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Degradation and recovery of Caribbean coral reefs

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DEGRADATION AND RECOVERY OF CARIBBEAN CORAL REEFS

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requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Gustavo Adolfo Paredes

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2009

The dissertation of Gustavo Adolfo Paredes is approved and is acceptable in quality and form for publication on microfilms:

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University of California, San Diego

2009

DEDICATION

This dissertation is the result of the advice and inspiration from many people in my life. To all I dedicate this particular endeavor, that I hope lives up to the height of their expectations. I especially dedicate my work to Sofia Rios, who taught me the meaning of hard work and dedication, to Professor and Friend Enric Sala whose example inspired me to go further in life and to my nieces and nephews who are my motivation to continue working in conservation.

EPIGRAPH

“A human being is a part of the whole, called by us “universe,” a part limited in time and space. He experiences himself, his thoughts and feelings as something separate from the rest – a kind of optical delusion of his consciousness. This delusion is a kind of prison for us, restricting us to our personal decisions and to affections for a few persons nearest to us. Our task must be to free ourselves from this prison by widening our circle of compassion to embrace all living creatures and the whole nature in his beauty.”

Albert Einstein

The second angel sounded his trumpet, and something like a huge mountain, all ablaze, was thrown into the sea. A third of the sea turned into blood, a third of the living creatures in the sea died, and a third of the ships were destroyed.

Revelation 8:8-9

The second angel poured out his bowl on the sea, and it turned into blood like that of a dead man, and every living thing in the sea died.

Revelation 16:3

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FIELDS OF STUDY

Marine Ecology, Conservation biology, and Sustainable fisheries.

ABSTRACT OF THE DISSERTATION

Degradation and recovery of Caribbean coral reefs

by

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Doctor of Philosophy in Marine Biology

University of California, San Diego, 2009

Professor Enric Sala, Chair

Professor Jeremy Jackson, Co-Chair

Coral reef ecosystems worldwide have been seriously impacted by human activities. The current deteriorated state of coral reef communities is the result of a long history of exploitation. The scientific community has recognized the extent of degradation, its consequences, and how little we have done to avoid further degradation only in the last two decades. Marine reserves are one of the main conservation actions that could help to reduce the impacts of human activities on the ecosystem, particularly those associated with fishing. However, in the Caribbean, full enforcement of protection only occurs in a handful of marine reserves. Positive changes in coral reef communities due to protection have been well documented, but they are mainly restricted to fish assemblages (i.e. increase of fish biomass). Yet, the effects of protection throughout the entire community are little known. In this dissertation I provide a quantitative description of the recent ecological trajectory of coral reef degradation across the Caribbean region.

Also, I assess the current conservation status of Caribbean reefs and the recovery of the community within marine reserves.

My results show that the response to protection is variable and depends on local conditions at the time of protection, the degree of enforcement, and the characteristics of the marine reserves (e.g., size). An increase of fish biomass inside reserves was generally associated with increased herbivory and decreased macroalgal abundance. However, corals did not exhibit any clear response to protection. Moreover, my results show that partial protection and/or poor enforcement could be counterproductive and have effects on the reef community that are worse than no protection at all. Fish diversity was related to the gradient of fish biomass in a non-linear way. Maximum fish diversity occurred at 200 g of fish m^{-2}. However, there was a decline in fish diversity above 300 g m^{-2}, which indicates an intermediate disturbance due to increased predator abundance.

Most Caribbean reef sites are in a serious state of degradation. My results indicate that the use of large and truly enforced marine reserves ensures the recovery of fish assemblages, but may be insufficient to enhance coral recovery. To enhance community-wide recovery and to increase the resilience of the ecosystem we need further conservation efforts, such as more and larger marine reserves, improved fisheries regulations and pollution control outside the reserves. Only with complementary measures at appropriate scales will we be able to enhance the recovery of the benthic communities to build resilience against global impacts such as climate change.

CHAPTER I

INTRODUCTION TO THE DISSERTATION

Ever since J. D. Watson published the *Double Helix*, it has become acceptable to admit how science is really done. In my case, I started out reconstructing the history of human impacts on the marine environment of the Mesoamerican Reef, from the first written records of humans inhabiting the region, the Mayas, around 300 B.C., to the present (Pandolfi et al 2001, see Appendix I). The Mesoamerican Reef is an 800-km coastal strip—roughly 400 km of which is coral reef—stretching from Isla Contoy, Mexico, in the north to Roatan Island, Honduras in the south. In this region the Maya people and other indigenous cultures thrived over hundreds of years. The inland and coastal communities found marine resources useful for both food and multiple secondary purposes as early as 8,000 B.C. (Cooke 1998). The size of the Maya population and evidence of use indicate considerable exploitation of coastal resources. Early civilizations had a substantial impact in the coral reef communities, although the nature of early exploitation and technological limitations allowed for maintaining multiple fisheries for hundreds of years according to the archeological records (Hamblin 1984). This is in contrast to modern commercial fisheries that have declined in only a few decades of open access and intensive exploitation.

The historical analysis provided a qualitative baseline for the ecological study of Caribean reefs, coral reefs monitoring, the effectiveness of marine protected areas. It also suggested that the Mesoamerican barrier reef was relatively unspoiled compared to places like Jamaica. To evaluate this statement I made two field trips to Belize where discovered that the communities of the coral reefs were not very different from that described from Jamaica. What is astonishing is that for no reef in the Caribbean is there a complete quantitative description of the changes that have occurred in the coral reef ecosystem over recent years. However, recent meta-analysis and my work presented in Chapter II confirm the generalized degradation of the Caribbean coral reefs (Gardner et al 2003, Cote et al 2005).

The wide degradation of Caribbean Reefs raised the question of whether there is anything practical that can be done to stop and reverse the damage, and weather the conservation efforts through MPAs can be truly effective for their recovery. Therefore, I decided on a first-hand study of MPAs to assess how well and how rapidly they might improve the health of degraded marine communities within a single biogeographic region. In the Caribbean 21% of coral reefs are inside MPAs, but only 0.5% of coral reefs are within truly protected marine reserves (Mora et al 2006). Therefore the rarity of truly protected marine reserves (hereafter marine reserves) was the first challenge for choosing the right survey sites for my study.

I initially focused on the twenty MPAs scattered along the Mesoamerican reef, and found that very few of them were both effectively protected (one of the themes running through this thesis will be consequences of ineffective MPAs) and accessible for intensive field work. My initial field research was carried out in three adequately enforced MPAs (no-take reserves or marine reserves). Two were in Belize (Glover’s Reef and Ambergris Caye) and one in Mexico (Isla Cozumel). Using SCUBA and visual census techniques I conducted quantitative surveys of the reef communities including fishes, macroalgae, corals and other benthic invertebrates in several sites inside and outside this marine reserves. I found initial evidence of positive impacts of the marine reserves upon the coral reef communities (Chapter III), but there were also substantial differences across community components at the local scale. Therefore, I needed to increase the number of replicates (namely MPAs) in my study to search for broader generalities. I had already looked at all three of the effective MPAs on the Mesoamerican reef, so it was necessary to go farther afield. Clearly, any further MPAs for my study had to be effectively protected marine reserves. Nevertheless, the degree of protection was not always easy to determine from a distance, because there is a lot of misinformation on MPA reports and publicity. I subsequently determined the best possibilities and selected three sites in the lower keys of Florida (Western Sambos, Sand Keys, and Looe Key), two sites in Cuba (Jardines de la Reina and Canarreos), and one site in Jamaica (Montego Bay). Other marine reserves in the region are also important but less accessible.

Previous to this work there have only been assessments for populations or functional groups (i.e. corals) to test the effects of reserves (Marks 2005, Linton and Fisher 2003). In this dissertation I include a community-wide assessment of both benthic and fish components. The field work was carried out with Marah J. Hardt and Enric Sala over two years.

Chapter II presents a Caribbean-wide meta-analysis of the recent degradation of coral reef communities. The time span is largely for the last three decades, for which more quantitative ecological data exists. A similar but less detailed meta-analysis of the recent changes in the Caribbean coral community was published by Gardner et al (2003). I compiled all quantitative ecological data published over the last few decades to assess changes in abundance of corals, fish and other major ecosystem components on

Caribbean coral reefs. In particular, I looked at the changes in abundance throughout time of the most frequently studied community components (fishes, corals, sea urchins and macroalgae). Additionally, I addressed the effects of anthropogenic drivers in the abundance of these reef components, and analyzed the recent collapse of Caribbean reefs. My results show a synchronous decline in abundance of coral, sea urchins and fishes. By 1983/4 when the sea urchin *D. antillarum* mass mortality took place, fishes and corals were already in decline.

The declines observed were correlated with increases in the intensity of human impacts in the Caribbean region. This has been a period of rapidly increasing human population throughout the Caribbean compared to rates previous to the middle of the twentieth century (Fig. I.1).

With increased population size, human population associated stressors obviously increased in number and intensity (Sandin et al 2008). It is also possible that hurricane frequency and increased sea surface temperature in the Caribbean are also a response of human induced global climate change (Hughes et al 2003, Solomon et al 2007). Therefore human population is the main forcing function for most of the stressors that have impacted marine environments more significantly in the last century. Reliable data on human stressors and its effects on marine communities are not 100% conclusive, although the single variable that has dramatically changed and is linked to multiple stressors is undeniable population size.

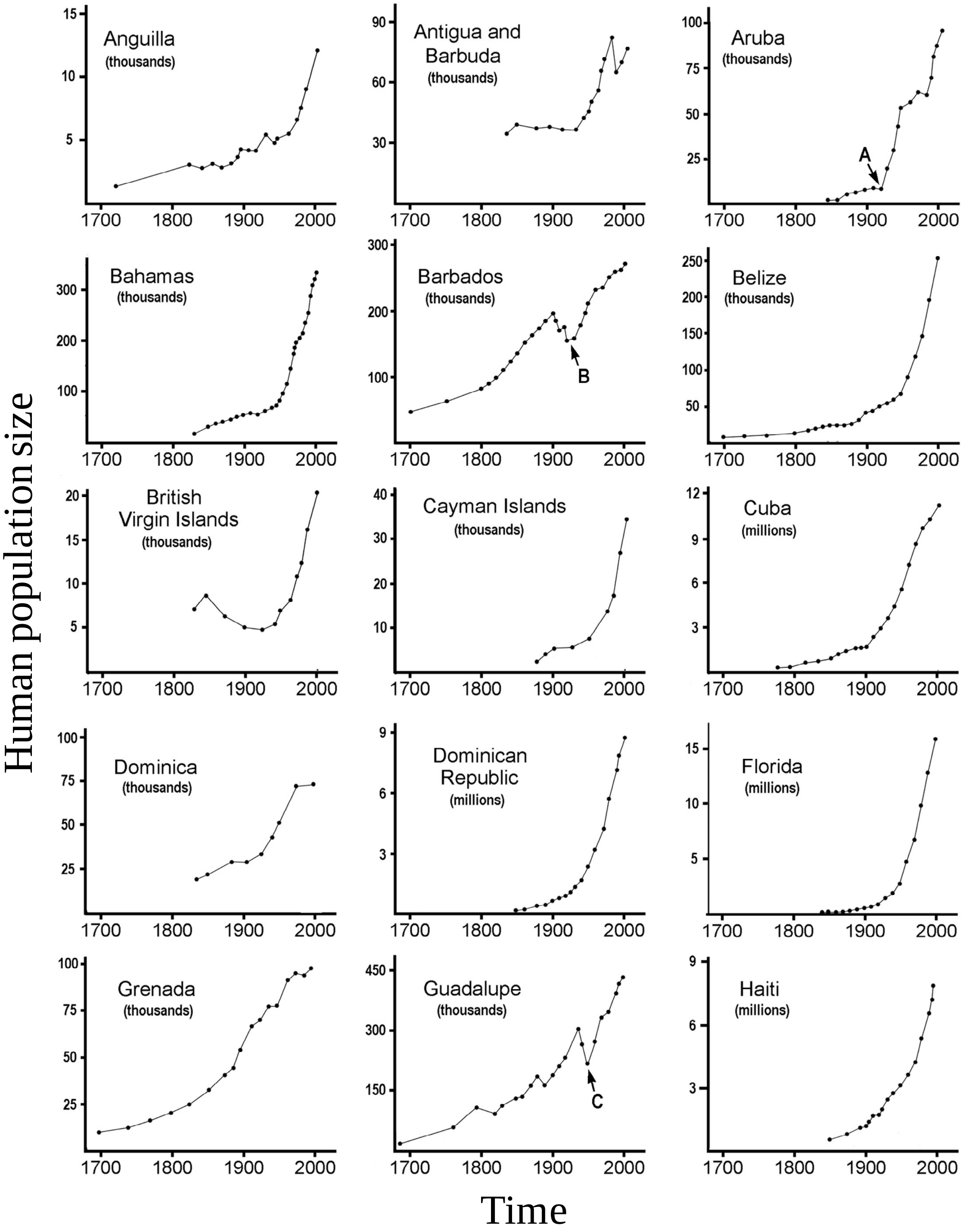
My results (Appendix I and Chapter II) support the notion that the understanding of the ecology of Caribbean coral reefs suffers from a shifted baseline (Jackson 1997, Jackson et al 2001). Most studies reviewed in my meta-analysis are small scale (10-100s meters) and community descriptions are characterized by the absence of large predators. More commonly predators are small groupers (*Epinephelus* spp.). By the time modern coral reef descriptions were published the communities had already undergone a great deal of deterioration (Jackson et al 2001).

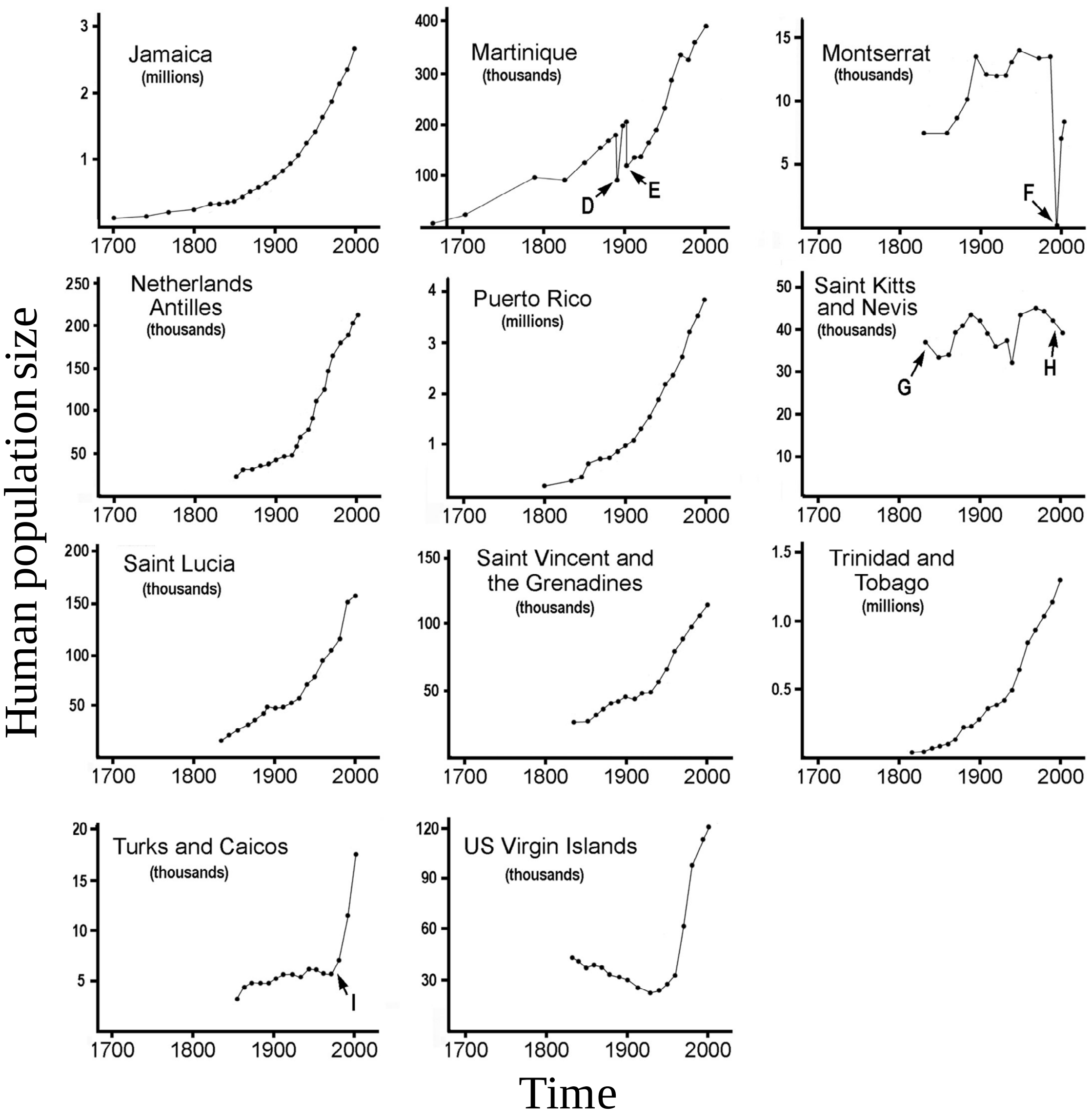
Data on the recovery of Caribbean coral reef communities is scarce and fragmented, both in space and time. Chapter II presents the results of a regional assessment of the state of these ecosystems to test the effectiveness of MPAs in restoring Caribbean coral reef communities based on my quantitative surveys. I particularly address the question of whether and how the prohibition of fishing helps the recovery of reef assemblages. I found that long-term protection within large marine reserves provides the greatest positive impact in the recovery of reef communities, but this finding is mostly limited to reef fishes. I also present evidence that ineffective protection would be more deleterious to the reef community than no protection at all.

Chapter IV presents a more detailed analysis of changes in the Caribbean communities due to protection, with special emphasis on fish diversity patterns. I used the species area relationship (SAR) to analyze changes in diversity of fish between protected and unprotected reef sites across the Caribbean. The model that best describes the patterns of fish diversity in my data was originally developed by Lomolino (2000). The model describes an asymptotic behavior of fish diversity. However, previous studies (10s-100s m^2) show a linear species-area relationship. My results indicate that at the regional scale (100s-1000s m^2) marine reserves have a greater rate of species accumulation per unit area, and a greater maximum number of species. Unprotected marine reserves and non-protected reefs did not show differences in the diversity patterns. At the local scale (reef site), the effect of protection upon fish diversity did not showed a clear pattern. My results also show that fish diversity appears to be negatively correlated to fishing pressure, although the relationship between fishing and diversity is clearly non linear. Additionally, the abundance of the benthic community components is loosely correlated to fish diversity. Marine reserves have a clear positive effect upon the abundance, biomass and diversity of fish community, but the link between benthic and fish communities requires a more detailed analysis.

I conclude in Chapter V with a discussion of the effectiveness of MPAs. The overall conclusion is that, MPAs can substantially reverse community degradation, but only when the middle letter “P” is a reality. I discuss how a MPA that is in truth a MNPA (Marine non-Protected Reserve) can have an overall negative effect. My final goal was to conduct a more comprehensive assessment of the community while moving the discussions toward restoration using MPAs and not simply descriptive studies. The challenges ahead for coral reef researchers are to provide the necessary science to elaborate regional policies for the exploitation and restoration of Caribbean coral reefs.

Figure I.1. Fluctuations in the human population over the last three centuries in the Caribbean region (data from http://www.populstat.info/populhome.html). Belize is the only country along the Mesoamerican reef that has a completely Caribbean shoreline, so the remaining Central American countries are omitted. Population data are also given for Florida (not part of the Caribbean in the strict sense) because parts of my dissertation studies were conducted there. Some interesting features in the growth curves are indicated by lettered arrows. **A)** shows the population spurt triggered by the discovery of oil in Aruba in 1929. **B)** indicates a period of extensive emigration from Barbados due to economic problems and labor unrest. **C)** indicates a surge of emigration from Guadaloupe to France, when the former was consolidated with the latter country in 1956. **D)** shows emigration from Martinique after much of one of its major cities, Fort-de-France, was destroyed by fire in 1890. **E)** shows the actual loss of about 30,000 lives when Mount Pelée erupted in 1902, completely destroying the city of Saint-Pierre. **F)** shows the complete evacuation of Montserrat due to a volcanic eruption there (only nine people were actually killed by the volcano). **G)** shows that the population of Saint Kitts and Nevis started out high, mainly because these are among the very first Caribbean islands colonized by Europeans. **H)** indicates emigration from the same island due to a devastating hurricane in 1998. **I)** indicates the population spurt in the Turks and Caicos that was triggered by the opening of a ClubMed there.


Human population size
Anguilla
(thousands)
15
10
5
Antigua and Barbuda
(thousands)
90
60
30
Aruba
(thousands)
100
75
50
25
A
Bahamas
(thousands)
300
200
100
Barbados
(thousands)
300
200
100
B
Belize
(thousands)
250
200
150
100
50
British Virgin Islands
(thousands)
20
15
10
5
Cayman Islands
(thousands)
40
30
20
10
Cuba
(millions)
12
9
6
3
Dominica
(thousands)
100
75
50
25
Dominican Republic
(millions)
9
6
3
Florida
(millions)
15
10
5
Grenada
(thousands)
100
75
50
25
Guadalupe
(thousands)
450
300
150
C
Haiti
(millions)
9
6
3
1700
1800
1900
2000
Time



Continuation Figure I.1 Fluctuations in the human population

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CHAPTER II

LONG-TERM ECOLOGICAL TRAJECTORY OF CARIBBEAN CORAL REEF COMMUNITIES

Abstract

I report Caribbean-wide coral reef community degradation over the last three decades using published quantitative data for major groups of reef organisms. Corals declined by 66%, and the sea urchin *Diadema antillarum* by 97%, whereas macro-algae increased by 367%, supporting previous findings. I also showed that reef fishes declined by 55% in the last 30 years. The trajectory of ecosystem change was initially driven by massive coral decline since 1978 concurrent with macro-algal increase. However, the major decline in fish abundance was delayed by one decade after the onset of the decline in coral cover. The trajectory of degradation was correlated with anthropogenic factors, among which human population density alone explains 61% of the variability. If human population density is excluded from the analysis, the major causal factors are still anthropogenic in nature. My results indicate that the combined effect of anthropogenic and environmental variables and the loss of the biogenic habitat may create a feedback loop inhibiting the recovery of Caribbean coral reefs.

Introduction

Caribbean coral reefs have suffered dramatic changes over historical time (Pandolfi et al. 2003). Large predators and herbivores such as the monk seal and green turtles are extinct or ecologically extinct due to overexploitation (Jackson 1997, McClenachan et al. 2006). Coral cover declined from 50% to 10% on average in the last decades (Gardner et al. 2003), and algal cover increased from 2% to 40% (Côté et al. 2005). In addition, the sea urchin *Diadema antillarum* lost 98% of its numbers in 1983 across the Caribbean (Lessios 1988). However, there are no published studies on the regional changes in reef fish abundance. Although we are aware of the historical trajectory of degradation of Caribbean reefs (Pandolfi et al. 2003) and there are excellent examples of local community changes (e.g., Hughes 1994, McClanahan & Muthiga 1998), we still do not have a description of the region-wide changes in the trajectory of the overall coral reef community that occurred during the last three decades.

The factors that caused the degradation of Caribbean reefs include overfishing, pollution, disease, and warming events (Lessios 1988, Knowlton et al 1990, Bythell and Sheppard 1993, Jackson et al 2001, Hughes et al 2003, McClanahan et al 2003, Gardner et al 2005). There has been a lengthy debate on what were the most important factors in explaining the changes (Precht and Aronson 1997, Knowlton 2001, Hughes at al 2003b). Although it is evident that all factors contribute to the problem, most studies have dealt with individual factors and taxa and only focused on part of the problem (Pandolfi et al. 2005). The importance of the different factors is likely to be context-dependent, but the relative importance of the main drivers at the regional scale has not yet been analyzed in the context of the ecosystem trajectory. Here I present a Caribbean-wide analysis of the coral reef ecosystem trajectory over the last three decades using published quantitative studies on the abundance of major reef organisms. In addition, I analyze the relationship between potential drivers of change (anthropogenic and environmental variables) and the ecosystem trajectory.

Materials and methods

Data collection and selection criteria

I conducted an extensive review of published literature, on line reports, and electronic databases to compile abundance data on macro-algae, sponges, gorgonians, mollusks, corals, sea urchins, and fishes on Caribbean coral reef habitats (fore and patch reefs). I chose to study only cover of coral and macro-algae, and abundance of fish and the sea urchin *Diadema antillarum* on fore reefs (1-35 m), because data for these four groups of organisms in this habitat were the most abundant across sites and years. Biomass is a better indicator of fish population dynamics than density (Sandin & Pacala 2005); however, most studies reported only fish density. In addition, information for other species/groups was scarce for most years and across the Caribbean. Patch reefs did not yield enough data to repeat the analysis throughout time and across all ecosystem groups. Shallow and deep reefs showed similar patterns of abundance through time, so I combined all fore reef data. The studies selected for analysis were given the same weight due to a generalized absence of measures of variance across studies. I selected only studies that: 1) mentioned the year when surveys were carried out, 2) described the methodology used to collect data, 3) mentioned the habitat and depth where data were collected, 4) reported the number of samples collected (*n*), and 5) gave the mean abundance per group. This resulted in more than 400 initial studies containing abundance data from Caribbean coral reefs, although only 155 publications were selected (Fig. II.1). Abundance data were obtained from digitized graphs when studies did not report summary tables, and in some cases the authors were contacted for complementary information. Some data were obtained directly from public coral reef databases (e.g., Atlantic and Gulf Rapid Reef Assessment, AGRRA). All data were standardized to density (individuals m^{-2}, for fishes and sea urchins) or to percent cover (for corals and fleshy macro-algae). The study on long-term decline of coral communities (Gardner et al. 2003) preceding this study included a total of 65 studies. Their selection criterion was limited to those studies with two or more years of observations. In this study the selection criteria allowed me to include more studies and examine four distinct ecosystem groups. Data were collected from 90, 27, 57 and 57 studies for coral, fishes, *D. antillarum,* and macro-algae respectively (Appendix II).

Data analysis

In order to explore potential bias of the data through time I analyzed the patterns of mean and median abundance, and habitat depth and type (fore or patch). Abundance trends of species groups were similar using the mean or the median of each year (t-test; corals $p = 0.66$, fishes $p = 0.36$, *D. antillarum* $p = 0.76$, macroalgae $p = 0.06$), indicating that dispersion of the data did not significantly influence the results. I examined the temporal trends in mean abundance of each group of organisms in relation to habitat and depth (shallow < 9 m and deep > 9 m respectively). For corals and *D. antillarum*, the yearly mean abundance was not significantly different between shallow and deep reefs (t-test; $p = 0.33$ and $p = 0.12$, respectively) and the trend was also similar. Annual mean cover of macroalgae was different between depths (t-test, $p < 0.01$), however the temporal trend of increase was similar. Fish abundance data was incomplete for some years for shallow reefs, but mean abundance was similar among depths for those years where data were available (t-test, $p= 0.8$). I thus combined all depths in the analysis.

I obtained over 6,000 abundance records for the above four species groups. In order to analyze the trajectories of abundance change I calculated the 3-year simple moving average (SMA) of the abundance trends of each species group between 1973 and 2005. The last 2 years (2004-2005) of the SMA trend were eliminated to avoid including zeros. To test for differences in abundance over time I performed one-way ANOVAs for each group.

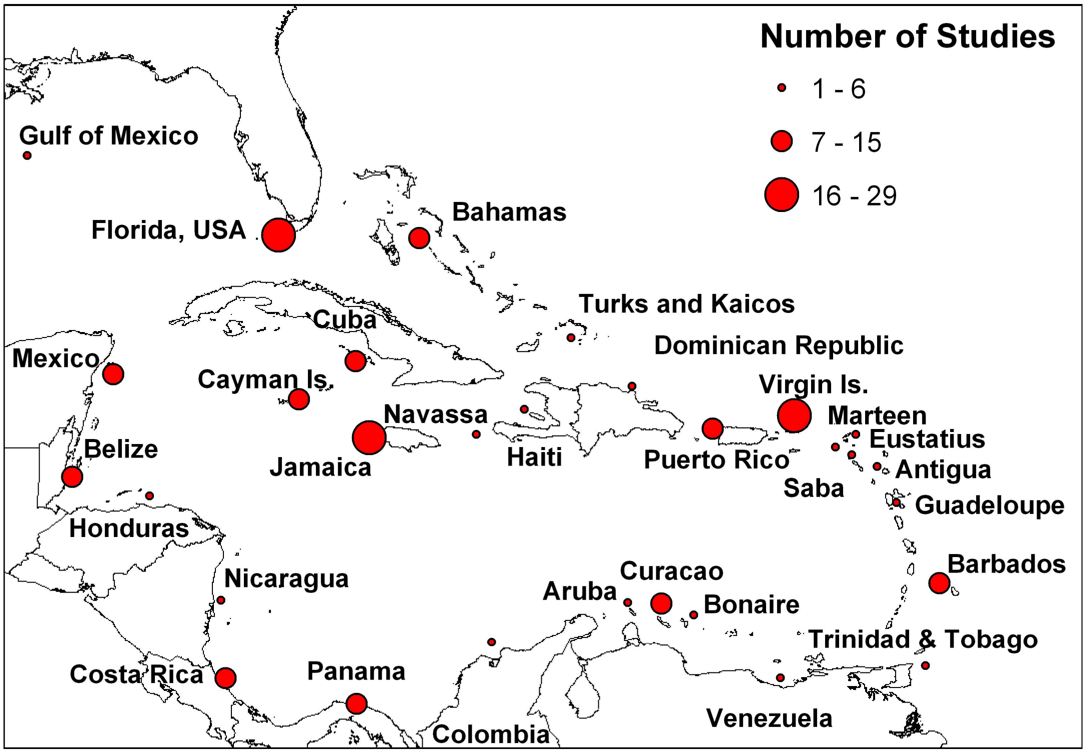

Figure II.1 Location of coral reef studies in the scientific literature (1973-2005). Circle size indicates the approximate number of studies per country, but does not depict the actual location of survey sites. Sometimes, studies reported abundances for more than one reef site, year or species group.

I performed a principal components analysis (PCA) to determine the trajectory of community change through time using the moving average of the four species groups. Species groups were the variables and years were the sample cases. I used a linear unconstrained ordination (PCA) given the linearity of the abundance data (gradient length = 1.2 S.D.) (Leps and Smilauer 1999, Braak and Smilauer 2002). I square root-transformed the density of fishes and *D. antillarum* to increase linearity of the data, and converted the species variables into a correlation matrix (centering and standardization, mean = 0 and variance = 1 respectively) to eliminate differences due to variable units (percent cover and density). I considered that changes in groups of organisms (abundance) and through samples (years) were equally important for the interpretation of results (symmetric scaling). Additionally, species scores were divided by the standard deviation to better represent the correlation of the species vectors to the principal components. I conducted this analysis using CANOCO V.4.5 (Braak and Smilauer 2002). Ordination results were plotted using CanoDraw 4.0.

To analyze the relationship between the changes in the Caribbean coral reef ecosystem and anthropogenic and environmental variables I conducted a direct gradient analysis (redundancy analysis, RDA) (Leps and Smilauer 1999, Braak and Smilauer 2002). I used direct gradient analysis instead of individual generalized linear (GLM) or additive models (GAM) for each variable because there is a great deal of interaction between the groups of organisms used in this study, and a multivariate analysis to explore the community trajectory was more appropriate. The RDA was carried out using the ecological data included in the PCA and a spectrum of explanatory variables of environmental and anthropogenic nature obtained from multiple databases (U.S. Census 2004, INEGI 2003, FAO 2005, NASA 2005, NOAA 2005, UK Met Office Historical SST, UNEP 2005). Drivers were selected given the availability and completeness of the data throughout time, across Caribbean countries, and their link to the health of ecosystems. These drivers included parameters for water quality, climate, and exploitation (see results). Human population size in the Caribbean increased over time and was strongly correlated to most anthropogenic drivers of change (see results). I could thus expect significant correlations between human population size and any other variables with a clear trend of increase or decrease, thus questioning the validity of human population size as an appropriate explanatory variable in the analysis. However, population size encapsulates the whole suite of anthropogenic activities, including those for which we do not have time series (e.g., fishing effort). Furthermore, we do not have good spatial information for some key drivers such as fishing. Therefore I decided to include human population size and the fraction of the other anthropogenic variables that explain the variance that is not explained by human population size alone. In order to do that I first performed a RDA with all anthropogenic variables that were correlated, and ranked the variables based on the proportion of the variance each explained, human population size being the most important. I then conducted a sequential regression analysis: I regressed human population size against the second most important variable and obtained the residuals for the second variable; then I regressed human population size and the residual of the second variable against the third most important variable, and obtained the residual of the third variable; and so on. I used human population size and the residuals for the other variables in the final RDA. In order to select the variables that were more related to the changes in the ecosystem I conducted a Monte-Carlo permutation test (n = 5000) with forward selection. The same analytical procedure was repeated without taking into account human population size at all in order to assess the effect of this variable upon the analysis.

Strengths and weaknesses of the analysis

Data across the studies included in this meta-analysis were collected using several different methodologies, presented in different formats, and to some degree they may be affected by observer bias. This problem can be addressed by carefully reviewing the methodologies within each study and by standardizing the data. I assumed the training of data collectors was relatively similar across the studies and eliminated only those where data appeared clearly as extreme outliers or were hard to corroborate. Additionally, some studies reported incomplete data or in graph format only. In these cases we contacted the authors and/or quantitative data were drawn from digitized graphs. A tendency to publish only significant results in main scientific journals affects the outcome of most meta-analysis. I addressed this potential bias by including some grey literature (unpublished reports & conference proceedings) and public databases (e.g., AGRRA). The main strength of my approach is the wide geographic and temporal scale of studies that allowed me to extract a general trend that is region-wide and that incorporates spatial variability in a resolved time series.

Results

Coral cover, and density of fish and *D. antillarum* greatly declined whereas macro-algal cover increased strikingly throughout the Caribbean during the last three decades (Fig. II.2). Coral cover declined significantly from an overall regional mean of 53% in mid 1970s to 18% in 2004 (ANOVA, F=13.03, $p < 0.01$) (Fig. II.2a), as previously reported (Gardner et al. 2003). Regional mean abundance of *D. antillarum* declined from 6.8 individuals m^{-2} in 1973 to nearly zero after the 1983 region-wide die-off (F=29.27, $p < 0.01$) (Fig. II.2b). Regional mean macro-algal cover increased from nearly zero in the late 1970s to 50% after the *D. antillarum* die-off, and has not decreased since (F=10.34, $p < 0.01$) (Fig. II.2c). Reef fish density decreased gradually from 1.8 individuals m^{-2} in the late 1970s to 0.6 individuals m^{-2} in 2005 (F=14.52, $p < 0.01$) (Fig. II.2d). The marked fish decline started after 1987, a decade after the beginning of the decline in coral cover (Piecewise linear regression, R^2=93.8). Despite the geographic variability of study locations, our results show consistent and synchronous dynamics throughout the region.

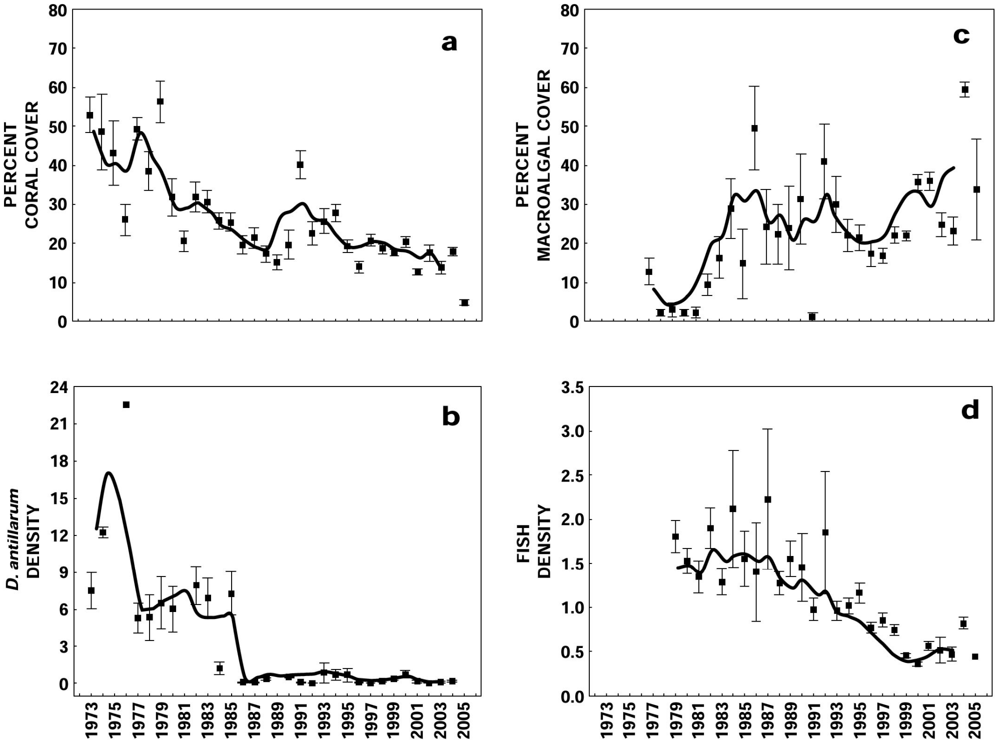

Figure II.2. Changes in the mean abundance throughout time of major ecosystem components (squares, ±S.E.): a) Percent coral cover, b) percent macro-algal cover, c) *D. antillarum* density (individuals m^{-2}), and d) fish density (individuals m^{-2}). The smoothed line indicates the SMA (see methods).

