



Status and Trends of Caribbean Coral Reefs:

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Status and Trends of Caribbean Coral Reefs

EXECUTIVE SUMMARY

Jeremy Jackson

“Perhaps the most striking aspect of plant life on a coral reef is the general lack of it. It seems anomalous to even the casual observer that tropical reefs, notable for their dazzling profusion of animal life, are almost devoid of conspicuous plants.”

Sylvia Earle

INTRODUCTION

Sylvia Earle’s early observations upon Caribbean reefs describe a forgotten world. Caribbean coral reefs have suffered massive losses of corals since the early 1980s due to a wide range of human impacts including explosive human population growth, overfishing, coastal pollution, global warming, and invasive species. The consequences include widespread collapse of coral populations, increases in large seaweeds (macroalgae), outbreaks of coral bleaching and disease, and failure of corals to recover from natural disturbances such as hurricanes. Alarm bells were set off by the 2003 publication in the journal *Science* that live coral cover had been reduced from more than 50% in the 1970s to just 10% today. This dramatic decline was closely followed by widespread and severe coral bleaching in 2005, which was in turn followed by high coral mortality due to disease at many reef locations. Healthy corals are increasingly rare on the intensively studied reefs of the Florida reef tract, US Virgin Islands, and Jamaica. Moreover, two of the formerly most abundant species, the elkhorn coral *Acropora palmata* and staghorn coral *Acropora cervicornis*, have been added to the United States Endangered Species List. Concerns have mounted to the point that

many NGOs have given up on Caribbean reefs and moved their attentions elsewhere.

It was against this gloomy backdrop that this study was undertaken to assess more rigorously than before the extent to which coral reef ecosystems throughout the wider Caribbean may have suffered the same fate, and if they have not, to determine what were the factors responsible. Various reports suggested that reefs in the southern Caribbean were in better ecological condition than elsewhere, with more live coral and reef fish. If this were true, understanding why some reefs are healthier than others would provide an essential first step for more effective management to improve the condition of coral reefs throughout the entire Caribbean region.

STRATEGY AND SCOPE OF THE PRESENT REPORT

Previous Caribbean assessments lumped data together into a single database regardless of geographic location, reef environment, depth, oceanographic conditions, etc. Data from shallow lagoons and back reef environments were combined with data from deep fore-reef environments

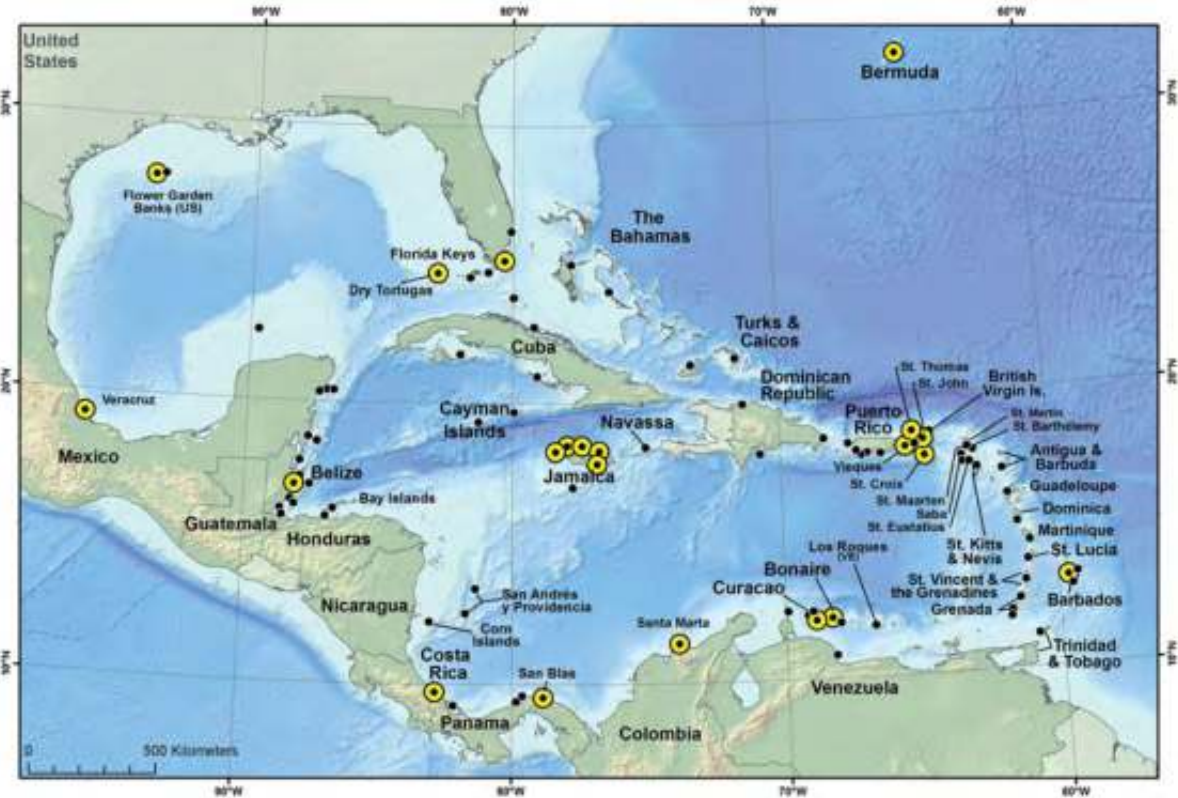


FIGURE 1. Distribution of 90 reef locations analyzed for this study. The large circles indicate 21 locations with the most complete time series data for analysis of long-term trends in coral cover.

and atolls. Geographic coverage was uneven, reflecting primarily the most studied sites with the most easily accessible data. Only total coral cover was recorded, with no attempt to assess the fates of different coral species. Nor was there any attempt to compile records of macroalgae, sea urchins, and fishes that are well known to have significant ecological interactions with corals.

We addressed these methodological problems by a detailed analysis of the status and trends of reef communities at distinct reef locations throughout the wider Caribbean. We also compiled essential metadata on the nature of the reef environment, depth, and history of human population growth, fishing, hurricanes, coral bleaching, and disease at each location. The quality of biological information varied among locations, but wherever possible data were obtained for coral and macroalgal cover, abundance of the critically important grazing sea urchin *Diadema antillarum*, and biomass of fishes, most importantly large grazing parrotfish.

Most of the quantitative data for Caribbean reefs is unpublished or buried in gray literature and government reports. To obtain these data, we contacted hundreds of people in all the countries of the Caribbean via several thousand emails, requests for data posted on relevant websites, and through presentations and interviews at international conferences. We also corresponded with managers of all the large monitoring programs in the region. In the end, we obtained data for corals, macroalgae, sea urchins, and fishes from a total of more than 35,000 quantitative reef surveys from 1969 to 2012. This is the largest amount of quantitative coral reef survey data ever compiled and exceeds by several fold that used for earlier Caribbean assessments.

Data are distributed among 90 reef locations in 34 countries (Fig. 1). Most of the data are from fore-reef and patch-reef environments in depths between 1-20 meters that are the focus of this study. Data are sparse up until the mass mortality of the formerly ubiquitous sea urchin *Diadema antillarum* in 1983-1984 when several monitoring programs first began. Data for corals are extensive

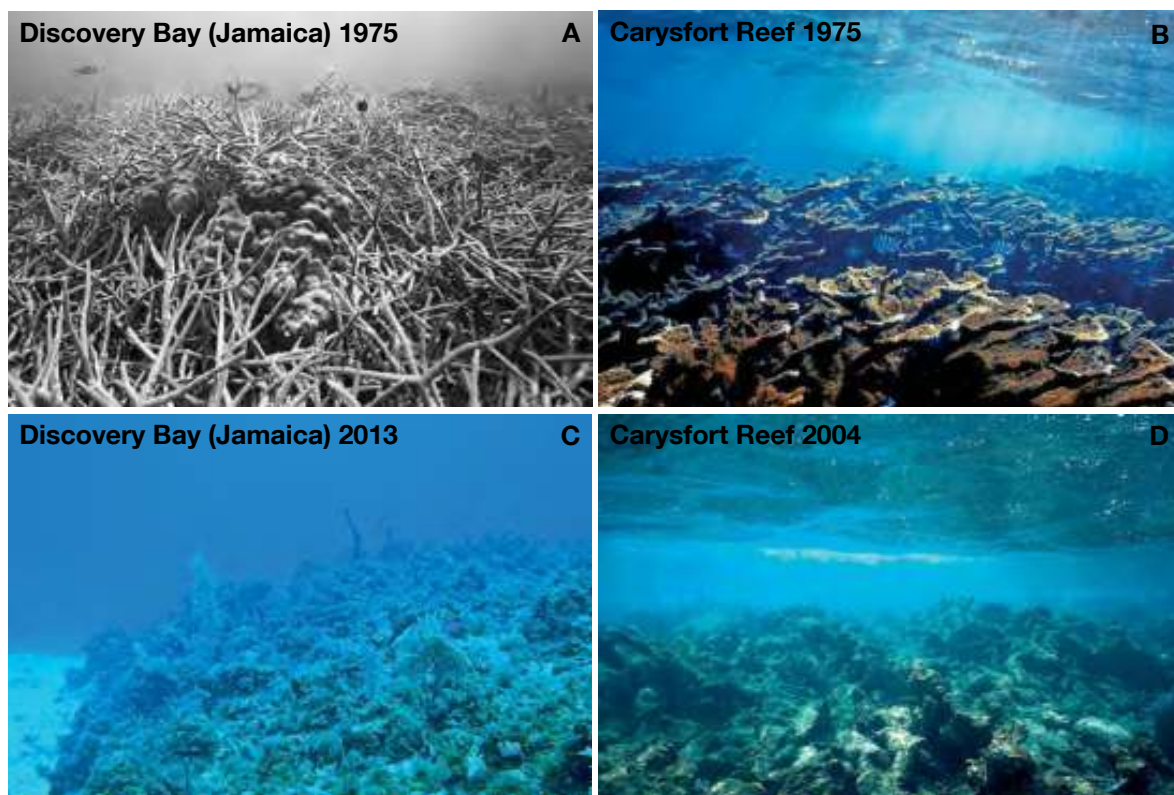


FIGURE 2. Phase shift from dominance by corals to dominance by macroalgae on the shallow fore-reefs in the northern Florida Keys and north coast of Jamaica. (A) Discovery Bay, Jamaica in 1975 and (C) the same location in 2013. (B) Carysfort Reef within the Florida Keys National Marine Sanctuary in 1975 and (D) in 2004 ((A, B, D by Phillip Dustan, and C by Robert Steneck).

and range from 1970 to the present. *Diadema* data are more limited up until mass mortality reduced its abundance to near zero and scientists realized what they had lost. Data for macroalgae are the most problematic because of inconsistent monitoring and taxonomy so that much of the data had to be discarded from our analysis. Quantitative data for both size and abundance of reef fishes needed to estimate fish biomass are unavailable until 1989 but are extensive after that.

The longest time series from the same reefs are large photo quadrats from 1973 to the present for fixed sites at Curaçao and Bonaire, with newer time series from the same islands beginning in the 1990s. Comparably long time series extending back into the early 1970s to early 1980s are available from the northern Florida Keys, Jamaica, St. John and St. Croix in the US Virgin Islands, and Panama. However, these records were compiled by different workers at different times and are therefore not as consistent or complete as data from the Dutch Caribbean.

Intensity of sampling varied greatly in time and space. We therefore partitioned the data into three time intervals of 12–14 years each based on major ecological events that extended throughout the wider Caribbean. These are:

1. 1970–1983: Interval from the oldest data up until and including the mass mortality of the formerly abundant sea urchin *Diadema antillarum* in 1983, as well as the first reports of White Band Disease (WBD) in the mid 1970s and early 1980s.
2. 1984–1998: From just after the *Diadema* die-off up to and including the widely reported 1998 extreme heating event.
3. 1999–2011: The modern era of massively degraded coral reefs.

PATTERNS OF CHANGE FROM 1970 TO 2012

Average coral cover for the wider Caribbean based on the most recent data for all the locations with coral data is 16.8% (range 2.8–53.1%). Taking into account the great variation among

locations and data sets reduces this estimate to 14.3% (+2.0, -1.8). Even this more rigorously refined mean is 43% higher than the 2003 regional estimate of 10% cover. Nevertheless, coral cover declined at three quarters of the locations with the greatest losses for locations that were surveyed earliest and for the longest time.

Average coral cover for all 88 locations with coral data declined from 34.8% to 19.1% to 16.3% over the three successive time intervals, but the disparity among locations was great. In contrast, macroalgal cover increased from 7% to 23.6% between 1984-1998 and held steady but with even greater disparity among locations since 1998. The patterns were similar for the 21 locations with coral data from all three intervals highlighted by circles in Fig. 1. These opposite trends in coral and macroalgal cover constitute a large and persistent Caribbean phase shift from coral dominated to macroalgal dominated communities that has persisted for 25 years (Figs. 2 and 3), a pattern also strongly supported by ordination analyses of benthic community composition.

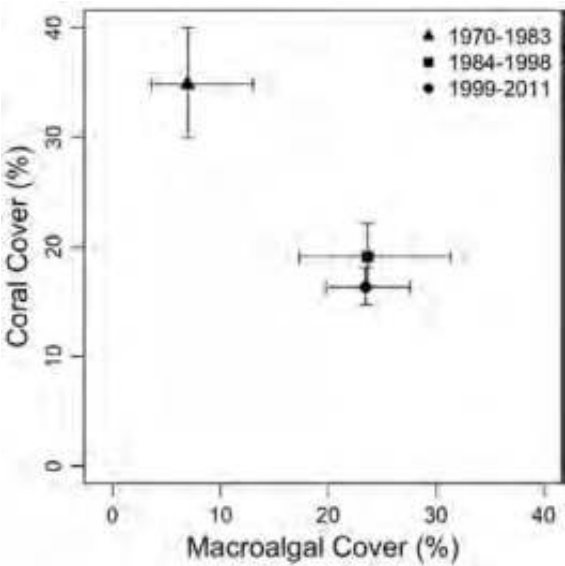


FIGURE 3. Large-scale shifts from coral to macroalgal community dominance since the early 1970s. Symbols and confidence intervals represent means and standard deviations for 3 time intervals that take into account variability due to location, and datasets using a mixed modeling framework.

The greatest overall changes in coral and macroalgal cover occurred between 1984 and 1998, after which there was little overall change at the great majority of locations except for places most strongly affected by the extreme warming events

of 2005 and 2010. The same was true for formerly abundant elkhorn and staghorn *Acropora* that began to decline in the 1960s, the mass mortality of the sea urchin *Diadema antillarum* in 1983-1984, and the extreme overfishing of large parrotfish at most locations in the early to middle 20th century. Thus the largest and most damaging changes on Caribbean reefs occurred before most coral reef scientists and managers had begun to work on reefs, a classic example of the Shifting Baselines Syndrome and a harsh reminder that the problems of today are just the latest chapter in a much longer story of decline.

Looking beyond this general picture, however, long-term trends at the 21 highlighted locations in Fig. 1 exhibit three strikingly contrasting patterns of change in coral cover (Fig. 4). Trajectories for nine of the locations resemble a hockey stick with precipitous declines of 58-95% between intervals 1 and 2 followed by no change (Fig. 4A). In contrast, five other locations exhibited comparable decline that was spread out approximately equally between intervals 1 and 2 and between intervals 2 and 3 (Fig. 4B). The third group of seven locations exhibited much greater stability with overall changes (increase or decrease) of just 4-35% (Fig. 4C).

DRIVERS OF CHANGE

The drivers of the ecological degradation of Caribbean reefs need to be understood in the context of the highly unique situation of the Caribbean compared to other tropical seas. The Caribbean is effectively a Mediterranean sea that is the most geographically and oceanographically isolated tropical ocean on the planet. Isolation began tens of millions of years ago with the gradual break-up on the once circumtropical Tethys Seaway, the widening of the Atlantic Ocean, and ultimately isolation from the Eastern Pacific by the closure of the Panamanian Seaway 5.4 to 3.5 million years ago.

Consequently, Caribbean reef biotas are also highly distinctive. Many coral genera once combined with Pacific taxa have proven to belong to uniquely Atlantic evolutionary lineages based on molecular genetics. Moreover, acroporid corals that make up more than a third of Indo-Pacific coral diversity are represented by only two

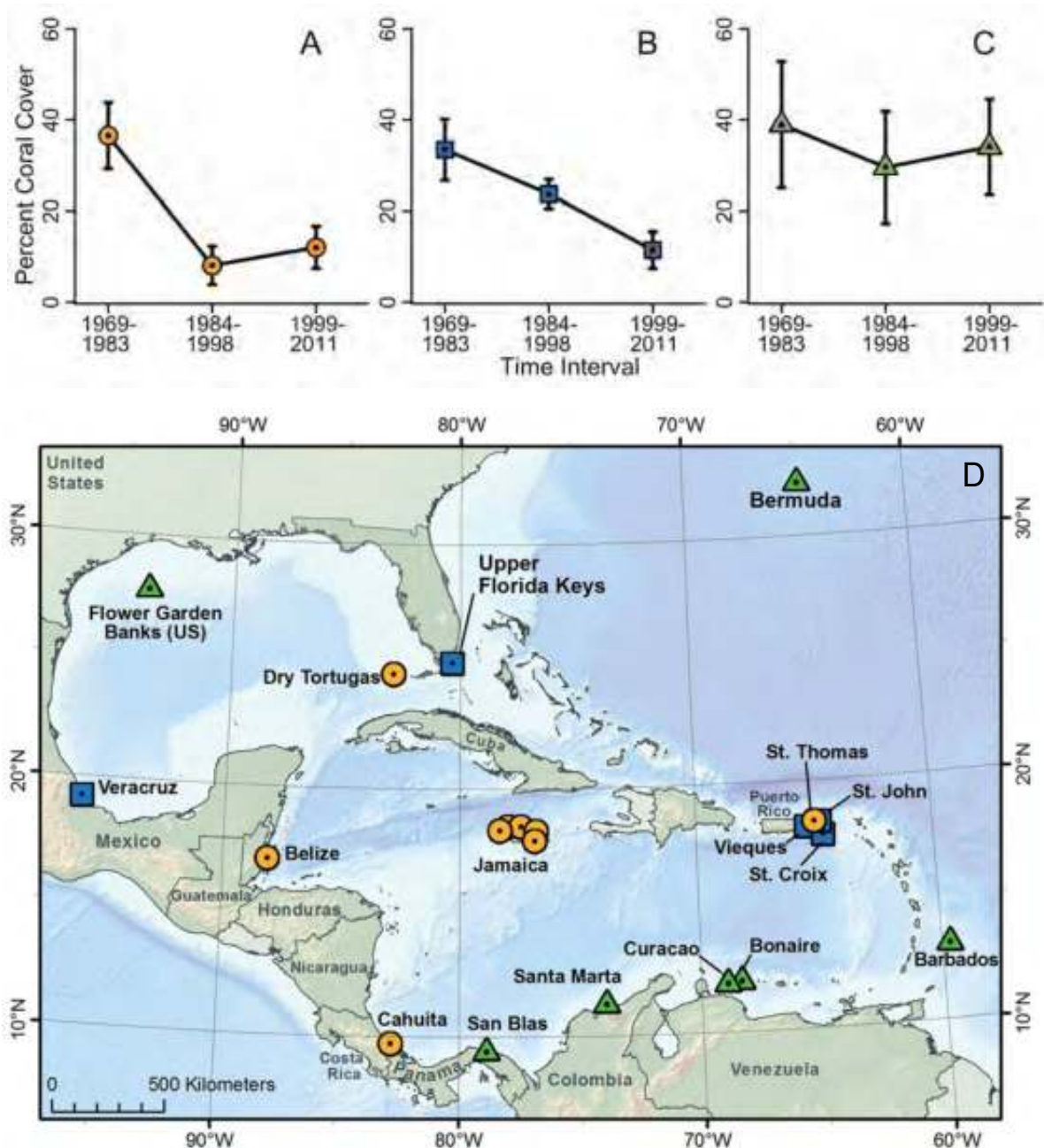


FIGURE 4. Trajectories of coral cover at 21 reef locations, grouped on the basis of the total amount of change over all three intervals and the tempo of change. (A) Hockey stick pattern with a steep decline between the first two intervals followed by little or no change. (B) Approximately continuous decline over all three intervals. (C) Comparative stability with smaller net changes in cover.

Caribbean species. Taxonomic diversity and ecological redundancy are low and the potential for rejuvenation from other regions is essentially nil. Caribbean species also had no evolutionary experience for dealing with exotic species and disease before the advent of people.

We focused on potential anthropogenic drivers of decline for which there were data for meaningful

comparisons. Drivers were treated separately for ease of analysis and discussion, but they are inextricably linked. In particular, coral disease is a complex and poorly understood symptom of several forms of human disturbance rather than a direct driver of change. Thus disease is treated in relation to several different drivers including introductions of alien species, ocean warming, coastal pollution, and overfishing. Overall, results are

stronger for evaluating effects of human population increase, overfishing, and ocean warming because there are more data, and less so for coastal pollution and invasive species.



FIGURE 5. Examples of mass tourism in the Caribbean. (A) Large cruise ships with thousands of passengers arrive every day in the Caribbean, shown here is St. Thomas, the US Virgin Islands (Source: Calyponte, Wikipedia). (B) Numerous hotel resorts offer ever more tourists the opportunity to stay in the Caribbean Sea, as here at Cancún Island, Mexico (Source: Foto Propia, Photo by Mauro I. Barea G., Wikipedia). (C) High density of tourists line South Beach, Miami, Florida (Source: Photo by Marc Averette, Wikipedia).

Too many people

Tourism is the lifeblood of many Caribbean nations (Fig. 5). However, our evidence demonstrates that extremely high densities of both tourists and residents are harmful to reefs unless environmental protections are comprehensive and effectively enforced. Unfortunately, this is only rarely the case. Numbers of visitors per square kilometer per year range from a low of 110 in the Bahamas to an astounding 25,000 at St. Thomas. All locations with more than the median value of 1,500 visitors per square kilometer per year have less than the median value of 14% coral cover except for Bermuda with 39% cover and Grand Cayman with 31%. The exceptional situation at Bermuda most likely

reflects progressive environmental regulations in place since the 1990s and the infrastructure required to make them work. Otherwise, the harmful environmental costs of runaway tourism seem to be inevitable.

Overfishing

Artisanal fishing for subsistence is crucial to most Caribbean economies but the consequences have been catastrophic for coral reefs. Overfishing caused steep reductions in herbivores, especially large parrotfishes, which are the most effective grazers on Caribbean reefs but vulnerable to all gear types except hook and line.

Nevertheless, the consequences of overfishing parrotfish for coral survival were little understood until the abrupt demise of the sea urchin *Diadema antillarum* due to an unidentified disease in 1983-1984. Until then, *Diadema* had increasingly become the last important macro-herbivore on Caribbean reefs due to overfishing. *Diadema* and parrotfish strongly compete for food, and variations in their abundance were inversely proportional until 1983. This inverse relationship provides a rigorous proxy to assess the consequences of historical overfishing of parrotfish for coral cover in the absence of quantitative data for parrotfish biomass before 1989.

Our analysis of overfishing focused primarily on 16 of the 21 highlighted reefs in Fig. 1 for which quantitative data on *Diadema* abundance were available before the die-off in 1983/84, in addition to coral cover for all three of the time intervals in Fig. 3. Nine of these reefs were classified as overfished for parrotfishes by 1983, with *Diadema* densities ranging from 6.9-12.4 per square meter, whereas the other seven reefs were classified as less fished with *Diadema* densities of just 0.5-3.8 per square meter. This ranking agreed well with the qualitative literature. Reefs where parrotfishes had been overfished before 1984 suffered greater subsequent decreases in coral cover and increases in macroalgae than reefs that still had moderately intact populations of parrotfish. Coral and macroalgal cover were independent of *Diadema* densities before 1984 when either the sea urchin or parrotfish grazed down macroalgae to extremely low levels. All that changed, however, after the *Diadema* die-off when coral cover declined in proportion to historical *Diadema* abundance, a trend that has continued to the present day.

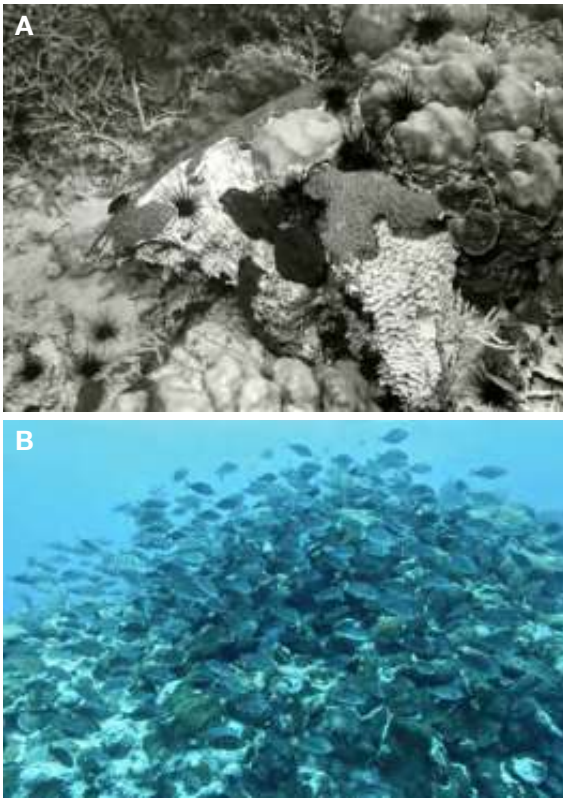


FIGURE 6. Formerly abundant grazers on Caribbean reefs. (A) Dense aggregation of the sea urchin *Diadema antillarum* on the west foreereef at Discovery Bay, Jamaica in about 10 meters a year before the massive die-off in 1983/1984 (Photo by Jeremy Jackson). (B) Large school of Stoplight Parrotfish *Sparisoma viride* on the south shore of Bermuda where fishing on parrotfish is banned (Photo by Philippe Rouja). Such large numbers of parrotfish are rare to absent today on the great majority of Caribbean reefs.

There is also strong field and experimental evidence for persistent indirect effects of the increase in macroalgae, including decreased larval recruitment and survival of juvenile corals and increased coral disease. Coral recruitment sharply declined after 1984, at least in part due to a decline in the parental brood stock. But there is also strong evidence for active interference by macroalgae. Larval settlement onto the tops of experimental panels in Curaçao declined five-fold between identical experiments in 1979-1981 and 1998-2004. Crustose coralline algae, that are a preferred substrate for larval settlement, covered the entire upper surfaces of the panels in the earlier experiment and macroalgae were absent. In contrast, upper surfaces in the later experiment were entirely covered by macroalgae.

Other experiments demonstrate that coral larvae actively avoid substrates where macroalgae are

present and larval recruits suffer increased mortality and growth inhibition due to physical interference by macroalgae. But the strongest evidence for macroalgal interference comes from recent large increases in coral recruitment and juvenile survival on reefs where *Diadema* have partially recovered or parrotfish have increased in marine protected areas. Experiments also demonstrate that macroalgae induce a wide variety of pathological responses in corals including virulent diseases. Release of toxic allelochemicals by macroalgae also disrupts microbial communities associated with corals sometimes causing bleaching or death.



FIGURE 7. Dense growths of macroalgae with surviving branch tips of *Porites* protruding through the algal canopy in the top right corner and previously overgrown dead branches of *Porites* and *Acropora cervicornis* in the bottom left (Dry Tortugas, 2000, Photo by Mark Chiappone).

Overfishing may have also indirectly affected the capacity of reefs to recover from damage by hurricanes; something they have routinely done for millions of years before or reefs would not exist. Over the past few decades, however, corals have increasingly failed to become reestablished on many reefs after major storms. We investigated this apparent shift using data for the 16 reefs with coral and *Diadema* data from before 1984. Coral cover was independent of the long-term probability of hurricanes before 1984 but not afterwards. Overfishing of parrotfish may have decreased the ability of corals to recover after hurricanes. Reefs protected from overfishing at Bermuda experienced four hurricanes since 1984 with no loss in average coral cover, whereas recently overfished reefs on the Central Barrier in Belize declined by 49% after 3 hurricanes.



FIGURE 8. Overfishing severely reduced fish biomass and diversity in the Caribbean. (A – C) Decline in the composition and size of coral reef trophy fish in the Florida Keys since the 1950s (modified from McClenachan 2008). (D – F) Parrotfish were the most important grazers on Caribbean reefs: (D) Stoplight parrotfish (*Sparisoma viride*) caught in a gill net. (E) A typical day of spearfishing off southeast Curaçao. (F) Fishing boats at Barbuda's Coco Point (Photos by Ayana Elizabeth Johnson).

Coastal pollution

Limited comparative data for water transparency based on secchi disk observations at three CARICOMP sites (Caribbean Coastal Marine Productivity Program by UNESCO) show that water quality is declining in areas of unregulated agricultural and coastal development. In particular,

water transparency steeply declined over 20 years at Carrie Bow Cay in Belize due to huge increases in agriculture and coastal development from Guatemala to Honduras such as illustrated in Fig. 9C. A similar pattern was observed at La Parguera on the west coast of Puerto Rico. In contrast, water quality improved in Bermuda.

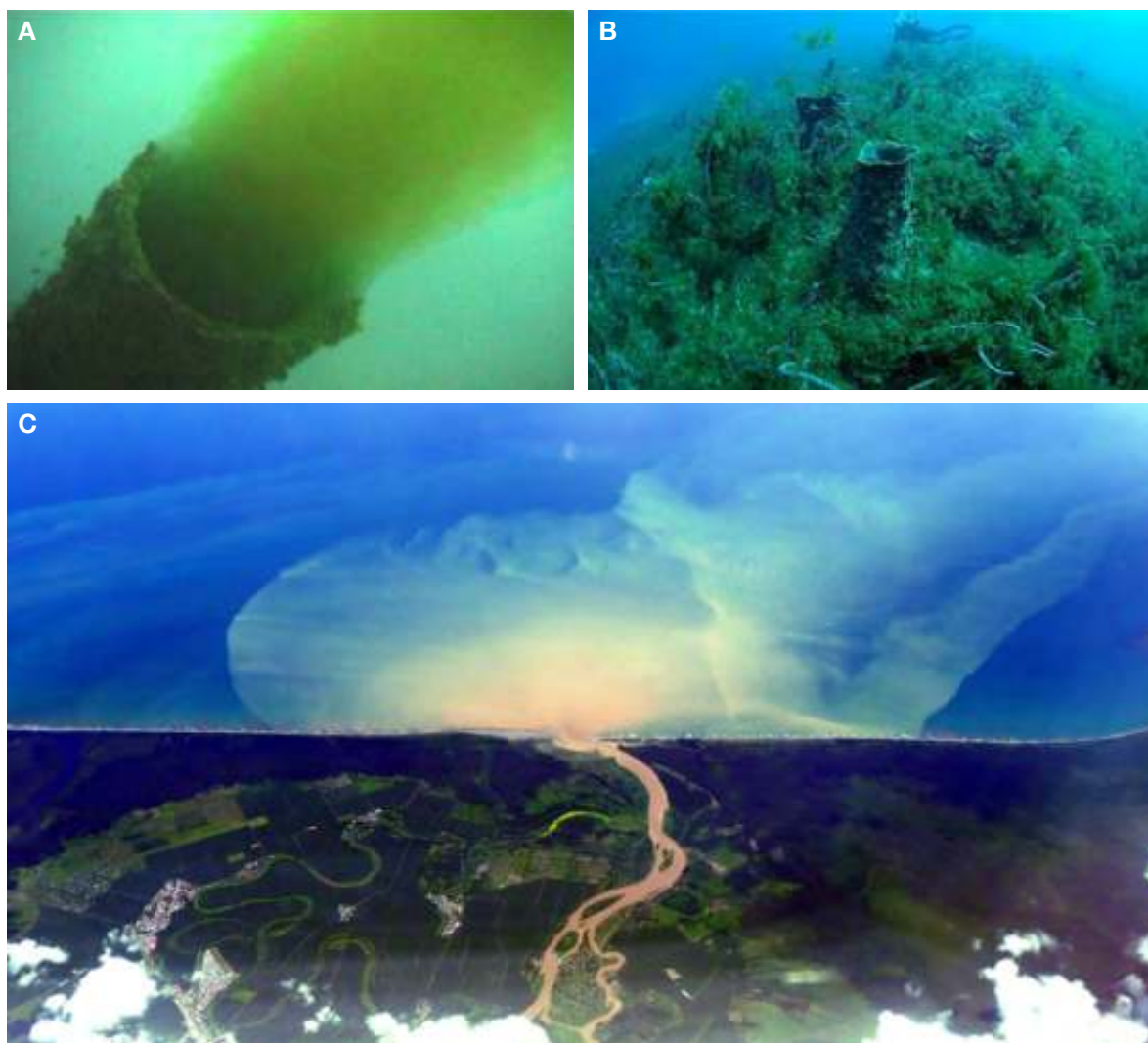


FIGURE 9. Impacts of coastal pollution on Caribbean reefs. (A) Sewage outfall in Delray Beach, Florida that discharges 13 million gallons per day of treated sewage up-current of a coral reef. (B) Macroalgae carpeting dead corals near the sewage outfall (Photos by Steve Spring, Marine Photobank). (C) Massive discharge of sediment loads by a river entering the Caribbean Sea off the Meso-American Coast (Photo by Malik Naumann, Marine Photobank).

Coral disease has been linked to excessive organic pollution but the data are spotty and limited in scope. In general there is a pressing need for more systematic and extensive monitoring of water quality throughout the wider Caribbean.

Ocean warming

Our first analyses were based on the Reefbase compilation of extreme bleaching events that showed no significant relationship between the numbers of extreme events per locality and coral cover at locations across the wider Caribbean, Gulf of Mexico and Bermuda. Because of the subjectivity of such bleaching assessments, however, we obtained data for degree heating weeks

(DHWs) for all 88 localities with coral cover from NOAA Coral Reef Watch.

We then used these data to assess the effects of the 1998, 2005, and 2010 extreme warming events on coral cover by calculating the proportional changes in coral cover for the two years following each event in relation to the two years before the event, and then plotting the proportional change in relation to the numbers of degree heating weeks (DHWs) experienced at each locality. There is a weak but insignificant negative correlation between changes in coral cover and numbers of DHWs, regardless of whether the data were analyzed for each warming event or combined, or whether we included all the localities or restricted

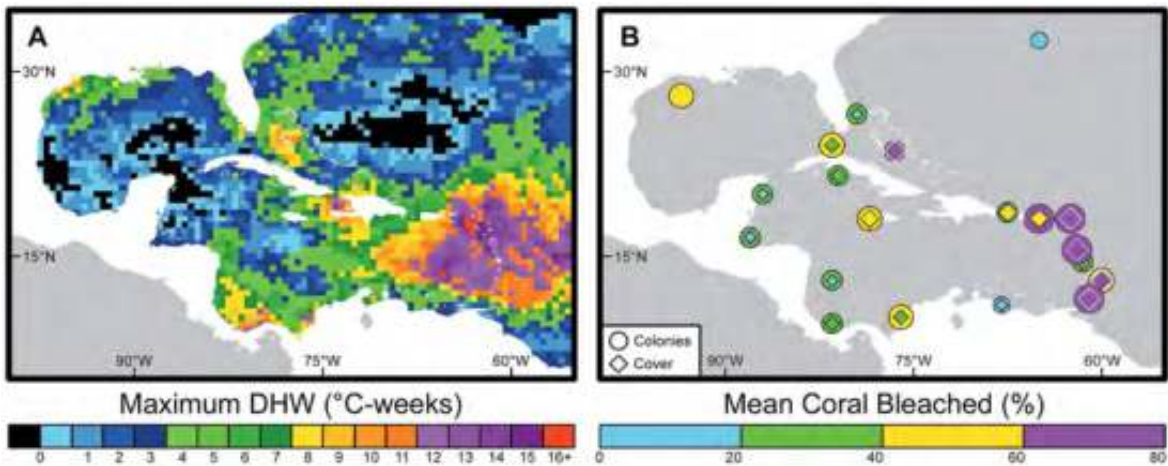


FIGURE 10. Extreme heating event and associated coral bleaching that most severely impacted the eastern Caribbean in 2005. (A) Degree heating weeks from Pathfinder Satellite observations. (B) Reports of the intensity of coral bleaching compiled from field observations (Courtesy Mark Eakin and colleagues).

the analysis to include only localities that experienced at least 8 DHWs. Moreover, the greatest losses in coral cover occurred at reef locations with less than 8 DHWs.

We caution that our results do not mean that extreme heating events are unimportant drivers of coral mortality due to coral bleaching and disease, as they clearly have been in the USVI, Puerto Rico, Florida Keys, and elsewhere. Moreover, increasingly severe extreme heating events will pose an even greater threat to coral survival in future decades. But our results do belie any regionally consistent effects of extreme heating events up to now and strongly imply that local stressors have been the predominant drivers of Caribbean coral decline to date.

Potentially deleterious effects of ocean acidification have not been treated here because of the lack of comparative data. If present trends of decreased pH continue, however, the

ability of corals and other calcareous reef species to deposit skeletons will be increasingly compromised.

Invasive species

The explosion of exotic Pacific lionfish throughout the wider Caribbean (Fig. 12) has wreaked havoc in Caribbean fish communities. But as serious as the potential long-term consequences may be, they pale in comparison to the introduction of the unidentified pathogen that caused the die-off of *Diadema antillarum* or the effects of “White-band disease” (WBD) on acroporid corals. *Diadema* mass mortality began only a few km from the Caribbean entrance of the Panama Canal. That, coupled with orders of magnitude increases in bulk carrier shipping in the 1960s and 1970s, strongly suggests that *Diadema* disease was introduced by shipping. The same may be true of coral diseases although their earliest occurrences were widespread throughout the Caribbean.

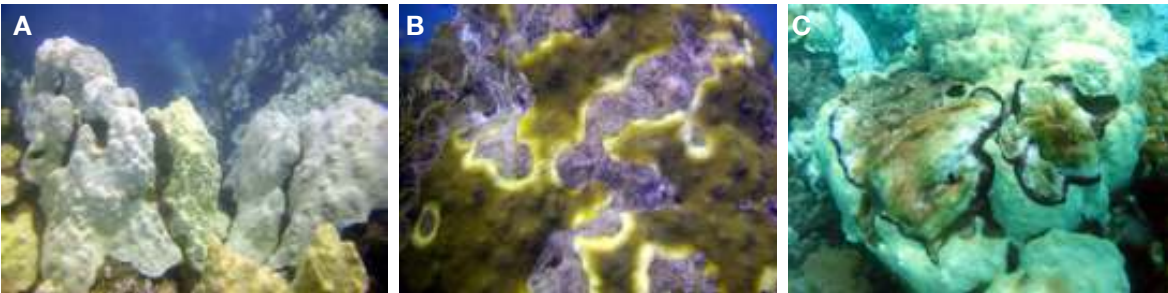


FIGURE 11. Effects of coral bleaching and disease on the formerly abundant coral *Orbicella faveolata*. (A) Bleached corals (Turrumote, Puerto Rico, 2005). Extensive partial colony mortality due to infection by (B) Yellow Band Disease (Turrumote, Puerto Rico, 2005) and (C) Black Band Disease (Los Roques Venezuela, 2010). (Photo A by Ernesto Weil; B & C by Aldo Cróquer).

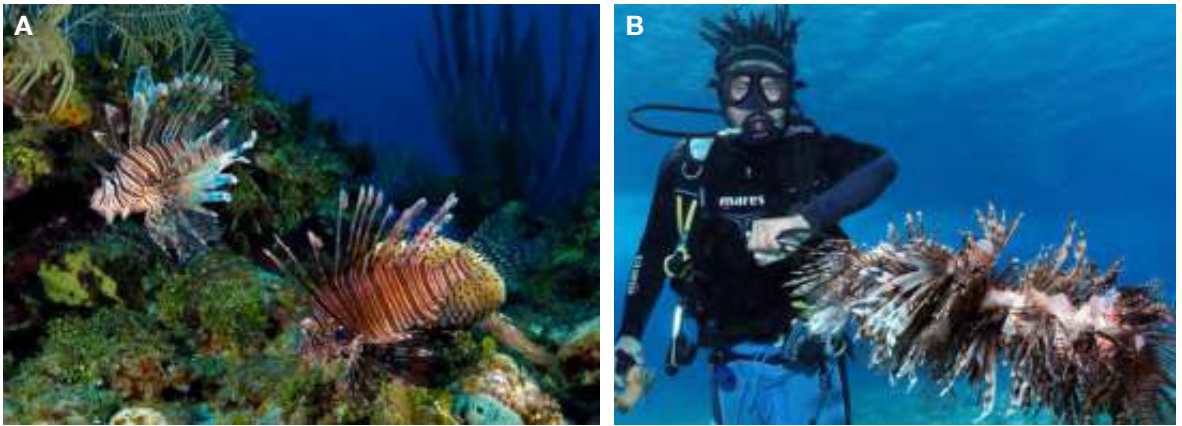


FIGURE 12. Population explosion of the highly successful Pacific lionfish (*Pterois volitans*) introduced into the Caribbean sometime between the 1980s and the early 1990s. (A) Abundant invasive lionfish on the reefs in the Cayman Islands (Photo courtesy of Niel Van Niekerk, with permission from IFAS, University of Florida). (B) Lionfish speared as part of a widespread effort to control the populations in the Dry Tortugas (Photo courtesy of ICRI).

