigned the lowest level of effective protection. The level of environmental threat was assessed for each location using values calculated by Burke and Maidens (2004), which combines measures of coastal development, marine based pollution, overexploitation and erosion to develop a risk index value. Environmental threats for the specific study locations were determined by overlaying a shapefile of the study areas on to a shapefile of the threat level throughout the Caribbean, and using arcGIS to calculate a weighted average of threat index in each study area.

RESULTS

The coral reefs from sites in Cayos Cochinos and Utila have different benthic cover of coral and algae. Cayos Cochinos has higher scleractinian cover, gorgonian cover and macroalgae cover than Utila, and Utila has a much higher turf algae cover than Cayos Cochinos (figure 3). Utila has higher algae cover of 60.22% compared to Cayos Cochinos' 43.97%. Cayos Cochinos has slightly higher non-framework scleractinians, *Porites* and *Agaracia* and framework coral *Montastraea* than Utila, but no observable greater *Acropora* framework coral (figure 4). Of these four scleractinian genera only *Porites* is significantly different between Cayos Cochinos and Utila ($p = 0.027$). Cayos Cochinos has a higher overall Shannon Weiner diversity for all taxa, and has a slightly higher diversity index for scleractinian taxa, gorgonian taxa and algae taxa (figure 5).

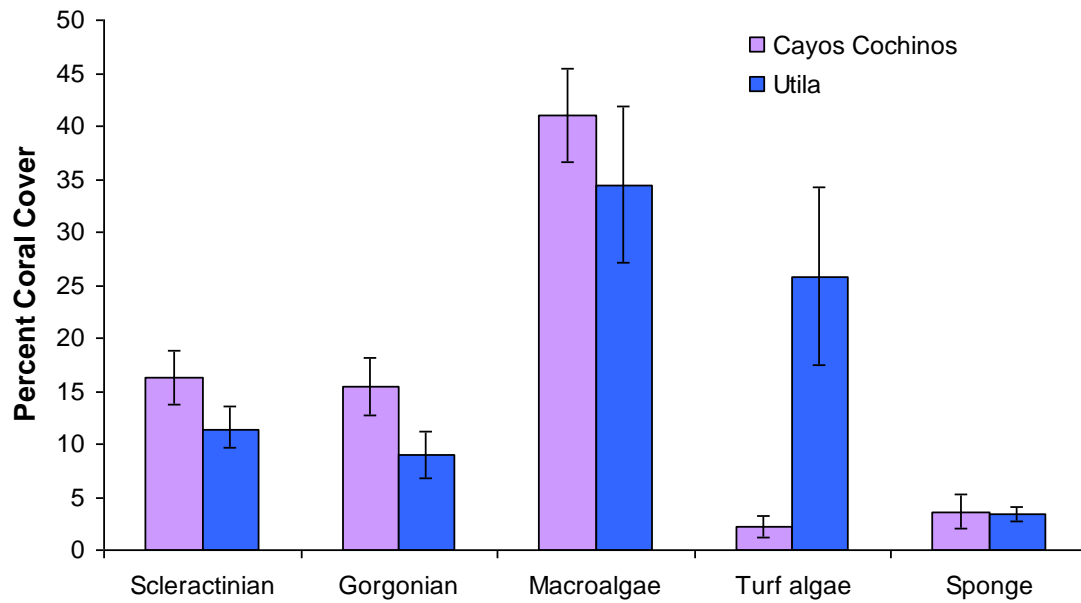


Figure 3: Percent cover of scleractinians (scleractinians), gorgonians (soft corals), macroalgae, turf algae and sponge for Utila and Cayos Cochinos. Data are shown with 95% confidence intervals.

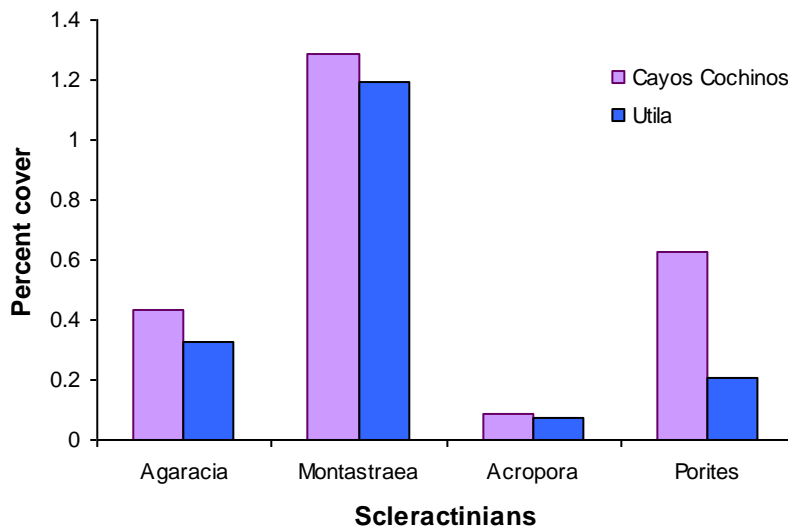


Figure 4: Percent cover of main framework and non-framework scleractinians taxa for Utila and Cayos Cochinos.

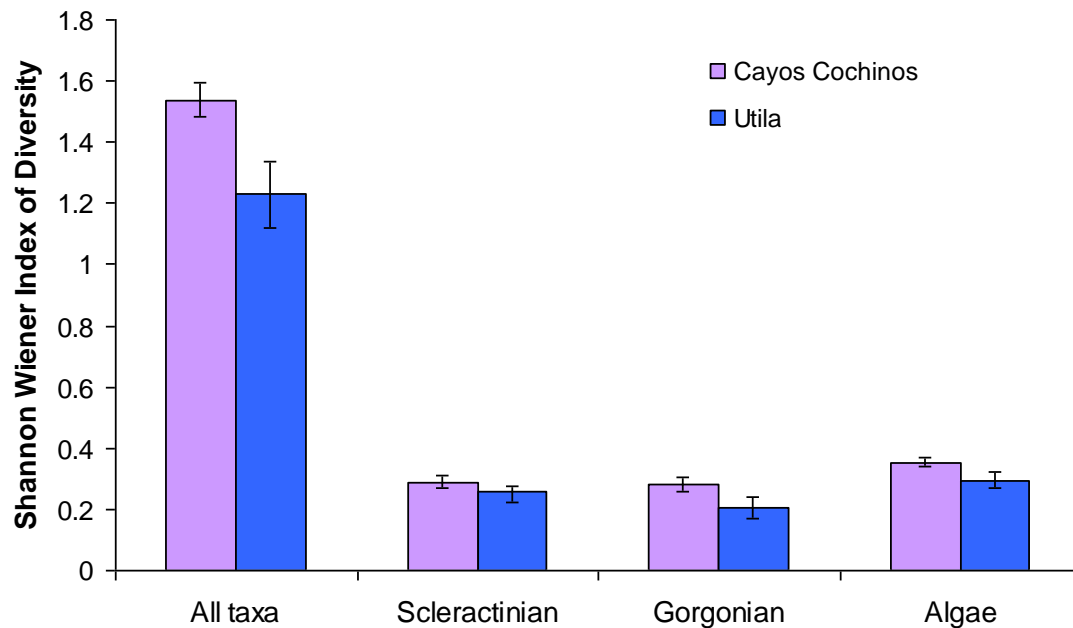


Figure 5: Measured diversity of all taxa, scleractinians, gorgonians, macroalgae on Utila and Cayos Cochinos using Shannon Wiener index. Data is shown with 95% confidence intervals.

The results of the ANOVA show that the macroalgae cover and sponge cover are not significantly different between Cayos Cochinos and Utila, and that the scleractinian cover (excluding transects from the Ironbound site, which were outliers) gorgonian cover and turf algae cover are significantly different between Cayos Cochinos and Utila (table 1). Indices of diversity on Cayos Cochinos and Utila are significantly different for all taxa, gorgonian taxa and algae taxa, and not significantly different for scleractinian taxa (ANOVA, table 1).

Table 1: ANOVA results for Cayos Cochinos and Utila comparisons using percent cover data averaged for each site and Shannon Wiener index of diversity data from CPCe averaged for each site. Tests used $\alpha = 0.05$ as a level of significance.

Source	Df	MS	F	p-value
Scleractinian cover	1	108.2	6.09	0.024
Gorgonian cover	1	190.6	11.75	0.003
Macroalgae cover	1	1.973	2.31	0.145
Turf cover	1	2885	14.01	0.001
Sponge cover	1	0.00	0.00	0.983
Shannon Wiener index all taxa	1	0.4463	11.68	0.003
Shannon Wiener index scleractinian	1	0.0069	2.73	0.115
Shannon Wiener index gorgonians	1	0.0273	7.59	0.013
Shannon Wiener index algae	1	0.0184	15.00	0.001

The results of multidimensional scaling show that the reef community on Cayos Cochinos sites was distinct from the reef community on Utila sites (figure 6). The stress on the MDS ordination is 0.14. Plots with stress values between 0.1 and 0.2 give a potentially useful 2-D picture although not too much reliance should be placed on details of the plot (Clarke and Warwick 2001). An analysis of similarity (ANOSIM) revealed significant differences in community structure between Cayos Cochinos and Utila ($r = 0.345$, $p = 0.001$).

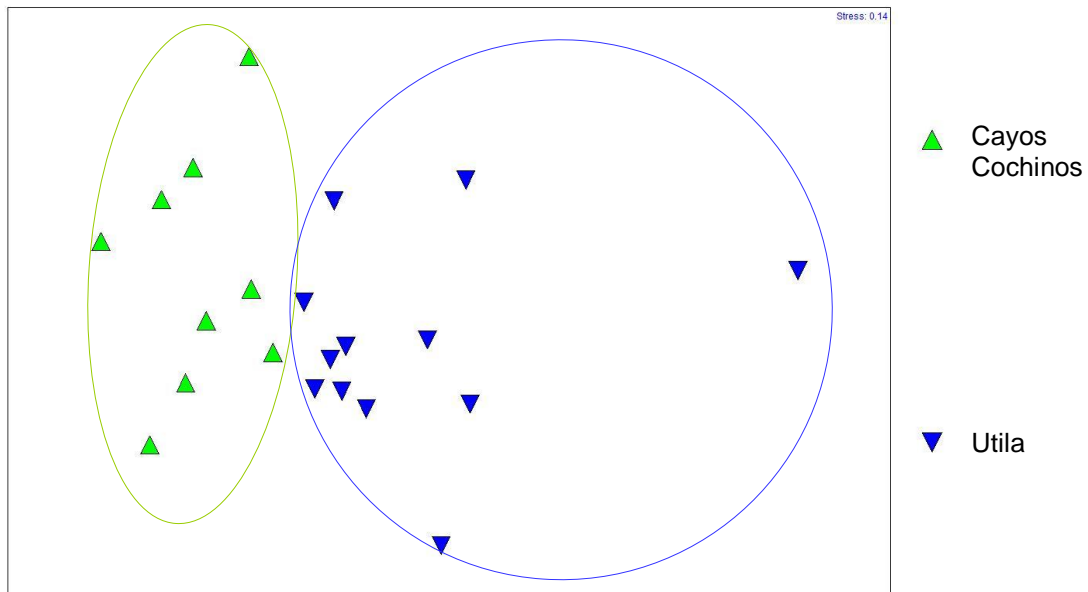


Figure 6: MDS ordination plot of Utila and Cayos Cochinos sites using square root transformed percent cover of coral reef taxa. Stress value is 0.14.

Parrotfish and sea urchins are two of the main herbivores on the Caribbean reefs. Cayos Cochinos has higher parrotfish abundance than Utila, and tends to have a greater variation of small-sized and large-sized fish (figure 7). Utila has a higher total parrotfish biomass than Cayos Cochinos (figure 8). Cayos Cochinos has a higher abundance of *Diadema* and *Eucidaris* urchins and Utila has a higher abundance of *Echinometra* urchins (figure 9).