The PCA revealed that Caribbean coral reefs moved gradually away from a coral-dominated state towards domination by macro-algae between 1978 and 1986 (Fig. II.3). This ecosystem change occurred orthogonally to fish abundance. However, from 1986 to the late 1990s there was a marked decline in fish abundance. Finally, from 1997 to 2003 there was an additional departure towards an algal-dominated state. The first principal component (PC1), which was highly correlated to coral and sea urchin abundance (r^2 =

0.82 and $r^2 = 0.76$ respectively, $p < 0.05$), explained 71.6% of the variability of the data, and PC2 explained 15.5%.

Human population size, the average anomaly of sea surface temperature during the hottest months of the year (August, September and October), and fertilizer consumption explained 61, 13, and 8%, respectively, of the overall variability of the ecosystem trajectory over time (Table II.1- II.2). Human population and the temperature anomaly were positively related with the main trajectory of ecosystem change after 1984, while fertilizer use was negatively related.

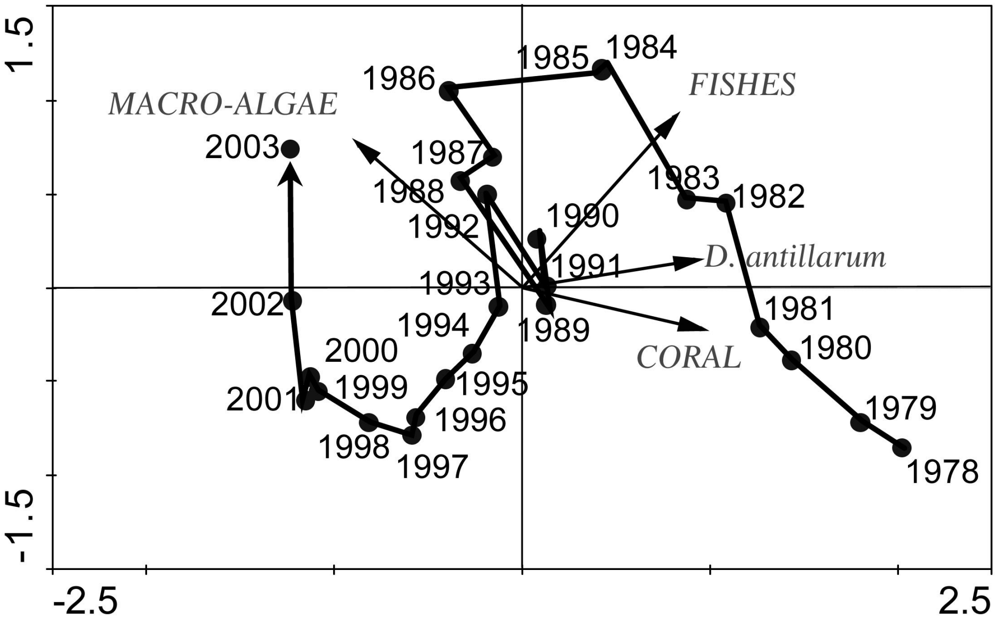

Figure II.3 PCA analysis showing the changes of the Caribbean reef community from 1978 to 2003. The position of each year in the multivariate space is determined by the abundance of all ecosystem groups (arrows). The length and position of arrows indicates the correlation of each species to the principal components. Each principal component is the linear combination that best represents the variability in the data. PC1 explains 71.6% of variability and PC2 15.5%. PC1 can be interpreted as an index of ecosystem degradation.

To prevent a spurious correlation with human population, I ran the same analysis without human population size. Results indicate that other anthropogenic variables highly correlated with human population size explain the variability of the trajectory of changes in the community. In this case, organic water pollutants (BOD) explained 59% of the trajectory variability followed by the Atlantic Southern Oscillation (ASO) and fertilizer consumption with 12% and 9% respectively.

Table II.1. Results of multivariate analysis of the changes of the Caribbean reefs. a) Summary of direct gradient analysis (RDA), p-value corresponds to Monte-Carlo probability for significance of the sum of all eigenvalues. b) Percent variability (PV) of ecosystem data explained by anthropogenic and environmental drivers, and statistical significance using forward selection and Monte-Carlo permutation test. C) Same analysis but without human population size.

a)					
Axes	1	2	3	4	
Eigenvalues	0.674	0.156	0.039	0.033	
Species-environment correlations	0.986	0.967	0.699	0.745	
Cumulative percentage variance					
species data	67.4	83	86.9	90.3	
species-environment relation	74.6	92	96.3	100	
Sum of all eigenvalues					0.903
Significance 1st and 2nd axis					
F					29.69
p-value					0.02
b)					
DRIVER	PV	p			
Human population size	61	0.03			
Sea surface temperature anomaly	13	0.03			
Fertilizer	8	0.03			
c)					
DRIVER	PV	p			
Biological oxygen demand	59	0.04			
Sea surface temperature anomaly	12	0.01			
Fertilizer	9	0.01			

Discussion

Caribbean reef ecosystems have undergone a severe transformation in the last 30 years. My analysis indicates non-linearities and time lags that make ecosystem changes unpredictable in the short term. The reported loss of corals and their replacement by algae (Hughes 1994, Gardner et al 2003, Cote et al 2005) was accompanied by a marked decline in reef fish populations across the Caribbean that begun ten years after the onset of the decline in coral cover. My results integrate a number of databases and results across the Caribbean which confirms that this trend is region wide. The main finding of this study is the delayed decline in fish abundance following the decline in corals.

The decline in reef fish may have been due to increased fishing pressure or a delayed response to the loss of coral cover, or both. Unfortunately, there are no data on fishing effort, so that it is not possible to determine whether there was a marked regional increase in fishing pressure starting in 1987. It is unlikely that the fish decline was a delayed consequence of long-term fishing pressure, since the initial densities reported in this study reflected an already overfished ecosystem (Munro 1983, Jackson 1997, Pandolfi et al. 2003). The maximum fish densities reported here are much lower than those in marine protected areas in the Caribbean where fish populations are on a trajectory of recovery (1.8, 1.3 and 1.2 individuals per square meter for Cozumel, Florida keys, and Cuba respectively, Chapter III) (Loreto et al 2003).

The hypothesis of the delayed response of reef fishes to the loss of live coral is supported by evidence from other regions. In Papua – New Guinea, an 8-year decline (90%) in coral cover was associated with a decline in the abundance of over 75% of reef fish species (Jones et al. 2004). Moreover, 50% of the species declined to less than half of their pre-decline numbers, both inside and outside of marine reserve.

This, along with the fact that 65% of the species settle into coral preferentially, strongly indicates that the fish decline was caused by the loss of the biogenic complexity provided by the coral. Other studies have also showed that decreasing vertical complexity means lower fish abundance (e.g., Luckhurst & Luckhurst 1978, Friedlander and Parrish 1998). I hypothesize that the loss of living coral in the Caribbean has also reduced essential habitat for many reef fishes due to a reduction of vertical structure that is accelerated by bioeroders when corals are dead (Sammarco 1996 and references therein). This is the first region-wide example of a delayed decline of reef fish assemblages after the loss of biogenic structure. This delayed response is similar to the “extinction debt” described for terrestrial ecosystems, where extinction is not predicted in the short term despite a reduction of habitat below a critical threshold that makes extinction inevitable (Tilman et al. 1994). This delayed decline is particularly alarming because it suggests a positive feedback loop that inhibits the ability of the reef ecosystem to reverse its trajectory of degradation.

The causes of the degradation of Caribbean coral reefs are diverse and context-dependent, and the sequence of occurrence of disturbances determines the sequence of ecosystem changes at local scales. Nevertheless, there are overall drivers of change that can be identified at the regional scale that can produce the ecosystem trends reported in this study. Global stressors (e.g., warming) and local stressors (e.g., fishing, pollution) stressors act synergistically and both contributed to the decline of Caribbean reef ecosystems. Our analysis indicates that the growth of human population across the

Caribbean was the major driver of change. Associated with population size there are a number of local factors including fishing, pollution, and coastal development that interact to produce changes of varying magnitude in different locales (Loya and Rinkevich 1980, Jackson et al 2001, Sealey 2004), although it is not possible to determine the relative importance of each factor because of a generalized absence of spatially-explicit data. Another driver that was significantly related to the ecosystem change was summer sea surface temperature anomalies that cause coral bleaching (Brown 1997, Barton and Casey 2005, McWilliams et al 2005). Coral reefs have dealt with bleaching before human impacts. However, the impacts of warming events are likely to increase with global warming (Brown 1997). The third significant factor, fertilizer use was surprisingly negatively related to the main ecosystem trajectory after the die off of *D. antillarum* in 1984. This suggests that the reduction in the use of fertilizers in the Caribbean over the last two decades, due to a more efficient use (CEPAL 2001), did not have any significant effect in reversing the ecosystem shift.

The relative importance of the above stressors in determining the ecosystem trajectory is difficult to tease apart because some stressors act as pulse disturbances (e.g., warming events) while others are chronic (e.g., overfishing), and also because they interact and create feed-back loops. But these feedback loops may be undetectable in studies that focus on single taxa and small temporal and spatial scales. For instance, it was hypothesized that, in Jamaica, the loss of herbivorous fishes and sea urchins reduced the ability of corals to prevent overgrowth by algae once corals die (Knowlton et al 1981, Hughes et al 1987). Aronson et al. (2006) argued that corals died because of disease and bleaching and that macroalgae colonized dead corals but did not kill coral, although overgrowth indeed observed (Hughes et al 1997). Moreover, as an example of unexpected feedback loops, it has recently been shown that macroalgae release dissolved organic compounds into the water, which stimulates the growth of bacteria living on the surface of corals and causes coral disease and death (Smith et al. 2006). These interactions between global and local stressors create a feedback loop of degradation that is unnoticeable in studies without a community perspective. There is consensus, however, that the removal of algae by grazing is a necessary condition for enhancing coral recruitment (Carpenter et al 2006**).** Fishes can recover relatively quickly if fishing is prohibited (Roberts 1995, Cote et al 2001), but the recovery of the sea urchin *Diadema antillarum* is difficult to predict. In addition, we do not know whether corals, which have lower turnover rates, will be able to reverse their trajectory of decline in the face of global warming (Orr et al 2005, Newman et al 2006).

In conclusion, my results show a long-term Caribbean-wide trajectory of degradation of the coral reef ecosystem, indicating that local community shifts reported in previous small-scale studies are general, while recovery is sporadic and occurring at very small scales (Rakitin and Kramer 1996, Chiappone et al 2000, Edmunds and Carpenter 2001, Idjadi et al 2006). The underlying factors contributing to this ecosystem deterioration are multiple and synergistic, although they have a clearly anthropogenic signal (Table II.3). Because of the interactions between disturbances and the feedback loops in the ecosystem, the only way of reversing the trajectory of degradation reported here is to reduce all anthropogenic disturbances simultaneously (Pandolfi et al. 2005).

Table II.2 Regional environmental and anthropogenic variables (drivers) selected for direct gradient analysis (RDA); Caribbean human population size (P, number of individuals), total reef fish catch (C, in tons), rain precipitation (R, mm/day), Low Latitude Air Temperature Index (T), Tropical storm frequency (TSF), Summer (August to October) averaged sea surface temperature anomaly (SST), fertilizer consumption (F, tons), annual aquaculture production (AP, tons), tourist visitors (T, number of individuals) and emissions of organic water pollutants (BOD, Kg/day). NA= no data available. See methods in main text.

YR	P	C	R	T	TSF	SST	F	AP	T	BOD
1978	59567385	166883	4.17	0	12	-3.15	575850	5788.71	NA	NA
1979	61050291	165753	4.02	0.16	9	3.58	594643	4892.00	NA	NA
1980	62404592	191134	4.03	0.2	11	5.67	645317	4781.21	7337000	10856
1981	63828174	209756	4.24	0.09	12	13.32	739653	6312.21	6924000	10547
1982	65227020	208700	3.85	0.2	6	-4.87	671678	6222.57	7016000	12522
1983	66658573	173143	3.86	0.35	4	-12.64	628448	6125.00	7239000	12566
1984	68106118	181901	4.11	0.09	13	-33.58	719606	7464.43	7483000	12587
1985	69590206	177542	4.05	0.01	11	-6.46	709605	6972.57	7939000	12919
1986	71132413	175852	4.03	0.15	6	-7.37	791021	6536.21	8335000	13284
1987	72679912	180382	3.85	0.5	7	0.41	806028	6039.43	9361000	13433
1988	74182175	184083	4.23	0.28	12	-3.09	743253	5898.71	9887000	14198
1989	75808921	198605	4.19	0.04	11	6.01	827978	5843.36	10506000	14541
1990	76929049	220342	3.93	0.29	14	6.92	746894	2873.79	11326000	14465
1991	78750433	220002	3.91	0.3	8	-3.15	541700	5598.57	11373000	14656
1992	80363833	214471	3.81	0.2	7	-7.19	417195	6819.00	12095000	15353
1993	81722037	239637	3.91	0.24	8	5.90	329000	6141.36	13007000	16039
1994	83538240	270423	3.97	0.25	7	7.88	290790	5200.71	13580000	16576
1995	84569983	256227	4.05	0.38	19	27.66	415057	6085.21	14135000	17303
1996	85665382	235261	4.09	0.27	13	36.92	412391	4738.29	14528000	17885
1997	87192511	221530	3.9	0.46	8	43.38	434214	5058.14	15636000	18633
1998	88692081	221485	4.06	0.68	14	28.24	361727	4860.86	16556000	18984
1999	90193576	190561	4.32	0.16	12	17.68	335759	5155.43	16561000	NA
2000	92330413	207426	4.2	0.19	15	24.34	316428	4497.00	17369000	NA
2001	93980575	198576	4.2	0.37	15	36.15	395389	4927.29	18737000	NA

Table II.3. Test for the correlation among anthropogenic variables and population size. Data and variables keys as in table S2.

C	F	AP	T	BOD
0.575	-0.7178	-0.3609	0.9765	0.987
p=.003	p=.000	p=.083	p=.000	p=.000

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CHAPTER III

COMMUNITY RECOVERY IN CARIBBEAN MARINE PROTECTED AREAS

Abstract

I examined regional and local effects of marine protected areas on the health of Northwestern Caribbean coral reef communities over multiple spatial scales. The response to protection at the local scale (10s km) was more variable than at a regional scales (100s km). Communities within marine reserves have a more consistent response to protection than unprotected reefs. Fish biomass, abundance and average trophic level increased, as well as, intensity of herbivory through increased abundance of herbivorous fish and sea urchins, inside well protected reserves. These data suggest that increased herbivory facilitates the reduction of macroalgal biomass. However, the coral community showed a weak response and coral biomass was only slightly different between protected and unprotected reefs. This may be explained in part by the slower growth rates of corals. However, the biomass and cover of corals was lower inside poorly enforced (unprotected) marine reserves than unprotected reefs. The presence of unprotected marine reserves may bias interpretation and thwart understanding of the effects of MPAs on coral reef ecosystems in databases that do not account for differences in enforcement levels. My results indicate that the level of enforcement has significant and important consequences for recovery of coral reef systems. Only in marine reserves where protection is enforced does recovery of fish populations and sea urchins occur. While the benthos continues to remain algal-dominated, increased herbivory inside protected marine reserves likely facilitates coral recovery. However, additional management

actions such as water quality control and active restoration programs may be necessary to help shift the balance back toward coral dominance.

Introduction

Human impacts on Caribbean coral reefs have caused the historical decline of large animals such as monk seals and sea turtles (Jackson 1997; Pandolfi et al. 2003; McClenachan et al. 2006), and the more recent decline of corals and reef fishes (Hughes 1994; Gardner et al. 2003; Cote et al. 2005; Newman et al. 2006). In addition, the 1983 mass mortality of the sea urchin *Diadema antillarum* throughout the Caribbean (Lessios 1988) contributed to the overgrowth of corals by seaweed (Hughes 1994). Over the last two decades, marine protected areas (MPAs) have become common management strategies for coral reefs. The goal of MPAs is to protect current coral reef ecosystems and enhance recovery of those that are degraded (Dayton et al. 2000; Agardy et al. 2003), but the vast majority of MPAs are simply “paper reserves” with very little management or enforcement (Mora et al. 2006). Most of the few cases where well-enforced laws have been maintained, the reserves are small in size, typically less than 1,200 hectares (Appeldorn & Lindeman 2003).

No pristine coral reefs exist in the Caribbean against which we can compare the health of impacted reefs (Jackson et al. 2001; Pandolfi et al. 2003; Pandolfi & Jackson 2006). Without such ecological baselines, well-enforced marine reserves may be our best guidelines for what constitutes a relatively healthy coral reef, and for informing management for ecosystem recovery (Pandolfi et al. 2005). In general, the efficacy of marine reserves is evaluated based on the changes in fish assemblages after protection (Russ & Alcala 1996). Most studies conclude that over time marine reserves help increase the abundance, biomass, size and diversity of fishes (Halpern & Warner 2002; Halpern 2003). Yet, the overarching management goal of full coral reef community recovery, including the benthos, within Caribbean marine reserves has not been met (Newman et al. 2006). Does this mean marine reserves are not working?

The challenge is to accurately evaluate the effectiveness of marine reserves as a coral reef management strategy. The documented increase in fish abundances inside reserves may have effects that propagate across the community, and may facilitate coral recovery (Bascompte et al. 2005; Mumby et al. 2007; McClanahan et al. 2007). However few studies have investigated the community-wide effects of marine reserves (Williams & Polunin 2000), and typically these studies focus on a single a reserve (e.g. Roberts 1995; Chapman & Kramer 1999; McClanahan et al. 2001; among many others). Therefore, we lack any general comparison of how reserves function across the Caribbean to promote coral reef ecosystem health. An analysis of major ecosystem components in multiple reserves across an appropriately large spatial scale serves to meet this challenge and will provide relevant evaluations of the effectiveness of marine reserves as a management strategy.

The level of enforcement within a marine reserve is a critical component of reserve management (Palumbi 2004; Pandofli et al. 2005), and one that may confound the effect of marine reserves on coral reef communities (Cote et al. 2001; Agardy et al. 2003; Bellwood et al. 2004). My goal was to determine whether well-enforced no-take marine reserves enhance the recovery of the major ecosystem components of Caribbean coral reefs, as opposed to marine reserves with poor enforcement, marine protected areas where fishing is allowed, and unprotected areas. I surveyed 11 marine protected areas and nearby unprotected areas across the Caribbean, ranging in protection level, age and size.

Materials and Methods

Study area and protection levels

I studied the coral reef communities at 5 and 15 meters within 11 marine reserves and their adjacent unprotected areas in the Caribbean (Fig. III.1). I surveyed both depths at each site wherever there was comparable habitat. For detailed attributes of the reserves and survey effort see table III.1 and for locations see figure III.1. I assessed the marine reserve attributes and the degree of enforcement from the literature, personal interviews with park personnel, and during the surveys. Although most reserves investigated in this study were designated as no-take, and in theory do not permit any fishing activity, in some cases illegal fishing was known to exist. Therefore I conducted two types of analysis: 1) a comparison of each marine protected area to its nearby unprotected reefs, and 2) a large-scale comparison between no-protected reefs (NP), protected marine reserves (PMR), and unprotected marine reserves (UMR). UMR were defined as a reef where fishing is partially allowed, such as Sand Keys and Rock Keys (Keller & Donahue 2003), or where poaching occurs such as Montego Bay and Canarreos (A. Ross pers. comm., personal observations, and Pina unpublished data, respectively). The greatest level of enforcement was observed in Jardines de la Reina (Cuba), Cozumel and the Florida Keys (Western Sambos and Looe Keys Sanctuary Preservation Areas), and these reserves were thus treated as protected marine reserves (PMR). I treated all other reef sites outside marine protected areas as non-protected reefs (NP).

Data collection

I carried out underwater fish surveys using a standard visual belt transect method

(Brock 1954, 1982). I conducted censuses in daylight between 10am and 4pm. For each replicate a diver swam a 50-meter transect, counting all fishes belonging to all species and estimating their size (± 5 cm) within 2.5m to either side of the center line (250 m^2 transect area). Swimming duration varied from 15-20 minutes, depending on fish abundance. I recorded species larger than 20 cm (total length) on an initial swim, and then smaller, more cryptic species on a second swim of the transect line.

I recorded the percent cover of benthic organisms using a standard point-intercept method with intervals of 20 cm along replicate 30 m-long transects. The 20 cm interval was determined a priori by calculating species diversity (Shannon-Wiener index, H’) and species richness curves for different intervals (1 cm, 5 cm, 10 cm, 20 cm, 25 cm, 30 cm, 50 cm) along transects of different length, and determining the minimum length of the transect and number of points needed for saturation of the curves. Overlapping of organisms were also recorded to account for the three-dimensional nature of the reef community (thus the total point counts for each transect varied depending on the degree of overlap among species). For the fleshy algae with vertical structure (e.g., *Sargassum*, *Dictyota*, *Stypopodium*), I also measured the height. I identified all scleractinian corals to species, and algae and octocorals to genus. Other non-coral sessile invertebrates were recorded using higher taxonomic categories (for detailed species list see Appendix III). I surveyed the species number, abundance and size of sea urchins along replicate 30 x 1m transects.

I also surveyed several reef sites (1-3) inside reserves when possible (Table III.1). A variable number of replicate transects for fish and benthic invertebrates (5 to 7) were conducted within each reef site (reserves and unprotected reefs). Due to logistical constraints, all sites were not surveyed simultaneously. All regions were surveyed within the same month, but different regions were surveyed during different months from November 2003 to August 2005.

I carried out estimates of biomass (g m^{-2}) using allometric conversions from the literature for fish (Froese & Pauly 2007), and from recent estimations of invertebrate and macroalgal biomass per unit surface area (Newman et al. 2006, Hardt unpublished). I adjusted the conversions for fleshy algal biomass using the height of the algal cover recorded on each transect. When conversion parameter values were unavailable for individual species, I used the parameters from a congeneric species with similar shape and maximum total length.

Data analysis

I focused the analysis on four community components: fish, corals, macroalgae (fleshy, turf, and crustose coralline algae), and sea urchins. Fleshy macroalgae and turf were treated as a single category, hereafter macroalgae. Species composition for each of the functional groups was analyzed as in Newman et al. (2006). This study is different from Newman et al (2006) in that I particularly address the question of marine reserve effects using a greater number of reef sites, multiple comparisons at the local and regional level, and the use of both abundance and biomass for the analysis and discussion of results. For each functional group I analyzed the differences in cover, density and biomass (g m^{-2}) between reserves and unprotected reefs and also among treatments (NP, UMR and PMR) at both 5 and 15 meters. Then, I assessed the statistical differences among reserves and unprotected reefs on a case by case basis using non-parametric

Mann-Whitney U-tests. Additionally, to compare between protection treatments I used the non-parametric Kruskal-Wallis analysis of variance by ranks with detailed comparisons for significant differences among treatments, when results were statistically significant

I conducted all treatment comparisons statistics after bootstrap re-sampling of the data (n=1000) to account for the unequal sampling size among treatments. Bootstrap analysis was facilitated using Microsoft office excel add-in resample routines (Bruce 2003).

In addition, I determined differences in the trophic structure of the fish assemblages (i.e. the complexity of the fish food web) across treatments using the marine trophic index (MTI, Pauly & Watson 2005). I calculated MTI for each location using the estimated species biomass from visual censuses and the information on the diet of fishes from the literature (Froese & Pauly 2007). That is, I calculated the MTI following the same formula as in calculating the average trophic level but after removing all the individuals from trophic levels below 3.25. The MTI has advantages that overcome some criticized aspects of the average trophic level analysis (Pauly & Watson 2005). I considered that this analysis was useful to evaluate the effectiveness of marine reserves in addition to analysis of the total biomass of fish because it provided a measure of the maturity (i.e. dominated by top predators; Friedlander & DeMartini 2002) of the assemblage. The ANOVA was used to determine the statistical significance of the differences in MTI observed among treatments and at 5 and 15 meters.

To further investigate the intensity of herbivory in relation to macroalgal abundance I also analyzed the relationship between herbivorous fish and sea urchin biomasses (alone and pooled) and macroalgal biomass, across treatments (PMR, UMR and NP). A regression analysis was used to determine significance of the trends observed.

Results

Comparison between individual marine protected areas and unprotected reefs

Fish biomass was significantly greater inside the MPAs than on unprotected reefs in 3 out of 8 cases at both depths. In only one case at 5 meters (Dry Tortugas) fish biomass was greater outside the reserve (Fig. III.2a, b). Sea urchin biomass was also greater inside MPAs in 2 out of 8 cases at 5 meters, and in 6 out of 8 cases at 15 meters (Fig. III.2c, d). However, sea urchin biomass was greater on unprotected reefs in one case at each depth. Coral biomass was greater inside the MPA in 2 out of 8 cases at 5 meters, but in two cases biomass was lower inside the reserve (Fig. III.3a, b). At 15 meters, coral biomass was greater outside the reserve in only one case, and no significant differences were found in the rest of the cases. Contrary to our expectations, macroalgal biomass was greater inside the reserves at 5 meters in 4 out of 8 cases, and only in one case was lower inside the reserve (Fig III.3c, d). At 15 meters, macroalgal biomass was greater inside MPAs in 4 out of 8 cases.

Comparison among protection treatments

Fish

Fish biomass ranged from 64 to 145 g m^{-2} at 5 meters and from 67 to 257 g m^{-2} at 15 meters (Fig. III.4). Total fish biomass was greater in PMRs than in UMRs and NPs at both 5 and 15 meters (Fig. III.4a, b, Table III.2). Fish biomass was greater in UMR than in NP at 15 meters, but no significant differences were found at 5 meters. MTI was greatest in PMR, followed by UMR at both 5 and 15 meters (Fig 3.4c, d). However, no significant differences were found between UMR and PMR at 5 meters.

Fish density ranged from 0.6 to 1.05 individuals m^{-2} and between 0.7 and 1.3 ind. m^{-2} at 5 and 15 meters, respectively (Table III.3). Results were similar to those of biomass with a few exceptions (Table III.2). Fish density was different among all treatments and depths, except between NP and UMR at 15 meters. Fish density was greatest in PMR at both depths followed by NP at 5 meters and UMR at 15 meters.

The biomass of herbivorous fish was greater in PMR at both depths (Fig. III.5a, b). Across treatments the biomass of parrotfishes contributed between 50 and 70% to the total biomass of herbivorous fishes. Biomass of herbivorous fish was greater at 5 meters than at 15 meters (Mann-Whitney U-Test, $p<=0.001$). The biomass of herbivorous fish was lower in UMR than NP and PMR at both depths, but no significant differences were found between NP and UMR at 5 meters.

Sea Urchins

Sea urchin biomass ranged between 0.9 and 2.3 g m^{-2} at 5 meters, and between 0.12 and 0.3 g m^{-2} at 15 meters (Fig. III.5c, d). Sea urchin density was greater at 5 than at 15 meters (Mann-Whitney U-Test, $p<=0.001$). Sea urchin abundance consists of 5 species of which *Diadema antillarum* was the most abundant across sites. Similarly to herbivorous fish, sea urchin biomass was greater in PMR than in UMR and NP at both depths. Sea urchin biomass was similar between NP and UMR at 5 meters, and at 15 meters biomass in UMR was greater than NP (Table III.2).

Sea urchin density ranged between 0.6 and 1.2 ind. m^{-2} and between 0.05 and 0.3 ind. m^{-2} at 5 and 15 meters, respectively (Table III.3). At 5 meters the greatest density was recorded in PMR, followed by UMR, while at 15 meters the greatest density was in UMR, followed by NP.

Coral

Biomass of coral ranged between 239 and 327 g m^{-2} at 5 meters, and between 342 and 422 g m^{-2} at 15 meters (Fig. III.6a, b). At 5 meters, the greatest coral biomass was found in PMR, followed by NP. Coral biomass was the lowest in UMR at both depths. At 15 meters, the greatest coral biomass was in NP, however no significant differences were found between NP and PMR treatments (Table III.2).

Coral cover ranged between 10% and 16% at 5 meters, and between 13% and 21% at 15 meters (Table III.3). Differences in cover among treatments were similar to those of biomass. Percent coral cover was the greatest in PMR at both depths, followed by NP, but no significant differences were found between NP and PMR at 5 meters. Coral cover was the lowest in UMR.

Macroalgae

Macroalgal biomass ranged between 294 and 498 g m^{-2} at 5 meters, and between 458 and 853 g m^{-2} at 15 meters. Macroalgal biomass was lower in PMR at both 5 and 15 meters than in UMR and NP (Fig III.6c, d). However, no significant differences were found between NP and PMR at 5 meters (Table III.2). Macroalgal biomass was the greatest in UMR, followed by NP.

Macroalgal cover ranged between 43% and 52% at 5 meters, and between 49% and 68% at 15 meters (Table III.3). Results were similar to those of biomass with a few exceptions. Macroalgal cover was the greatest in UMR, followed by PMR at 5 meters and NP at 15 meters. However, no significant differences were found between UMR and PMR at 5 meters.

Crustose Coralline Algae

Biomass of CCA ranged between 6.9 and 9.4 g m^{-2} at 5 meters, and between 1.7 and 3.9 g m^{-2} at 15 meters. CCA cover ranged between 12.79 and 17.5% at 5 meters, and from 3.26 to 7.37 at 15 meters (Table III.3). Statistical differences in CCA cover and biomass were the same. CCA inside NP was the greatest at both depths, followed by UMR, but no significant differences were found between UMR and PMR at 15 meters (Table III.2). Cover and biomass of CCA results were identical given that we used a transformation based on cover using a single conversion factor for all CCA species. Lack of detailed information on the biomass of CCA species and identification in the field made it difficult to conduct a more detailed analysis.

Herbivore linkages

The regional pattern in fish, coral, macroalgal and sea urchin biomass across treatments and depths was further investigated by examining the correlation between coral and macroalgal biomasses to the herbivorous fish and sea urchin biomass (Fig.

III.7a, b). Both sea urchin and herbivore fish biomass were negatively correlated with algal biomass (Spearman Rank correlation, R= -0.88, p=0.02 and R=-0.94, p=0.004, respectively), but they were not significantly correlated with coral biomass (p=0.3 and p=0.7, respectively). Similar results were found when analyzing the relationship among these herbivores and cover of macroalgae and corals. I pooled herbivore biomass in one group (total herbivore biomass= herbivorous fish + sea urchin biomass) and this was also negatively correlated with biomass of macroalgae (R=-0.94, p=0.004) but not correlated with corals (p=0.7). Further analysis of the differences in grazing intensity between herbivore fish and sea urchins may be necessary to reveal the effect of herbivore abundance and changes in macroalgal abundance. However, those estimates were not possible for this study, due to lack of parameters for some fish herbivore species.

Discussion

My results showed variable patterns of abundance of major ecosystem components when comparing reserves versus nearby unprotected reefs throughout the Caribbean (Fig. III.2). However, protection treatments showed clear patterns, despite potential geographic variability. Well-protected marine reserves (PMR) showed greater fish biomass than ineffective marine protected areas (UMR) and unprotected reefs (NP), as well as more mature (i.e. successionally advanced) fish assemblages with more abundant predators. Fully protected reserves (PMR) also exhibited increased herbivory, through increased sea urchins and herbivorous fish biomass and reduced macroalgal biomass. Coral biomass was slightly greater in PMRs only at 5 meters. These results indicated that in marine reserves where effective protection is missing (UMRs), there are fewer sea urchins, less coral, and more macroalgae than both PMRs or NPs. These results indicated that analyses of reserve effectiveness, without consideration for reserve enforcement status, can greatly bias the results towards showing reserve failures.

Although snapshot comparisons do not necessarily mean that observed differences are due to changes in the reserves after protection, the data showed patterns in the fish community that have been detected in other reserves elsewhere such as increases in fish biomass (Halpern 2003). I therefore assumed that the observed changes in abundance and biomass were mostly due to the degree of protection, at least for the fish community.

The negative response in UMR may be linked to increased fishing due to a reverse ‘reserve effect:’ where no enforcement exists, such reserves work instead as a fishermen attractor (Byers & Noonburg 2007). UMRs probably had lower fish biomass than PMR, because of increased fishing pressure. Although I did not find data on fishing effort, I observed fishing or received reports of both permitted and illegal fishing in the reserves categorized as UMR (A. Ross pers comm, F.P. unpublished, Keller and Donahue 2006). The lack of enforcement may aggravate the recovery of the community through increased exploitation and other sources of disturbance such as over-frequentation and uncontrolled development (Garrabou et al. 1998).

Reef fishes

In contrast to the expectation of greater fish biomass among reserves and nearby unprotected reefs, my results showed no significant differences in 43% of the cases (Fig. III.2a, b). Most of the reserves where no difference was detected between inside and outside fish biomass occurred in small reserves, such as Looe Keys (Florida), and Hol-Chan (Belize). This could be partly due to a decrease in the efficacy of small reserves as the mobility of larger fishes increases (Gerber et al. 2002, 2003), insufficient area inside the reserve to permit sufficient recruitment for increased population growth (Kaplan et al. 2006), and/or increase use of marine resources in and around the reserve (Cote et al. 2001, Jameson et al. 2002).

Given the increase in fish biomass in some reserves, I would expect an increase in the biomass of large fish, in the proportion of top predators relative to total fish biomass, and changes in the structure of the food web (Friedlander & DeMartini 2002; Stevenson et al. 2007; Friedlander et al. 2007). My results indicated that PMR have achieved the greatest changes in the fish food web and are consistent with the overall gradient of fish biomass and assemblage structure in the Caribbean (Newman et al. 2006). Jardines de La Reina National Park has the most mature fish food web, with 46% of the total fish biomass accounted for by top predators including sharks, and large snappers and groupers larger than one meter (Newman et al. 2006). However, as has been shown in the Mediterranean, the trajectory of recovery of the fish community in a particular reserve is highly dependent on local factors and the initial conditions at the onset of protection (Guidetti & Sala 2007). Changes in the biomass of top predators in the UMR and smaller PMR will likely take longer (Micheli et al. 2004; Russ et al. 2005). It is not possible to predict whether reserves surrounded by very poor fish assemblages will be able to recover to the point observed in Jardines de la Reina. Nevertheless, my results show that fish assemblages in PMR, will exhibit increases in biomass and eventually in the complexity of the fish food web as clearly shown in the larger reserves, although full recovery may take decades (Russ et al. 2005; McClanahan 2005, 2007).

Benthic communities

In the last 30 years, Caribbean reefs have lost over 50% of coral cover, which has been replaced by macroalgae (Hughes 1994; Gardner et al. 2001; Cote et al. 2005; Aronson et al. 2004), and sea urchin populations have not recovered to pre-mortality levels (Lessios 1988, 2005). Can reserves enhance the recovery of this degraded benthic community through changes in the biomass of fishes? Previous studies indicate that increased herbivory may be a mechanism of community recovery (Edmunds & Carpenter 2001; Carpenter & Edmunds 2006; Idjadi & Edmunds 2006; Mumby 2006; Mumby et al. 2007). Increased grazing inside reserves caused by increases in the biomass of herbivorous fishes and/or sea urchins has been shown to reduce macroalgal cover and enhance coral recruitment, and thus, the recovery of coral populations (Mumby et al. 2007). However, these studies recognize that adult coral populations do not show a response to increased fish herbivores and urchin abundance at these limited temporal and spatial scales.

My results indicate large cover and biomass of macroalgae across sites, and low coral cover and biomass, independent of the degree of protection. The greatest coral cover in shallow reefs was detected at the unprotected area near Montego Bay (Fig. III.3a), a reef with a very low biomass of herbivorous fishes (Newman et al. 2006), but high sea urchin biomass (Fig. III.2c). This was particularly surprising, given that Jamaica has served as the poster child for degraded coral populations in the Caribbean (Hughes

1994). Coral cover and biomass was greater inside reserves relative to nearby unprotected areas only in reserves that contained larger, old colonies as in the Florida Keys (5m depth). At 15 meters, coral cover and biomass were not significantly different between reserves and unprotected areas at any site, except Cozumel, where coral biomass was greater outside the reserve. Thus, current relatively large coral cover at Caribbean sites is due to remnant living colonies as opposed to new growth or recovery from mortality events (Newman et al. 2006). Additionally, macoralgal cover could have stayed low due to competition for space with large coral colonies (Williams and Polunin 2001, Lee 2006) and localized herbivory (Hay 1984). In general, coral cover and biomass were lower in UMR, while very small or no differences existed between PMR and NP.

The initial condition of the reef at the time of reserve implementation is a confounding factor here that may account for the variability of high coral cover. Often reserves are placed over areas that have not yet degraded, due to variable factors. Remnant colonies may or may not have survived due to reserve protection, and high coral cover appears to be a historical consequence of the many factors of disturbance that affect reefs, and can occur inside or outside of reserve areas. Although these results showed no indication of reserve effect on coral recovery to date, recovery of the coral community may be occurring at small scales undetected by this study, such as those indicated in previous studies (Macintyre et al. 2005, Carpenter & Edmunds 2006, Idjadi & Edmunds 2006). Also, corals may recover over much larger time scales than I observed.

Macroalgal biomass inside reserves was either greater or the same as at unprotected reefs at both depths. Macroalgal biomass and cover were greatest in UMRs, while the lowest in PMRs. Without a time series I cannot determine whether algal biomass was already higher in UMR than in adjacent NPs before protection, or whether it has been a consequence of the lack of effective regulations and enforcement (see above).

In a related study, increased herbivorous fish biomass (and total biomass) was negatively correlated with algal biomass across the gradient of fish biomass in the Caribbean (Newman et al. 2006). Similarly, my results also indicated a strong negative correlation among herbivores and macroalgae biomass across treatments and depths (Fig. III.7). These results are consistent with movement towards coral recovery; although macroalgal cover has not been reduced to a point that facilitates coral re-growth and recruitment on a regional scale (but see Mumby et al. 2007). Additionally, CCA abundance was greater at 5 than at 15 meters, which suggest a greater potential for coral recruitment in shallow reefs (Morse et al. 1988). In contrast, the lower CCA abundance and biomass found in PMRs may not facilitate coral recovery. Due to the scale of my survey protocol a more detailed assessment of the CCA abundance is necessary to confirm these results

Previous studies suggested that increased abundance of fishes was associated with lower sea urchin abundance inside Caribbean reserves because of increased predation (McClanahan et al. 2001). In contrast, my results showed greater biomass of sea urchins in PMR, despite the generally high variability in abundance across reef sites. After the mass mortality of *Diadema antillarum*, sea urchin herbivory decreased dramatically (Lessios 1988) and recent recovery of the population is patchy (Macintyre et al. 2005; Idjadi & Edmunds 2006). I observed greater abundances of sea urchins under two conditions in shallow (5 m) reefs: 1) isolated reefs (Montego Bay) where old but healthy

Montastrea annularis colonies dominate; and 2) in the Jardines de la Reina reserve, where shallow reefs are dominated by structurally complex *Acropora palmata* stands (Fig III.2c). These findings suggest enhanced sea urchin settlement/survival associated with increased three-dimensional structure (Lee 2006). Even so, my results showed that sea urchin densities across the majority of reefs were not sufficiently high to allow for the removal of enough macroalgae to enhance the abundance of corals.