Because of their isolation for millions of years, and by analogy to the fates of Native Americans after their first contact with Europeans, Caribbean species should be exceptionally prone to the impact of introduced diseases. And this appears to be the case. We know of no examples of the virtual elimination due to disease of any marine species throughout the entire extent of the Indian or Pacific oceans comparable to the demise of Caribbean *Diadema* and *Acropora*. This interpretation is also consistent with the apparent lack of any major environmental shift in the 1970s that might have triggered the outbreak of disease. Most importantly, the emergence of these diseases occurred many years before the first reported extreme heating events.

It would be possible to test this introduced species hypothesis for WBD since the pathogen is known and available for DNA-sequencing. It may also be possible for *Diadema* even though the pathogen is unknown by genetic analysis of entire frozen specimens of *Diadema* that died from the disease. This is not an entirely academic exercise: the two pivotal events in the demise of most Caribbean reefs are as much a mystery today as they were when they first occurred 30 or more years ago.

SUMMARY

Outbreaks of *Acropora* and *Diadema* diseases in the 1970s and early 1980s, overpopulation in the form of too many tourists, and overfishing are the three best predictors of the decline in Caribbean coral cover over the past 30 or more

years based on the data available. Coastal pollution is undoubtedly increasingly significant but there are still too little data to tell. Increasingly warming seas pose an ominous threat but so far extreme heating events have had only localized effects and could not have been responsible for the greatest losses of Caribbean corals that had occurred throughout most of the wider Caribbean region by the early to mid 1990s.

In summary, the degradation of Caribbean reefs has unfolded in three distinct phases:

1. Massive losses of *Acropora* since the mid 1970s to early 1980s due to WBD. These losses are unrelated to any obvious global environmental change and may have been due to introduced pathogens associated with enormous increases in ballast water discharge from bulk carrier shipping since the 1960s.
2. Very large increase in macroalgal cover and decrease in coral cover at most overfished locations following the 1983 mass mortality of *Diadema* due to an unidentified and probably exotic pathogen. The phase shift in coral to macroalgal dominance reached a peak at most locations by the mid 1990s and has persisted throughout most of the Caribbean for 25 years. Numerous experiments provide a link between macroalgal increase and coral decline. Macroalgae reduce coral recruitment and growth, are commonly toxic, and can induce coral disease.
3. Continuation of the patterns established in Phase 2 exacerbated by even greater

overfishing, coastal pollution, explosions in tourism, and extreme warming events that in combination have been particularly severe in the northeastern Caribbean and Florida Keys where extreme bleaching followed by outbreaks of coral disease have caused the greatest declines.

IMPLICATIONS FOR MANAGEMENT

Our results contradict much of the rhetoric about the importance of ocean warming, disease, and hurricanes on coral reefs and emphasize the critical importance of historical perspective for coral reef management and conservation. The threats of climate change and ocean acidification loom increasingly ominously for the future, but local stressors including an explosion in tourism, overfishing, and the resulting increase in macroalgae have been the major drivers of the catastrophic decline of Caribbean corals up until today.

What this means is that smart decisions and actions on a local basis could make an enormous difference for increased resilience and wellbeing of Caribbean coral reefs and the people and enterprises that depend upon them. Thus, four major recommendations emerge from this report:

1. **Adopt robust conservation and fisheries management strategies** that lead to the restoration of parrotfish populations, including the listing of the parrotfish in relevant annexes of the Protocol concerning Specially Protected Areas and Wildlife (SPA protocol) of the UNEP Caribbean Environment Programme. A recommendation to this effect was passed unanimously at the October 2013 International Coral Reef Initiative Meeting in Belize (see Box).
2. **Simplify and standardize monitoring** of Caribbean reefs and make the results available on an annual basis to facilitate adaptive management.
3. **Foster communication and exchange of information** so that local authorities can benefit from the experiences of others elsewhere.
4. **Develop and implement adaptive legislation and regulations** to ensure that threats to coral reefs are systematically addressed, particularly threats posed by fisheries, tourism

and coastal development as determined by established indicators of reef health.

We understand that action upon these recommendations will be a matter of local and national socioeconomic and political debate. But the implications of our scientific results are unmistakable: *Caribbean coral reefs and their associated resources will virtually disappear within just a few decades unless all of these measures are promptly adopted and enforced.*

RECOMMENDATION

on addressing the decline in coral reef health throughout the wider Caribbean: the taking of parrotfish and similar herbivores

Adopted on 17 October 2013, at the 28th ICRI General Meeting (Belize City)

Background

The latest report of the Global Coral Reef Monitoring Network (GCRMN), entitled: *Status and Trends of Caribbean Coral Reefs: 1970-2012* is the first report to document quantitative trends of coral reef health based on data collected over the past 43 years throughout the wider Caribbean region.

The results of the study clearly show:

- Coral reef health requires an ecological balance of corals and algae in which herbivory is a key element;
- Populations of parrotfish are a critical component of that herbivory, particularly since the decline of *Diadema* sea urchins in the early 1980s;
- The main causes of mortality of parrotfish are the use of fishing techniques such as spearfishing and, particularly, the use of fish traps.

The Report further identifies that overfishing of herbivores, particularly parrotfish, has been the major drivers of reef decline in the Caribbean to date, concluding that management action to address overfishing at the national and local levels can have a direct positive impact on reef health now and for the future. *In some areas of the wider Caribbean (for example Bermuda and the Exuma Cays Land and Sea Park in the Bahamas, and more lately in Belize and Bonaire), active management including bans on fish traps, has led to increases in parrotfish numbers and consequent improvement in reef health and resilience to perturbations including hurricanes. This is in contrast to other areas within the Caribbean, where heavily fished reefs lacked the resilience to recover from storm damage.*

Positive impacts on reef health demonstrably have spill over effects on local economies, including the potential for alternative livelihoods to fishing, thanks to increased tourism revenues, replenishment of fish stocks and restoration of ecosystem services such as shoreline protection.

It is recognised that in the Caribbean there are varying levels of community reliance on fishing in general and the taking of parrotfish in particular. However, in light of the evidence now available, and in accordance with ICRI's Framework for Action cornerstone of 'integrated management' (which includes fisheries management), the International Coral Reef Initiative would like to highlight the benefits of strong management to protect reefs from overfishing, and urges immediate action to effectively protect parrotfish and similar herbivores.

Accordingly, the International Coral Reef Initiative urges Nations and multi-lateral groupings of the wider Caribbean to:

1. **Adopt** conservation and fisheries management strategies that lead to the restoration of parrotfish populations and so restore the balance between algae and coral that characterises healthy coral reefs;
2. **Maximise** the effect of those management strategies by incorporating necessary resources for outreach, compliance, enforcement and the examination of alternative livelihoods for those that may be affected by restrictions on the take of parrotfish;
3. **Consider** listing the parrotfish in the Annexes of the SPAW Protocol (Annex II or III) in addition to highlighting the issue of reef herbivory in relevant Caribbean fisheries fora;
4. **Engage** with indigenous and local communities and other stakeholders to communicate the benefits of such strategies for coral reef ecosystems, the replenishment of fisheries stocks and communities' economy.

PART I: OVERVIEW AND SYNTHESIS FOR THE WIDER CARIBBEAN REGION

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Caribbean coral reef ecosystems are severely degraded due to human overfishing, pollution, climate change, and the synergies among them. Coral cover has reportedly declined by more than 80% since the 1970s (Fig. 1), virtually all the large fishes, sharks, and turtles are gone (Fig. 2), and the threats of global climate change loom increasingly ominously for the future (Fig. 3) (Hughes 1994; Jackson 1997; Aronson and Precht 2001; Jackson et al. 2001; Gardner et al. 2003; Pandolfi et al. 2003; McClenachan 2008; Eakin et al. 2010). The severity of the situation has raised serious questions about the future of Caribbean reefs and indeed reefs worldwide (Knowlton 2001; Hughes et al. 2003, 2010; Bellwood et al. 2004; Pandolfi et al. 2005; Hoegh-Guldberg et al. 2007; Hughes et al. 2010).

Nevertheless, there are reasons for hope based upon the remarkable abundance and resilience of corals at some remote Pacific island reefs that are protected from local impacts of overfishing and pollution (Friedlander and DeMartini 2002; Knowlton and Jackson 2008; Sandin et al. 2008a; Pandolfi et al. 2011; Gilmour et al. 2013). Despite increased

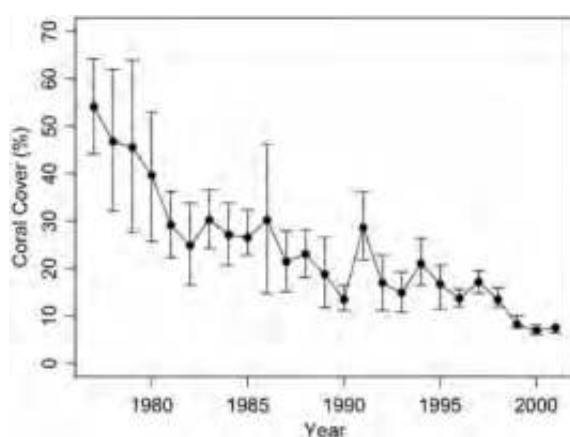


FIGURE 1. Estimates of annual percent coral cover for the entire wider Caribbean region (re-plotted from Gardner et al. 2003).

warming and coral bleaching throughout the Pacific, these reefs have recovered from past episodes of bleaching and still support extraordinarily abundant and resilient populations of fishes and corals.

There are also reports of considerable variability in the condition of Caribbean reefs (Kramer 2003; Newman et al. 2006; Schutte et al. 2010) that is



FIGURE 2. Overfishing significantly reduced fish biomass and diversity in the Caribbean. (A - C) Decline in the composition and size of coral reef trophy fish in the Florida Keys since the 1950s (modified from McClenachan 2008). (D - F) Parrotfish were the most important grazers on Caribbean reefs: (D) Stoplight parrotfish (*Sparisoma viride*) caught in a gill net. (E) A typical day of spearfishing off southeast Curaçao. (F) Fishing boats at Barbuda's Coco Point (Photos by Ayana Elizabeth Johnson).

obscured by plotting a single line for reef condition over time, regardless of location, reef type, depth, environmental conditions, and human impact as in Fig. 1 (Gardner et al. 2003). For example, live coral cover is less than the reported Caribbean average of 10% in the Florida Keys (Dustan 2003; DuPont et al. 2008) and the US Virgin Islands (Edmunds 2002; Rogers and Miller 2006; Miller et al. 2009), but commonly exceeds 30% on reefs in Curaçao and Bonaire (Bak et al. 2005; Sandin et al. 2008b; Steneck et al. 2011;

Vermeij 2012), the Flower Gardens Banks (Aronson et al. 2005; Hickerson et al. 2008), and Bermuda (Murdoch et al. 2008; Smith et al. 2013).

The causes of these regional differences are poorly understood despite their obvious significance for conservation and management. Caribbean reefs with the highest coral cover tend to be characterized by little land-based pollution; some degree of fisheries regulations and enforcement; lower frequencies

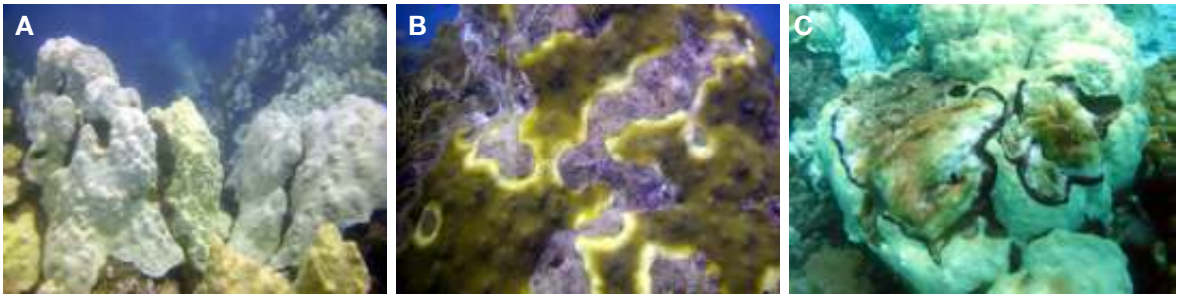


FIGURE 3. Effects of coral bleaching and disease on the formerly abundant coral *Orbicella faveolata*. (A) Bleached corals (Turrumote, Puerto Rico, 2005). Extensive partial colony mortality due to infection by (B) Yellow Band Disease (Turrumote, Puerto Rico, 2005) and (C) Black Band Disease (Los Roques Venezuela, 2010). (Photos A and B by Ernesto Weil; C by Aldo Cróquer).

of hurricanes, coral bleaching, and disease; and moderate economic prosperity. However, these apparent trends have not been rigorously investigated.

There is also a fundamental methodological problem in the common failure to distinguish between the potential anthropogenic drivers of reef degradation such as human overpopulation, overfishing, coastal pollution, introductions of alien species, and ocean warming and acidification due to the burning of fossil fuels, versus their effects such as losses of corals and increases in macroalgae, coral bleaching, and disease (Hughes et al. 2010). This confusion is compounded by scientific provinciality. Most scientists study reefs in a geographically limited area and then project their results to the entire Caribbean. This tendency for over generalization is further compounded by an overall lack of comparative data to address multiple factors in a unified analysis (Hughes et al. 2010).

New insights in science commonly emerge from examining exceptions to general patterns rather than the norms (Knowlton and Jackson 2008). Thus the major goal of this report is to document the variable condition of Caribbean reefs as a means towards better understanding of the factors driving Caribbean reef decline and what actions might be adopted to prevent their demise.

To this end, Part I of the report is divided into five main sections:

1. data, methods, and analysis;
2. description of quantitative changes in the status and trends of major components of Caribbean coral reef ecosystems (corals, macroalgae, sea urchins, and fish) since 1970 throughout the tropical western Atlantic;

3. analysis of the different potential drivers of change to attempt to determine their comparative impact on reefs to the present day and likely impacts in the future;
4. synthesis of results; and
5. recommendations for management.

1. DATABASE, METHODOLOGY, AND ANALYSIS

Most of the quantitative data for Caribbean reefs is unpublished or buried in gray literature and government reports that have not been systematically exploited in previous long-term assessments of changing conditions throughout the region. We contacted hundreds of people in all the countries of the Caribbean via several thousand emails, requests for data posted on relevant websites, and through presentations and interviews at the 64th Gulf and the Fisheries Institute (GCFI) annual conference in Puerto Morelos, Mexico in 2011 and the 12th International Coral Reef Symposium (ICRS) and ICRI meetings in Cairns, Australia in 2012. We also corresponded with managers of large monitoring data sets, including the National Oceanic and Atmospheric Administration (NOAA) Center for Coastal Monitoring and Assessment Biogeography Branch, Caribbean Coastal Marine Productivity Program (CARICOMP), Atlantic and Gulf Regional Reef Assessment (AGRRA), Caribbean Adaptation to Climate Change Mainstreaming Adaptation to Climate Change (CPACC MACC) programs, Coral Reef Evaluation and Monitoring Project (CREMP) carried out by Florida Fish and Wildlife (FWC), and the Inventory and Monitoring Program (I&M) conducted by the National Park Service South Florida Caribbean Network (NPS SFCN).

1a. SCOPE OF THE DATA

We obtained data from 78 principal investigators supplemented by data from 143 published scientific papers and reports. In total, these include data from more than 35,000 surveys of corals, macroalgae, the sea urchin *Diadema antillarum*, and reef fish from 287 data sets, distributed among 90 reef locations in 34 countries, states, or territories (Tables 1 and 2, Fig. 4). This is by far the largest amount of quantitative coral reef survey data ever compiled and exceeds several fold the data employed for previous analyses of Caribbean reefs (Gardner et al. 2003; Schutte et al. 2010).

Sampling units are defined as follows:

Survey: A set of replicate data points collected at a unique reef site, date, depth, or range of depths. Individual surveys are replicates or averaged values for a series of replicates within datasets at a unique site, date and depth.

Data Set: An individual data collection by a single researcher or research team in a particular country, territory, or state.

Site: One or more surveys at the same depth and GPS coordinates on the same reef.

Location: A geographic cluster of exact survey coordinates (sites) revealed by GIS and further defined by prevailing oceanographic conditions (windward or leeward, onshore or offshore, etc.) and political boundaries.

Country, State, or Territory: An independent nation (Cuba, Curaçao, Jamaica, Panama) or political entity attached to or within a single country (Bonaire, Florida, Guadeloupe, Puerto Rico), either of which may be further subdivided to reflect geographic isolation (St. Thomas, St. Croix, and St. John within the US Virgin Islands within the USA).

Compilation of the great majority of the data presented very substantial challenges for organization

and management. We obtained two types of ecological data: (1) raw data provided directly by researchers and (2) summarized data extracted from peer-reviewed articles and government or gray literature reports. The datasets were based upon various sampling designs and methodologies, reported widely variable ecological and environmental parameters, utilized differing codes and groupings for reported variables, and were presented in a unique format. Consequently, we had to convert each database into a standardized, uniform format with accompanying crucial meta-data on precise geographic locations for GIS, sampling methodology, reef environmental parameters, and reef management history and status. To accomplish this, we developed a data template (Appendix 1) by soliciting input from study collaborators at the workshop in Panama, the ICRS and ICRI meetings in Cairns Australia, and countless additional emails. Compiling and organizing this information required a coordinated and extremely time-consuming effort to evaluate each dataset individually and to edit, reformat, and check for data consistency and quality before merging datasets into a master database.

The great majority of the data are for reef corals, macroalgae, *Diadema*, and fishes from fore-reef and patch-reef environments in depths between 1-20 m (Fig. 5). Therefore, all of the analyses for this report are restricted to these types of reefs and depths. Data are sparse and geographically limited until the mass mortality of *Diadema antillarum* in 1983. This striking event, combined with growing awareness of the severity of *Acropora* mortality due to White Band Disease (WBD), stimulated a surge of monitoring efforts. Numbers of surveys for corals and *Diadema* are about 12,000, for reef fish about 20,000, but only about 4,000 for macroalgae.

TABLE 1. Summary of numerical extent of data collected for the wider Caribbean, Gulf of Mexico, and Bermuda. For definitions of terms see text.

Number of	Coral	Macroalgae	Urchin	Fish	Overall
Countries/Territories	33	31	32	25	34
Locations	88	73	73	73	90
Datasets	193	129	107	68	287
Principal Investigators	65	55	19	20	78
Individual surveys	12,116	4,109	11,962	20,279	35,577
Datasets from papers	59	30	96	4	143
Start Year	1965	1970	1965	1988	1965
End Year	2012	2012	2012	2011	2012
Years surveyed	42	35	38	18	43

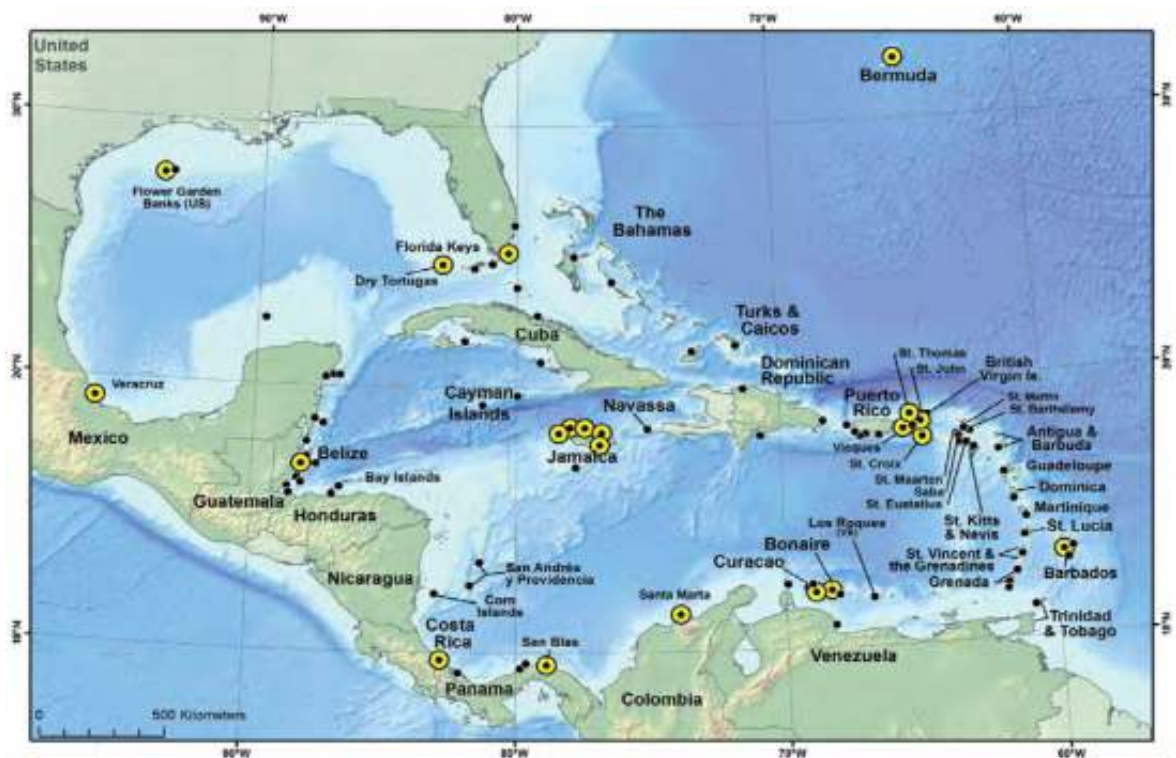


FIGURE 4. Geographic distribution of the 90 reef locations analyzed for this study and listed in Table 2. Large circles indicate 21 reef locations with the most complete time series data for analysis of long-term trends in coral cover.

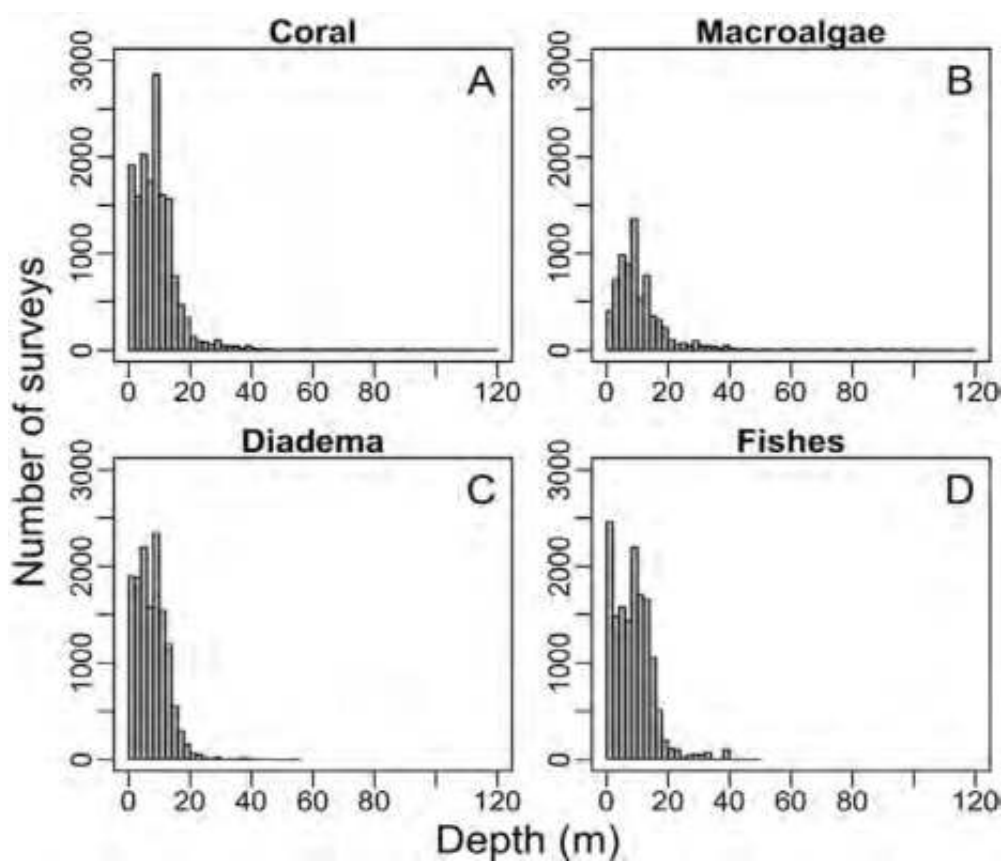


FIGURE 5. Frequency of surveys by depth for (A) corals ($= 9.5 \pm 8.34$), (B) macroalgae ($= 11.3 \pm 10.7$), (C) *Diadema antillarum* ($= 7.7 \pm 4.9$), and (D) reef fishes ($= 8.8 \pm 6.3$).

TABLE 2. List of coral reef locations used for this study with extent of sampling, range of years sampled, depth, changes in coral cover for locations sampled more than once, and recent biomass of parrotfish. Locations without percent coral cover were included for data for macroalgae, sea urchins, or fish.

Label	Country or Territory	Location	# of data sets	# of surveys	Start year	End year	# of years	Year span	Depth range (m)	Oldest coral cover (%)	Most recent coral (%)	Change coral cover (%)	Oldest macroalgal cover (%)	Most recent MA cover (%)	Change MA cover (%)	Parrotfish biomass after 1999 (g/m ²)
1	Antigua & Barbuda	Antigua & Barbuda	2	227	2005	2008	3	4	2 - 14	16.5	3.8	-12.7	24.8	13.8	-11	19.4
2	Aruba	Aruba	1	13	1986	1986	1	1	5 - 5	24	24					
3	Bahamas	Cay Sal Bank	1	685	2011	2011	1	1	4 - 28	7.1	7.1		68.7	68.7	0	14.8
4		Exuma Land Sea Park	1	138	1993	2007	14	15	0 - 20	7.3	7.8	0.5	11.2	33.7	22.5	9.8
5		Other	4	2237	1994	2011	14	18	0 - 27	9.7	11.7	2	10.5	44.7	34.2	27.7
6	Barbados	Leeward	7	186	1974	2007	24	34	1 - 22	37.4	15	-22.4	0	14.5	14.5	
7		South	1	104	1978	2007	12	30	3 - 25	11.1	17.4	6.3	6.8	1.8	-5	
8		Windward	1	3	2002	2003	2	2	12 - 13							
9	Belize	Atoll Leeward	4	963	1970	2009	9	40	0 - 18	55.5	20.7	-34.8	43.9	45.6	1.7	6
10		Atoll Windward	7	710	1970	2011	12	42	0 - 25	93.2	20.9	-72.3	6.8	51.5	44.7	6.3
11		Central Barrier	6	751	1978	2012	21	35	0 - 49	32.5	15.9	-16.6	4.9	55.5	50.6	7.2
12		Gulf Honduras	1	191	2006	2006	1	1	5 - 18	7.6	7.6					4.5
13		Inner Barrier	2	697	1994	2009	14	16	1 - 15	42.4	16.2	-26.2	4.1	1.6	-2.5	10.7
14		Northern Barrier	6	581	1997	2012	14	16	1 - 26	33.3	16.9	-16.4	20.3	48.8	28.5	8.9
15		Southern Barrier	3	414	1997	2011	9	15	1 - 24	23.5	13.5	-10	12.8	66.8	54	6.4
16	Bermuda	Bermuda	5	365	1977	2012	19	36	0 - 40	19.4	38.6	19.2	8.4	12.1	3.7	21.9
17	British Virgin Islands	British Virgin Islands	2	292	1992	2012	21	21	5 - 13	18	14.3	-3.7	5	10.2	5.2	13.8
18	Cayman Islands	Grand Cayman	5	356	1995	2009	8	15	2 - 20	19	30.7	11.7	13.9	31.4	17.5	12.7
19		Little and Brac	4	700	1988	2011	13	24	2 - 27	36.1	24.6	-11.5				15.7
20	Colombia	Providencia	1	52	1999	2006	6	8	1 - 21	20.5	20.5		41.9	41.9	0	
21		San Andrés	4	85	1992	2006	9	15	2 - 20	28.2	12.6	-15.6	19.8	23.8	4	
22		Santa Marta Region	10	61	1977	2005	21	29	3 - 23	28	31.1	3.1	0	3.3	3.3	
23	Costa Rica	Cahuita	2	90	1977	2011	17	35	2 - 10	40.4	18	-22.4	13.2	12.5	-0.7	39.8
24	Cuba	Jardines de la Reina	3	898	2001	2011	3	11	0 - 17	15.6	30.1	14.5	32	35.7	3.7	20.4
25		North	2	597	1989	2001	7	13	0 - 23	6.8	15.9	9.1	38.5			6.9
26		Southwest	4	1168	1998	2011	6	14	0 - 21	9.8	25.2	15.4	43.2	19.1	-24.1	8.4
27	Curacao	Curacao Northwest	6	202	1983	2011	16	29	2 - 20	18.1	13.3	-4.8	6	8.3	2.3	31.6
28		Curacao Southwest	13	335	1973	2011	27	39	1 - 40	40.7	31.5	-9.2	0	7.8	7.8	15.2
29		Curacao Windward	1	6	2001	2001	1	1	20 - 20							8.6

Label	Country or Territory	Location	# of data sets	# of surveys	Start year	End year	# of years	Year span	Depth range (m)	Oldest coral cover (%)	Most recent coral cover (%)	Change coral cover (%)	Oldest macro-algal cover (%)	Most recent MA cover (%)	Change MA cover (%)	Parrotfish biomass after 1999 (g/m ²)
30	Dominica	Dominica	1	9	2007	2009	2	3	5 - 14	11.4	9	-2.4	10.6	0.1	-10.5	
31	Dominican Republic	North	2	202	2004	2006	2	3	0 - 12	23.4	21.3	-2.1	8.9	8.9	0	3.1
32		Punta Cana	1	235	2003	2003	1	1	1 - 8	8	8					3.9
33		South	2	140	1994	2004	6	11	4 - 33	7.8	28.1	20.3	17.7	9.9	-7.8	9.2
34	French Antilles	Guadeloupe	1	192	1988	2011	20	24	1 - 15	23	18.6	-4.4	52.5	33.8	-18.7	24.4
35		Martinique	1	38	2001	2007	7	7	5 - 10	35.7	17.4	-18.3	33.7	33.8	0.1	20.4
36		St. Barthelemy	1	47	2002	2011	10	10	10 - 10	25.3	10.8	-14.5	14.9	53	38.1	17.1
37	Grenada	Grenada other	1	12	2005	2009	3	5	2 - 20	41.7	27.7	-14				
38		Leeward	1	11	2007	2009	2	3	17 - 30	10.1	12.8	2.7	37.6	65.9	28.3	
39	Guatemala	Guatemala	1	59	2006	2006	1	1	7 - 15	9.9	9.9					3
40	Honduras	Bay Islands	3	981	1987	2010	4	24	0 - 19	20.6	21.6	1	34.5	43	8.5	11.8
41		Near shore	1	328	2006	2006	1	1	2 - 20	12	12					22.5
42	Jamaica	Montego Bay	7	348	1973	2007	18	35	0 - 16	10.6	19.4	8.8	0	53.4	53.4	4.6
43		North central	17	724	1969	2011	38	43	1 - 120	44.6	19.6	-25	1.1	24.2	23.1	6.9
44		Northeast	3	308	1977	2007	9	31	1 - 17	47	11.8	-35.2	26.9	55.9	29	5.4
45		Pedro Bank	1	301	2005	2005	1	1	1 - 21	14.7	14.7					15.4
46		Port Royal Cays	3	20	1977	2011	11	35	4 - 13	24.9	4.7	-20.2	55.7	7.7	-48	
47		West	4	269	1977	2012	12	36	1 - 18	40.3	7.8	-32.5	20.7	55.7	35	8.1
48	Mexico	Alacran	2	7	1985	1985	1	1	2 - 35	11.2	11.2		45.6			
49		Chinchorro Bank	2	486	2000	2008	5	9	0 - 29	17	7.9	-9.1	7.7	7.7	0	1.4
50		Cozumel Leeward	4	678	1984	2011	11	28	0 - 28	25.5	12.1	-13.4	32.9	21.6	-11.3	3.5
51		Cozumel Windward	1	77	2005	2005	1	1	1 - 17	9.2	9.2					0.7
52		North East Yucatan	6	1105	1979	2010	15	18	0 - 28	20.1	7.9	-12.2	30.9	10.6	-20.3	6.2
53		South East Yucatan	2	1028	1985	2009	7	11	0 - 21	29.8	15.9	-13.9	40.4	36.3	-4.1	5.1
54		Veracruz	3	152	1965	1999	4	35	1 - 21	34.1	17.2	-16.9				
55	Navassa	Navassa	1	5	2002	2012	5	11	27 - 28	46.4	10.7	-35.7	41.7	65.7	24	
56	Netherlands	Bonaire Leeward	9	408	1973	2011	23	39	3 - 40	54.8	37.1	-17.7	6.1	17.7	11.6	32.3
57		Bonaire Windward	4	236	1988	2008	4	21	3 - 31	31.9	9.7	-22.2	35	66.3	31.3	19.1
58		Saba	2	219	1993	2003	7	11	3 - 20	19.5	9.4	-10.1	25.1	5.5	-19.6	13.5
59		Saba Bank	1	54	1999	1999	1	1	14 - 21	24.3	24.3					14.5
60		St. Eustatius	1	213	1999	2007	4	9	11 - 19	21.8	21.8					23

Label	Country or Territory	Location	# of data sets	# of surveys	Start year	End year	# of years	Year span	Depth range (m)	Oldest coral cover (%)	Most recent coral cover (%)	Change coral cover (%)	Oldest macro-algal cover (%)	Most recent MA cover (%)	Change MA cover (%)	Parrotfish biomass after 1999 (g/m ²)
61	Nicaragua	Corn Islands	2	269	1993	2003	5	11	2 - 16	28.2	24.4	-3.8	37.4			5.1
62	Panama	Bahia Las Minas	3	215	1985	2011	19	27	2 - 14	23.7	12.3	-11.4	42	3.2	-38.8	
63		Bocas del Toro	4	473	1999	2011	13	13	1 - 17	29.7	13.6	-16.1	12.5	10.4	-2.1	12.3
64		Costa Arriba	3	154	1985	2011	19	27	2 - 17	24.7	13.9	-10.8	56	31.6	-24.4	
65		San Blas	3	1118	1980	2005	23	26	0 - 21	38.8	30.9	-7.9	0.6			13.3
66	Puerto Rico	Guanica	1	6	2005	2006	2	2	2 - 18	27.6	17.3	-10.3				
67		Jobos Bay	1	25	2009	2009	1	1	0 - 12	8.7	8.7		15	15	0	2.1
68		La Paguera	5	1265	1989	2012	20	24	0 - 112	16.4	19.2	2.8	5.4	10.4	5	5.6
69		Mona Islands	1	38	2008	2008	1	1	30 - 103	4.5	4.5		60.7	60.7	0	
70		Turumote	1	11	2002	2010	6	9	0 - 19	23.8	23.8					9.5
71		Vieques & Culebra	5	358	1978	2008	7	31	2 - 48	42.6	8.1	-34.5	1.9	10.6	8.7	19
72	St. Kitts & Nevis	St. Kitts & Nevis	2	446	2007	2011	3	5	4 - 24	10.3	11.1	0.8	48.5	36.8	-11.7	13
73	St. Lucia	St. Lucia Leeward	2	12	1993	2009	3	17	8 - 21	48.5	10.1	-38.4	41.4	8.1	-33.3	
74	St. Martin	St. Martin	1	52	1999	2007	3	9	8 - 12	12.5	12.5					12.1
75	St. Vincent & the Grenadines	Grenadines	4	304	1976	2007	5	32	2 - 17	30.4	19.5	-10.9				16.7
76		St. Vincent	2	108	2007	2009	3	3	2 - 11	29.2	24.9	-4.3	2.3	0.4	-1.9	6.8
77	Trinidad & Tobago	Trinidad & Tobago	1	16	1994	2012	16	19	10 - 10	24.1	19.1	-5	0	0.9	0.9	
78	Turks & Caicos	Turks & Caicos Islands	2	565	1999	1999	1	1	2 - 23	17.7	17.7		11.7	11.7	0	7.4
79	U.S.A	Dry Tortugas	9	671	1975	2011	19	37	1 - 28	20.8	8	-12.8	0.6	31.7	31.1	7.5
80		Flower Garden Banks	3	347	1974	2011	6	38	18 - 43	56.7	53.1	-3.6	13.2	25.6	12.4	35.8
81		Lower Florida Keys	5	1094	1972	2011	24	40	1 - 27	31.8	10.3	-21.5	15.3	15.2	-0.1	24.2
82		Middle Florida Keys	4	390	1991	2011	17	21	3 - 24	8.4	8	-0.4	7	22.8	15.8	8.4
83		Southeast Florida	4	256	1989	2011	17	23	2 - 17	12.5	2.8	-9.7	3.4	4.6	1.2	3.6
84		Upper Florida Keys	13	1880	1965	2011	31	47	0 - 27	27.9	6.1	-21.8	0.8	15.3	14.5	20.3
85	U.S. Virgin Islands	St. Croix	10	505	1976	2011	32	36	0 - 40	23.2	4.7	-18.5	3	8.9	5.9	13.1
86		St. Thomas	5	473	1978	2010	19	33	0 - 33	27.4	13.6	-13.8	1.5	47.7	46.2	11.4
87		St. Thomas shelf edge	2	620	2002	2011	10	10	30 - 40	26.1	33.6	7.5	42.9	26.8	-16.1	9.2
88		St. John	11	2991	1978	2011	31	34	0 - 27	34.1	10.1	-24.0	0.6	28.9	28.3	8.3
89	Venezuela	Los Roques	2	209	1999	2008	7	10	1 - 15	69	78	9				60.7
90		Morrocco	2	165	1996	2011	16	16	5 - 13	55	38.5	-16.5				

There are no quantitative survey data for reef fish biomass prior to 1989. Data for *Diadema* abundance and macroalgal cover are also rare until the sea urchin began to die *en masse*. Most of the coral data are for total coral cover, but there are also considerable data broken down by genus or species since the early 1970s. Many of the fish surveys only recorded certain groups such as parrotfish or groupers, but the identification and recording of these charismatic taxa appears to be generally good. The greatest problems of data quality are with macroalgae, which were not recorded consistently except by a small number of experts in algal ecology and systematics. We defined macroalgae as erect calcareous or fleshy algae greater than 2 cm tall. These include, but are not limited to species of the genera *Cladophora*, *Dictyota*, *Halimeda*, *Liagora*, *Microdictyon*, and *Sargassum*. In many cases macroalgae were recorded as turf and vice versa, and the CARICOMP protocol distinguished macroalgae by such different criteria that we could not use their algal data in our analysis. Considerable energy was invested in vetting the algal data to throw out all of the questionable data sets, which explains why the numbers of surveys for macroalgae are so much smaller than the other groups.

Most of the surveys employed haphazardly placed or fixed transects or quadrats. Examples include the remarkable nearly 40-year data set provided by Rolf Bak for fixed quadrats in Curaçao and Bonaire, larger scale transect surveys for particular reefs by individual scientists, and large monitoring programs such as CARICOMP, CREMP, and FWC. Surveys were varyingly conducted with widely varying frequency and consistency from 1970 to the present, although the numbers of surveys were small and restricted to only a few locations until the 1980s, and coverage did not substantially increase until the 1990s (Fig. 6A).

Two other major survey programs beginning in the 1990s employed entirely different sampling approaches. AGRRA began in 1997 and used widely varying rapid sampling protocols that have changed throughout the history of the project and also differ among regions surveyed (Fig. 6B). In contrast, data are collected from stratified random sites for the NOAA Biogeography Program surveys in Puerto Rico and the US Virgin Islands, and by the Florida Keys Coral Reef

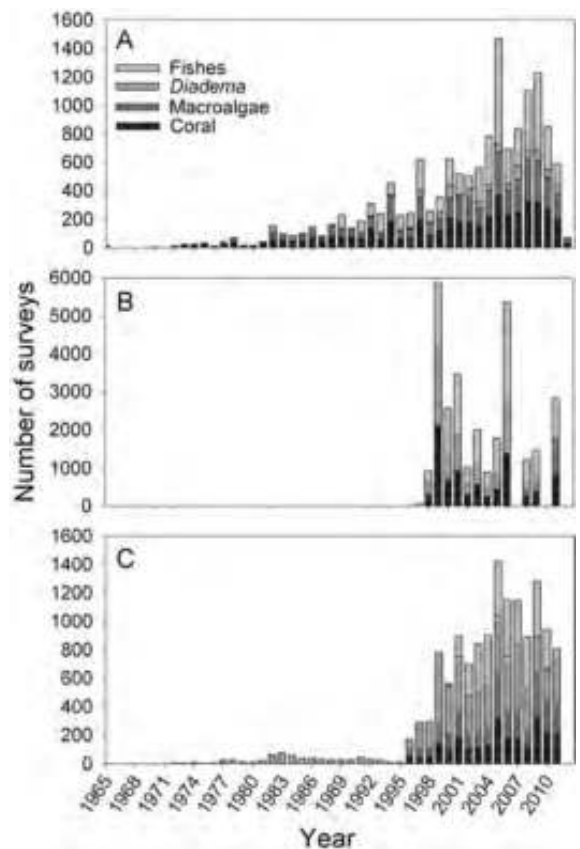


FIGURE 6. Number of surveys by year for coral, macroalgae, *Diadema*, and fishes for (A) all permanent or haphazardly collected data, (B) data from the AGRRA program, and (C) data collected from locations randomly selected for each census so that there are no repeated observations from the same geographic point.