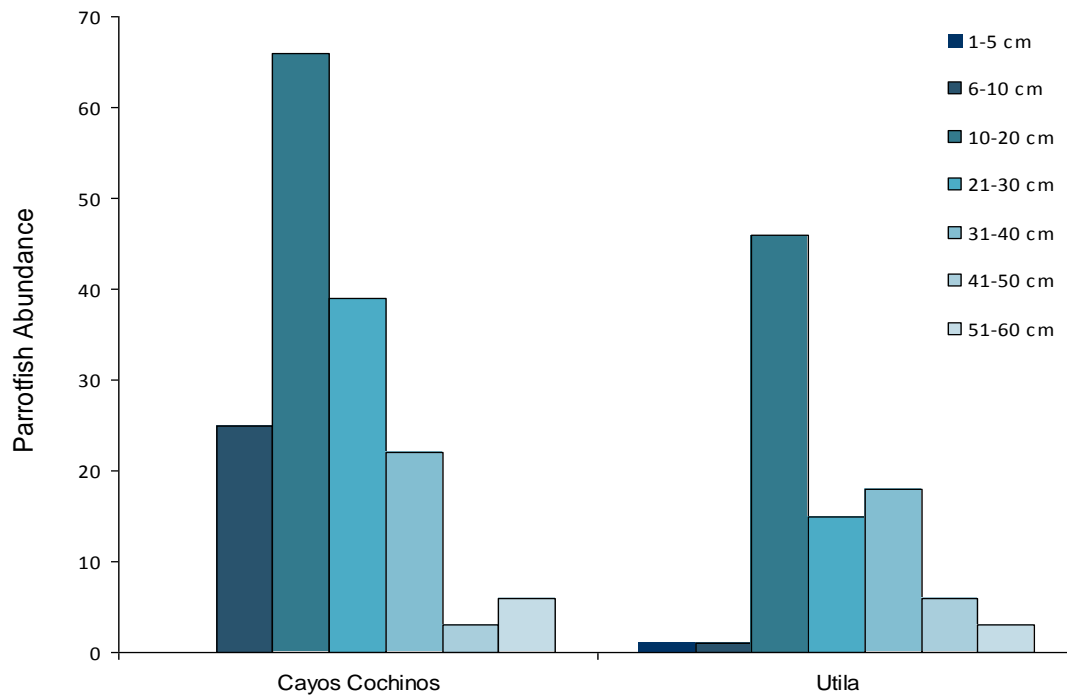


Figure 7: Size-class abundance of parrotfish on selected sites in Cayos Cochinos and Utila.

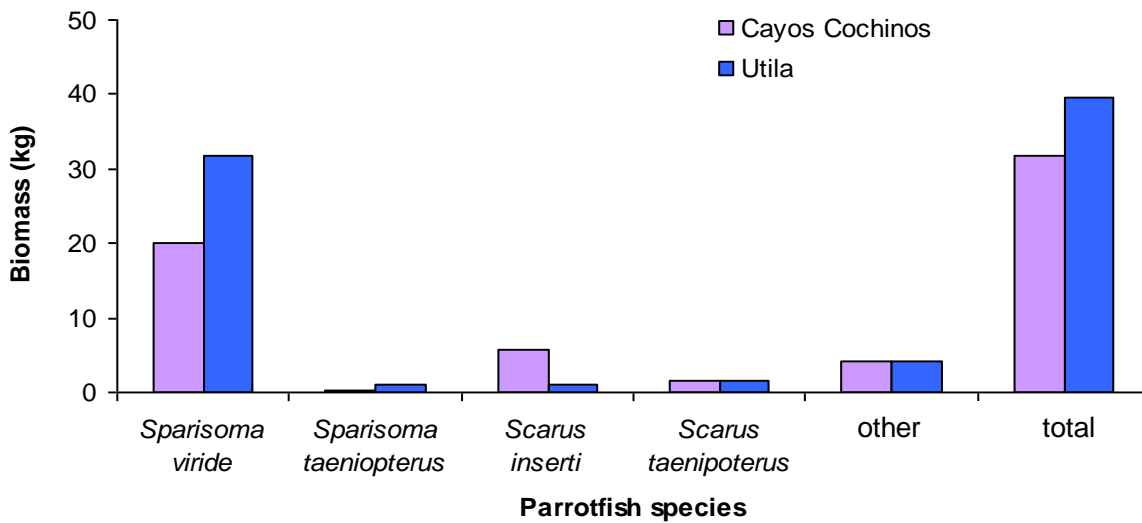


Figure 8: total biomass of all parrotfish and identified parrotfish species on 9 Utila and 9 Cayos Cochinos sites.

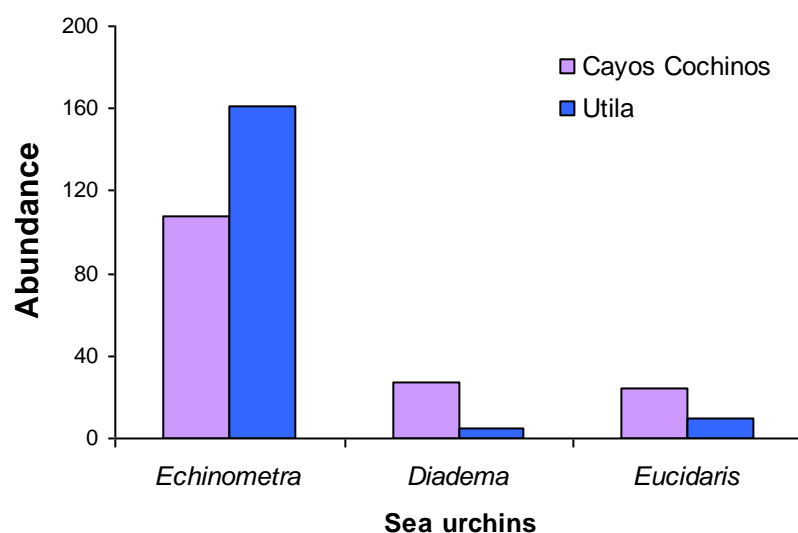


Figure 9: Sea urchin abundance on selected sites in Cayos Cochinos and Utila reefs measured by active surveying of reef.

The Mesoamerican study locations are in areas with different levels of environmental threats and different measures of protection. Figure 10 shows the coral cover and algae cover for all five sites and the associated index of risk and index of effective protection (Mora *et al.* 2004, Bryant *et al.* 1998). Cayos Cochinos has a higher measure of effective protection than Utila, and Banco Chinchorro has the highest measure of effective protection. Utila has more environmental risk than the Cayos Cochinos archipelago. There is no significant relationship between the coral cover on Mesoamerican locations and protection effectiveness or environmental risk (figure 11). This relationship appeared to be the strongest when coral cover was used, and was also not significant when environmental risk and protection effectiveness were plotted with algae cover and the ratio of algae to coral cover.

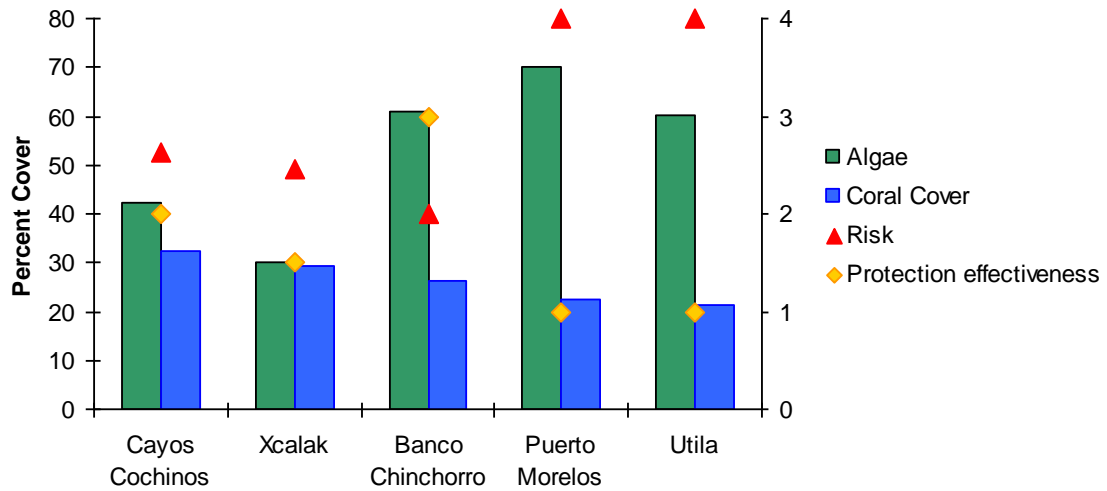


Figure 10: Coral cover and algae cover for the five Mesoamerican sites, Cayos Cochinos, Xcalak, Banco Chinchorro, Puerto Morelos and Utila plotted with the associated risk index of the location (Burke and Maidens 2004) and the index indicating the effectiveness of the protection (Mora *et al.* 2006). Environmental risk is on scale of 1 to 3, with 1 representing medium risk; 2 representing high risk and 3 representing very high risk. Protection effectiveness is on a scale of 1 to 4 with 1 representing very limited, 2 representing limited, 3 representing partial and 4 representing adequate protection.

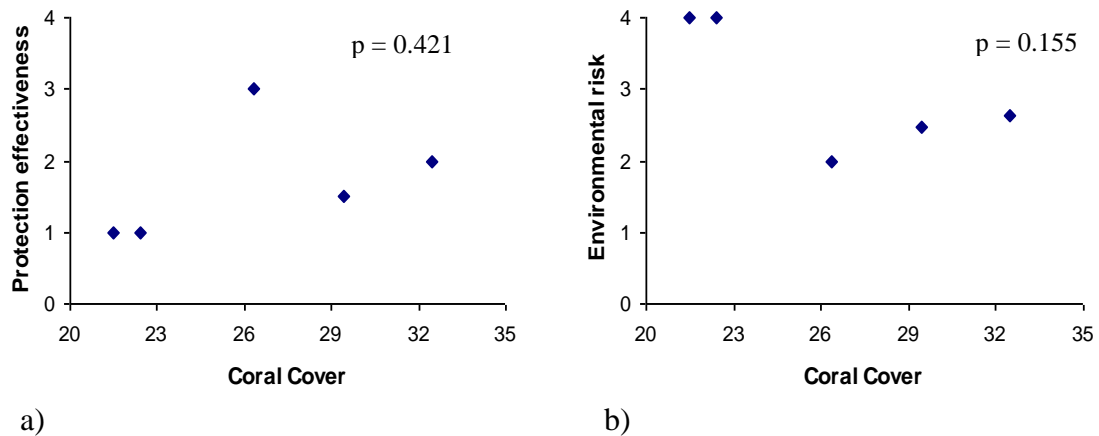


Figure 11: coral cover plotted against a) protection effectiveness and b) environmental risk for the five Mesoamerican reefs. Plots contain p value of regression analysis with level of significance of $\alpha = 0.05$.

Utila and Cayos Cochinos, although statistically different from each other, are relatively similar to the three other sites on the Mesoamerican reef. The MDS ordination

in figure 12 does not show any distinct grouping of coral communities in each location and there is a fair amount of overlap of sites. A cluster dendrogram showing the similarity of coral communities between each Mesoamerican study location shows that the locations are between 70 to 80% similar, and that Utila and Cayos Cochinos are not more similar to each other than to the rest of the Mesoamerican locations (figure 13).