In summary, within the scope of this study, the coral community does not show a response to protection. This may be an indication that the increase in fish and sea urchin biomass may not be enough to significantly decrease macroalgal cover, within the time frame of protection of the reserves under study. This raises questions about the adequacy of single conservation actions such as marine reserves in restoring coral reef communities over short time scales, and suggests the need for additional conservation measures, such as proactive restoration, to improve the effectiveness of marine reserves (Denny & Babcock 2004).

Baselines and expectations of Caribbean reef reserves

The community at the Jardines de la Reina reserve in Cuba is unique in many respects. On the one hand, it has the most mature reef fish assemblage in the Caribbean, with large total biomass and a large proportion of apex predators (Newman et al. 2006). This is similar to the best-preserved fish assemblages in the central Pacific (Friedlander & DeMartini 2002; Stevenson et al. 2007), and makes it the best available baseline for non-fished reef fish assemblages in the Caribbean. Cozumel also has a large total fish biomass, but most of it is accounted for by large schools of medium-sized grunts, and thus is not as mature as Jardines de la Reina. On the other hand, the benthic community at Jardines de la Reina shows dominance of *Acropora palmata* at 5 m, but very low coral cover and high macroalgae at 15 m. Jardines is far from constituting a baseline for corals, although the living three-dimensional structure at 5m is still present. This raises the question: Can an algal-dominated reef in the Caribbean support a fish biomass comparable to that of near-pristine coral-dominated reefs such as Kingman Reef (Sandin et al 2008)? Will reserves enhance full recovery of fish assemblages regardless of the structure of the benthic community?

Jones et al. (2004) showed that coral loss results in a reduction of fish abundance in a Papua New Guinea reserve, and argued that the loss of the three-dimensional structure provided by living corals impairs reef fish recruitment. Graham et al. (2006) reports similar findings for Seychelles reefs. The biomass and structure of reef fish and sea urchin assemblages is greatly dependent on the three-dimensional structure of the habitat (Friedlander & Parrish 1998, Lee 2006), and the recruitment of some species is tightly linked to the availability of nursery habitats such as mangroves (Mumby et al. 2004). The area surrounding Jardines de la Reina had the lowest frequency of hurricanes over the last 30 years (NHC 2005) compared to the other regions visited, which may explain why the vertical structure is still present, in spite of the low living coral cover. The reserve is very large (33,580 ha) and situated far from large human settlements. In addition, Jardines de la Reina is surrounded by a large extension of mangrove forests, which likely enhances recruitment of many species, including the goliath grouper, rainbow parrotfish, and tarpon (Mumby et al. 2004), common there but rare elsewhere. The Cozumel reserve, in contrast, had a total fish biomass similar to Jardines de la Reina at 15 meters, although environmental conditions are different (less mangrove habitat, more human development, and higher hurricane frequency). While coral cover was low, Cozumel reefs contained high biomass of large sponges, which also provided three-dimensional structure to the reefs. Whether Cozumel will reach a level of maturity in the fish assemblage similar to at Jardines de la Reina remains to be seen. Just a year after we conducted our survey, hurricane Emily and Wilma devastated the region around Cozumel and post-hurricane surveys indicated a decline of 10% in coral cover (Alvarez-Flip & Nava-Martinez 2006).

Regardless, the reefs at Jardines de la Reina provide a baseline for Caribbean reef fishes. This does not mean that it should become a static goal of Caribbean reserves, because the responses of fish assemblages to protection can be context-dependent and influenced by local processes (Guidetti & Sala 2007). However, the functional structure of the reef fish assemblage at Jardines, in terms of proportion of trophic levels (Newman et al. 2006), is an ecologically feasible target towards which all conservation efforts in the Caribbean should aim.

Conclusions: the role of Caribbean reef reserves

The absence of widespread community response to protection underscores the seriously degraded state of Caribbean coral reefs (Hughes & Tanner 2000; Knowlton 2001; Aronson et al. 2004; Pandolfi et al. 2005). Most of the reef sites we studied were characterized by low biomass of coral, low fish biomass and large macroalgal biomass. Few reef sites break away from this pattern: reefs that have been protected from fishing effectively or escaped some deterioration because of their relative isolation (Aronson et al. 2005). Yet even in the best reserves, the underwater landscape is not the same as before degradation in the early 1970s. While it is possible that Caribbean reefs will recover, the future seascape of Caribbean coral reefs will most likely be very different from that observed in the 1950s (see Goureau 1959).

Well-enforced reserves help fish biomass and assemblage structure to recover, but these changes have not yet reversed the decline in the benthic community. Caribbean reef ecosystems have been subjected to an increasing number of synergistic disturbances, of which overfishing is the earliest but no longer necessarily the greatest (Bellwood et al. 2004). Prohibition of fishing can thus help recover part of the ecological community, but complementary measures are needed to restore a successionally advanced benthic community (Pandolfi et al. 2005).

Although they may not be enough on their own, well-enforced, large marine reserves are a critical component of this recovery strategy (Denny & Babcock 2004). Large marine reserves are more likely to include multiple habitats (i.e. reefs, mangroves, and lagoons), providing additional protection throughout the life cycle of organisms (Mumby et al. 2004). Moreover, the larger the reserve, the less affected the entire community will be by single disturbance events such as oil spills, and hurricanes (Allison et al. 2003). Reserves are also affected by uncontrolled external conditions such as pollution and climate change (Jameson et al. 2002; Soto 2001). But reef fish assemblages that have nearly fully recovered and are dominated by top predators appear to enhance resilience from such warming events (Knowlton and Jackson 2008, Sandin et al. 2008). This study indicates that MPAs that are not effectively enforced or where some kinds of fishing are allowed may be counterproductive in terms of conservation achievements. This shows the importance of establishing truly large no-take marine reserves to start enhancing resilience and set the stage for recovery, as soon as possible.

Table III.1 Description of study sites including MPAs and unprotected reefs, survey effort (N) per community assemblage, attributes of marine reserves and location in map (ID, Fig. 1). Data obtained from reefbase.org, Keller and Donahue (2006), and authors during field work. Non protected reef sites (NP) correspond to sites nearby MPAs either protected marine reserves (PMR) or unprotected marine reserves (UMR).

DEPTH	COUNTRY	RESERVE NAME	Non-protected area for comparison	PROTECTION TYPE	ENFORCEMENT	AREA (ha)	TREATMENT	ID	*N* FISH	*N* BENTHOS	*N* URCHIN
5	CUBA	**Canarreos Ntl. Park (since 2001)**		NO TAKE	poaching	33110	UMR	**1**	15	15	30
			Rosario & Cantiles	none					15	15	30
		Jardines de la Reina Ntl. Park (since 1996)		NO TAKE open to sportfishing catch and release	effective	30580	PMR	**2**	15	15	40
			Ballenatos	none					15	15	30
	JAMAICA	**Montego Bay Marine Park (since 1996)**		NO TAKE	poaching	1530	UMR	**3**	15	15	15
			Montego Bay NR	none					5	5	5
	BELIZE	**Glover's Reserve (since 1993)**		NO TAKE	effective	270	PMR	**4**	5	5	11
			Glover's atoll NR	none					15	16	26
	MEXICO	**Cozumel Reefs Marine Park (since 1996)**		NO TAKE	effective	11988	PMR	**6**	15	14	15
			Habitat not found								
	USA	**Dry Tortugas National Park (since 1992)**		NO TAKE open to sportfishing catch and release	some fishing	26203	UMR	**7**	15	15	15
		Sand Key (FKNMS) (since 1997)		NO TAKE open to sportfishing catch and release	some fishing	150		**8**	5	5	5
		Western Sambos (FKNMS) (since 1997)		NO TAKE	effective	3000	PMR	**10**	5	5	5
		Looe Key (FKNMS) (since 1997)		NO TAKE	effective	115		**11**	5	7	5
			Florida keys NR	none					7	8	8
15	CUBA	**Canarreos Reserve**		NO TAKE	poaching	33110	UMR	**1**	15	15	30
			Canarreos NR	none					15	15	30
		Jardines de la Reina Ntl. Park		NO TAKE open to sportfishing catch and release	effective	30580	PMR	**2**	15	15	40
			Jardines NR east	none						15	30
	JAMAICA	**Montego Bay Marine Park**		NO TAKE	poaching	1530	UMR	**3**	15	15	15
			Montego Bay NR	none					5	5	5
	BELIZE	**Glover's Reserve**		NO TAKE	effective	270	PMR	**4**	5	5	8
			Glovers NR	none					15	16	28
		Hol Chan Reserve (since 1989)		NO TAKE	effective	411	PMR	**5**	5	5	8
			Hol Chan NR	none					15	15	28
	MEXICO	**Cozumel Reefs Marine Park**		NO TAKE	effective	11988	PMR	**6**	10	10	15
			Akumal	none					14	15	14
	USA	**Dry Tortugas National Park**		NO TAKE open to sportfishing catch and release	some fishing	26203	UMR	**7**	15	15	15
		Rock Key (FKNMS) (since 1997)		NO TAKE	some fishing	30		**9**	5	5	5
			Florida keys NR	none					15	15	20

Table III.2. Results of the treatment comparisons (TC) of biomass and abundance (cover and density) of main community components coral, macroalgae (MA), crustose coralline algae (CCA), sea urchins and fish. Significant differences indicate Kruskal-Wallis test results for multiple comparisons of mean ranks. Transect data was bootstrap resampled (n=1000) to account for unequal sample size among treatments.

	d	TC		CORAL	MA	CCA	URCHIN	FISH
BIOMASS	5	*NP*	*UMR*	<0.001	<0.001	<0.001	ns	ns
		UMR	*PMR*	<0.001	<0.001	ns	<0.001	<0.001
		PMR	*NP*	<0.01	ns	<0.001	<0.001	<0.001
	15	*NP*	*UMR*	<0.001	<0.001	<0.05	<0.001	<0.05
		UMR	*PMR*	<0.001	<0.001	<0.001	<0.001	<0.001
		PMR	*NP*	ns	<0.001	<0.001	<0.01	<0.001
COVER AND DENSITY	5	*NP*	*UMR*	<0.001	<0.001	<0.001	<0.001	<0.01
		UMR	*PMR*	<0.001	ns	ns	<0.001	<0.001
		PMR	*NP*	ns	<0.001	<0.001	<0.001	<0.001
	15	*NP*	*UMR*	<0.001	<0.001	<0.001	<0.001	ns
		UMR	*PMR*	<0.001	<0.001	<0.001	<0.001	<0.001
		PMR	*NP*	<0.001	<0.001	<0.001	<0.001	<0.001

Table III.3. Percent cover of benthic assemblages: Coral, Macroalgae (MA), and Crustose coralline algae (CCA). Density (ind. m^{-2}) of fish and sea urchins. Means and standard errors (below in parenthesis) of community components inside non-protected reefs (NP), unprotected marine reserves (UMR) and protected marine reserves (PMR). Statistical differences indicated in table 3.2.

		5			15		
		NP	UMR	PMR	NP	UMR	PMR
COVER	CORAL	15.52 (1.48)	10.34 (1.2)	16.33 (1.89)	18.98 (0.82)	12.96 (0.94)	21.22 (1.84)
	MA	43.36 (2.2)	52.63 (3.87)	49.18 (2.4)	56.33 (1.87)	69.56 (3.16)	49.47 (2.67)
	CCA	17.50 (1.3)	14.848 (1.94)	12.79 (1.42)	7.37 (0.72)	5.57 (0.55)	3.26 (0.74)
DENSITY	URCHINS	0.59 (0.09)	0.84 (0.15)	1.21 (0.17)	0.09 (0.01)	0.28 (0.08)	0.05 (0.01)
	FISH	0.78 (0.05)	0.68 (0.04)	1.01 (0.07)	0.71 (0.03)	0.77 (0.04)	1.32 (0.15)

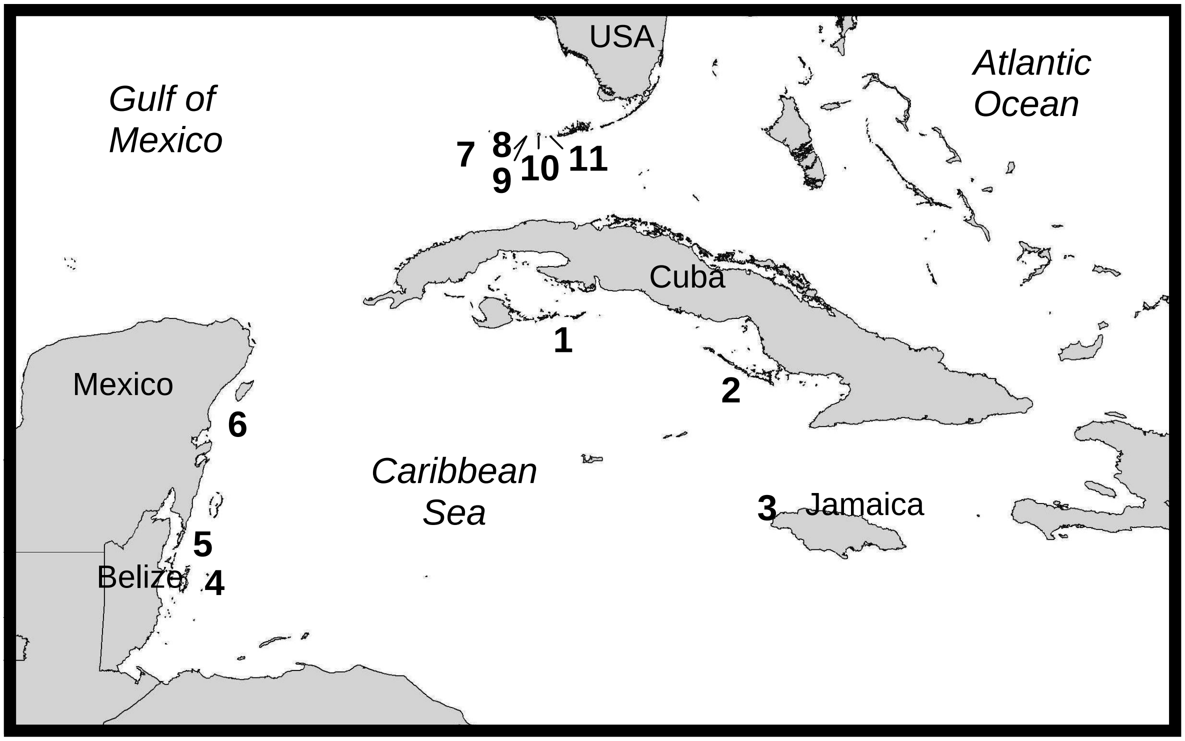

Figure III.1. Location of study sites in Western Caribbean countries. Surveys were conducted inside marine protected areas and nearby unprotected reefs. MPAs for this study were: Canarreos National Park (1), and Jardines de la Reina National Park (2), Cuba; Montego Bay Marine Park (3) in Jamaica; Glover's Reef Wildlife Preservation Area (4), Hol-Chan Marine Park (5) in Belize; Cozumel Reefs Marine Park (6) in Mexico; Dry Tortugas National Park (7), Sand Keys Sanctuary Preservation Area (8), Rock Key Sanctuary Preservation Area (9), Western Sambos Ecological Reserve (10), and Looe Key Sanctuary Preservation Area (11) in USA.

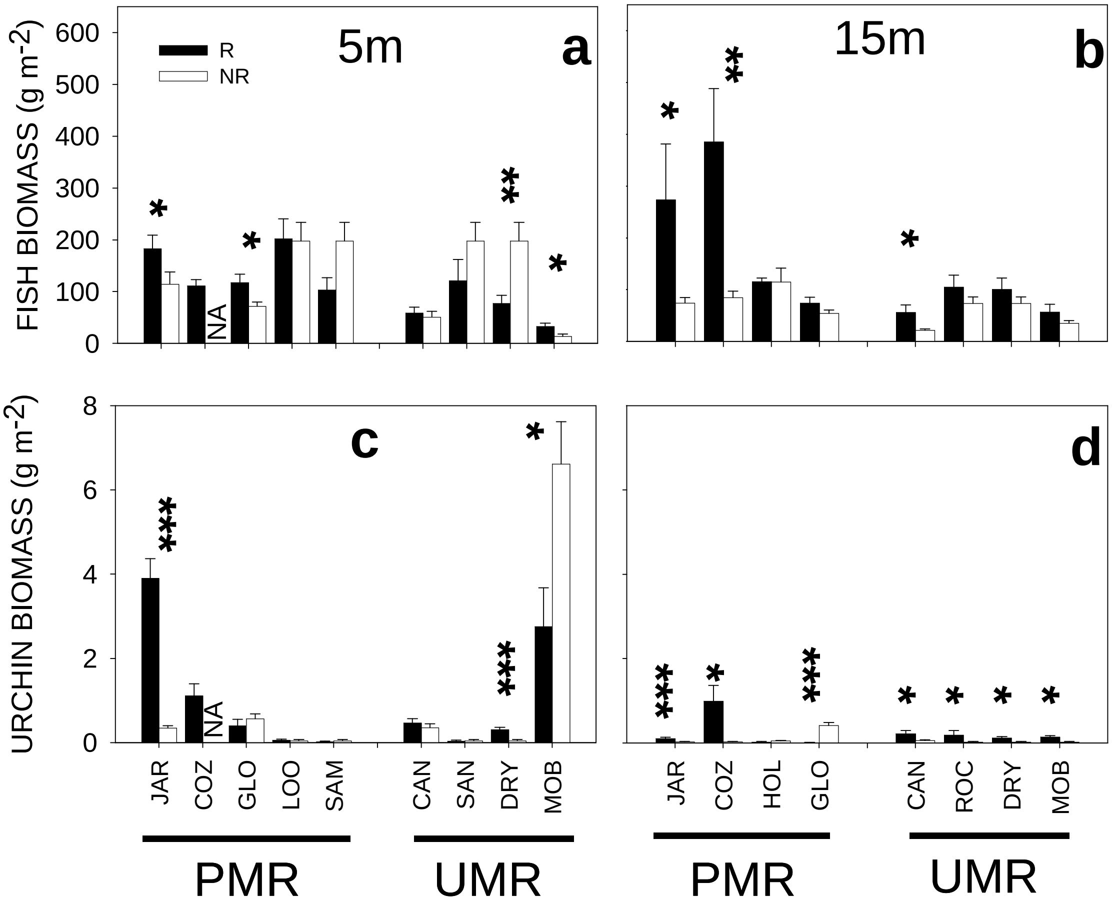

Figure III.2. Comparisons of fish (a-b) and sea urchin (c-d) biomass between individual marine protected areas and unprotected reefs. Statistical significance of differences was obtained using nonparametric Mann-Whitney U-Test for each case (* p<=0.05, ** p<=0.001, *** p<=0.001). Habitat not found indicated by N/A at 5 meters. Note some comparisons at 15 meters were not possible at 5 meters. See Table 1 for MPA attributes.

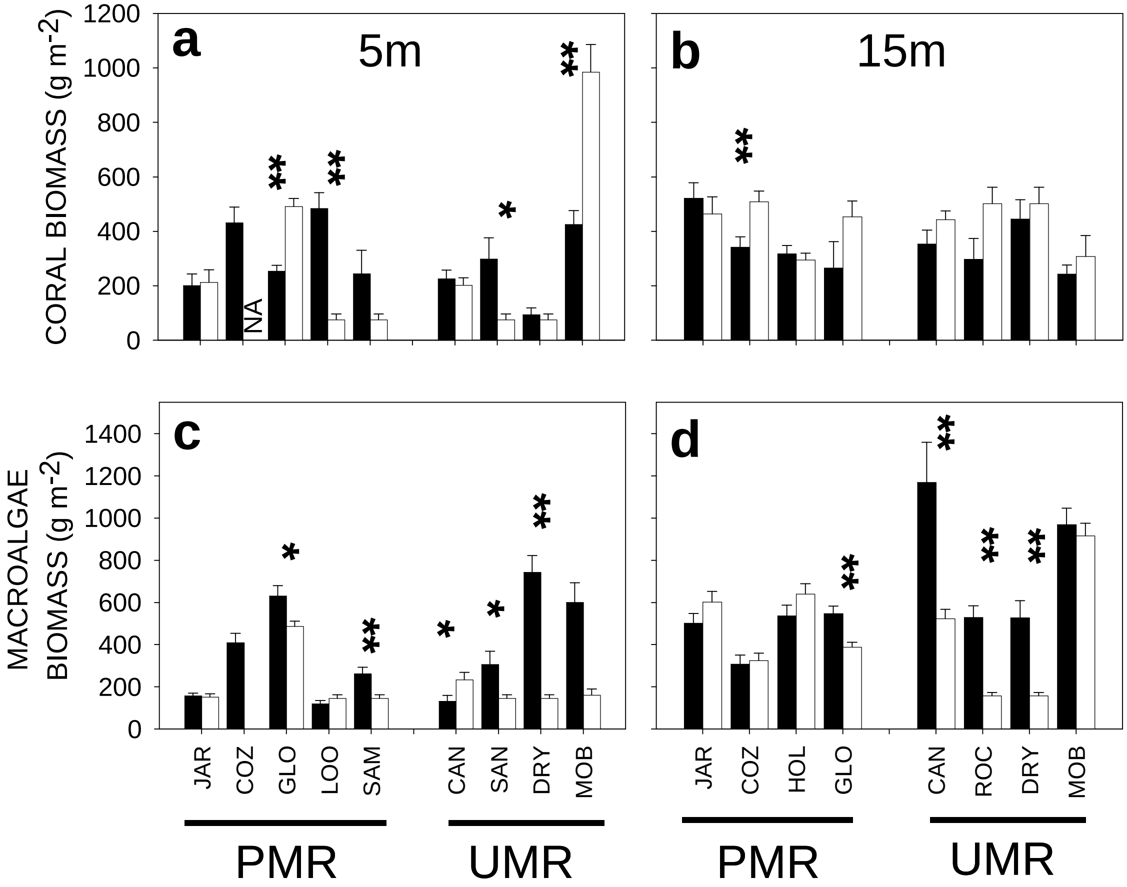

Figure III.3. Comparisons of fish (a-b) and sea urchin (c-d) biomass between individual marine protected areas and unprotected reefs. Statistical significance of differences was obtained using nonparametric Mann-Whitney U-Test for each case (* p<=0.05, ** p<=0.001). Bold and empty bars indicate reserve and no reserve reefs respectively. Habitat not found indicated by N/A at 5 meters.

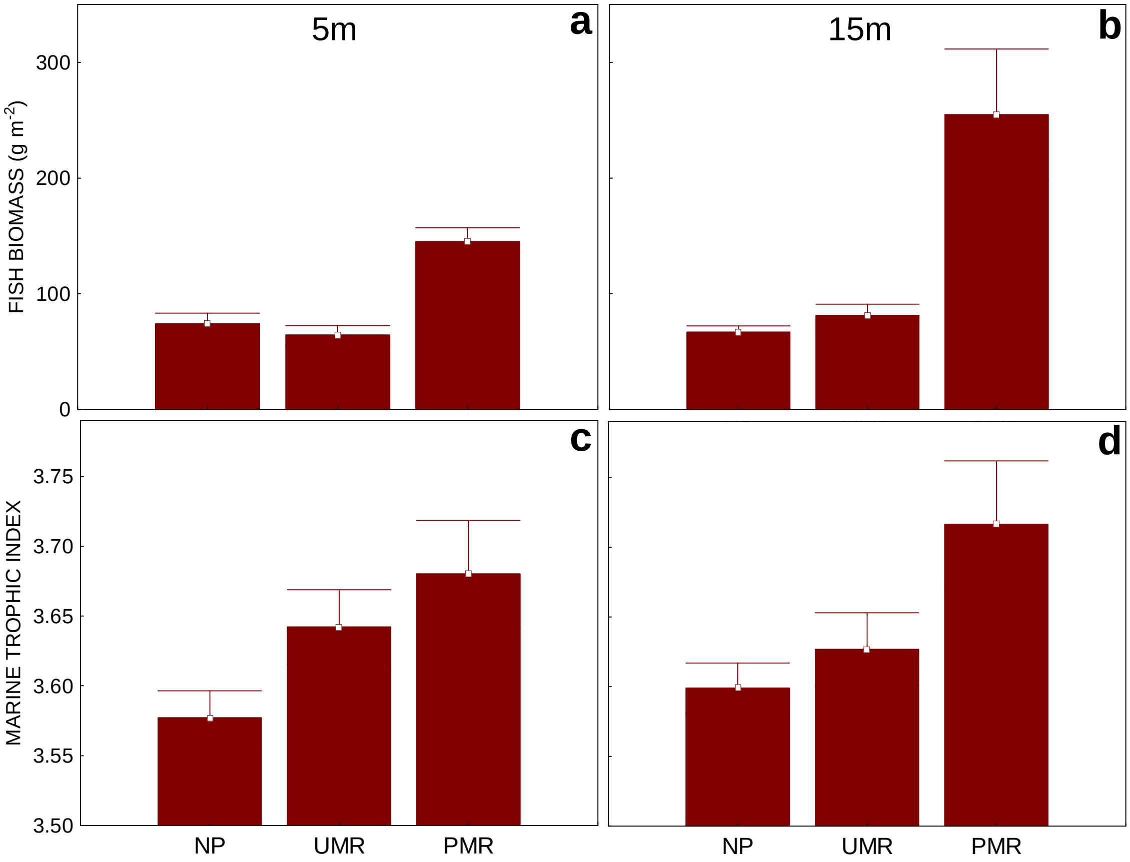

Figure III.4. Comparison of fish biomass (a-b) and MTI (c-d) among treatments. Whiskers indicate standard error of the non-bootstrapped means. Statistical differences are shown in Table 3.2. See methods for details on analysis.

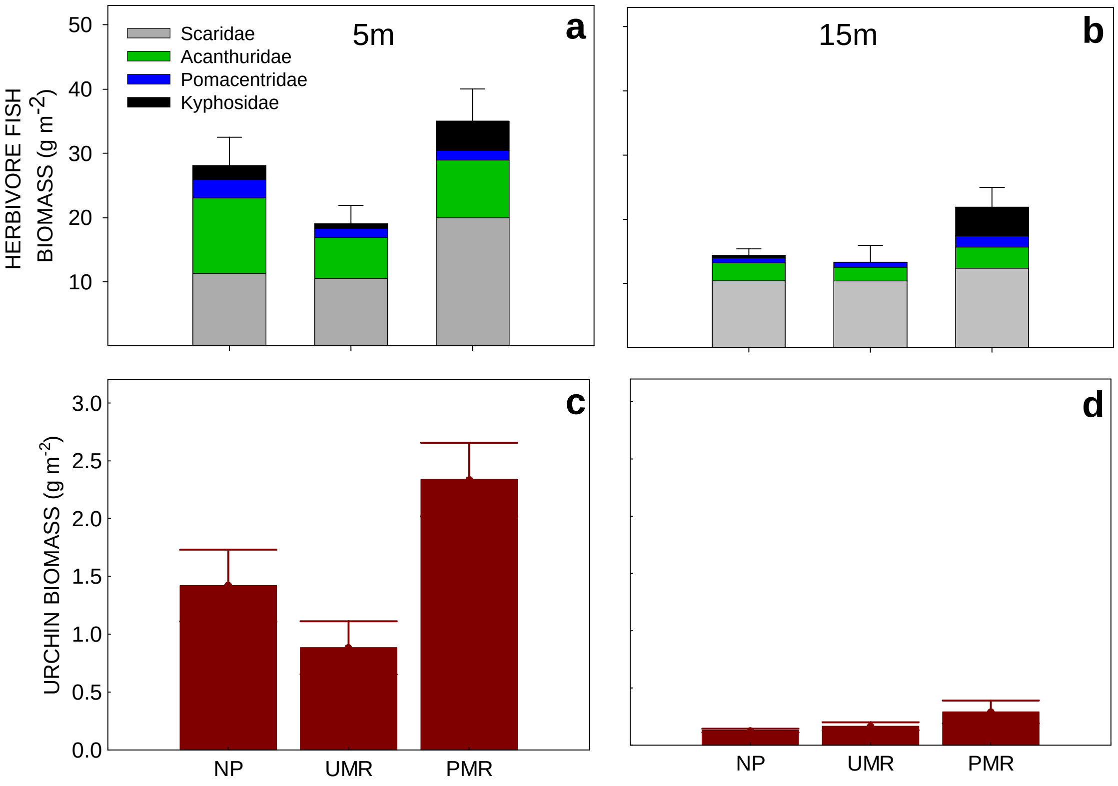

Figure III.5. Comparison of herbivore (a-b) and sea urchin (c-d) biomass among treatments. Statistical differences are shown in Table 3.2. For herbivore biomass the average abundance of fish herbivore families is indicated within each treatment. Whiskers indicate standard error of the non-bootstrapped means.

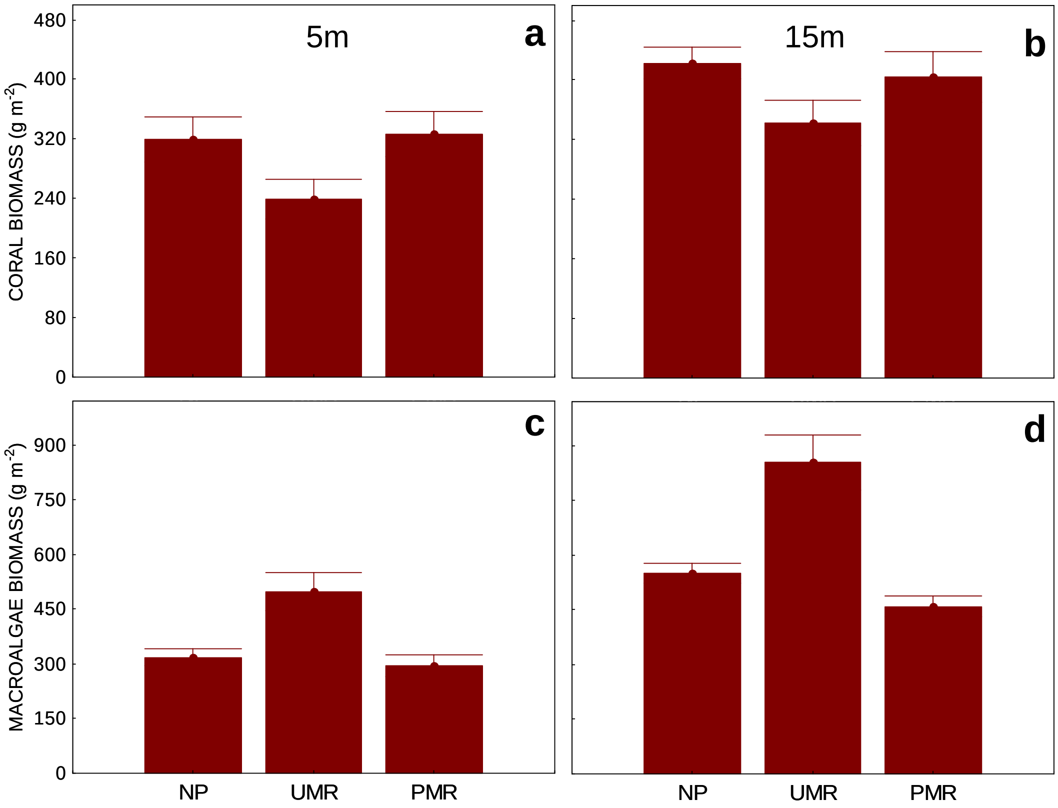

Figure III.6. Comparison of coral (a-b) and macroalgal biomass (c-d) among treatments. Statistical differences are shown in Table 32. Whiskers indicate standard error of the non-bootstrapped means.

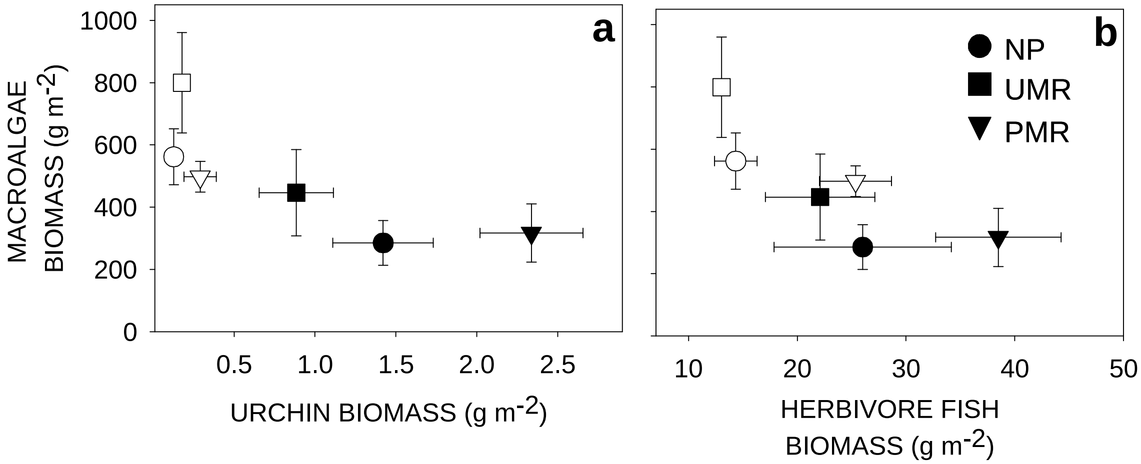

Figure III.7. Correlation between herbivore and macroalgal biomass, fish (a) and sea urchin (b), within Caribbean reefs at 5 (bold symbols) and 15 (empty symbols) meters depth, and across different degrees of protection (shape symbols). Data are averages for macroalgae, urchins, and herbivorous fish biomasses (±S.E.) from transects.

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CHAPTER IV

REEF FISH DIVERSITY ACROSS GRADIENTS OF FISHING IN THE CARIBBEAN

Abstract

In this chapter I examine the effects of protection on the biodiversity of the fish assemblages across Caribbean reefs. I used the species area relationship (SAR) to compare diversity between protected and non-protected reefs at a significantly large spatial scale (100s-1000s square meters). I found that, at the scale of our study, the Lomolino model fits our data better than other models typically used to describe the SAR. I used Lomolino parameter estimates to compare diversity patterns across categories of management (protected marine reserves, unprotected marine reserves, and no-protected reefs). At the regional scale the estimates indicate that both the species accumulation per unit area ($\text{Hill}_{\text{slope}}$) and maximum richness ($S_{\text{max}}$) were greater inside protected marine reserves than in the unprotected marine reserves and non-protected reefs. Alternatively, Lomolino third parameter (A50) indicates that the area necessary to attain 50% of maximum number of species was smaller inside reserves than in unprotected reefs. The SAR was variable at the local scale and did not show a clear pattern. However, analysis of pooled parameter estimates showed a greater rate of species accumulation inside protected marine reserves. Additionally, I found that the diversity of fish (richness) was a function of the fish biomass. This relationship was not asymptotic at high levels of fish biomass (>250g m^{-2}). Particularly at 15 meters, the relationship between fish biomass and diversity was hyperbolic, indicating a saturation point around

300 g m^{-2}. This indicates that fishing may have an important effect on the diversity of fish, whereas protected marine reserves enhance fish diversity through increased fish biomass. The SAR here presented indicated that all reserves are large enough (above 10,000m^2) to protect the maximum number of species. Deeper reefs showed higher diversity of fish, however those were found within small protected marine reserves. Although, marine reserves help the recovery of fish diversity, fishing is not the only stressor on Caribbean reefs. This may explain in part why healthy fish communities (i.e. where fish diversity and biomass are high) are rare. To ensure the future of Caribbean coral reefs additional conservation actions should be conducted to build resilience and to offset the synergistic effects of multiple anthropogenic stressors.

Introduction

Caribbean coral reef ecosystems have suffered considerable degradation due to chronic anthropogenic disturbances over the past centuries (Pandolfi et al 2003, 2005), and the human impacts on reefs have increased in the last few decades (Hughes 1994, Gardner et al 2003, Cote et al 2005, Bellwood et al 2004). Large predators such as sharks and groupers, as well as large herbivores (parrotfishes and turtles) are ecologically extinct in most Caribbean reefs (Jackson et al 1997, MacClenachan et al 2006, Newman et al 2006). Additionally, important species of corals (*Acropora palmata* and *A. cervicornis*) and sea urchins (*Diadema antillarum*) have suffered massive decline in population abundance mostly due to diseases and global warming (Aronson et al 2002, Lessios 2005, Hughes et al 2003). Consequently, the landscape of Caribbean coral reefs today is very different compared to that documented in early ecological work (Goureau 1959, Lewis 1960) or the geological record (Aronson and Precht 2004, Pandolfi and Jackson 2006). Furthermore, the decline of corals implies a net loss of reef habitat that might be in turn be linked to a decline in the abundance of fish diversity documented elsewhere (Sluka et al 2001, Almany 2004, Jones et al 2004, Gratwicke and Speight 2005).

Conservation actions such as establishment of marine reserves have shown promising results in restoring the abundance of fish (Roberts and Polunin 1993, Roberts 1995, Chapman and Kramer 1999, Gell and Roberts 2003, Halpern 2002). However, few studies have been designed to investigate how diversity patterns change across spatial scales with such protection (but see Tittensor et al. 2007 and Cote et al 2001 for other regions). Because biodiversity has been linked with function and the provision of important ecosystem services (Worm et al. 2006) it is important that we understand how diversity is affected by human activities. The species area relationship (SAR) is a well-known tool for the study of species diversity. Tittensor et al. (2007) recently showed evidence that fishing pressure affected SAR by depressing the rate of species increase (slope) in locales within three oceans, but no such work has been conducted in Caribbean reefs at a significantly large scale. In this study I examined Tittensor's findings within several marine reserves in the Caribbean. Following a similar approach I tested the consistency of their findings within a regional context.