Monitoring Assessment team (PIs: S. Miller and M. Chiappone) and Southeast Florida Coral Reef Monitoring and Evaluation Project (PI: Gilliam) in the Florida Reef Tract (Fig. 6C). In this latter case, surveys include sandy and rocky bottoms in addition to actual reef habitat so are not directly comparable to the other data.

The longest time series with consistent data are Rolf Bak's study beginning in 1973 for large fixed photo quadrats at 4 stations and 4 depths at Curaçao and Bonaire totaling 243 m² (Bak et al. 2005). Photographs were taken annually, but data for corals and macroalgae identified from the photographs have been analyzed so far only for 5-year intervals. An additional site in east Curaçao was added starting in 1993. Robert Steneck also began monitoring reefs at Bonaire in 1999 (Steneck and Arnold 2009). Comparably long time series extending back into the early 1970s to early 1980s are available from the northern Florida Keys (Dustan 1977, 1985; Porter and Meier

1992), Jamaica (Hughes and Jackson 1985; Liddell and Ohlhorst 1986, 1992; Hughes 1994; Loya, unpublished data), St. John and St. Croix in the United States Virgin Islands (Rogers et al. 1991, 2008; Edmunds 2002; Rogers and Miller 2006; Miller et al. 2009), and Panama (Guzmán et al. 1991; Shulman and Robertson 1996; Guzmán 2003). However, these records were compiled by different workers at different times and are therefore not as consistent or complete as data from the Dutch Caribbean.

1b. ANALYSIS

Trends in percent cover were assessed for total corals and macroalgae. Trends in density were assessed for *Diadema antillarum* and reef fishes. Analyses were based on a hierarchical structuring of the data and were summarized based on means of surveys within individual datasets for each location. Each survey was assigned to a “location” so each dataset contributed one value to each location unless that dataset covered more than one location. Finally, means were calculated for each location. All statistical analyses were conducted using the software program R version 2.15 (R Development Core Team 2011).

Because the intensity of sampling varies so greatly in time and space, we partitioned the data into three 12 to 14-year time intervals based on major ecological events that extended throughout the wider Caribbean. These are:

1. 1970-1983: Interval from our oldest data until the massive die-off of the sea urchin *Diadema antillarum* in 1983 including the first reports of White-Band Disease (WBD) from the mid 1970s to early 1980s.
2. 1984-1998: From the end of the *Diadema* die-off up to and including the widely reported 1998 extreme heating event.
3. 1999-2011: The modern era of massively degraded coral reefs including the extreme heating events in 2005 and 2010.

We also selected a subset of 21 reef locations for more detailed statistical analyses (large circles in Fig. 4) based upon availability of coral cover data for all three time intervals as well as associated metadata important for the interpretation of the possible drivers of reef degradation.

General and generalized linear mixed effects models (Pinheiro and Bates 2000) were used to test

explanatory variables across time and with response variables (R packages lme4: Bates and Maechler 2010, and glmmADMB; Skaug and Fournier 2013). Where the response variable was percent cover we used generalized linear mixed models assuming a beta distribution since the response variable is a percentage. Otherwise, general linear mixed models were used on square-root transformed response variables to reduce the mean-variance relationship and meet the assumptions of linear modeling. We accounted for temporal and spatial autocorrelation by adding random components of year nested within survey and dataset (for definitions see previous section), thus each survey within each dataset was treated as a repeated measure. The model accounted for differences in sampling by location by further nesting within location. For each model 95% confidence intervals were calculated for means that accounted for variation due to dataset and location based on 5000 simulations (R package arm: Gelman et al. 2010). Criteria for comparing model fits were based on minimizing the Akaike Information Criterion (AIC). An estimate of restricted maximum likelihood was used to fit the models. Bonferroni-adjusted pair-wise multiple comparisons were conducted for specific post-hoc hypotheses where appropriate.

Means were modeled for time bins defined above, as well as the values for the oldest (first) year and most recent year a location was studied. In most cases, the oldest or most recent year for a given location was comprised of a single dataset, but in the case of multiple datasets per year the datasets were averaged. Current coral cover was estimated by considering, for 88 locations, the most recent estimate of cover per location as long as the most recent survey was after 1998. Analyses across time bins were conducted for each location with mixed effects models including random effect of dataset. Tukey Honest Significant Differences for post-hoc pairwise comparisons of means were conducted with adjustments for multiple means.

To assess trends in *Acropora* abundance over time, frequency of occurrence and dominance across various time bins were constructed. Because sample sizes are small before 1950, and the locations represented in various time bins are not consistent, care should be taken when interpreting results. Thus we constructed confidence intervals for proportions assuming a binomial distribution with

the Pearson-Klopper method. Temporal trends in *Acropora* species percent cover were also examined for data after 1975 in the GCRMN database where means and standard deviations were calculated as for trends discussed above.

Multivariate ordination was conducted to investigate temporal trends in benthic community composition. Locations were included in the ordination if data were available for percent cover of corals at the species (or species group) level as well as for total macroalgae for the same replicate. Coral species were combined into 19 groups by species or genera, and by growth form, to reduce zero occurrences for rare species, especially for species with limited geographic range.

We used two forms of ordination analysis to assess changes in coral and macroalgal assemblage composition. Principal Components Analysis (PCA) uses Euclidean distances to compute a similarity matrix projected on a PCA ordination graph that illustrates the total amounts of the variance “explained” along the first, second, and third PCA axes. PCA has the advantage that results are easily interpretable with taxa represented by arrows that indicate increasing abundance in the direction of the arrow. In contrast, non-metric, multidimensional scaling (MDS) is based on rank order correlation and uses a Bray-Curtis similarity matrix to generate an ordination (Clarke et al. 2005). MDS has the important advantage of not treating zeros as values of occurrence since multiple zero occurrences common in ecological data can play havoc with resemblance based on Euclidean distance. But, the order of the axis does not necessarily imply importance, which renders the results less intuitive and more difficult to interpret.

PCA and MDS were performed on square root transformed mean percent cover data across two time bins to explore the change in benthic assemblage composition over time (R package *vegan*: Oksanen et al. 2013). Species were scaled proportional to the eigenvalues for graphical purposes, so angles reflect correlations in multidimensional space (Legendre and Legendre 1998).

Relationships between coral and macroalgal cover and anthropogenic drivers were explored using various methods depending on the question and data structure (see text of relevant sections for detailed methodological information). Wherever relevant, we

employed generalized linear mixed effects models with a beta distribution as described above to test the relationship between coral cover and drivers.

2. OVERALL CHANGES IN BIOLOGICAL ABUNDANCE

We first discuss status and trends of corals and macroalgae, which are the two major sessile components of Caribbean reef communities. Next we consider the demise of three major taxa that have severely declined over the past 40 years: the branching coral genus *Acropora* that once overwhelmingly dominated most shallow reefs, the sea urchin *Diadema antillarum*, and parrotfishes. The latter two are (or were) the most important macroscopic herbivores on Caribbean reefs.

2a. PATTERNS OF CHANGE FOR CORALS AND MACROALGAE

Mean live coral cover for the tropical western Atlantic based upon the most recent estimates of cover for each of the 88 locations in Table 2 is 16.8% (median 14.5%, range 2.8% for southeast Florida to 53.1% for the Flower Garden Banks). The mean is 68% higher than the mean of 10% cover reported previously for 2001 (Gardner et al. 2003) but almost identical to the mean of 16.0% cover for the years 2001-2005 from a more recent and more rigorous assessment (Schutte et al. 2010).

We further refined the estimate of mean percent coral cover using statistical methods to take into account the great variation among locations and data-sets, resulting in a mean of 14.3% (+2.0, -1.8) This lower value reflects the skewed shape of the variation in coral cover across the region, wherein most locations fall well below the mean with several notable exceptions of locations with considerably higher than average coral cover (Fig. 7). This variation is further apparent when the quantiles of current coral cover are considered. The upper quartile is 21.2%, while the 95% quantile is 31.5%. Five locations fall above the 95% quantile including Bermuda, the leeward coast of Bonaire, the southwest coast of Curaçao, the Flower Garden Banks in the northern Gulf of Mexico, and Morrocoy National Park on the mainland coast of Venezuela (However, the high value for Morrocoy resulted from the relocation of the CARICOMP study site to a different reef after all the corals at the original location had died.).

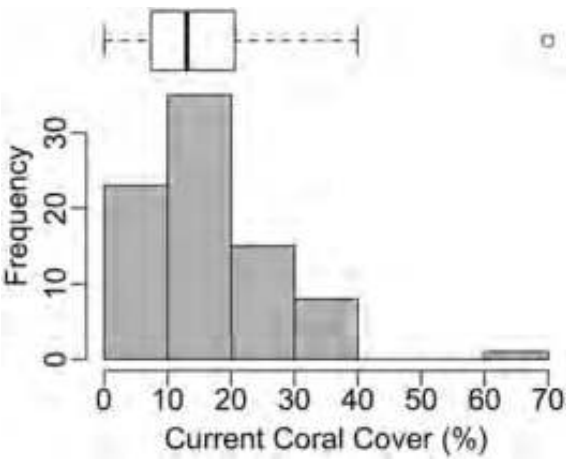


FIGURE 7. Histogram of current estimates of percent coral cover from 88 locations across the Caribbean with box plot reflecting 0, 25%, 50%, 75% quantiles.

Coral cover declined at 52 of 71 (73%) locations in Table 2 for which time series data are available (Fig. 8). The decline was greatest for locations with the oldest estimates of percent cover (Fig. 8A) and the longest periods of observation (Fig. 8B). This is the now classic pattern of “shifting baselines” for fisheries management (Pauly 1995; Jackson and Jacquet 2011; Jackson et al. 2012). Another striking example of the Shifting Baselines Syndrome in the Caribbean concerns the status and trends of green turtle populations on nesting beaches that have been surveyed for varying lengths of time (Jackson 1997; McClenachan et al. 2006). Beaches observed for less than 40 years exhibit

a wide mixture of positive and negative trends, whereas all beaches observed for more than 40 years have suffered very large declines of 75-95%.

Long-term changes in corals and macroalgae

Average changes in coral and macroalgal cover over the three time intervals are presented in Table 3 for all locations and the 21 long-term data locations in Fig. 4. Mean coral cover in depths of 0-20 m for all locations declined from 33.0% before 1984, to 18.6% from 1984-1998, and 16.4% from 1999 to today (Fig. 9A, Table 3). The average pattern of decline did not vary greatly with depth. Coral cover before 1984 was 33.2% on reefs from 0-5 m depth versus 32.6% cover in depths of 5.1-20 m (Table 3). After 1999 coral cover declined slightly more on reefs shallower than 5 m. *Acropora palmata* once overwhelmingly dominated reefs in 0-5 m with cover as great as 50 to 85% (Woodley et al. 1981; Gladfelter 1982). Thus, our data suggest that the decline of *Acropora palmata* had begun before the first quantitative surveys at most reef locations. In contrast, a locally variable mix of species including the *Orbicella* (formerly *Montastraea*) *annularis* species complex, other massive and plating corals, and *Acropora cervicornis* formerly dominated reefs from 5 to 20 m (Goreau 1959; Kinzie 1973; Bak 1977; Bak and Luckhurst 1980; Liddell and Ohlhorst 1986, 1988).

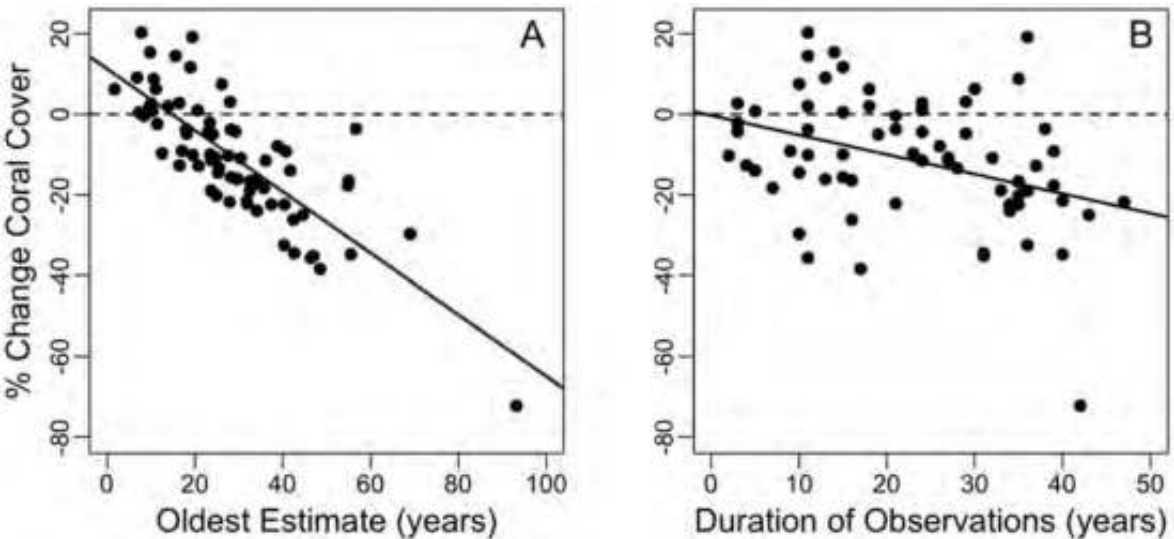


FIGURE 8. Percent change in coral cover at 71 locations in Table 2. Change in percent cover of corals in relation to (A) cover measured in the earliest year of observation ($R^2 = 0.63$, $p < 0.01$) and (B) the duration of the study period for that location ($R^2 = 0.17$, $p < 0.01$).

TABLE 3. Corrected values of percent cover of corals and macroalgae by depth for 3 time periods for all locations and for the subset of 21 circled locations in Fig. 4. Values are means with 95% confidence intervals in parentheses calculated with mixed-effect beta regression that takes into account variability due to location and datasets

Depth (m)	All locations			21 locations		
	1970-1983	1984-1998	1999-2011	1970-1983	1984-1998	1999-2011
Coral cover (%)						
0-20	33.0 (28.7, 37.6)	18.6 (16.2, 21.2)	16.4 (14.8, 18.1)	31.5 (27.7, 35.6)	18 (15.1, 21.3)	15.8 (13.0, 19.0)
0-5	33.2 (22.7, 45.6)	14.1 (11.2, 17.6)	15.4 (13.2, 17.9)	26.6 (20.2, 34.1)	13.4 (9.5, 18.5)	12.2 (8.6, 17.0)
5.1-20	32.6 (28.1, 37.3)	19.4 (16.3, 22.9)	16.5 (14.8, 18.4)	34.6 (30.3, 39.1)	19.6 (16.6, 23.0)	16.7 (12.9, 21.3)
Macroalgal cover (%)						
0-20	7.0 (3.6, 13.0)	23.6 (17.3, 31.4)	23.5 (19.8, 27.6)	5.6 (2.7, 11.0)	21.6 (14.0, 31.8)	23.9 (18.4, 30.5)
0-5	12.1 (5.3, 25.2)	40.1 (24.4, 58.2)	24.0 (17.9, 31.4)	10.2 (3.9, 24.2)	42.4 (29.0, 56.9)	21.1 (16.0, 27.4)
5.1-20	4.0 (1.8, 9.0)	21.5 (15.1, 29.5)	23.2 (19.2, 27.8)	4.0 (1.8, 9.0)	19.3 (11.3, 31.0)	25.8 (18.8, 34.2)

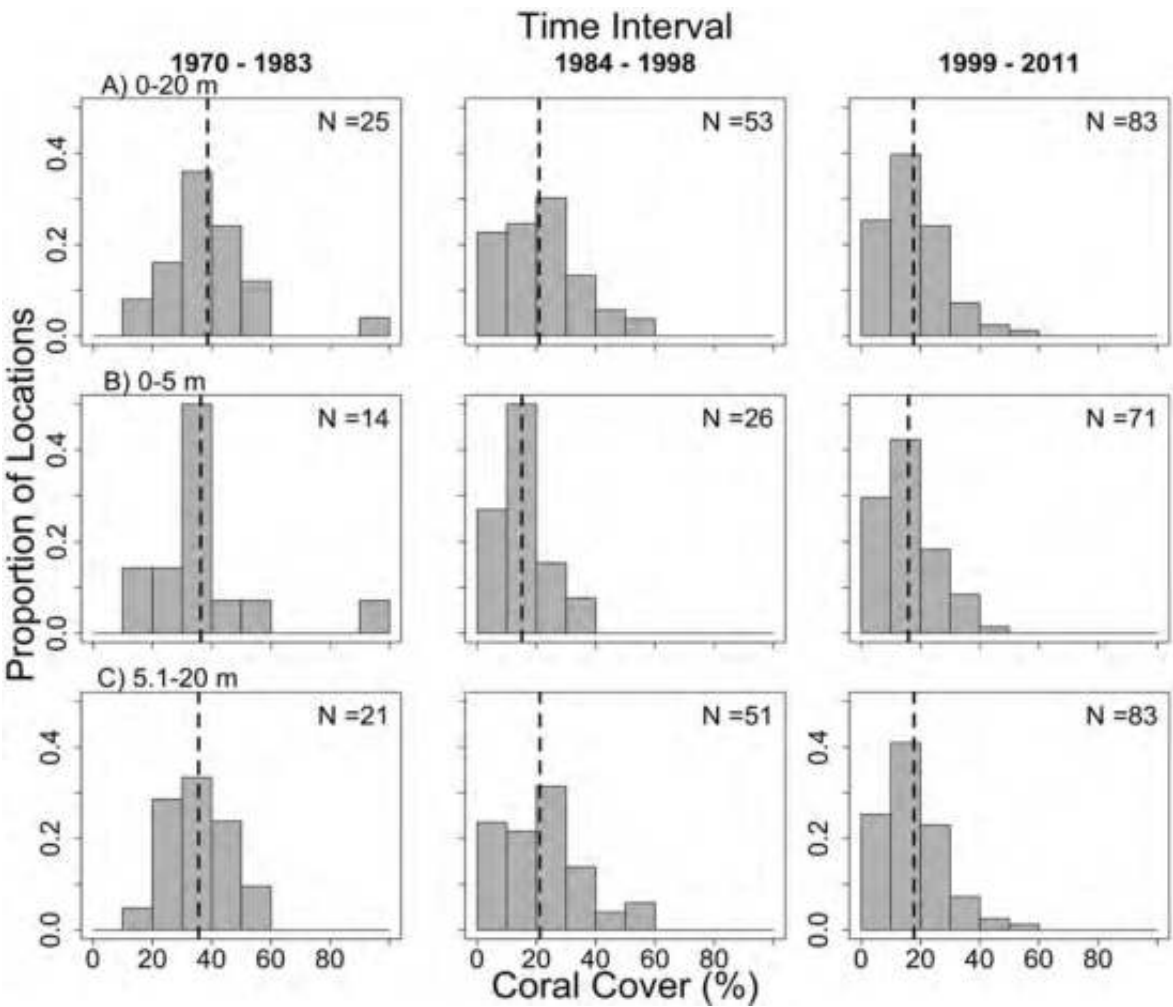


FIGURE 9. Distribution of coral cover among all the locations in Table 2 for all three time intervals and depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent the means within locations for each time bin. Vertical line indicates uncorrected mean, and N is the number of locations.

Changes in coral cover were similar on the 21 reefs in Fig. 4 except that coral cover was lower in shallow depths before 1984 and the subsequent declines were more abrupt between time intervals 1 and 2 (Table 3, Fig. 10).

Macroalgal cover in 0-20 m was 7.0% prior to the mass mortality of *Diadema antillarum* in 1983 and then tripled to 23.6% afterwards (Fig. 11A, Table 3). However, the patterns vary strongly with depth. Macroalgal cover from 0-5 m depth averaged

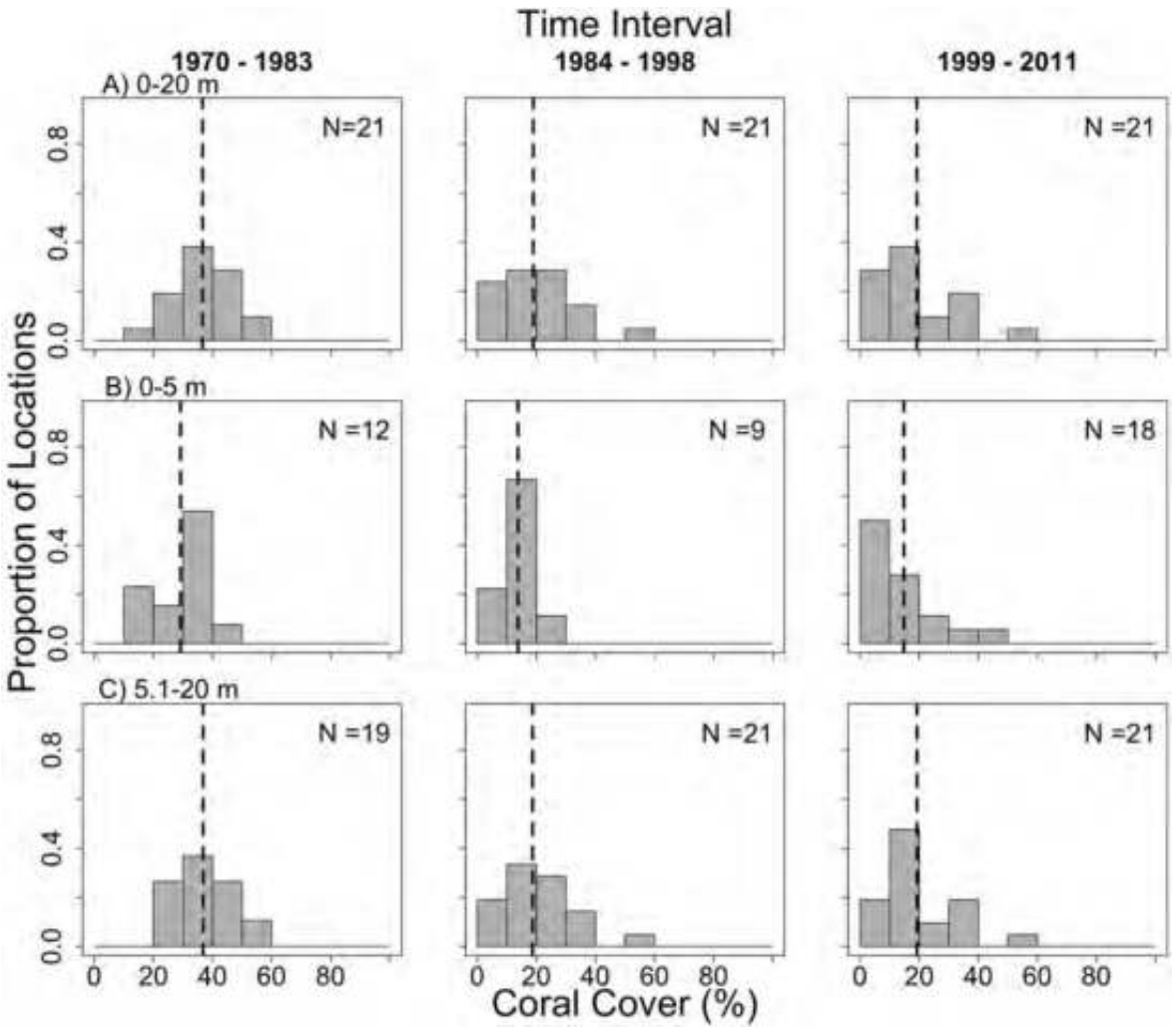


FIGURE 10. Distribution of coral cover for the 21 long-term data locations (large circles in Fig. 4) for all three time intervals at depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent the means within locations for each time bin. Vertical line indicates uncorrected mean, and N is the number of locations.

12.1% before 1984 and increased afterwards to 40.1% (Table 3). In contrast, macroalgal cover was only 4.0% on reefs in 5.1-20 m before 1984, and then increased 5-fold after the *Diadema* died (Fig. 11C, Table 4). Macroalgal cover since 1999 has averaged about 23.2% but varied enormously among the 67 locations from 1-69%. Changes in macroalgae on the 21 reefs were similar to that for the entire dataset (Table 3, Fig. 12).

The clearly opposite trends in coral and macroalgal cover (Figs. 9 and 10 versus Figs. 11 and 12) demonstrate a highly significant and persistent shift throughout the wider Caribbean from reef communities where corals were the most abundant occupiers of space to reef communities where macroalgae are more abundant than corals (Fig. 13). Such a striking reversal from coral to

macroalgal dominance is commonly referred to as a phase shift (sensu Hughes et al. 2010); a pattern first documented in even more extreme form from Jamaica between the 1970s and 1990s (Hughes 1994).

Geographic Variation in Reef Degradation

The preceding histograms demonstrate very large geographic differences in the status and trends for coral cover at different reef locations. To document the nature of this variability in greater detail, we constructed two different kinds of timelines for the status and trends in coral cover for two different subsets of reefs presented below. The focus here is on documenting the patterns of variation among sites. Implications and insights derived from the timelines are discussed in the following section of the report on anthropogenic drivers of change.

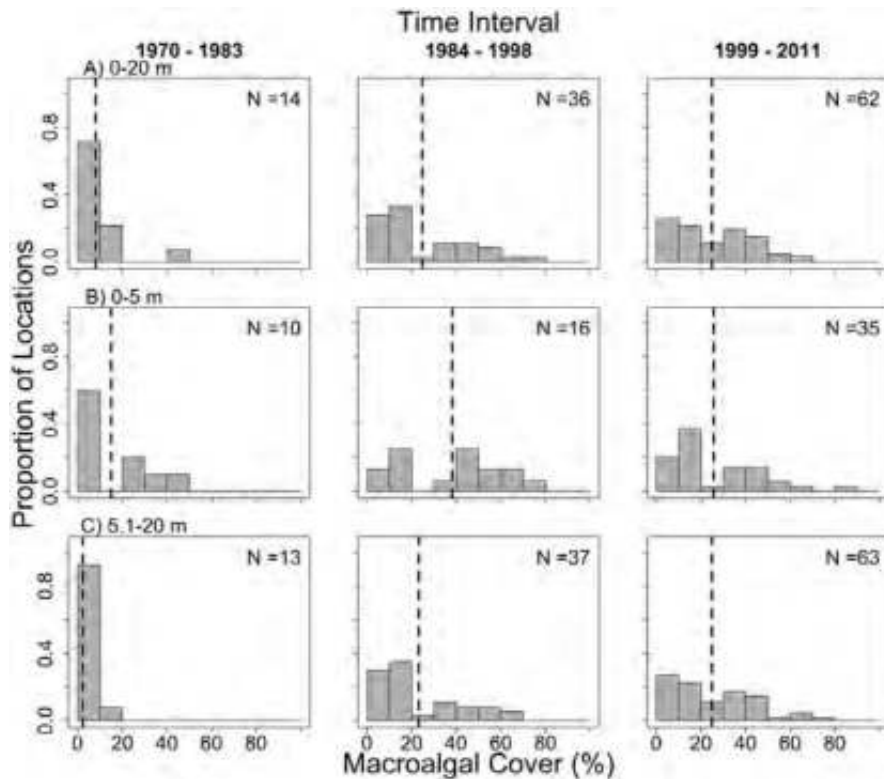


FIGURE 11. Distribution of percent macroalgal cover among all the locations in Table 2 for all three time intervals at depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent the means within locations for each time bin. Vertical line indicates uncorrected mean, and N is the number of locations.

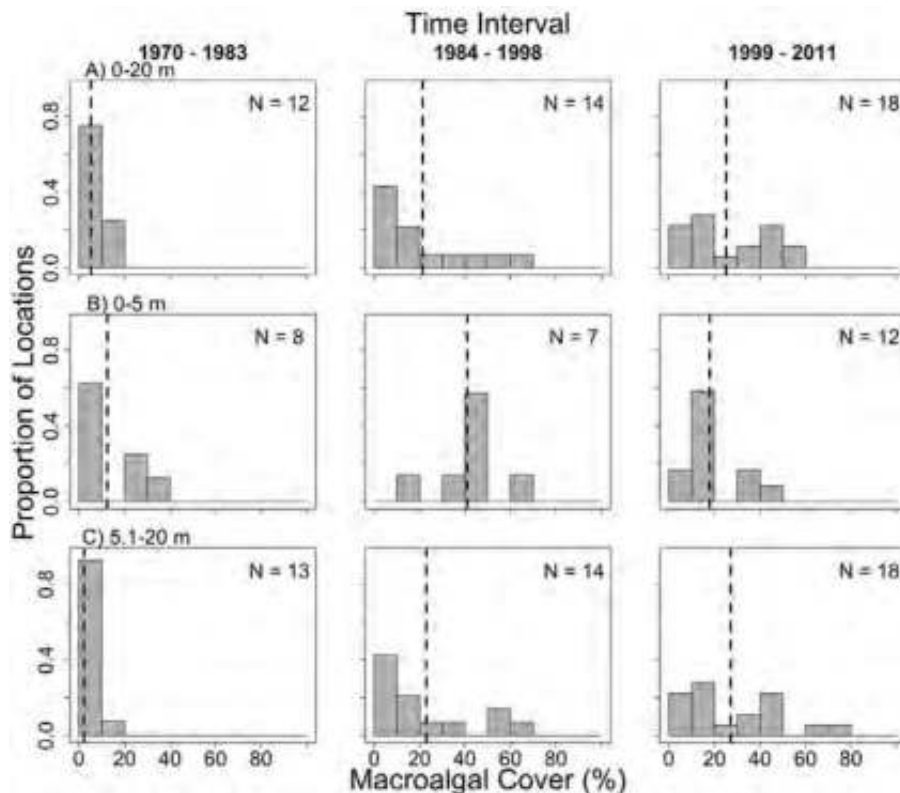


FIGURE 12. Distribution of percent macroalgal cover for the 21 long-term data locations (large circles in Fig. 4) for all three time intervals at depths of (A) 0-20 m, (B) 0-5 m, and (C) 5.1-20 m. Values represent uncorrected means within locations for each time bin. Vertical line indicates mean, and N is the number of locations.

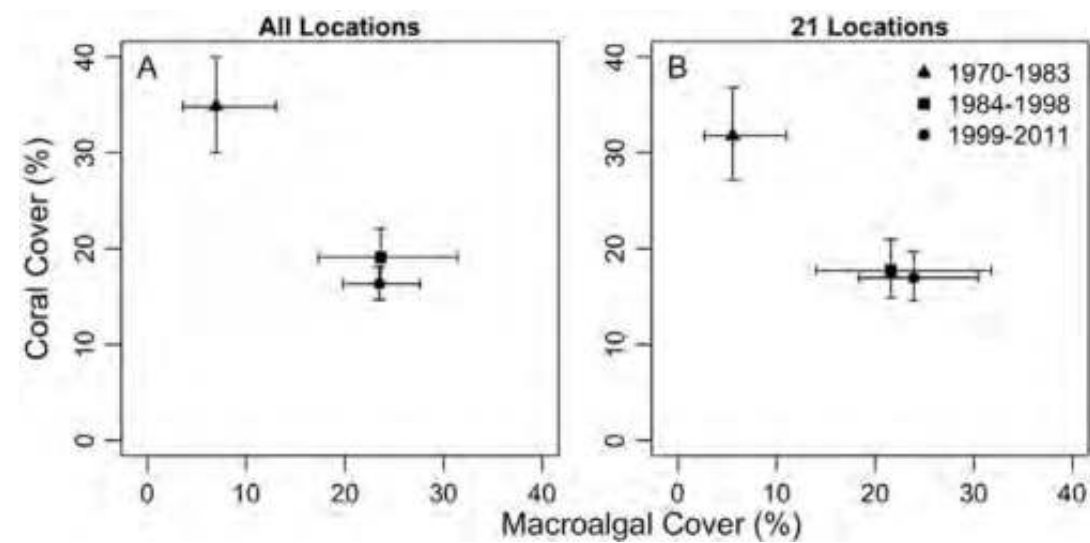


FIGURE 13. Large-scale shifts from coral to macroalgal community dominance since the early 1970s at (A) all locations and (B) the 21 long-term data locations (large circles in Fig. 4). Symbols and confidence intervals represent corrected means and standard deviations for 3 time intervals that take into account variability due to location and datasets using a mixed modeling framework.

Timelines for specific reef sites: These document detailed patterns of variation in coral cover and rates of change on a local scale for 40 particularly well-studied reef sites for which data were available over a span of at least eight years (Table 4, Appendix 2). The earliest of the timelines begins in 1972 but the great majority of sites were not surveyed quantitatively until the 1990s. Average net change in coral cover for the 40 sites is -21% but variation was extreme among sites (range +1 to -64%). Eight sites exhibited remarkable stability with a net change of only +1 to -5% cover. In contrast, four sites declined by $\geq 55\%$ and another six sites by 32% or more.

Whenever possible we chose reefs for plotting timelines for which taxonomic data were available for reef composition at the specific or generic level. Taxa were lumped into eight taxonomic and morphological groups for ease of graphing the data: acroporids (*Acropora palmata* and *A. cervicornis*), other branching corals (principally *Porites* and *Madracis*), agariciids (*Agaricia* and *Helioseris*), *Orbicella* (formerly *Montastraea*) *annularis* species complex, *Montastraea cavernosa*, *Porites astreoides*, and other corals (principally massive species of *Diploria*, *Siderastrea*, and *Colpophyllia*).

Taxonomic data were available for at least some of the surveys from 32 of the 40 sites. The fates of different taxa varied considerably. Species that suffered the greatest proportional losses include most of the former ecologically dominant taxa on

Caribbean reefs, including *Acropora palmata* and *A. cervicornis*, branching *Porites* and *Madracis*, the *Orbicella annularis* species complex, and the large plate-like *Agaricia* species. However, most acroporid mortality occurred long before the first surveys at most of the sites. Species that declined the least include species that form massive colonies including the genera *Diploria*, *Siderastrea*, and some *Porites*. Shifts in taxonomic composition are analyzed further in the section on ordination analyses.

Timelines for reef locations with coral cover data for all three time intervals: Twenty-one of the reef locations (clusters of nearby reef sites) enumerated in Table 2 were surveyed at least once before 1984, from 1984 through 1998, and from 1999 to 2011 (Fig. 4, Table 5).

Long-term trends in coral abundance varied greatly among these 21 locations (Table 5) that are grouped into three contrasting patterns of change to highlight their different histories (Fig. 14). Trajectories for nine of the 21 locations (Belize, Costa Rica, Florida Dry Tortugas, Jamaica, and St. Thomas) resemble a hockey stick with steep declines in coral cover between intervals 1 and 2 followed by little change thereafter (Fig. 14A). Proportional losses in coral cover between 1984 and 1998 ranged from 58 to 95% (average 73%). Coral cover at five additional locations (Florida Upper Keys, St. Croix, St. John, Veracruz Mexico, and Vieques Puerto Rico) exhibited comparable

TABLE 4. Geographic locations, depths, year span, and net changes in coral cover for detailed timelines for 40 reefs. ¹ T. P Hughes original site, now a CARICOMP site.

Place	Reef	Depth (m)	Year span	Start coral cover (%)	End coral cover (%)	Net change (%)
Barbados	Bellairs	3-15	1974-2006	37	15	-23
Belize	Carrie Bow	13	1978-2012	33	11	-22
	Hol Chan	8-11	2005-2012	15	16	+1
Bermuda	Hog Breaker	8	1993-2007	20	20	0
	Twin Breaker	10	1993-2007	25	20	-5
Bonaire	Karpata	10	1974-2008	63	31	-32
	Karpata	20	1974-2008	71	8	-63
BVI – Tortola	Guana Island	8-9	1992-2012	18	14	-4
Cayman Islands	Little Cayman	10-20	1992-2011	28	25	-4
Colombia	Santa Marta	10	1994-2005	33	32	-1
Costa Rica	Cahuita	4-10	1981-2011	40	18	-22
Curaçao	CARMABI Buoy 1	10	1973-2008	36	12	-24
	CARMABI Buoy 1	20	1973-2008	34	10	-24
	CARMABI Buoy 2	10	1973-2008	37	29	-8
	CARMABI Buoy 2	20	1973-2008	35	17	-18
Florida – Upper Keys	Carysfort	0-2	1975-2011	37	3	-34
	Carysfort	14-16	1975-2011	43	4	-39
Florida – Dry Tortugas	Bird Key	13-15	1975-2011	48	10	-38
Jamaica	West	1-18	1977-2012	40	8	-32
	Montego Bay	3-15	1977-2005	47	19	-28
	Rio Bueno	9-18	1978-2010	60	27	-33
	Discovery Bay ¹	9	1977-2011	61	11	-50
	Northeast	1-17	1977-2003	47	12	-35
	Port Royal	5-10	1977-2011	25	5	-20
Mexico	Leeward Cozumel	1-20	1984-2011	25	14	-11
Panama	SE Bastimentos	1	1999-2011	32	24	-8
	SE Bastimentos	9	1999-2011	35	28	-7
	San Blas, Sail Rock	4	1993-1998	18	28	+10
Puerto Rico	La Parguera	10	1994-2012	40	26	-13
Tobago	Bucco Reef	10	1994-2012	24	19	-5
USA – Gulf Mexico	East Flower Garden Bank	20-21	1980-2010	65	55	-10
USVI – St. Croix	Buck Island	7-14	1989-2011	25	6	-19
	Salt River	9-20	1982-2010	25	6	-19
USVI – St. John	Newfound	8	1990-2011	22	6	-16
	Tektite	13	1987-2010	32	28	-4
	Yawzi	13	1987-2011	45	7	-38
USVI – St. Thomas	Black Point	9-14	1979-2010	25	13	-12
	Flat Cay	9-13	1979-2010	65	15	-50
Venezuela – Morrocoy	Cayo Sombrero	5-13	1996-2011	55	39	-16
Venezuela – Los Roques	Dos Mosquises Sur	12	1999-2012	44	25	-19
Summary			1973-2012	38	18	-20

proportional decline (50-80%, average 65%) that was spread out more evenly among the three time intervals (Fig. 14B). The third group of seven locations exhibited greater overall stability, although overall mean abundance among these locations differed nearly three fold (Fig. 14C). Coral cover at

six of these locations including Barbados, Bonaire, Curaçao, Flower Gardens Bank, San Blas, and Santa Marta declined by just 4-35% over the three time intervals and increased at Bermuda by 35% (Fig. 14C). However, the increase at Bermuda is largely due to more comprehensive sampling of

TABLE 5. Changes in coral and macroalgal cover at the 21 long-term data locations indicated by large yellow circles in Fig. 4. Coral cover data are available for all three time intervals at all 21 locations. Macroalgal data are available for all three of the time intervals for just 9 of the 21 locations. Percent change over the three intervals is expressed as both the absolute change in cover and the proportional change (cover in time interval 3 minus cover in interval 1/cover in interval 1). The pattern of change refers to Fig. 14. P-values are the result of post-hoc comparison of means between the 1st and 2nd time interval and the 2nd and 3rd time interval with significance at the 95% level in bold.

Label	Location	Coral cover (%)					Macroalgal cover (%)					Change type		
		1970 - 1983	1984 - 1998	1999 - 2011	Abs change	Prop. loss	1970 - 1983	1984 - 1998	1999 - 2011	Abs. change	Prop. loss	1-2	2-3	
6	Barbados Leeward	26.9	14.7	20.9	-6.0	-0.22	10.5	22.4	6.1	-4.4	-0.4	0.48	0.08	C
11	Belize Central Barrier	33.8	14.1	17.3	-16.5	-0.49	2.8	36.9	43.7	+40.9	+14.6	0.18	0.90	A
16	Bermuda	19.4	21.9	28.8	+9.5	+0.35	NA	8.3	10.6			0.54	0.99	C
56	Bonaire Leeward	54.1	35.2	35.2	-18.9	-0.35	1.0	6.1	15.8	+14.8	+14.8	< 0.01	0.10	A,C
22	Colombia Santa Marta	32.5	30.2	31.8	-0.7	-0.02	19.8	19.8	NA			0.84	0.93	C
23	Costa Rica Cahuita	40.4	11.2	16.1	-24.3	-0.60	NA	NA	NA			< 0.01	0.79	A
28	Curaçao Southwest	43.0	34.6	35.5	-7.5	-0.17	0.1	4.4	5.0	+5.0	+49.0	0.64	0.05	C
84	Florida Upper Keys	32.7	21	6.4	-26.2	-0.80	NA	15.0	15.2			0.06	0.03	B
79	Florida Dry Tortugas	28.9	12.0	10.0	-18.9	-0.65	NA	NA	20.5			< 0.01	0.99	A
42	Jamaica Montego Bay	36.3	8.4	15.3	-21.0	-0.58	NA	56.8	66.4			< 0.01	0.68	A
43	Jamaica North Central	44.6	10.8	14.4	-30.2	-0.67	8.2	57.8	43.6	+35.4	+4.3	< 0.01	0.99	A
44	Jamaica Northeast	47.0	2.5	10	-37.1	-0.78	NA	NA	45.9			< 0.01	0.20	A
46	Jamaica Port Royal Cays	24.9	2.7	2.6	-22.3	-0.90	NA	NA	45.0			< 0.01	0.97	A
47	Jamaica West	40.3	6.5	9.0	-31.3	-0.78	NA	NA	70.3			< 0.01	0.62	A
54	Mexico Veracruz	34.1	28.0	17.2	-16.9	-0.50	NA	NA	NA			0.70	0.18	B
65	Panama San Blas	39.2	19.1	30.9	-8.3	-0.21	NA	69.3	NA			0.06	0.35	C
71	Puerto Rico Vieques	42.6	22.8	12.6	-30.0	-0.70	1.9	4.1	13.5	+11.6	+6.1	0.54	0.80	B
80	USA East Flower Garden Bank	57.5	51.1	55.1	-2.4	-0.04	NA	NA	NA			0.34	0.31	C
85	USVI St. Croix	23.7	20.7	9.1	-14.6	-0.62	1.6	7.2	10.9	+9.3	+5.8	0.28	0.17	B
88	USVI St. John	34.1	26.1	11.8	-22.3	-0.65	0.7	12.7	30.3	+29.6	+42.3	0.19	< 0.01	B
86	USVI St. Thomas	32.5	4.6	13.9	-18.6	-0.57	1.5	NA	35.3	+33.8	+22.5	0.01	0.87	A
	Summary	36.6	19.0	19.2	-17.4	-0.51	2.3	15.3	22.8	+19.6	+17.7	< 0.01	0.53	

a wider diversity of habitats in recent years rather than an increase at earlier monitored sites.