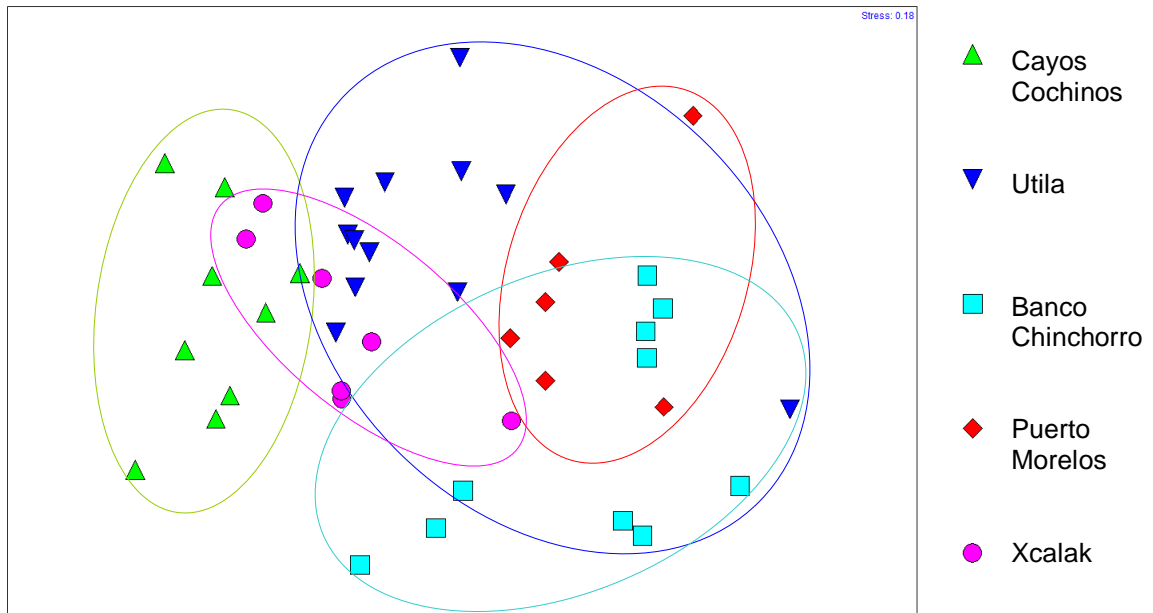


Figure 12: MDS ordination plot of the benthic communities of Utila, Cayos Cochinos, Banco Chinchorro, Xcalak and Puerto Morelos sites using square root transformed percent cover of coral reef taxa. Stress value is 0.18.

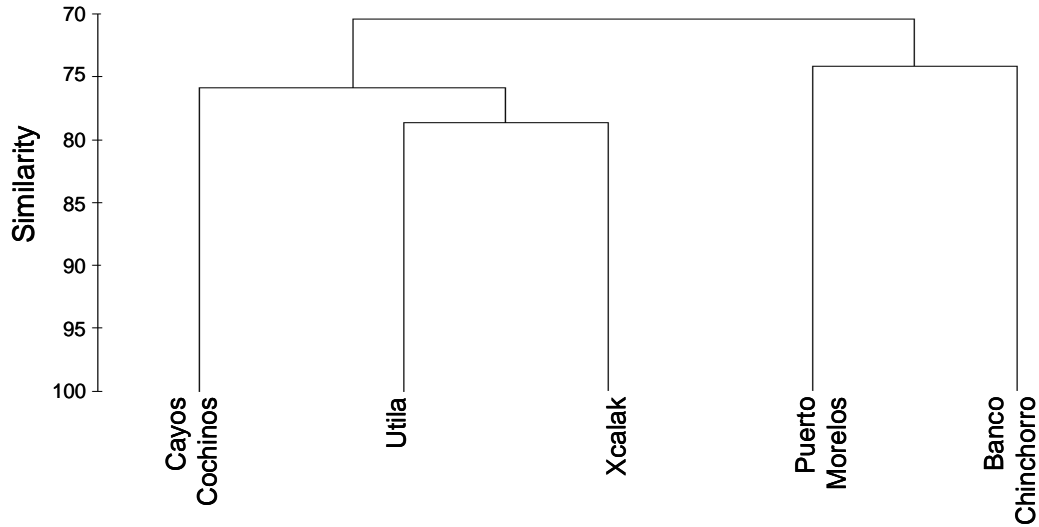


Figure 13: Cluster dendrogram displaying the percent similarity between Cayos Cochinos, Utila, Xcalak, Puerto Morelos and Banco Chinchorro. Similarities are based on average taxon cover values for each location.

Transects from the different study sites in the Mesoamerican reef are taken at varying depths. The sites in Utila and Cayos Cochinos are all between 6 to 8 m depth, but the sites in Banco Chinchorro, Puerto Morelos and Xcalak vary from 3 m to 20 m depth (appendix g). The change in the reef community at different depths was determined by a MANOVA which reveals that depth has no significant effect on scleractinian cover or algae cover but does have a significant effect on gorgonian cover and sponge cover (table 4).

Table 2 (a and b). Results of a multivariate analysis of variance comparing cover of scleractinian, gorgonian, sponge and algae between Mesoamerican reef locations (2a), and a nested multivariate analysis of variance comparing depth nested within location and reef cover for study sites in Xcalak, Puerto Morelos, Cayos Cochinos, Utila and Banco Chinchorro (2b).

a)

Effect	Value	F	Hypothesis df	Error df	Sig.
Intercept	0.989	668.469	4.000	29.000	<<0.001
Location	0.796	2.800	12.000	93.000	0.003
Depth(location)	1.246	2.067	28.000	128.000	0.003

b)

Source	Dependant variable	Type III SS	Df	MS	F	Sig.
Location	scleractinian	401.846	3	133.949	6.606	0.001
	soft coral	239.169	3	79.723	3.192	0.037
	sponge	15.968	3	5.323	1.702	0.186
	algae	1512.896	3	504.299	3.322	0.032
Depth(location)	scleractinian	199.977	7	28.588	1.409	0.236
	soft coral	441.029	7	63.004	2.523	0.035
	sponge	55.477	7	7.925	2.523	0.034
	algae	1735.92	7	247.989	1.634	0.162

DISCUSSION

The coral reefs within the Cayos Cochinos MPA have significantly more scleractinian cover and gorgonian cover than the fringing reefs of Utila. This result is supported by a recent study by Selig and Bruno (2010), which surveyed 4456 reefs around the world, including 306 Caribbean reefs, and compared the coral cover on MPA reefs to the coral cover on unprotected reefs (Selig and Bruno 2010). This study found that MPAs are, for the most part, effective in preventing coral losses (Selig and Bruno 2010). In 2005 coral cover increased by 0.05% in the Caribbean MPAs and decreased by 0.27% in the unprotected Caribbean reefs in one year (Selig and Bruno 2010). Evidence of higher scleractinian and gorgonian cover is generally accepted to be a good indicator of reef health (Gardner *et al.* 2003). Scleractinians are important for the health of the reef because they form the three-dimensional reef structure, which provides important habitats

for reef fish (Mumby 2006, Syms and Jones 2000). However, the ANOVA results for the scleractinian cover comparisons should be taken with some reservations because one site on Utila was omitted from the analysis. The Ironbound head site has over two times as much scleractinian cover as other Utila sites, so it is an outlier that prevents the data from being normally distributed. When the ANOVA includes the Ironbound site, the difference in scleractinian cover between sites is not significant, but the test is not valid because the data are not normally distributed. The Ironbound site was omitted from the analysis.

The lower coral cover on Utila may simply be due to a recent impact of a natural disturbance or to local or regional variation in abundance (Hughes and Connell 1999), but this is unlikely to cause differences between Cayos Cochinos and Utila because these islands have experienced similar natural disturbances and were broadly sampled to avoid local variation. It is possible that the increased coral cover and diversity on Cayos Cochinos compared to Utila is due to the limited choices of sites on Cayos Cochinos. This study was done with Operation Wallacea, which required the use of permanent mooring sites. There were only 4 mooring sites available on Cayos Cochinos compared to the 90 or more moorings on Utila, and all moorings on Cayos Cochinos were concentrated towards the northern side of the islands. These northern sites were close to the edge of deeper water, which may represent a healthier area of the MPA. Sampling was also biased towards areas with calmer seas, because the dive boats had more access to these areas, and study sites in Utila were slightly concentrated on the calmer southern side of the island for this reason. The sampling sites on both Utila and Cayos Cochinos were designed for a longitudinal study monitoring changes in coral cover over time at individual heads, not a one-time comparison of Cayos Cochinos and Utila. Thus the study

sites were not selected to give the best possible representation of Cayos Cochinos and Utila. A more uniform distribution of sampling sites may give a lower coral cover and higher macroalgae cover on Cayos Cochinos.

Focusing on the overall scleractinian cover may mask changes in coral community composition. Recently there have been reported shifts from framework scleractinians, such as *Acropora* and *Montastraea*, to non-framework scleractinians, namely *Porites* and *Agaricia* (Edmunds and Carpenter 2001). Cayos Cochinos has higher cover of *Acropora*, *Montastraea*, *Porites* and *Agaricia* species compared to Utila, however differences in non-framework and framework scleractinians between Cayos Cochinos and Utila are not significant ($p=0.069$, $p= 0.763$, respectively). Of the four scleractinians only *Porites* cover is significantly different between Cayos Cochinos and Utila ($p = 0.027$). This indicates that although Cayos Cochinos has greater scleractinian cover, this difference is partly the result of higher cover of opportunistic non-framework species. These non-framework species are suspected to be more vulnerable to disturbance than the framework corals, so they may decrease the resilience of the reef (Knowlton 2001).

Cayos Cochinos reefs are significantly more diverse than Utila. This is consistent with the hypothesis that the community with lower fishing pressure, lower environmental threats and less algae competition will have a higher biodiversity (Bellwood and Hughes 2001). Cayos Cochinos has a significantly different coral community composition than Utila, which may be a result of the increased diversity. There are more coral taxa found on Cayos Cochinos than Utila, and seven out of those eight taxa present only on Cayos Cochinos are scleractinians taxa only occasionally found in the Caribbean (Humman and

Deloach 2002). This indicates that the marine protected area has more rare coral taxa present than Utila.

The higher algae cover in Utila, particularly the turf algae, is likely an indication of lower coral reef health. Although algae are an important component of coral reefs, the dominance of algae is typically associated with reef decline (Foster *et al.* 2008). When coral cover decreases, algae begin to monopolize the substrate and overtake the reef (Rodgers and Miller 2006). Shifts towards an algae dominated reef are mostly due to algae recruits inhibiting coral settlement and not direct competition though algae overgrowth (Diaz-Pulido and McCook 2004), although this also occurs (Hughes *et al.* 2007). It is interesting that Utila and Cayos Cochinos have similar amounts of macroalgae, but Utila has much more turf algae. Turf algae form a low biomass, high turnover community (Carpenter 1986) and are more palatable to herbivores (McClanahan *et al.* 2001), so it is expected that a MPA will have less macroalgae not less turf algae (Mumby 2006). For example, a measurement of algae dominance is the shift from turf algae to fleshy macroalgae (Edmunds and Carpenter 2001). There is some evidence that the filamentous turf algae abrades coral polyps as it moves in currents and surges, but this is also true macroalgae such as *Dictyota* and *Halimeda* (Forster *et al.* 2008). The higher turf algae are likely an indication of poorer reef environment in Utila, but it is unclear why macroalgae is not also increased outside of the MPA, or why it is so prevalent inside the MPA.

Algae replacement of corals is typically understood in the context of herbivore abundance, because herbivores graze algae, which prevents it from overtaking the reef and leaves space for coral colonization (Hughes *et al.* 2007). Reefs with higher grazing

pressure are typically covered with cropped coralline red algae, fine filamentous algae and short algal turfs (Mumby 2006). Herbivores such as the *Diadema* sea urchin and parrotfish largely control the biomass of algae on the Caribbean reefs (McCook *et al.* 2001). *Echinometra* and *Eucidaris* urchins are also present on the reef, and in greater abundances than *Diadema*, but they are smaller and are not considered to be major herbivores of the Caribbean reefs (Carpenter 1988). Recently parrotfish have become the most important grazer on the Caribbean reefs because the *Diadema* population has collapsed (Mumby *et al.* 2004). Parrotfish are more abundant in Cayos Cochinos, but Utila has a higher parrotfish biomass. The higher biomass on Utila is due to the presence of 13 large *Sparisoma viride* parrotfish on the Ironbound site. Out of the total 31.78 kg biomass of *Sparisoma viride* on Utila, 14.68 kg are from Ironbound. When Ironbound is removed from the analysis, the parrotfish biomass is 3.41 kg higher on Cayos Cochinos than Utila. Since Ironbound was again deemed to be an outlier, it was omitted from the analysis. The higher abundance and biomass of parrotfish present on Cayos Cochinos compared to Utila may be responsible for the lower algae cover on Cayos Cochinos, because increased herbivores are grazing the algae and facilitating coral settlement. Mumby (2006) modeled the effect of parrotfish grazing on live coral cover and found that unexploited populations of parrotfish usually intensively grazed about 30% of a coral reef, and that intermediate levels of parrotfish exploitation caused a steady decline in live coral cover of 0.5% per year. It is also possible that coral decline on Utila is not due to algae competition, and that the decline in coral cover due to other causes such as bleaching and disease, is making space for increased algae settlement on the reef. More

information on grazers in Cayos Cochinos and Utila is needed to determine if grazing responsible for the increased coral cover on Cayos Cochinos.