The goal of this study was to investigate the effects of fishing prohibition on Caribbean reef fish diversity. In particular, I quantified the species-area relationship within several marine protected areas and compared to the adjacent unprotected reef areas. Additionally, I analyzed the richness patterns across the gradient of fishing pressure.

Materials and Methods

Study area and protection levels

I used two coral reef settings to study the effects of fishing: marine protected areas (unfished) and unprotected reefs (fished). First, I studied 11 marine protected areas and their adjacent unprotected areas in the Caribbean (Fig. III.1). There were two types of marine protected areas: truly protected marine reserves (PMR hereafter), and non-enforced marine reserves or marine protected areas where some types of fishing are allowed (UMR hereafter); adjacent non-protected areas are called NP reefs hereafter. Given that unprotected marine reserves (UMRs) shown in the previous chapter are more similar to NP reefs I focused the analysis on PMR and NP reefs, to increase clarity. Second, I took advantage of the large gradient of fish biomass on Caribbean coral reefs (Newman et al. 2006), and used total fish biomass as a proxy for historical plus present fishing pressure (Friedlander & DeMartini 2002, Dulvy et al. 2004, Graham et al 2005, Sandin et al. 2008) to look at the changes in diversity along this gradient. I surveyed coral reef communities at 5 and 15 m depth at each site where comparable habitats were available. For detailed attributes of the reserves and survey sampling effort see Table III.1, and for locations see Figure 3.1 (chapter III).

Data collection

I carried out underwater fish surveys using a standard visual belt transect method (Brock 1954, 1982). Censuses were conducted during daylight hours between 10am and 4pm. A diver swam a 50-meter transect, identifying and counting all fish and also estimating their size (± 5 cm) within 2.5m to either side of the center line (250 m^2 transect area). Swimming duration varied from 15-20 minutes, depending on fish abundance. Species larger than 20 cm (total length) were recorded on an initial swim, and smaller, more cryptic species were recorded on a second swim of the transect line.

The percent cover of benthic organisms was recorded using a standard point-intercept method with intervals of 20 cm along replicate 30 m-long transects (Newman et al. 2006). Overlapping of organisms was recorded to account for the three-dimensional nature of the reef community (thus the total point counts for each transect varied depending on the degree of overlap). For the fleshy algae with vertical structure (e.g., *Sargassum*, *Dictyota*, *Stypopodium*), the height was also measured. All scleractinian corals were identified to species, and algae and octocorals were identified to genera. Other non-coral sessile invertebrates were recorded using higher taxonomic categories (for detailed taxon list see Appendix III).

Several stations were surveyed inside reserves depending on their size (Table III.1). A variable number of replicate transects (5 to 15) for fish and benthic invertebrates were conducted within each station. Due to logistical constraints, all sites were not surveyed simultaneously. All local sites (individual PMRs and adjacent NP reefs) were surveyed within the same month, but different regions were surveyed during different months from November 2003 to August 2005.

Data analysis

Species-area relationship for each protection level (hereafter category) was calculated as the number of species at increasing area intervals (250 m^2 increments). Transects within categories were randomly permuted to calculate the averaged number of species per area increment. Transect permutations (n=1000) were conducted using Poptools (v 3.0.3) excel add-in (Hood 2007). I also calculated the SAR for each location (reef site) using the same procedure.

Previous studies have shown that the most appropriate models for SAR at small and intermediate scales are the power-law and exponential functions (Tjorve 2003, Tittensor et al 2007). The resolution of the transect data in this study is above 250m^2, and is also above the scale examined in previous studies. Therefore, I made a selection of the most appropriate model by testing the fit of our SAR data to 8 models, following a methodology similar to Tittensor et al (2007). The best-fit model was obtained by comparing both the adjusted r^2 estimate and AIC (Akaike Information Criteria, Akaike 1973) across categories. I tested two-parameter non-asymptotic models (power, exponential, log-log, and untransformed), two-parameter asymptotic models (Monod and negative exponential), and three-parameter asymptotic models (Lomolino and Weibull). For detailed discussion of these models see Tjorve (2003). In order to increase the sample size and the spatial range of our analysis, model fit tests were conducted using pooled data (MR and NP categories).

I compared the SAR patterns among categories within both the regional and local scale. At the regional scale I calculated the SAR between 250 and 11,000 m^2 for each category and for both depths (5 and 15 meters). I used bootstrap iterations (n=1000) to compute the model parameters (Lomolino) and confidence intervals (±C.I.) of the mean number of species. I compared SAR patterns among categories using non-parametric Mann-Whitney U-test. Alternatively, I computed the model estimates for each location ($area<1250m^2$). I compared SAR between MR and NP categories using pooled model parameter estimates and tested for significant differences using Wald-Wolfowitz runs test. I repeated both test for 5 and 15 meters depths.

Additionally, I analyzed the relationship between fish biomass and richness using a regression approach. Because coral cover appears to be linked to the diversity of small reef fishes (Jones et al. 2003, Graham et al 2006), I also analyzed the correlation between the fish diversity and the cover of different benthic components across the gradient of fish biomass. The variability of cover across sites and categories was examined in chapter III.

Results

I determined the fit of eight different models to the SAR of MR and NP reefs (5 and 15 m depths) using a least-squares approach and AIC (Table IV.1). Model fit of all models examined was relatively acceptable (r^2>0.74) and consistent across categories. However I found greater differences between models using AIC (as a rule of thumb differences in AIC greater than 1 are significant). The Lomolino model showed both the greater adjusted r^2 (0.99) and the lowest AIC for all treatments compared to other models (Table IV.1). Alternatively, the Weibull model showed good fit and low AIC, followed by the linear log-log model with low AIC. At this scale data behaves asymptotically, which explains the lower fit of linear models. Data across reef locations showed a similar adjusted R^2 fit to the Lomolino model. This model remarkably follows the SAR data pattern (Fig. IV.1). Below 1500m^2 the SAR appears linear in nature but behaves asymptotic over larger scales.

I used the SAR to compare diversity patterns between PMR, UMR and NP treatments at 5 and 15 meters (Fig. IV.1). I found the same patterns at both depths: 1) UMR and NP curves overlapped, 2) the PMR curve reaches more rapidly the asymptotic limit than both UMRs and NP curves, and 3) PMR curve did not overlapped with the UMRs and NP curves across the entire range of the data. Also, the confidence intervals of the mean species along the range examined overlapped between UMRs and NP, but did not overlap with PMR at 5 and 15 meters along the entire range. Apparently, at 5 meters curves converged at about 85 species. However, at 15 meters the SAR curves did not converge and the maximum number of species appears to be closer to 100 species. The maximum number of species at both depths was found above 8,000 m^2.

Lomolino (2000) describes the parameters interpretation for the Lomolino function. From Table IV.2 the *a* parameter, is the maximum expected richness (S_{max}); *b*, is the slope of the curve at the point of inflexion ($Hill_{slope}$), and *c*, is the area yielding a richness equal to the 50% of the maximum richness (A50). When I compared categories based on Lomolino parameter estimates (Table IV.2) I found the most dramatic differences in the A50 parameter estimate, which was significantly smaller in PMR at 5 and 15 m (1150 and 1405, respectively) than in NP reefs (1667 and 2516, respectively). The SAR curves from PMR presented a greater $Hill_{slope}$ parameter compared to NP treatments. These two parameters explain the differences in the curves we described from figure IV.1 (above). The third parameter, S_{max} estimate varied within the range of 109-134 species. At 5 meters S_{max} was greater in PMR, while at 15 meters this estimate was greater in NP (inverted pattern with depth). I tested the differences among PMR, and NP parameters estimates for both depths and found that all differences were significant (Mann-Witthney U-test, $p<0.001$, $n=1000$).

I found great variability in the SAR patterns across locations (Fig. IV.2). Given the overlapping between UMR and NP curves described above, I present only the comparison of PMR and NP at the location level. Unprotected reefs at both depths did not show a clear pattern. However, for both depths curves appear close to each other and Glover's reef curve was above all curves. This may suggest an increased number of species for this isolated location. The position of the curves relative to site location did not show a particular pattern except for Glover's reef. Similarly, SAR curves from PMR category showed an unclear pattern at the location level. Curves were widely separated in some cases, suggesting a variable effect of protection at the local level. Cozumel curves overlapped with Florida curve at 5 meters and also with Jardines curve at 15 meters. Unfortunately, some reserves were too small to obtain a greater number of replicates, particularly at 15 meters, and I could not analyze the SAR pattern conclusively. Alternatively, I determined the corresponding model parameters for each location and tested for significant differences of pooled estimates across categories using the non-parametric Wald-Wolfowitz runs test. I found significant differences ($p<0.05$) in A50 and Hill_{slope}, but no differences in S_{max}. Overall PMR shows greater Hill_{slope} and smaller A50, at 5 meters, but only greater Hill_{slope} at 15m (Table 3). Thus location data indicate that marine reserves have a greater accumulation rate of species per unit area, which is consistent with the findings at the regional scale.

Alternatively, I examined the patterns of richness across the gradient of fish biomass observed in the data. Total fish biomass is an indicator of the recovery of the fish community and/or fishing pressure as noticed in previous work (Friedlander & DeMartini 2002, Dulvy et al. 2003, Newman et al. 2006). Because pooling marine protected areas in a single statistical block entails regional and scale considerations (Guidetti & Sala 2007), I also analyzed changes along a gradient of ecosystem health/maturity by assessing the relationship between total fish biomass and fish diversity (Fig. IV.3). I expected a monotonic increase of diversity with greater fish biomass. Surprisingly, I found that fish diversity increases with total fish biomass in a linear way below 200 g m^{-2}, and then saturates and decreases slightly when fish biomass reaches 300 g m^{-2}. Because total observed fish biomass at 5 m was 288 g m^{-2}, the relationship at 5 m was linear for both transect and averaged data by location (adjusted $r^2=0.24$, $p<0.01$). At 15 m, however, where total fish biomasses ranged between 13.25 and 587.5 g m^{-2}, the relationship is clearly hyperbolic (adj. $r^2=0.42$, $p<0.001$). This pattern, in addition to a lower S_{max} inside PMR, also at 15 meters (described above), may corroborate the occurrence of a decrease in fish diversity with increased fish biomass. However, sites with fish biomass greater than 300g m^{-2} were scarce and this limits the power of our analysis.

Similarly, I found a correlation among benthic community components and fish richness. Fish diversity was negatively correlated with CCA cover found at 5 meters and positively correlated with coral and calcareous erect macroalgae cover. On the other hand, at 15 meters fish richness was negatively correlated with fleshy macroalgae, and positively correlated with CCA, coral and sponge cover (Table IV.3). Cover data was square root transformed to improve normality and to compute Pearson's correlation coefficients. Previous analysis suggested a weak interaction between the benthic and the fish communities (Newman et al 2006). Therefore I did not conduct a multivariate analysis to test the effect of the benthic communities on fish diversity, since I cannot assume benthos affect fish or vice versa.

I explored the possibility of determining the effects of location, depth and protection on the SAR using a linear model analysis. However, the behavior of the SAR was not linear and linear model could only be tested along a small spatial range (250-1250m^2). Preliminary results using linear model analysis were limited. Lomolino function provided a better fit and the interpretation of the differences between PMR and NP was more intuitive.

Discussion

Previous meta-analyses have shown that, on average, marine reserves have greater number of species than unprotected areas (Halpern and Warner 2002, Worm et al. 2006). However, these studies were not designed to collect rigorous diversity data, and did not estimate the total expected number of species. A recent study comparing fish diversity using a power model between marine protected areas and non-protected reefs showed that fishing depresses the slope (z value) of SAR (Tittensor et al. 2007); this study was based on permutations of nested sampling units on small spatial scales (<100 m^2). My results indicate more complex diversity patterns at a larger spatial scale, complementing and expanding previous findings.

Lomolino (2000) criticizes the generalized use of linear models to explain SAR patterns. He points out that the traditional species transformation procedure may affect the interpretation of such patterns. Also, *z* values may oversimplify patterns in species richness but provide an easier way to interpret differences among treatments. Here I present the alternative analysis using the sigmoid model developed by Lomolino, which at this scale provides a better quantitative description of the diversity patterns observed. Furthermore, with this function I was also able to compare diversity patterns of the fish community between reserves and unprotected sites.

From a regional perspective the fish community is more diverse within PMR independently of the depth. A detailed analysis of the SAR parameter estimates allowed us to identify the differences in diversity between marine reserves and unprotected reefs. First, PMRs were found to have a greater rate of species accumulation per unit area ($Hill_{slope}$). These results are consistent with previous findings on the slope of the power and exponential functions (Tittensor et al 2007). Also, within PMR the expected maximum richness (S_{max}) is reached sooner (smaller areas), than in NP reefs. However, the differences in S_{max} across categories were small and may be due to biogeographical similarities across reef sites and also that we collected data from adjacent reefs (PMR and NP). On the other hand, my results also show that diversity within unprotected marine reserves is no different from unprotected reefs. Previous results indicate a similar finding in relation to the abundance and biomass of fish (Chapter III). I justified the use of pooled data for this analysis given the regional similarities of the Western Caribbean reef communities, in contrast to traditional meta-analysis approach that combine results from multiple studies, across regions, and distinct biographies.

The SAR patterns observed at individual reef sites (100s m^2) were variable. Reef sites under protection (PMR) show a range of SAR patterns. Do PMRs increase variability of the diversity patterns at the reef site scale? I hypothesize that protection affects diversity patterns of the fish community. Release from fishing may induce a change in richness through changes in fish biomass. Newman et al (2006) indicate that with increased total fish biomass there is a parallel increase in biomass of fish trophic groups. However, at this scale reef sites are affected by a variable number of stressors (i.e. pollution, hurricane frequency) which may also account for the differences in SAR observed across protected reef sites. A more detailed study that accounts for the effects of reserve size, time since protection, degree of protection, island area and a wide range of replicate samples will be necessary to test these assumptions. However, the appropriate sampling protocol has been limited by the availability of truly protected marine reserves.

On the other hand, NP reefs historically have been affected by multiple disturbances varying in number and magnitude. Over time, the effects of these chronic disturbances may lead to a process of community homogenization across reef sites where only a number of generalist species survive. The similarity of the SAR pattern observed across unprotected reef sites particularly at 5 meters may be indicative of the occurrence of such a homogenization process.

Unexpectedly, I found evidence that may aid in the design and improvement of marine reserves, particularly determining the minimum reserve size. The parameter estimates (Table IV.2) indicate that maximum expected richness (S_{max}) is greater at 15 meters than at 5 meters depth, suggesting that deeper reefs shelter a greater richness. However, at 5 meters maximum richness can be attained faster and within a smaller area. These results were found consistently in PMRs and non-protected reefs, suggesting a Caribbean wide pattern. However, deeper reefs occurred less frequently within the boundaries of the marine reserves and the area of deep reefs under protection was considerably smaller. This suggests that currently deep coral reefs are being neglected from protection.

Fish diversity, fishing gradient and benthic community.

I studied the largest gradient in fish biomass in the Caribbean (Newman et al. 2006) and used total fish biomass as a proxy for the maturity of the reef fish assemblage, as it has been shown elsewhere (Friedlander & DeMartini 2002, Sandin et al. 2008). My results show that fish diversity increases until it saturates and then declines, above 300 g m^{-2}, suggesting a hump-shaped relationship. This decline in fish diversity along the gradient of fishing (a gradient opposite to that of maturity of the fish assemblage) could not have been predicted by linear models or exponential models without saturation. However, the hump shaped curve can be explained by intermediate disturbance models (Grigg & Maragos 1974, Connell 1978) and abundance-based models (Preston 1962, MacArthur & Wilson 1967). I propose that fish diversity increases faster in protected areas than in unprotected areas, until top predators accumulate enough biomass to monopolize the assemblage and start reducing the abundance of prey (Sandin et al. 2008). A lower S_{max} found at 15 m where fish biomass is higher (Chapter III), also suggest that diversity may decrease above a threshold of recovery of the fish community. This finding may be a consequence of methodological differences (expanded spatial scale) and the fact that most previous studies were conducted on reefs that are moderately or intensely degraded.

The increase in the biomass of predators is clearly associated with the increase in total fish biomass (Roberts 1995, Friedlander et al, Micheli et al 2004, Newman et al 2006), and the hump-shaped curve of fish diversity is apparent in large gradients of fish biomass (Sandin et al. 2008). This non-linear relationship is apparent only through the study of a gradient that includes relatively undisturbed sites such as Jardines de la Reina in Cuba, (Chapter III), and using non-linear models. I understand that making a species list is easier than conducting a rigorous quantitative census including fish sizes; I suggest that diversity be used in conjunction with biomass, which is a better indicator of the maturity/recovery of an assemblage, as predicted by the theory of succession (Odum 1969, Margalef 1996).

More surveys of undisturbed places such as Jardines de la Reina are needed, to fully understand the relationship between human impacts, food web structure and diversity, and to prevent a biased view of reef fish assemblages according to the shifting baseline syndrome (Pauly et al 1998). The fact that I surveyed few sampling sites with biomass above 350 g of fish m^{-2} reflects, unfortunately, the paucity of these undisturbed ecosystems. In any case, I believe this is a robust pattern, which has been shown in pristine and near pristine reefs (Sandin et al. 2008).

In a related study, Newman et al (2006) found a weak correlation among fish and benthic communities, particularly a negative correlation among macroalgae and fish biomass. Here I found evidence of both positive and negative correlations among fish diversity and cover of benthic community components. Although there is a correlation, the link between corals and the fish community has been elusive. Interestingly coral cover was positively correlated to the diversity of fish but not to biomass. It is possible that both communities are interrelated and respond to protection as well as environmental and anthropogenic disturbances in a simultaneous way. More detailed experimental studies are necessary to clarify the patterns of change across communities.

Although previous studies have shown the deleterious effects of decreased coral habitat upon fish abundance (Jones et al 2004), my results show that, for the Caribbean, fishing is a more important effect, mostly because coral biomass and cover are not significantly different between sites across the fishing gradient (Newman et al. 2006, Chapter III).

In conclusion, reef fish biodiversity increases with decreasing human impacts. Although the number of species shows a hump-shaped relationship, other biodiversity measures such as food web structure (related to the biomass of top predators and the inversion of the biomass pyramid; Sandin et al. 2008) increase monotonically (Sala & Knowlton 2006). Therefore it is necessary to combine measures of biodiversity to answer questions at appropriate spatial scales, and not stay attached to number of species as the only measure of recovery of assemblages.

Table IV.1. Model fitting for SAR using log-likelihood and AIC of marine reserves (MR) and non-protected reefs (NP). Model functions (f) were: A) non-asymptotic linear models, B) asymptotic two-parameter models, and C) asymptotic three-parameter models.

MODEL		**PARAMETER ESTIMATION**				**AIC**			
		5		**15**		**5**		**15**	
A)	**f**	**MR**	**NP**	**MR**	**NP**	**MR**	**NP**	**MR**	**NP**
POWER	**ax^b**								
R		0.96	0.956	0.966	0.964				
L		95.72	165.07	111.43	266.90	99.72	169.07	115.43	270.90
a		10.46	10.30	11.69	13.70				
b		0.24	0.23	0.24	0.20				
EXPONENTIAL	**a+b log(x)**								
R		0.994	0.993	0.996	0.996				
L		10.45	28.78	-1.37	5.45	14.45	32.78	2.63	9.45
a		-64.82	-67.19	-72.56	-69.50				
b		39.31	38.11	43.53	40.37				
LOG-LOG	**log(S)= a+b(log x)**								
R		0.939	0.931	0.950	0.938				
L		0.07	0.14	0.06	0.17	4.07	4.14	4.06	4.17
a		0.88	0.84	0.94	1.00				
b		0.28	0.27	0.27	0.24				
UNTRANSFORMED	**a+bx**								
R		0.774	0.747	0.780	0.746				
L		172.28	291.04	205.56	501.94	176.28	295.04	209.56	505.94
a		54.85	56.31	61.93	69.33				
b		0.004	0.003	0.004	0.002				
B)									
MONOD	**(a x)/(b+x)**								
R		0.987	0.986	0.982	0.968				
L		45.07	79.90	79.53	254.26	49.07	83.90	83.53	258.26
a		97.56	97.61	109.55	112.23				
b		897.04	1321.38	994.51	1717.15				
NEG EXP	**a(1-exp(-bx))**								
R		0.911	0.907	0.899	0.852				
L		130.82	218.48	166.66	437.77	134.82	222.48	170.66	441.77
a		86.79	87.51	97.73	102.21				
b		0.0008	0.0005	0.0007	0.0004				
C)									
LOMOLINO	**a/1+(b^log(c/x))**								
R		**0.999**	**0.999**	**0.999**	**0.999**				
L		-71.76	-229.29	-183.02	-255.70	**-65.76**	**-223.29**	**-177.02**	**-249.70**
a		110.11	109.88	128.09	134.26				
b		5.25	5.15	4.65	3.94				
c		1150.63	1667.02	1405.88	2516.71				
WEIBULL	**a(1-exp(-bx^c))**								
R		0.997	0.998	0.999	0.998				
L		-23.61	-80.18	-78.06	-127.02	-17.61	-74.18	-72.06	-121.02
a		97.22	97.17	111.13	116.88				
b		0.02	0.01	0.02	0.02				
c		0.55	0.55	0.53	0.47				

Table IV.2. Wald-Wolfowitz test for differences among treatments using location parameter estimates. See text for parameters description.

	Parameters	NP	MR	Z	p
5 m	Smax	77.74	82.37	0.00	1.00
	HILLslope	1.84	2.07	-2.29	0.02
	A50	1196.45	771.90	-2.29	0.02
15 m	Smax	80.80	74.50	1.53	0.13
	HILLslope	2.18	2.51	2.29	0.02
	A50	2828.24	411.06	-0.76	0.45

Table IV.3. Correlation analysis among fish diversity and cover of benthic organisms across a gradient of fish biomass. Significant differences shown in bold cases. Benthic community components: Crustose Coraline Algae (CCA), Coral, Sponge, Turf algae (TURF), Calcareous Erect (C.E.) and Fleshy macroalgae as in Appendix III.

DEPTH	5		15	
N	172		224	
Fish Richness vs	R	p	R	p
CCA	**-0.186**	**0.015**	**0.132**	**0.049**
CORAL	**0.251**	**0.001**	**0.164**	**0.014**
SPONGE	-0.077	0.318	**0.192**	**0.004**
TURF	0.106	0.168	0.031	0.648
C.E. MACROALGAE	**0.302**	**0.000**	-0.108	0.108
FLESHY MACROALGAE	0.023	0.769	**-0.164**	**0.014**

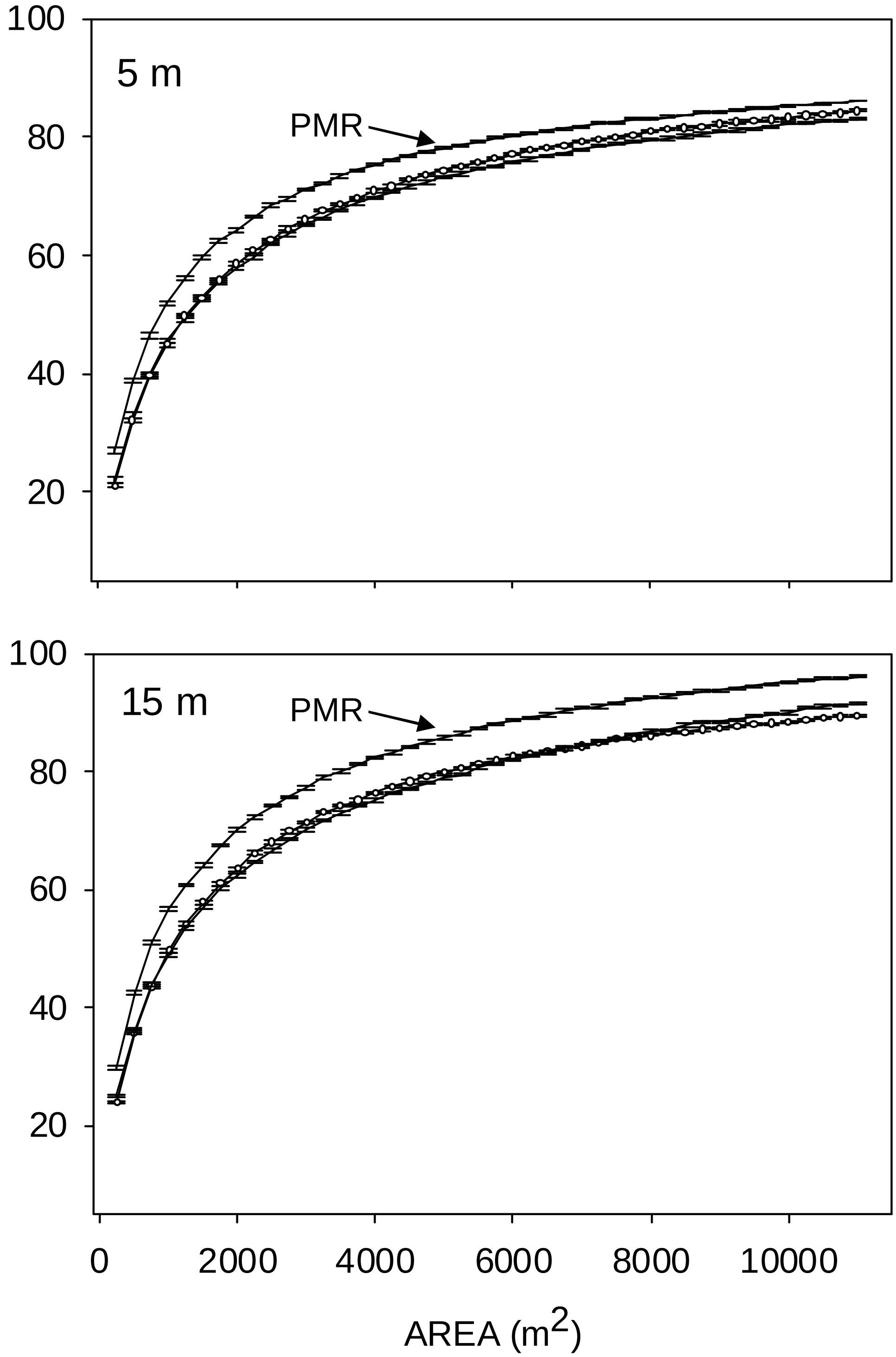

Figure IV.1 Comparison of the species area relationship between categories of protection and depths. Pooled data from all marine reserves (PMR), marine protected areas (UMR, empty bullets) and unprotected reefs (NP, line). See test for analysis details.

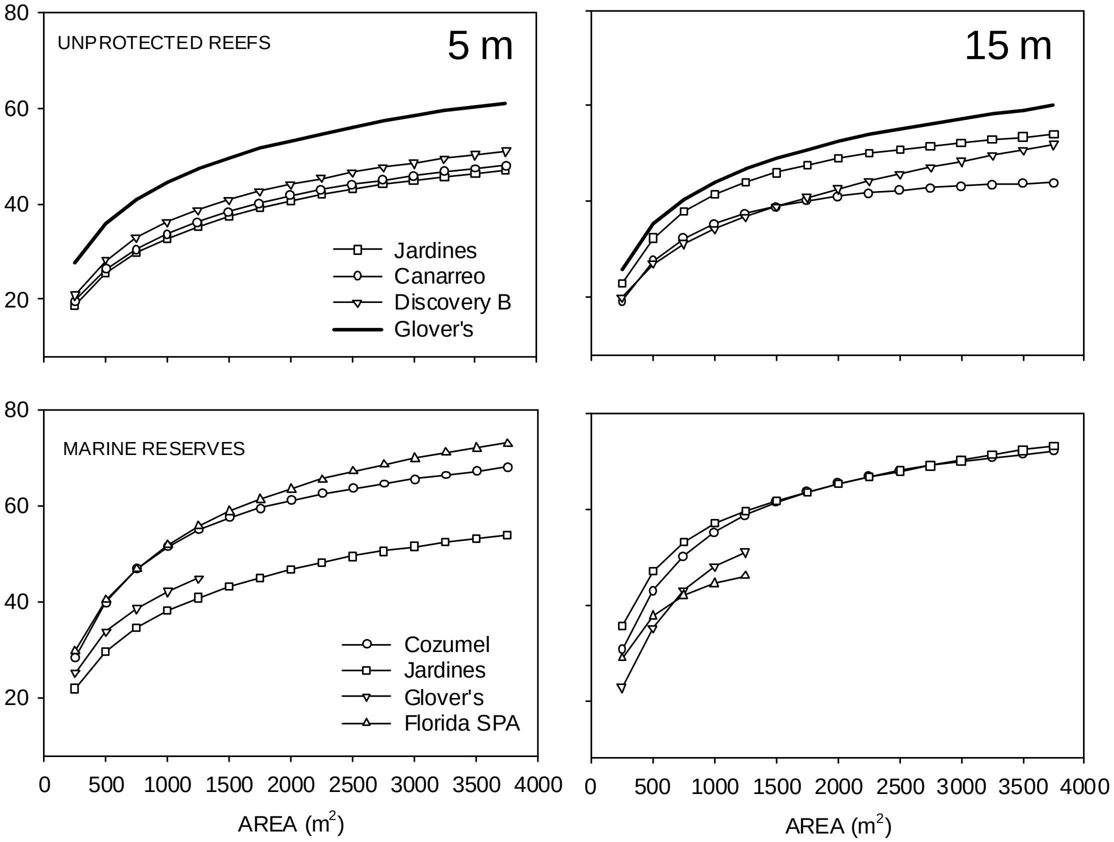

Figure IV.2 Comparison of species area relationship across Western-Caribbean reef sites. In some marine reserves the area under protection was too small to survey more than 5 transects. Unprotected marine reserves are not presented for clarity and given the regional patterns shown in fig 4.1.

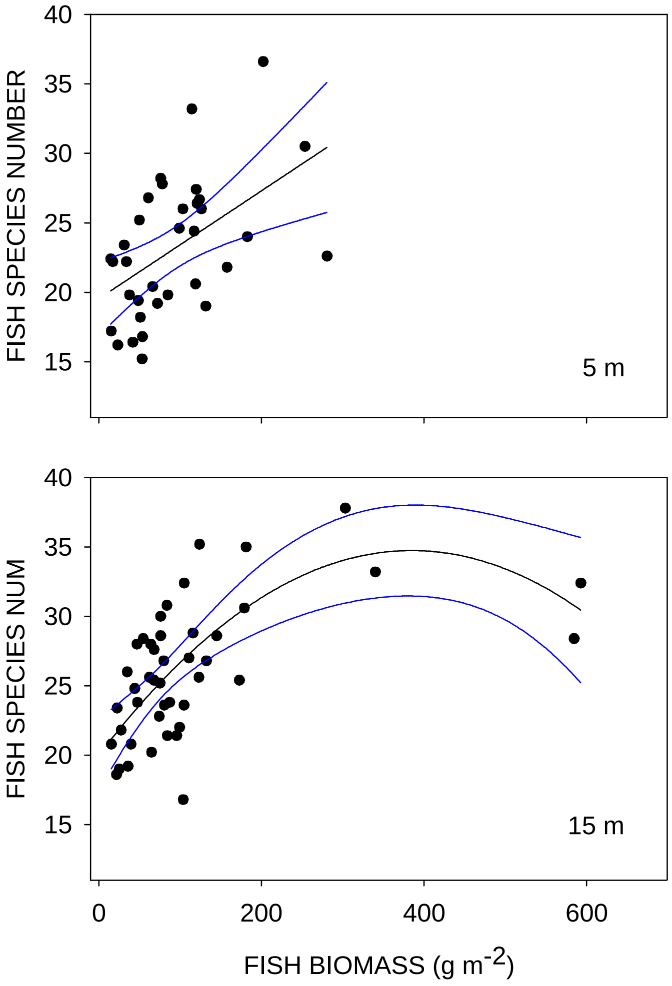

Figure IV.3. Regression analysis (line, ±C.I.) between fish biomass and fish species richness. Fish biomass represents the regional gradient. Species number and fish biomass shown are averaged from local reef sites (n=5). Analysis was repeated using transect data and results were similar.

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CHAPTER V

GENERAL DISCUSSION AND CONCLUSIONS

In this dissertation I described the effects of chronic human impacts on Caribbean reefs. I also conducted a community-wide assessment to evaluate the effects of marine reserves and the conservation status of coral reef biodiversity. My results provide evidence of the relative success of conservation actions within the region and the issues that need further attention.

The degradation of a coral reef ecosystem in a nutshell

Anthropogenic exploitation of Caribbean coral reefs can be traced back to the time of human arrival to the Caribbean coast, based on archeological and historical records. Humans were progressively affecting the community structure of coral reefs (Pandolfi et al 2003). We cannot know the full extent of the effects of primitive and archaic exploitation on the community structure. Some evidence indicates that in the last few centuries the intensity of exploitation has increased (Jackson 1997, Jackson et al. 2001, McClenachan et al. 2006). However, in the last 40 years coral reefs have dramatically changed (Hughes et al 1994, Knowlton 2001, Aronson et al 2002, Huges et al 2003, Lessios 2005). From my perspective it seems that the synergistic effects of multiple anthropogenic disturbances are the ultimate reason of the modern state of degradation in Caribbean coral reef ecosystems.

Ecosystem degradation was more evident in recent times with the evidence of the deterioration of the reef framework (Hughes et al 1994, Aronson et al 2002, Pandolfi et al

2003, Pandolfi and Jackson 2006). The descriptions of Caribbean benthic communities from early ecological studies depict complex and thriving coral reefs (Goureau 1959, Lewis 1960), and the early signs of decline were not identified as such by modern ecologists. Then in the late 1970s reef building corals were affected by diseases across the Caribbean. Initially there was a dramatic decrease in the abundance of weedy corals, and eventually the damage was evident in all coral populations. Consequently, it was estimated that the abundance of coral declined up to 80% in shallow reefs over the following decades (Gardner et al 2003). Chronic overfishing of fish populations was likely to simplify fish food webs (Roberts 1995, Jennings and Polunin 1996, Pauly et al 1998). It is likely that there was a reduction in the abundance of herbivorous fishes due to overfishing. However, the reduction in fish herbivory remained unnoticed, while high levels of grazing were maintained by sea urchin populations (Done 1992). However, in the early 1980s the sea urchin *Diadema antillarum* was affected by an unknown disease that eliminated over 95% of its population (Lessios 1988). After the sea urchin die off, a shift from coral- to macroalgal-dominated communities occurred. The combined effect of available space from coral mortality and reduced grazing intensity was a key factor for this shift (Aronson et al 2004, Knowlton 1992). Across the Caribbean Sea, sea urchin populations have not recovered from the die off (Lessios 2005), but some exceptions have been documented (Edmunds and Carpenter 2001, Idjadi et al 2006). Remarkable exceptions are also marine reserves where extractive activities have been banned and are effectively enforced. However, in these cases my data indicates that only a fraction of the ecosystem has managed to recover (Chapter III).

Additionally, increased water temperature from human-driven climate change (Baker 2007, Solomon 2007) represents a major threat to coral reef ecosystems in the Caribbean and worldwide (Hoegh-Gulberg 1999, Knowlton et al 2001, Orr et al 2005, Donner et al 2007). In the Caribbean the plethora of anthropogenic disturbances magnifies the effects of bleaching and coral mortality, limiting recovery and reef accretion.

Given the gaps of information, a rigorous test of the cause-effect of Caribbean coral reef decline is impractical. While a strict hypothesis-testing approach is difficult to conduct because we have been running a large uncontrolled experiment for centuries, it is clear that increased human population in the region is the major cause of ecosystem degradation in the Caribbean. Moreover, it is all human impacts together that degrade reefs, and I believe that the obsession with quantifying the relative role of every single stressor under every circumstance does not let us see the forest for the trees (Pandolfi et al. 2005).

Previous ecological studies in the Caribbean have typically dealt with small taxonomic, spatial and temporal scales (but see M. Hardt's PhD Thesis, 2006). The problem is that we cannot generalize or extrapolate their results from patch reefs to understand the ecosystem functioning on a larger scale. Although there are multiple monitoring efforts across the region (Marks 2005, Chiappone et al 1997), our understanding of the current health of the reef ecosystem is fragmented. Unfortunately, most monitoring studies target a portion of the community and have not provided a complete picture of the ecosystem functioning nor been designed to test specific questions such as the effects of marine reserves. Yet, meta-analytical approaches have filled some gaps of information and provided a description of the decline in coral reef health. A good reason for the absence of large scale studies that target the entire community was probably due to difficulties in collecting this type of data, the logistical limitations, and statistical capabilities to analyze the data that existed in the past. In this dissertation I collected data on the entire coral reef community across a significant geographic area with a small group of researchers. While the time it took to complete the survey was relatively short, the results and power of the conclusions that we can draw present a much better representation of the ecosystem functioning across a gradient of human pressure. While I could not find many encouraging results on the effectiveness of reserves, I can ascertain the urgency of bolder conservation actions.

I must recognize that small scale studies will remain necessary, especially in the Caribbean, where the recovery of the benthic community is likely to occur on a small, patchy scale. We must, somehow, track the conditions that favor the sporadic recovery events and find a way to replicate them on a larger scale.

What has my dissertation added to the body of knowledge on the degradation and recovery of Caribbean coral reefs? The trajectory of an ecosystem along succession is asymmetrical: it takes a long time for information/structure to accumulate, but collapse tends to be sudden and dramatic (Odum 1969, Margalef 1996). Our knowledge of ecosystem trajectories is also asymmetrical in the same sense: we know much more about degradation than about reassembly/recovery. During five years I attempted to address degradation at an appropriate temporal and spatial scale, and also to examine recovery at the community level.