The geographic distribution of the three different patterns of change overlap broadly throughout the wider Caribbean but there are also differences (Fig. 14D). Locations that exhibited the hockey stick pattern of dramatic early decline followed by no

change (orange circles) are distributed very widely from Florida in the north to Costa Rica in the south and from Belize in the west to St. Thomas in the east. Locations where coral cover declined progressively through all three intervals (blue squares) are more constrained in latitude and distributed in a band from Veracruz in the west to Vieques, St. Croix, and St. John in the east. Lastly, locations that

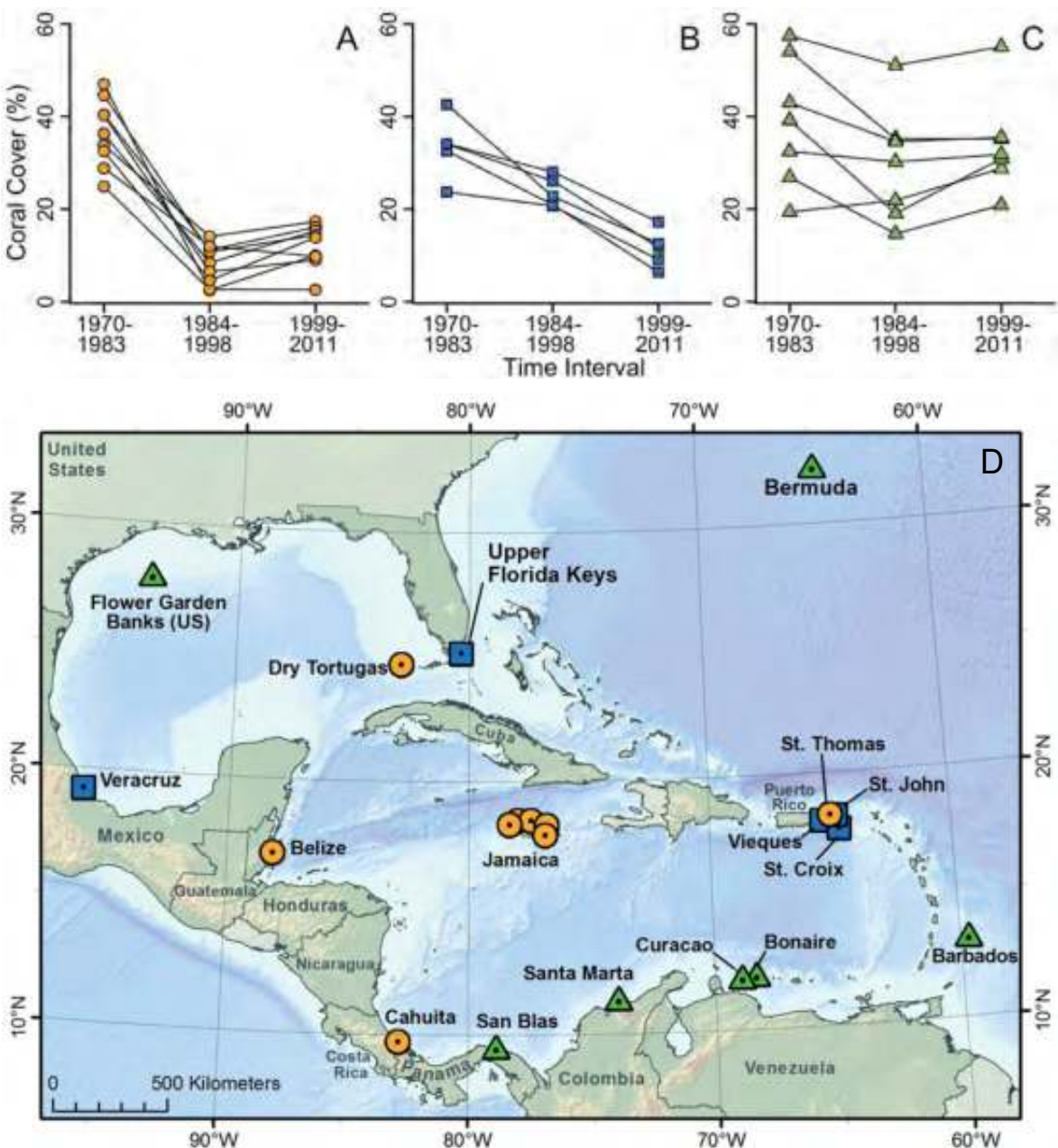


FIGURE 14. Disparate trajectories of coral cover at 21 mapped locations for which data for coral cover are available for all three time intervals (1 = before 1984, 2 = 1984-1998, 3 = 1998-2011). Values are means of percent coral and macroalgal cover averaged over all the data for each location within each time interval. Locations are grouped by eye into three general categories based on the total amount of change in coral cover over the three time intervals and the tempo of change. (A) hockey stick pattern of 49-90% decline between intervals 1 and 2 followed by little or no change. (B) approximately constant and continuous decline ranging from 50-80% over all three intervals. (C) comparative stability of +35% to -35%. Note that the trajectory for Bonaire is a hybrid of patterns A and C. (D) map showing geographic distribution of the three patterns of change. For further details see text.

TABLE 6. Summary statistics for PCA analyses of coral and macroalgal community composition.

	Percent variation explained			
	PCA 1	PCA 2	PCA 3	sum
Coral + Macroalgae, 21 locations	42.1	17.9	11.8	71.8
Coral + Macroalgae, all locations	41.3	12.7	11.1	65.1
Coral only, 21 locations	24.9	21.8	16.2	62.9
Coral only, all locations	21.8	17.2	13.5	52.5

exhibited the greatest stability in coral cover (green triangles) are concentrated in the extreme south and north of the wider Caribbean plus Bermuda.

The disparate reef histories in Fig. 14 clearly demonstrate the folly of attempting to understand the causes of coral reef decline for the entire Caribbean as a single ecosystem, an approach that ignores the enormous heterogeneity in environments and history of human and natural disturbance among different reef locations. This is even more apparent in timelines of coral cover compiled for individual reef sites (Table 4, Appendix 2). Moreover, locations that suffered the greatest proportional loss in coral cover over the three time intervals (cover interval 1- cover interval 3/cover interval 1) also suffered the greatest absolute loss in cover (cover interval 1-cover interval 3) (Fig. 15). The strong correlation between proportional and absolute decline further strengthens the conclusion that trajectories of change at different locations reflect their unique histories of events rather than some pervasive force throughout the entire wider Caribbean.

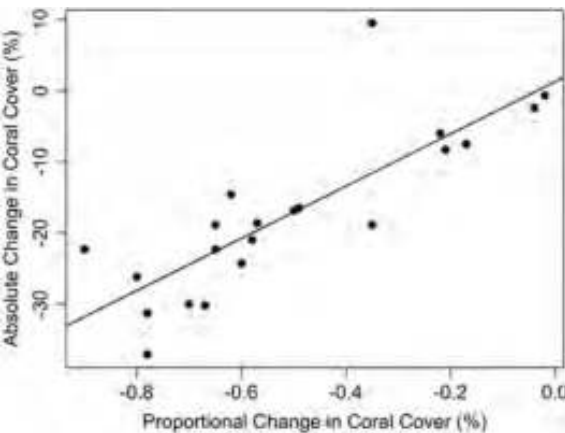


FIGURE 15. Absolute change in percent cover of corals from before 1984 to after 1999 versus the proportional change in coral cover ($R^2 = 0.65$, $p < 0.01$).

Ordination of coral and macroalgal community composition:

We used PCA and MDS to investigate patterns of change in community composition of corals and macroalgae for the entire dataset and the 21 reef locations in Table 5 (Fig. 16-17). Coral taxa were grouped based on an analysis of their average abundance and frequency of occurrence in the overall dataset to minimize zero occurrences in the ordination matrix. The resulting nineteen taxa include: *Acropora cervicornis*, *Acropora palmata*, *Agaricia tenuifolia*, other *Agaricia*, *Colpophyllia*, *Diploria*, *Eusmilia*, *Helioseris*, *Madracis*, *Meandrina*, *Millepora*, *Montastraea cavernosa*, *Mycetophyllia*, *Orbicella* [formerly *Montastraea*] “*annularis*” complex, *Porites astreoides*, other (overwhelmingly branching) *Porites*, *Siderastrea*, *Stephanocoenia*, and other corals. Macroalgae were considered as a single taxon.

Results are presented here for the PCA analyses only. The best results are for the 21 locations with data for coral and macroalgae in the same analysis in which the first three principal components explain more than 70% of the total variance. (Table 6, Fig. 16A-B). The strongest separation along PCA 1 is between macroalgae versus corals. PCA 2 accounts for an additional 20% of the variance reflecting the opposite trends in occurrence of branching *A. palmata* and the *Orbicella annularis* species complex. The same analysis based on all the localities produces a similar pattern but explains less of the total variability (Fig. 16C-D), a difference we attribute to the lack of consistency of locations among time intervals due to very limited sampling at most of the locations in Table 2 and greater variety in reef environments compared to the more restricted analysis.

Ordinations based only upon coral taxa without macroalgae yielded consistently poorer results, underlining the fundamental importance of the phase shift between corals and macroalgae that dominates patterns of change (Fig. 17).

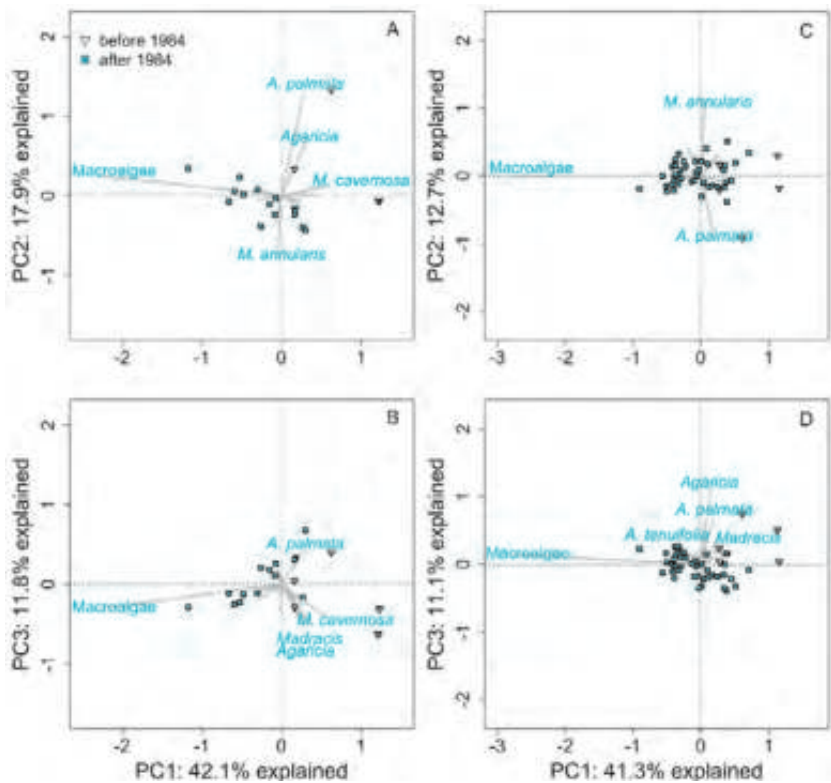


FIGURE 16. Principal components analysis of coral taxa and macroalgae. (A-B) PCA based on all available data for the 16 of 21 locations in Table 5. (C-D) PCA based on all available data for the 44 locations with coral data from more than a single year in Table 2.

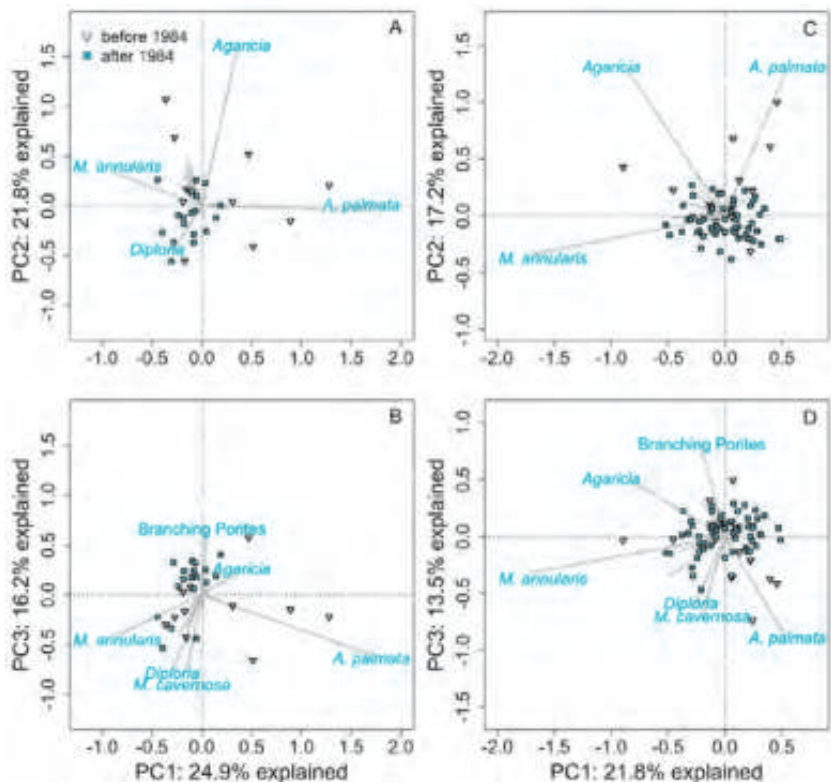


FIGURE 17. Principal components analysis of coral taxa without macroalgae. (A-B) PCA based on all available data for 18 of the 21 locations in Table 5. (C-D) PCA based on all available data for the 64 locations with coral data available at a fine taxonomic level.

2b. EXTREME DECLINE OF FORMERLY DOMINANT SPECIES

Three taxa of formerly great ecological significance on Caribbean reefs suffered massive declines up to several decades before the first quantitative surveys at most of the 90 locations in Table 2. Losses were so great that the species are virtually ecologically extinct; meaning they no longer play any significant ecological role in determining the distribution and abundance of surviving species. Understanding the subsequent decline of Caribbean reefs hinges upon a clear understanding of the magnitude of these early changes that in most places have hardly left a trace.

Decline of *Acropora palmata* and *A. cervicornis*

Acropora palmata and *A. cervicornis* were among the most abundant and ecologically dominant corals on Caribbean reefs in depths down to 20 m for the last one million years until the 1970s and 1980s (Goreau 1959; Geister 1977; Adey 1978; Jackson 1992, 1994; Pandolfi 2002; Pandolfi and Jackson 2001, 2006). Distribution and abundance were highly variable. Nevertheless, the former ecological dominance of *Acropora* is obvious from the composition of Holocene and Pleistocene reef rock, the coral fraction of which is 80-90% *Acropora* by volume in the majority of shallow-water sections (Mesoella 1967; Macintyre and Glynn 1976; Lewis 1984; Liddell et al. 1984; Jackson 1992 and references within; Pandolfi and Jackson 2001, 2006; Aronson and Precht 2001).

Both species experienced intense mortality due to White-Band Disease (WBD) since the mid to late 1970s until today (Gladfelter 1982; Porter and Meier 1992; Aronson and Precht 2001; Porter et al. 2001; Patterson et al. 2002; Weil and Rogers 2011). Hurricanes and outbreaks of predators also devastated acroporids in Jamaica and the USVI in the 1980s (Knowlton et al. 1981, 1990; Woodley et al. 1981; Rogers et al. 1991; Rogers and Miller 2006), and there is strong paleontological evidence for die-offs several decades earlier in Barbados (Lewis 1984), Bocas del Toro, Panama (Cramer et al. 2012), and more broadly throughout the region (Jackson et al. 2001).

Unfortunately, there are remarkably few quantitative data on the abundance of either species until they were already greatly diminished by disease, a

spate of hurricanes in close succession, and degrading water quality to be reviewed in the next section. To address this, we compiled a very large qualitative database on the occurrences of both species back into the 19th century to supplement the quantitative data (Appendix 3). The proportion of reef sites with presence and dominance of *Acropora palmata* and *A. cervicornis* was computed for the time period from 1851-2012. Data include qualitative and quantitative information from the primary peer-reviewed scientific literature, government reports, and less commonly historical literature as well as quantitative data received directly from contributors to this study and compiled in the larger GCRMN database. Quantitative data include percent cover for either *Acropora* species, while qualitative data include presence/absence and relative abundance data, as well as descriptions of relative abundance categories (Appendix 3). Data are primarily from underwater field surveys, although a small number are from boat-based observations and high-resolution aerial photographs. Data from the literature were extracted from texts, tables, figures, and maps.

Only data from “reef crest” and “midslope” reef zones were included in the analysis. Generally, reef crest data spanned 0-6 m water depth and midslope data spanned between 6-20 m, as 6 m was the depth at which dominance typically shifted from *A. palmata* to *A. cervicornis* in the quantitative data. However, the distinction between reef crest and midslope was made on a reef site-by-site basis, taking into account additional information on reef zone or reef morphology, if available. For some locations, the cutoff was closer to 10 m, the same value used in Jackson et al. (2001). Data were not included if determination of the reef zone could not be made. Data were recorded at the reef site level and computed by averaging over replicates within the same reef site and reef zone. In total, 1,855 reef sites from 67 locations were compiled for the reef crest zone and 4,543 reef sites from 80 locations for the midslope zone. These included locations that were not represented in the master GCRMN quantitative database (Table 2).

Results are presented in Fig. 18. Sample size is small before 1950, and the locations represented in various time bins are not consistent.

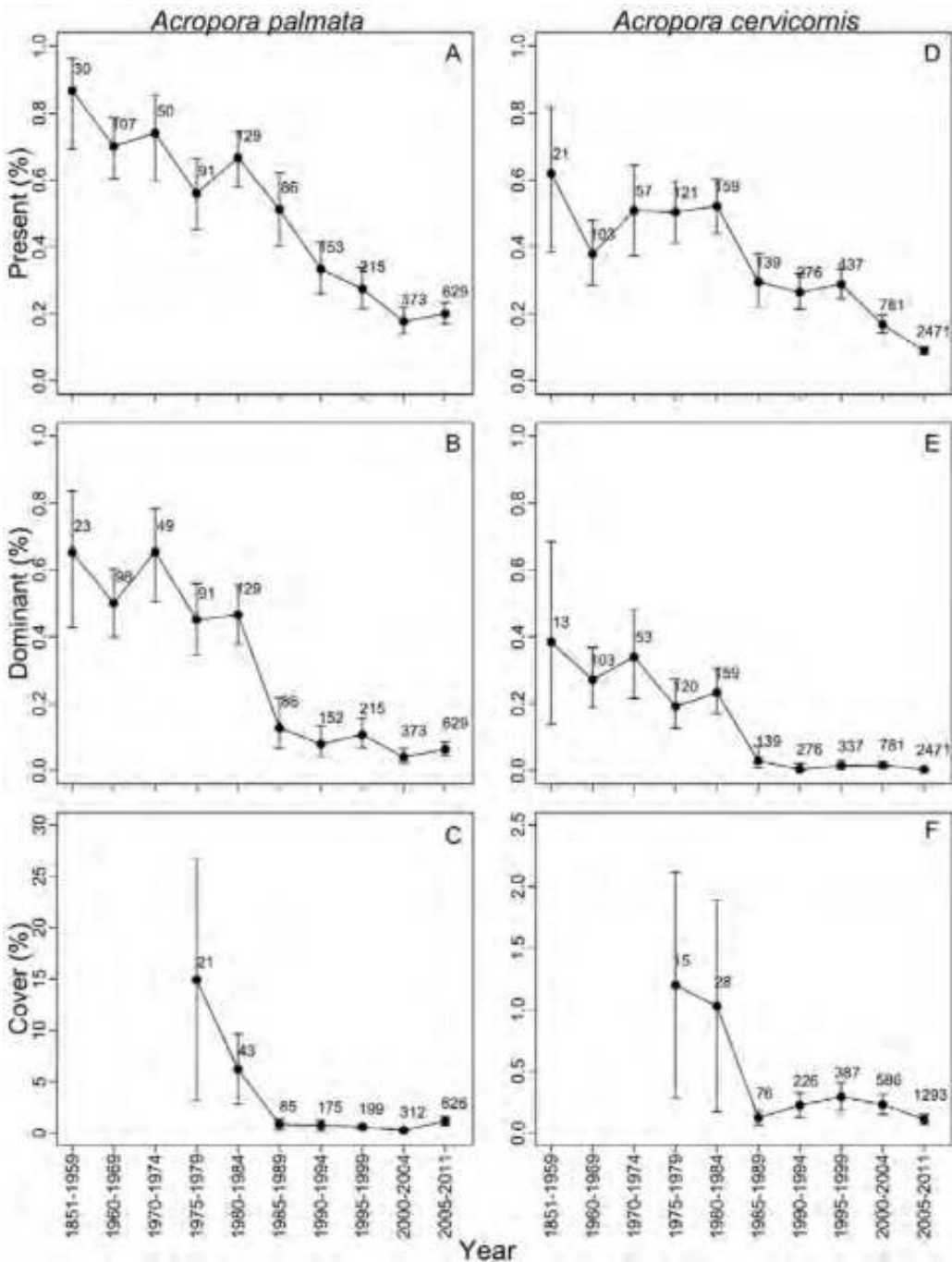


FIGURE 18. Decline in *Acropora palmata* and *A. cervicornis* throughout the wider Caribbean region based on qualitative and quantitative data. (A) frequency of occurrence of *A. palmata*; (B) frequency of reefs at which *A. palmata* was described as the dominant coral; (C) changes in percent cover recorded in the GCRMN quantitative database; (D) frequency of occurrence of *A. cervicornis*; (E) frequency of reefs at which *A. cervicornis* was described as the dominant coral; (F) changes in percent cover recorded in the GCRMN quantitative database. Sample size (numbers of sites) indicated adjacent to points. Confidence intervals are 95% binomial intervals for A, B, D, and E and standard errors for C and F.

Nevertheless, the data confirm the remarkably great abundance of both species before the 1970s. *Acropora palmata* was present at more than 80% of all areas surveyed in depths less than 10 m throughout the wider Caribbean region and was recorded as “dominant” at 60% of these

localities Fig. 18 A-C. The data also suggest that the decline in *A. palmata* occurrence and dominance began in the 1960s in accord with the paleontological data (Lewis 1984; Cramer et al. 2012). The patterns for *A. cervicornis* are similar to *A. palmata* (Fig. 18D-F). The species was

present at 60% of all localities surveyed before 1959 and dominant at nearly 40% of them. As for *A. palmata*, there is a suggestion that dominance began to decline before the 1970s but there are less data than for *A. palmata*. Quantitative data are extremely sparse showing a maximum average percent cover of just over 1% although some reefs were still blanketed by about 50% cover, emphasizing the dearth of quantitative data before the late 1980s.

Decline of *Diadema antillarum*

Diadema antillarum was variably abundant on Caribbean reefs until 1983 when it rapidly suffered mass mortality from an unidentified pathogen throughout its range in the tropical western Atlantic (Lessios et al. 1983; Lessios 1988). Reported densities before the die-off ranged from a low of about 1/m² to a spectacular 90/m² in a harbor at Discovery Bay Jamaica. Hughes et al. (2010) compiled all the available data from the literature for trends in *Diadema* abundance since the earliest quantitative surveys to present. We supplemented their analysis with additional data from the GCRMN database with essentially similar results (Fig. 19). Average density throughout the region was about 8-10/m², declining to near zero between 1983 and 1984. Average density remained extremely low throughout the second time interval (1984-1998), and then rose almost imperceptibly during the third period. However, some locations have densities today back up to 3-5/m² (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Idjadi et al. 2010; Vardi 2011).

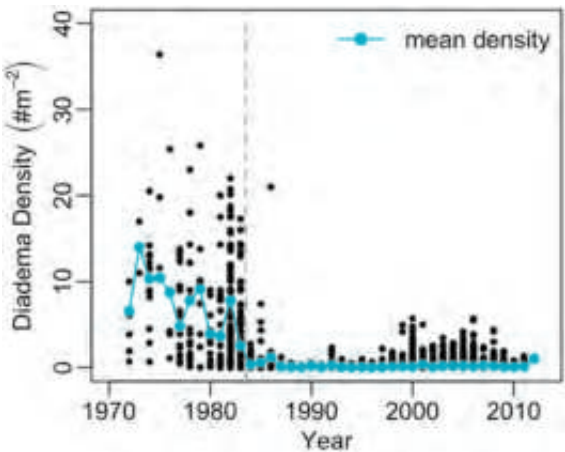


FIGURE 19. Abundance of *Diadema antillarum* throughout the wider Caribbean from 1972 to 2012. Densities of > 25 /m² before 1983 are not shown and are not included in average densities. Studies that intentionally surveyed aggregations were not included.

Parrotfish abundance and biomass

Reef fishes were overfished before the middle of the 20th century throughout large areas of the Caribbean including especially Jamaica and the USVI (Duerden 1901; Thompson 1945; Randall 1961, 1963; Munro 1983; Hughes 1994; Hay 1984; Jackson 1997). This was decades before the first underwater quantitative surveys in the late 1970s and 1980s. Reef fishes were still reported to be abundant at many remote localities such as the Belize Barrier Reef (Lewis and Wainwright 1985; Lewis 1986), but the once large schools of large bodied groupers and parrotfishes had mostly disappeared. Fishing prior to the 1970s was mostly artisanal using small nets and fish traps. Parrotfish were not specifically targeted but their wide bodies made them particularly vulnerable to traps (Johnson 2010).

We examined parrotfish abundance since 1988 in two ways. In the first case, we compiled all the quantitative data on parrotfish biomass in the GCRMN database after the year 2000 to examine the frequency distribution of biomass (Table 2; Fig. 20). Mean parrotfish biomass taking into account differences among locations and datasets was only 14g/m², a small fraction of the highest Caribbean value recorded of 71 g/m² and an even smaller percentage of their abundance on protected Indo-Pacific reefs (Sandin et al. 2008a).

Time series of parrotfish biomass longer than ten years are available for only three locations at St. John USVI, Guadeloupe, and Bonaire (Fig. 21).

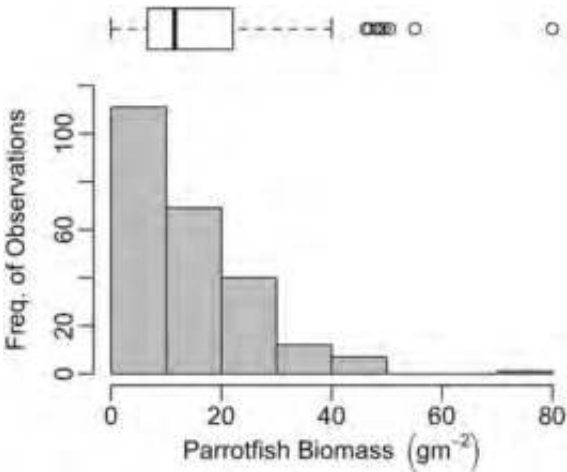


FIGURE 20. Frequency distribution of parrotfish biomass based on all available data after the year 2000 in the GCRMN database (1988-2012) with box plot reflecting the median and the first and third quantiles and dots for outliers.

Values at St. John have been extremely low, hovering around 5-10 g/m² since the beginning of the surveys in 1988 in accordance with Randall's (1961) much earlier work in the 1950s when he observed the USVI were already severely overfished (Fig. 21A). In contrast, parrotfish biomass at Guadeloupe also started off at around 10 g/m², but has since gradually increased for unknown reasons to between 25-30 g/m² (Fig. 21B). Bonaire exhibits a strikingly different pattern (Fig. 21C). Parrotfish biomass in 2003 was similar to the highest recorded in the Caribbean (71 g/m²) but has since plummeted to less than 30 g/m² due to recent targeted fishing on parrotfishes (Fig. 24C; Steneck and Arnold 2009; Steneck et al. 2011).

3. ANTHROPOGENIC DRIVERS OF CORAL REEF DEGRADATION

The ultimate driver of environmental degradation is human population growth coupled with inevitable increases in resource consumption, pollution, and habitat degradation as humanity clamors to feed, clothe, and satisfy 7 billion people and counting (Meadows et al. 1972; Vitousek et al. 1997; Wackernagel et al. 2002). But population alone is seldom a good predictor of environmental condition because of enormous disparities in consumption, cultural traditions, and the ways people exploit, pollute, and directly physically impact their natural environment.

Another major difficulty in deciphering cause and effect is the common failure to distinguish between potential drivers of coral decline (overpopulation, overfishing, coastal pollution and development, rising temperatures due to the burning of fossil fuels, introduced species, etc.) and their effects (increases in macroalgae, coral bleaching, coral disease) (Hughes et al. 2010). This problem is especially vexing in the case of coral diseases that have exploded since the first reports of their occurrence in the 1970s (Antonius 1973; 1977; Gladfelter 1982).

Coral diseases have taken a dreadful toll and it is easy to forget that their sudden emergence is almost certainly the result of some combination of anthropogenic stressors (introductions of exotic pathogens, eutrophication, warming, increases in macroalgae, etc.) rather than a natural force. Nevertheless, because of their great and increasing importance, we have treated coral diseases separately in section 3f. A similar confusion exists for the role of hurricanes that are natural phenomena but have been hypothesized to have increased in occurrence and intensity due to climate change. This postulated increase has been blamed for the failure of reefs to recover from the storms. We therefore treat the role of hurricanes separately in Section 3g.

Here we attempt to identify the major drivers of Caribbean coral reef decline by analyzing different anthropogenic stressors one at a time. The results are obviously a work in progress, but we believe they are remarkably clear in identifying the major factors responsible for reef degradation to date and ways in which the nature of stresses on Caribbean reefs are likely to change over the next few decades. Future analyses for publication in

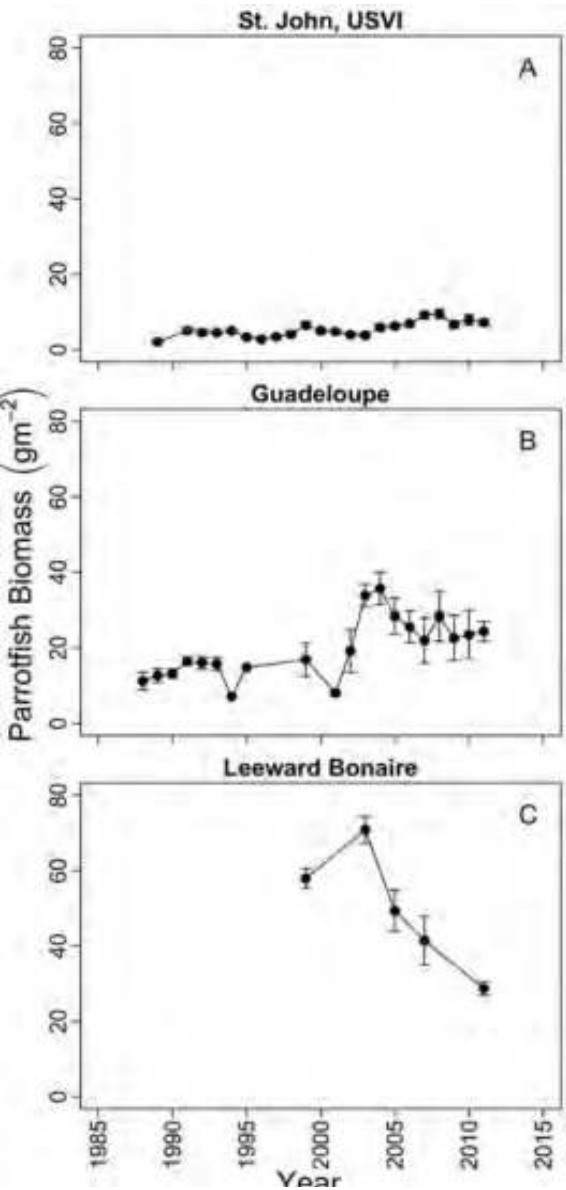


FIGURE 21. Trends in parrotfish biomass since 1988 at (A) St. John, (B) Guadeloupe, and (C) Bonaire. Error bars represent one standard error.

the scientific literature will examine all of the drivers together by multivariate analysis.

3a. POPULATION DESITY OF RESIDENTS AND VISITORS (TOURISTS)

We compiled data from the World Wide Web on the average numbers of residents and visitors per year over the past decade at 34 and 29 Caribbean reef locations respectively (Table 7). Considerable effort was invested in locating data for coral reef regions and not for entire countries, as has been the general practice for studies of the impact of people on coral reefs. It is meaningless to compare an ecological metric such as coral cover for an archipelago like Los Roques Venezuela to the entire population of

Venezuela, or the condition of the Florida Keys to the population of the entire State of Florida. In general, data for numbers of residents was more forthcoming than for visitors, and in several cases numbers of visitors were combined for two or more different locations such as St. Thomas and St. John because of the lack of an international airport on St. John. Population densities were calculated for land area rather than reef area because the topographic data for land area are more reliable and precise due to satellite mapping. In contrast, published estimates of reef area commonly vary several-fold for the same location because of different definitions of what constitutes a reef and different technologies and methods of observation employed.

TABLE 7. Numbers of visitors, residents, the numbers/km² and the most recent coral cover for 34 Caribbean locations plus Bermuda. Data compiled from the World Wide Web based on censuses of residents and tourist board and industry data for numbers of visitors. Most data are for the past five to seven years.

Name	Land area (km ²)	# of residents	Resident density (km ⁻²)	# of visitors	Visitor density (km ⁻²)	Total population	Total density (km ⁻²)	Coral cover (%)
Antigua and Barbuda	443	88000	199	842689	1902	930689	2101	3.8
Bahamas	13940	313312	22	1528000	110	1841312	132	11.7
Barbados	431	284589	660	575000	1334	859589	1994	15
Bermuda	53	67837	1280	306000	5774	373837	7054	38.6
Bocas del Toro	250	13000	52					13.6
Bonaire	294	14006	48	74342	253	88348	301	37.1
British Virgin Islands	153	23552	154	351408	2297	374960	2451	14.3
Cayman Brac	36	1500	42					14.4
Cayman Islands Total	259	56649	219	321650	1242	378299	1461	27
Corn Islands	13	6626	510	50000	3846	56626	4356	24.4
Cozumel	484	79535	164	4000000	8264	4079535	8429	12.1
Curaçao	444	141766	319	419621	945	561387	1264	31.5
Dominica	724	73126	101	354189	489	427315	590	9
Florida Upper Keys	59	19990	339	1185213	20088	1205203	20427	6.1
Grand Cayman	197	56949	289					30.7
Grenada	344	110000	320	360220	1047	470220	1367	12.8
Guadeloupe	1628	452776	278	693000	426	1145776	704	18.6
Kingston Harbor	1645	1184386	720	226164	137	1410550	857	4.7
Little Cayman	26	200	8					24.5
Los Roques	41	1800	44	70000	1707	71800	1751	31
Florida Lower Keys	272	67883	250	2205047	8107	2272930	8356	10.3
Martinique	1128	436131	387	487359	432	923490	819	17.4
Middle Keys	25	10255	410	254585	10183	264840	10594	8
Montego Bay Jamaica	595	184662	310	863214	1451	1047876	1761	19.4
San Andrés, Colombia	57	75000	1316	377619	6625	452619	7941	12.6
San Blas	337	15541	46					30.9
St Ann Jamaica	1213	173232	143	895296	738	1068528	881	19.6
St Bart	21	8902	424	200000	9524	208902	9948	10.8
St Croix	215	50601	235	236000	1098	286601	1333	4.7
St Kitts Nevis	261	50726	194	636924	2440	687650	2635	11.1
St Lucia	617	174000	282	931222	1509	1105222	1791	10.1
St Thomas	81	51634	637	2040900	25196	2092534	25834	13.6
St. Vincent and Grenadines	389	120000	308	199753	514	319753	822	19.5
Tobago	300	60874	203	450000	1500	510874	1703	19.1

Population densities of residents varied 165-fold, from a low of 8 persons/km² at Little Cayman to a high of 1,316/km² at San Andrés Colombia with 24 of the locations between 100-1000/km² (median = 264/km²). Variations in numbers of visitors per year are even more extreme, ranging 229-fold from 110 persons/km² in the Bahamas to an astounding 25,196/km² at St. Thomas. Seventeen of the 29 locations have between 1001 to 10,000 visitors/km²/year (median = 1500/km²/year). Nine of the locations had less than 1000 visitors/km² and 2 have more than 20,000/km².

Coral cover is plotted against the density of residents and annual density of visitors in Fig. 22. We used 2 by 2 contingency table analysis explore the relationship between human population density and coral cover. Boundaries of the four quadrants were determined by median values of coral cover and by median densities of residents and tourists. Coral cover is significantly negatively correlated with both the density of residents ($N = 34$, $X^2 = 7.5$, $df = 1$, $p = 0.01$) and the density of visitors per year ($N = 29$, $X^2 = 5.99$, $df = 1$, $p = 0.01$). Moreover, all the locations with more than 2,635 visitors/km²/year have only 6.1 to 13.6% cover.

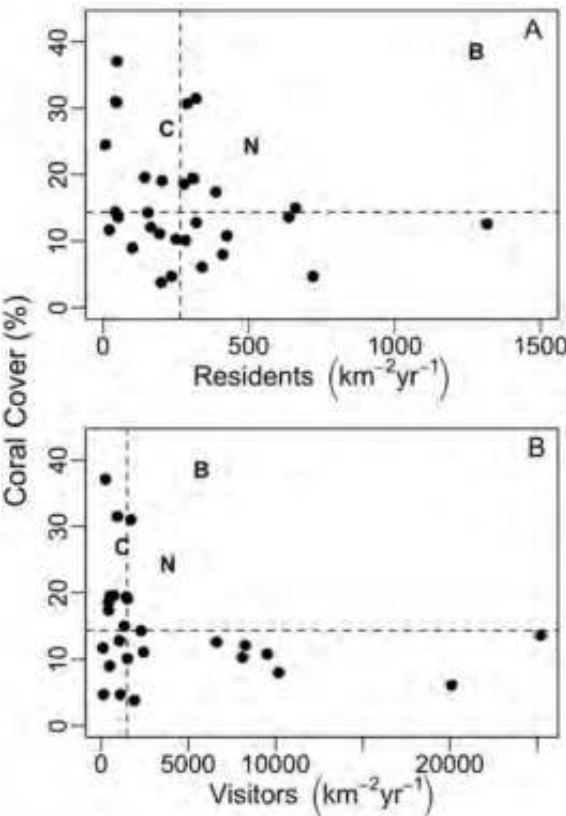


FIGURE 22. Coral cover in relation to human population density. (A) Numbers of residents/km², (B) numbers of visitors/km²/year. B = Bermuda, C = Cayman Islands, N = Corn Islands Nicaragua

Most tourists to Caribbean locations never get beyond the swimming pool to even see a coral reef so their impact on reefs is indirect. The most important indirect effects include runoff of sediments due to unregulated coastal development of roads and hotels, dredging harbors for yachts and gargantuan cruise ships, and nutrient pollution from runoff from golf courses and untreated or minimally treated sewage from hotels, cruise ships, and cesspits (see references in the section on water quality below). In this light, the remarkably high coral cover at Bermuda despite very high densities of visitors and residents is almost certainly a result of strongly enforced environmental and fisheries regulations as discussed below.

3b. FISHING

Artisanal coral reef fisheries are traditionally among the most important sources of protein and livelihood throughout Caribbean coastal communities (Jackson 1997; Hardt 2009). As populations have grown, however, overfishing has resulted in the widespread collapse of reef fish stocks with dire consequences not only for peoples' livelihoods and nutrition but also the ecological condition of coral reefs (Duerden 1901; Thompson 1945; Munro 1983; Hughes 1994; Hawkins and Roberts 2003). The ecological consequences of overfishing are complex and depend on a host of factors including the types of fishing gear employed, the variety of species exploited, trophic cascades, interactions with other kinds of human disturbance, and the unique environmental characteristics of different reefs (Jackson et al. 2001; Mumby et al. 2006, 2007, 2012; Estes et al. 2011). Nevertheless, overfishing is strongly correlated with ecological collapse of reef ecosystems as defined by decrease in coral cover and recruitment and increases in macroalgal abundance and coral disease (Hughes 1994; Sandin et al. 2008a).

The ecological consequences of overfishing in the Caribbean for coral reef communities are most clearly associated with reductions in the abundance and sizes of herbivores, most importantly parrotfishes, surgeonfishes, and sea urchins. Innumerable experiments have shown that exclusion or removal of these grazers results in explosive increases in the abundance of macroalgae (Randal 1961; Lewis 1986; Lirman 2001; Hughes et al. 2007) that potentially compete with corals in numerous ways discussed below. This is perhaps most obvious in

the Caribbean where the mass mortality of the sea urchin *Diadema antillarum* coupled with the overfishing of parrotfishes has resulted in the large increases in macroalgal abundance documented in the previous section (Table 3; Figs. 11-13).