Marine protected areas may benefit corals directly by preventing destructive fishing and anchoring, and terrestrial run-off, and indirectly by stopping overfishing and restoring coral reef food webs (Selig and Bruno 2010). An effective MPA should increase the amount of fish within the protected area by restricting fishing (Halpern 2003), so the higher parrotfish abundance in the Cayos Cochinos MPA is likely a result of the enforced protection. This is consistent with a study on a coral reef atoll in Belize which found increased fish in the protected “no take” areas compared to unprotected areas (McClanahan *et al.* 2001). Mumby *et al.* (2006) also found that marine reserves are effective at increasing parrotfish densities or size, and that the increased grazing by these parrotfish resulted in a fourfold reduction in macroalgae cover (Mumby *et al.* 2006). Since the Cayos Cochinos MPA restricts fishing on commercial species such as parrotfish, this could be one of the reasons Cayos Cochinos has less algae cover, especially less turf algae which is more palatable to herbivorous fish. The increased parrotfish on Cayos Cochinos is slightly unexpected because there are no mangroves on Cayos Cochinos, but much of Utila is composed of mangroves, which have been shown to be an important nursery habitat for fish (Mumby *et al.* 2003). A 2008 study by Harm *et al.* assessed the abundance of fish on Utila and Cayos Cochinos and found more parrotfish in Utila compared to Cayos Cochinos. This result was attributed to the presence of mangroves in Utila (Harm *et al.* 2008). Therefore although the observed higher biomass of parrotfish is consistent with the predicted effects of MPAs, this result is not supported by existing literature on Cayos Cochinos.

There are other potential benefits from protecting Cayos Cochinos that could be responsible for the increase in coral cover. Cayos Cochinos has limited development compared to Utila. Utila is an internationally recognized tourist dive destination and has tourism-related development along the southern coast (Saunders *et al.* 2008). The increased sediment run-off and pollution from the development on Utila could be causing the coral to decline, because sediment particles smother reef organisms and decrease coral cover (Rodgers 1990). The Slumberland site is closest to the shore development of the town of Utila, and has the third lowest scleractinian cover (9.09%) and the lowest gorgonian cover (0.32%) of the 12 Utila sites. There is also slight amount of damage caused by recreational divers on Utila that could explain the lower coral cover, but for the most part the dive operation is well regulated and destructive practices are restricted (Saunders *et al.* 2008). The protection around Cayos Cochinos also includes land protection and prevents coastal development, which is an important feature of MPAs (Selig and Bruno 2010). The higher coral cover on Cayos Cochinos could be a direct effect of the MPA restricting coastal development.

There are other differences with between Cayos Cochinos and Utila locations that may influence the coral cover difference. Cayos Cochinos is closer to the mainland (Harm *et al.* 2008) so it should have higher levels of coastal run-off, especially during heavy rainfalls, which can cause coral decline (Bryant *et al.* 1998). The depth and temperature is similar on both locations (Harm *et al.* 2008), but local eddies and upwelling along ridges may create locally different environments that would affect benthic cover in locations. [The photographic transects sampled about 170 m of the 3.1 km long coast of Cayos Cochinos, and 240 m of the 11 km coast of Utila, which is a](#)

fairly good sampling of the reef, so it is likely that these local variations would not affect the overall result.

The results suggest that the MPA is effective at protecting the Cayos Cochinos reefs. This is an important conclusion for the protection of the Mesoamerican reefs, as the establishment of protected areas is one of the main conservation tools employed in the Mesoamerican Great Barrier Reef System. The three other coral reef locations were examined to determine if Cayos Cochinos MPA results can be generalized to other locations in the MBRS. Multidimensional scaling analysis and a cluster dendrogram performed on benthic cover indicates that the five locations are all relatively similar to each other or that each location is highly variable so overall variation across the MBRS is due to local variation at each location. The benthic community on Utila is more similar to the Xcalak location than to Cayos Cochinos which indicates that Cayos Cochinos and Utila do not have unique reef communities from other areas of the Mesoamerican reef. The five study locations are situated in areas with different amounts of environmental threats, such as erosion, run-off, coastal development, pollution and overexploitation (Bryant *et al.* 1990). Puerto Morelos and Banco Chinchorro have the highest and lowest index of environmental risk respectively, but are more closely related to each other than to the rest of the locations. Utila and Xcalak are the most similar locations but also have very different indices of environmental risk. It is likely therefore that the level of environmental threat is not a major determinant of the coral community in the locations along the Mesoamerican reef. The protection level also varied among study locations according to the index of effective protection developed by Mora *et al.* (2006). Xcalak is less protected than Cayos Cochinos and more protected than Utila, so the similar coral

community between Xcalak and Utila could be caused by varying levels of protection. However the most protected location, Banco Chinchorro, is most similar to Puerto Morelos which has one of the lowest levels of protection. The discrepancy between the level of protection and the coral community similarity indicate that the level of protection is not the main determinant of coral community in the MBRS. This does not discredit the earlier result that marine protection increases coral cover and diversity, but this increase is from a localized baseline, and many other factors influence the overall benthic community structure across the MBRS.

The sites are also at different depths, and while this had no significant effect on algae and scleractinian cover it did effect the gorgonian and sponge cover of the reef. Sampling at Mexico was biased towards accessible, deep sites that were probably in decent condition, because the sampling was done through recreational dive charters. Variations in depth could influence the benthic community in Puerto Morelos, Xcalak and Banco Chinchorro. Sampled sites in Honduras had very similar depths, so depth should not influence the benthic communities on Utila and Cayos Cochinos. Despite these variations, the sites are shown to be between 71 and 79% similar in coral community composition, and so the results from the Cayos Cochinos MPA can be tentatively extrapolated to other locations on the Mesoamerican reef. Further studies with more MBRS locations and a more detailed analysis of the oceanographic environment at each location are needed to fully support this conclusion.

The marine protected area on Cayos Cochinos appears to protect the coral reef through directly restricting coastal development and indirectly increasing fish abundance. Thus the establishment of effectively enforced marine protected areas is critical for the

conservation of the coral reefs within the MBRS. There are still many threats to coral reefs that MPAs do not protect against. Hurricanes, ocean acidification, climate change and disease all need to be addressed if coral reefs are to survive. Hopefully proper management of coral reefs will increase the coral reef's resilience so that it can recover from these threats and disasters.

SUMMARY

The marine protected area in Cayos Cochinos appears to be decreasing coral loss or favouring coral cover, and increasing parrotfish abundance on the fringing reef. This indicates that establishing marine protected areas along the Mesoamerican Barrier Reef System may increase the coral cover and resilience of these threatened reefs.

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APPENDICES

Appendix a: Percent cover of benthic taxa taken from photograph transects averaged between sites in Cayos Cochinos, Honduras.

<i>Taxa</i>	<i>Arena</i>	<i>Pelica</i> <i>n 1</i>	<i>Pelica</i> <i>n 2</i>	<i>Pelica</i> <i>n 3</i>	<i>Pelica</i> <i>n 2 (2)</i>	<i>Pelica</i> <i>n 2 (2)</i>	<i>Pelican</i> <i>2.5</i>	<i>Timon 1</i>	<i>Timon 2</i>
<i>Acropora cervicornis</i>	0	0.72	0	0	0	0.92	0	0	0
<i>Acropora palmata</i>	0	0.18	0	0	0.19	0	0	0	0
<i>Acropora prolifera</i>	0	0	0.16	0	0	0	0	0.15	0
<i>Agaricia agaricites</i>	0	0.71	2.18	1.27	0.19	2.41	0.58	7.70	3.66
<i>Agaricia fragilis</i>	0	0	0	1.08	0	0.15	0	0	0.19
<i>Agaricia grahamae</i>	0	0	0.16	0	0	0	0	0	0
<i>Agaricia tenuifolia</i>	0	1.65	0.16	0.30	0	0.59	0.18	0	0
<i>Agaricia undata</i>	0	0	0	0	0	0	0	0	0
<i>Agaricia lamarcki</i>	0	0.18	0	0	0	0	0	0	0
<i>Colpophyllia breviserialis</i>	0	0	0	0	0	0	0	0	0
<i>Colpophyllia natans</i>	0	0	0	0	0	0	0	0	0
<i>Dendrogyra cylindrus</i>	1.25	0.35	0.16	0.66	0.19	1.49	0	0	0
<i>Dichocoenia stellaris</i>	0	0	0	0	0.19	0	0	0	0
<i>Dichocoenia stokesi</i>	0	0.18	0.33	0	0	0.16	0	0	0
<i>Diploria clivosa</i>	0	0.72	0	0	0	0	0	0	0
<i>Diploria labyrinthiformis</i>	0	0	0.49	0.50	0	0	0	0	0.17
<i>Diploria strigosa</i>	0.63	0.18	1.16	0.46	3.00	0.78	0.56	0.15	0.17
<i>Eusmilia fastigiata</i>	0	0	0.16	0	0	0	0	0	0
<i>Favia fragum</i>	0	0	0.16	0	0	0	0	0	0
<i>Isophyllia sinuosa</i>	0	0	0	0	0	0	0	0	0
<i>Leptoseris cucullata</i>	0	0	0	0	0	0	0	0	0
<i>Madracis decactis</i>	0	0.55	0.50	0	0.81	0	0	2.56	0
<i>Madracis mirabilis</i>	0	0	0.33	0	0	0.16	0	1.48	0.19
<i>Manicina areolata</i>	0	0	0.65	0	0	0	0	0	0
<i>Meandrina meandrites</i>	0	0	0	0	0	0.16	0	0	0
<i>Millipora alcicornis</i>	0	0.34	1.82	1.11	0.39	1.08	1.72	1.13	0.72
<i>Millipora complanata</i>	0	0	1.35	0.15	0.19	0	0.19	0	0
<i>Millipora squarrosa</i>	0	0.51	1.03	0	0	0	0	0	0
<i>Montastraea annularis</i>	6.56	0.87	2.01	4.42	3.32	2.76	1.68	0.49	2.97
<i>Montastraea cavernosa</i>	0.94	0	1.49	0.17	4.79	0	0	0.15	0.52
<i>Montastrea faveolata</i>	0	0.70	1.70	0.60	0.60	0.93	1.66	0.59	0.17
<i>Montastrea franksi</i>	0.31	3.01	0.34	0.64	0.40	0.16	0.37	0	1.05
<i>Mussa angulosa</i>	0	0	0	0	0	0	0	0	0
<i>Mycetophyllia aliciae</i>	0	0	0	0.33	0	0	0	0	0
<i>Mycetophyllia danaana</i>	0	0	0	0	0	0	0	0	0
<i>Mycetophyllia ferox</i>	0	0	0	0.15	0	0.30	0.38	0	0
<i>Mycetophyllia lamarckiana</i>	0	0	0	0	0	0	0	0	0
<i>Oculina diffusa</i>	0	0	0	0	0	0	0	0	0
<i>Porites astreoides</i>	0.63	1.42	2.21	2.65	1.35	1.22	0.56	0.54	1.60
<i>Porites branneri</i>	0	0.35	0	0	0	0	0	0	0
<i>Porites divaricata</i>	0	0	0	0	0	0	0	0.15	0.19
<i>Porites furcata</i>	0.31	0	0	0	0	0	1.67	7.73	3.76
<i>Porites porites</i>	0	0	0	0	0	0	0	1.63	0.19
<i>Scolymia cubensis</i>	0	0	0	0	0	0	0	0	0
<i>Scolymia lacera</i>	0	0	0	0	0	0	0	0	0
<i>Siderastrea radians</i>	0	0	0	0.33	1.21	0.45	0.19	0.83	0.36
<i>Siderastrea siderea</i>	0	0.37	0	0	0	0.90	0	0.73	0.70
<i>Solenastrea bournoni</i>	0	1.55	0	0	0.19	0	0	0.15	0
<i>Solenastrea hyades</i>	0	0.18	0	0	0.19	0	0	0	0
<i>Stephanocoenia michelinii</i>	0	0.18	0	0	0	0	0	0	0
<i>Tubastraea aurea</i>	0	0	0	0	0	0	0	0	0
<i>Briareum</i>	0.63	0	0	0.48	0	2.43	3.95	0	0
<i>Erythropodium</i>	0.94	0.18	0.16	0.17	0	0.30	0.19	0	0