The role of marine reserves

is the removal of humans sufficient for ecosystem recovery?

In his recent book “The world without humans” Alan Weisman (2007) asks the question what would happen to the biosphere if humans suddenly disappeared. He clearly shows that our footprint will be evident on the planet, including the oceans, for millennia. The questions follow: What do we need to do to reverse the trajectory of degradation of a coral reef ecosystem? Would it be sufficient to ban human access and leave a coral reef “alone”? In other words, will marine reserves do the job with no further intervention?

Part of the solution to the ecological crisis in the Caribbean has been approached by the creation of marine protected areas (MPAs) where human exploitation of the ecosystem is limited (partially-protected MPAs) or eliminated (no-take marine reserves). Reserves are expected to help in the recovery of ecosystems and complement fisheries management. Yet, the use have been questioned by critics due to poor evaluation of their effectiveness, and because their value as tools for the enhancement of fisheries through spillover is limited to a few hundred meters outside of their boundaries (Gell & Roberts 2005, Goñi et al. 2006). A major problem is that recent attempts to evaluate the effectiveness of MPAs focus on meta-analytical assessments and single populations/guilds approaches (e.g., Halpern 2003). A complete ecosystem assessment cannot be conducted with the amount of information available from individual studies as meta-analysis suggests (Guidetti and Sala 2007).

To try to help solve this problem, I focused on a regional assessment of the effects of marine reserves that captures the regional variability of the structure of the reef communities, and across the gradient of conditions that is likely to influence the outcome of marine reserves. Here I presented the first assessment of reef community response to management using marine reserves across the Caribbean. I hypothesized that the response of the community to protection depends on the local conditions at the onset of protection.

My results show that the changes in reef assemblages in relation to protection were variable, possibly due to differences in the local histories of exploitation, the range in characteristics of marine reserves including size and the degree of enforcement of protection. Yet, the fish community within large and effectively protected marine reserves consistently showed a positive increase in biomass compared to nearby reefs. This increase in fish biomass has important consequences in the diversity and structure of the fish food web. The expected maximum number of species was greater and a larger number of species were found per square meter of reef. Fish diversity increases until a threshold is reached beyond which top predators are likely to regulate the abundance and diversity of lower trophic levels, and fish diversity declines slightly. However, the effects of protection upon the abundance and diversity of other ecosystem components such as corals was very limited. In particular, corals have slow turnover rates and growth, so that we expect longer times of recovery that surpass the time that most reefs have been under protection. Because stressors are all increasing, particularly the rise in sea surface temperature, the expectations of significant coral recovery are not great.

Thus, my results clearly show that marine reserves alone are not likely to cause the recovery of the coral reef ecosystems. The most dynamic parts of the ecosystem, namely reef fishes, respond quickly and positively, exhibiting trajectories that correspond to a trend in the maturity of succession. Benthic communities, however, appear to be relatively unaffected by protection and the increase in fish biomass. There are some signs of hope (Edmunds & Carpenter 2001, Newman et al. 2006, Mumby et al. 2006, 2007), but they are too local and have not yet reversed the trends in coral community structure at any significant spatial scale. Macroalgal biomass has diminished with an increase of fish biomass in reserves, but this reduction has not yet been sufficient to reduce algal cover and enhance the recovery of corals. This is a textbook example of hysteresis.

Moreover, not all MPAs are the same. MPAs will have an impact on the ecosystem within their boundaries that is a function of their size, location, initial ecological conditions, and the local history of marine resource exploitation. Moreover, not all MPAs are true no-take marine reserves. Unsuccessful examples of MPAs are common. In the Caribbean only 25 marine reserves exist (covering <10% of the reefs), while the rest are not effectively protected MPAs (Mora et al 2006). In some cases we found evidence that insufficient protection/enforcement may be more deleterious than not protecting the reefs at all. This is probably due to a reverse “reserve effect” whereby legal and illegal fishermen are more attracted to fish inside the reserve because of the expectation of greater catches; the irony is that there will be no greater catches if there is more fishing inside the reserve.

I have shown with ecological data how protection has an important effect upon the fish community. I am convinced that the establishment of a network of large, fully protected marine reserve is urgent. But how realistic this task may be depends on the governments of the Caribbean countries and/or local communities committed and organized to protect their resources. On the other hand, from a more naturalistic perspective, I observed a relationship between the isolation of a reef site and the improvement in the health of the benthic community, particularly corals. Similarly, the occurrence of non extractive exploitation of the reefs (i.e. diving) seems to correlate to decreased fishing and a relatively healthier seascape. However, a rigorous test of this assumption is more difficult and would need a dissertation with a more socio-economic approach. Particularly in Cozumel, the density and frequency of diving activities is such that fishermen have no opportunities to fish around the reefs. In this case enforcement of protection has not been necessary, but protection is effective. A similar situation was observed in Montego Bay (Jamaica) and San Pedro (Belize) but at a smaller scale. Recovery without protection was observed in reefs where human impacts are reduced due to the distance from human populations, such as in Dry Tortugas and Montego Bay. The coral community seems to benefit more from isolation and this may be an indication that water quality may decline near coastal cities having an impact on the replenishment and survival of the coral community These observations may be combined with future conservation and restoration actions such as sea urchin re-population, water quality control and marine reserves without which the recovery of Caribbean reefs would be very difficult.

The future of Caribbean coral reefs

Coral reefs are facing global warming in addition to the direct anthropogenic impacts already mentioned. While some conservation actions such as marine reserves aim at protecting the communities from local anthropogenic disturbances (particularly overfishing), there is little they can do to protect reefs against global disturbances such as the rise in seawater temperature and acidification (Bellwood et al 2004, Jameson et al 2002, Donner et al 2007), apparently increasing hurricane frequency and severity (Gardner et al 2005), and pollution (Ross and DeLorenzo 1997). However, it is important to recognize that relatively undisturbed communities are more resilient and have better chances to recover from impacts such as coral bleaching (Knowlton and Jackson 2008, Sandin et al. 2008). A reserve can thus reduce the impacts of global disturbances, in the same way that the reintroduction of top predators on terrestrial ecosystems have helped buffer the impacts of climate change (Sala 2006).

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APPENDIX I

HISTORICAL ECOLOGICAL TRAJECTORY OF THE MESOAMERICAN REEF SYSTEM

Abstract

I reviewed the ecological history of the exploitation of the Mesoamerican Barrier Reef using the paleontological, archaeological, anthropological, historical and ecological records of human exploitation of the marine environment. I collected information of the fishing activities and impacts related to the reef fauna, and characterized the use of marine resources during four main cultural periods: Prehistory, Maya civilization, Colonial and Modern. During Prehistory exploitation may have started around 2,000 B.C but records were scarce due to the sea level rise. The Maya people lived along the coast of the Mesoamerican reef and made use of manatee, turtles, sea snails and reef fishes as sources of food and tools. Initially, indigenous fishing technology was limited to near shore hand collecting and harpooning, with rudimentary use of nets and other tools. Boats and a network of maritime trade were later developed. Archeological records indicate that the Maya seafood production went from a few tens of tons to hundreds of tons a year. Initially, in Cozumel Island seafood remains were dominated by crabs and fishes (45%). Later sharks, stingrays, crocodiles and turtles became an important part of the catch. Throughout the colonial period the Spaniards documented that native people targeted several marine species: manatees, reef, pelagic and estuarine fishes, turtles, sharks and monk seals. Colonials also developed a variety of uses for marine animals and improved fishing gear (i.e. iron hooks) during this period. Yet, most colonial records still

remain in old archives and a more detailed assessment is necessary to quantify their fisheries. The modern period formally starts with the collection of fishing statistics in 1940 by the Food and Agriculture Organization. At the beginning commercial seafood production was relatively low (10 tons/year) across the region. A rapid increase in seafood production occurred in 1970s with the introduction of more mechanized fishing technology (large vessels, outboard motors and nylon nets). Over the past decades the total MBR production of seafood increased to 25,000 tons/year. Catch composition in comparison to earlier cultural periods was significantly different. Lobster, reef and pelagic fishes, conch and shrimp were the most common catch in modern fisheries. By the end of the modern period monk seals were killed to extinction, manatee and turtle populations were greatly reduced, reefs sharks became ecologically extinct and many fish spawning aggregations disappeared. More recently the decline of coral abundance, eutrophication, overfishing of herbivore fish populations, and the mass mortality of *Diadema antillarum* in 1983, combined to allow a shift in the ecosystem from coral to algal dominated. It is notorious that Maya fishing continued for hundreds of years, while modern fisheries have declined in a less than hundred years and induced massive changes in the food web structure. In summary, the impacts of humans throughout time have induced the homogenization of biodiversity in the MBR and ecosystem decline. Thus, ecologists must relay their expectations of recovery on more realistic baselines. Future coral reef conservation must focus on ecosystem-wide conservation actions (i.e. marine reserves) and science-based management to accelerate recovery.

Introduction

Coral reefs have been increasingly degraded worldwide by overfishing, disease, pollution, and global warming (Hughes 1994, Lessios 1988, Jackson et al 2001, Bellwood et al 2004). In spite of the impacts of recent disturbances such as pollution and global warming, fishing appears to predate all other disturbances to coral reefs (Jackson 2001, Pandolfi et al. 2003). Large herbivores and carnivores were extirpated long ago from most reefs (Jackson 1997), and presently apex predator biomass of non-fished reefs, within marine reserves, can be up to 18 times higher than in fished reefs (Friedlander et al. 2002, Newman et al 2006). Although there is strong evidence for global patterns of historical reef decline (Pandolfi et al. 2003), the detailed ecological history of a coral reef and the role of fishing throughout human history has yet to be described. Understanding ecological history and its relationship to anthropogenic disturbances is essential for understanding the present state of coral reefs, the factors responsible for changes and ecological interactions, and for assessing the feasibility of successful management and restoration (Jackson et al. 2001, Pandolfi et al. 2003).

The MBR suffers from overfishing, with one species, the Caribbean monk seal already extinct, several other vertebrates such as sea turtles, manatees and sharks are also threatened (O’Donnell 1981, O’Shea 1991, Musick et al 2000, MacClennachan et al 2006). Fisheries, such as that of the Nassau grouper are on the verge of commercial extinction (Sala et al. 2001), and I do not know how many species are commercially extinct already. In addition, many reefs recently shifted from a coral-dominated to an algal-dominated state (Lessios 1988, Knowlton 1992, McClanahan et al. 1999), suffered extensive bleaching (Aronson et al. 2000), and have failed to recover from hurricanes

(Knowlton 1990). In this study I illustrate whether the present state of the MBR coral reefs is a consequence of recent anthropogenic impacts, or the result of recent changes in exploitation of the marine resources. This work does not intend to be an exhaustive historical review, but an estimation of the magnitude of the changes associated with the main patterns of exploitation of the MBR ecosystem. Here I describe a historical trajectory of impacts upon the reef ecosystem and assess the role of anthropogenic impacts in the Mesoamerican Barrier Reef (MBR) ecosystem.

Study area

The MBR is located in Central America, extending from Contoy Island North of the Yucatan Peninsula (Mexico), south to the Bay Islands (Honduras) (Fig. A.1). It includes the second longest barrier reef in the world, which extends approximately over 800 kilometers, paralleling the coast at a distance of 10 to 40 km. The MBR ecosystem is composed of coral reef islands and atolls, soft bottoms, mangroves, and complex coastal lagoon systems (Almada-Villela et al 2002).

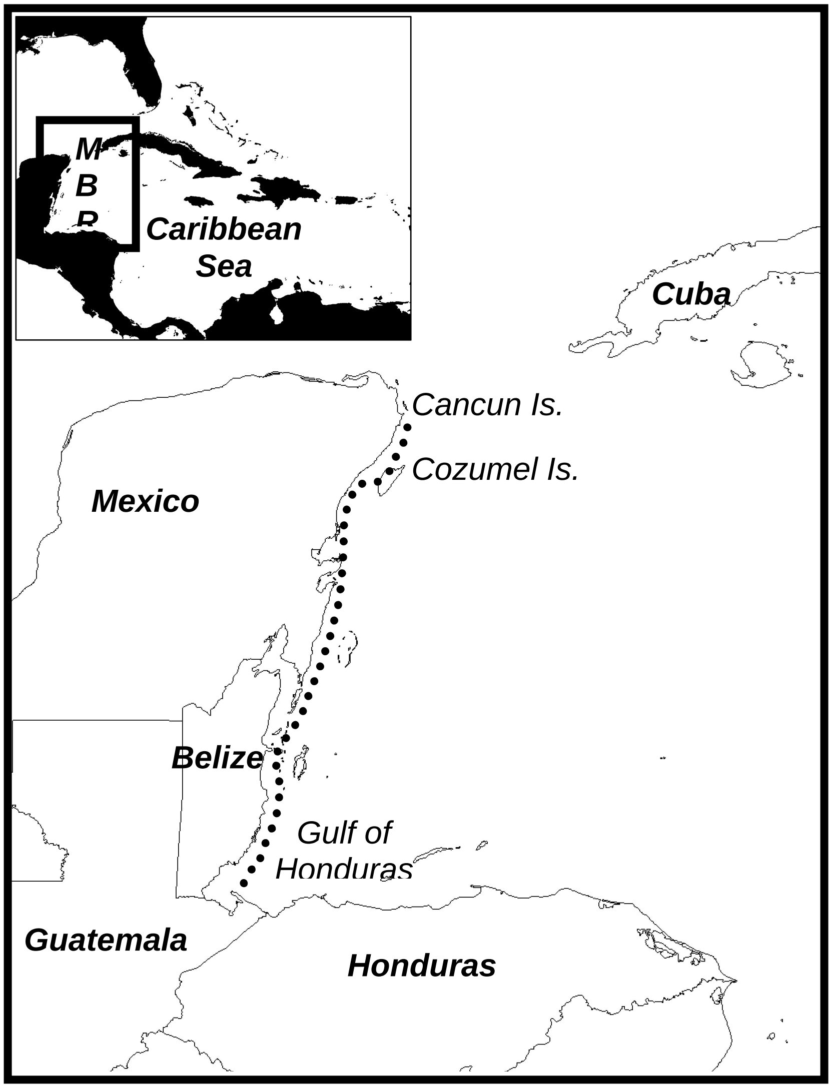

Figure A.1. Location of the Mesoamerican reef (dotted line), Western Caribbean Sea (inset), and the countries with important historically use of marine resources from the MBR ecosystem.

Material and methods

I conducted a search on paleontological, archaeological, historical, ecological and fisheries records, from the pre-human period to present, and pooled data in four culturally defined time periods: prehistory (11,000 B.C. to 1,800 B.C.), Maya period (1800 B.C. to the 1650s A.D.), colonial (1650s to 1900), and modern (1900 to present). I obtained estimates of human population abundance for the territories that connect to the MBR (Yucatan peninsula and Belize) as a reference for the context for the exploitation in the region.

For each period I characterized human population density and spatial distribution, fishing activities (e.g., technology, target species, preservation methods, trade), and uses of marine products (e.g., food, ornamental, ritual). For the Prehistory, fisheries were characterized using records of specific remains found in archaeological middens. Additionally, to describe the colonial and modern fisheries I relied on accounts of fisheries from qualitative descriptions from historical records, naturalist and explorer reports, and fisheries reports (i.e. country fisheries statistics).

Pre-historical fisheries throughout time were characterized by estimating the seafood consumption within coastal settlements using the archaeological remains descriptions. First, I identified the coastal settlements in the area were marine animal use was an important part of the diet, based on the midden remains. Then I characterized the exploitation of the MBR at near pristine state by quantifying the abundance and relative importance of marine animals in the diet of the first natives. I estimated the biomass of seafood from midden remains using the minimum number of individuals (MNI) and the average weight of the species. From archeological records I obtained the marine animals

MNI corresponding to one human settlement from Cancun during the pre-Classic Maya ca. 800 B.C. (Andrews 1975) most likely to be from one generation/family. Average weight of each species found in middens was obtained from the literature (Froese and Pauly 2003). The relative importance of each species in the diet of natives was then calculated based on biomass estimates.

To characterize marine resources use throughout Maya period I used a detailed midden description from a Maya coastal settlement in Cozumel Island (Hamblin 1984) that describes the food remains occurring in a period of nine centuries. Cozumel is an ideal example for prehistoric marine exploitation since the population was isolated and I could assume marine animals were ultimately necessary for food as sources of protein. Using habitation records (Culbert and Rice 1990) I estimated the number of humans inhabiting Cozumel at each Maya sub-period described in Hamblin (1984). First, I estimated the hypothetical seafood consumption per individual per year. Alroy (2001) hypothesized that prehistoric human required a minimum of 64 gr of protein a day. Based on the proportion of terrestrial to marine remains found in Maya midden records (Andrews 1975, Mckillop 1984, Hamblin 1985, Shaw 1995) I conservatively assumed that 50% of the protein in Maya diet was from seafood. Thus, the estimated Maya seafood production a year equals the total human population during each period, times the protein intake from seafood (32gr/day) times 365 days. Assuming the proportion of remains from the different species found in the middens corresponds to the relative consumption of seafood types (during each period) I determined the production of fish, crab, shark, stingrays, crocodiles and turtles. Finally, I compared the species composition from Cancun and Cozumel archaeological records.

To describe the marine animal exploitation in the MBR during the colonial period I relied on written accounts and sporadic tax records from the historical literature. Evidence of the magnitude of the colonial exploitation of reefs is still in museum archives and a more comprehensive study will be necessary to quantify the details of the fisheries exploitation during this period of history. Due to time constrains and broader objectives of this dissertation I describe the colonial fisheries in a very general summary.

Finally, in order to describe the modern marine exploitation in the MBR I analyzed the Food and Agriculture Organization (FAO) fisheries statistics from 1946 to present. I pooled the catch records of reef related species throughout time for the 4 countries neighboring the MBR: Mexico (yucatan peninsula only), Belize, Honduras and Guatemala (Atlantic only).

Results

Pre-historical exploitation of marine resources

I assumed that coral communities were not affected by human activities throughout this period due to the low human population density (21 ind/100km^2). Corals of the genus *Acropora* dominated shallow Holocene reefs for thousands of years including prehistory (Aronson et al 2002, Pandolfi and Jackson 2006). Reef fish paleo-communities may have been similar to modern, but records of the assemblage structure are scarce (Aguilera and Rodrigues 1999, Nolf 1992). Unfortunately, I did not find estimations of the abundances of reef fishes.

The prehistoric period begun with the first human occupation of Central America at least 8,000 years ago (Willey 1960, Cooke 1998, Fix 2002), and ended at the beginning of the Pre-classic Maya period in 1800 B.C. (Hamblin 1984). It is also likely that primitive humans arrived to the region by 11,000 B.C. (Fiedel, 1999, Gonzalez-Jose et al. 2003). Population density was no more than 21 people per 100 km^2 (Alroy 2001), and likely distributed near rivers and in coastal areas (Sauer 1962, Fix 2002). At the same time other hunter-gatherer communities developed within inland territories (Brush1965, Cooke 1998). Records of habitation are found more frequently in the Pacific coast of Mesoamerica for this period of time (Voorhies et al 2002, Cooke 1992). Caribbean records of habitation may have been erased due to sea level rise. Sea level rose from -20 meters roughly 7,000 B.C. to -0.4 m in 400 B.C. (Pomerol 1982), drowning durable records of human activities near the coast, although, some records have been unearthed in recent excavations (Mckillop 2005). Therefore I was not able to fully detail the exploitation of marine organisms by humans during this period. However, given the diversity and advanced fishing technology found in later periods (Lange 1971) I assume from the archeological evidence that humans probably started using fishing gears very early in time (Eaton 1978).

Change from nomadic to sedentary life occurred ca. 3000 B.C. (Brush 1965). Hammond (1976) indicates that the Yucatan peninsula was already occupied by 2600 B.C. Village life developed around primitive agriculture; settlers were bordering large waterways and survived hunting small mammals and other rainforest resources (Willey 1960, Coe 1964, Cooke 1998). Archaeological evidence indicates that manatee was used in Cancun Island as early as 2000 B.C. (O'Donnell 1981). Early human settlements were primarily around rivers and inland territories, but the development of the exploitation of marine resources along shorelines could have occurred early in time.

Maya period

The early Maya

This period ranged from the beginning of the Archaic Maya period (1800 B.C.) to the end of the pre-Classic around 250 A.D. (Coe 1999). Population growth was slow and human population density was in the range of 20 to 69 ind/km^2 scattered over the Yucatan peninsula, approximately 185,000 km^2 (Deevey 1975). There were larger settlements inland, maintained by incipient agriculture (Culbert and Rice 1995) while coastal settlements were generally small and based on marine resources and some agriculture (Freidel 1978, Teeter 2001). Records of coastal habitation and seafood remains do not appear in the Caribbean coast until the late pre-Classic (Andrews 1975, Hamblin 1985, Graham and Pendergast 1989, Dunn and Mazzullo1993). The archeological evidence was swamped due to sea level rise (McKillop 2005). By this time, Inland settlements developed agriculture and exploited river resources (Masson 1999).

Archaeological records of the diet and animal use were found from middens of Maya settlements along the entire MBR coast. Midden remains indicate that the Maya hunted manatee (*Trichechus manatus*) (Mckillop 1985), turtles, a large number of species of gastropods, crabs and reef fish (Table I.1). Large species were abundant in archeological middens; in order of importance there were conch (*Strombus gigas*), turtles (Chelonidae), Goliath grouper (*Epinephelus itajara*), lightning whelk (*Busycon contrarium*), manatee, other mollusks (up to 99 snail species) and sharks (Carchariinidae). They probably collected mollusks inside lagoons by hand (Sauer 1962, Andrews 1969); fishes were caught using turtle shell hooks, nets and harpoons (Ball 1972).

The degree upon which Maya settlements relied upon marine resources was variable. For example, while in Cancun the remains found in middens were nearly 100% from marine animals (Andrews et al 1975), in other settlements such as Cozumel 40% of vertebrates were marine and 60% terrestrial (Hamblin 1985). Invertebrates (snails, mollusks and crabs) were always present, but species were not always quantified in the archeological studies reviewed. Although I found that in some cases the marine vertebrate to invertebrate ratio is 1:1 (Andrews et al 1975). Thus, the proportion of marine animals to terrestrial vertebrates in the diet of natives was probably 58:42.

Fishers had limited technology at the beginning of the period (hand collecting and harpoons) but later on, evidence of notched shards suggest development of net use, alongside pumice spheres that probably worked as buoys (Eaton 1976, Freidel 1978).

Most of the archaeological remains show no signs of secondary use of marine organisms, except for tools made out of conch and turtle shell (Thompson 1932, O'Day and Keegan 2001).

I calculated the fishing effort in terms of seafood biomass, based on the midden remains of a settlement) from Cancun Island during the early Maya period (above). Based on the species composition, the species biomass estimates, and assuming conservatively that 50% of the catches were marine vertebrates and 50% marine invertebrates I determined the relative importance of species in the diet/fisheries corresponding to this midden (table I.2). In general, conch (*Strombus gigas*) was the most important item followed by turtles, Goliath grouper (*Epinephelus itajara*), lighting whelk (*Busycon contrarium*) and manatee.

These estimates are rather conservative because of obvious preservation problems. Up to 70% of invertebrate record can be lost by natural decomposition (Kiddwell and Bosence 1991). Bone preservation in the Caribbean is bad due to the effects of the tropical climate (i.e. high humidity). Additionally, archeological records in coastal regions may be scarce possibly due to fishing preservation techniques, and trade (Teeter 2001).

Using archaeological remains data from Cozumel Island (Hamblin 1985) I also found that an estimated population of 1600 people living in the Island during the early Maya period was able to catch up to 16.8 tons of fish and 1.8 tons of crab a year (Table I.3). I based this estimate on the assumption that 50% of the minimum daily protein requirement by primitive humans (64g/day) was of marine origin (see methods).

The Classic and Post-classic Maya

This period comprehends the climax of Maya civilization and extended from 250 A.D. to the arrival and colonization by Europeans (early 16th C.). Maya population reached a density of 140 ind/km^2 in large cities of the Yucatan peninsula and 100-200 ind/km^2 in the Belize River Valley (Sanders 1962). During the Classic large part of the population was concentrated on inland territory but during the Post-Classic 80% of the population lived within 50 km of the coast (Sanders 1962, Rathje and Sablof 1973). However, during post-classic human population was in decline across Mesoamerica (Coe 1999). The decline of the Maya civilization may be correlated to both political instability and crop failure due to unusual climate (Leyden 2002, Haug et al. 2003). Agricultural produce was not sufficient to support a population of millions; which probably led to migration to coastal areas (Culbert and Rice 1999). Consequently I found more evidence from archeological records indicating extensive use of marine products during this period (Lange 1971, Rathje 1971).

The Maya economy was increasingly supported by a wide range of products either marine or terrestrial, which was facilitated by marine trade (Bloom 1932, Rathje 1971, Turtellot and Sabloff 1972, Hamblin 1985, McKillop 2005). The total biomass of seafood estimated for the post classic period was five times that of the pre-classic (Table I.3). I estimated that Cozumel Island's fish production went from an estimated 21 to 95 tons/year from early pre-classic to the end of Classic respectively. Crab production also increased during this period from 2 to 20 tons/yr, but interestingly the ratio of fish to crab exploitation remained 10:1 for centuries. Similarly, I found that other marine animals such as sharks, stingrays, crocodiles and turtles were increasingly important part of the catches (Hamblin 1985). The most common bony fishes found in archaeological remains are groupers, jacks, snappers, parrotfishes, grunts and stingrays (Teeter 2001).

I found that many other MBR coastal settlements like Cozumel existed along the MBR. There were at least five Maya settlements with similar population and evidence of marine animal exploitation: Tulum, Cerros, Ambergris Cay, Moho Cay and Wild Cane Cay (Miller 1974, Mckillop 1984, 1987, 1996, Graham and Pendergast 1989, Guderjan 1995, Pyburn et al 1998). This evidence may entail that the regional production of seafood could have reached a total of 696 tons/year conservatively. Additionally, inland Maya settlements (Altun-Ha, Cuello, Dzibilchaltun, Mayapan, Caracol, Colha, Kichpanha and Lubaantun) also show evidence of heavy marine animal utilization (imported marine items). For example in Colha 93% of the remains found in an archaeological midden were fish and turtles (Teeter 2001). In some coastal settlements manatee bones account for up to 89% of the animal remains (Mckillop 1985).

The Maya fishing technology was diversified and included sink nets, hook and lines (Andrews 1975), trained remoras (Fernandez de Oviedo 1959), buoys, traps (O'Day and Keegan 2001) and canoes (Eaton 1970, Mckillop 2005). Most fishing gear was made from non perdurable materials such as bones and fibers therefore only partial fishing gear was found in archeological records. Some evidence of Maya fisheries was also recorded in paintings in temple walls (Baughman 1952, Covarrubias 1957**,** Miller 1974).

The Maya people employed marine products such as coral, pearls, marine shells (*Spondylus* sp. and *Olivella* sp.), sawfish (*Pristis* sp.) and porcupine-fish (*Diodon* sp.) as ornamental items. Manatee bones were used to build musical instruments and figurines (Mckillop 1985). Also, cooking tools were made from conch-shell blades, shark skin for sand paper, and war tools from shark teeth and turtle carapaces (Andrews 1975). Remarkably, sea turtles were very abundant by the time Europeans arrived to the Caribbean (Jackson 1997). Yet, the variety of uses of turtle shells (tools and ornaments) could be the reason why so few turtle remains were found in coastal middens.

The Maya people also employed marine products for ritualistic or ceremonial purposes; the main items found in burials were conch, shark teeth and sting-ray spines, sea shells, sand dollars and sea urchin spines (Andrew 1969, Borhegyi 1961, Kozuch 1991). The use of marine products was varied during Maya Climax (Lange 1971). Mckillop (1996) noted that use of marine products changed with distance from the shore; coastal communities consumed seafood, but inland seafood was more frequently intended for elite consumption and ceremonial purposes.

The heterogeneous distribution of resources in Maya territory made necessary the invention of long distance trade (Rathje 1971). Maya moved along rivers in small canoes transporting goods to the coast where a number of products were transshipped to large canoes, with capacity for up to 40 people (Roys 1943), for sea transportation; they could navigate from 10 to 300 miles (Winzerling 1946, Friedel 1978, Guderjan and Garber 1995). Salt was a key product of the sea trade along which obsidian, agricultural products and pottery were included. Reliable sources of salt also made possible fish preservation and transportation (Baughman 1952, Rathje 1971, Mckillop 2002) enhancing a putative increase of fish catches. The marine trade system connected cities in the Northern Yucatan Peninsula and Gulf of Mexico to the Belize valley and Honduras (Andrews 1988, Guderjan et al 1989, Mckillop 1996). Archeological evidence points out that the Maya built a passage through the Xcalack Peninsula on Chetumal Bay to connect the lagoon (fig. I.1) to the northern route (Guderjan et al. 1989). At least 12 marine ports along the route have been identified where thousands of people lived, as well as many transshipment points were a few hundred people inhabited (Eaton 1978, Guderjan and Pendergast 1989, Guderjan 1995). Many other small coastal villages have been described along the trade route, and it would be reasonable to expect that all seashore communities derived at least part of their subsistence from fishing (Eaton 1970).

I could not determine if fish was traded, nor how much fish was transported by canoe, but I presume that a certain amount of fish and other marine products were transported long distances (Baughman 1952, Borhegyi 1961, Healy et al. 1984, Teeter 2001). For example conch, turtle shell, shark teeth, salted fish, and other marine products were found in burials of inland cities near Mexico City (Borhegyi 1961). The Maya transported grains and seafood alongside cultural, technological and elite products, but I am not certain that food was the main reason of the trade (Borhegyi 1961, Guderjan and Gerber 1995, Mckillop 1996). However, marine trade products reached far inland as shown by ornamental, ritualistic and other hard records well preserved.

The Colonial period

This period started in the 16th century with the Spanish arrival to Maya territory and technically ended first in the Yucatan and then in Belize in approximately 1810 and 1981 respectively (Shattuck 1933, Graham and Pendergast 1989). Since resource exploitation was parallel in both regions I close this period at the beginning of the 20th century. Human population declined from 800,000 individuals to 250,000 (conservative estimation) due to famine, wars and diseases related to the colonial invasion (Graham and

Pendergast 1989, Roberts 1989). Some estimates indicate up to 90% of mortality after Spanish arrival (Lovell and Lutz 1995, Kiple 1997). During the 16th century the Yucatan Peninsula was dominated by the Spaniards but most attempts to establish permanent settlements on or near the coast were unsuccessful (O'Donnell 1981). The Maya took refuge from the colonists and migrated to the south-east coast of the peninsula where the barrier reef and dense forests made access difficult for the Spaniards. Contemporary observations indicate that this territory was frequented by buccaneers (Esquemeling 1967) and ship wrecks were frequent (Winzerling 1946). In the 17th and 18th century the British took control over the territory that now is the country of Belize (Leslie 1997, King 1999). Forestry of logwood was the most important colonial industry (Armytage 1953, Bolland 1977). Thus, deforestation and run-off related disturbances probably began during this period.

Landa (1941) gave a good description of fisheries on the Yucatan peninsula during the colonial period. He identified several targeted species including snooks, sardines, soles, sting-rays, swordfish, mackerel, tunny fish, cuttlefish, barracuda and dolphin fish (Baughman 1952). Black coral was also gathered in the cays of Belize (Winzerling 1946). Other food species were manatee, turtles and their eggs, oysters, cuttlefish eggs, crabs and lobsters (Roys 1943). Sharks were abundant and their liver was boiled by the Maya and colonials to obtain oil (Thompson 1932, Jones 1985). Records of colonial fisheries on sharks were not found, however Thompson (1932) indicates that two Maya natives on a small canoe were able to catch up to 7 individuals in a day.

Other than colonial accounts there is little historical evidence of the magnitude of fishing activities during this period. However, tax records buried in old archives may have additional information of the intensity of fishing. However, the population decline and the territorial disputes between British and Spaniards may have limited the fishing activities in the region (O'Donnell 1981). Also the distribution of settlement was mostly in the periphery of the peninsula to the North and along the Gulf of Mexico coast (Graham et al 1989). The core of the colonial territory rarely included the coast of the MBR (Roys 1965, Patch 1993). I found only seven colonial villages bordering the MBR during the colonial period (Roys 1965), but no statistics on taxes or population estimates during this period. The later may indicate that information on the colony is still buried in Spanish archives.

Although depopulation was strong, faunal remains indicate that the same diversity of marine animals was exploited by the surviving Maya (Roys 1965, Graham et al 1989). During this time fish were caught with harpoons, hooks made of cane, and various types of traps (Thompson 1933, Winzerling 1946). Spanish writers described a variety of fishing gear such as nets and dragnets, hook and lines. Excess fish was salted, roasted or sun-dried and later transported up to 100 kilometers inland (Baughman 1952). Salt and fish were considered among the most important commercial items (Mckillop 2002). Salt was collected all along the northern coast of Yucatan peninsula and traded with inland and southern territories (Landa 1941, Collier 1964).

Other accounts indicate that marine vertebrates (manatee, monk seal and turtles) were popular targets of colonial fisheries. Natives from the Honduras coast (Miskito) were skilled hunters of manatee and turtles and both the Spanish and the British kept Miskito natives on the ships to provide seafood (Dampier 1927, Baughman 1946, McKillop 1985). Manatee and turtles meat was prepared fresh or preserved salted, smoked or dried and sold to privateers and logwood cutters along Belize’s coast (Craigg 1966, Esquemeling 1967). Manatee was imported to Jamaica from Central America to feed slaves (Winzerling 1943, Parsons 1956, Mckillop 1985). There were many manatees on the west coast of the Yucatan peninsula and in the Belize area during this time (Collier 1964, Mckillop 1984). Yet, colonialist noticed a reduction in abundance soon after the opening of the coast to settlement and trade in the 18th C. (O’Donnell 1981). Several other products were made from manatee: skin was used for shoes, bones for musical instruments and crafts, and oil for lamps (Winzerling 1946, Baughman 1946, O’Donnell 1981). The other marine mammal that was heavily fished during this period was the monk seal (*Monachus tropicalis*); it was fished for skins and oil (Collier 1964). Monk seals were in great numbers along the coast of Yucatan to Quintana Roo, Honduras and the Bay Islands during the 19th C. and it was hunted on Yucatan and later in Honduras on offshore reefs (McClenachan et al 2006).

Records from 1750, British Honduras exported 6,000 pounds of carey (turtle shell ornamental by-products) to England, but did not specify if they traded whole carapaces or craft products (Armytage 1953). Although records are sporadic, from 1821 to 1851 up to 3,000 pounds of carey were exported each year from British Honduras. Given that a single hawksbill turtle yields about 3 pounds of carey (Meylan and Donnelly 1999), the British were killing at least a thousand turtles every year. Another figure indicates that starting in 1867 and ending in 1896, a total of 13,787 live turtles were exported to England (Craigg 1966, Naylor 1988).

The use of iron probably improved fishing efficiency during the colony comparing to the Maya period. The Maya people were eventually required to pay taxes to the Spaniards. Six arrobas of fish (11.3 kg per arroba) were collected per tax payer. A total of 220 tribute payers were reported in the census of the Cozumel Island in 1549 (Roys et al 1940) this translates conservatively to a population of approximately 1100 natives, considering a mean of 5.6 people per Maya household (Haviland 1972). The tribute paid by this population could total approximately 14.9 tons of fish, probably paid over the year. During the colony the Maya both the maritime trade ended and the fisheries on the Island of Cozumel (Shattuck 1933).

The Modern period

This period comprehends the last 100 years of modern history. Rapid human population growth increased coastal development and intensive commercial fisheries are characteristic of this period. In 1900 there were 40,000 people in Belize and 10,000 in Quintana Roo (Mexico), most of them living along the coast bordering the MBR. The region doubled in population by 1950 and today there are approximately one million people. Floating population during a year is estimated around 500,000. The population grew at a faster rate on the Mexican territory than in Belize. For instance, Cancun Island shifted from a small fishing village in 1940s to a large tourist development complex with a population of more than 30,000 people (Anonymous 2000, INEGI 2003).

In 1940 there were 500 fishermen registered in Belize, all boats were less than 2 m and propelled by sail and oar. Before the 1950s most fishing gear was traditional (i.e. hook and line, mesh traps). After 1950, FAO encouraged the introduction of new types of gear and began the collection of fisheries statistics. In 1950 Belize exported 115 tons of seafood (Anonymous 1952). During the 1960s fisherman population in Belize increased to 600, then 700 in 1970s and by the year 2000 there were a total of 3,000 (Wade and Ariola 2003).

Commercial fisheries production by country varies on a year to year basis (fig. 2.2). Within the MBR region Mexico and Honduras are the top producers followed by Belize. Guatemalan fisheries are very small comparatively. Seafood production in the region maintained a maximum catch below 5,000 tons per year before 1965. With the use of intensive commercial methods of capture (i.e. outboard motor, trawling, commercial fishing boats) the total production of fish in the MBR increased to 10,000 tons around 1970s, then to 15,000 tons in the 1980s, and reached 20,000 tons during the 1990s. A decline in production in Mexico and Honduras was observed in 1990s, but at the same time seafood production intensified in Belize. This maintained an apparent level of fish production for the MBR region. Fish production was initially consumed locally, but I found that two thirds of the Belizean production was exported by 2000 (Wade and Ariola 2003).

Due to the characteristics of the fisheries in the MBR, I divided them in two regions: the Yucatan Peninsula in the North (Quintana Roo, Mexico and Northern Belize), and the Gulf of Honduras (GOH) in the South (South Belize, Guatemala and Honduras). The fish production of the North region reaches over 20,000 tons of seafood (FAO 2000, Anonymous 2000), and in the south 6,489 tons for the entire GOH. Belize’s southern coast production totals only 4% of GOH, the 96% remaining is from Honduras and Guatemala (Heyman and Graham 2000).