Fishing pressure and the state of reef fish populations varied greatly among Caribbean reef locations in the 1970s due to a complex mix of fishing practices, economic well being, and cultural traditions that are beyond the scope of this report. Nevertheless, certain patterns are clear. Densely populated West Indian islands with a long tradition of sugar economies based upon slavery (e.g., Jamaica, Barbados, Hispaniola, the Virgin Islands, and most of the Lesser Antilles) developed labor intensive artisanal fisheries based largely on the use of fish traps and small nets that resulted in extreme overfishing by the early 20th century (Duerden 1901; Thompson 1945; Randall 1963; Munro 1983; Jackson 1997; Hawkins and Roberts 2003; Hardt 2009). In contrast, continental reefs along the coasts of Florida, Mexico, the Mesoamerican Barrier Reef, and northern South America were generally less densely populated and less heavily fished until the 1970s to 1990s (Goode 1887; Jackson 1997; McClenachan 2008).

***Diadema* abundance before 1984 as a proxy for historical fishing pressure**

Most of the historical information on overfishing is anecdotal or qualitative and there were very few hard scientific data to back them up until Mark Hay (1984) conducted a comparative study from 1980-1982 on the intensity of grazing by the sea urchin *Diadema antillarum* versus grazing by parrotfishes and surgeonfishes at several locations across the wider Caribbean. Densities of *Diadema* on eight heavily fished reefs ranged from 5-20/m² (median = 10) versus 0 to 8/m² (median = 1) on less fished reefs (Hay 1984, his Table 2, $F_{1,12} = 20.7, p < 0.01$).

Hay did not count herbivorous fishes but instead used strips of the seagrass *Thalassia testudinum* as standardized “baits” to measure rates of herbivory. Rates of consumption of *Thalassia* bait by fishes and *Diadema* were inversely proportional in relation to the extent of overfishing on the reefs. Fish consumption of bait on lightly fished reefs in Belize, Panama, Honduras, and a protected area in the US Virgin Islands was 5-10 times higher than on heavily overfished reefs in Haiti and the

US Virgin Islands. Consumption and abundance of *Diadema* showed the opposite pattern, with very little consumption on less fished reefs and high consumption exceeding that by grazing fishes on overfished reefs.

There is also considerable evidence from ecological surveys and from natural and manipulative experiments for intense competition for food between *Diadema* and grazing fishes, especially parrotfish. Abundance of *Diadema* and grazing fishes were inversely proportional across a depth gradient on reefs near Carrie Bow Cay in Belize (Lewis and Wainwright 1985). *Diadema* were most abundant in the high spur and groove habitat (4.3/m²) where the high habitat relief likely provided better protection from predators than less complex habitats. In contrast, parrotfish abundance was only 0.07/m², the lowest in any of the five reef habitats surveyed. *Diadema* abundance was extremely low (0.1 to 0.7/m²) in all the other reef zones where parrotfish abundance ranged from 0.09-0.32/m².

Hay and Taylor (1985) strengthened the evidence for strong competition between *Diadema* and parrotfish in two *Diadema* removal experiments at St. Thomas and St. Croix that were conducted just before the *Diadema* die-off occurred. Numbers of parrotfish at two control (non-removal) sites at St. Thomas were 0.02 and 0.04/m² versus 0.18/m² at the removal site (Kruskal-Wallis Test, $p < 0.05$). Similarly at St. Croix, there were 0.08 parrotfish/m² at the single control site versus 0.29/m² at the removal site (Kruskal-Wallis Test, $p < 0.05$). These patterns were confirmed by surveys before and after the die-off of *Diadema* within four reef zones at Tague Bay, St. Croix (Carpenter 1990b). Numbers of parrotfish increased 3.9-fold from 0.17/m² transect before the die-off to an average of 0.66/m² afterwards on the backreef and reef crest. Similar comparisons for the three forereef zones surveyed showed a 2.8-fold increase from 0.29 to 0.81 parrotfish/m² at 2 m; a 2.3-fold increase from 0.25 to 0.57/m² at 5 m; and a 4.1-fold increase from 0.17 to 0.67/m² at 10 m. All of these differences were significant by 1-way ANOVA at $p < 0.0001$.

Summarizing the above, Hay's (1984) study confirmed that overfishing on many Caribbean reefs occurred before the mass mortality of *Diadema* in 1983, a fact consistent with Jack Randall's (1961,

1963) pioneering investigations in the 1950s and all of the historical data (Duerden 1901; Thompson 1945; Munro 1983; Jackson 1997; McClenachan 2008; Hardt 2009). But this is difficult to document beyond Hay’s and the other specific study sites because there are virtually no quantitative survey data on the biomass of Caribbean herbivorous reef fishes prior to 1988 (Tables 1 and 2, Fig. 6).

What we can do, however, is to use the patterns of *Diadema antillarum* abundance prior to 1984 as a proxy for historical fishing pressure based upon (1) the well-documented inverse correlation between *Diadema* abundance and herbivorous fish abundance prior to the mass mortality of *Diadema* in 1983 (Ogden et al. 1973; Hay 1984, Lewis and Wainwright 1985), (2) the increase in herbivorous fish abundance after the die-off of *Diadema* in 1983 (Carpenter 1990a, b; Robertson 1991), and (3) Hay and Taylor’s (1985) *Diadema* removal experiments. Besides all of the above, we know of no evidence to suggest that *Diadema* abundance was not inversely proportional to fishing pressure. Thus the proxy relationship is robust.

Contrasting fates of reefs since 1984 in relation to historical fishing pressure

Data on *Diadema* density/m² before 1984 were available for 16 of the 21 reef locations in Table 5 and Fig. 14 (Table 8, Appendix 4). *Diadema* densities ranged from a low of 0.5/m² at San Blas, Panama to a high of 12.4/m² at the Port Royal Cays, Jamaica. There is a clear break in the values between reefs in San Blas, Bermuda, the Upper Florida Keys, Bonaire, Belize, Curaçao, and Cahuita Costa Rica (0.5/m² to 3.8/m², median = 1.5/m², classified here as “less fished” reefs) versus reefs in Barbados, Jamaica, and the US Virgin Islands (6.9/m² to 12.4/m², median -9.1/m², classified here as “overfished” reefs, t-test: t = 9.0, df = 13.6, *p* < 0.01). These values correspond closely with what is known qualitatively about fishing pressure at these locations before 1984 (Appendix 5).

We conducted a linear mixed-effects model analysis to compare median coral cover between “less fished” versus “overfished” reefs based on the density of *Diadema* at the 16 locations before the 1983 die-off (see methods section for model formulation). As expected, there was no significant correlation between coral cover at less fished and overfished

TABLE 8. Data for the analysis of the effects of historical and recent fishing pressure on coral cover for the 16 locations in Table 5 with *Diadema* data from before the die-off.

Label	Location	<i>Diadema</i> density (#/m ²)	Parrotfish biomass (g/m ²)	Long -term prob. hurricane	# of hurricanes since 1984	Coral cover since 2005 (%)
6	Barbados Leeward	11.2		0.06	0	15.0
11	Belize Central Barrier	1.7	7.2	0.06	3	15.0
16	Bermuda	0.6	21.9	0.12	4	38.6
56	Bonaire Leeward	1.5	32.3	0.02	0	37.1
23	Costa Rica Cahuita	3.8	39.8	0.00	0	18
28	Curaçao Southwest	3.0	15.2	0.02	0	31.5
84	Florida Upper Keys	1.2	20.3	0.15	2	6.1
42	Jamaica Montego Bay	7.1	4.6	0.08	3	19.4
43	Jamaica North Central	6.9	6.9	0.10	3	19.6
44	Jamaica Northeast	7.9	5.4	0.09	4	
46	Jamaica Port Royal Cays	12.4		0.05	3	4.7
47	Jamaica West	9.2	8.1	0.06	3	7.8
65	Panama San Blas	0.5	13.3	0.00	0	
85	USVI St. Croix	7.0	13.1	0.08	5	4.7
88	USVI St. John	9.1	8.3	0.11	5	10.1
86	USVI St. Thomas	9.8	11.4	0.12	3	13.6
	Mean	5.8	14.8	0.07	2.4	17.2

locations before 1984 (Fig. 23A; GLMM (generalized linear mixed model) $p=0.19$) because high *Diadema* abundance compensated for the low abundance of herbivorous fish. But this changed after the 1983 mass mortality of *Diadema* when median values of coral cover significantly diverged between less fished and overfished reefs (Fig. 23B-C; GLMM $p<0.01$). Similar results were found for coral cover since 2005 (Fig. 23D; GLMM $p=0.01$). There is also a significant difference between time periods 1 and 3 in the proportional loss in coral cover between “less fished” locations (median = -35%, range +35% to -80%) and

“overfished” locations (median = -65%, range -22% to -90%) ($F_{1,14} = 4.96, p = 0.04$). Comparisons between time periods 1 and 2 and 1 and 4 are not significant but all of the trends are in the same direction.

Data for macroalgae are too incomplete for meaningful statistical comparison of changes in macroalgal abundance between “less fished” and “overfished” reefs although the trends are consistently in the expected direction with two to three times higher macroalgal cover at locations that had been earlier overfished (Table 8, Fig. 23 D-E).

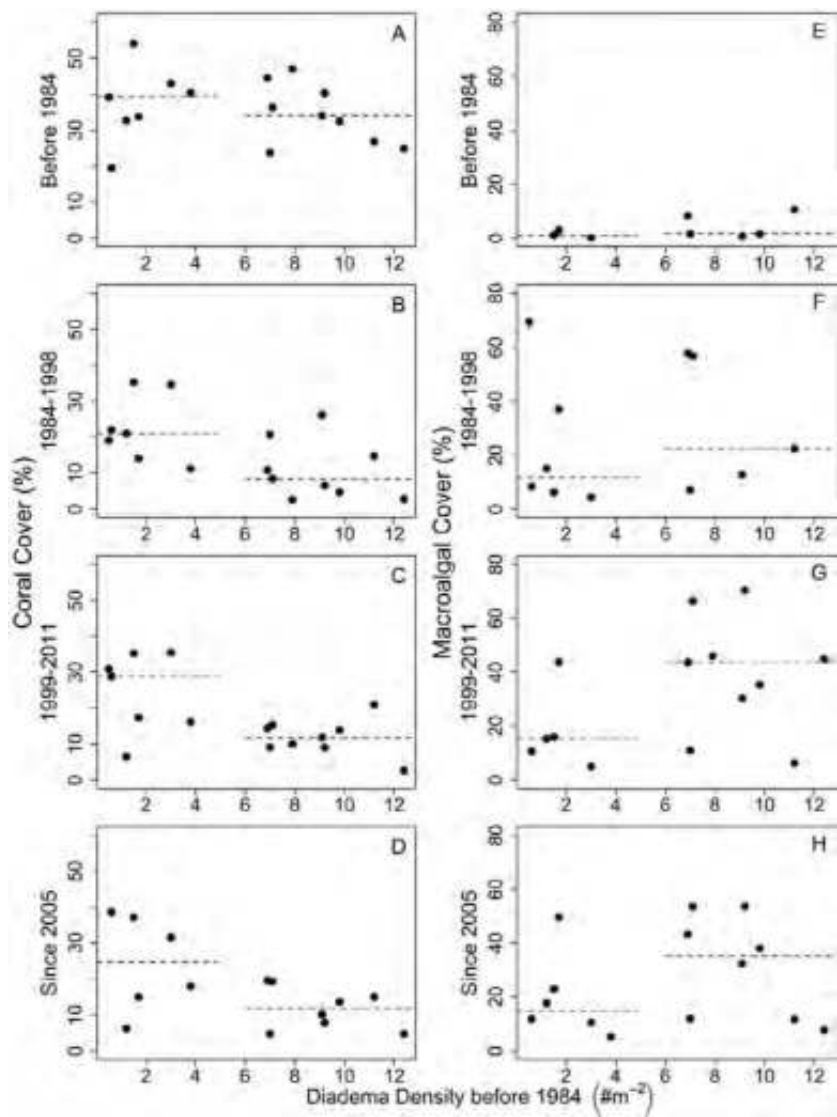


FIGURE 23. Percent coral (A-D) and macroalgal (D-E) cover in relation to the abundance of *Diadema antillarum* before the die-off in 1983 for the 16 reef locations in Table 8. (A) coral cover 1970-1983 (N = 16, median = 39.2/m² versus 34.1/m², $p = 0.19$), (B) coral cover 1984-1998 (N = 16, median = 21.0/m² versus 8.4/m², $W = 53, p < 0.01$), (C) coral cover 1999-2011 (N = 16, median = 28.8 versus 11.8, $p = 0.02$), and (D) coral cover since 2005 (N = 15, median coral cover 31.5/m² versus 10.1/m² $p = 0.01$). (E) macroalgal cover 1970-1983 (N = 8, median MA cover 1.0 versus 1.6%), (F) from 1984-1998 (N = 11, median MA cover = 11.7 versus 22.4%), (G) from 1999-2011 (N = 14, median MA cover = 15.2% versus 43.6%), and (H) since 2005 (N = 14, median MA cover = 14.8% versus 35.1%).

The role of parrotfish today

Further support for the harmful consequences of overfishing herbivorous fishes upon coral cover is apparent from the positive and negative correlations on reefs today between the abundance of grazing parrotfishes and the percent cover of corals and macroalgae for all of the locations in Table 9 with paired data (Fig. 24). The non-parametric correlation is significant for coral cover versus parrotfish (Fig. 24A) but not for macroalgae versus parrotfish due to the smaller sample size for macroalgae and considerably greater scatter in the data (Fig. 24B). Results were opposite for the smaller dataset of 16 reefs (Fig. 24 C-D).

Generally speaking, the few reefs in the upper quartile of parrotfish biomass today (locations

with $> 15.6\text{g/m}^2$) have significantly more coral than reefs where parrotfish are less abundant ($t = 2.24$, $df = 60.7$, $p = 0.03$). This is especially evident when the relationship between parrotfish biomass and macroalgal cover is compared with a linear-mixed model between locations that had been overfished before 1984 (high *Diadema* abundance) and those that were not (Fig. 24D). All of the historically overfished localities have low parrotfish biomass and low coral cover (Fig. 24C), and macroalgal cover is significantly greater than at less fished locations ($t = -2.12$, $df = 36.2$, $p = 0.03$), and strongly negatively correlated to parrotfish abundance (Fig. 24D, $\beta = -1.14$, $SE = 0.40$, $p < 0.01$).

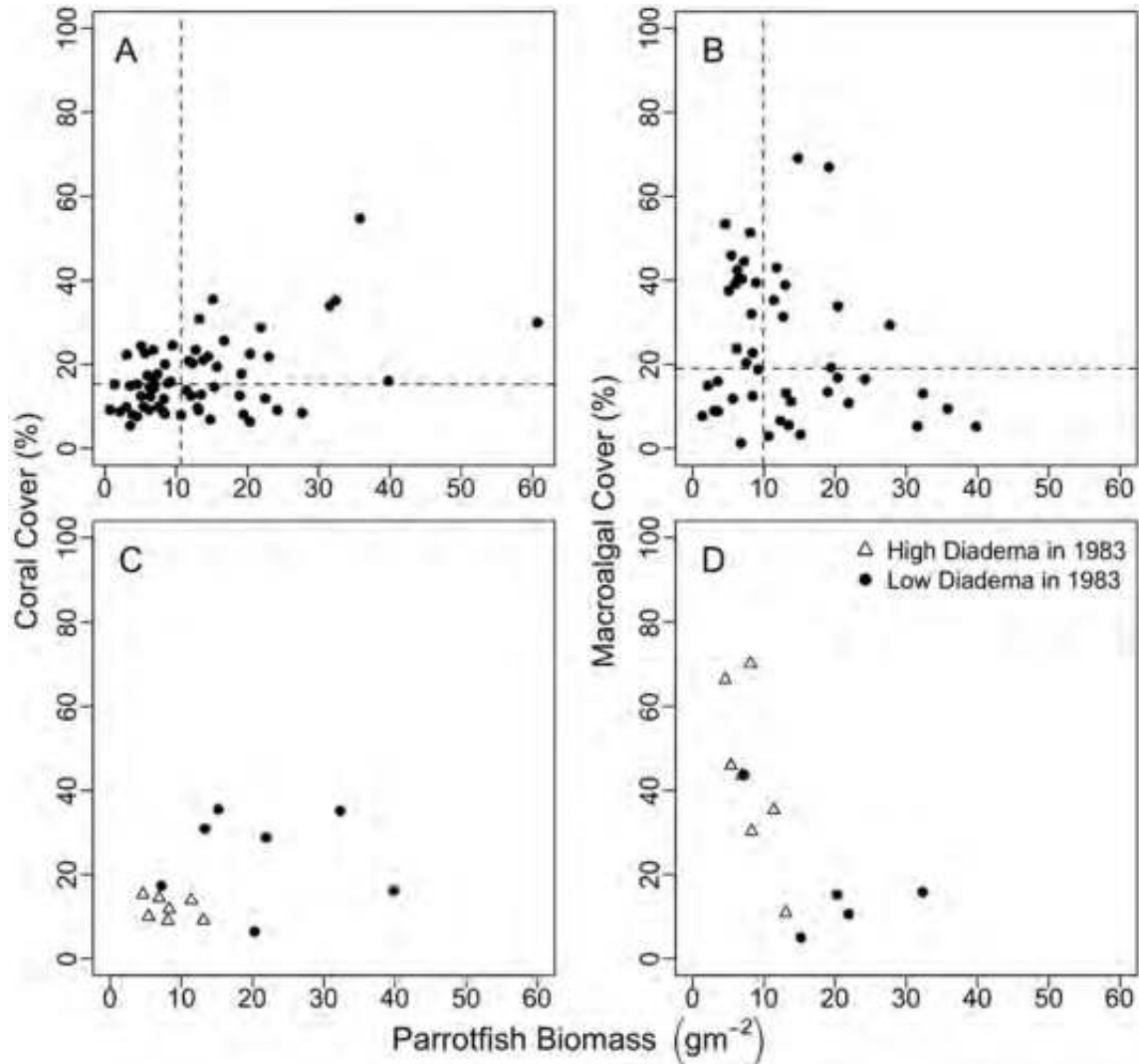


FIGURE 24. Percent coral cover and macroalgal cover versus parrotfish biomass since 1998 for all reef locations with paired data Table 9: (A) $N = 67$, $r_s = 0.31$, $p = 0.02$; (B) $N = 46$, $r_s = -0.19$, $p = 0.20$. The same analysis for only the 16 locations in Table 8: (C) $r_s = -0.36$, $p = 0.21$; (D) $r_s = -0.81$, $p = 0.01$. Dashed lines in (A) and (B) are medians for each axis.

Indirect effects of fishing due to increased macroalgal abundance

Reduction in coral recruitment

Approximately one quarter of Caribbean corals are brooding species that produce comparatively small numbers of large planula larvae that disperse short distances from their parents. Larval mortality is lower than for broadcasting species and populations may be effectively self-seeding (Jackson 1991). In contrast, the remaining broadcasting species spawn gametes that are fertilized in the ocean and larvae disperse farther and suffer higher mortality before settlement than brooding species so that there is little or no correlation between adult abundance and recruitment at different sites (Jackson 1991).

Numbers of coral recruits before the *Diadema* mortality were overwhelmingly dominated by brooding species that comprised > 90% of all recruits (Bak and Engel 1979; Rylaarsdam 1983; Rogers et al. 1984; Hughes and Jackson 1985). Recruits of brooding species are still more abundant than broadcasting species, but rates of coral recruitment have greatly declined. The most extensive long-term data are from Jamaica and Curaçao (Hughes and Tanner 2000; Vermeij 2006). Cover of two brooding species in Jamaica (*Agaricia agaricites* and *Leptoseris cucullata*) declined 83% between 1977 and 1993 while the average number of recruits/year declined 75%. Thus the decline in recruitment was similar to the loss in coral cover. This was not the case in Curaçao, however, where coral cover declined by 50% but coral recruitment in identical settlement panel experiments declined by more than 80% between 1979-1981 and 1998-2004 so that the decline in recruitment cannot be attributed entirely to a simple decline in the abundance of parental colonies.

The differences on the upper surfaces of the settlement panels were even greater and provide a clue to the factors responsible. Upper surfaces in 1979-1981 were almost entirely dominated by crustose coralline algae that favor coral recruitment (Morse et al. 1988; Hughes et al. 2007; Arnold and Steneck 2011) and macroalgae were absent, whereas from 1998-2004 the upper surfaces were covered by macroalgae. Total numbers of recruits after each following year were > 500 in the 1979-1981 experiments compared to

about 25 in the 1998-2000 experiments. These included a total of 981 recruits of *Agaricia* and *Porites* in the earlier experiment versus none of these taxa in 1998-2000. Numbers of “juvenile” corals (< 4 cm) on the reefs at Curaçao decreased by only 55% but these small corals can be as much as 13 years old (Vermeij et al. 2011). There was also a dramatic shift in juvenile coral composition: mean density of juveniles of brooding species decreased on average by about 10 recruits/m² whereas that of spawning species increased by 1-2 recruits/m².

The data from Curaçao strongly suggest that increased macroalgal abundance is a major factor in the reduced recruitment of corals, an observation consistent with earlier observations of Rogers et al. (1984) who concluded: “High rates of coral recruitment tended to be associated with low [non-calcareous] algal biomass and relatively high grazing pressure by urchins and fishes.” Recent experiments strongly support this hypothesis. Recruitment of *Porites astreoides* larvae in Florida was inhibited by a variety of the most abundant macroalgae and cyanobacteria on Caribbean reefs (Kuffner et al. 2006). All of the macroalgal and cyanobacterial species tested caused recruitment inhibition or avoidance behavior by larvae and several species also significantly increased mortality of recent recruits. Behavioral avoidance reactions by the coral larvae suggest some form of chemical inhibition. There is also experimental evidence for more direct physical inhibition of recruitment by macroalgae at Roatán, Honduras (Box and Mumby 2007). Shading by *Lobophora* and *Dictyota* caused considerable losses in juvenile coral tissues and increased mortality of recruits and presence of *Dictyota* around the periphery of coral recruits decreased their growth rates by as much as 99%, and decreased cohort survival. Additional settlement experiments in Belize confirm that crustose coralline algae are strongly favorable to coral recruitment whereas macroalgae and turf algae inhibit recruitment (Arnold and Steneck 2011).

The role of macroalgae in inhibiting coral recruitment is even more strongly supported by striking increases in coral recruitment following reductions in macroalgae by recovering populations of *Diadema* and parrotfish. *Diadema* have begun to recover in increasingly large areas across the Caribbean (Edmunds and Carpenter 2001;

Carpenter and Edmunds 2006) reaching densities of 1.7/m² to 8.9/m² on a spatial scale of several km at sites in Belize, Jamaica, St. Croix in the northern Caribbean and Bonaire, Grenada, and Barbados in the south. Juvenile coral densities ranged from 4.5/m² to 32.3/m² in areas where *Diadema* have recovered versus 2.5/m² to 12.9/m² where they have not. A more recent study at Discovery Bay, Jamaica corroborated these results (Idjadi et al. 2010). Macroalgae were reduced from 68% to 6% cover. A combination of crustose corallines, turf algae, and bare space constituted 74% of the reef surface following grazing instead of 16%, and corals more than doubled from 4 to 11% cover in urchin zones compared to areas where urchins were absent.

A similar result emerges from the partial recovery of parrotfish in marine protected areas in the Bahamas (Mumby et al. 2006, 2007; Mumby and Harborne 2010). Increased parrotfish abundance and size in the Exuma Cays Land and Sea Park resulted in a 2- to 3-fold increase in parrotfish grazing intensity compared with unprotected sites. This increase in grazing further resulted in a decrease in macroalgal cover from 20-25% to about 1-5% and a 2- to 3-fold increase in coral recruitment. Moreover, size-adjusted rates of change in cover of five dominant coral species increased in areas within the marine park and decreased outside. The tipping point between positive and negative effects on coral growth occurred at about 10% macroalgal cover. Finally, the benefits of marine protected areas for increasing herbivory on reefs greatly exceed the potentially harmful effects of increased predator abundance on parrotfish (Mumby et al. 2006). This is because large bodied parrotfish can achieve an escape in size from predators.

Thus all of the evidence to date strongly supports the hypothesis that high macroalgal cover strongly reduces the recruitment of juvenile corals into the coral reef community. The negative effects of macroalgae far exceed the effects of decreased parental populations.

Increases in coral disease

There is also increasingly strong experimental evidence that high macroalgal abundance due to overfishing may induce outbreaks of coral disease as will be discussed in Section 3f on coral disease.

3c. COASTAL POLLUTION

It has long been understood that areas of greater sedimentation, seawater turbidity and light attenuation are less favorable to corals than clearer waters (Odum and Odum 1955; Sheppard et al. 2009). Low light affects photosynthesis by microbial symbionts, and sediments and oil interfere with ciliary feeding and may require increased production of mucus for sediment removal (Dodge et al. 1974; Bak and Elgershuizen 1976; Loya 1976; Dodge and Vaisnys 1977; Bak 1978; Rogers 1983b, 1990; Jackson et al. 1989; Guzmán et al. 1991; Burns et al. 1993, 1994; Guzmán and Holst 1993; Wolanski et al. 2003; D'Croz et al. 2005; Cramer et al. 2012). All of these different forms of stress may decrease coral growth rates and survival

Several factors contribute to increased turbidity including unregulated coastal development, dredging, other forms of coastal pollution such as oil spills, re-suspension of bottom sediments by storms, proximity to areas of naturally heavy rainfall and erosion, and excess nutrients from sewage, agriculture, and clearing of land. Nutrient pollution may be especially problematic because of excess production by phytoplankton and benthic algae that further reduce light levels (D'Croz et al. 2005) and may promote macroalgal growth and disease. The resulting positive feedback loop has negative impacts on coral survival including increased growth of macroalgae that may overgrow, abrade, or poison corals as well as inhibit their recruitment (Section 3b) and promote coral disease (Kline et al. 2006; Section 3f).

Most of the evidence regarding nutrient pollution versus grazers for the increased abundance of macroalgae implicates top down control by fishes, sea urchins, and smaller invertebrates (Hughes and Connell 1999; Aronson and Precht 2000; Burkepile and Hay 2006, 2008, 2009). However, nutrient and chlorophyll data are unavailable for most Caribbean reef locations because optical data from satellites cannot yet reliably determine chlorophyll levels in reef waters and there is a dearth of systematically collected data from water samples at different reef locations. Thus it not yet possible to systematically explore whether there is a strong case for the role of bottom-up processes except in the most heavily polluted locations such as parts of the Florida Reef Tract

(Lapointe 1997; Leichter et al. 2003). There is also no consistent monitoring of toxic substances released into Caribbean waters although some of the toxic effects of oil spills suggest that, just as for the Exxon Valdez spill (Peterson et al. 2003), chemical toxins of all sorts may be a greater problem for Caribbean reefs than is generally understood (Jackson et al. 1989; Guzmán et al. 1991; Burns et al. 1993, 1994; Guzmán and Holst 1993; Fernandez et al. 2007; García et al. 2008; Ramos et al. 2009).

Fortunately, simple measurements of water clarity/transparency are an excellent measure of

several aspects of water quality including the effects of sediments, nutrients, and organic matter (Fabricius et al. 2012). There are also limited comparative data to examine trends in water transparency based upon secchi disk measurements that record the distance through the water column in meters at which the secchi disk is no longer visible from the surface or along a horizontal plane at depth (CARICOMP). Measurements were made at only seven of the CARICOMP sites and were made consistently for more than ten years at only three: inside the lagoon and on the fore reef at Carrie Bow Cay, Belize and at a single forereef site at La Parguera Puerto Rico (Table 9).

TABLE 9. Average secchi disk depths, degree heating weeks in 1998, 2005, and 2010, changes in coral cover in the two years following the extreme heating events of 1998, 2005, and 2010, and parrotfish abundance and coral cover since 1998 for 88 Caribbean reef locations (numbers same as in Table 2). See the text for the different drivers sections for further details.

Label	Country	Location	Median DHW			Proportional change in coral cover (%)			Secchi disk depth (m)	Parrotfish biomass (g/m ²)	Coral cover since 2005 (%)
			1998	2005	2010	1998	2005	2010			
1	Antigua & Barbuda	Antigua & Barbuda	0.64	11.35	11.66					19.4	3.8
2	Aruba	Aruba	0	2.35	8.33						
3	Bahamas	Cay Sal Bank	1.31	2.48	3.33					14.8	7.1
4		Exuma Land Sea Park	8.09	8.98	6.86		0.07			9.8	7.8
5		Other	7.01	3.56	2.25	1.25	-0.01	0.02		27.7	11.7
6	Barbados	Barbados Leeward	0.52	3.3	11.85	0.08	-0.26				
7		South	0.52	3.3	11.85						
9	Belize	Atoll Leeward	1.09	0.55	3.33	0.03	-0.56			6	20.7
10		Atoll Windward	1.09	0.55	3.33	-0.50	-0.30	0.25		6.3	20.9
11		Belize Central Barrier	1.09	0.55	3.33	0.02	-0.27	-0.04	16	7.2	15.9
12		Gulf Honduras	2.93	0	4.02					4.5	7.6
13		Inner Barrier	2.93	0	4.02	-0.91				10.7	16.2
14		Northern Barrier	0.56	2.25	0.53	-0.64	-0.30	-0.18		8.9	16.9
15		Southern Barrier	2.93	0	4.02	-0.67		-0.06		6.4	13.5
16	Bermuda	Bermuda	5.1	1.68	4.55	-0.15	0.24	-0.28	36.8	21.9	38.6
17	British Virgin Islands	British Virgin Islands	1.61	8.92	3.18	-0.24	-0.36	0.08		13.8	14.3
18	Cayman Islands	Grand Cayman	2.27	0.51	1.11	-0.14				12.7	30.7
19		Little and Brac	2.16	2.49	2.19		-0.11	0.49		15.7	24.6
20	Colombia	Providencia	2.54	1.63	4.3						
21		San Andrés	1.9	2.11	5.42						
22		Santa Marta Region	1.51	2.52	5.05	-0.05					
23	Costa Rica	Costa Rica Cahuita	0	1.38	2.66		-0.15	0.00		39.8	18
24	Cuba	Jardines de la Reina	3.34	5.29	5.57					20.4	30.1
25		North	3.19	2.28	1.71					6.9	
26		Southwest	1.77	2.01	1.2					8.4	25.2
27	Curaçao	Curaçao Northwest	0	2.35	8.33	0.00	-0.02	-0.55		31.6	13.3
28		Curaçao Southwest	0	0.51	5.75	0.25	0.47	-0.02		15.2	31.5

Label	Country	Location	Median DHW			Proportional change in coral cover (%)			Seechi disk depth (m)	Parrot-fish biomass (g/m ²)	Coral cover since 2005 (%)
			1998	2005	2010	1998	2005	2010			
30	Dominica	Dominica	2.81	8.68	10.54						
31	Dominican Republic	North	1.17	0.63	0		-0.09			3.1	21.3
32		Punta Cana	1.16	2.91	3.93					3.9	
33		South	1.83	2.26	9.96	-0.56				9.2	
34	French Antilles	Guadeloupe	5.19	9.91	14.1		-0.48	0.23			
35		Martinique	2.73	9.49	11.58		-0.38				
36		St. Barthelemy	0.5	6.04	2.57		-0.43	-0.08			
37	Grenada	Grenada other	2.17	9.78	15.08						
38		Leeward	2.17	9.78	15.08						
39	Guatemala	Guatemala	2.93	0	4.02					3	9.9
40	Honduras	Bay Islands	1.77	0	2.9					11.8	21.6
41		Near shore	1.77	0	2.9					22.5	12
42	Jamaica	Jamaica Montego Bay	2.88	2.74	2.66	-0.18				4.6	19.4
43		Jamaica North central	3.78	2.5	3.9	0.25	0.20			6.9	19.6
44		Jamaica Northeast	0.52	1.79	3.79					5.4	
45	Jamaica	Pedro Bank	1.75	0	4					15.4	14.7
46		Port Royal Cays	2.48	1.62	5.89						
47		Jamaica West	5.23	2.83	4.38	0.27				8.1	7.8
48	Mexico	Alacran	2.17	0	0						
49		Chinchorro Bank	1.16	1.67	0					1.4	7.9
50		Cozumel Leeward	1.11	0	0		-0.47	0.09		3.5	12.1
51		Cozumel Windward	1.11	0	0					0.7	9.2
52		North East Yucatan	1.11	0	0	0.22	-0.45			6.2	7.9
53		South East Yucatan	0.56	1.67	0					5.1	15.9
54		Veracruz	0.54	0	0						
56	Netherlands	Bonaire Leeward	0.53	5.76	13.7	0.11	0.13	0.69		32.3	37.1
57		Bonaire Windward	0.53	5.76	13.7					19.1	9.7
58		Saba	3.43	12.6	7.72	0.34				13.5	
59		Saba Bank	3.43	12.6	7.72					14.5	
60		St. Eustatius	4.05	11.61	10.84					23	
61	Nicaragua	Corn Islands	1.21	1.75	4.72					5.1	
62	Panama	Bahia Las Minas	2.18	6.37	2.63	0.01	0.15	0.01			
63		Bocas del Toro	2.89	1.2	6.59		0.00	-0.44		12.3	13.6
64		Costa Arriba	0.52	2.87	4.18	0.17	-0.09	0.02			
65		Panama San Blas	0	0	3.78					13.3	
66	Puerto Rico	Guanica	4.63	8.3	3.5						
67		Jobos Bay	0.74	7.67	9.83					2.1	8.7
68		La Paguera	1.15	8.09	9.18	-0.02	-0.53	-0.03	10.2	5.6	19.2
70		Turumote	1.15	8.09	9.18					9.5	23.8
71		Vieques & Culebra	4.63	8.3	3.5		-0.84			19	8.1
72	St. Kitts & Nevis	St. Kitts & Nevis	1.03	9.96	3.81			0.41		13	11.1

Label	Country	Location	Median DHW			Proportional change in coral cover (%)			Secchi disk depth (m)	Parrot-fish biomass (g/m²)	Coral cover since 2005 (%)
			1998	2005	2010	1998	2005	2010			
73	St. Lucia	St. Lucia Leeward	2.45	6.87	11.2						
74	St. Martin	St. Martin	3.26	12.84	6.77					12.1	
75	St. Vincent	Grenadines	1.13	4.34	13.25					16.7	19.5
76	& the Grenadines	St. Vincent	1.84	7.39	12.3					6.8	24.9
77	Trinidad & Tobago	Trinidad & Tobago	2.26	4.12	10.05	0.65	-0.31	-0.02			
78	Turks & Caicos Islands	Turks & Caicos Islands	0	3.23	1.06					7.4	
79	U.S.A	Dry Tortugas	4.25	0.54	2.21		-0.19	0.07		7.5	8
80		Flower Garden Banks	2.48	3.88	6.37					35.8	53.1
81		Lower Florida Keys	8.47	4.7	6.54	-0.51	-0.42	0.36		24.2	10.3
82		Middle Florida Keys	0.55	0.5	0	-0.40	-0.41	0.07		8.4	8
83		Southeast Florida	1.93	2.43	2.8		-0.50	-0.38		3.6	2.8
84		Upper Florida Keys	4.15	0.53	1.58	-0.64	-0.24	0.02		20.3	6.1
85	U.S. Virgin Islands	USVI St. Croix	2.47	7.03	5.95	-0.35	-0.53	-0.32		13.1	4.7
86		USVI St. Thomas	4.63	8.3	3.5		-0.43			11.4	13.6
88		USVI St. John	4.63	8.3	3.5	-0.17	-0.47	0.33		8.3	10.1
89	Venezuela	Los Roques	1.74	2.91	13.57		0.01	-0.47		60.7	31
90		Morrocoy	0	1.2	12.48	-0.21	0.04	-0.14	12.9		

Trends in water transparency were assessed by testing the linear relationship of secchi distance to year while assuming an AR-1 autocorrelation (R package *nlme*; Pinheiro and Bates 2013). Water transparency significantly declined at all three consistently monitored sites, while coral cover has declined by approximately two thirds (Fig. 25; Koltes and Opishinski 2009; K. Koltes, personal communication; E. Weil, personal communication). The decline in transparency at Carrie Bow Cay is related to the conversion of lands bordering the Gulf of Honduras to agriculture and urban development. Massive amounts of sediments, primarily from Guatemala and Honduras, were introduced to the Gulf following the 2 m rainfall during Hurricane Mitch (Smith et al. 2002). These sediments became entrained in the gyre of the Gulf and continue to be re-suspended. More recent rapid conversion of the Belize coastline to intensive agriculture and tourism is also a major factor. Coastal development is also responsible for the downward trend at La Parguera (Hertler et al. 2009).

Coral cover declined by approximately two thirds at both Carrie Bow Cay and La Parguera, but the declines were episodic and uncorrelated with the gradual decline in water quality. Most of the

decline at Carrie Bow Cay occurred before the transparency data began and coral cover increased by approximately 10% between 1994 and 2003 before declining precipitously by > 25% cover between 2003 and 2007 (Appendix II).

In contrast, water transparency did not change appreciably over 7 years at Morrocoy, Venezuela, but there were very large increases in heavy metals and hydrocarbons in relation to Venezuela’s massive oil production (Bastidas et al. 1999; García et al. 2008; Ramos et al. 2009) that may have been a major factor in the dramatic losses in coral cover along the Venezuelan coast. Water transparency increased by about 50% over eight years at Bermuda.

3d. OCEAN WARMING

Reef corals host endosymbiotic photosynthetic dinoflagellates (*Symbiodinium*) that provide sugar to their coral host and are essential for coral growth and survival. Coral bleaching results from the ejection of the symbiotic dinoflagellates from the host coral due to stress. The most common form of bleaching occurs in response to extended increases in sea-surface temperature (SST) that are routinely measured in terms of Degree Heating Weeks (DHWs), defined as numbers of weeks during which SSTs exceed 1°C above the local

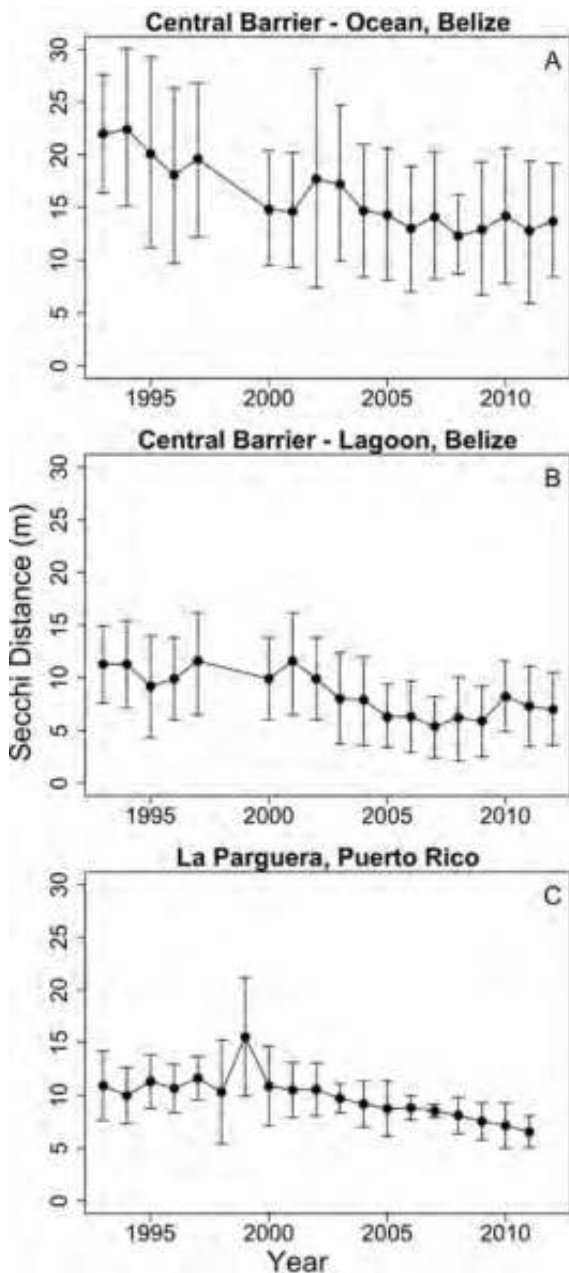


FIGURE 25. Decline in water transparency over time at the CARICOMP at fore-reef and lagoonal sites at Carrie Bow Cay and a fore-reef site at La Parguera, Puerto Rico. All of these trends are highly significant (GLMM, $p < 0.01$). See text for details.

climatological thermal maximum (Brown 1997; Hoegh-Guldberg 1999; Knowlton 2001; Hughes et al. 2003; Baker et al. 2008; Donner et al. 2007). However, different types of *Symbiodinium* are more or less resistant to elevated temperatures so that the bleaching response can be exceedingly varied and complex (Rowan et al. 1997; Knowlton and Rohwer 2003; Baker et al. 2008).