Taxa	Arena	Pelica n 1	Pelica n 2	Pelica n 3	Pelica n 2 (2)	Pelica n 2 (2)	Pelican 2.5	Timon 1	Timon 2
<i>Eunicea</i>	0	3.09	1.34	0.64	2.37	1.84	0	0	6.94
<i>Gorgonian</i>	1.25	9.82	4.74	3.76	3.51	3.18	3.07	2.49	2.82
<i>Iciligorgia</i>	0	0	0	0	0	0	0	0	0
<i>Muricea</i>	0.31	0	0	0.66	0	0.46	0	0	0.55
<i>Muriceopsis</i>	0	0	0	0	0	0	0	0	0
<i>Plexaura</i>	0	0	0	0	0	0	0	0	0
<i>Plexaurella</i>	0	0.51	1.82	3.42	0.58	0.44	0	1.32	0.89
<i>Pseudoplexaura</i>	0	0.35	1.00	0.30	0.58	1.83	0	0.74	0
<i>Pseudopterogorgia</i>	5.31	0.55	6.81	4.85	11.33	9.47	2.47	12.79	4.45
<i>Pterogorgia</i>	0.94	0.17	0	0	0.40	0.15	0	0	0
<i>Sponge</i>	1.56	7.65	2.33	7.17	0	2.09	2.99	1.23	4.91
<i>Amphiroa</i>	1.88	2.44	1.85	1.42	2.19	1.21	5.44	1.12	1.12
<i>Dictyota</i>	33.13	7.71	6.77	17.72	11.91	21.96	26.23	20.16	21.20
<i>Halimeda</i>	12.19	8.60	7.73	10.62	2.77	5.00	4.71	9.46	3.07
<i>Liagora</i>	0	0	0	0	0	0	0	0	0
<i>Lobophora</i>	6.25	19.01	11.94	13.11	6.89	9.58	10.77	2.48	6.59
<i>Macroalgae</i>	2.50	0.86	3.85	0.50	7.46	0.62	1.87	3.99	2.73
<i>Padina</i>	0.31	4.91	0.85	0.15	1.75	0	1.69	1.23	0
<i>Porolithon</i>	0	0	0	0	0	0	0	0	0
<i>Sargassum</i>	0	0	0	0	0	0	0	0	0
<i>Schizothrix</i>	0	0	0	0	0	0	0	0	0
<i>Stypopodium</i>	0.63	0	0	0.17	0	0	1.15	0	0.74
<i>Turbinaria</i>	0	0.51	1.34	0.17	0.19	0	0	0.24	0
<i>Turf</i>	0.31	3.19	0.84	0.17	2.60	2.44	2.44	0.98	6.11
<i>Wrangelia</i>	0	0	0	0	0	0	0	0	0
<i>Ascidian</i>	0	0	0	0	0	0	0	0	0
<i>Coralline algae</i>	18.13	1.39	5.05	15.67	14.70	14.30	12.04	5.23	8.91

Taxa	Slu mb.	Blk Cor.	Cor. Vw	Iron bnd. (f)	Jack Neil	Lit Hse	Little Bigh	Pinna cle	Sting ray pt.	Sting ray Alley	West end	Iron bnd (h)
<i>Plexaura</i>	0	0	0	0	0.17	0	0	0	0	0	0	0
<i>Plexaurella</i>	0	0	0	1.52	0	0	0.53	0.47	0.98	0.18	0.88	1.46
<i>Pseudoplexaura</i>	0	0.68	0.75	0	0	0	0.19	0.15	0	0	0.29	0.82
<i>Pseudopterogorgia</i>	0	3.58	1.36	10.1	0.70	1.10	1.63	6.53	1.51	0	5.60	1.14
<i>Pterogorgia</i>	0	0	2.11	0.15	0	3.92	0.14	1.82	3.16	0	0	0
<i>Sponge</i>	5.29	4.02	3.76	1.22	3.85	4.26	5.56	2.03	3.30	2.57	1.57	2.70
<i>Amphiroa</i>	0	1.20	1.66	1.83	1.22	2.61	2.94	1.25	3.15	2.09	1.20	0.17
<i>Dictyota</i>	29.2	16.7	19.6	0.30	20.0	35.5	22.5	15.96	18.58	20.36	12.34	5.23
<i>Halimeda</i>	1.62	15.7	2.12	0.15	6.84	6.93	11.2	4.14	7.56	11.38	1.34	14.21
<i>Liagora</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lobophora</i>	0.31	7.47	0.45	0	5.23	5.21	4.79	3.46	5.13	4.74	3.42	2.00
<i>Macroalgae</i>	1.14	1.94	0.76	0.61	0.35	0.75	1.50	0.47	1.33	1.02	4.60	2.75
<i>Padina</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Porolithon</i>	0.66	2.25	0.46	1.67	0	0	0.14	0.32	0	0	3.98	6.89
<i>Sargassum</i>	0	0	0	0	0.18	0	0.43	0.15	0	0.36	0.54	0
<i>Schizothrix</i>	0	0	0.15	0	0	0	0	0	0	0	0	0
<i>Styopodium</i>	1.32	0.72	0.91	0	2.99	0.56	2.60	0.15	0.51	5.62	0	0
<i>Turbinaria</i>	0	0.34	0.15	0	0	0	0	0	0.18	0.62	0	0
<i>Turf</i>	30.6	6.25	36.8	74.1	24.4	11.8	14.1	39.25	24.98	20.90	3.97	22.47
<i>Wrangelia</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ascidian</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Coralline algae</i>	3.17	6.74	1.21	0.30	8.53	8.57	8.58	9.12	10.06	5.12	8.14	1.50

Appendix c: Percent cover of benthic taxa taken from photographic transects averaged between sites in Banco Chinchorro, Mexico.

Taxa	1	2	3	4	5	6	7	8	9	10
<i>Acropora cervicornis</i>	0.30	0.37	0	1.53	0	0	0	0.91	0.31	0
<i>Acropora palmata</i>	0	0	0	0	0	0	0	0	0	0
<i>Acropora prolifera</i>	0	0	0	0	0	0	0	0	0	0
<i>Agaricia agaricites</i>	1.52	0.37	0.61	1.23	1.23	1.98	0.28	0.30	0.31	0.27
<i>Agaricia fragilis</i>	0	0	0	0.31	0	0.57	0	0	0	0
<i>Agaricia grahamae</i>	0	0	0	0	0	0	0	0	0	0
<i>Agaricia tenuifolia</i>	0	0	0	0	0	0	0	0	0	0
<i>Agaricia undata</i>	0	0	0	0	0	0	0	0	0	0
<i>Agaricis lamarcki</i>	0	0	0	0	0.31	0	0.85	0	1.53	1.35
<i>Colpophyllia breviserialis</i>	0	0	0	0	0	0	0	0	0	0
<i>Colpophyllia natans</i>	0	0	0	0	0	0	0	0	0	0.27
<i>Dendrogyra cylindrus</i>	0	0	0	0	0	0	0	0	0	0
<i>Dichocoenia stellaris</i>	0	0	0	0	0	0	0	0	0	0
<i>Dichocoenia stokesi</i>	0	0	0	0	0	0	0	0	0	0
<i>Diploria clivosa</i>	0	0	0	0	0	0	0	0	0	0
<i>Diploria labyrinthiformis</i>	0	0	0	0	0	0	0	0	0	0
<i>Diploria strigosa</i>	0	0	0	1.23	0	1.70	0	0	0.31	0.54
<i>Eusmilia fastigiata</i>	0	0	0	0	0.62	0	0	0	0	0
<i>Favia fragum</i>	0	0	0	0	0	0	0	0	0	0
<i>Isophyllia sinuosa</i>	0	0	0	0	0	0	0	0	0	0
<i>Leptoseris cucullata</i>	0	0	0	0	0	0	0	0	0	0
<i>Madracis decactis</i>	0	0	0.30	0.61	0.31	0.57	0	0	0.31	0.27
<i>Madracis mirabilis</i>	0	0	0	0	0	0	0.28	0	0	0
<i>Manicina areolata</i>	0	0	0	0	0	0	0	0	0	0
<i>Meandrina meandrites</i>	0	0.74	0	0	0	0	0	0	0	0
<i>Millipora alcornis</i>	2.73	2.59	3.04	4.60	3.69	1.70	2.82	0.61	1.84	1.89
<i>Millipora complanata</i>	1.52	0	0	0	0.31	0	0.28	0	1.53	0.54
<i>Millipora squarrosa</i>	0	0	0	0	0	0	0	0	0	0
<i>Montastraea annularis</i>	0	0.37	0.30	0.31	0.62	1.70	0	0	0	0.81
<i>Montastraea cavernosa</i>	0	1.48	0.61	0.61	0.62	0.57	0	0	0	0
<i>Montastrea faveolata</i>	0	0	0	0.31	0	3.40	0	0	0	0.27
<i>Montastrea franksi</i>	0	0	0	1.23	0	0.28	0	0	0	0.27
<i>Mussa angulosa</i>	0	0	0	0	0	0	0	0	0	0
<i>Mycetophyllia aliciae</i>	0	0	0	0	0	0	0	0	0	0
<i>Mycetophyllia danaana</i>	0	0	0	0	0	0	0	0	0	0
<i>Mycetophyllia ferox</i>	0	0	0	0	0	0	0	0	0	0
<i>Mycetophyllia lamarckiana</i>	0	0	0	0	0	0	0	0	0	0
<i>Oculina diffusa</i>	0	0	0	0	0	0	0	0	0	0.27
<i>Porites astreoides</i>	0	0.74	0.30	1.53	2.46	1.42	3.66	3.34	4.91	5.66
<i>Porites branneri</i>	0	0	0	0	0	0	0	0	0	0
<i>Porites divaricata</i>	0	0	0	0.31	0	0	0	0	0	0
<i>Porites furcata</i>	0	0	0	0.31	0	0	0	0	0	0.27
<i>Porites porites</i>	0	0	0	0	0	0	0	0	0.61	0.27
<i>Scolymia cubensis</i>	0	0.37	0	0	0	0	0	0	0	0
<i>Scolymia lacera</i>	0	0	0	0	0	0	0	0	0	0
<i>Siderastrea radians</i>	0.30	0.74	0.30	1.53	2.15	0.28	1.69	0.91	1.84	1.89
<i>Siderastrea siderea</i>	0	0	0	0	0	0	0	0	0	0
<i>Solenastrea bournoni</i>	0	0	0	0	0	0	0	0	0	0
<i>Solenastrea hyades</i>	0	0	0	0	0	0	0	0	0	0
<i>Stephanocoenia michelinii</i>	0	0	0	0	0	0	0	0	0	0
<i>Tubastraea aurea</i>	0	0	0	0	0	0	0	0	0	0
<i>Briareum</i>	0	0	0	0	0	0	0	0	0	0
<i>Erythropodium</i>	0	0	0	0	0	0	0	0	0	0
<i>Eunicea</i>	1.21	1.85	0.61	2.76	2.15	1.98	0.56	0.30	0.61	0
<i>Gorgonian</i>	0	0	0	0	0.31	0.28	11.27	1.52	6.13	5.66
<i>Iciligorgia</i>	0	0	0	0	0	0	0	0	0	0
<i>Muricea</i>	0	0	0.61	0.92	0	0.85	0	0	0.31	0
<i>Muriceopsis</i>	0	0	0	0	0	0	0	0	0	0
<i>Plexaura</i>	0	0	0	0	0	0	0	0	0	0
<i>Plexaurella</i>	0	0	0	0	0	0	0.28	2.13	0	0.27
<i>Pseudoplexaura</i>	1.21	2.22	1.52	4.60	2.46	2.55	0.56	0.61	0.61	1.89
<i>Pseudopterogorgia</i>	3.03	8.52	8.51	14.11	21.85	15.58	10.42	2.13	2.76	4.58
<i>Pterogorgia</i>	0.61	0	1.52	0	0.62	0.85	0	0	0	0.54
<i>Sponge</i>	4.24	1.85	3.04	5.83	5.54	5.95	4.23	3.34	1.23	0