A total of 350 species of reef fishes are targeted by a small scale fishing industry operating along the entire MBR (Oliver 2003). Fishing gear includes traps, casting nets, hand lines, gillnets, trawl and beach nets. Fishery species on the North region include, in order of importance: groupers (Serranidae), snappers (Lutjanidae), shrimp, lobster, conch, and sharks, and in much less proportion: squid, octopus, oysters and other reef fishes (16 general categories). The southern fisheries include several species of snappers (*Lutjanus* sp.), lobster, conch, turtle, manatee, other reef fishes and crabs.

In the Gulf of Honduras fisheries production reached 6,488 tons in 1999, but local declines has been reported by fishermen. While the number of fishermen has been increasing every year, fishing grounds are at least 50 km away from the coast. Most fishers use hand-lines (60% in the GOH) but other also use gill nets, long-lines, seine nets, tow hand line, traps and diving. The fishery is multi-specific to ensure a sustained income all year long (Heyman and Graham 2000). Also in other parts of the MBR, such as Belize, fishers have noticed the decline in the individual size and abundance of fish. However target species have remained the same in the latest years (Aiken 1996).

Guatemala seafood production from the Caribbean was nearly 40% of the total GOH production, but a small portion corresponds to reef related species. It included nearly 1,250 tons of manjua (*Anchoa lyolepis*), followed by shrimp with 190 tons. Other fisheries include red snapper (*Lutjanus campechanus*), mutton snapper (*L. analis*), billfish (*Istiophorus albicans*), jack (*Caranx* sp.), tarpon (*Megalops atlanticus*), and snook (Centropomidae) totally approximately 700 tons. A total of 1,323 boats are reported for Guatemala of which, a large portion are small boats, and there are a few vessels for large scale fisheries such as shrimp and tuna (FAO 2000). A large percent of the production is exported to US markets (Craig 1966, Gregg 1968, Heyman and Graham 2000).

Total fish production in the MBR increased at the beginning of the 1990s and soon after declined. A small peak was recorded just in the last few years due to an increase in Belizean fisheries (fig. A.2). The production of demersal fish species in Belize has increased from 71 tons in 1993 to 3,800 tons in 1999 (FAO 1999). The MBR also supports a sport fishing industry but statistics are scarce and unofficial.

The estimated sustainable reef production for the Caribbean is 4-5 tons of fish per square kilometer and the total reef area estimated for the MBR is approximately 3,920 km^2 (Spalding 2001). Thus the sustainable total fish production would be about 15,680 tons a year. Fisheries declined dramatically just after production passed 12,000 tons a year (Fig A.2), around 1995 (FAO 2000). This indicates that estimations on fisheries sustainability are not accurate since they consider only fishes, and do not consider trophic interactions, fishing effort, by-catch, catastrophic events (e.g. hurricanes) and population recovery rates.

Commercial fisheries and coral reefs today

Fisheries statistics of particular species are missing, yet the changes in production are evident across the whole spectrum of species. The lobster commercial fishery started around 1925 with a minuscule production. However, this fishery has maintained a production of over 500 tons/year for Belize and the Mexican coast of the MBR in the last two decades (FAO 2000). The lobster fishery was once considered sustainable in Belize (Craig 1966). However, the catch in Honduras dropped from nearly 1,500 tons in 1987 to 300 in 1998 (FAO 1999). The size of lobsters has decreased considerably and fishing effort is greater today than two decades ago (Craig 1966**,** Acosta and Robertson 2003). Production peak occurred in 1990 and declined soon after that. The average weight of lobster tails in Belize was around 4-6 lb in 1950 (Godfrey 2001) but today it is 0.25 lb. Today the legal minimum size for a lobster catch is 8 cm (FAO 2001).

Today, conch is the most important mollusk fishery in the MBR. Commercial conch fishing started in Belize as early as 1961, including two related species (*Strombus gigas* and *S. costatus*) (Craig 1966). Peak production reached 1200 tons/year and occurred in the late 1960s and early 1970 followed by a dramatic decline. On the other side, the crustacean fishery (shrimp and crab) has been dominated by Honduras fisherman since the mid 1960s, although catches ranges between 2500 and 5000 ton/year, the regional production has declined since 1995.

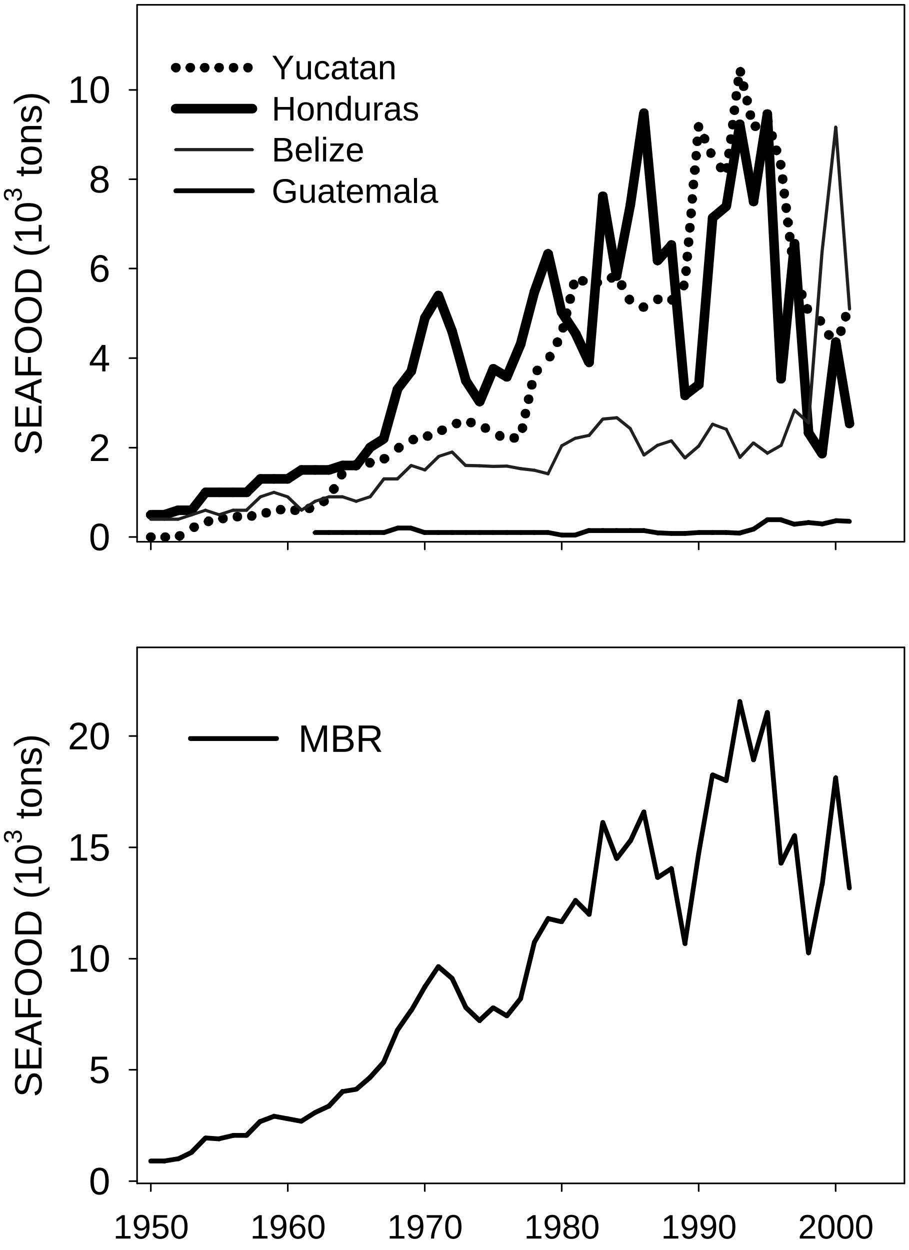

Figure A.2. Changes in the seafood production (marine vertebrate and invertebrate species) throughout the modern period by countries (above) and total production from the MBR region (below). Catch composition includes only reef associated species (see methods).

By 1960 the monk seals were extinct; the last remaining group inhabited the Alacranes atoll just North West of the Yucatan peninsula (Collier 1964). The Goliath grouper fishery is now almost non existent; only a few tons are produced from Honduras (Heyman and Graham 2000). Reef sharks are ecologically extinct; manatee and turtle are seriously threatened by poaching. Today manatee is scarce and difficult to see, small populations are concentrated in Belize and Nicaragua (O'Shea and Salisbury 1991, Magnus 1978). Turtles were a popular ornamental item and fishery until the 1960s. Important turtle nesting beaches were spread along Quintana Roo coast and offshore reefs (Lange 1971). Several spawning aggregations of groupers have been fished out along the MBR or numbers have been reduced from tens of thousands to a few thousands (Sala 2001). In the 1960s up to 300 boats were deployed to fish a Nassau grouper aggregation during 3 weeks in Cay Glory, out of the coast of Belize (Craig 1966). Today, Cay Glory does not support any fishery (Heyman and Graham 2000).

Many fisheries statistics pool several related species into broad categories, which makes it difficult to describe and analyze the results. However, a general and striking decline has been observed in the last decade for the whole MBR seafood production. Although official statistics do not report fishing effort for most of the target species, changes in effort can be inferred by studying the location of fishing grounds, as well as the abrupt variations from one year to the other. In the early 1900s fishing grounds were no farther than 3 nm from shore and less that 3 fathoms deep (Craig 1966). As the number of fishermen increased, along with total human population, commercial fishing and international markets appeared, fishing grounds moved off shore to deeper waters and larger boats were employed. With the introduction of the outboard motor more oceanic environments were targeted (i.e. atolls, windward reefs) by local fishermen. Production and fishing effort increased over the entire MBR region due to technological developments.

Presently, sea food is marketed fresh or frozen, preserved dried, salted, pickled or canned (Craig 1966). Modern means of transportation have made possible the distribution of daily local production to regional markets and elsewhere in the world. With this capacity more than 300 tons of seafood were produced per month only in Quintana Roo last decade (Anonymous 2000).

Conservation efforts and current status of MBR reefs

Belize introduced its first fishery protection measure in 1948, for lobster (3.5 inches minimum length, only non-gravid individuals, molting individuals could not be fished and 4 months of no export fishery). In Belize fishing activities are regulated also for the conch fishery with size limits; also the use of nets is limited inside the reefs. Traps outside the reef and SCUBA fishing are prohibited. Similar measures were established for lobsters, conch and shrimp in Honduras fisheries (FAO 2002).

Nearly 20 marine protected areas (MPAs) along the MBR have been established but enforcement is variable and rarely full protection is granted. There are a large number of other conservation actions and fisheries regulations but most of them are not enforced. Recently, fish spawning grounds were closed to fishing during spawning season across the MBR region (Anonymous 2003).

Anthropogenic activities (fishing, pollution, coastal development) in addition to climate changes and diseases have seriously deteriorated the MBR ecosystem. Coral populations of the genus *Acropora* suffered a dramatic decrease in recent times (Aronson et al 2002). A remarkable ecosystem shift was observed after the mass mortality off of the sea urchin *Diadema antillarum* in 1983/4 with over 95% mortality throughout the Caribbean (Lessios 1988). *D. antillarum* populations once reached densities up to 71 ind. m^{-2} (Randall 1964), but after the die-off densities were less than 0.5 ind. m^{-2}. Coral cover before 1983 reached over 50% in shallow reefs and macro-algae was less that 10%. Fish herbivores (i.e. parrotfish) were already overfished. The loss of corals and urchins allowed macro-algae to overgrow the reefs and in a few years macro-algal cover was over 60% and corals declined to less than 10% (MacClanahan and Muthiga 1998, Gardner et al 2001). Ultimately, coral reefs shifted to an alternate macroalgal-dominated state across the entire Caribbean basin (Hughes 1994). Recently, an increase of coral recruitment has been observed in Jamaica associated to increased sea urchin abundance (Edmunds and Carpenter 2001, Newman et al 2006). Unfortunately, the scale of recovery due to conservation actions across the MBR and the Caribbean has not been significant (Risk 1999).

Discussion

I found an excellent record of the prehistoric, historic and contemporary exploitation of marine resources in the MBR. The number of species targeted by fisheries increased throughout time, as well as the number of habitats under exploitation, from the shoreline to the off shore reefs. The use of marine resources began primarily for food production in shallow habitats and near shore where humans were able to easily gathered snails, crabs, and possibly small fish (Sauer 1962). Later, with the development of fishing technology a greater number of marine resources were available for food and tool materials (Eaton 1976). This model of primitive exploitation hardly had a significant impact on the ecology of the MBR. With Maya civilization development the use of marine resources increased. A number of marine species were the target of Maya fisheries including large animals, snails, crabs and reef fishes. The archeological evidence points out to an increased exploitation of marine resources that lasted throughout for centuries (Hamblin 1985).

Although human population declined during the Colonial period the fishing intensity likely increased due to technological advantages brought by the Europeans. During this period the abundant populations of large animals were used to feed slave populations and for export to the new world. At the end of the Colonial period the abundance of sharks, manatees, turtles and large groupers was dramatically reduced. The turtle fishery was already in decline at the beginning of the 19th century and possibly other species were in the same situation.

On the other side, during the modern period seafood production increased considerably. Yet, catch composition consisted of small reef fishes (i.e. groupers) and invertebrates (i.e. lobster and conch). Over this period the loss of biodiversity due to overfishing and human impacts altered the ecosystem functioning. Recent conservation actions such as marine protected areas managed to reduce fishing pressure but truly enforced marine reserves are scarce and often small.

By the time of the first ecological assessments the MBR ecosystem was already changed. It is likely that modern coral reef researchers perception of ecosystem functioning is deficient (Jackson 2001). Already deteriorated communities were documented as “healthy” ecosystems when the first SCUBA technology appeared (Goureau 1959). By then monk seals were extinct, turtle populations already declined and several nesting beaches vanished (MacClennacan et al 2006), manatees were rare. Reef sharks did not figure in the assessments of the trophic structure of reefs (Opitz 1996). Trophic structure of the Caribbean coral reefs as documented by modern ecologist is based on an ecosystem where higher trophic levels are missing, and ecosystem dynamics might be totally different from earlier periods (Jackson et al 2001, Pandolfi et al. 2003). In summary, I have an understanding of how an altered ecosystem works and detailed description of the process of decline. I only understand the history of the ghosts that today swim sporadically over the reef but not their role in shaping the structure of the Caribbean coral reefs.

Conservation efforts at the local scale are numerous over the past decades (i.e. protected areas), yet a large scale management project is still pending. While some marine reserves have shown important results in helping the recovery of the system (Williams and Polunnin 2000, Halpern 2003, Newman et al 2006), reefs have continued to decline (Gardner et al 2003). Steps towards recovery require more comprehensive ecosystem assessment, a regional program for a network of large marine reserves (areas closed to fishing) and a restoration program aimed to restore the lost resilience of the community.

Table A.1. Taxonomic composition of Maya middens in Cancun (A) and Cozumel Island (B) during the Pre-Classic period (Andrews 1975, Hamblin 1984)

Species	A	B
Mammals (terrestrial)		
Deer		*
Dogs		*
Pecaries		*
Other		*
Mammals (marine)		
Trichechus manatus	*	
Crocodiles		
Crocodylus acutus		*
Turtles (terrestrial)		
Kinosternon cruentatum		*
Chelydra serpentina		*
Pseudemis scripta		*
Geomyda pulcherrima		*
Turtles (marine)		
Chelonia mydas	*	*
Caretta caretta	*	*
Lizards		
Anolis sp.		*
Ctenosaura similis		*
Iguana iguana		*
Sceloporus sp		*
Amphibians		
Bufo marinus		*
Leptodactylus sp		*
Smilisca baudinii		*
Fishes		
Muraena miliaris		*
Enchelycore nigricans		*
Caranx sp	*	
Calamus sp	*	
Sphyraena sp	*	*
Sphyraena barracuda		*
Epinephelus sp		*
E. itajara	*	
E. morio	*	
Fish (cont.)		
E. striatus	*	
Mycteroperca sp		*
Lutjanus sp		*
Haemulon sp		*
Lachnolaimus maximus	*	
Bodianus rufus		*
Bodianus sp		*
Halichoeres sp		*
Sparisoma sp		*
Sparisoma viride		*
Scarus sp		*
Acanthurus sp		*
Balistes sp		*
Balistes vetula	*	*
Melichthys niger		*
Diodon hystrix		*
Ginglymostoma cirratum		*
Galeocerdo cuvier		*
Carcharhinus sp	*	*
Carcharhinus maculipinnis		*
Sphyrna mokarran	*	*
Sphyrna zygaena		*
Dasyatis americana		*
Crustacea		
Callinectes sapidus		*
Menippe mercenaria		*
Gastropoda		
Cittarium pica	*	
Strombus costatus	*	
S. gigas	*	
Melongena corona	*	
Busycon contrarium	*	
Fasciolaria tulipa	*	
Other rare (93 species)	*	
Birds (23 species)	*	*

Table A.2. Abundance and relative importance of seafood types based on pre-classic Maya (<800 B.C.) settlement in Cancun. Midden remains correspond to 1 generation (approximately 50-80 yr). Andrews (1976) indicates that nearly 100% of the protein consumption was apparently from marine origin and conservatively 50% corresponded to invertebrates and 50% to vertebrates

	MNI	**Species weigth (kg)**	**Total B**	**%**
Vertebrates				
Manatee	1	540.0	540.0	8.2
Turtle	10	136.2	1362.0	20.6
Sharks	2	109.8	219.6	3.3
Epinephelus itajara	2	455.0	910.0	13.8
Epinephelus striatus	6	25.0	150.0	2.3
Caranx spp.	1	12.4	12.4	0.2
Calamus spp	3	0.7	2.0	0.0
Lachnolaimus maximus	7	10.0	70.0	1.1
Balistes vetula	7	5.4	38.1	0.6
Invertebrates				
Cittarium pica	364	205.6	74.8	1.7
Strombus costatus	493	350.0	172.5	4.0
S. gigas	1871	533.9	998.9	23.0
Melongena corona	555	310.4	172.3	4.0
Busycon contrarium	581	682.8	396.7	9.2
Fascialoria tulipa	478	378.8	181.1	4.2
Nerita versicolor	96	38.4	3.7	0.1
Pleuropoca gigantea	84	924.5	77.7	1.8
Turbinella angulata	96	546.0	52.4	1.2
Oliva reticularis	106	67.2	7.1	0.2
Spondylus americanus	111	153.3	17.0	0.4
Tellina radiata	100	135.6	13.6	0.3

Table A.3. Estimated sea food production based on midden remains and estimated population from Cozumel during Maya civilization. **1**) Expected seafood production for the total population per year (**C**) given the daily percapita protein needs during prehistory (seafood diet provided 50% of protein, see methods); **2**) Relative importance (%) of seafood types in Maya diet over time, based on minimum number of individuals (MNI) found in middens; and **3**) estimated composition of total seafood production (tons/yr) based on seafood relative importance and C. Population estimation based on Culbert (1990) and Maya periods according to Hamblin (1984).

1)

MAYA PERIOD	YEARS	COZUMEL POPULATION	Protein intake (kg/day)	Marine Protein (kg/day)	C (kg/yr)
PRECLAS-CLASS	<800 A.C.	1600	102.4	51.2	18688
FLORECENT	800-1000 A.C.	2100	134.4	67.2	24528
E-POSTCLASS	1000-1200 A.C.	3600	230.4	115.2	42048
POSTCLASS	1250-1500 A.C.	3100	198.4	99.2	36208
L-POSTCLASS	1500-1650 A.C.	10000	640	320	116800

2)

	MNI	FISH	CRAB	SHARK	STINGRAY	CROCODILES	TURTLE
PRECLAS-CLASS	162	90.1	9.9	0	0	0	0
FLORECENT	67	86.6	8.9	0	4.5	0	0
E-POSTCLASS	71	85.9	9.85	0	1.4	2.81	0
POSTCLASS	106	81.1	8.5	5.6	1.9	2.8	0
L-POSTCLASS	626	81.63	8.62	7.5	0.64	1.4	0.16

3)

	C (tons/yr)	FISH	CRAB	SHARK	STINGRAY	CROCODILES	TURTLE
PRECLAS-CLASS	18.69	16.84	1.85	-	-	-	-
FLORECENT	24.53	21.24	2.18	-	1.10	-	-
E-POSTCLASS	42.05	36.12	4.14	-	0.59	1.18	-
POSTCLASS	36.21	29.36	3.08	2.03	0.69	1.01	-
L-POSTCLASS	116.80	95.34	10.07	8.76	0.75	1.64	0.19

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APPENDIX II

Additional information from Caribbean studies included in the meta-analysis, Chapter II.

Table AII. .Data presented here are: authors of each study, country where studies were conducted, site names (when available), type of data collected from each study (1. Means from table, 2.Means from graph, 3.Means from original database, 4.Raw transect data, 5.data cited from other paper), depth (D) in meters, year of survey (Y), and community components surveyed for each particular study: coral (C), macro-algae (M), D. antillarum (D), and fish respectively (F).

AUTHOR	COUNTRY	SITE	TYPE	D	Y	GROUPS
Afzal et al 2001	Honduras	Utila	1,2	5, 15, 25	1997-1999	C
Aguilar 1998	Yucatan	Majahual	1,4	6, 18, 25	1997	C M
Alcolado et al 2003, Lang 2003 (ed)	Cuba	Acuario	1	5	1999	D
Alcolado et al 2003, Lang 2003 (ed)	Cuba	Cadena	1	11	1999	D
Alcolado et al 2003, Lang 2003 (ed)	Cuba	Jardinin de Gorgonias	1	8	1999	D
Alcolado et al 2003, Lang 2003 (ed)	Cuba	Nhbana	1	1.5	1999	D
Alcolado et al 2003, Lang 2003 (ed)	Cuba	Yemaya	1	5	1999	D
Alvarado et al 2004	Costa Rica	Costa rica	1,5	7	1977, 1980, 1992, 1999, 2003	D
Andrefouet and Guzman 2005	Panama	Ailigandi	1	10	2001	C
Andrefouet and Guzman 2005	Panama	Naragana	1	10	2001	C
Andrefouet and Guzman 2005	Panama	Panama	1	10	2001	M
Andrefouet and Guzman 2005	Panama	Tubuala,	1	10	2001	C
Andres and Witman 1995	Jamaica	WFR	1	5, 10, 15 20 30	1992	C M
Aponte and Ballantine 2001	Bahamas	Lee Stocking	1	45	1999	M
Aronson and Pretch 2000	Jamaica	Discovery bay	1,2	5	1993-1996, 1998, 1999	C M D
Aronson et al 2002	Belize	Channel cay	1,2	10	1997-2001	C M
Aronson et al 2005	Gulf Mex	Flower Gardens	1,2	20	2002-2003	C M
Bak 1987	Aruba	Aruba 6 sites	1	5	1986	C
Bak and Luckhurst 1980	Curacao	Curacao	1,4	10, 20 30	1973, 1978	C
Bak and Van Eys 1975	Curacao	Curacao	2	2, 6, 12	1974	C D
Bak et al 1984	Curacao	3 SITES	1	3, 10, 12, 20, 22	1983-1984	D
Bauer 1980	Antigua	Sandy Is	1	6.1	1979	D
Bauer 1980	Barbados	Needham	1	7.6	1978	D
Bauer 1980	Bermuda	Elys	1	12	1977	D
Bauer 1980	Cayman Is	Georgetown	1	2	1977	D
Bauer 1980	Cayman Is	Rum Point	1	1.5	1977	D
Bauer 1980	Curacao	Piscadera	1	1.5	1977	D
Bauer 1980	Trinidad and Tobago	Buccoo Reef	1	1.5	1979	D
Bauer 1980	Trinidad and Tobago	Irvine	1	2	1979	D
Bauer 1980	USA	Florida	1	7.8	1977	D
Bauer 1980	USA	Florida	1	4.2	1978	D
Bauer 1980	USA	Florida	1	6.1	1978	D
Bauer 1980	USA	Florida	1	7.5	1978	D
Bauer 1980	USA	Florida	1	7.6	1978	D
Bauer 1980	USA	Florida	1	10	1978	D
Bauer 1980	USA	Florida	1	10.6	1978	D
Bauer 1980	Virgin Is	Peter Island	1	1	1977	D
Bauer 1980	Virgin Is	St Croix	1	1.5	1978	D
Bauer 1980	Virgin Is	St John	1	1.5	1979	D
Bauer 1980	Virgin Is	St John	1	6.1	1979	D
Bauer 1980	Virgin Is	St Thomas	1	2	1978	D
Bauer 1980	Yucatan	Cozumel	1	7.6	1979	D
Beaver et al 2003, Jaap et al 2002	USA	1D1-Bird key reef	3	9	1999-2003	C M D
Beaver et al 2003, Jaap et al 2002	USA	1D2-Black coral rock	3	21	1999-2003	C M D
Beaver et al 2003, Jaap et al 2002	USA	2D1-Sand key od	3	7	1996-2003	C M D
Beaver et al 2003, Jaap et al 2002	USA	2S1-Sand key	3	3	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	3H1-Content keys	3	5	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5D1-Sombrero od	3	14	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5D2-Looe key od	3	12	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5D3-Eastern sambo od	3	13	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5D4-Western sambo od	3	12	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5D5-Rock key od	3	11	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5H1-Moser channel	3	4	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5S1-Sombrero	3	5	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5S2-Looe key	3	6	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5S3-Eastern sambo	3	1	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5S4-Western sambo	3	3	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	5S5-Rock key	3	5	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	7D1-Alligator od	3	10	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	7D2-Tennessee od	3	13	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	7H2-Long key	3	4	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	7S1-Alligator	3	4	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	7S2-Tennessee	3	5	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9D1-Carysfort od	3	12	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9D3-Molasses od	3	12	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9D4-Conch od	3	14	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9H2-El radabob	3	3	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9S1-Carysfort	3	2	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9S2-Grecian rocks	3	4	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9S3-Molasses	3	6	1996	C M D
Beaver et al 2003, Jaap et al 2002	USA	9S4-Conch	3	5	1996	C M D
Blair and Flynn 1989	USA	Florida Dade	1,3	10, 15, 18	1988	C M
Blair et al 1994	USA	Florida Dade	1,5	11, 17, 19	1992	C
Bythell et al 1993	Virgin Is	Buck Is	1,4	9	1989	C
Carpenter 1984	Virgin Is	Teague bay	1	1.5, 2, 5, 10	1982	D
Chapman and Kramer 1999	Barbados	BMR	1	5	1996	F
Chiappone et al 1997	Bahamas	ECLSP 6 sites	2	5	1995	C M
Chiappone et al 2001a	Cuba	Guantanamo	1	3, 5, 6, 9, 11	1996	C M
Chiappone et al 2001b	USA	Florida	1	1	1999, 2000	D
Chiappone et al 2001b	USA	Tortugas bank	1	2, 15	2000	M D
Chiappone et al 2002a	USA	Florida	1	5	1999, 2000	D
Chiappone et al 2002b	USA	Florida	1	2, 5, 10	1999	D
Christensen et al 2003	Puerto Rico	Parguera BSR	2	10	2001	F
Claro and Garcia-Arteaga 1994	Cuba	Camaguey 12 sites	1	1, 2, 5, 15, 15	1989	F
Claro et al 1998	Guadalupe	Guadalupe 2 sites	1,4	15	1990	F
Claro, Lindeman et al 2001	Cuba	Canarreos	1,4	2, 10, 20	1985, 1989	F
Claro, Lindeman et al 2001	Cuba	Jardines Reina	1,4	10	1997	F
Claro, Lindeman et al 2001	USA	Key West	1,4	10	1995	F
Claro, Lindeman et al 2001	USA	W Sambo	1,4	10	1995	F

Table AII. Continuation

Cortes 1993	Costa Rica	Cahuita	1,5	5	1981, 1993	C
Cortes and Risk 1984	Cayman Is	Grand Cayman	1,4	15	1982	C
Cortes and Risk 1984	Costa Rica	Cahuita	1,4	5	1982	C
Crawford 1995	Jamaica	Discovery Bay	1	8, 15	1980-1981	C
Deschamps et al 2003, Lang 2003 (ed)	Trinidad and Tobago	Horshoe	1	3, 3.5, 9, 11, 11.5	1999	D
Diaz et al 2000	Colombia	Colombia	1	2, 6, 10, 15	1995	C M
Diaz et al 2000	Colombia	Colombia	1	6	1995	C
Dodge et al 1982	Bermuda	North rock	1	2	1980	C
Dodge et al 1982	Bermuda	South shore	1	2	1980	C
Dodge et al 1982	Bermuda	Three hills	1	2	1980	C
Dorensboch et al 2004	Curacao	Curacao 44 sites	1	2.5, 5, 10, 15	2000	C
Dustan 1985	USA	FKNMS	1	3, 12, 15, 22	1975	C
Dustan and Halas, 1987	USA	Florida	1	15	1975, 1983	C
Edmunds 2000	Virgin Is	St John	1,2,4	5	1995	C M
Edmunds 2002	Virgin Is	Tektite	1	10	1987, 1988	C M
Edmunds 2002	Virgin Is	Yawzi	1	10	1987	C
Edmunds and Carpenter 2001	Jamaica	RioBueno	1	2	2001	D
Feingold et al 2003, Lang 2003 (ed)	Bahamas	Abaco	1	5	1999	D
Fenner 1988	Yucatan	Cozumel	1	2, 5, 15	1985	C
Fenner 1991	Yucatan	Cozumel	1	2, 5, 15	1988	C
Fenner 1993	Cayman Is	CaymanBrac	1	5, 10, 20, 25	1988	C
Fenner 1993	Roatan	Overheat	1	3, 15	1987	C
Fernandez and Alvarado 2004	Costa Rica	Punta Cocles	1,4	1.5	2002	C M
Fonseca 2003, Lang 2003 (ed)	Costa Rica	Cahuita	1	5.5	1999	D
Fonseca 2003, Lang 2003 (ed)	Costa Rica	Cahuita CM	1	5	1999	D
Fonseca 2003, Lang 2003 (ed)	Costa Rica	Cahuita M	1	4	1999	D
Fonseca 2003, Lang 2003 (ed)	Costa Rica	Manzanillo	1	1.5	2000	D
Forcucci 1994	USA	Florida, 23 Sites	1	5	1990, 1991, 1992	D
Garrison et al 2000 in Gardner 2003	Puerto Rico	Culebra	1,5	6	1991, 1998	C
Garrison et al 2000 in Gardner 2003	Puerto Rico	Dewey	1,5	6	1991, 1998	C
Garrison et al 2000 in Gardner 2003	Puerto Rico	Windward	1,5	6	1991, 1998	C
Garza-Perez and Ariaz-Gonzalez 2001	Yucatan	Majahual	1	10	1997, 1998	C M
Garzon-Ferreira and Kielman 1993	Colombia	Rosario Is	1	3, 5, 10, 15, 7, 11	1983, 1984, 1986-1988, 1992	C M
Garzon-Ferreira and Kielman 1993	Colombia	Rosario Is	1	15	1990	C M
Garzon-Ferreira and Kielman 1993	Colombia	Rosario Is	1	10	1992	C M
Gladfelter et al 1991	Virgin Is	Buck Is	1,4	5	1985, 1989, 1990	C
Gladfelter et al 1991	Virgin Is	Buck Is	1,4	5	1989, 1990, 1991	F
Guardia-Llanso and Sanson, 2000a and Guardia-Llanso and Sanson, 2000b	Cuba	Habana	1	10, 20	1997	C M
Guzman and Guevara 1998	Panama	Bocas del toro	1	10	1997	C M
Guzman et al 2003	Panama	Ailigandi	1	10	2001	C
Guzman et al 2003	Panama	Naragana	1	10	2001	C
Guzman et al 2003	Panama	Panama	1	2, 15, 10, 20	2001	C
Guzman et al 2003	Panama	Panama	1	10	2001	M
Guzman et al 2003	Panama	Tubuala	1	10	2001	C
Haley and Solandt 2001	Jamaica	Discovery bay	1,2	5, 10, 15	1995, 1996, 1998-2000	D
Harper et al 2000 and Bohnsack et al 1999	USA	12-12 Sambos	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	14 Sambos	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	15-13 Sambos	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	8 Fathom Rock	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Alligator Reef	1,3	10	1982, 1995, 1997, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	American Shoal	1,3	10	1995, 1997, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Big Pine Shoal	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Black Coral Rock	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	BNP: Ajax reef	1,3	10	1988-1992,1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	BNP: Ball Buoy reef	1,3	10	1988-1991, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	BNP: Brewster reef	1,3	10	1988-1992, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	BNP: IGW Trust reef	1,3	10	1988-1991. 1995, 1997, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	BNP: NE Corner reef	1,3	10	1988-1992, 1995, 1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	BNP: Triumph reef	1,3	10	1989-1992, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Carysfort S	1,3	10	1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Cecily's Site	1,3	15	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Conch reef	1,3	10	1991, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Cosgrove shoal	1,3	10	1994-1995	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Crocker	1,3	10	1994, 1997, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Dave's site	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Davis	1,3	10	1994, 1996-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Delta shoals	1,3	10	1984, 1991, 1994, 1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Devil's reef	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Eastern Dry Rocks	1,3	10	1995, 1995, 1997, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Eastern Dry Rocks (FED)	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Eastern Sambos	1,3	10	1993, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Elbow	1,3	10	1980, 1981, 1994-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Fantom reef	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Fowey Rocks	1,3	10	1995, 1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	French	1,3	10	-1983,1991, 1993, 1994, 1996-	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Gary's Anchor	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Georges rock	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Grouper site	1,3	10	1985-1989, 1996, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Guy's Grotto	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Hangover reef	1,3	15	1994	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Hump 1	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Hump 2	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Hump 3	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Joe's Hump HUMP	1,3	10	1994, 1996	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Key Biscayne	1,3	10	1983, 1984	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Key Largo Dry Rocks	1,3	10	1981, 1994, 1997, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Little bank	1,3	10	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Long Key (Bird Key)	1,3	15	1994-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Looe Key E	1,3	10	1996-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Looe Key W	1,3	10	1994, 1996-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Looe Key other	1,3	10	1979-1987, 1991-1993, 1995	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Looe Key research	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Marker H	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Marquesas rocks	1,3	10	1995	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Maryland shoals	1,3	10	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Mavro vetranic	1,3	15	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Middle Sambos	1,3	10	1993, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Molasses	1,3	10	1979-1998, 1991, 1993-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	No Name reef	1,3	15	1995	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Pelican shoals	1,3	10	1995, 1998	C M F

Table AII. Continuation

Harper et al 2000 and Bohnsack et al 1999	USA	Pete's Pinnacle	1,3	10	1995, 1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Pickles reef	1,3	10	1995, 1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Pott's Peak	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Pulaski shoal	1,3	15	1994-1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Ralph's ridge	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Replenishment shoal	1,3	10	1994	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Rock Key	1,3	10	1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Sand	1,3	10	1994-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Sherwood Forest	1,3	15	1997-1999	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Sombrero	1,3	10	1984, 1991, 1993, 1994, 1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tennesse reef (FED)	1,3	15	1995, 1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Texas rock	1,3	15	1994, 1996-1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Bank (pinnacles)	1,3	15	1994-1995	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Bank site 11	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Bank site 18	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Bank site 25	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Bank site 51	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas flat	1,3	10	1997	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Park site 52	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Tortugas Park site 82	1,3	15	1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Turtle reef	1,3	10	1993, 1995, 1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Twenty Eight Foot shoals	1,3	10	1995	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Twin Peaks	1,3	15	1994	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Western Dry Rocks	1,3	10	1997-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Western Sambos E	1,3	10	1993, 1995-1998	C M F
Harper et al 2000 and Bohnsack et al 1999	USA	Western Sambos W	1,3	10	1993, 1995-1998	C M F
Hawkings and Lewis 1982	Barbados	BMR	1	3	1976	D
Hawkins et al 1999	Bonaire	Bonaire 2 sites	1,2	10	1994	C F
Hawkins et al 1999	Bonaire	Carls hill 2 sites	1,2	10	1994	C F
Hawkins et al 1999	Bonaire	Jerrys 2 sites	1,2	10	1994	C F
Hawkins et al 1999	Bonaire	karpata 2 sites	1,2	10	1994	C F
Hay 1984	Belize	Belize	1	2	1980	D
Hay 1984	Haiti	Haiti	1	5	1980	D
Hay 1984	Honduras	Honduras	1	2	1980	D
Hay 1984	Virgin Is	VirginIs	1	3, 5, 10	1980	D
Hernandez-Delgado and Sabat 1998	Puerto Rico	Culebra	1,2	10	1998	C F M
Hernandez-Delgado et al 1998	Puerto Rico	Culebra	1,2	6	1997, 1998	C F
Herrera et al 1981	Cuba	Habana	1	5	1980	D
Horta-Puga 2003, Lang 2003 (ed)	Veracruz	Galle	1	4, 10	1999	D
Horta-Puga 2003, Lang 2003 (ed)	Veracruz	Is Ver	1	4, 10	1999	D
Horta-Puga 2003, Lang 2003 (ed)	Veracruz	Sacr	1	4, 10	1999	D
Hubbard and Gladfelter, 1993	Virgin Is	Buck Is	1	5, 10	1988, 1989, 1990, 1993	C
Hughes 1989	Jamaica	RioBueno	1	7, 10, 2O	1983-1987	C
Hughes 1993	Jamaica	Jamaica Is	1	1, 10, 20	1978, 1990	C
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1977	C M
Hughes 1994a	Jamaica	Discovery Bay	2	10, 15, 35	1978	C M
Hughes 1994a	Jamaica	Discovery Bay	2	10, 15, 35	1979	C M
Hughes 1994a	Jamaica	Discovery Bay	2	10, 15, 35	1980	C M
Hughes 1994a	Jamaica	Discovery Bay	2	10, 15, 35	1981	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1982	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1983	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1984	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1985	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1986	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1987	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1988	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1989	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1990	C M
Hughes 1994a	Jamaica	Discovery Bay	2	7, 10, 15, 35	1993	C M
Hughes 1994b	Jamaica	Jamaican reefs	2	5	1980, 1993	D
Hughes and Jackson 1985	Jamaica	Rio Bueno	1	10, 10, 15, 20, 35	1977	C M
Hughes et al 1987	Jamaica	Dancing	1	8, 15	1973	D
Hughes et al 1987	Jamaica	Dancing	1	3, 8, 10, 15	1986	D
Hughes et al 1987	Jamaica	Discovery Bay	1	2, 7, 10, 20	1986	C
Hughes et al 1987	Jamaica	Discovery Bay	1	2, 10, 20	1986	M
Hughes et al 1987	Jamaica	Mooring	1	3, 10	1973	D
Hughes et al 1987	Jamaica	Pear	1	10	1973	D
Hughes et al 1987	Jamaica	Rio Bueno	1	2, 7, 10, 20	1986	C
Hughes et al 1987	Jamaica	Rio Bueno	1	7, 10, 20	1973	D
Hughes et al 1987	Jamaica	Rio Bueno	1	7, 10, 20	1986	D
Hughes et al 1987	Jamaica	Rio Bueno	1	7, 10, 20	1986	M
Hunte and Younglao 1988	Barbados	BMR	1,2	10	1984, 1985	D
Hunte and Younglao 1988	Barbados	Gliter	1,2	10	1984, 1985	D
Hunte and Younglao 1988	Barbados	Golden	1,2	10	1984, 1985	D
Hunte and Younglao 1988	Barbados	Heron	1,2	10	1984, 1985	D
Hunte and Younglao 1988	Barbados	Paines	1,2	10	1984, 1985	D
Hunte and Younglao 1988	Barbados	Sandridge	1,2	10	1984, 1985	D
Hunte et al 1986	Barbados	BMR 2 sites	1,4	10	1983, 1984	D
Hunte et al 1986	Barbados	SW Coast	1,4	10	1984	D
Jaap et al 1984	USA	BNP	1	3	1978	C M
Jordan et al 1981	Yucatan	Puerto Morelos Reef	1,4	5, 10, 15	1980	C
Karlson and Levitan 1990	Virgin Is	Lamesur	1,4	4	1988	D
Kjerfve 1998	Curacao	Spaanse Water Reef	1	15	1990	F
Kjerfve 1998	Yucatan	Puerto Morelos Reef	1	5, 10, 15, 20	1980	C
Klopm and Kooistra 2003, Lang 2003 (ed)	Belize	Lighthouse	1	4.5, 7, 7.5, 8, 8.5, 9, 9.5	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Bonaire	Barcadera Reef	1	9.5	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Bonaire	Carls hill	1	11.5	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Bonaire	habitat	1	10	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Bonaire	Karpata	1	9	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Bonaire	Klein	1	12	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Bonaire	Twin	1	9	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Eustatius, N.A.	Eustatius	1	12, 14, 15, 16, 17	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Marteen, N.A.	Marteen	1	9, 11	1999	D
Klopm and Kooistra 2003, Lang 2003 (ed)	Saba, N.A.	Saba	1	, 7, 9, 10, 11, 12, 13, 15, 17, 2	1999	D
Knowlton et al 1981	Jamaica	Discovery Bay	1	8, 14	1980	D
Knowlton et al 1990	Bahamas	West Exuma sound	1,4,5	10	1980	C
Knowlton et al 1990	Panama	Aguadargana	1,4,5	10	1980	C
Knowlton et al 1990	Panama	Holandes	1,4,5	10	1980	C
Knowlton et al 1990	Panama	Limones	1,4,5	10	1980	C
Kramer et al 2003, Lang 2003 (ed)	Bahamas	Bight Andros	1	9	1998	D