Mass mortality of corals commonly occurs when such high temperatures persist for more than one

month. Bleaching events were rare before 1980 (Glynn 1993) but have since increased greatly in intensity and frequency due to rising temperatures that are in turn due to burning of fossil fuels and increases in other greenhouse gas emissions (Hoegh-Guldberg et al. 2007; Donner 2009, 2011). Increasingly severe coral bleaching events occurred in the Caribbean in 1995, 1998, 2005, and 2010 (Wilkinson and Souter 2008; Eakin et al. 2010).

Much progress has been made in prediction of coral bleaching events using long-term records of SST variability and the duration of heating events in association with the ReefBase compilation (<http://www.reefbase.org>) of coral mass bleaching events (Donner 2011; Chollett et al. 2012a,b). However, the ReefBase dataset has been criticized for three reasons: (1) bias towards reporting the occurrence of mass bleaching events, but less frequently their non-occurrence, (2) uneven spatial distribution of reports, and (3) absence of data from many of the large, well organized monitoring programs (Oliver et al. 2009; Donner 2011).

A major step forward has been provided by NOAA Coral Reef Watch (CRW) that has conducted near real-time global monitoring of thermal stress (<http://coralreefwatch.noaa.gov>) since 2000 based on satellite SST data at a resolution of 0.5-degree (~50km). These data have the important advantage of measuring the strength of the driver rather than the ecological response and complement observations *in situ*. They also provide an independent and consistent measure of thermal stress over the entire ocean rather than a hodgepodge of scattered measurements using different instruments and methodologies. As such, they provide an invaluable tool for managers and scientists to alert them of likely severe bleaching events before they occur and to facilitate preparations for essential *in situ* observations of ecosystem response. The DHWs product has been associated with significant coral bleaching (≥ 4 DHWs), and with widespread bleaching and significant coral mortality (≥ 8 DHWs; Liu et al. 2003; Eakin et al. 2009). However, extreme bleaching events do not always result in massive coral mortality, as evidenced by very large variations in mortality among locations that were comparably heated following the extreme heating event in 2005 (Eakin et al. 2010). CRW has

also produced historical thermal stress products based on retrospective SST data as far back as 1985.

For this study, CRW extended these thermal stress products historically based on retrospective SST satellite data prior to 2000. SST data at 0.5-degree resolution were developed from the Pathfinder version 5.2 dataset (Casey et al. 2010), mimicking the methodology used for the operational CRW near real-time SST product (as described in Eakin et al. 2009). These data were combined with the near real-time SST data to extend the time-series back to 1985. Annual maximum DHW values for 1985-2011 (0.5-degree) were calculated for reef-containing pixels corresponding to each location in Table 9. Data were then combined for each location by taking the median number of DHW per location for 1998, 2005, and 2010. Pathfinder SST data were provided by GHRSSST and the US National Oceanographic Data Center, supported in part by a grant from the NOAA Climate Data Record (CDR) Program for satellites. Our use of these data solely reflects the opinions of the authors of this report and do not constitute a statement of policy, decision, or position on behalf of NOAA or the US Government.

We analyzed changes in coral cover for the two years following each of the prolonged and extreme heating events in 1998, 2005, and 2010 relative to the two years preceding the event in relation to the numbers of DHWs experienced (Table 9). There was also a significant heating event across the southern Caribbean in 1995 with numbers of DHWs ranging from > 10 to 19.5 in a broad swath from mainland Colombia and San Andres in the west to Venezuela in the east, and with slightly lower numbers of DHWs in Panama and Barbados (CARICOMP 1997). Unfortunately, coral cover data are too sparse for detailed before and after comparisons around this event. Nevertheless, the timelines for these reefs that go back before 1995 show little decline or even increases in coral cover after 1995, suggesting low coral mortality. Support for this inference comes from the timelines for Morrocoy and Los Roques in Venezuela that begin a few years after 1995 with exceptionally high coral cover of 55% and 44% coral cover respectively (Table 4, Appendix 2). There are also scattered reports of bleaching events at Florida before 1995 (Billy Causey,

personal communication) but we lack the quantitative data for comparative analysis.

We explored the relationship between degree heating weeks and proportional changes in coral cover for the 1998, 2005, and 2010 heating events both separately and for all three events combined using non-parametric correlations. Linear statistics are not appropriate in this case due to spatial and temporal autocorrelation causing residual variation to be correlated. Correlations were calculated for proportional changes in coral cover (decreases or increases) as a function of numbers of DHWs using two data sets. In the first case we used all of the data regardless of the numbers of DHWs experienced at any location. The purpose of this broader analysis was to determine the extent to which extreme heating events may have been responsible for changes in the abundance of corals throughout the wider Caribbean in comparison with other drivers of change. In contrast, the second analysis only employed data above the postulated critical threshold of 8 DHWs to examine more closely the impact of extreme heating events on coral cover. We also assessed the extent to which proportional changes in coral cover were related to numbers of DHWs above and below 8 DHWs by constructing contingency tables.

There is a small, non-significant negative correlation between proportional changes in coral cover and numbers of DHWs for the entire data set (Fig. 26A). We also examined the same data using 2×2 contingency table analysis for changes in coral cover at locations that experienced < 8 or ≥ 8 DHWs with marginally significant results ($\chi^2 = 3.11$, $df = 1$, $p = 0.07$). Remarkably, however, the trend is *opposite to the expected pattern* because the two locations that experienced the highest numbers of DHWs experienced a substantial proportional *increase* in coral cover. Moreover, the proportion of locations that lost coral cover is not different for places that experienced more or less than 8 DHWs (74% and 73% respectively), and six of the eight locations that suffered losses in coral cover $> 50\%$ coral were exposed to < 8 DHWs. Finally, and even more remarkably, there is a significant *positive* correlation between proportional changes in coral cover and numbers of DHWs using only the data for locations that experienced > 8 DHWs ($r_s = +0.66$, $p = 0.01$).

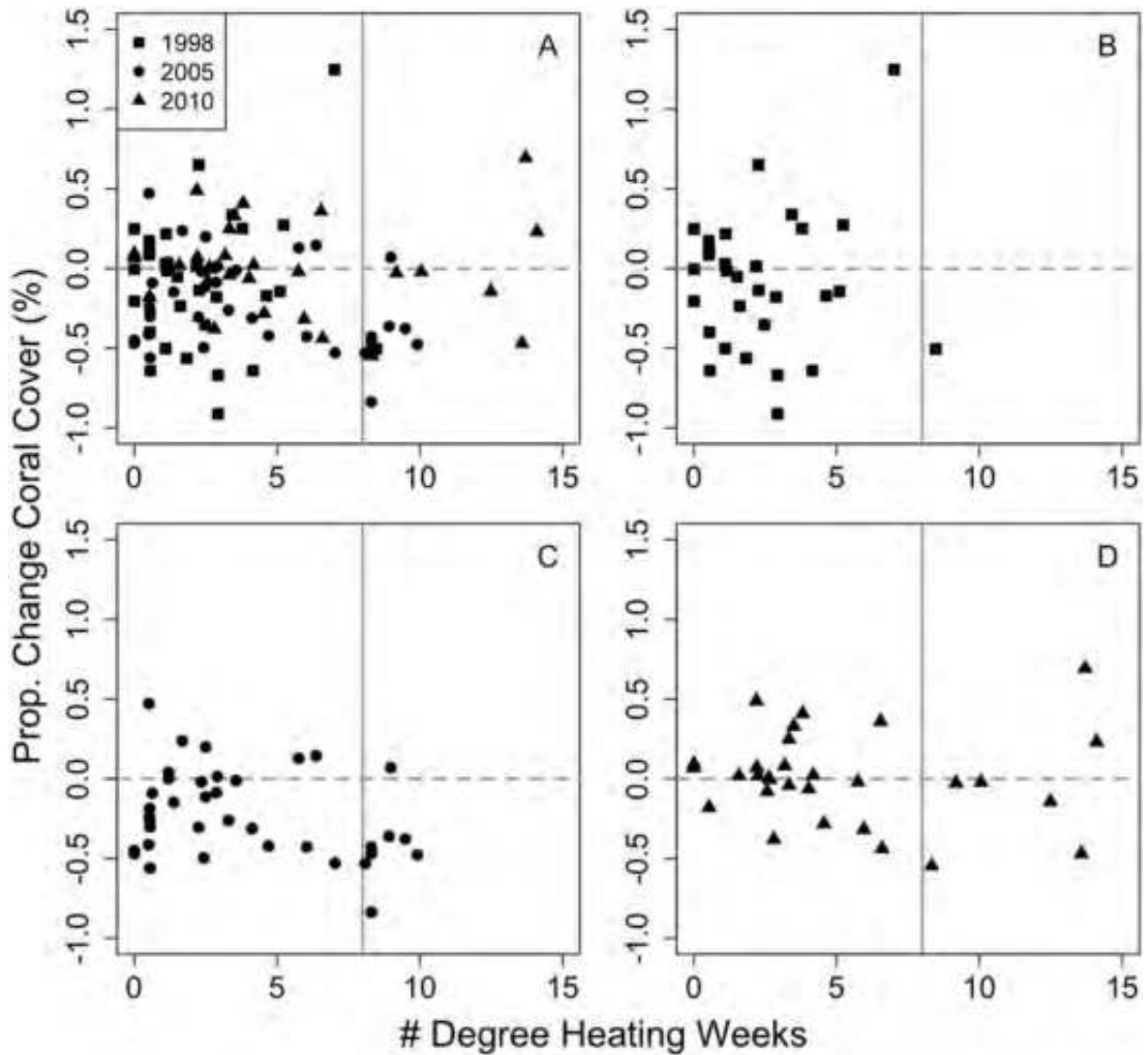


FIGURE 26. Proportional changes in coral cover in the two years following major heating events in relation to the number of degree heating weeks (DHWs) at all the locations for which paired data are available (Table 9) (A) all three events combined, $r_s = -0.10$, $p = 0.34$; (B) in 1998, $r_s = -0.07$, $p = 0.71$; (C) in 2005, $r_s = -0.20$, $p = 0.25$, and (D) in 2010: $r_s = -0.20$, $p = 0.29$. See text for details of the analysis.

Graphs of the loss of coral cover against the number of DHWs after 1998, 2005, and 2010 vary in their relationship between coral cover and thermal stress (Fig. 26B-D). For the earliest event in 1998, there are very few Caribbean reef locations that experienced ≥ 8 DHWs, and overall no relationship was found to proportional loss of coral cover (Fig. 26B). Similarly, no regional correlation between DHW and proportional loss in coral cover was found in 2005 (Fig. 26C) and 2010 (Fig. 26D). Contingency table analyses for 2005 and 2010 were also non-significant (2005: $X^2 = 0.78$, $df = 1$, $p = 0.38$; 2010: $X^2 = 1.92$, $df = 1$, $p = 0.17$). Contingency table analysis could not be done for 1998 because of the lack of data in the upper right quadrant.

Lack of an overall regional correlation between numbers of DHWs and changes in coral cover does not mean that bleaching is an unimportant cause of coral mortality because numerous studies have clearly demonstrated mass mortality following coral bleaching (Hoegh-Guldberg et al. 2007). Moreover, even greater rising temperatures in the future will almost certainly have increasingly severe effects. But the data do belie any strong, regionally consistent effects of coral bleaching upon coral cover *up to the present*. Instead, mortality due to bleaching has been highly localized. At Belize, for example, coral cover dropped precipitously from about 35-45% to zero after the massive bleaching event at two cays on the leeward side of the southern barrier reef (Aronson et al. 2002), but

mortality was negligible at Glovers Atoll farther off-shore (Mumby 1999). A similar drop occurred at Carrie Bow Cay from the combined effects of coral bleaching and Hurricane Mitch (K. Koltes, personal communication). Mortality was also very extensive after the 2005 massive bleaching event at St. John, with proportional losses in coral cover of up to 60% on some reefs (Miller et al. 2009), and at La Parguera, Puerto Rico (Weil et al. 2009). In both of these cases, however, mortality may have been largely due to a major outbreak of disease that closely followed the thermal stress (see Section 3f).

3e. INVASIVE SPECIES

The Caribbean is effectively a Mediterranean sea and has been the most isolated tropical ocean on the planet ever since the final closure of the Central American Seaway by the rise of the Isthmus of Panama between about 5 to 3 million years ago severed its connection with the eastern tropical Pacific (Coates and Stallard 2013; Jackson and O’Dea 2013). Isolation from the tropical Indian Ocean to the east occurred even earlier due to the movements of the continents of Africa and Asia, the subtropical Mediterranean, and the inhospitable eastern Atlantic. Thus, by analogy to the fates of the myriad island birds and reptiles decimated to the point of extinction by introduced species of snakes, rats, cats, and goats (Fritts and Rodda 1998; Pimentel et al. 2005), Caribbean marine species should be exceptionally prone to the impact of introduced competitors and predators. Moreover, by analogy to the fates of the original Americans after their first contact with European diseases (Crosby 1986; Mann 2005), Caribbean corals should be especially vulnerable to introduced diseases.

Most of the recent focus on introduced marine species has concentrated on highly visible macro-organisms, such as the explosive increase in the abundance of the Pacific lionfish *Pterois volitans* throughout the entire wider Caribbean over the past decade (De Leon et al. 2011; Hackerott et al. 2013) or the uncontrolled spread of the alga *Caulerpa taxifolia* in the northern Mediterranean (Meinesz et al. 1993, 2001). The potential effects of lionfish on Caribbean invertebrates and fishes may be severe, especially in exacerbating the consequences of overfishing by depleting juvenile parrotfishes and surgeonfishes (Albins and Hixon 2018, 2013). However, it is too soon to tell whether native predators might eventually have

an impact of lionfish, especially in marine reserves where predators could regain their former abundance (Mumby et al. 2013).

Far too little attention has been paid, however, to the introduction of the myriad marine organisms we cannot see, including virtually all microorganisms and pathogens. The case of the unidentified pathogen that caused the mass mortality of *Diadema antillarum* in 1983-1984 is a case in point. *Diadema* mortality began next door to the Caribbean entrance to the Panama Canal, whence it spread like wildfire on ocean currents eastward to Trinidad and Tobago and northward throughout the western Caribbean, Greater Antilles, and Florida all the way to Bermuda, with mortality in the eastern Caribbean arriving from both the north and the south in 1984 (Lessios et al. 1984; Lessios 1988). Introduction via ballast water from the Pacific is seemingly the most reasonable explanation.

This begs the question of why so many marine diseases first appeared in the 1970s and early 1980s, a pattern for which there is no compelling environmental explanation. Temperatures were not excessively warm in the 1970s and heating in relation to El Niño in 1983 was small compared to the episodes in 1995, 1998, 2005, and 2010. There is also no evidence of a pervasive decline in Caribbean water quality before the 1980s or later.

In contrast, the volume of international shipping exploded in the late 1960s with the advent of bulk carriers and enormous cruise ships that discharged untold volumes of ballast water into coastal waters before stricter regulations may have begun to take effect (Carlton 1996). Greater speed of transport among distant ports may also be a contributing factor. Many introduced species have been transported by ballast water, and this is especially true for microbes that have been calculated to be transported in numbers on the order of 10^{20} /year into the lower Chesapeake Bay alone (Ruiz et al. 2000; Drake et al. 2007). None of this proves that *Diadema* disease or WBD were introduced into the Caribbean from another ocean. But given the numbers of microbes in ballast waters, it is remarkable that all marine diseases have not been introduced throughout the global ocean. Introductions of aquarium species and so-called “live rock” for aquaria are another potentially major avenue for incidental introductions of pathogens.

Once introduced, different environmental factors may retard or promote the growth of introduced species including species that cause disease. But it is important not to confuse the causes of an initial outbreak from factors that may subsequently promote or inhibit its spread and increase.

3f. INCREASING INCIDENCE OF CORAL DISEASE

Corals are complex ecological communities (holobionts) comprising the coral host and an extraordinary diversity of associated eukaryotic and prokaryotic microorganisms (Rohwer et al. 2001, 2002; Knowlton and Rohwer 2003; Rosenberg et al. 2007). These associates include a great diversity of intracellular, endosymbiotic dinoflagellates (*Symbiodinium*) and a bewildering variety of bacteria, archaea, and viruses that confer essential nutritional and immunological benefits to the host coral by photosynthesis, provision of nutrients, nitrogen fixation, and resistance to infection. The ecological balance among all of these mutualistic ecological components of the holobiont community is essential for coral health. Breakdown in that balance due to a change in the environmental or genetic landscape of the holobiont or the invasion or increase in a pathogen compromises the health of the holobiont in the form of myriad forms of coral bleaching or disease. Understanding of the underlying mechanisms of these ecological interactions that compromise coral health is in its infancy, so that scientists are required to describe phenomena in terms of their gross phenotypic expression (e.g., bleaching, White-Band Disease, Black-Band Disease, Yellow-Band Disease, etc.) rather than the precise underlying ecological components of cause and effect (Weil and Rogers 2011).

In recognition of this complexity, disease is commonly defined as “any impairment to health resulting in physiological dysfunction” due to a pathogen (virus or microorganism), environmental perturbation, toxic substance, or genetic changes in the affected organism (Weil and Rogers 2011). Defined so broadly, coral bleaching, mercury poisoning, or smothering by sediments can be treated as a disease – a definition so broad as to be of little use. For this report, therefore, we define coral diseases more narrowly as impairments to coral health caused by a demonstrable or presumptive infectious pathogen that results in varying pathological responses or death (see Martin et

al. 1987; Wobeser 1994 for further discussion of these criteria).

Coral diseases so defined occur in a bewildering variety of forms that may affect a few or many coral taxa (Weil and Rogers 2011). In most cases the diseases are identified by the pathological expression exhibited by the affected coral. The actual pathogens have been identified in only a few cases, and similar manifestations of disease in the changing appearance of the affected coral may be caused by different pathogens in different circumstances. Failure to identify pathogens is the major impediment to any real advance in understanding the causes and consequences of coral disease. Little is known about transmission, but there is evidence that various predators of corals including fishes, polychaete worms, and snails may transmit diseases from one coral prey to the next, as well as transport by currents (Williams and Miller 2005; Rosenberg et al. 2007; Weil and Rogers 2011) or in the ballast water of ships (Drake et al. 2007).

The first report of coral disease in the Caribbean was for BBD in Belize, Florida, and Bermuda in the early 1970s and throughout the western Atlantic soon after (Antonius 1973, 1977; Weil and Rogers 2011). BBD appears as a dark microbial mat and infects 19 species of Caribbean corals. BBD was followed closely by a virulent outbreak of WBD that caused mass mortality of *Acropora palmata* in the US Virgin Islands in the late 1970s, and spread throughout the western Atlantic to cause mass mortality of both *A. palmata* and *A. cervicornis* in the early 1980s to the present (Gladfelter 1982; Goreau et al. 1998; Aronson and Precht 2001; Weil and Rogers 2011). In total, about 13 different diseases of corals have been identified whose distribution and prevalence varies greatly among different locations within the wider Caribbean (Weil and Cróquer 2009; Cróquer and Weil 2009; Weil and Rogers 2011).

Despite numerous breakthroughs in documenting the agents of coral disease we do not understand why outbreaks of disease occur. The two most likely explanations are (1) introduction of a pathogen to an area where it was previously absent, as in the case of bubonic plague, and (2) increase in the abundance of a previously rare pathogen due to changes in the physical or biotic environment

as with outbreaks of cholera in polluted waters. A third possibility is the evolution of a new pathogen that sweeps through host populations with devastating effects. Such an explanation is extremely unlikely for Caribbean corals because it would require the synchronous evolution of more than a dozen major coral pathogens within one or two decades.

Data are so far inadequate to identify whether invasions or environmental change were the major factor in the emergence of particular Caribbean coral diseases, but there are valuable hints related to the timing of appearance and severity of diseases. This is especially true for the first outbreaks in the 1970s and early 1980s, most notably WBD, BBD, and the pathogen that caused the massive die-off of the sea urchin *Diadema antillarum* in 1983/84 (Lessios et al. 1984; Lessios 1988; Weil and Rogers 2011). In each case, mass mortality approaching 95–100% occurred 15–25 years before the first episodes of extreme heating events due to global warming or any other documented regional environmental change. It is therefore of considerable interest that the effects of WBD and *Diadema* disease have been so much more extreme than in other tropical seas. Nothing like the mass mortality of *Diadema* has affected any echinoderm throughout the entire Indian Ocean or tropical Pacific, nor has any genus of Indo-Pacific acroporid suffered such broad and lasting extirpation as Caribbean *Acropora palmata* and *A. cervicornis*.

More progress has been made in understanding the causes of more recent and seemingly chronic disease outbreaks in relation to rising temperatures and the increased abundance of macroalgae after the demise of *Diadema* (Table 3; Figs 12–14). Evidence for a temperature effect comes from increases in the incidence in disease after extreme heating events and coral bleaching (Weil and Rogers 2011). However, such outbreaks of disease may result either from a general weakening of coral due to the physiological distress caused by bleaching or thermal stress per se. Experiments are needed to help resolve these alternatives.

In contrast, numerous recent experiments have demonstrated that physical contact or even close proximity to various macroalgae may also trigger the outbreak of a wide variety of pathological responses including virulent diseases in corals

(Nugues et al. 2004; Kline et al. 2006; Smith et al. 2006; Rosenberg et al. 2007; Knowlton and Jackson 2008; Barott and Rohwer 2012; Morrow et al. 2012; Rasher et al. 2012; but see Vu et al. 2009 for somewhat contrary results). Toxic allelochemicals from macroalgae also disrupt the complex microbial communities present on the surface of coral colonies, and may cause bleaching and death of coral tissues when in direct contact (Rasher and Hay 2010; Rasher et al. 2011).

In summary, increases in macroalgae principally due to overfishing can disrupt the ecological balance of reef coral assemblages in many ways. Macroalgae inhibit coral growth and may cause direct mortality by shading or abrasion. They also inhibit coral recruitment and disrupt symbiotic assemblages resulting in outbreaks of disease and coral death. These are all testable hypotheses in marine protected areas and wherever else that populations of herbivores may recover and graze down macroalgae to previously low levels of abundance. If the macroalgal disease hypothesis is correct, incidence of coral disease should decline in concert with the decline in macroalgae.

Bleaching and disease are increasingly closely associated in their occurrence but the reasons are obscure because coral cover at some reefs *increased* or was stable after experiencing very high numbers of DHWs (Table 9; Fig. 26). For example, the leeward coast of Bonaire experienced < 1, 5.8, and 13.7 DHWs in 1998, 2005, and 2010 with a proportional *increase* in coral cover of 11, 13, and 0.1% respectively in the two years thereafter. The southwest coast of Curaçao also experienced > 10 DHWs during all three events and percent coral cover *increased* proportionately by 25% after 1998, by 47% after 2005, and declined by just 2% after 2010. Northwest Curaçao and nearby Los Roques experienced 2.3 and 2.9 DHWs in 2005 with 2% and 4% change in coral cover. However, these same locations experienced a precipitous proportional decline in coral cover of 55% and 14% respectively after experiencing 8.3 and 12.5 DHWs in 2010. The decline in NW Curaçao was due to a combination of factors including exceptional storms, increased coastal development, and coral bleaching (Mark Vermeij, personal communication), but the decline at Los Roques was due to massive coral bleaching followed by disease (Bastidas et al. 2012).

In contrast, coral cover on reefs in the USVI and at La Parguera and Vieques in Puerto Rico declined proportionately by 47-53% after enduring 7 to 8.3 DHWs in 2005. These much greater losses in coral cover after experiencing less heat stress than in NW Curaçao and Los Roques strongly imply that the consequences of extreme heating stress are somehow mediated by other environmental factors than heat stress alone. Coral mortality in the USVI and Puerto Rico after 2005 was due primarily to outbreaks of coral disease (Rogers and Miller 2006; Muller et al. 2008; Rogers et al. 2009; Miller et al. 2009; Weil et al. 2009). We postulate that these greater losses in the USVI and Puerto Rico may reflect regional differences in macroalgal abundance, which is generally considerably lower in the southern Caribbean. Support for this hypothesis comes from the experiments discussed above and the anomalous increase in total algal cover at Los Roques of 34 to 54% before and after the 2010 extreme heating event when coral cover declined precipitously, versus the minor proportional losses in coral cover in SW Curaçao where macroalgal cover is much lower.

3g. THE ROLE OF HURRICANES

Strong hurricanes have been a natural occurrence on coral reefs for millions of years and are potentially highly destructive to corals (Woodley et al. 1981; Rogers et al. 1982, 1991). Reefs have routinely recovered from hurricane damage in the past or reefs would not exist. The occurrence of hurricanes varies greatly throughout the wider Caribbean region (Chollett et al. 2012a). Hurricanes are frequent and intense in a broad swath from the northern Lesser Antilles across Puerto Rico, eastern Cuba, Jamaica, and the Cayman Islands to eastern Yucatan as well as southern Florida. In contrast, hurricanes are rare all across the southern third of the Caribbean from Barbados to Nicaragua and points south. Despite these differences, however, average coral cover from 1970 through 1983 was remarkably similar among the 16 locations with old *Diadema* data in Tables 5 and 8. Corals differ greatly in their rates of recruitment, growth, and reproduction. These differences in life history characteristics are believed to have been responsible for a natural pattern of succession of reef communities extending for up to several decades after a storm had passed (Woodley et al. 1981; Rogers 1983a).

Nevertheless, the frequency and intensity of hurricane occurrence have been proposed as important drivers of coral decline on Caribbean reefs, especially since the 1980s when corals have failed to recover in many cases due to some combination of human stressors (Gardner et al. 2005). We therefore examined this hypothesis in two ways using the 16 reefs in Table 8. The first analysis addresses the null hypothesis that coral cover at the 16 locations prior to the mass mortality of *Diadema antillarum* in 1983 was independent of the long-term annual probability of hurricane occurrence at each location over the past 160 years. The second analysis addresses the null hypothesis that the changes in coral cover after 1983 were independent of the numbers of hurricanes that actually occurred at each location after 1983. Hurricanes vary in intensity and the details of their tracks through an area that affect their potential impact on reefs (Fabricius et al. 2008), but such detailed data are available for only a small proportion of hurricanes. Nevertheless, the long-term probability of hurricane occurrence, and their actual frequency since 1983, should provide a good first order estimate of the impact of hurricanes on coral cover both in the past and on reefs today.

Hurricane incidence was measured using the Atlantic Hurricane data set (1851-2012), which tracks the location and intensity of the eye of tropical cyclones every six hours (Jarvinen et al. 1984). Hurricane force winds may extend several kilometers from the hurricane track. We captured the spatial influence of hurricanes by using the buffering system described by Keim et al. (2007) and Edwards et al. (2011). Buffers capture the area of influence of each hurricane by taking into account the intensity of the storm, its asymmetry, and the reduction in wind speed away from the track (Keim et al. 2007; Edwards et al. 2011). The hurricane dataset was used previously by Chollett (2012a) but is here updated to include Bermuda and four more years of data from 2009-2012 (Table 8). Hurricane incidence was extracted for each pixel within the polygon drawn for each reef location in Table 5 (Fig. 27). The number of pixels extracted and the average and standard deviation of hurricane incidence were reported for each of four time periods: (1851-2012, 1970-1983, 1984-1998, and 1999-2012).

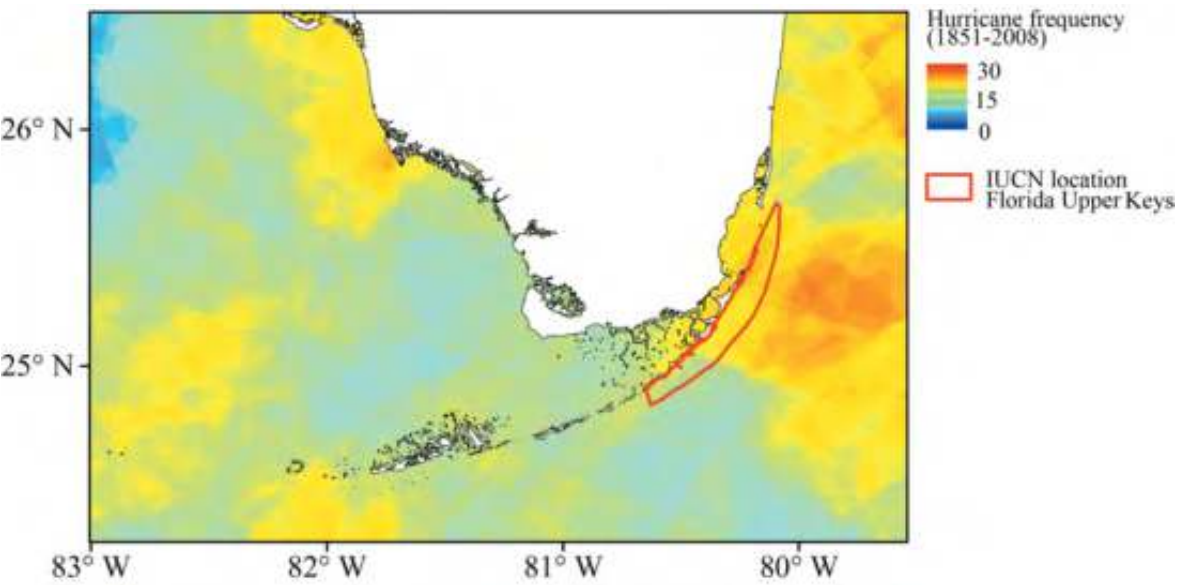


FIGURE 27. Example of the methodology for extraction of the incidence of hurricanes for the Upper Florida Keys.

Coral cover on reefs before 1984 is negatively correlated with the long-term probability of hurricane occurrence but the relationship is not significant (Fig. 28A). This suggests that hurricane frequency was not a major determinant of coral cover on reefs prior to 1984.

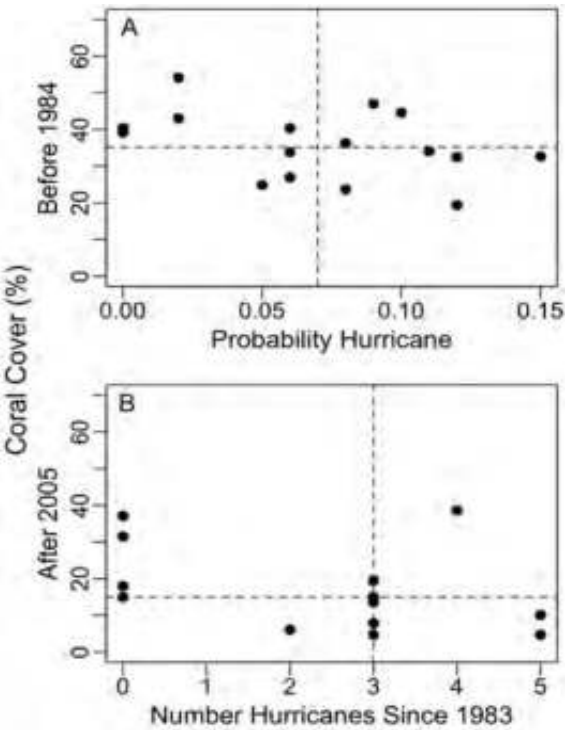


FIGURE 28. Coral cover versus hurricane occurrence for the 16 reef locations in Table 8. (A) There is no relation between the long-term probability of hurricane occurrence at the 16 reefs in Table 5 up to 1983 ($r_s = -0.4$, $p = 0.15$). (B) Since 1984, the number of hurricanes is also uncorrelated with coral cover ($r_s = -0.25$, $p = 0.38$) except when the protected reefs at Bermuda are removed from the analysis ($r_s = -0.57$, $p = 0.04$).

The number of hurricanes that have occurred at the 16 locations since 1984 is highly positively correlated with the long-term probability of hurricane occurrence at the same locations, demonstrating that the incidence of hurricanes over the past 30 years has not departed from the normal pattern ($r_s = 0.67$, $p = 0.01$). Average coral cover since 2005 is negatively but insignificantly correlated with the numbers of hurricanes that have occurred since 1984, due to the very high coral cover at Bermuda despite four hurricanes since 1984 (Table 8, Fig. 28B). Removal of Bermuda from the analyses had no effect on the results for the years prior to 1984, but the negative correlation between coral cover and number of hurricanes since 1984 was significant (Fig. 28B). It is important in this context to remember that acroporids have always been absent from Bermuda where reefs are overwhelmingly dominated by massive corals, which are more resistant to hurricanes than branching species (Woodley et al. 1981).

Fish traps were banned in Bermuda in 1990 and parrotfish are still abundant. In contrast, reefs on the Belize Central Barrier have been overfished since the 1990s (Mumby et al. 2012) in addition to having experienced three hurricanes. Coral cover declined proportionately by 49% (Table 5). Coral bleaching was extensive at Carrie Bow Cay ten days after the passage of Hurricane Mitch (K. Koltes, personal communication), but the reason(s) for bleaching are obscure because

of a huge influx of sediments and freshwater due to > 1 m of rain within 24 hours (Koltes and Opishinski 2009; K. Koltes, personal communication). Massive influxes of freshwater have been previously shown to have caused nearly 100% coral bleaching in Jamaica following hurricane Flora in 1963 (Goreau 1964). Jamaica was already overfished in the 1960s (Jackson 1997) but *Diadema* were extremely abundant and macroalgae virtually absent. These are only isolated examples but suggest that protection of herbivores and wiser land use as in Bermuda may have conferred greater resilience of reefs to hurricanes.

3h. THE SPECIAL CASE OF THE FLORIDA REEF TRACT (FRT)

The ecological situation of the FRT is unique due to its particular environmental setting and the unprecedented scale of human impacts that include all of the drivers discussed in this report (Ault et al. 2005; Keller and Causey 2005; Causey 2008; Kruczynski and Fletcher 2012).

The FRT is a predominantly continental reef system in south Florida and the Florida Keys that is situated towards the northern geographic occurrence of Atlantic coral reefs. Fluctuations in environmental conditions and the long-term probability of hurricane occurrence are among the highest in region. The FRT is also positioned at the junction of Caribbean waters from the south, Gulf of Mexico waters from the West, and the subtropical western Atlantic. Moreover, the reefs of the Florida Keys sit just offshore of Florida Bay into which the Everglades drain. For all of these reasons, the assemblages of species and habitats of the FRT were considerably different from anywhere else in the wider Caribbean region long before human impacts intensified.

Unprecedented increases in land use, coastal development, and pollution of south Florida occurred over the past half century as human populations exploded. The hydrology of the Everglades and Florida Bay has drastically changed and nutrient and sediment influx greatly increased with direct impacts on coastal estuarine habitats and water quality in the Florida Keys. These local dynamics have combined with regional and global environmental change to impact reefs along most of the FRT.

Today the FRT is adjacent to the major metropolitan area of greater Miami with a rapidly growing human population exceeding 5 million while also serving as a popular tourist destination with unparalleled access to the reefs for recreation and exploitation. Intensity of human use and environmental impacts greatly exceeds that of any other region in the wider Caribbean, if not the world. Numbers of fishers, boaters, and divers increase every year. Nearly a million vessels are registered in Florida with a majority in the southern portion of the state. Damage due to boat groundings, propeller scour, anchoring, and shipwrecks is extensive and wastewater runoff enormous. Overfishing has virtually eliminated formerly abundant Goliath and Nassau Groupers and stocks of other target species such as snappers, lobsters, and conchs are overfished.

Establishment of the nearly 10,000 square kilometer Florida Key's National Marine Sanctuary (FKNMS) in 1997 led to the creation of a modest network of no-take marine reserves with a total protected area of only 6% of the total area of the Keys. This action, combined with increasingly restrictive fishing regulations, has led to small increases in a limited number of stocks, and a general slowing of the decline in fish stocks overall. The FKNMS has also been successful in encouraging collaborative management strategies allowing Florida to successfully document and implement corrective actions to improve wastewater and storm water treatment and disposal.

In conclusion, the FRT epitomizes a kind of worst-case scenario in which unprecedented population growth and inadequate governance and regulations have resulted in the critical endangerment of an entire coral reef ecosystem. Despite the positive and courageous actions of the Sanctuary, coral cover is well under 10% and declining. Much more stringent actions will be required for any hope of coral survival.

4. SYNTHESIS

We first review the major results of the analyses of pattern and then focus on the apparent importance of the different drivers of coral reef decline.

4a. PATTERNS OF CHANGE

The three overarching results of this report are that

1. Most of the degradation of Caribbean reefs occurred between the 1970s to early 1990s well before most ecological surveys began.
2. Phase shifts from greater coral to greater macroalgal abundance happened early and are geographically pervasive.
3. Geographic disparity in the fates of reefs at different locations was and is truly enormous.

Timing and rates of reef degradation

Average coral cover throughout the wider Caribbean, Gulf of Mexico, and Bermuda declined by 49% from an overall average of 33.0% before 1984 to 17.7% since 2005 (Tables 2 and 3, Fig. 7). Refinement of our 2005 estimate to take into account the great variation among locations and datasets lowers the 2005 estimate to 14.3% coral cover with an overall decline of 59%. These estimates of loss are considerably lower than Gardner and colleagues' estimate of an 80% decline from 50% to 10% (Gardner et al. 2003) but in good agreement with the estimate of Schutte et al. (2010) of a 60% decline from about 40% to 16% cover. The earlier estimates were based on considerably less data and were disproportionately dominated by surveys from the Florida Reef Tract, US Virgin Islands, and Jamaica that are among the most severely degraded reefs in the entire region.

Coral cover declined at 73% of locations with time series data (Fig. 8). The declines were greatest for locations that began to be studied earliest and over the longest period of time. Indeed, 88% of the total overall Caribbean decline in coral cover occurred between 1984 and 1998, and this increases to 100% for the 21 reef locations with long-term data extending back before 1984 (Table 3). Likewise, 99% of the overall Caribbean increase in macroalgal cover occurred before 1998, with a somewhat lower value of 81% for the 21 long-term reefs.

The same was true for the dramatic declines of iconic species. *Acropora palmata* and *A. cervicornis* began to decline in the 1960s and were virtually ecologically extinct at most Caribbean locations by the mid 1980s (Fig. 18). *Diadema antillarum* was the most important grazer on

overfished Caribbean reefs and common elsewhere until 1983-1984 when more than 95% of all Caribbean *Diadema* died due to an unidentified pathogen (Lessios 1988; Fig. 19). Parrotfish had been extremely reduced at Jamaica, the USVI, and other overfished locations by the 1960s or before (Randall 1961, 1963; Munro 1983; Hay 1984; Lewis and Wainwright 1985), and are rare on most Caribbean reefs today (Fig. 20).

These sobering results of very early decline long before most coral reef ecologists today had ever seen or read about a coral reef are a classic example of the Shifting Baselines Syndrome (Pauly 1995; Jackson and Jacquet 2011; Jackson et al. 2012) and a harsh reminder that what is going on today is the end of a much longer story.

Phase shifts

The dramatic reversal between coral and macroalgal abundance (Fig. 13) occurred over about a decade and is strong evidence for a phase shift in coral reef community structure (Done 1992; Knowlton 1992, 2004; Hughes 1994; Hughes et al. 2010; Schutte et al. 2010). Forty-one percent of the total variation in the PCA ordination of coral and macroalgal community composition at the 21 long-term locations is explained by the shift from coral to macroalgal dominance (Fig. 16).

Some have questioned the generality of phase shifts on coral reefs claiming that the Caribbean example of corals to macroalgae is unrepresentative of the general pattern of overall change (Aronson and Precht 2006; Bruno et al. 2009). However, our results are based on vastly more data and greater geographic coverage than any previous analysis and overwhelmingly support the occurrence of a phase shift at most Caribbean locations from coral to macroalgal dominance. The question is not whether a phase shift occurred, but what might be done about it to return reefs to their thoroughly documented former dominance by abundant corals.

Geographic variation in reef decline

Clues to the possible recovery of Caribbean reefs lie in the enormous variability among Caribbean reef locations today (Table 3 and 5; Figs. 9-12, 14; Appendix 1).

Coral cover for 53 locations since 2005 varies from a low of < 3% off of Port Royal, Jamaica to a high of 53% at the east Flower Garden Banks in the northern Gulf of Mexico (Table 9). Seventeen locations have < 10% coral cover and another 21 between 10 to < 20%. Thus, three quarters of all the Caribbean locations for which we could find data have degraded by at least 50% below the average coral cover before 1984. But 15% of the locations have > 20% cover and another 13% have > 30% cover including Bermuda, Grand Cayman, Jardines de la Reina on the south coast of Cuba, southwest Curaçao, the leeward coast of Bonaire, Flower Garden Banks, and Los Roques Venezuela. This pattern is virtually identical to the distribution of cover in the third time interval of 1999-2011 (Fig. 7). The obvious question is why these reefs with > 30% cover are doing so well compared to all the rest?

4b. DRIVERS OF CORAL REEF DECLINE

Our analyses focused on potential drivers of decline for which there were adequate data for meaningful comparisons. The results are particularly strong for evaluating the effects of overpopulation, overfishing, and global warming, and less so for coastal pollution and invasive species.

Too many people

Tourism is the lifeblood of many Caribbean nations but our evidence strongly suggests that extremely high densities of tourists and residents are harmful to reefs unless environmental regulations to protect reefs are comprehensive, stringent, and effectively enforced. All locations with > 2635 visitors/km²/year have < 14% coral cover except for Bermuda with 39% (Table 7, Fig. 22). Likewise, islands with substantially > 500 residents/km² have < 15% coral cover except for Bermuda. The situation at Bermuda reflects exceptionally effective regulations and the infrastructure to enforce them, as well a greater level of economic well being that obviates the need for subsistence fishing. But without similar protections, the harmful environmental costs of runaway tourism and population growth seem inevitable.