Taxa	1	2	3	4	5	6	7	8	9	10
<i>Amphiroa</i>	0.61	0.74	0	0	0	0	0.28	0	0	0
<i>Dictyota</i>	2.42	0	0	0	3.08	1.13	7.32	10.94	5.21	5.39
<i>Halimeda</i>	0	1.85	1.22	8.90	7.08	11.90	1.97	0.30	3.07	1.08
<i>Liagora</i>	0	0	0	0	0	0	0	0	0	0
<i>Lobophora</i>	7.88	6.30	3.34	7.06	10.77	19.26	1.41	3.34	3.68	1.35
<i>Macroalgae</i>	0.61	4.07	0.91	2.15	1.85	0.28	1.69	3.34	0.92	3.23
<i>Padina</i>	0	0	0	0	0	0	0	0	0	0
<i>Porolithon</i>	0.30	0	0	0.61	0	0	0.28	0.30	1.53	0.81
<i>Sargassum</i>	0	0	0	0	0	0	0.56	0	0	0
<i>Schizothrix</i>	0.30	0	0	0	0	0	0	0.61	0	0
<i>Styopodium</i>	0	0	0	0	1.23	0	2.82	2.13	2.76	5.39
<i>Turbinaria</i>	0	0	0	0	0	0	0	0	0	0.27
<i>Turf</i>	69.70	57.04	41.95	24.54	18.77	9.63	45.07	61.40	54.60	47.98
<i>Wrangelia</i>	0	0	0	0	0	0	0	0	0	0
<i>Ascidian</i>	0	0	0	0	0.31	0	0	0	0	0
<i>Coralline algae</i>	0.30	0	1.82	4.29	1.85	0	0	0.61	0.92	1.35

Appendix d: Percent cover of benthic taxa taken from photographic transects averaged between sites in Puerto Morelos, Mexico.

Taxa	13	Albert's reef	Cabeza Grande	Grouper Alley	Puente	Rodwin's
<i>Acropora cervicornis</i>	0	0	0	0	0.18	0
<i>Acropora palmata</i>	0	0	0	0	0	0
<i>Acropora prolifera</i>	0	0	0	0	0	0
<i>Agaricia agaricites</i>	0	1.55	2.21	0.62	0.37	0.76
<i>Agaricia fragilis</i>	0	0	0	0	0	0
<i>Agaricia grahamae</i>	0	0	0	0	0	0
<i>Agaricia tenuifolia</i>	0	0.16	0.24	0	0	0.12
<i>Agaricia undata</i>	0	0	0	0	0	0
<i>Agaricis lamarcki</i>	0	0	0	0	0.19	0
<i>Colpophyllia breviserialis</i>	0	0	0	0	0	0
<i>Colpophyllia natans</i>	0	0.31	0	0	0.74	0.35
<i>Dendrogyra cylindrus</i>	0	0	0	0	0	0
<i>Dichocoenia stellaris</i>	0	0	0	0	0	0
<i>Dichocoenia stokesi</i>	0	0	0.31	0	0	0
<i>Diploria clivosa</i>	0	0	0	0	0	0
<i>Diploria labyrinthiformis</i>	0.55	0	0.12	0	0	0
<i>Diploria strigosa</i>	0	0.31	0.78	0	0.19	0
<i>Eusmilia fastigiata</i>	0	0	0	0	0	0
<i>Favia fragum</i>	0	0	0	0	0	0
<i>Isophyllia sinuosa</i>	0	0	0	0	0	0
<i>Leptoseris cucullata</i>	0	0	0	0	0	0
<i>Madracis decactis</i>	1.08	0.16	0.77	0	0.73	0.95
<i>Madracis mirabilis</i>	0	0	0	0	0	0
<i>Manicina areolata</i>	0	0	0	0	0	0
<i>Meandrina meandrites</i>	0	0	0	0	0	0
<i>Millipora alcicornis</i>	0.37	0.36	0.32	0.16	0.73	0.58
<i>Millipora complanata</i>	0	0	0	0	0.37	0
<i>Millipora squarrosa</i>	0.19	0	0	0	0	0
<i>Montastraea annularis</i>	0.18	0.78	1.11	0	0	0.41
<i>Montastraea cavernosa</i>	1.09	1.09	0.90	0.16	1.28	0.36
<i>Montastrea faveolata</i>	0.18	1.24	1.58	0	1.83	0.71
<i>Montastrea franki</i>	0	0	0	0	0	0
<i>Mussa angulosa</i>	0	0	0	0	0	0
<i>Mycetophyllia aliciae</i>	0	0	0	0	0	0
<i>Mycetophyllia danaana</i>	0	0	0	0	0	0
<i>Mycetophyllia ferox</i>	0.19	0	0.11	0	0	0
<i>Mycetophyllia lamarckiana</i>	0	0	0.12	0	0	0
<i>Oculina diffusa</i>	0	0	0	0	0	0
<i>Porites astreoides</i>	0.37	0.89	0	0.16	1.10	0
<i>Porites branneri</i>	0	0	0	0	0	0
<i>Porites divaricata</i>	0	0	0	0	0	0
<i>Porites furcata</i>	0	0	0	0	0	0.53
<i>Porites porites</i>	0	0.64	0.43	0	1.28	0
<i>Scolymia cubensis</i>	0.37	0.36	0.10	0.59	1.28	0
<i>Scolymia lacera</i>	0	0	0	0	0	0
<i>Siderastrea radians</i>	1.27	0.69	1.99	0.62	0.91	0.65
<i>Siderastrea siderea</i>	0	0	0.48	0	0	0
<i>Solenastrea bournoni</i>	0.91	0.16	0.55	0.78	0.74	0
<i>Solenastrea hyades</i>	0	0	0	0	0.55	0
<i>Stephanocoenia michelinii</i>	0	0	0	0	0	0
<i>Tubastraea aurea</i>	0	0	0	0	0	0
<i>Briareum</i>	0.19	0.53	0	0.16	0.55	0.18
<i>Erythropodium</i>	0	0.93	0.21	0	0.19	0.18
<i>Eunicea</i>	0.36	0	0.33	0	0	2.14
<i>Gorgonian</i>	1.63	1.24	0.98	0	0.73	0.74
<i>Iciligorgia</i>	0	0	0	0	0	0
<i>Muricea</i>	0	0	0	0	0	0.88
<i>Muriceopsis</i>	0	0	0	0	0	0
<i>Plexaura</i>	0	0	0	0	0	0.13
<i>Plexaurella</i>	0.73	0	0.10	0	0.19	1.18
<i>Pseudoplexaura</i>	1.43	1.57	4.55	0	2.00	3.37
<i>Pseudopterogorgia</i>	8.32	5.48	13.48	2.04	5.80	11.75
<i>Pterogorgia</i>	0.36	0	0.94	0	0	2.22
<i>Sponge</i>	2.17	4.78	1.32	0.16	7.68	0.65

Taxa	13	Albert's reef	Cabeza Grande	Grouper Alley	Puente	Rodwin'Reef
<i>Amphiroa</i>	0.54	0.80	1.48	0.59	4.92	1.77
<i>Dictyota</i>	4.85	5.69	19.90	32.72	13.68	16.76
<i>Halimeda</i>	1.08	13.02	2.82	5.08	3.28	0.98
<i>Liagora</i>	0	0	0	0	0	0
<i>Lobophora</i>	0.18	0.31	1.17	1.95	1.46	0.71
<i>Macroalgae</i>	0.72	0.67	0.33	0.31	1.27	0.83
<i>Padina</i>	0	0	0	0	0	0
<i>Porolithon</i>	1.45	4.65	1.07	0	3.29	0.13
<i>Sargassum</i>	0	0	0	2.85	0.37	0
<i>Schizothrix</i>	0	0	0	0	0	0
<i>Styopodium</i>	0	0	0	0	0.55	0
<i>Turbinaria</i>	0	0	0	0	0	0
<i>Turf</i>	66.56	46.09	32.02	49.61	35.11	45.50
<i>Wrangelia</i>	0	0	0	0	0	0
<i>Ascidian</i>	0	0	0	0	0	0
<i>Coralline algae</i>	0.54	0.93	0.22	0.47	0.55	0

Appendix e: Percent cover of benthic taxa taken from photographic transects averaged between sites in Xcalak, Mexico.

Taxa	First site	Santa Rosa	Blanqui-zares	Partilla	Poza Rico	La Chimimea	Scott's Playground
<i>Acropora cervicornis</i>	0	0.49	0.31	0	0.06	0	0
<i>Acropora palmata</i>	0	0	0	0	0	0	0
<i>Acropora prolifera</i>	0	0	0	0	0	0	0
<i>Agaricia agaricites</i>	2.03	1.46	1.68	0.46	0.39	0.40	0.95
<i>Agaricia fragilis</i>	0.18	0.16	0	0	0	0	0
<i>Agaricia grahamae</i>	0	0	0	0.15	0	0	0
<i>Agaricia tenuifolia</i>	0.10	0.31	0.47	0.15	0.20	0.10	0.21
<i>Agaricia undata</i>	0	0	0	0	0.08	0	0
<i>Agaricis lamarcki</i>	0	0	0	0	0.08	0.10	0.21
<i>Colpophyllia breviserialis</i>	0	0	0	0	0	0	0
<i>Colpophyllia natans</i>	1.19	0.47	0	0	0	0	0.10
<i>Dendrogyra cylindrus</i>	0	0	0.16	0	0	0	0
<i>Dichocoenia stellaris</i>	0	0	0	0	0	0	0
<i>Dichocoenia stokesi</i>	0	0	0	0	0.07	0.31	0
<i>Diploria clivosa</i>	0	0	0	0	0	0	0
<i>Diploria labyrinthiformis</i>	1.25	0	0.31	0.14	0.24	0	0.93
<i>Diploria strigosa</i>	0.10	0	0	1.53	0.06	0.29	1.16
<i>Eusmilia fastigiata</i>	0	0	0	0	0	0	0
<i>Favia fragum</i>	0	0	0	0	0	0	0
<i>Isophyllia sinuosa</i>	0	0	0	0	0.08	0	0
<i>Leptoseris cucullata</i>	0	0	0	0	0	0	0
<i>Madracis decactis</i>	0	0	0	0	0	0	0
<i>Madracis mirabilis</i>	0.10	0	0.15	0	0	0	0
<i>Manicina areolata</i>	0	0	0	0	0.08	0	0
<i>Meandrina meandrites</i>	0.09	0	0	0	0	0	0
<i>Millipora alcicornis</i>	0.09	0.31	0	0.60	0.91	0.19	0.21
<i>Millipora complanata</i>	0	0	0	0	0.08	0.10	0.11
<i>Millipora squarrosa</i>	0	0	0	0	0.06	0	0
<i>Montastraea annularis</i>	1.16	0.31	0	0.57	0.08	0.29	0.63
<i>Montastraea cavernosa</i>	1.82	0.16	0.30	0.14	0.64	0.10	0.52
<i>Montastrea faveolata</i>	1.96	1.92	1.25	0.29	0	1.24	0.21
<i>Montastrea franksi</i>	0.48	0.47	0	0	0	0	0
<i>Mussa angulosa</i>	0	0.16	0	0	0	0	0
<i>Mycetophyllia aliciae</i>	0	0	0	0	0	0	0
<i>Mycetophyllia danaana</i>	0	0	0	0	0	0	0
<i>Mycetophyllia ferox</i>	0	0	0	0	0	0	0
<i>Mycetophyllia lamarckiana</i>	0	0.33	0	0	0	0	0
<i>Oculina diffusa</i>	0	0	0	0	0	0	0
<i>Porites astreoides</i>	5.43	3.26	5.69	1.95	0.14	1.32	1.26
<i>Porites branneri</i>	0	0	0	0	0	0	0
<i>Porites divaricata</i>	0.22	0	1.08	0	0	0	0
<i>Porites furcata</i>	1.16	0.97	2.01	0	1.08	0.10	0.11
<i>Porites porites</i>	0.10	0	0	0	0	0.10	0
<i>Scolymia cubensis</i>	0.12	0	0	0	0.07	0	0.11
<i>Scolymia lacera</i>	0	0	0	0	0	0	0
<i>Siderastrea radians</i>	0.33	0.49	0.16	0	0.13	0.40	0.63
<i>Siderastrea siderea</i>	0	1.27	0.15	0.14	0.34	0.21	0.84
<i>Solenastrea bournoni</i>	0	0	0	0	0	0	0
<i>Solenastrea hyades</i>	0	0	0	0	0	0.62	0
<i>Stephanocoenia michelinii</i>	0	0	0	0	0	0	0
<i>Tubastraea aurea</i>	0	0	0	0	0	0	0
<i>Briareum</i>	0.09	0.33	0	0	0	0	0
<i>Erythropodium</i>	0.21	0	0.16	0.60	0.43	0.10	0
<i>Eunicea</i>	0.31	1.78	0	0.73	1.78	0.41	1.58
<i>Gorgonian</i>	0.89	1.61	0.47	2.47	1.25	0.60	4.00
<i>Iciligorgia</i>	0	0	0	0	0	0	0
<i>Muricea</i>	0.33	0.31	0.78	0.31	0.31	0.10	1.37
<i>Muriceopsis</i>	0	0	0	0	0.07	0	0
<i>Plexaura</i>	0	0	0	0	0	0	0
<i>Plexaurella</i>	0.39	2.86	1.23	1.04	1.39	1.11	0.94
<i>Pseudoplexaura</i>	0	0	0	0.14	0.74	0	0.63
<i>Pseudopterogorgia</i>	2.62	9.78	7.65	12.09	7.43	9.30	9.64
<i>Pterogorgia</i>	0.19	0	0	0.31	0	0	0