Table AII. Continuation

Kramer et al 2003, Lang 2003 (ed)	Bahamas	Central Andros	1	9	1998	D
Kramer et al 2003, Lang 2003 (ed)	Bahamas	North Andros	1	9	1998	D
Kramer et al 2003, Lang 2003 (ed)	Bahamas	South Andros	1	9	1998	D
Kuhlmann 1974	Cuba	Macao	1,4	5	1974	C
Lapointe et al 2003	Trinidad and Tobago 8 S	Buccoo Reef	2	5	2001	C M
Laydoo 1990	Trinidad and Tobago	Angel	1	3, 9, 16, 21	1984	C
Laydoo 1990	Trinidad and Tobago	Buccoo Reef	1	3, 9, 16, 21	1984	C
Laydoo 1990	Trinidad and Tobago	Culloden	1	3, 9, 16, 21	1984	C
Levitan 1988	Virgin Is	Lamesur	1,4	4	1983-1987	D
Lewis and Wainwright 1985	Belize	Carrie bow	1	5	1983	D
Liddel et al 1997	Bahamas	LSI	1	10, 20, 30	1994	C M
Liddell and Holrst 1987	Jamaica	Discovery bay	1	15, 30, 45	1980, 1982	C M D
Liddell and Ohlhorst 1986	Jamaica	Discovery bay 3 SITES	1	5, 10, 15, 22	1982	C M D
Linton 2003	Haiti	Haiti	1	5	2003	C M D
Linton 2003	Haiti	Haiti	1	10	2003	C M D
Linton 2003	Jamaica	Big Port	1	5	2002	C D F
Linton 2003	Jamaica	Bloody Bay	1	3, 10	2003	C D
Linton 2003	Jamaica	Bloody Bay	1	10	2003	C D
Linton 2003	Jamaica	El Punto Neg 2 sites	1	3, 10	2003	C D
Linton 2003	Jamaica	HR	1	5	2002	C D F
Linton 2003	Jamaica	Ireland Pen	1	3, 10	2003	C D
Linton 2003	Jamaica	Little bay	1	3, 10	2003	C D
Linton 2003	Jamaica	Pigeon L	1	5	2002	C D F
Linton 2003	Jamaica	Pigeon SE	1	5	2002	C D F
Linton 2003	Jamaica	Pigeon SW	1	5	2002	C D F
Linton 2003	Jamaica	Pigeon W	1	5	2002	C D F
Linton and Fisher 2003 (ed)	Bahamas	Fernandez Bay 1, San Salvador	1,3,4	10	1994-1996, 1998	D
Linton and Fisher 2003 (ed)	Bahamas	Fernandez Bay 2, San Salvador	1,3,4	10	1994-1996, 1998	D
Linton and Fisher 2003 (ed)	Bahamas	Fernandez Bay Reef	1,3,4	10	1994-1998	C M
Linton and Fisher 2003 (ed)	Barbados	BMR	1,3,4	10	1993-1994, 1998-2000	C M D
Linton and Fisher 2003 (ed)	Belize	Calabash Reef	1,3,4	10	1997	C M D
Linton and Fisher 2003 (ed)	Belize	Carrie bow	1,3,4	10	1994-1997	C M D
Linton and Fisher 2003 (ed)	Belize	Carrie bow	1,3,4	10	1995-1997	C M D
Linton and Fisher 2003 (ed)	Bermuda	Bermuda Reef	1,3,4	10	1993-2000	C M
Linton and Fisher 2003 (ed)	Bonaire	Barcadera Reef	1,3,4	10	1994-1997	C M
Linton and Fisher 2003 (ed)	Cayman Is	GrandC	1,3,4	10	1995, 1997, 2000	C M
Linton and Fisher 2003 (ed)	Colombia	Canal	1,3,4	10	2000	D
Linton and Fisher 2003 (ed)	Colombia	Chengue Bay Reef	1,3,4	10	1993-2000	C M D
Linton and Fisher 2003 (ed)	Colombia	La Iguana 2B	1,3,4	10	2000	D
Linton and Fisher 2003 (ed)	Colombia	Providencia Reef	1,3,4	10	2000	C M
Linton and Fisher 2003 (ed)	Colombia	San Andres Reef	1,3,4	10	1998-2000	C M
Linton and Fisher 2003 (ed)	Colombia	San Felipe	1,3,4	10	2000	D
Linton and Fisher 2003 (ed)	Colombia	Wild Life 1B	1,3,4	10	2000	D
Linton and Fisher 2003 (ed)	Costa Rica	Cahuita	1,3,4	10	1999-2000	C M
Linton and Fisher 2003 (ed)	Costa Rica	Eduardo Reef	1,3,4	10	2000	D
Linton and Fisher 2003 (ed)	Costa Rica	Megashoal Reef	1,3,4	10	1999-2000	D
Linton and Fisher 2003 (ed)	Cuba	Cayo Coco Reef	1,3,4	10	1994-1997	C M D
Linton and Fisher 2003 (ed)	Curacao	Spaanse Water Reef	1,3,4	10	1994-1995	C M
Linton and Fisher 2003 (ed)	Curacao	Spaanse Water Reef	1,3,4	10	1995	D
Linton and Fisher 2003 (ed)	Dom Rep	Boca Chica Reef	1,3,4	10	1994	C M
Linton and Fisher 2003 (ed)	Dom Rep	El Peñón Reef	1,3,4	10	1996, 1997, 2000	C M
Linton and Fisher 2003 (ed)	Jamaica	Discovery bay	1,3,4	10	1993-1999	C M D
Linton and Fisher 2003 (ed)	Nicaragua	Great Corn Island Reef	1,3,4	10	1993, 1995, 1997-1998	C M
Linton and Fisher 2003 (ed)	Panama	Isla Colon Reef	1,3,4	10	1999-2000	C M
Linton and Fisher 2003 (ed)	Puerto Rico	Media Luna Reef	1,3,4	10	1994, 1995, 1998-2000	D
Linton and Fisher 2003 (ed)	Puerto Rico	Parguera	1,3,4	10	1994-1998	C M
Linton and Fisher 2003 (ed)	Puerto Rico	Turrumote Reef	1,3,4	10	1994-1995, 1998-2000	D
Linton and Fisher 2003 (ed)	Saba, N.A.	Ladder Labyrinth 1	1,3,4	10	1996	D
Linton and Fisher 2003 (ed)	Saba, N.A.	Ladder Labyrinth 2	1,3,4	10	1996	D
Linton and Fisher 2003 (ed)	Saba, N.A.	Ladder Labyrinth Reef	1,3,4	10	1993-1996, 1998	C M
Linton and Fisher 2003 (ed)	Trinidad and Tobago	Buccoo Reef	1,3,4	10	1994-1996	C M
Linton and Fisher 2003 (ed)	Trinidad and Tobago	Buccoo Reef	1,3,4	10	1997-1998	C M D
Linton and Fisher 2003 (ed)	Trinidad and Tobago	Buccoo Reef	1,3,4	10	2000	C M
Linton and Fisher 2003 (ed)	Venezuela	Cayo Sombrero Reef	1,3,4	10	1996-2000	C M
Linton and Fisher 2003 (ed)	Venezuela	Cayo Sombrero Reef	1,3,4	10	1997	C M D
Linton and Fisher 2003 (ed)	Venezuela	Playa Caimán Reef	1,3,4	10	1995-1996	C M
Linton and Fisher 2003 (ed)	Venezuela	Punta Ballena Reef	1,3,4	10	1995	C M
Linton and Fisher 2003 (ed)	Yucatan	Puerto Morelos Reef	1,3,4	10	1993-1995	C M
Linton and Fisher 2003 (ed)	Yucatan	Puerto Morelos Reef	1,3,4	10	1996-1999	C M D
Lirman and Biber 2000	USA	Northern reefs combined	1	5	1999	M
Loreto et al 2003	Yucatan	Chinchorro bank 4 sites	1	10	1999	F
Loya 1976	Puerto Rico	East Reef	1	8, 14, 19	1973	C
Loya 1976	Puerto Rico	West reef	1	20	1973	C
Mallela et al 2004	Jamaica	Rio Bueno	2	5, 10, 15, 20, 25	2001	C M
Manfrino et al 2003, Lang 2003 (ed)	Cayman Is	Cayman Brac	1	4, 7, 8, 9, 10, 16	1999	D
Manfrino et al 2003, Lang 2003 (ed)	Cayman Is	Grand Cayman	1	6.5, 7, 7.5, 9, 9.5, 10.5, 11.5, 12, 14, 20	1999	D
Manfrino et al 2003, Lang 2003 (ed)	Cayman Is	Little Cayaman	1	3, 6, 9, 10, 10.5, 11, 12, 12.5, 13, 13.5, 14, 16	1999	D
Marks 2005	Bahamas	Autec 2 (D18)	3	12.6	1998	C M F
Marks 2005	Bahamas	Autec 2 South (D19)	3	10.6	1998	C M F
Marks 2005	Bahamas	Autec 3 (D21)	3	10.5	1998	C M F
Marks 2005	Bahamas	Bristol Galley (D17)	3	11.2	1998	C M F
Marks 2005	Bahamas	Bucket (D4)	3	10.1	1997	M
Marks 2005	Bahamas	Coffee (D9)	3	11	1997	M
Marks 2005	Bahamas	Conch (D3)	3	5.3	1997	M
Marks 2005	Bahamas	Congo Town (D24)	3	10.1	1998	C
Marks 2005	Bahamas	Delta (D31)	3	8.6	1997	M
Marks 2005	Bahamas	Elbow Cay, Middle	3	5.7	1999	C M F
Marks 2005	Bahamas	Elbow Cay, North	3	8.4	1999	C M F
Marks 2005	Bahamas	Elbow Cay, South (Inner)	3	3.9	1999	C M F
Marks 2005	Bahamas	Elbow Cay, South (Outer)	3	5	1999	C M F
Marks 2005	Bahamas	Fowl Cay, Fore Reef	3	4.4	1999	C M F
Marks 2005	Bahamas	Fowl Cay, Pinnacles	3	12.1	1999	C M F
Marks 2005	Bahamas	Gaulin's Forereef #1	3	10.3	1998	M
Marks 2005	Bahamas	Gaulin's Forereef #2	3	8	1998	M
Marks 2005	Bahamas	Gaulin's Forereef #3	3	5.7	1998	M
Marks 2005	Bahamas	Green Cay (D15)	3	11.1	1998	C M F
Marks 2005	Bahamas	High Point Cay (D27)	3	9.3	1998	C M F
Marks 2005	Bahamas	Long Bay Cay (D25)	3	10.4	1998	C M F
Marks 2005	Bahamas	Long Rock (D13)	3	8.5	1998	C M F
Marks 2005	Bahamas	Lynyard Cay, North	3	8	1999	C M F

Table AII. Continuation

Marks 2005	Bahamas	Lynyard Cay, South	3	8.7	1999	C M F
Marks 2005	Bahamas	Man O' War Cay, N. of S. Channel	3	5.4	1999	C M F
Marks 2005	Bahamas	Man O' War Cay, S. of S. Channel	3	3.1	1999	C M F
Marks 2005	Bahamas	Middle Bight (D22)	3	9.1	1998	C M F
Marks 2005	Bahamas	Middle Long Rock (D14)	3	9.6	1997	C M F
Marks 2005	Bahamas	Nichols Town (D2)	3	9.6	1997	C M F
Marks 2005	Bahamas	North Bight (D20)	3	9.7	1998	C M F
Marks 2005	Bahamas	North Grassy Creek (D29)	3	9.6	1997	C M F
Marks 2005	Bahamas	North Grassy Creek (D30)	3	7.2	1997	C M F
Marks 2005	Bahamas	North Joulters (D1)	3	6.5	1997	C M F
Marks 2005	Bahamas	North Mangrove (D23)	3	9.4	1998	C M F
Marks 2005	Bahamas	North Rock (D28)	3	7.2	1997	C M F
Marks 2005	Bahamas	North Staniard (D5)	3	7.5	1997	C M F
Marks 2005	Bahamas	Oasis (D26)	3	5.8	1998	C M F
Marks 2005	Bahamas	Pigeon (D32)	3	8.7	1997	C M F
Marks 2005	Bahamas	Saddleback (D33)	3	8.3	1997	C M F
Marks 2005	Bahamas	South AUTEC 1 (D11)	3	13.1	1997	C M F
Marks 2005	Bahamas	South Long Rock (D12)	3	8	1997	C M F
Marks 2005	Bahamas	South Love Hill (D8)	3	8.5	1997	C M F
Marks 2005	Bahamas	South Staniard 1 (D6)	3	8.1	1997	C M F
Marks 2005	Bahamas	South Staniard 2 (D7)	3	8.9	1998	C M F
Marks 2005	Bahamas	Sugar Rock (D16)	3	11	1998	C M F
Marks 2005	Bahamas	West Klein (D10)	3	10.8	1998	C M F
Marks 2005	Belize	7 Cut The Trench Deep (WP15)	3	12.8	2000	C M F
Marks 2005	Belize	Aquarium	3	7.7	1999	C M F
Marks 2005	Belize	Babylon's Gardens	3	9.4	1999	C M F
Marks 2005	Belize	Black Durgon	3	8	1999	C M F
Marks 2005	Belize	Cathedral	3	7.1	1999	C M F
Marks 2005	Belize	Caye Bokel Deep - E. Turneffe	3	16.6	2000	C M F
Marks 2005	Belize	Caye Chapel Deep (BZ-3)	3	15.7	2000	C M F
Marks 2005	Belize	Driftwood Reef	3	8.8	1999	C M F
Marks 2005	Belize	E. Turneffe Deep (WP6)	3	10.8	2000	C M F
Marks 2005	Belize	E. Turneffe Deep (WP8)	3	17	2000	C M F
Marks 2005	Belize	Gladdens Spit Deep (WP14)	3	11.6	2000	C M F
Marks 2005	Belize	Goffs Caye Deep (BZ-1)	3	9.3	2000	C M F
Marks 2005	Belize	Gotham City	3	8.7	1999	C M F
Marks 2005	Belize	Long Caye Ridge	3	7	1999	C M F
Marks 2005	Belize	Marie's promenade	3	8.8	1999	C M F
Marks 2005	Belize	Middle Caye Deep - E. Glovers	3	8.8	2000	C M F
Marks 2005	Belize	N.E. Glovers Deep (WP17)	3	11.7	2000	C M F
Marks 2005	Belize	N.W. Glovers Deep (WP18)	3	17.1	2000	C M F
Marks 2005	Belize	Painted Wall	3	4.2	1999	C M F
Marks 2005	Belize	S.E. Glovers Deep (WP19)	3	12.3	2000	C M F
Marks 2005	Belize	S.W. Glover Deep (WP20)	3	5	2000	C M F
Marks 2005	Belize	Samphire Rocks Deep (BZ-2)	3	10.3	2000	C M F
Marks 2005	Belize	San Pedro Canyon	3	13.2	1999	C M F
Marks 2005	Belize	Silver Caves	3	7.2	1999	C M F
Marks 2005	Belize	South Water Caye	3	5.7	1999	C M F
Marks 2005	Belize	South Water Caye Deep (WP16)	3	13.5	2000	C M F
Marks 2005	Belize	Surge City	3	8.8	1999	C M F
Marks 2005	Belize	Tobacco	3	5.7	1999	C M F
Marks 2005	Belize	W. Glovers Deep (WP22)	3	5.9	2000	C M F
Marks 2005	Belize	W. Turneffe Deep (WP2)	3	9.9	2000	C M F
Marks 2005	Belize	W. Turneffe Deep (WP4)	3	9.2	2000	C M F
Marks 2005	Belize	W. Turneffe Deep (WP5)	3	10.6	2000	C M F
Marks 2005	Bonaire	Barcadera	3	9.6	1999	C M F
Marks 2005	Bonaire	Carl's Jam	3	11.6	1999	C M F
Marks 2005	Bonaire	habitat	3	10	1999	C M
Marks 2005	Bonaire	karpata	3	9.1	1999	C M F
Marks 2005	Bonaire	Twin Peaks	3	8.8	1999	C M F
Marks 2005	Bonaire	W. Klein	3	11.2	1999	C M F
Marks 2005	Cayman Is	Cayman Brac: Airport Reef (End of Island) (CB9)	3	8.5	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Bert Brothers (CB3)	3	16.4	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Greenhouse (CB7)	3	6.7	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Lighthouse Reef (CB5)	3	9.5	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Peter's Anchor (CB1)	3	10.4	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Pillar Coral Reef (CB4)	3	10.6	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Pillars of Hercules (CB2)	3	4.1	2000	C M F
Marks 2005	Cayman Is	Cayman Brac: Sargent Major Reef (CB6)	3	7.7	2000	C M F
Marks 2005	Cayman Is	Grand Cayman: Babylon (GC23)	3	9.3	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Bear's Paw (GC27)	3	10.5	1999	C M
Marks 2005	Cayman Is	Grand Cayman: Breakers (GC30)	3	12.5	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Casey's Reef (GC26)	3	14	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Cemetery Reef (GC32)	3	9	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Deila's Delight (GC24)	3	7.2	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: East End Reef (GC19)	3	6.6	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Hepp's Mini Wall (GC28)	3	11.4	1999	C M
Marks 2005	Cayman Is	Grand Cayman: Isabel's Reef (GC22)	3	11	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Kaho's Reef (GC20)	3	8.9	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Kelly's Caverns (GC29)	3	8.8	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Playing Field (GC31)	3	7.5	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Queen's Throne (GC25)	3	12.2	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Snapper Hole (GC21)	3	10	1999	C M F
Marks 2005	Cayman Is	Grand Cayman: Sunset House (GC33)	3	9.1	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Berges Meredith Anchor (LC17)	3	9.2	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Black Tip Tunnels (LC6)	3	12.6	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Charles Bay (LC4)	3	10.8	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Disneyland (LC3)	3	9.9	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Grundy's Gardens (LC1)	3	9.3	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Jigsaw Puzzle (LC2)	3	10.3	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Joy's Joy (LC10)	3	12.4	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Lighthouse (LC16)	3	14.3	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Lucas's Ledge (LC14)	3	13.6	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Meadows (LC8)	3	5.8	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Mixing Bowl-Three Fathom Wall (LC5)	3	12.4	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Nancy's Cup of Tea (LC9)	3	12.4	1999	C M F
Marks 2005	Cayman Is	Little Cayman: No Name (LC15)	3	10.9	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Paul's Anchor (LC12)	3	13.1	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Penguin's Leap (LC7)	3	16	1999	C M F
Marks 2005	Cayman Is	Little Cayman: Rock Bottom Wall (LC13)	3	12.6	1999	C M F

Table AII. Continuation

Marks 2005	Cayman Is	Little Cayman: Wreck Anchor (CL18)	3	10.8	1999	C M F
Marks 2005	Costa Rica	Chance Mouth	3	5.5	1999	C M F
Marks 2005	Costa Rica	Meager Shoal	3	7	1999	C M F
Marks 2005	Cuba	Acuario	3	5.8	1999	C M F
Marks 2005	Cuba	Ancón (profundo)	3	8	2001	C M F
Marks 2005	Cuba	Arrecife Frustrado	3	9.2	2001	CM
Marks 2005	Cuba	Arrecifes Mulatas Centro (profundo)	3	12.3	2001	C M F
Marks 2005	Cuba	Arrecifes Mulatas Este (profundo)	3	13.3	2001	C M F
Marks 2005	Cuba	Boca de Juan Grin	3	10.5	2001	C M F
Marks 2005	Cuba	Canal de la Mulatas (profundo)	3	12.2	2001	C M F
Marks 2005	Cuba	Cayo Anclitas Este	3	11.9	2001	C M F
Marks 2005	Cuba	Cayo Anclitas Oeste (Punta Prácticos A)	3	14.1	2001	C M F
Marks 2005	Cuba	Cayo Anclitas Oeste (Punta Prácticos B)	3	13.3	2001	C M F
Marks 2005	Cuba	Cayo Arbolito (profundo)	3	12.5	2001	C M F
Marks 2005	Cuba	Cayo Bahía de Cádiz (Faro) (profundo)	3	12.9	2001	C M F
Marks 2005	Cuba	Cayo Bahía de Cádiz (Oeste) (profundo)	3	13.9	2001	C M F
Marks 2005	Cuba	Cayo Ballenatos (profundo)	3	12	2001	C M F
Marks 2005	Cuba	Cayo Blanco 1 (profundo)	3	10.1	2001	C M F
Marks 2005	Cuba	Cayo Blanco 2 (profundo)	3	6.7	2001	C M F
Marks 2005	Cuba	Cayo Blanco 3 (profundo)	3	14.2	2001	C M F
Marks 2005	Cuba	Cayo Borracho (profundo)	3	10.2	2001	C M F
Marks 2005	Cuba	Cayo Bretón Este	3	15	2001	C M F
Marks 2005	Cuba	Cayo Bretón Oeste	3	12.8	2001	C M F
Marks 2005	Cuba	Cayo Caballones Centro (Punta Escondida)	3	9.6	2001	C M F
Marks 2005	Cuba	Cayo Caballones Este	3	10.9	2001	C M F
Marks 2005	Cuba	Cayo Cachiboca	3	9.8	2001	C M F
Marks 2005	Cuba	Cayo Cachiboca (Punta Ballenas)	3	12.8	2001	C M F
Marks 2005	Cuba	Cayo Caguama (Punta Macao)	3	8.4	2001	C M F
Marks 2005	Cuba	Cayo Campos 1 (profundo)	3	13.5	2001	C M F
Marks 2005	Cuba	Cayo Campos 2 (profundo)	3	12.3	2001	C M F
Marks 2005	Cuba	Cayo Campos 3 (profundo)	3	12	2001	C M F
Marks 2005	Cuba	Cayo Campos 4 (profundo)	3	12.6	2001	C M F
Marks 2005	Cuba	Cayo Cantiles E. (profundo)	3	11.6	2001	C M F
Marks 2005	Cuba	Cayo Cinco Balas Dentro Este	3	6.8	2001	C M F
Marks 2005	Cuba	Cayo Cinco Balas Dentro Oeste	3	7.3	2001	C M F
Marks 2005	Cuba	Cayo Coco (Caricom) (profundo)	3	9.5	2001	C M F
Marks 2005	Cuba	Cayo Coco (Flamenco) (profundo)	3	9.3	2001	C M F
Marks 2005	Cuba	Cayo Confites (profundo)	3	12.5	2001	C M F
Marks 2005	Cuba	Cayo Cruz del Padre (Faro) (profundo)	3	13.2	2001	C M F
Marks 2005	Cuba	Cayo Cruz del Padre (Oeste) (profundo)	3	15	2001	C M F
Marks 2005	Cuba	Cayo Fragoso (Punta de Palo Quemado) (profundo)	3	14.7	2001	C M F
Marks 2005	Cuba	Cayo Fragoso (Sarmedina) (profundo)	3	14.9	2001	C M F
Marks 2005	Cuba	Cayo Grande Este 1 (Punta Bayameses Oeste)	3	11.4	2001	C M F
Marks 2005	Cuba	Cayo Grande Este 2 (Punta Bayameses Este)	3	11.3	2001	C M F
Marks 2005	Cuba	Cayo Grande Oeste 1	3	12.6	2001	C M F
Marks 2005	Cuba	Cayo Grande Oeste 2	3	13.9	2001	C M F
Marks 2005	Cuba	Cayo Guajaba (Este) (profundo)	3	13.9	2001	C M F
Marks 2005	Cuba	Cayo Guajaba (Oeste) (profundo)	3	12.2	2001	C M
Marks 2005	Cuba	Cayo Hicacos (profundo)	3	18.2	2001	C M F
Marks 2005	Cuba	Cayo la Vela (profundo)	3	15	2001	C M F
Marks 2005	Cuba	Cayo Matías 1 (profundo)	3	11.6	2001	C M F
Marks 2005	Cuba	Cayo Matías 2 (profundo)	3	12.5	2001	C M F
Marks 2005	Cuba	Cayo Piedra Grande (Pasa de Boca Piedra)	3	14.8	2001	C M F
Marks 2005	Cuba	Cayo Rico (profundo)	3	11.6	2001	C M F
Marks 2005	Cuba	Cayo Romano (profundo)	3	14.9	2001	C M F
Marks 2005	Cuba	Cayo Sigua - Cayo Diego Pérez 1 (profundo)	3	14	2001	C M F
Marks 2005	Cuba	Cayo Sigua 1 (profundo)	3	7.7	2001	C M F
Marks 2005	Cuba	Cayo Sigua 3 (profundo)	3	8.2	2001	C M F
Marks 2005	Cuba	Cayo Verde (profundo)	3	7.5	2001	C M F
Marks 2005	Cuba	Cayos Hijos de los Ballenatos (profundo)	3	16.1	2001	C M F
Marks 2005	Cuba	Cayos Pajonal (Punta Tocinera) (profundo)	3	15.2	2001	C M F
Marks 2005	Cuba	E. Cayo Diego Pérez	3	10.1	2001	C M F
Marks 2005	Cuba	E. Ensenada de Cazones (profundo)	3	9.7	2001	C M F
Marks 2005	Cuba	Faro de la Vela (profundo)	3	13.4	2001	C M F
Marks 2005	Cuba	Jardín de las Gorgonias	3	8.3	1999	C M F
Marks 2005	Cuba	La Cadena Misteriosa	3	11.3	1999	C M F
Marks 2005	Cuba	Médanos de la Vela Centro	3	7.7	2001	C M F
Marks 2005	Cuba	Médanos Vizcaínos 1 (profundo)	3	14.7	2001	C M F
Marks 2005	Cuba	Médanos Vizcaínos 2 (profundo)	3	13.3	2001	C M F
Marks 2005	Cuba	Médanos Vizcaínos 3 (profundo)	3	12.7	2001	C M F
Marks 2005	Cuba	Médanos Vizcaínos 4 (profundo)	3	13.1	2001	C M F
Marks 2005	Cuba	N. Cayo de Dios (profundo)	3	10	2001	C M F
Marks 2005	Cuba	N. Cayo Pinos 1	3	12.3	2001	C M F
Marks 2005	Cuba	N. Cayo Pinos 2	3	10.9	2001	C M F
Marks 2005	Cuba	N. Médano de la Vela A (profundo)	3	10.6	2001	C M F
Marks 2005	Cuba	N. Médano de la Vela B (profundo)	3	10.3	2001	C M F
Marks 2005	Cuba	N.E. Ensenada de Cazones	3	7.3	2001	C M F
Marks 2005	Cuba	Pasa Cachiboca	3	9.6	2001	C M F
Marks 2005	Cuba	Playa Larga 1 (profundo)	3	14.2	2001	C M F
Marks 2005	Cuba	Playa Larga 2 (profundo)	3	14.2	2001	C M F
Marks 2005	Cuba	Playa Larga 3 (profundo)	3	13.3	2001	C M F
Marks 2005	Cuba	Punta Bretón	3	14.6	2001	C M F
Marks 2005	Cuba	Punta Francés 1 (profundo)	3	8.6	2001	C M F
Marks 2005	Cuba	Punta Francés 2 (profundo)	3	15	2001	C M F
Marks 2005	Cuba	S. Ensenada de Cazones (profundo)	3	10.7	2001	C M F
Marks 2005	Cuba	S.E. Cayo Largo (profundo)	3	16.8	2001	C M F
Marks 2005	Cuba	S.E. Cayo. Diego Pérez (profundo)	3	13	2001	C M F
Marks 2005	Cuba	S.E. Cayo. Diego Pérez 1 (profundo)	3	13.9	2001	C M F
Marks 2005	Cuba	S.E. Cayo. Diego Pérez 4 (profundo)	3	12.9	2001	C M F
Marks 2005	Cuba	S.E. Ensenada de Cazones	3	10.6	2001	C M F
Marks 2005	Cuba	Yemayá	3	5.7	1999	C M F
Marks 2005	Curacao	Jeremi	3	10	1998	C M
Marks 2005	Curacao	Jeremi - 10m	3	10.7	2000	C M
Marks 2005	Curacao	Jeremi - 15m	3	15	2000	C M
Marks 2005	Curacao	Jeremi - 20m	3	20	2000	C
Marks 2005	Curacao	Kalki	3	10	1998	C M
Marks 2005	Curacao	Kalki - 15m	3	15	2000	C M
Marks 2005	Curacao	Kalki - 20m	3	19.9	2000	C
Marks 2005	Curacao	Lagun	3	10	1998	C M F
Marks 2005	Curacao	Lagun - 10m	3	9.9	2000	C M F

Table AII. Continuation

Marks 2005	Curacao	Lagun - 15m	3	15.3	2000	C M F
Marks 2005	Curacao	Oostpunt	3	10	1998	C M F
Marks 2005	Eustatius, N.A.	EUX01: Barracuda Reef	3	17.4	1999	C M F
Marks 2005	Eustatius, N.A.	EUX02: Anchor Point	3	14.4	1999	C M F
Marks 2005	Eustatius, N.A.	EUX03: Hangover	3	14.2	1999	C M F
Marks 2005	Eustatius, N.A.	EUX04: The Blocks	3	15.2	1999	C M F
Marks 2005	Eustatius, N.A.	EUX05: The Ledges	3	13.7	1999	C M F
Marks 2005	Eustatius, N.A.	EUX06: Five Fingers	3	14.9	1999	C M F
Marks 2005	Eustatius, N.A.	EUX07: Valley of the Sponges	3	14	1999	C M F
Marks 2005	Eustatius, N.A.	EUX08: The Humps	3	11.5	1999	C M F
Marks 2005	Eustatius, N.A.	EUX09: Mushroom Gardens	3	16.2	1999	C M F
Marks 2005	Eustatius, N.A.	EUX10: Mushroom Gardens South	3	16.2	1999	C M F
Marks 2005	Jamaica	Bloody Bay	3	8.9	2000	C M F
Marks 2005	Jamaica	Booby North Point	3	11.7	2000	C M F
Marks 2005	Jamaica	Boscolbel West	3	7.7	2000	C M F
Marks 2005	Jamaica	Boston Bay	3	9.4	2000	C M F
Marks 2005	Jamaica	Braco Village West	3	9.7	2000	C M F
Marks 2005	Jamaica	Chalet Caribe, Classroom, Reading	3	7	2000	C M F
Marks 2005	Jamaica	Dairy Bull - Deep	3	10	2000	C M F
Marks 2005	Jamaica	Davis Cove East	3	12.4	2000	C M F
Marks 2005	Jamaica	DBay - CARICOMP	3	8.8	2000	C M F
Marks 2005	Jamaica	Dicky's Reef	3	9.9	2000	C M F
Marks 2005	Jamaica	Drumville Cove	3	11.8	2000	C M F
Marks 2005	Jamaica	Falmouth East, Trelawny	3	8.2	2000	C M F
Marks 2005	Jamaica	Green Island	3	5.6	2000	C M F
Marks 2005	Jamaica	Green Island East	3	12.3	2000	C M F
Marks 2005	Jamaica	Hedo 3 - Nursery	3	3.4	2000	C M F
Marks 2005	Jamaica	Holiday Inn	3	8.7	2000	C M F
Marks 2005	Jamaica	Homer's Cove	3	10.3	2000	C M F
Marks 2005	Jamaica	Laughlands E	3	13.6	2000	C M F
Marks 2005	Jamaica	Little River	3	13.1	2000	C M F
Marks 2005	Jamaica	Long Bay East Coast	3	6.5	2000	C M F
Marks 2005	Jamaica	Long Bay Montego	3	9.6	2000	C M F
Marks 2005	Jamaica	Long Bay Negril	3	10.6	2000	C M F
Marks 2005	Jamaica	Lucea Bay East	3	8.9	2000	C M F
Marks 2005	Jamaica	Mosquito Cove - Deep	3	7.1	2000	C M F
Marks 2005	Jamaica	Mountain Spring Bay	3	10.1	2000	C M F
Marks 2005	Jamaica	Ocho Rios West - Sewage End	3	14.5	2000	C M F
Marks 2005	Jamaica	Oraccobessa East	3	8.5	2000	C M F
Marks 2005	Jamaica	Orange Bay East Coast	3	7.5	2000	C M F
Marks 2005	Jamaica	Orange Bay West Coast - Deep	3	8.4	2000	C M F
Marks 2005	Jamaica	Pear Tree - Deep	3	8.5	2000	C M F
Marks 2005	Jamaica	Port Maria East	3	9.8	2000	C M F
Marks 2005	Jamaica	Rio Bueno	3	5.4	2000	C M F
Marks 2005	Jamaica	Rio Nuevo West	3	10.6	2000	C M F
Marks 2005	Jamaica	Round Hill - Deep	3	9.6	2000	C M F
Marks 2005	Jamaica	Salt Bay West	3	10.8	2000	C M F
Marks 2005	Jamaica	Salt Marsh, Trelawny	3	7.8	2000	C M F
Marks 2005	Jamaica	Sandals Montego Bay, St. James	3	7.2	2000	C M F
Marks 2005	Jamaica	Sandy Bay	3	8.7	2000	C M F
Marks 2005	Jamaica	Savannah La Mar	3	9.2	2000	C M F
Marks 2005	Jamaica	Sergeant Major Reef	3	8	2000	C M F
Marks 2005	Jamaica	Sheerness Bay	3	9.7	2000	C M F
Marks 2005	Jamaica	Silver Sands	3	10.6	2000	C M F
Marks 2005	Jamaica	Snapper Drop	3	11.7	2000	C M F
Marks 2005	Jamaica	St. Ann's Bay-West	3	10.4	2000	C M F
Marks 2005	Jamaica	Stewart Bay	3	10.2	2000	C M F
Marks 2005	Jamaica	Tower Isle East - Deep	3	7	2000	C M F
Marks 2005	Jamaica	Tropical Beach - Deep	3	5.2	2000	C M F
Marks 2005	Jamaica	Wag Water	3	10	2000	C M F
Marks 2005	Jamaica	Windsor Castle	3	9.2	2000	C M F
Marks 2005	Jamaica	Witches Maze, Rose Hall, Wyndham Hotel, St. James	3	9.3	2000	C M F
Marks 2005	Marteen, N.A.	SXM01: Mike's Maze	3	9.1	1999	C M F
Marks 2005	Marteen, N.A.	SXM02: Hens & Chicks	3	10.6	1999	C M F
Marks 2005	Nicaragua	BCI003	3	13.1	2003	C M F
Marks 2005	Nicaragua	BCI004	3	11.1	2003	C M F
Marks 2005	Nicaragua	BCI005	3	11.8	2003	C M F
Marks 2005	Nicaragua	BCI006	3	12.5	2003	C M F
Marks 2005	Nicaragua	BCI007	3	15.7	2003	C M F
Marks 2005	Nicaragua	LCI002	3	5.1	2003	C M F
Marks 2005	Nicaragua	LCI003	3	5.1	2003	C M F
Marks 2005	Nicaragua	LCI004	3	9.6	2003	C M F
Marks 2005	Panama	Bocas del Toro: Deer Creek (Deep)	3	5.9	2002	C M F
Marks 2005	Panama	Bocas del Toro: Hector's Site 42 (Deep)	3	9.6	2002	C M F
Marks 2005	Panama	Bocas del Toro: Isla Popa 3	3	7.4	2002	C M F
Marks 2005	Panama	Bocas del Toro: Salt Creek (Deep)	3	4.4	2002	C M F
Marks 2005	Panama	Bocas del Toro: Zapatilla 3	3	6	2002	C M F
Marks 2005	Panama	Bocas del Toro: Zapatilla 4	3	6.6	2002	C M F
Marks 2005	Panama	Kuna Yala: Acuakargana	3	9.8	2002	C M F
Marks 2005	Panama	Kuna Yala: Aguadargana B	3	4.3	2002	C M F
Marks 2005	Panama	Kuna Yala: Alidup	3	8.4	2002	C M F
Marks 2005	Panama	Kuna Yala: Aritupu	3	7	2002	C M F
Marks 2005	Panama	Kuna Yala: Carti Shoal 1	3	8.2	2002	C M F
Marks 2005	Panama	Kuna Yala: Carti Shoal 2	3	7.2	2002	C M F
Marks 2005	Panama	Kuna Yala: Chichime Sand Bar	3	6.7	2002	C M F
Marks 2005	Panama	Kuna Yala: East Banedup	3	7.7	2002	C M F
Marks 2005	Panama	Kuna Yala: Eden Channel	3	9.3	2002	C M F
Marks 2005	Panama	Kuna Yala: Limon Grande	3	6.8	2002	C M F
Marks 2005	Panama	Kuna Yala: Miria Backreef	3	8.1	2002	M
Marks 2005	Panama	Kuna Yala: Miria Forereef	3	5.8	2002	C M F
Marks 2005	Panama	Kuna Yala: Misdup	3	6.6	2002	C M F
Marks 2005	Panama	Kuna Yala: Niatupu	3	8.7	2002	C M F
Marks 2005	Panama	Kuna Yala: Niatupu 2	3	3.1	2002	C M F
Marks 2005	Panama	Kuna Yala: Niatupu 3	3	11.1	2002	C M F
Marks 2005	Panama	Kuna Yala: Nubasitupu	3	8.3	2002	C M F
Marks 2005	Panama	Kuna Yala: Ordupdarbogoad 1	3	9.1	2002	C M F
Marks 2005	Panama	Kuna Yala: Orosdup	3	6.1	2002	C M F
Marks 2005	Panama	Kuna Yala: Sail Rock	3	8.6	2002	C M F
Marks 2005	Panama	Kuna Yala: Salar	3	6.9	2002	C M F
Marks 2005	Panama	Kuna Yala: Ubicantupu	3	6.2	2002	C M F