Overfishing

Artisanal fishing for subsistence is crucial to most Caribbean economies but the consequences have been catastrophic for coral reefs. Overfishing

caused steep reductions in herbivores, especially parrotfishes, which are vulnerable to all gear types except hook and line. The greatest reductions occurred where fish traps were the favored gear, although low catches today are resulting in increased spearfishing and larger nets.

The severe consequences of the overfishing of parrotfishes for coral survival were generally unappreciated until the abrupt demise of the sea urchin *Diadema* in 1983-1984 that had increasingly become the last important herbivore on Caribbean reefs (Fig 19; Hay 1984; Hughes 1994; Jackson 1997). *Diadema* and parrotfish compete intensely for food (Randall 1961; Lewis and Wainwright 1985; Hay and Taylor 1985; Carpenter 1990b), and their abundance was inversely proportional until 1983. This inverse relationship provides a rigorous proxy for the assessment of the consequences of historical overfishing of parrotfish in the absence of quantitative data for reef fish abundance before 1983 (Table 8).

Most of our analysis of overfishing focused on the fates of 16 reefs for which we have quantitative data on *Diadema* abundance before the die-off, plus coral cover for the three time intervals 1970-1983, 1984-1998, and 1999-2011 (Tables 3, 5, 8). Nine of the 16 reefs were classified as overfished for parrotfishes by 1983, with *Diadema* densities ranging from 6.9-12.4/m², whereas the other seven reefs were classified as less fished with *Diadema* densities of 0.5-3.8/m². These classifications agreed well with what we could glean from the qualitative literature (Appendix 4).

Reefs where parrotfishes had been overfished before 1984 suffered greater decreases in coral cover (Fig. 23 A-D) and increases in macroalgae (Fig. 23 E-H) than reefs that still had functional populations of parrotfish. Coral cover was independent of *Diadema* densities before 1984 (Fig. 23A) when either *Diadema*, or parrotfish, or both managed to graze down macroalgae to extremely low levels. But all that changed dramatically after the *Diadema* die-off when coral cover became negatively correlated with historical *Diadema* abundance right up to the present day (Fig. 23B, C, D). Conversely, macroalgal cover became positively correlated with historical *Diadema* abundance since there were no longer any abundant herbivores to hold it in check, but the scatter was

much greater and correlations weaker and generally not significant (Figs. 23 E-H).

There is also compelling field and experimental evidence for persistent indirect effects of increased macroalgal abundance that strongly impede coral recovery through decreased recruitment and increased disease (Box 1). Coral recruitment has greatly declined since 1984, at least in part due

to a decline in the parental brood stock, but there is also strong evidence for active interference by macroalgae.

Macroalgae also induce a wide variety of pathological responses including virulent diseases and may release toxic allelochemicals that disrupt microbial communities associated with corals causing bleaching or death.

Box 1. Harmful effects of increased macroalgal (MA) abundance on larval recruitment and outbreaks of disease of Caribbean reef corals (for further details see text).

Type of study	Observation	Reference
<u>Reduction of coral recruitment and survival of juvenile corals</u>		
Field surveys in St. Croix	Coral recruits most abundant in locations of high grazing pressure and low abundance of non-calcareous (fleshy) algae	Rogers et al. 1984
Fouling panel experiments in Curaçao	20-fold reduction in larval recruitment onto upper surfaces of panels in 1998-2000 compared with 1979-1981 (after versus before mass mortality of <i>Diadema</i>) due to blanketing of the panels by MA	Vermeij 2006
Settlement experiments in Belize	Greater larval recruitment onto substrates covered by crustose coralline algae and low recruitment onto surfaces covered by MA	Arnold and Steneck 2006
Laboratory experiments on Larval behavior	Larval avoidance of substrates with all species of MA or cyanobacteria tested	Kuffner et al. 2000
Field observations in the Bahamas	2 to 3-fold increase in coral recruitment at sites where parrotfishes have increased and MA have decreased in protected areas	Mumby et al. 2006, 2007; Mumby and Harborne 2010
Field observations at numerous sites around the Caribbean where <i>Diadema</i> have recently recovered to densities >1/m2	Reduction of MA to very low percent cover and several-fold increases in juvenile corals and coral cover	Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Idjadi et al. 2001
<u>Pathological responses of corals to proximity to macroalgae</u>		
Laboratory experiments with corals and macroalgae from numerous Caribbean locations	Close proximity or contact with MA results in coral death ¹	Nugues et al. 2004; Smith et al. 2006; Rosenberg et al. 2007; Barott and Rohwer 2012; Morrow et al. 2012
Laboratory experiments at various Caribbean locations	Toxic allelochemicals from macroalgae disrupt microbial communities on coral surfaces and may cause bleaching or death on contact with corals	Rasher and Hay 2010; Rasher et al. 2011
¹ But see Vu et al. 2009		

Finally, overfishing may have also indirectly affected the capacity of reefs to recover from damage by hurricanes; something they have routinely done for millions of years (Woodley et al. 1981; Jackson 1991). Over the past few decades, however, corals have increasingly failed to become reestablished on many reefs after major storms (Gardner et al. 2005). We investigated the causes of this apparent shift using the data for the 16 reefs with data from before 1984 in Tables 5 and 8. Coral cover was independent of the long-term probability of hurricane occurrence before 1984 (Fig. 28A), but not afterwards (Fig. 28B). The reasons are obscure because the locations that have experienced the most hurricanes since 1984 were also among the most extremely overfished (Table 8; median for overfished locations = 3 hurricanes since 1984, median for less fished locations = 0 hurricanes since 1984). But it is unlikely to be just a coincidence that the greater vulnerability to storms began just after the *Diadema* die-off, especially given the extraordinary resilience of coral cover at Bermuda after 4 hurricanes since 1984.

Coastal pollution

Almost everyone agrees that coastal pollution is an increasingly serious problem for coral reefs but there are precious few rigorously and consistently collected data comparable to that for Degree Heating Weeks (Table 9). Thus, it is difficult to do more than compile a list of local situations on coral reefs and attempt to generalize as has been done for sedimentation stress (Rogers 1990; Fabricius 2005) and oil spills (Guzmán et al. 1991; Burns et al. 1993, 1994; Guzmán and Holst 1993), but not yet for nutrients.

Nevertheless, limited comparative data for water transparency at three CARICOMP sites based on simple secchi disk observations suggest that water quality on Caribbean reefs is declining greatly (Table 9; Fig. 25). Water transparency declined significantly over 20 years at Carrie Bow Cay due to steep increases in the clearing of land for agriculture and for coastal development in Belize and continued deforestation of the high coastal mountains along the Gulf of Honduras in Guatemala and Honduras (Burke and Sugg 2006; Fig. 25 A-B). Similar declines were observed at La Parguera, Puerto Rico (Fig. 25C). Secchi disk measurements were a standard part of the CARICOMP protocol and it is unfortunate that the

measurements were made at so few CARICOMP sites. The results from strongly suggest a very serious decline in water quality that is being widely ignored.

Global climate change

We began our study expecting to document very large and pervasive consequences of coral bleaching but that was resoundingly not the case. Our first analyses were based on the ReefBase compilation of extreme bleaching events that showed no significant relationship between the numbers of extreme events/locality and coral cover at locations across the wider Caribbean, Gulf of Mexico and Bermuda. We next requested and obtained Pathfinder Sea Surface Temperature data from the National Oceanographic Data Center through the assistance of Mark Eakin and Scott Heron. The result is the comprehensive data for degree heating weeks (DHWs) for all 88 localities with coral cover in Table 9.

Graphs of the proportional loss in coral cover in relation to numbers of DHWs in the two years following the 1998, 2005, and 2010 major heating events are surprisingly flat, essentially mirroring our earlier results (Fig. 26). All the slopes are weakly negative but non-significant in spite of the well-documented cases of extreme coral bleaching followed by disease that has severely affected reefs in the USVI and Puerto Rico after 2005 and elsewhere (Miller et al. 2009; Weil et al. 2009). Repeating the analyses using only the data for locations that suffered ≥ 8 DHWs gives even weaker and anomalous results.

The reason for the general lack of correlation is that coral cover at several locations has substantially increased or held steady after extreme heating events (points on or above the lines of zero percent change in Fig. 26). Many of these exceptional locations have either high parrotfish abundance or low macroalgal cover, or both (Fig. 26, Tables 2 and 5). This implies that high grazing pressure and/or low macroalgal abundance may have somehow increased the resilience of corals to the otherwise fatal combination of massive bleaching followed by disease, which has been the generally accepted pattern for the consequences of extreme heating events. Our results do not imply that coral bleaching is unimportant or that it will not become even more dangerous

in the future (Hoegh-Guldberg et al. 2007). But they do belie any regionally consistent effects of coral bleaching up to now, and suggest that strong measures to protect parrotfish and other grazers could make an important difference for the survival of corals in an increasingly warmer world.

None of this would necessarily apply to the deleterious effects of ocean acidification which has not been treated here because it is too soon to know what the effects are now much less in the future. If present trends of decreased pH continue, however, the ability of corals and other calcareous reef species to deposit skeletons will be increasingly but perhaps not fatally compromised (Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011).

Invasive species

The explosion of exotic Pacific lionfish throughout the wider Caribbean has wreaked havoc in Caribbean fish communities. But as serious as the potential consequences may be, they pale in comparison to the introduction of the pathogen that caused the die-off of *Diadema antillarum* or the effects of WBD on acroporid corals. The first occurrence of *Diadema* mass mortality at the Caribbean entrance of the Panama Canal (Lessios 1988) coupled with the enormous increases in bulk carrier shipping and the salt water aquarium trade in the 1960s and 1970s (Carlton 1996; Drake et al. 2007) can hardly be a coincidence.

The Caribbean is effectively a Mediterranean sea and has been the oceanographically and geographically most isolated tropical ocean on the planet since the continuous emergence of the Isthmus of Panama 3-5 million years ago (Jackson and O'Dea 2013). This strongly suggests that, by analogy to the fates of the original Americans after their first contact with Europeans (Crosby 1986; Mann 2005), Caribbean species should be exceptionally prone to the impact of introduced diseases. And this appears to be the case. We know of no other examples of the virtual elimination due to disease of any marine species throughout the entire extent of the Indian or Pacific oceans comparable to the demise of Caribbean *Diadema* and acroporids. This interpretation is also consistent with the failure to discern any environmental shift in the 1970s that could have triggered the outbreak of disease.

Concluding remarks

Overpopulation in the form of too many tourists and overfishing appear to be the two best predictors to date of the overall decline in Caribbean coral cover over the past 30 or more years. Coastal pollution is undoubtedly increasingly significant but there are too little data. Increasingly warming seas have caused extensive coral bleaching and mortality and pose an increasingly ominous threat in the future. But so far extreme heating events appear to have been of surprisingly limited and local significance.

5. RECOMMENDATIONS FOR MANAGEMENT

Our results challenge much of the conventional wisdom about the relative importance of global climate change versus more local impacts of overdevelopment, coastal pollution, and overfishing as the primary drivers of coral reef degradation to date and emphasize the critical importance of historical perspective for coral reef management and conservation (Jackson et al. 2001; Pandolfi et al. 2005; Knowlton and Jackson 2008; Hughes et al. 2010). The threats of climate change and ocean acidification loom very large for the future but have not been the major drivers of the decline of Caribbean corals up to now.

Overemphasis on climate change distracts attention from acute local to regional problems about which much could be done to improve conditions on reefs. It also provides an excuse for managers and governments not to make the hard decisions required to stop overfishing, coastal pollution, and unsustainable development and to do the simple, basic monitoring essential for adaptive management.

Smart decisions can make an enormous difference for the wellbeing of coral reefs and the people and enterprises that depend upon them. No place is close to perfect and everywhere is threatened, but the higher coral cover and comparative resilience to extreme heating events or frequent hurricanes on most reefs in Bermuda, Bonaire, Curaçao, the Venezuelan parks, the Flower Garden Banks, and the Jardines de la Reina in Cuba provide clear examples of what could begin to be achieved by strong and effective environmental regulation

(albeit that the regulations greatly differ among these different sites).

Four major recommendations emerge from this report:

1. Adopt robust conservation and fisheries management strategies that lead to the restoration of parrotfish populations, including the listing of the parrotfish in relevant annexes of the Protocol concerning Specially Protected Areas and Wildlife (SPA protocol) of the UNEP Caribbean Environment Programme. A recommendation to this effect was passed unanimously at the October 2013 International Coral Reef Initiative Meeting in Belize (see Box 2 below).

The most important recommendation based on the evidence of this report is the urgent and immediate need to ban fish traps and fishing of any kind for parrotfish and to severely restrict and regulate all other kinds of fishing throughout the wider Caribbean including spearfishing, gill nets, long lines, and all other destructive fishing practices.

The need for strong fisheries regulations has been obvious for decades (Thompson 1945; Randall 1963; Munro 1983; Hay 1984; Hughes 1994; Jackson 1997; Jackson et al. 2001), but only the managers of Bermuda, Los Roques, the Flower Gardens Banks, Bonaire, Jardines de la Reina, and most recently Belize have taken effective action. Given current trends, reef corals can be expected to become ecologically extinct in the Florida Keys, US Virgin Islands, and most of Jamaica within a decade.

With a few local exceptions, reef associated fish stocks are severely overfished and depleted throughout the wider Caribbean. The market value of remaining fisheries is miniscule compared to the damage fishing does to reefs in terms of lost tourist revenues, coastal protection, and the other ecosystem services reefs provide (Pandolfi et al. 2005). Without effective management and welfare, subsistence fishing of ever-depleted stocks will remain vitally important for the very survival of artisanal fishers living on the edge, but the costs of providing alternative dignified livelihoods for these fishers pale in comparison to the enormous losses of coral reef resources and biodiversity caused by continued overfishing.

2. Simplify and standardize monitoring of Caribbean reefs and make results freely available in real time to promote adaptive management.

There is an urgent need to develop *simple, standardized* monitoring protocols to assess in real time the condition of reefs throughout the wider Caribbean. CARICOMP and AGGRA made important progress but protocols were not consistently followed. Highly elaborate and costly programs in the US Virgin Islands and Florida are impractical to achieve elsewhere.

Most of the information for this report came from individual scientists who generously shared their data. But it took nearly two years to begin to use it reliably because of the diversity of metrics, formatting errors, and internal inconsistencies. Much of the data was unusable because we could not verify locations, depths, and missing metadata. The situation is inexcusable and no one should ever have to go through such an exercise again. In contrast, the Center for Tropical Forest Science and partners monitor 48 standardized forest plots in 22 countries containing 4.5 million trees that are routinely surveyed with up-to-date data readily accessible online (Losos and Leigh 2004).

The results of this report further suggest that regular and consistent monitoring of a small number of key variables would be sufficient to establish status and trends for well-informed adaptive management:

1. Percent cover of corals and macroalgae,
2. Abundance and biomass of parrotfish and *Diadema* abundance,
3. Coral recruitment measured as the density of small colonies < 40 mm,
4. Prevalence of coral disease, and
5. Water transparency measured by a secchi disk

Additional information including abundance of other herbivores and outbreaks of bleaching and coral disease are also highly informative. The bottom line, however, is that reefs with abundant coral, little macroalgae, abundant herbivores, strong coral recruitment, and clear water are healthy by any standard, and those that depart from that pattern are not. We should make sure that all Caribbean nations have all of this simple, basic information before embarking on more complex and challenging

endeavors of greater interest to scientists than any value to the managers on the ground.

3. Foster communication and exchange of information

Resources are needed to revitalize the Caribbean node of the GCRMN and other mechanisms to foster exchange of information and cooperation. The GCRMN Workshop in Panama was the first time most of the participants had met or interacted with each other. Ignorance of the work of participants from different countries was great and participants expressed frustration about working in isolation of what was going on elsewhere.

4. Develop and implement adaptive legislation and regulations to ensure that threats to coral reefs are systematically addressed, particularly threats posed by fisheries, tourism and coastal development as determined by established indicators of reef health.

We understand that action upon these recommendations will be a matter of local and national socioeconomic and political debate. But the implications of our scientific results are unmistakable: *Caribbean coral reefs and their associated resources will virtually disappear within just a few decades unless all of these measures are promptly adopted and enforced.*

RECOMMENDATION

on addressing the decline in coral reef health throughout the wider Caribbean: the taking of parrotfish and similar herbivores

Adopted on 17 October 2013, at the 28th ICRI General Meeting (Belize City)

Background

The latest report of the Global Coral Reef Monitoring Network (GCRMN), entitled: *Status and Trends of Caribbean Coral Reefs: 1970-2012* is the first report to document quantitative trends of coral reef health based on data collected over the past 43 years throughout the wider Caribbean region.

The results of the study clearly show:

- Coral reef health requires an ecological balance of corals and algae in which herbivory is a key element;
- Populations of parrotfish are a critical component of that herbivory, particularly since the decline of *Diadema* sea urchins in the early 1980s;
- The main causes of mortality of parrotfish are the use of fishing techniques such as spearfishing and, particularly, the use of fish traps.

The Report further identifies that overfishing of herbivores, particularly parrotfish, has been the major drivers of reef decline in the Caribbean to date, concluding that management action to address overfishing at the national and local levels can have a direct positive impact on reef health now and for the future. *In some areas of the wider Caribbean (for example Bermuda and the Exuma Cays Land and Sea Park in the Bahamas, and more lately in Belize and Bonaire), active management including bans on fish traps, has led to increases in parrotfish numbers and consequent improvement in reef health and resilience to perturbations including hurricanes. This is in contrast to other areas within the Caribbean, where heavily fished reefs lacked the resilience to recover from storm damage.*

Positive impacts on reef health demonstrably have spill over effects on local economies, including the potential for alternative livelihoods to fishing, thanks to increased tourism revenues, replenishment of fish stocks and restoration of ecosystem services such as shoreline protection.

It is recognised that in the Caribbean there are varying levels of community reliance on fishing in general and the taking of parrotfish in particular. However, in light of the evidence now available, and in accordance with ICRI's Framework for Action cornerstone of 'integrated management' (which includes fisheries management), the International Coral Reef Initiative would like to highlight the benefits of strong management to protect reefs from overfishing, and urges immediate action to effectively protect parrotfish and similar herbivores.

Accordingly, the International Coral Reef Initiative urges Nations and multi-lateral groupings of the wider Caribbean to:

1. **Adopt** conservation and fisheries management strategies that lead to the restoration of parrotfish populations and so restore the balance between algae and coral that characterises healthy coral reefs;

2. **Maximise** the effect of those management strategies by incorporating necessary resources for outreach, compliance, enforcement and the examination of alternative livelihoods for those that may be affected by restrictions on the take of parrotfish;
3. **Consider** listing the parrotfish in the Annexes of the SPAW Protocol (Annex II or III) in addition to highlighting the issue of reef herbivory in relevant Caribbean fisheries fora;
4. **Engage** with indigenous and local communities and other stakeholders to communicate the benefits of such strategies for coral reef ecosystems, the replenishment of fisheries stocks and communities' economy.

Annex: Executive Summary - Status and Trends of Caribbean Coral Reefs; 1970-2012, GCRMN Report

6. REFERENCES

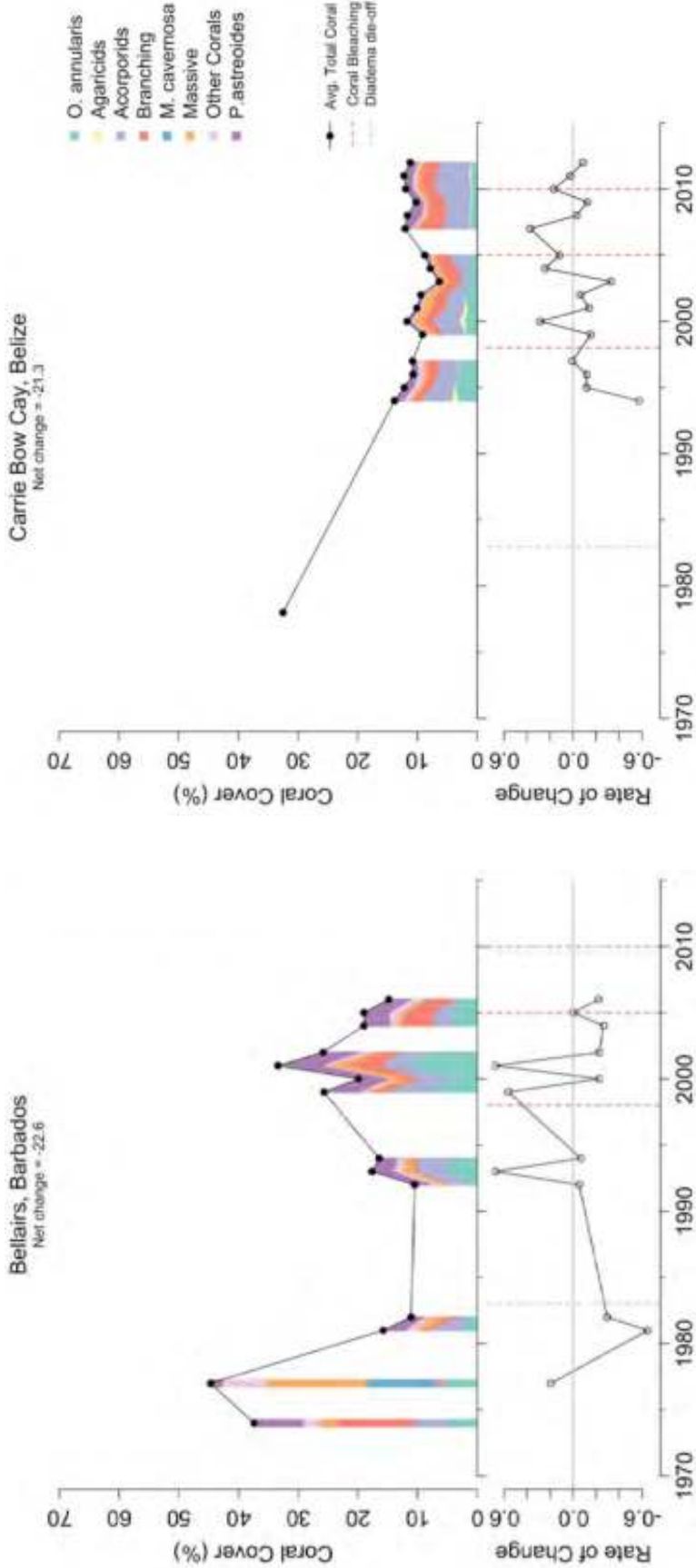
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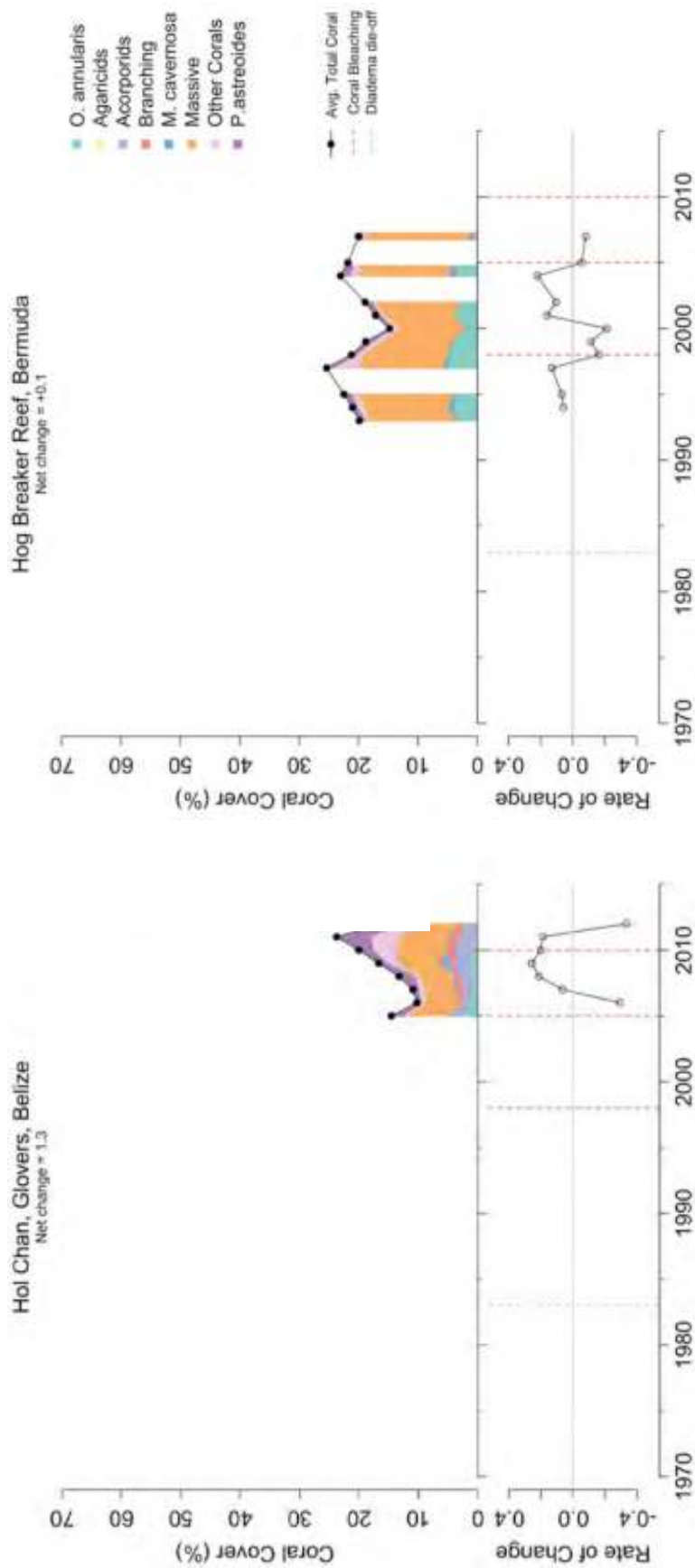
APPENDICES

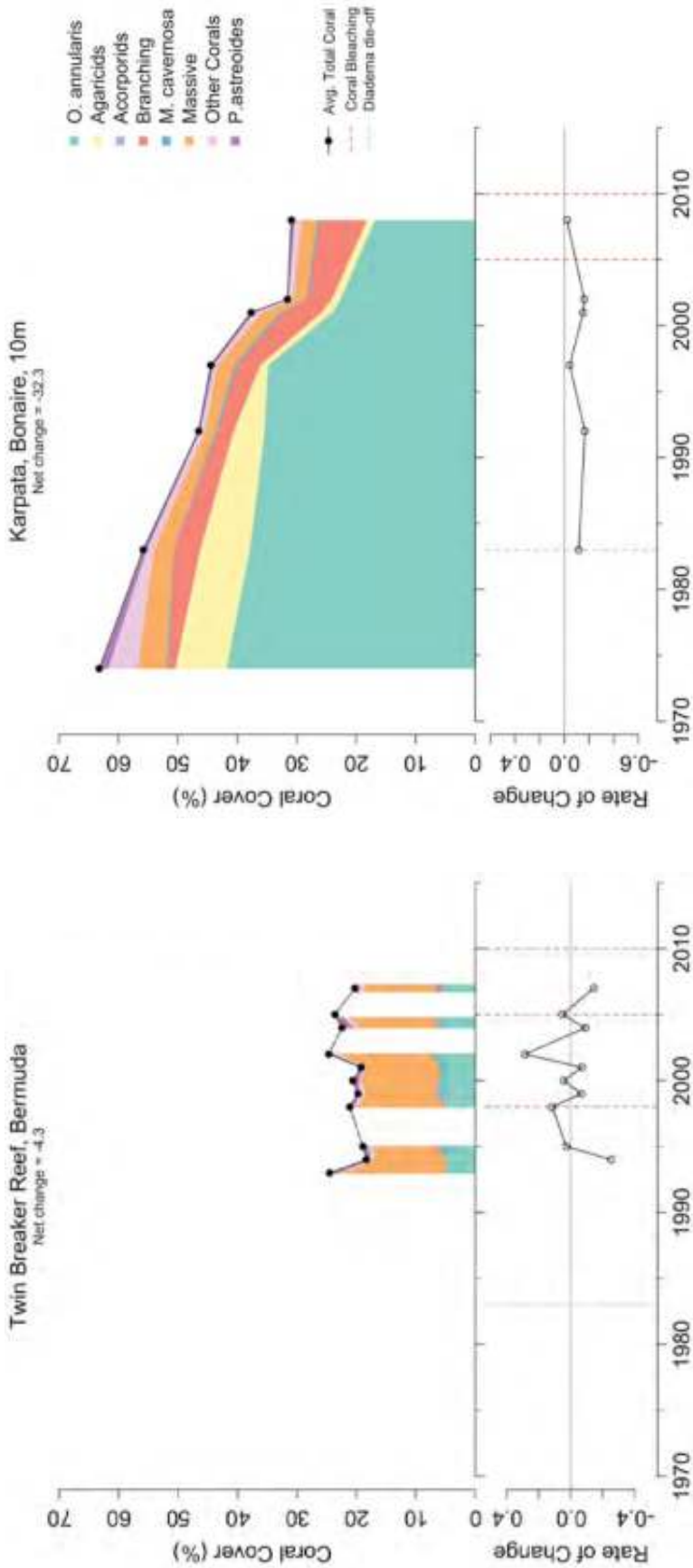
Appendix I: Database structure

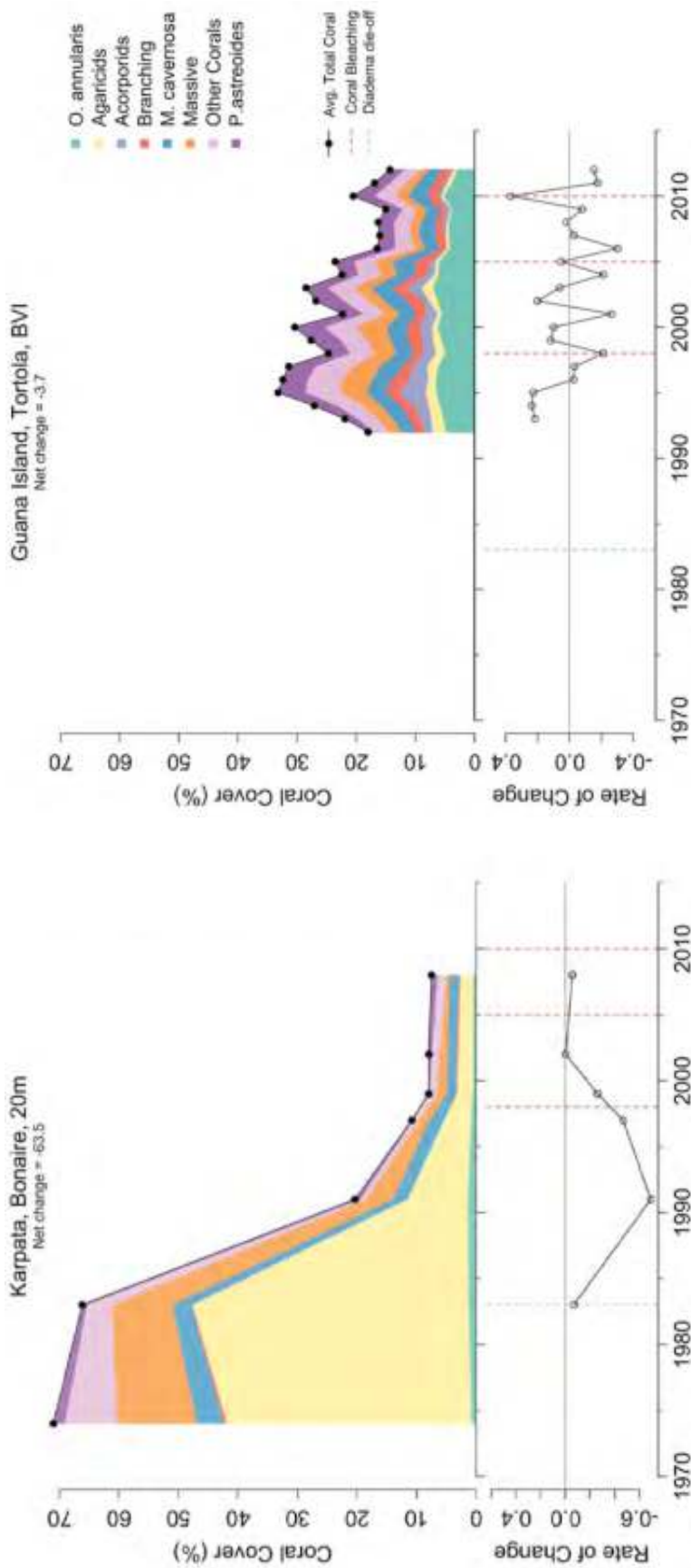
Field	Field Options
Contact Person	
DataLevel	Raw; Summarized with error; Summarized without error
Latitude	
Longitude	
Country	Antigua & Barbuda; Bahamas; Barbados; Belize; British Virgin Islands; Cayman Islands; Columbia; Costa Rica; Cuba; Dominica; Dominican Republic; French Antilles; Grenada; Guatemala; Haiti; Honduras; Jamaica; Mexico; Netherlands Antilles; Panama; Puerto Rico; St. Kitts & Nevis; St. Lucia; St. Vincent & the Grenadines; Trinidad & Tobago; Turks & Caicos; USA; USVI; Venezuela
Location	
ReefSite	
Replicate ID	
Management	No-take MPA; Restricted take MPA; Restricted take MPA; Restricted land-use MPA; No management; Other (explain)
StartYearManagement	
StartYear	
EndYear	
ReefType	Barrier Reef; Deep Reef; Fringing Reef; Hard Bottom; Patch Reef; Spur and Groove; Bank Reef; Atoll; Back Reef
ReefZone	A. cervicornis Zone; A. palmata Zone; Escarpment; Fore Reef Slope; Gorgonian Zone; Reef Crest; Reef Flat; Ridge; Trough; Lagoon
ReefSlope	Flat ; Gentle; Steep; Wall
WaveExposure	Exposed; Protected; Semi-protected
SampleDesign	Random; Selective; Haphazard; Stratified Random
SamplingMethod	Belt Transect; Chain Transect; Linear-Point Intercept Transect; Photo Quadrat; Photo Transect; Quadrat; Video Transect; Continuous transect; Visual estimate
Permanent	Yes; No
SamplingUnit	Single; Multiple
NoOfReplicates	
SampleArea	
SampleAreaUnit	meters; feet
NumberPointsSampled	
MinDepth	
MaxDepth	
MedianDepth	
DepthUnit	meters; feet
Published	Yes-reports; Yes-papers; No
Reference	
UrchinSamplingMethod	Belt Transect; Chain Transect; Linear-Point Intercept Transect; Photo Quadrat; Photo Transect; Quadrat; Video Transect
UrchinSamplingNoOfReplicates	Single; Multiple
UrchinAreaSurveyed	
UrchinAreaSurveyedUnit	meters; feet
PercentTotalCoralIncludesMillepora?	Yes; No

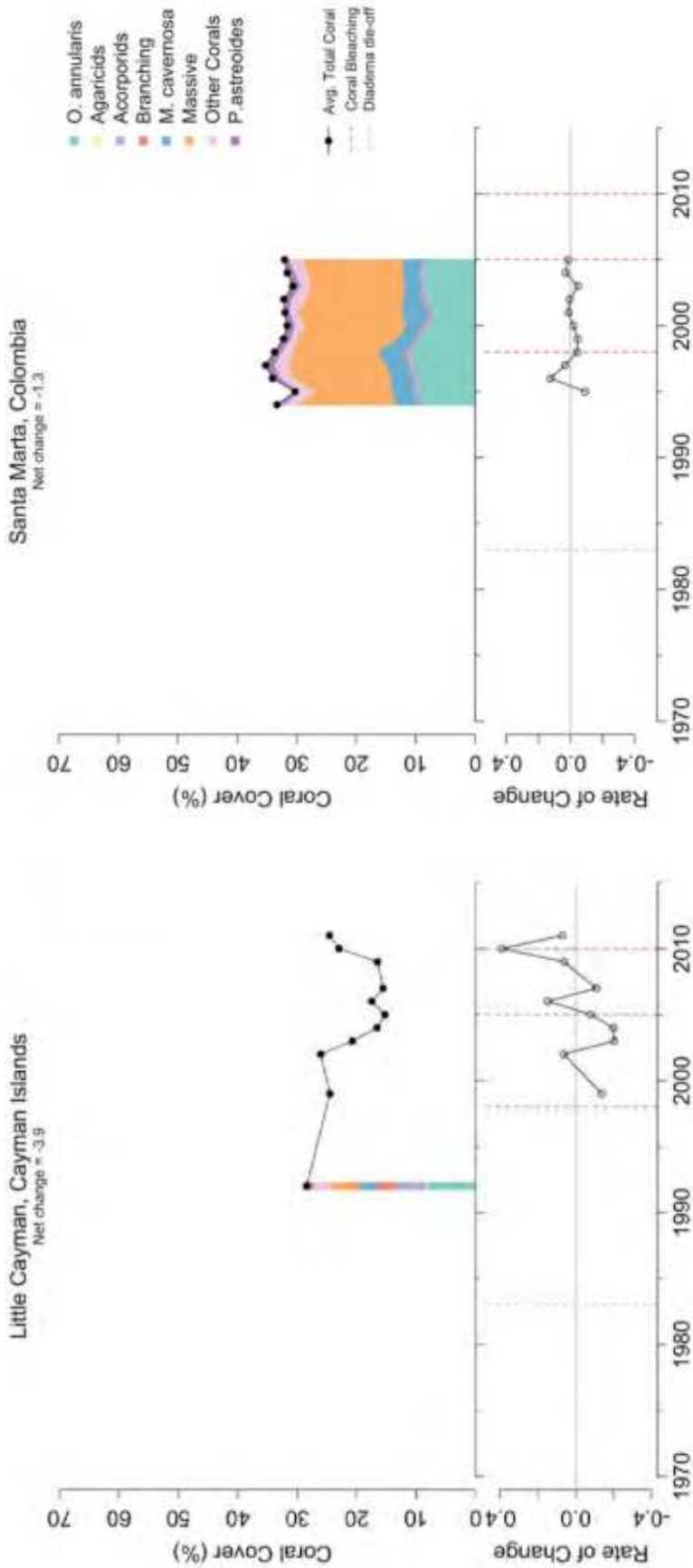
Appendix II: Timelines of coral cover and composition for 40 reef sites

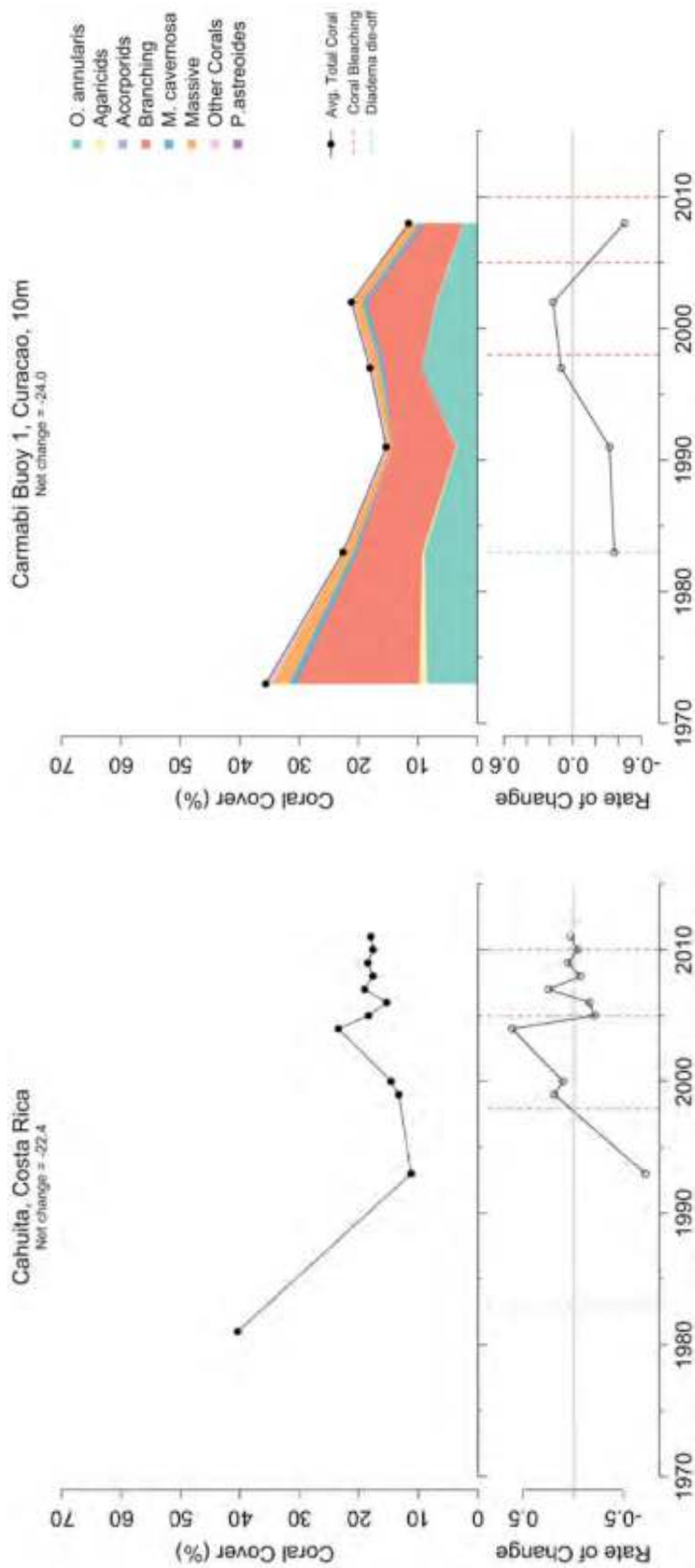












COUNTRIES, STATES, AND TERRITORIES

- Antigua & Barbuda
- Bahamas
- Barbados
- Belize
- Bermuda
- Bonaire
- British Virgin Islands
- Cayman Islands
- Colombia
- Costa Rica
- Cuba
- Curaçao
- Dominica
- Dominican Rep.
- Flower Garden Banks
- Florida Keys
- French Antilles
- Grenada
- Guatemala
- Honduras
- Jamaica
- Mexico
- Navassa Island
- Nicaragua
- Panama
- Puerto Rico
- Saba, St. Maarten, and St. Eustaius
- St. Kitts & Nevis
- St. Lucia
- St. Vincent & the Grenadines
- Trinidad & Tobago
- Turks & Caicos
- US Virgin Islands
- Venezuela

ANTIGUA & BARBUDA

Coauthors: Marilyn Brandt, MACC, AGRRA
and Reef Check

Geographic Information

Coastal Length:	285 km
Land Area:	463 km ²
Maritime Area:	109,845 km ²
Population:	69,886
Reef Area:	116 km ²
Number of hurricanes in the past 20 years:	6

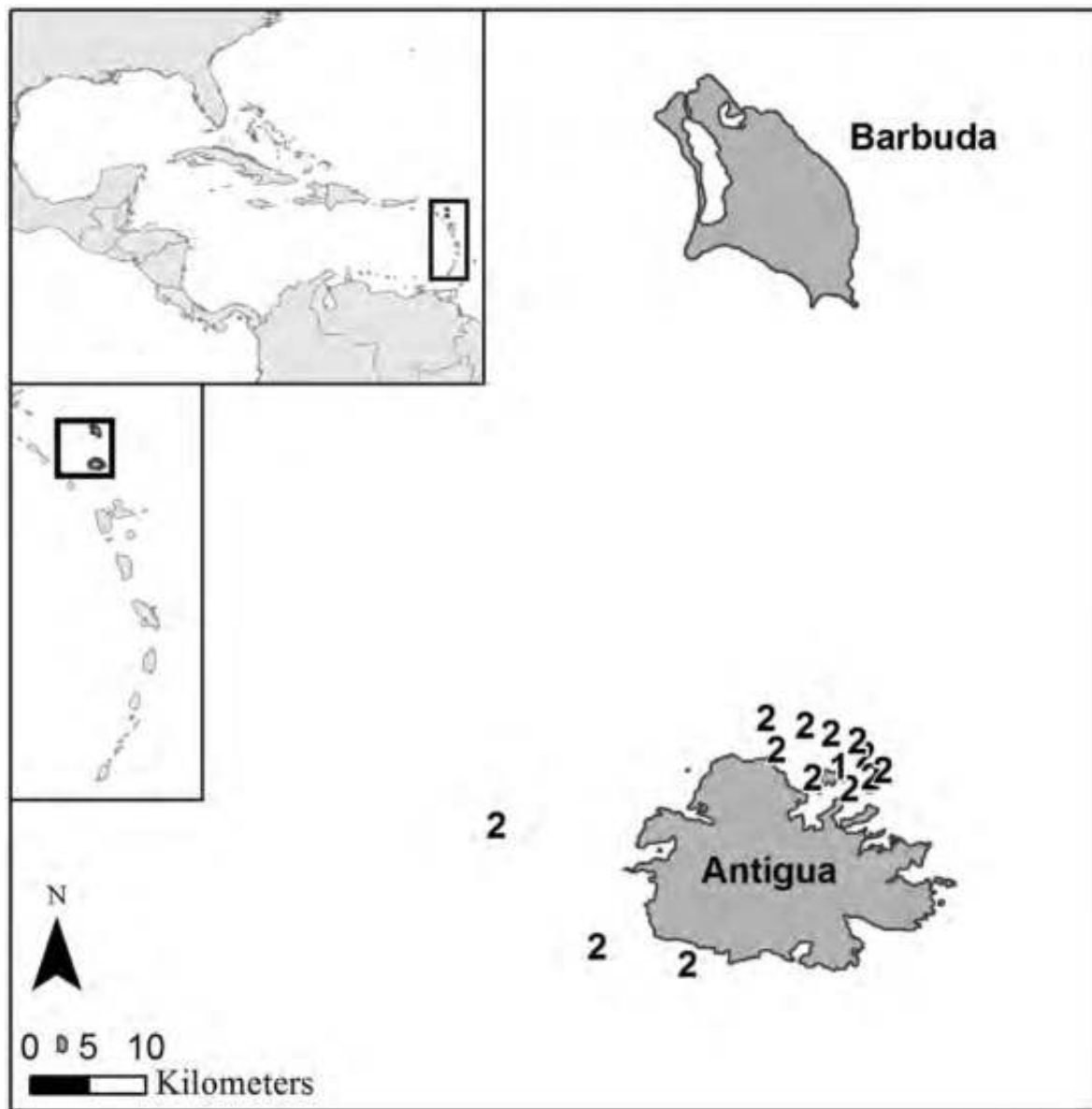


Fig. 1.1 Map of Antigua & Barbuda, codes represent studies listed in Table 1.1. Missing map code(s) due to unavailable coordinates.