<i>Taxa</i>	<i>First site</i>	<i>Santa Rosa</i>	<i>Blanqui zares</i>	<i>Partilla</i>	<i>Poza Rico</i>	<i>La Chimimea</i>	<i>Scott's Playground</i>
<i>Sponge</i>	1.53	0.80	0.61	2.79	0.86	0.51	0.74
<i>Amphiroa</i>	6.31	0.80	0.15	1.80	0.67	2.73	4.40
<i>Dictyota</i>	19.46	20.40	14.77	11.64	1.25	4.37	3.16
<i>Halimeda</i>	4.26	5.89	12.33	17.31	2.87	25.67	10.24
<i>Liagora</i>	0	0	0	0	0	0	0
<i>Lobophora</i>	8.69	3.36	9.91	1.58	0.47	2.59	0.84
<i>Macroalgae</i>	5.49	3.61	1.70	5.80	6.55	7.89	8.95
<i>Padina</i>	0	0	0	0	0	0	0
<i>Porolithon</i>	0.67	0	0.16	0	0	0	0
<i>Sargassum</i>	0	0	0	0	0.06	0	0
<i>Schizothrix</i>	0	0	0	0	0	0	0
<i>Styopodium</i>	1.34	1.30	0.62	1.30	0.43	0	0
<i>Turbinaria</i>	0.31	0	0.15	0.14	0	0	0
<i>Turf</i>	3.34	7.77	9.73	15.60	47.83	17.70	12.93
<i>Wrangelia</i>	0	0	0	0	0	0	0
<i>Ascidian</i>	0	0	0	0	0	0	0
<i>Coralline algae</i>	20.94	12.35	20.29	9.68	9.56	16.49	24.91

Appendix f: Shannon-Wiener diversity index for Cayos Cochinos and Utila study sites averaged over photographic transects.

<i>Site</i>	<i>All taxa</i>	<i>Algae</i>	<i>Scleractinian</i>	<i>Gorgonians</i>
Area	1.28	0.32	0.24	0.22
Pelican 1	1.55	0.36	0.30	0.28
Pelican 1	1.57	0.35	0.28	0.28
Pelican 2	1.75	0.36	0.33	0.31
Pelican 2	1.58	0.37	0.30	0.27
Pelican 3	1.59	0.37	0.29	0.30
Pelican 3	1.51	0.35	0.27	0.24
Pelican2 1	1.60	0.36	0.32	0.25
Pelican2 1	1.43	0.36	0.29	0.35
Pelican2 2	1.58	0.37	0.30	0.34
Pelican2 2	1.58	0.37	0.26	0.30
Pelican 2.5	1.50	0.34	0.26	0.17
Pelican 2.5	1.37	0.32	0.19	0.27
Timon1	1.46	0.36	0.36	0.27
Timon1	1.59	0.37	0.35	0.33
Timon2	1.52	0.35	0.27	0.25
Timon2	1.66	0.37	0.32	0.32
Slumberland	1.19	0.27	0.21	0.02
Slumberland	1.18	0.29	0.23	0.02
Blank Coral	1.44	0.33	0.26	0.19
Blank Coral	1.44	0.35	0.29	0.29
Coral View	1.27	0.30	0.29	0.19
Coral View	1.44	0.28	0.29	0.29
Ironbound flat	0.61	0.15	0.13	0.24
Ironbound flat	0.78	0.22	0.13	0.32
JackNeil	1.23	0.29	0.31	0.08
JackNeil	1.35	0.31	0.22	0.18
Lighthouse	1.32	0.30	0.22	0.25
Lighthouse	1.18	0.28	0.22	0.21
Little Bight	1.28	0.32	0.28	0.24
Little Bight	1.22	0.29	0.27	0.20
Pinnacle	1.26	0.32	0.23	0.23
Pinnacle	0.86	0.24	0.09	0.33
Stingray Point	1.12	0.29	0.29	0.16
Stingray Point	1.30	0.31	0.23	0.28
Stingray Alley	1.02	0.26	0.29	0.21
Stingray Alley	1.13	0.28	0.28	0.19
Westend	1.82	0.35	0.26	0.26
Westend	1.58	0.37	0.30	0.19
Ironbound head	1.14	0.33	0.31	0.06
Ironbound head	1.32	0.36	0.37	0.24

Appendix g: Average scleractinian, gorgonian, sponge and algae percent cover for each study site, and average transect depth in feet, as well as depth rank on a scale of 0-5. CC represents Cayos Cochinos, Ut represents Utila, BC represents Banco Chinchorro and PM represents Puerto Morelos locations. (-) indicates no measurements were taken.

<i>Site</i>	<i>Location</i>	<i>Scleractinian</i>	<i>Gorgonian</i>	<i>Sponge</i>	<i>Algae</i>	<i>Depth (ft)</i>	<i>Depth Rank</i>
Arena	CC	10.63	9.38	1.56	57.19	22.5	2
Pelican 1	CC	15.26	14.69	7.65	47.24	27.5	2
Pelican 2	CC	18.90	15.87	2.33	35.19	20.0	2
Pelican 3	CC	14.80	14.27	7.17	44.01	22.5	2
Pelican2 1	CC	17.21	18.77	0.00	35.77	25.0	2
Pelican2 2	CC	14.62	20.10	2.09	40.80	22.5	2
Pelican 2.5	CC	9.74	9.68	2.99	54.30	25.0	2
Timon1	CC	26.14	17.34	1.23	39.67	15.0	1
Timon2	CC	16.60	15.64	4.91	41.56	22.5	2
Slumberland	Ut	9.09	0.32	5.29	64.80	30.0	2
Blank Coral	Ut	13.67	11.82	4.02	52.55	25.0	2
Coral View	Ut	12.04	7.24	3.76	63.06	25.0	2
Ironbound flat	Ut	4.26	15.09	1.22	78.67	-	-
JackNeil	Ut	13.72	4.52	3.85	61.14	22.5	2
Lighthouse	Ut	9.11	10.02	4.26	63.42	23.0	2
Little Bight	Ut	14.28	9.55	5.56	60.21	22.5	2
Pinnacle	Ut	6.04	15.60	2.03	65.16	-	-
Stingray Point	Ut	12.50	10.10	3.30	61.42	22.5	2
Stingray Alley	Ut	15.26	7.68	2.57	67.10	-	2
Westend	Ut	14.48	9.93	1.57	31.40	23.5	2
Ironbound head	Ut	25.79	6.05	2.70	53.73	-	-
BC 1	BC	6.67	6.06	4.24	81.82	50.0	4
BC 2	BC	7.78	12.59	1.85	70.00	60.0	5
BC 3	BC	5.47	12.77	3.04	47.42	60.0	5
BC 4	BC	15.64	22.39	5.83	43.25	60.0	5
BC 5	BC	12.31	27.38	5.54	42.77	60.0	5
BC 6	BC	14.16	22.10	5.95	42.21	60.0	5
BC 7	BC	9.86	23.10	4.23	61.41	30.0	2
BC 8	BC	6.08	6.69	3.34	82.37	30.0	2
BC 9	BC	13.80	10.43	1.23	71.78	30.0	2
BC 10	BC	15.09	12.94	0.00	65.50	-	-
13	BC	6.72	13.01	2.17	75.38	30.0	2
Albert's reef	PM	8.64	9.74	4.78	71.20	45.0	4
Cabeza Grande	PM	12.25	20.58	1.32	58.80	22.5	3
Grouper Alley	PM	3.06	2.19	0.15	93.08	60.0	5
Puente	PM	12.42	9.44	7.67	63.91	45.0	4
Rodwin's Reef	PM	5.55	22.78	0.65	66.68	17.5	1
First site	Xc	17.93	5.03	1.53	49.86	61.7	5
Santa Rosa	Xc	13.73	10.29	0.61	49.52	60.0	5
Blanquizaes	Xc	12.54	16.68	0.80	43.12	50.0	5
Partilla	Xc	6.15	17.69	2.79	55.16	30.0	2
Poza Rico	Xc	6.08	15.91	1.07	52.91	42.2	2
La Chimimea	Xc	5.87	11.62	0.51	60.96	41.7	3
Scott's Playground	Xc	8.19	18.17	0.74	40.52	26.7	2

Appendix h: Live taxa identified in photographic transects

<i>Scleractinians</i>	<i>Gorgonians</i>	<i>Macroalgae</i>	<i>Other</i>
<i>Acropora cervicornis</i>	<i>Briareum</i>	<i>Amphiroa</i>	Coralline algae
<i>Acropora palmata</i>	<i>Erythropodium</i>	<i>Dictyota</i>	Turf algae
<i>Acropora prolifera</i>	<i>Eunicea</i>	<i>Halimeda</i>	Sponge
<i>Agaricia agaricites</i>	<i>Gorgonian</i>	<i>Liagora</i>	
<i>Agaricia fragilis</i>	<i>Iciligorgia</i>	<i>Lobophora</i>	
<i>Agaricia grahamae</i>	<i>Muricea</i>	<i>Macroalgae</i>	
<i>Agaricia tenuifolia</i>	<i>Muriceopsis</i>	<i>Padina</i>	
<i>Agaricia undata</i>	<i>Plexaura</i>	<i>Porolithon</i>	
<i>Agaricis lamarcki</i>	<i>Plexaurella</i>	<i>Sargassum</i>	
<i>Colpophyllia breviserialis</i>	<i>Pseudoplexaura</i>	<i>Schizothrix</i>	
<i>Colpophyllia natans</i>	<i>Pseudopterogorgia</i>	<i>Styopodium</i>	
<i>Dendrogyra cylindrus</i>	<i>Pterogorgia</i>	<i>Turbinaria</i>	
<i>Dichocoenia stellaris</i>	<i>Briareum</i>		
<i>Dichocoenia stokesi</i>	<i>Erythropodium</i>		
<i>Diploria clivosa</i>	<i>Eunicea</i>		
<i>Diploria labyrinthiformis</i>	<i>Gorgonian</i>		
<i>Diploria strigosa</i>	<i>Iciligorgia</i>		
<i>Eusmilia fastigiata</i>	<i>Muricea</i>		
<i>Favia fragum</i>	<i>Muriceopsis</i>		
<i>Isophyllia sinuosa</i>	<i>Plexaura</i>		
<i>Leptoseris cucullata</i>	<i>Plexaurella</i>		
<i>Madracis decactis</i>	<i>Pseudoplexaura</i>		
<i>Madracis mirabilis</i>	<i>Pseudopterogorgia</i>		
<i>Manicina areolata</i>	<i>Pterogorgia</i>		
<i>Meandrina meandrites</i>			
<i>Millipora alcicornis</i>			
<i>Millipora complanata</i>			
<i>Millipora squarrosa</i>			
<i>Montastraea annularis</i>			
<i>Montastraea cavernosa</i>			
<i>Montastrea faveolata</i>			
<i>Montastrea franksi</i>			
<i>Mussa angulosa</i>			
<i>Mycetophyllia aliciae</i>			
<i>Mycetophyllia danaana</i>			
<i>Mycetophyllia ferox</i>			
<i>Mycetophyllia lamarckiana</i>			
<i>Oculina diffusa</i>			
<i>Porites astreoides</i>			
<i>Porites branneri</i>			
<i>Porites divaricata</i>			
<i>Porites furcata</i>			
<i>Porites porites</i>			
<i>Scolymia cubensis</i>			
<i>Scolymia lacera</i>			

Scleractinians	Gorgonians	Macroalgae	Other
<i>Siderastrea radians</i>			
<i>Siderastrea siderea</i>			
<i>Solenastrea bournoni</i>			
<i>Solenastrea hyades</i>			
<i>Stephanocoenia michelinii</i>			
<i>Tabastraea aurea</i>			

Appendix i: ANOVA results for Cayos Cochinos and Utila comparisons of percent cover data averaged for each site and Shannon Wiener indices of diversity data from CPCe averaged for each site. Tests used $\alpha = 0.05$ as a level of significance.