Table AII. Continuation

Marks 2005	Panama	Kuna Yala: Ulagsukun B	3	8.1	2002	C M F
Marks 2005	Panama	Kuna Yala: Wichudub 1	3	12.4	2002	C M F
Marks 2005	Puerto Rico	Bajo Blade	3	8.8	2003	C M F
Marks 2005	Puerto Rico	Cayo Diablo	3	8.8	2003	C M F
Marks 2005	Puerto Rico	Culebra: Carlos Rosario North	3	8	2003	C M F
Marks 2005	Puerto Rico	Culebra: Corchos	3	4.9	2003	C M F
Marks 2005	Puerto Rico	Culebra: Corchos South	3	10.6	2003	C M F
Marks 2005	Puerto Rico	Culebra: Culebrita Reef	3	7.8	2003	C M F
Marks 2005	Puerto Rico	Culebra: Punta Vapor	3	6.2	2003	C M F
Marks 2005	Puerto Rico	Culebra: S.E. Luis Peña	3	4.8	2003	C M F
Marks 2005	Puerto Rico	Punta Aguila	3	10.1	2003	C M F
Marks 2005	Puerto Rico	S.W. Cayo Lobo	3	4.5	2003	C M F
Marks 2005	Puerto Rico	South Palominito	3	9.5	2003	C M F
Marks 2005	Puerto Rico	Vieques: 1	3	13.9	2003	C M F
Marks 2005	Puerto Rico	Vieques: 2	3	4.5	2003	C M F
Marks 2005	Saba, N.A.	BNK01: Saba Bank 1	3	20.1	1999	C M F
Marks 2005	Saba, N.A.	BNK02: Saba Bank 2	3	15	1999	C M F
Marks 2005	Saba, N.A.	BNK03: Saba Bank 3	3	17.5	1999	C M F
Marks 2005	Saba, N.A.	SAB01: Core Gut	3	9.5	1999	C M F
Marks 2005	Saba, N.A.	SAB02: Hole in the Corner	3	10.7	1999	C M F
Marks 2005	Saba, N.A.	SAB03: Tent Reef	3	9.4	1999	C M F
Marks 2005	Saba, N.A.	SAB04: Hot Springs	3	11.2	1999	C M F
Marks 2005	Saba, N.A.	SAB05: Ladder Labyrinth	3	12.1	1999	C M F
Marks 2005	Saba, N.A.	SAB06: Babylon	3	13.1	1999	C M F
Marks 2005	Saba, N.A.	SAB07: Porites Point	3	14.5	1999	C M F
Marks 2005	Saba, N.A.	SAB08: Torrens Point	3	5.6	1999	C M F
Marks 2005	Saba, N.A.	SAB09: Green Island	3	6.9	1999	C M F
Marks 2005	St Vincent	Horseshoe Reef, Site A	3	11.4	1999	C M F
Marks 2005	St Vincent	Horseshoe Reef, Site C	3	8.8	1999	C M F
Marks 2005	St Vincent	Horseshoe Reef, Site E	3	11.1	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC13-The Arch	3	11	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC14-Airplane	3	15.6	1999	C M
Marks 2005	Turks&Caic	Caicos Bank: TC16-Ambergris 2	3	19.9	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC17-(No Name)	3	15.5	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC18-F Hole	3	13.2	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC19-French Cay	3	14.4	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC20-West Sand Spit	3	13.4	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC21-Spanish Anchor (W. Caicos Wall)	3	15.4	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC22-W. Caicos Wall-middle	3	18.3	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC23-The Pinnacles (Grace Bay)	3	10.1	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC24-Coral Gables (N. side of Provo)	3	11.1	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC25-Grace Bay	3	10.1	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC26-Football Field	3	18.9	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC27-Grouper Hole	3	11.6	1999	C M F
Marks 2005	Turks&Caic	Caicos Bank: TC28-Aquarium West	3	17.3	1999	C M F
Marks 2005	Turks&Caic	Mouchoir Bank: TC11-Mouchoir Bank 1	3	22.7	1999	C M F
Marks 2005	Turks&Caic	Mouchoir Bank: TC12-Mouchoir Bank 2	3	13.6	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC01-Lighthouse Point (anchor)	3	17	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC02-North Point (anchor)	3	16.2	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC03-Coral Garden	3	11.5	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC04-West of Little Sand Cay	3	9.6	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC05-N. of Salt Cay (anchor)	3	12.2	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC06-Casey's Wall (anchor. W. of Salt Cay)	3	11.9	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC07-Black Forest	3	11.7	1999	C M F
Marks 2005	Turks&Caic	Turks Bank: TC08-Chief Minister's House	3	10.1	1999	C M F
Marks 2005	USA	Biscayne Bay: Fowey Reef	3	5.2	2003	C M F
Marks 2005	USA	Biscayne Bay: Pacific Reef	3	6	2003	C M F
Marks 2005	USA	Biscayne Bay: Triumph Reef	3	5.5	2003	C M F
Marks 2005	USA	East Flower Garden Banks (bouy #2)	3	19.3	1999	C M F
Marks 2005	USA	Lower Keys: Maryland Shoal	3	8	2003	C M F
Marks 2005	USA	Lower Keys: West of Big Pine Shoal	3	5.7	2003	C M F
Marks 2005	USA	Lower Keys: West of Sombrero HB	3	8.5	2003	C M F
Marks 2005	USA	Middle Keys: Tennessee Reef RO HB	3	5.7	2003	C M F
Marks 2005	USA	Upper Keys: French Reef SPA	3	7	2003	C M F
Marks 2005	USA	Upper Keys: Little Conch Reef	3	8.7	2003	C M F
Marks 2005	USA	Upper Keys: South of Carysfort SPA	3	8.2	2003	C M F
Marks 2005	USA	Upper Keys: The Elbow	3	5.3	2003	C M F
Marks 2005	USA	Upper Keys: West Alligator Light HB	3	9.5	2003	C M F
Marks 2005	USA	West Flower Garden Banks (buoy #5)	3	22.5	1999	C M F
Marks 2005	Venezuela	Boca de Cote Profundo (BCP)	3	11.3	1999	C M F
Marks 2005	Venezuela	Boca del Medio (BM)	3	7.2	1999	C M F
Marks 2005	Venezuela	Cayo Sal Sur (CSS)	3	9.4	1999	C M F
Marks 2005	Venezuela	Dos Mosquises Sur (DMS)	3	11.2	1999	C M F
Marks 2005	Venezuela	Pelona de Rabusqui (PR)	3	6.4	1999	C M F
Marks 2005	Venezuela	Punta Cayo Sal (PCS)	3	13.7	1999	C M F
Marks 2005	Virgin Is	BVI, Anegada: Herman's Reef	3	13.1	2000	M
Marks 2005	Virgin Is	BVI, Anegada: Horseshoe Reef	3	10.5	2000	C M F
Marks 2005	Virgin Is	BVI, Anegada: Jack Bay	3	9.1	2000	C M F
Marks 2005	Virgin Is	BVI, Anegada: West Cow Wreck	3	8.4	2000	C M F
Marks 2005	Virgin Is	BVI, Guana Island: Iguana Head	3	9.5	1999	C M F
Marks 2005	Virgin Is	BVI, Virgin Gorda: Eustacia Reef	3	8.5	2000	C M F
Marks 2005	Virgin Is	USVI, St. Croix: Cane Bay	3	9.9	1999	C M F
Marks 2005	Virgin Is	USVI, St. Croix: Long Reef	3	13.4	1999	C M F
Marks 2005	Virgin Is	USVI, St. Croix: Salt River East	3	10.1	1999	C M F
Marks 2005	Virgin Is	USVI, St. John: F Bay East, Inner	3	4.8	1999	C M F
Marks 2005	Virgin Is	USVI, St. John: F Bay East, Outer	3	6.4	2000	C M F
Marks 2005	Virgin Is	USVI, St. John: F Bay West, Inner	3	4.7	2000	C M F
Marks 2005	Virgin Is	USVI, St. John: F Bay West, Outer	3	7.6	1999	C M F
Marks 2005	Virgin Is	USVI, St. John: Great Lameshur, Donkey	3	2.9	2000	C M F
Marks 2005	Virgin Is	USVI, St. John: Great Lameshur, Tektite	3	11	1999	C M F
Marks 2005	Virgin Is	USVI, St. John: Great Lameshur, VIERS	3	5.6	1999	C M F
Marks 2005	Virgin Is	USVI, St. John: Great Lameshur, Yawzi	3	12.6	1999	C M F
Marks 2005	Virgin Is	USVI, St. Thomas: Brewer's Bay	3	8.3	1999	C M F
Marks 2005	Virgin Is	USVI, St. Thomas: Buck Island	3	13.8	1999	C M F
Marks 2005	Virgin Is	USVI, St. Thomas: Caret Bay	3	9.1	1998	C M F
Marks 2005	Virgin Is	USVI, St. Thomas: Flat Cay	3	12.3	1999	C M F
Marks 2005	Virgin Is	USVI, St. Thomas: Sprat Bay, Water Island	3	10.2	2000	C M F
Marks 2005	Yucatan	Akumal: Dicks	3	10.5	1999	C M
Marks 2005	Yucatan	Akumal: Doña Laticia	3	11.8	1999	C M
Marks 2005	Yucatan	Akumal: Las Redes	3	12	1999	C M

Table AII. Continuation

Marks 2005	Yucatan	Akumal: Média Luna	3	10.3	1999	C M
Marks 2005	Yucatan	Akumal: Motorcycle	3	12	1999	C M
Marks 2005	Yucatan	Akumal: Yal Ku	3	10	1999	C M
Marks 2005	Yucatan	Boca Paila Centro	3	10.5	1999	C M F
Marks 2005	Yucatan	Boca Paila Norte	3	11.3	1999	C M F
Marks 2005	Yucatan	Boca Paila Sur	3	8.9	1999	C M F
Marks 2005	Yucatan	Canal de Glenview	3	15.7	2000	C M
Marks 2005	Yucatan	El Placer Centro	3	12.1	1999	C M F
Marks 2005	Yucatan	El Placer Norte	3	12	1999	C M F
Marks 2005	Yucatan	El Placer Sur	3	12.4	1999	C M F
Marks 2005	Yucatan	El Quebradote	3	12.1	2000	C M
Marks 2005	Yucatan	Entrada de Cayo Labos	3	8.2	2000	C M F
Marks 2005	Yucatan	Galleguilla-deep (GA9)	3	10.5	1999	C M
Marks 2005	Yucatan	Galleguilla-shallow (GA3)	3	4.5	1999	C M
Marks 2005	Yucatan	Isla Che Norte	3	7.5	2000	C M F
Marks 2005	Yucatan	Isla de Sacrificios-deep (IS9)	3	10.5	1999	C M
Marks 2005	Yucatan	Isla de Sacrificios-shallow (IS3)	3	4.5	1999	C M
Marks 2005	Yucatan	Isla Verde-deep (IV9)	3	10.5	1999	C M
Marks 2005	Yucatan	Isla Verde-shallow (IV3)	3	4.5	1999	C M
Marks 2005	Yucatan	Mahahual Centro	3	10.6	1999	C M F
Marks 2005	Yucatan	Mahahual Norte	3	9.8	1999	C M F
Marks 2005	Yucatan	Mahahual Sur	3	9.9	1999	C M F
Marks 2005	Yucatan	Punta Allen Centro	3	12.1	1999	C M F
Marks 2005	Yucatan	Punta Allen Norte	3	10.3	1999	C M F
Marks 2005	Yucatan	Punta Allen Sur	3	11.4	1999	C M F
Marks 2005	Yucatan	Punta Yuyum Centro	3	10	1999	C M F
Marks 2005	Yucatan	Punta Yuyum Norte	3	9.9	1999	C M F
Marks 2005	Yucatan	Punta Yuyum Sur	3	10.4	1999	C M F
Marks 2005	Yucatan	Segundo Blanquizal	3	11.1	2000	C M F
Marks 2005	Yucatan	Tampalam Centro	3	8.9	1999	C M F
Marks 2005	Yucatan	Tampalam Norte	3	10.1	1999	C M F
Marks 2005	Yucatan	Tampalam Sur	3	8.1	1999	C M F
Marks 2005	Yucatan	Xahuayxol Centro	3	11.1	1999	C M F
Marks 2005	Yucatan	Xahuayxol Norte	3	9.5	1999	C M F
Marks 2005	Yucatan	Xahuayxol Sur	3	10.5	1999	C M F
Marks 2005	Yucatan	Xcalak Centro	3	9.4	1999	C M F
Marks 2005	Yucatan	Xcalak Norte	3	10.7	1999	C M F
Marks 2005	Yucatan	Xcalak Sur	3	9.9	1999	C M F
Marks 2005	Yucatan	Xcalak: Cañones (Canyons)	3	13.5	1999	C M F
Marks 2005	Yucatan	Xcalak: Chimnea (Chimney)	3	10.5	1999	C M F
Marks 2005	Yucatan	Xcalak: Coral Gardens	3	7.9	1999	C M F
Marks 2005	Yucatan	Xcalak: Doña Nica (Sur de Nicas)	3	15	1999	C M F
Marks 2005	Yucatan	Xcalak: El Quebrado	3	10.1	1999	C M F
Marks 2005	Yucatan	Xcalak: Siete Cocos (Dos Cocos)	3	11.8	1999	C M F
McField et al 2001, Mcfield 2001	Belize	BAC	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	BAC	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	Calabash Reef	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	Calabash Reef	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	GAL	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	GAL	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	Glovers 2 sites	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	Glovers 2 sites	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	GOF	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	GOF	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	HMC	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	HMC	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	Holchan	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	Holchan	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	NICS	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	NICS	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	POM	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	POM	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	SWA	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	SWA	1	15	1999	C
McField et al 2001, Mcfield 2001	Belize	TAC	1	15	1997	C M F
McField et al 2001, Mcfield 2001	Belize	TAC	1	15	1999	C
Meier 1996	USA	Florida	1	2	1994	C
Mejia and Garzon-Ferreira 2000	Colombia	ALS	1	10	1995	F
Mejia and Garzon-Ferreira 2000	Colombia	APB	1	10	1995	F
Mejia and Garzon-Ferreira 2000	Colombia	LPTS	1	10	1995	F
Mejia and Garzon-Ferreira 2000	Colombia	TB	1	10	1995	F
Miller 2003	Navassa	North shelf	1	5	2002	C
Miller 2003	Navassa	North shelf	1	5	2002	F
Miller 2003	Navassa	North shelf	1	5	2002	M
Miller 2003	Navassa	NW point	1	5	2002	C
Miller 2003	Navassa	NW point	1	5	2002	F
Miller 2003	Navassa	NW point	1	5	2002	M
Miller and Gerstner 2002	Navassa	Navassa	1	15	2000	C M F D
Miller et al 2003	USA	FKNMS 12 sites	2	8, 15	1998, 1999	M
Miller et al 2003	Virgin Is	St Croix 6 sites	1	2	2000, 2001	D
Morrison 1988	Jamaica	Discovery Bay	1,2	5, 17	1982, 1984	D
Morrison 1988	Jamaica	Discovery Bay 3 sites	1,2	7	1982, 1984	M
Moses and Bonem 2001	Jamaica	DairyB	1	1.5, 3, 5, 6, 7, 9, 11, 12	1998	D
Moses and Bonem 2001	Jamaica	LTS	1	1.5, 3, 5, 6, 7, 9, 11, 12	1998	D
Moses and Bonem 2001	Jamaica	Pear	1	1.5, 3, 5, 6, 7, 9, 11, 12	1998	D
Moses and Bonem 2001	Jamaica	Rio Bueno	1	1.5, 3, 5, 6, 7, 9, 11, 12	1998	D
Murdoch and Aronson 1999	USA	Ajax	2	19	1995	C
Murdoch and Aronson 1999	USA	Aligator	2	19	1995	C
Murdoch and Aronson 1999	USA	American shoal	2	19	1995	C
Murdoch and Aronson 1999	USA	Bird Key	2	19	1995	C
Murdoch and Aronson 1999	USA	Carysfort	2	19	1995	C
Murdoch and Aronson 1999	USA	Cosgrove	2	19	1995	C
Murdoch and Aronson 1999	USA	Elbow	2	19	1995	C
Murdoch and Aronson 1999	USA	Looe Key	2	19	1995	C
Murdoch and Aronson 1999	USA	Love	2	19	1995	C
Murdoch and Aronson 1999	USA	No Name	2	19	1995	C
Murdoch and Aronson 1999	USA	Pickles	2	19	1995	C
Murdoch and Aronson 1999	USA	Pulaski	2	19	1995	C
Murdoch and Aronson 1999	USA	Sand Key	2	19	1995	C
Murdoch and Aronson 1999	USA	Sombrero Key	2	19	1995	C

Table AII. Continuation

Murdoch and Aronson 1999	USA	Tennessee	2	19	1995	C
Murdoch and Aronson 1999	USA	Western Sambo	2	19	1995	C
Murillo and Cortes 1984	Costa Rica	Cahuita	1,4	2	1983	D
Nagelkerken et al 2005	Curacao	Curacao 9 sites	2	3, 4, 6, 7, 9, 12, 15, 18, 21	1973, 2003	C
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	Anegada	1	8.5, 9, 10.5, 13	2000	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	Eustatia	1	8.5	2000	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	Iguana	1	10	1999	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St Croix	1	9.5, 10, 13.5	1999	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St John	1	5, 5.5, 7.5, 11, 13	1999	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St John	1	3, 5, 6.5	2000	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St Thomas	1	14	1999	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St Thomas	1	8.5, 9.5, 10, 12	2000	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St Thomas	1	9.5	2000	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St Thomas	1	10	2000	D
Nemeth et al 2003, Lang 2003 (ed)	Virgin Is	St Thomas	1	12	2000	D
NOAA, 2005 and Garcia-Sais et al 2005	Puerto Rico	La Parguera	3	10	2001-2005	C M F
NOAA, 2005 and Garcia-Sais et al 2005	Puerto Rico	La Parguera	3	10	2000	F
NOAA, 2005 and Jeffrey et al 2005	Virgin Is	St Croix	3	8	2001-2005	C M F
NOAA, 2005 and Jeffrey et al 2005	Virgin Is	St John	3	10	2001-2005	C M F
Nunez-Lara 1998, Nunez-Lara and Ariaz-Gonzalez 1998	Yucatan	B Paila	1,4	6	1997	F
Nunez-Lara 1998, Nunez-Lara and Ariaz-Gonzalez 1998	Yucatan	Majahual	1,4	6	1997	F
Nunez-Lara 1998, Nunez-Lara and Ariaz-Gonzalez 1998	Yucatan	Tampalam	1,4	6	1997	F
Ohlhorst 1980	Jamaica	Discovery Bay	1	15, 24, 30, 39	1977	C M D
Ohlhorst 1980	Jamaica	Pear t Bottom	1	6, 15, 24	1977	C M D
Osulivan 2002	Jamaica	Negril	1	4	2002	C M
Osulivan 2002	Jamaica	Negril 2 sites	1	4	2001	D
Paredes unpublished	Belize	Cypress	4	15	2004	C M F D
Paredes unpublished	Belize	Dos cocos	4	15	2004	C M F D
Paredes unpublished	Belize	Hol Chan	4	15	2004	C M F D
Paredes unpublished	Belize	Mata cave	4	15	2004	C M F D
Paredes unpublished	Belize	Middle Key	4	5, 15	2004	C M F D
Paredes unpublished	Belize	NW Glover's	4	5, 15	2004	C M F D
Paredes unpublished	Belize	SW Glover's	4	5, 15	2004	C M F D
Paredes unpublished	Belize	W Glover's	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Canarreos 4	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Canarreos 5	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Canarreos 6	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Canarreos 1	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Canarreos 2	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Canarreos 3	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 4	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 5	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 6	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 1	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 2	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 3	4	5, 15	2004	C M F D
Paredes unpublished	Cuba	Jardines 7	4	15	2004	C M F D
Paredes unpublished	Cuba	Jardines 8	4	15	2004	C M F D
Paredes unpublished	Cuba	Jardines 9	4	15	2004	C M F D
Paredes unpublished	Jamaica	Braco	4	5, 15	2004	C M F D
Paredes unpublished	Jamaica	Dairy Bull	4	5, 15	2004	C M F D
Paredes unpublished	Jamaica	MBMP C	4	5, 15	2004	C M F D
Paredes unpublished	Jamaica	MBMP hani	4	5, 15	2004	C M F D
Paredes unpublished	Jamaica	MBMP N	4	5, 15	2004	C M F D
Paredes unpublished	Jamaica	MBNP W	4	5, 15	2004	C M F D
Paredes unpublished	Jamaica	Rio Bueno	4	5, 15	2004	C M F D
Paredes unpublished	Yucatan	Cozumel C	4	5, 16	2004	C M F D
Paredes unpublished	Yucatan	Cozumel N	4	5, 17	2004	C M F D
Paredes unpublished	Yucatan	Cozumel S	4	5, 18	2004	C M F D
Pattengill and Semmens 2003, Lang 2003 (ed)	Gulf Mex	E Flowers	1	19.5	1999	D
Pattengill and Semmens 2003, Lang 2003 (ed)	Gulf Mex	W Flowers	1	22.5	1999	D
Phillips and Perez-Cruet 1984	Costa Rica	Cahuita	1,4	5	1982	F
Porter and Meier 1992	USA	Florida	1,2	2	1985, 1986, 1989	C
Porter and Meier 1992	USA	Florida	1,2	2	1984, 1990, 1991	C M D
Rakitin and Kramer 1996	Barbados	Barbados-BMR 2 SITES	1,3	10	1992	F
Randal 1963	Virgin Is	St John	1,4	9	1960	F
Riegl et al 2003, Lang 2003 (ed)	Turks&Caic	Turks&Caicos	1	9.5, 10, 10.5, 11, 11.5, 12, 13, 13.5, 14.5, 15, 16, 17, 18, 19, 20, 22	1999	D
Rogers and Miller 2001	Virgin Is	Lamesur	1	10	1989, 1995, 1998	C M
Rogers and Miller 2001	Virgin Is	Newfound	1	10	1998	C M
Rogers and Zullo 1987 in Gardner 2002	Virgin Is	Hawknest Bay	1,5	3, 7, 11	1984, 1985	C
Rogers et al 1984	Virgin Is	USVI 2 sites	1	9, 18, 27, 37	1981	C
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Allen C	1	12	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Allen N	1	10.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Allen S	1	11	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Mahaual C	1	10.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Mahaual N	1	9.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Mahaual S	1	10	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Paila C	1	9.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Paila N	1	11.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Paila S	1	9	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Placer C	1	12	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Placer N	1	12	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Placer S	1	13	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	TampN	1	10.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	TampS 2 SITES	1	8	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Xahua C	1	11	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Xahua N	1	9.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Xahua S	1	10.5	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Xcalak C	1	9	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Xcalcalak N	1	11	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Xcalak S	1	10	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Yuyum C	1	10	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Yuyum N	1	10	1999	D
Ruiz-Zarate et al 2003, Lang 2003 (ed)	Yucatan	Yuyum S	1	10.5	1999	D
Rutzler and Macintyre 1982	Belize	Carrie Bow	1	5, 15	1980	C M
Rylaarsdam 1983	Jamaica	Buoy reef	1	11	1976	C
Rylaarsdam 1983	Jamaica	East	1	15	1976	C
Rylaarsdam 1983	Jamaica	Sand channel	1	14	1976	C
Sedberry et al 1992	Belize	Glover's	1	20	1990	F
Sedberry et al 1992	Belize	Lighthouse	1	20	1990	F

Table AII. Continuation

Sluka et al 1998	USA	Elbow	1,2	6, 10, 20	1994	C M
Solandt and Campbell 2001	Jamaica	Discovery Bay 2 sites	1	5	1995	C M D
Steneck 1993	Jamaica	Discovery Bay	1, 2	3, 10	1978, 1982, 1987	C D
Steneck 1993	Virgin Is	St Croix	1, 2	3, 10	1982, 1987, 1988	C D
Steneck and Lang 2003, Lang 2003 (ed)	Yucatan	Akumal	1	11, 11.5, 13, 18	1999	D
Steneck and Lang 2003, Lang 2003 (ed)	Yucatan	Xcalac	1	8.5, 11, 11.5, 13, 13.5, 15, 16.5	1999	D
Thompson 1990	USA	Sombrero Key	1,4	2, 5, 7	1988	F
Tomascik and Sander 1987	Barbados	BMR	1,4	3, 4, 5	1983	C M D
Torres et al 2001	Dom Rep	Dominicus	1	20	1996	C
Torres et al 2001	Dom Rep	El Toro	1	20	1996	C
Torres et al 2001	Dom Rep	La Raya	1	20	1996	C
Torres et al 2001	Dom Rep	Ruben	1	20	1996	C
Tratalos and Austin 2001	Cayman Is	West Grand Cayman 3 sites	1	11	1996	C
Tupper and Rudd 2002	Turks&Caic	ACLSNP 3 sites	1	4, 15	2000	C M
Valdez and Villalobos 1978	Costa Rica	Puerto Vargas	1	2	1977	D
Villamizar et al 2003, Lang 2003 (ed)	Venezuela	Roques	1	1.5, 2, 2.5, 4, 5.5, 6.5, 7.5, 9.5, 12, 13.5	1999	D
Weil, et al 1984	Venezuela	Morocoy	1	5, 15	1982	D
Weill et al 84 and Urich 1977	Venezuela	La Orchila	5	5	1977	D
Williams and Polinin 2001	Barbados	BMR	1	15	1997	C M
Williams and Polinin 2001	Belize	Ambergris	1	15	1998	C M
Williams and Polinin 2001	Belize	Ambergris	1	12	1999	C M
Williams and Polinin 2001	Belize	Holchan	1	15	1998	C M
Williams and Polinin 2001	Cuba	Pta Este 2 sites	1	15	1998	C M
Williams and Polinin 2001	Cuba	Pta Frances 2 sites	1	15	1998	C M
Williams and Polinin 2001	Jamaica	Montego 2 sites	1	15	1997	C M
Williams and Polinin 2001	Jamaica	Negril 2 sites	1	15	1997	C M
Williams and Polinin 2001	Virgin Is	Grand Cayman 6 sites	1	15	1997	C M
Williams et al 2001	Belize	Ambergris	1	12	1999	C M
Zea et al 1998	Colombia	San Andres Reef	1,4	5, 10, 20	1992	C M
Zilberberg and Edmunds 2001	Jamaica	Discovery Bay	1	8	1998	C M
Zilberberg and Edmunds 2001	Virgin Is	St John	1	8	1998	C M

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APPENDIX III

Additional information on the species composition of Caribbean coral reefs included in Chapter III.

Table AIII. Assemblages composition, fish community (A) and benthic community (B). Fish species trophic level (TL) and feeding habits: Herbivores (H), Zoobenthivores-herbivores (Z-H), Zoobenthivores (Z), Zoobenthivores-Piscivores (Z-N), Planktivorus (P), Piscivorous (PS). Benthos categories for macroalgae: Fleshy algae (FA), Turf, Crustose coraline algae (CCA), Crustose non-coralline algae (CNC), articulated coralline, and calcified erect (CA).

A)

Group	Fish	Feeding	TL
Herbivores	*Acanthurus chirurgus*	H	2
	A. bahianus	H	2
	A. coeruleus	H	2
	Kyphosus sectator	H	2
	Microspathodon chrysurus	H	2.4
	Scarus coelestinus	H	2
	S. coeruleus	H	2
	S. guacamaia	H	2
	S. iserti	H	2
	S. taeniopterus	H	2
	S. vetula	H	2
	Sparisoma atomarium	H	2
	S. aurofrenatum	H	2
	S. chrysopterum	H	2
	S. rubripinne	H	2
	S. viridae	H	2
	Stegastes dorsopunicans	H	2
	S. leucostictus	H	2
	S. partitus	H	2
	S. planifrons	H	2
	S. variabilis	H	2
	Stegastes spp.	H	2.5
Omnivores	*Abudefduf saxatilis*	Z-H	3.4
	Aluterus scriptus	Z-H	2.8
	Cantherhines pullus	Z-H	2.6
	Canthigaster rostrata	Z-H	2.9
	Chaetodon capistratus	Z-H	2.5
	C. ocelatus	Z-H	3.2
	C. striatus	Z-H	3.1
	Chaetodon spp.	Z-H	3.1
	Holacanthus bermudensis	Z-H	3
	H. ciliaris	Z-H	3
	H. tricolor	Z-H	3
	Melichtys niger	Z-H	2.1
	Pomacanthus arctus	Z-H	2.6
	P. paru	Z-H	2.8
	Sphoeroides spengleri	Z-H	2.3
	Aetobatus narinari	Z	3.2
	Balistes vetula	Z	3.4
	Bodianus pulchelus	Z	3.4
	B. rufus	Z	3.4
	Cantherhines macrocerus	Z	3
	Canthidermis sufflamen	Z	3.2
	Diodon holocanthus	Z	3.3
	D. hystrix	Z	3.2
	Gerres spp.	Z	3.1
	Halichoeres bivittaus	Z	3.4
	H. cyanocephalus	Z	3.4
	H. garnotti	Z	3.5
	H radians	Z	3.3
	Holocentrus spp.	Z	3.5
	Hypoplectrus spp	Z	3.6
	Lachnolaimus maximus	Z	3.3
	Lactophrys triqueter	Z	3.2
	Malacanthus plumieri	Z	3.6
	Mulloidichthys martinicus	Z	3.2
	Myripristis jacobus	Z	3.6
	Pempheris schomburgki	Z	3.1
	Pseudopeneus maculatus	Z	3.2
	Thalassoma biffasciatum	Z	3.3
	Xanthichthys ringens	Z	3.1
Omnivores cont.	*Anisotremus surinamensis*	Z-N	3.3
	A. virginicus	Z-N	3.4
	Aulostomus maculatus	Z-N	4.3
	Bothus lunatus	Z-N	3.4
	Calamus calamus	Z-N	3.3
	C. penna	Z-N	3.4
	Caranx spp	Z-N	4
	Cephalopholis cruentatis	Z-N	3.5
	Dasyatis spp.	Z-N	3.5
	Epinephelus fulvus	Z-N	3.5
	E. guttatus	Z-N	3.9
	Gymnotorax funebris	Z-N	3.6
	Gynothorax spp.	Z-N	3.6
	Halicoeres chrysopterus	Z-N	3.3
	Haemulon aurolineatum	Z-N	3.4
	Haemulon carbonarium	Z-N	3.4
	Haemulon flavolineatum	Z-N	3.3
	Haemulon macrostomum	Z-N	3.1
	Haemulon melanurum	Z-N	3.1
	H. parrae	Z-N	3.2
	H. plummieri	Z-N	3.5
	H. sciurus	Z-N	3.4
	Lutjanus analis	Z-N	3.9
	L. apodus	Z-N	3.7
	L. griseus	Z-N	3.8
	L. mahogoni	Z-N	3.8
	L. synagris	Z-N	3.8
	Muraenidae	Z-N	3.4
	Mycteroperca phenax	Z-N	3.7
	Mycteroperca spp	Z-N	4
	Ocyurus chrysurus	Z-N	3.5
	Rachycentron canadum	Z-N	4
	Rypticus sp.	Z-N	3.6
	Sciaenidae	Z-N	3.6
	Scorpaena plumieri	Z-N	3.8
	Serranus tabacarius	Z-N	3.4
	Synodus spp.	Z-N	3.4
Planktivores	*Chromis cyanea*	P	3.1
	C. multilineata	P	3.1
	Chromis spp.	P	3.1
	Clepticus parrae	P	3.3
	Gramma spp.	P	3
	Inermis vittata	P	3.2
Top predators	*Caranx latus*	PS	4
	C. bartolomei	PS	4
	C. rubber	PS	4.4
	Carcharhinus perezi	PS	4.5
	Carcharhinus spp	PS	4.5
	Epinephelus itajara	PS	4.1
	E. morio	PS	3.5
	E. striatus	PS	4
	Ginglymostoma cirratum	PS	3.8
	Lutjanus cyanopterus	PS	4.2
	L. jocu	PS	4.3
	Mycteroperca bonaci	PS	4.5
	M. tigris	PS	4.5
	M. venenosa	PS	4.4
	Megalops atlanticus	PS	4.5
	Scomberomorus regalis	PS	4.5
	Scomberomorus spp.	PS	4.5
	Seriola rivoiana	PS	4.5
	Sphyraena barracuda	PS	4.5

Table AIII. Continuation

B)

Group	Species
Coral	*Acropora cervicornis*
	Acropora palmata
	Agaricia agaricites
	Agaricia humilis
	Agaricia tenuifolia
	Colpophyllia natans
	Dendrogyra cylindrus
	Dichocoenia stokesi
	Diploria clivosa
	Diploria labyrinthiformis
	Diploria strigosa
	Eusmilia fastigiana
	Favia fragum
	Helioceris cucullata
	Isophyllastrea rigida
	Madracis formosa
	Madracis mirabilis
	Madracis spp.
	Manicina areolata
	Meandrina meandrites
	Montastraea annularis
	Montastraea cavernosa.
	Montastraea faveolata/franksi
	Mussa angulosa
	Mycetophyllia spp.
	Porites astreoides
	Porites porites/furcata
	Porites spp.
	Scolymia spp.
	Siderastrea radians
	Siderastrea siderea
	Solenastrea spp.
	Stephanocoenia intersepts
Sea Urchins	*Echinometra lucunter*
	Echinometra viridis
	Diadema antillarum
	Eucadiris tribuloides
	Tripneustes ventricata
	Lytnochinus variegata
	Lytnochinus williamsi
OctoCoral	*Briareum spp.*
	Ellisella spp.
	Erythropodium spp.
	Eunicea spp.
	Gorgonia spp.
	Iciligorgia spp.
	Muricea spp.
	Plexaura spp.
	Plexaurella spp.
	Pseudoplexaura spp.
	Pseudopterogorgia spp.
	Pterogorgia spp.
Sponges	*Sponge encrust.*
	Sponge massive
	Sponge Rope
	Sponge Tube

Group	Species	Type
Algae	Acanthophora spp.	FA
	Anadyomene spp.	FA
	Caulerpa spp.	FA
	Codium spp.	FA
	Dictyosphaeria spp.	FA
	Dictyota spp.	FA
	Laurencia spp.	FA
	Lobophora spp.	CNC
	Other Chlorophyta	FA
	Other Rhodophyta	FA
	Padina spp.	FA
	Peyssonnelia spp.	CNC
	Sargassum spp.	FA
	Stypopodium spp.	FA
	Trichogloea spp.	FA
	Turbinaria spp.	FA
	Ventricaria spp.	FA
	Avrainvillea spp.	CEA
	Halimeda spp.	CEA
	Penicillus spp.	CEA
	Rhipocephalus spp.	CEA
	Udotea spp.	CEA
	Ceramiales	Turf
	Ectocarpales	Turf
	Ulvales	Turf
	Other filamentous algae	Turf
	Encrusting corallines	CCA
	Metapeyssonelia spp	CCA
	Amphiroa spp.	ACA
	Galaxaura spp.	ACA
	Jania spp.	ACA
Non Living	Bare space	
	Dead coral	
	Sand	
Other benthos	Anemone	
	Antipatharians	
	Ascidians	
	Bryozoans	
	Hydroids	
	Millepora alcicornis	
	Millepora complanata	
	Sabellidae	
	Serpulidae	
	Stylaster roseo	
	Zoanthids	
	Cyanobacteria	