Table 1.1 Collected data sources from Antigua & Barbuda, codes represent individual studies. Refer to Fig. 1.1 for locations; * denotes original data; full references found in published data sources.

Map Code	Contributor	Time Period	Year Count	Coral	<i>Diadema antillarum</i>	Macroalgae	Fishes
1	MACC* ¹	2007-2008	2	X		X	
2	Brandt, Marilyn/ AGRRA* ²	2005	1	X	X		X
3	Bauer 1980 ³	1979	1		X		
4,5	Reef Check*	2003-2004	2		X		

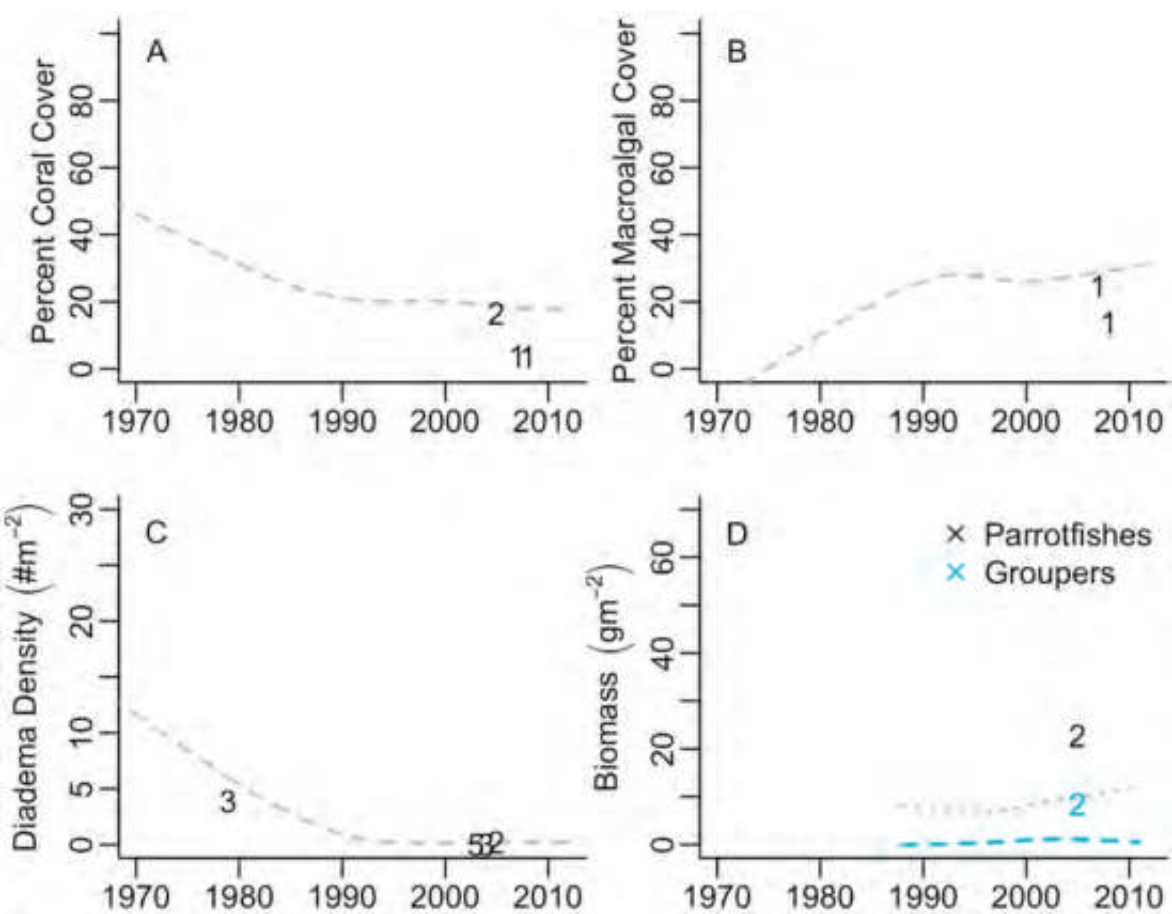


Fig. 1.2 Average percent cover of live corals (A) and macroalgae (B), density of *Diadema antillarum* (C), and biomass of parrotfishes and groupers (D) in Antigua & Barbuda. Dotted line represents the average of Caribbean data collected for this report (codes as in Table 1.1 and Figure 1.1).

General Literature

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Published Data Sources

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³ Bauer JC (1980) Observations on geographical variations in population density of the echinoid *Diadema antillarum* within the western north Atlantic. Bulletin of Marine Science 30: 509-515.

BAHAMAS

Coauthors: Dan Brumbaugh, John Bruno, Mark Chiappone, Craig Dahlgren, Phil Dustan, Brooke Gintert, Alastair Harborne, Mark Hixon, Allison King, Lindy Knowles, Patricia Kramer, Philip Kramer, Judy Lang, Casuarina McKinney-Lambert, Peter Mumby, Ivan Nagelkerken, Eric Pante, Kathleen Sullivan Sealey, Chris Stallings, AGRRA, CARICOMP, Khaled bin Sultan Living Oceans Foundation and Reef Check

Geographic Information

Coastal Length:	11,145 km
Land Area:	13,370 km ²
Maritime Area:	622,273 km ²
Population:	304,107
Reef Area:	4,081 km ²
Number of hurricanes in the past 20 years:	13

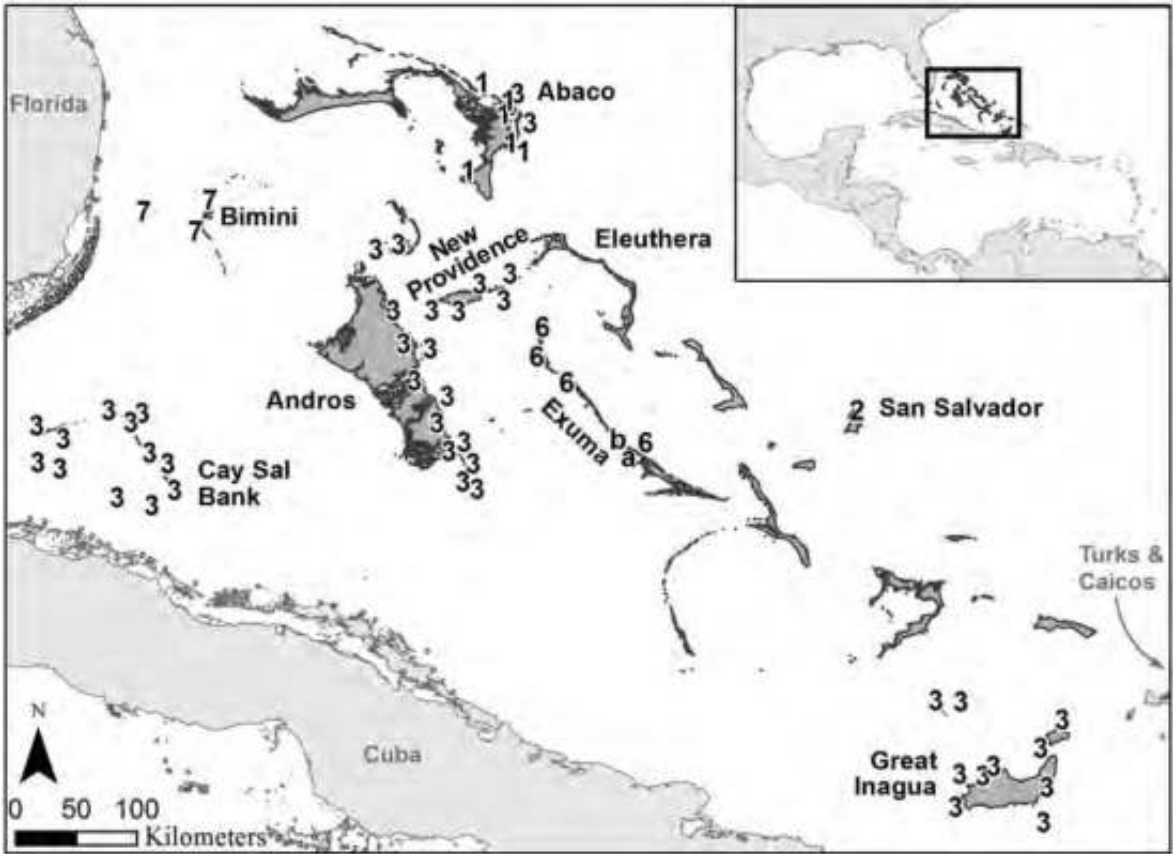


Fig. 2.1 Map of Bahamas, codes represent studies listed in Table 2.1. Missing map code(s) due to unavailable coordinates.

Table 2.1 Collected data sources from Bahamas, codes represent individual studies. Refer to Fig. 2.1 for locations; * denotes original data; full references found in published data sources.

Map Code	Contributor	Location	Time Period	Year Count	Coral	<i>Diadema antillarum</i>	Macroalgae	Fishes
1	Bruno, John*	Abaco	2010-2011	2	X	X	X	
2	CARICOMP* ¹	Fernandez Bay	1994-1998, 2001, 2003-2006	10	X	X	X	
3	AGRR/LOF* ^{2,3,4,5,12,13,14,15}	Abaco; Andros; Cay Sal Bank; Inaguas; New Providence	1998-1999, 2008, 2011	4	X	X	X	X
6	Harborne, Alastair; Mumby, Peter* ^{6,7,8}	Exuma Cays Land and Sea Park (ECLSP)	2004, 2007	2	X	X		X
7	Nagelkerkan, Ivan*	Bimini	2006	1	X			
8	Hay 1984 ⁹	Eleuthera	1981	1		X		
9	Reef Check*	Andros; Paradise Island	1999-2000, 2002-2007	8		X		
a	Hixon, Mark; Stallings, Chris*	Southern Exumas	1993-2005	13				X
b	Dustan, Phil; King, Allison; Pante, Eric* ¹⁰	Iguana Cay, Exuma	1991, 2004	2	X			
c	Bauer 1980 ¹¹		1978	1			X	
d	AUTEC/Patricia Kramer	Andros	2002-2011	7	X			

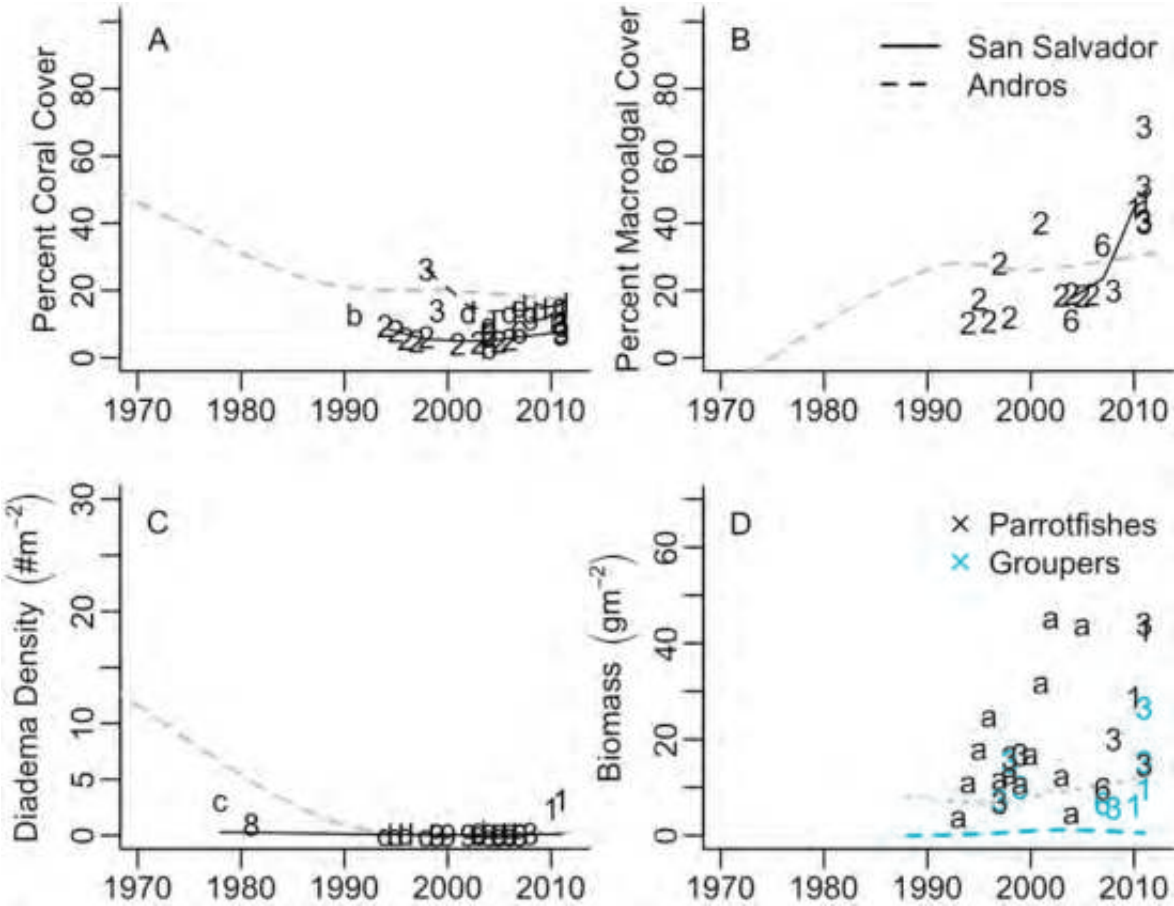


Fig. 2.2 Average percent cover of live corals (A) and macroalgae (B), density of *Diadema antillarum* (C), and biomass of parrotfishes and groupers (D) in Bahamas. Dotted line represents the average of Caribbean data collected for this report (codes as in Table 2.1 and Figure 2.1).

BARBADOS

Coauthors: Caroline Bissada-Gooding, Angelique Brathwaite, Hazel Oxenford, Nicholas Polunin, Richard Suckoo, Ivor Williams, CARICOMP and Reef Check

Geographic Information

Coastal Length:	96 km
Land Area:	443 km ²
Maritime Area:	186,827 km ²
Population:	282,819
Reef Area:	62 km ²
Number of hurricanes in the past 20 years:	0

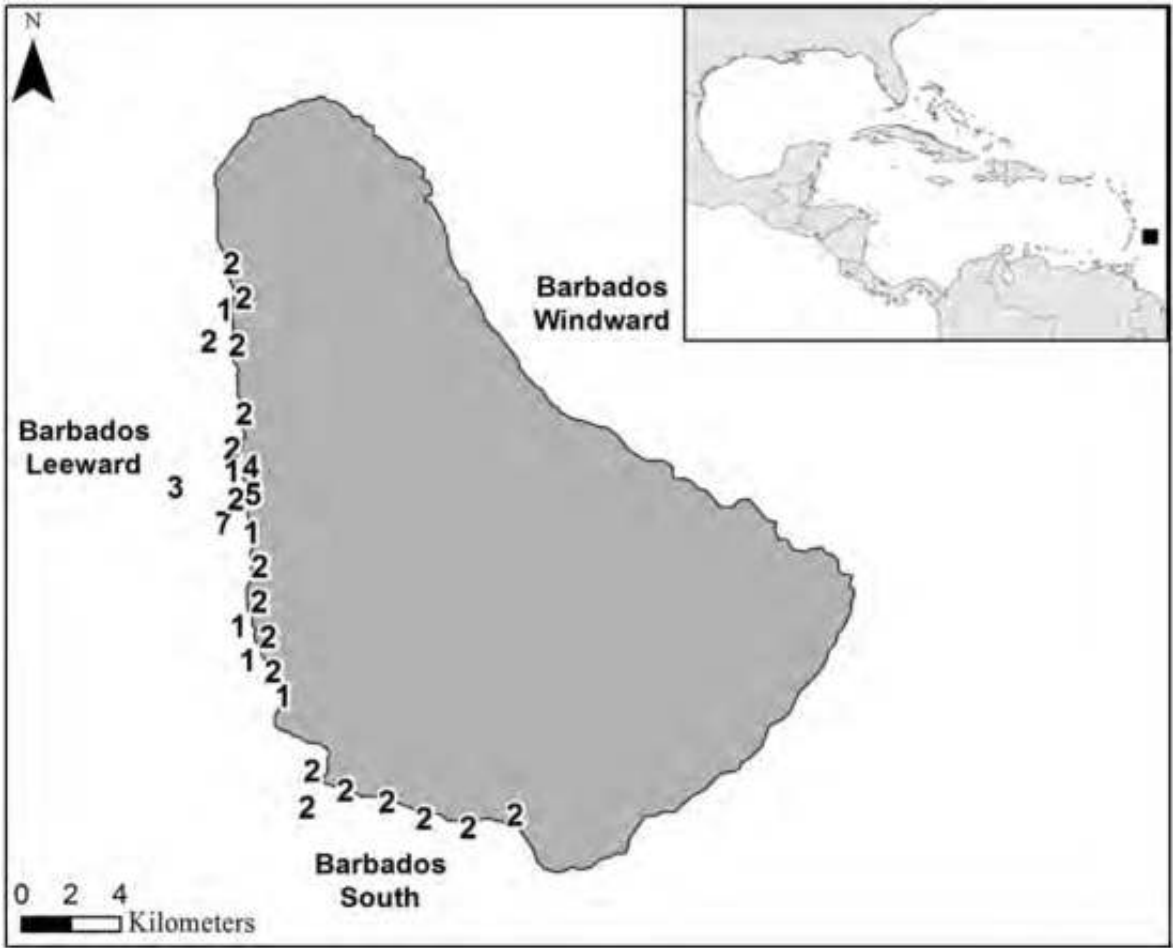


Fig. 3.1 Map of Barbados, codes represent studies listed in Table 3.1. Missing map code(s) due to unavailable coordinates.

Map Code	Contributor	Time Period	Year Count	Coral	<i>Diadema antillarum</i>	Macroalgae	Fishes
1	Allard 1994 ¹	1992	1	X			
2	Brathwaite, Angelique* ²	1982, 1987, 1992, 1997, 2002, 2007	6	X	X	X	
3	Liddell & Ohlhorst 1988 ³	1977	1	X		X	
4	Oxenford, Hazel/ CARICOMP* ⁴	1993-1994, 1998-2002, 2004-2006	10	X	X	X	
5	Scoffin 1993 ⁵	1974, 1981, 1992	3	X			
6	Tomascik & Sander 1987 ⁶	1982	1	X	X	X	
7	Williams, Ivor; Polunin, Nicholas* ⁷	1997	1	X		X	
9	Hawkins & Lewis 1982 ⁸	1975-1976	2		X		
a	Hunte et al. 1986 ⁹	1983-1984	2		X		
b	Hunte & Younglao 1988 ¹⁰	1983-1985	3		X		
c	Reef Check*	1997, 2001-2005	6		X		
d	Scoffin 1980 ¹¹	1978	1		X		
e	Bauer 1980 ¹²	1978	1		X		



BELIZE

Coauthors: Nadia Bood, John Bruno, Phil Dustan, Kirah Forman, Marah Hardt, Allison King, Karen Koltes, Isaias Majil, Tim McClanahan, Melanie Mcfield, Peter Mumby, Gustavo Paredes, Nicholas Polunin, Bob Steneck, John Tschirky, Ivor Williams, AGRRA, Healthy Reefs Initiative, CARICOMP and Reef Check

Geographic Information

Coastal Length:	1,984 km
Land Area:	22,153 km ²
Maritime Area:	34,701 km ²
Reef Area:	1,668 km ²
Number of hurricanes in the past 20 years:	5

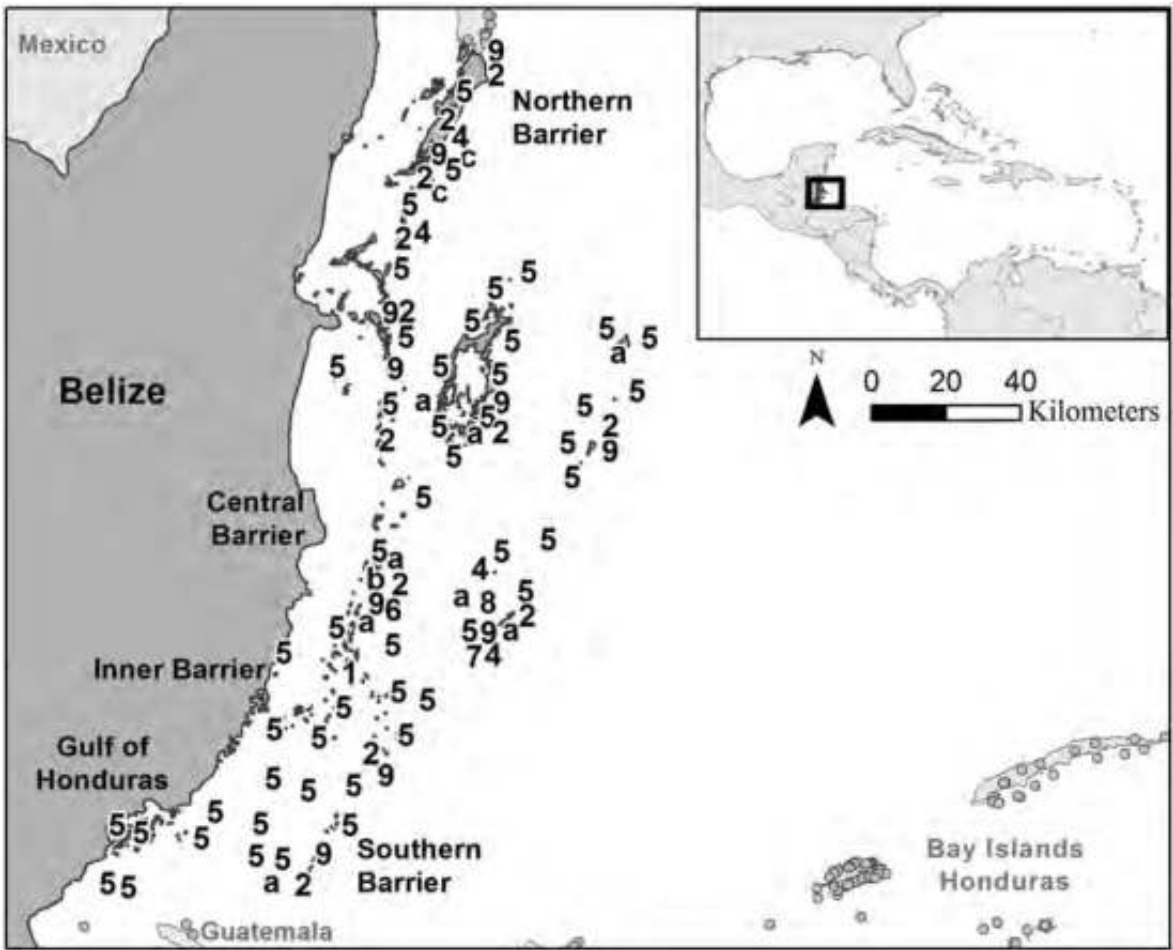


Fig. 4.1 Map of Belize, codes represent studies listed in Table 4.1. Missing map code(s) due to unavailable coordinates.

Table 4.1 Data sources for Belize used in current study. Map codes represent individual studies. For exact location of study, refer to Fig. 4.1; * denotes original data; for full references, refer to published literature sources in the last section.

Map Code	Contributor	Location	Time Period	Year Count	Coral	<i>Diadema antillarum</i>	Macroalgae	Fishes
1	Aronson et al. 2000 ¹	Barrier	1994-2001	8	X	X	X	
2	Bruno, John*	Atoll, Barrier	2009-2011	3	X		X	
3	Forman, Kirah* ^{2,3,4,5,6}	Barrier	2005-2012	8	X		X	
4	Hardt, Marah; Paredes, Gustavo* ⁷	Atoll, Barrier	2004	1	X		X	X
5	Heathy Reefs Initiative & AGRRA* ⁸	Atoll, Barrier (197 sites)	1999-2000, 2006, 2008-2009	5	X	X	X	X
7	Koltes, Karen; Tschirky, John/ CARICOMP* ⁹	Barrier	1994-2012	17	X	X	X	
6	McClanahan et al. 2001 ¹⁰	Atoll	1998-1999	2	X		X	
8	McClanahan & Muthiga 1998 ^{11,12}	Atoll	1970, 1996	2	X		X	
9	Mcfield, Melanie* ^{13,14,15,16}	Barrier	1997-1999	2	X		X	X
a	Mumby, Peter* ^{17,18}	Atoll, Barrier	2002	1	X		X	
b	Rützler & Macintyre 1982 ¹⁹	Barrier	1978	1	X		X	
c	Williams, Ivor; Polunin, Nicholas* ²⁰	Barrier	1998	1	X		X	X
d	Reef Check*	Atoll, Barrier (36 sites)	1997, 2001, 2004-2007	6		X		
e	Hay 1984 ²¹	Atoll, Barrier	1981	1		X		
f	Brown 2007 ²²	Barrier	2003	1		X		
g	Lewis & Wainright 1985 ²³	Barrier	1983	1		X		
h	Bood, Nadia*		2001, 2005	2		X		
i	Majil, Isaias*		2004-2005	2		X		
j	Steneck, Bob*		2002-2003, 2005, 2008, 2010	5	X		X	
k	Dustan, Phil* ²⁴	Atoll	1993	1	X		X	
m	Lessios 1988 ²⁵	Barrier	1983-1984	2		X		

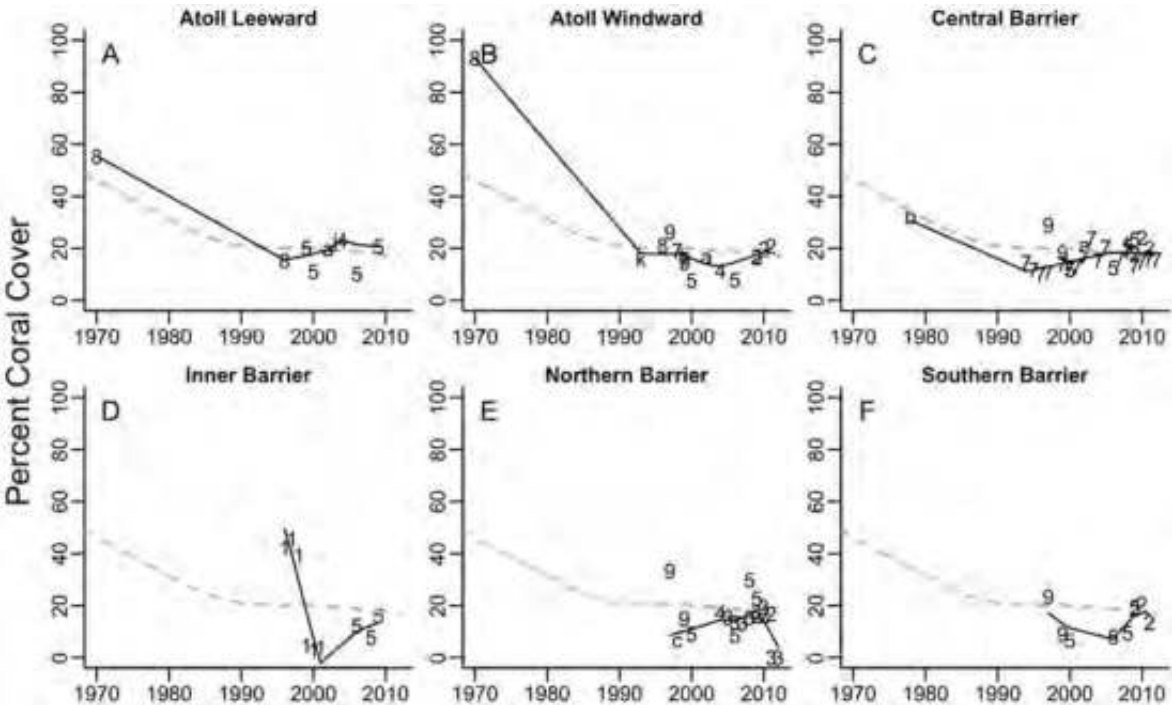


Fig. 4.2 Average percent cover of live corals for 6 locations in Belize: Atoll Leeward (A), Atoll Windward (B), Central Barrier (C), Inner Barrier (D), Northern Barrier (E) and Southern Barrier (F). Dotted line represents the average of Caribbean data collected for this report; solid lines are drawn through data presented. (Codes same as in Table 4.1 and Figure 4.1)

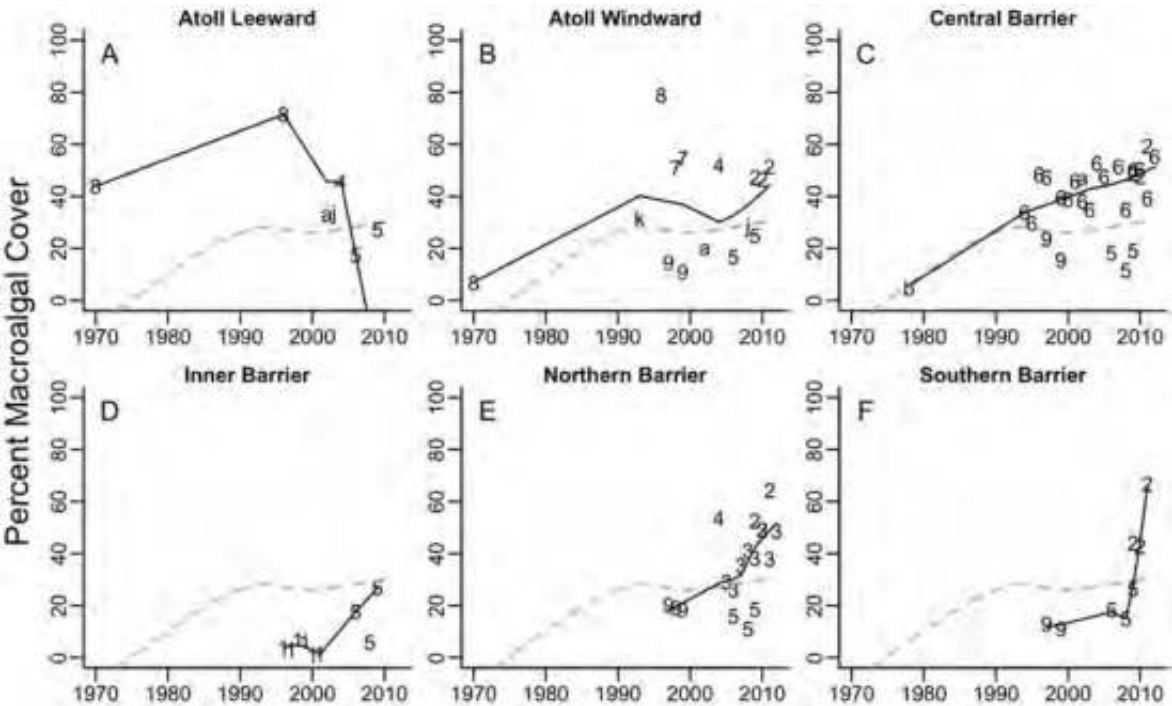


Fig. 4.3 Average percent cover of macroalgae for 6 locations in Belize: Atoll Leeward (A), Atoll Windward (B), Central Barrier (C), Inner Barrier (D), Northern Barrier (E) and Southern Barrier (F). Dotted line represents the average of Caribbean data collected for this report; solid lines are drawn through data presented. (Codes same as in Table 1 and Figure 1)

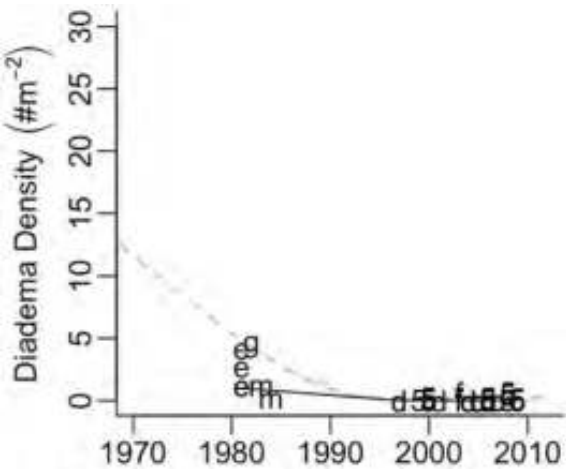


Fig. 4.4 Average density of *Diadema antillarum* for all Belize locations combined. Dotted line represents the average of Caribbean data collected for this report; solid lines are drawn through data presented. (Codes same as in Table 4.1 and Figure 4.1)

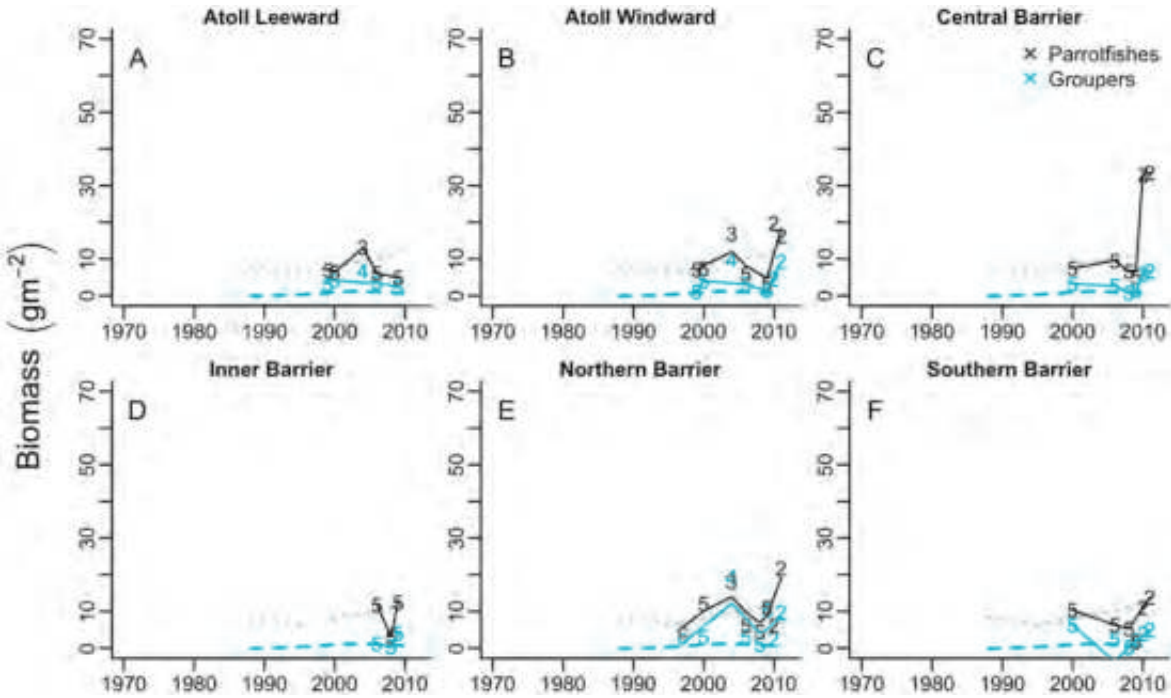


Fig. 4.5 Average biomass of parrotfishes and groupers for 6 locations in Belize: Atoll Leeward (A), Atoll Windward (B), Central Barrier (C), Inner Barrier (D), Northern Barrier (E) and Southern Barrier (F). Dotted line represents the average of Caribbean data collected for this report; solid lines are drawn through data presented. (Codes same as in Table 4.1 and Figure 4.1)

Timeline

- 1950s: Development of commercial fishing
- 1960s: Forming of fishing cooperatives
- 1972: Research started at Carrie Bow Cay, coral cover around 60%
- 1981: British Honduras becomes Belize
- 1981: Half Moon Caye Natural Monument declared (first MPA)
- 1983-1984: Mass mortality of *Diadema*

1987:	Hol Chan Marine Reserve established, coral cover <70%
1990:	Coastal Zone Management Unit (CZMU) established by the Government
Early 1990s:	Rapid increase of tourism
1995:	First mass coral bleaching event
Late 1990s:	Rapid clearing and development, dredging and filling of Cayes begin
1998:	Bleaching event (began late-summer)
1998:	Hurricane Mitch (Category 5, Oct/Nov – affected whole reef)
2001:	Hurricane Iris (Category 4, isolated path in southern reef)
2008:	Lionfish first reported in Belize
2009:	National ban on harvesting herbivores
2010:	Fisheries Act revisions begin; Belize population quadrupled and tourist numbers increased by 20-fold compared to 1960s
2011:	Unprecedented phytoplankton bloom

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