Source	Df	SS	MS	F	p-value
Scleractinian cover					
Location	1	108.2	108.2	6.09	0.024
Error	18	319.9	17.8		
Total	19	428.1			
Gorgonian cover					
Location	1	190.6	190.6	11.75	0.003
Error	19	308.1	16.2		
Total	20	498.7			
Macroalgae cover					
Location	1	1.973	1.973	2.31	0.145
Error	19	16.24	0.855		
Total	20	18.22			
Turf cover					
Location	1	2885	2885	14.01	0.001
Error	19	3914	206		
Total	20	6798			
Sponge cover					
Location	1	0.00	0.00	0.00	0.983
Error	19	77.96	4.10		
Total	20	77.97			
Shannon Wiener index all taxa					
Location	1	0.4463	0.4463	11.68	0.003
Error	19	0.7262	0.0382		
Total	20	1.1725			
Shannon Wiener index scleractinian					
Location	1	0.0069	0.0069	2.73	0.115
Error	19	0.0482	0.0482		
Total	20	0.0551			
Shannon Wiener index gorgonians					
Location	1	0.0273	0.0273	7.59	0.013
Error	19	0.0684	0.0036		
Total	20	0.0958			
Shannon Wiener index algae					
Location	1	0.0184	0.0184	15.00	0.001
Error	19	0.0234	0.0012		
Total	20	0.0428			

Appendix j: ANOVA results for Cayos Cochinos and Utila scleractinian comparisons using percent cover data averaged for each site. Tests used $\alpha = 0.05$ as a level of significance.

Source	Df	SS	MS	F	p-value
Non-framework scleractinian cover					
Location	1	1.664	1.664	3.75	0.069
Error	18	7.986	0.444		
Total	19	9.650			
Framework scleractinian cover					
Location	1	0.031	0.031	0.08	0.783
Error	18	7.233	0.402		
Total	19	7.264			
<i>Agaracia</i> cover					
Location	1	0.059	0.059	0.67	0.424
Error	19	1.673	0.088		
Total	20	1.732			
<i>Montastraea</i> cover					
Location	1	0.046	0.046	0.12	0.736
Error	19	7.450	0.392		
Total	20	7.496			
<i>Acropora</i> cover					
Location	1	0.001	0.001	0.07	0.793
Error	19	0.2930	0.015		
Total	20	0.2941			
<i>Porites</i> cover					
Location	1	0.898	0.898	5.76	0.027
Error	19	2.963	0.156		
Total	20	3.861			

REFERENCES

Aguilar-Perera, A. and W. Aguilar-Dávila. 1993. Banco Chinchorro: Arricife coralino en al Caribe. In: Salazar-Vallejo, S. I. and N. E. González, editors. Biodiversidad Marina y Costera de México. México (DF): Comisión Nacional para el Conocimiento y Use de la Biodiversidad y Centro de Investigaciones de Quintana Roo. p 807-816.

Andérouët, S., P. J. Mumby, M. McField, C. Hu, F. E. Muller-Karger. 2002. Revisiting coral reef connectivity. *Coral Reefs* 21:43-48. doi:10.1007/s00338-001-0199-0.

Bellwood D. R. and T. P. Hughes. 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292:1532-1535. doi:10.1126/science.1058635.

Bellwood D. R., T. P. Hughes, C. Folke and M. P. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827-833. doi:10.1038/nature02691.

Brondo, K. V. and L. Woods. 2007. Garifuna land rights and ecotourism as economic development in Honduras' Cayos Cochinos marine protected area. *Ecological and Environmental Anthropology* 3:1-18.

Brown-Saracino, J. P. Peckol, H. A. Curran and M. L. Robbart. 2007. Spatial variation in sea urchins, fish predators, and bioerosion rates on coral reefs of Belize. *Coral Reefs* 26:71-78. doi:10.1007/s00338-006-0159-9.

Bryant, D., L. Burke, J. McManus and M. Spalding. 1998. Reefs at risk: a map-based indicator of potential threats to the worlds coral reefs. World Resources Institute, Washington, DC; International Center for Living Aquatic Resource Management, Manila; and United Nations Environment Programme-World Conservation Monitoring Center, Cambridge. p. 17-31.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algae communities. *Ecological Monographs* 56:345-364. www.jstor.org/stable/1942551.

Carpenter, R. C. 1988. Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. *Proceedings of the National Academy of Science of the United States* 85:511-514.

Clarke, K. R. and M. Ainsworth. 1993. A method linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92:205-219.

Clarke, K. R. and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd Edition. PRIMER-E: Plymouth, UK. p. 43-47.

Clifton, K. E. and L. M. Clifton. 1998. A survey of fishes from various coral reef habitats within the Cayos Cochinos marine reserve, Honduras. *Revista de Biología Tropical* 46(4): S109-S124.

Coronado, C. J. Candela, R. Iglesias-Prieto, J. Sheinbaum, M. López and F. J. Ocampo-Torres. 2007. On the circulation in the Puerto Morelos fringing reef lagoon. *Coral Reefs* 26:149-163. doi:10.1007/s00338-006-0175-9.

Diaz-Pulido, G. and L. J. McCook. 2004. Effects of live coral. Epilithic algal communities and substrate type on algal recruitment. *Coral Reefs* 23:225-233. doi:10.1007/s00338-004-0370-5.

Dunn, S. R., C. S. Schnitzler and V. M. Weis. 2007. Apoptosis and the autophagy as mechanisms of dinoflagellate symbiont release during cnidarian bleaching: every which way you lose. *Proceedings of the Royal Society of Biology* 274:3079-3085. doi:10.1098/rspb.2007.0711.

Edmunds P. J. and R. C. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgae cover and increases abundance of juvenile corals on the Caribbean reef. *Proceedings of the National Academy of Sciences* 98:5067-5071. doi:10.1073/pnas.071524598.

Foster, N. L., S. J. Box and P. J. Mumby. 2008. Competitive effects of macroalgae on the fecundity of the reef-building coral *Montastrea annularis*. *Marine Ecology Progress Series* 367:143-152. doi:10.3354/meps07594.

Game, E. T., E. McDonald-Madden., M. L. Puotinen and H. P. Possingham. 2008. Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Conservation Biology* 22:1619-1629. doi:10.1111/j.1523-1739.2008.01037.x.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant and A. R. Watkinson. 2003. Long-term region wide declines in Caribbean corals. *Science* 301:958-960. doi:10.1126/science.1086050.

Halpern, B. S. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13:S117-S137. doi:10.1890/1051-0761(2003)013[0117:TIOMRD]2.0.CO;2.

Harm, J. H., E. Kearns and M. R. Speight. 2008. Differences in coral-reef fish assemblages between mangrove rich and mangrove-poor islands of Honduras. *Proceedings of the 11th International Coral Reef Symposium*; 2008 July 7-11; Fort Lauderdale. Florida. p. 296-300.

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158-2162. doi:10.1126/science.1063699.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. M. Kleypas *et al.* 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929-933

Hughes, T. P. and J. H. Connell. 1999. Multiple stressors on coral reefs: a long term perspective. *Limnology and Oceanography* 44:932-940.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschanowskyj, M.S. Pratchett, R. S. Steneck and B. Willis. Phase shifts, herbivory, and the resilience of coral reefs to climate change. 2007. *Current Biology* 17:360-365. doi:10.1016/j.cub.2006.12.049.

Humman, P. N. Deloach. 2002. Reef Coral identification: Florida, Caribbean, Bahamas: including marine plants. 2nd ed. Jacksonville (FL): New World Publications. p.86-174.

Knowlton, N. 2001. The future of coral reefs. *Proceedings of the National Academy of Sciences* 98:5419-5425. doi:10.1073/pnas.091092998.

Kohler, K. E. and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32:1259–1269. doi:10.1016/j.cageo.2005.11.009.

Ledlie, M. H., N. A. J. Graham, J. C. Bythell, S. K. Wilson, S. Jennings, N. V. C. Polunin and J. Hardcastle. 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26:641-653. doi:10.1007/s00338-007-0230-1.

McClanahan, T. R., M. McField, M. Huitric, K. Bergman, E. Sala, M. Nyström, I. Nordemar, T. Elfving and N. A. Muthiga. 2001. Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glover Reef Atoll, Belize. *Coral Reef* 19:367-379. doi:10.1007/s003380000131.

McCook L. J., J. Jompa, G. Diaz-Pulido. 2001. Competition between coral and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19: 400-417. doi:10.1007/s003380000129.

Mora, C. S. Andérouët, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston and R. A. Myers. 2006. Coral reefs and the global network of marine protected areas. *Science* 312:1750-1751. doi:10.1126/science.1125295.

- Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16:747-769. doi:10.1890/1051-0761(2006)016[0747:TIOEGS]2.0.CO;2.
- Mumby, P. J., A. J. Edwards, J. E. Arias-González, K. C. Lindeman, P. G. Blackwell, A. Gall, M. I. Górczyska, A. R. Harborne, C. L. Pescod, H. Renken *et al.* 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427: 533-536 doi:10.1038/nature02286.
- Mumby, P. J., C. P. Dalgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch *et al.* 2006. Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs. *Science* 311:98-101. doi:10.1126/science.1121129.
- Pandolfi, J. M., R. H. Bradbury, E. Saka, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes *et al.* 2003. Global trajectories of the long term decline of coral reef ecosystems. *Science* 301:955-958. doi:10.1126/science.1085706.
- Rodgers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62:185-202.
- Rodgers, C. S. and J. Miller. 2006. Permanent 'phase shifts' or reversible declines in coral cover? Lack of recovery of two coral reefs in St. John, US Virgin Islands. *Marine Ecology Progress Series* 306:103-114. doi:10.3354/meps306103.
- Rodríguez-Martínez, R. E. 2008. Community involvement in marine protected areas: the case of Puerto Morelos reef, México. *Journal of Environmental Management* 88:1151-1160. doi:10.1016/j.jenvman.2007.06.008.
- Saunders J., J. Shrives, J. Harm, S. Green and N. Brown. 2008. Honduras Marine Science Report. [Internet]. [cited 2010 Mar 16]. Available from [http://www.opwall.com/Library/Honduras.marine management and overall.shtml](http://www.opwall.com/Library/Honduras.marine%20management%20and%20overall.shtml).
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591-596. doi:10.1038/35098000.
- Selig, E. R. and J. F. Bruno. 2010. Global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS One* 5(2): e9278. doi:10.1371/journal.pone.0009278.
- Steiner, S. C. C. and S. M. Willams. 2006. The density and size distribution of *Diadema anillarum* in Dominica (Lesser Antilles): 2001-2004. *Marine Biology* 149:1071-1078. doi:10.1007/s00227-006-0279-3 .

Syms, C. and G. P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81:2714-2729. doi:10.1890/0012-9658(2000)081[2714:DHSATD]2.0.CO;2.

Weis, V. and D. Allemand. 2009. What determines coral health? *Science*: 324:1153-1155. doi:10.1126/science.1172540.