

An underwater photograph of a vibrant coral reef. In the foreground, a large, textured brain coral is prominent. Above it, several other coral species, including branching and table corals, are visible. Several colorful fish are swimming around the coral: a large, multi-colored parrotfish on the left, two yellow and white butterflyfish at the top, and a black and white striped angelfish on the right. The water is clear and blue.

TROPICAL AMERICAS

CORAL REEF RESILIENCE WORKSHOP REPORT

April 29 – May 5, 2012

Panama City, Republic of Panama
Tupper Center, Smithsonian Tropical Research Institute





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TROPICAL AMERICAS CORAL REEF RESILIENCE WORKSHOP

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EXECUTIVE SUMMARY

The International Union for the Conservation of Nature (IUCN) assumed leadership of the Global Coral Reef Monitoring Network (GCRMN) in 2010 with three primary objectives:

1. Strengthen scientific understanding of the status and trends of coral reef ecosystems at different places around the world.
2. Improve communication among the scattered members of the Network.
3. Make reef data publicly available online in a timely fashion.

The purpose of our new scientific endeavor is to establish quantitatively rigorous baselines for earlier reef conditions and to document the extent to which different reefs have varyingly declined from a relatively more pristine to degraded state. This variability is the key to understanding why some reefs have much more abundant corals than others; knowledge that is essential for preserving and restoring coral reefs and their ecosystem services in the foreseeable future.

Because of the enormity of the task, we plan to focus on separate biogeographic regions in a stepwise fashion, and then combine all of the results for a global synthesis by 2016. We have begun in tropical America because this is the region with which we are most familiar and to refine our methods of analysis before moving on to other regions. This report describes the results of our very preliminary Caribbean analysis. It will be followed closely by an assessment of the tropical eastern Pacific. This work will be completed in 2012.

The three major components of the scientific effort are to:

1. Document quantitatively the status and trends for all routinely monitored components of coral reef ecosystems, including reef corals, macroalgae, other sessile benthos, sea urchins, and fishes based on data provided by individual researchers as well as the scientific literature, monitoring programs, and reports;
2. Conduct workshops to bring together people who collected the data to directly involve them in data analysis and synthesis; and
3. Interpret variations in status and trends in relation to independent environmental, management, and socioeconomic data to better understand what are the primary

natural and anthropogenic factors driving coral reef decline and how they may be more effectively alleviated,

We assembled 36 scientists from 18 countries and territories to assess status and trends of Caribbean reefs at our first workshop held at the Smithsonian Tropical Research Institute (STRI) in the Republic of Panama 29 April to 5 May, 2012. Discussions were based upon initial exploratory analyses of approximately half the 253 data sets obtained so far from 29 countries. Trajectories of status and trends were constructed for reefs from seven countries with additional data for reef fish.

Three general points are clearly evident from these preliminary analyses:

1. The routine analytical procedure of ecological change on reefs that combines data from distant sites obscures important ecological differences among geographic locations and habitats of crucial importance for policy and management.
2. Some Caribbean reef ecosystems are relatively intact compared to average conditions in the region. For example, many reefs in the Dutch Caribbean and Cayman Islands have 30 % or more live coral cover, little macroalgae, and a moderate (albeit strongly depleted) abundance of fish. In contrast, reefs in Jamaica and the US Virgin Islands have well below 10% live coral cover, abundant macroalgae, and virtually no fish larger than a few cm.
3. The causes of these regional differences in reef conditions are not well understood beyond the obvious role of human exploitation and disturbance. Caribbean reefs with the highest surviving coral cover and least macroalgae tend to be characterized by little land-based pollution, some degree of fisheries regulations and enforcement, moderate economic prosperity, and lower frequency of hurricanes, coral bleaching, and disease. Unraveling the potential interactive role of these and other factors is a major goal of our study once all the necessary data are available.

More extensive and detailed results will be presented in a draft Caribbean Synthesis Report in December 2012, to be published and made available online by March 2013. We also plan to follow up with a second Caribbean workshop immediately preceding the 2013 ICRI Meeting in Belize to bring together members of the different GCRMN Caribbean nodes to explore ways the results of the scientific analysis can be used to improve the effectiveness of Caribbean reef monitoring and policy.

WORKSHOP REPORT

I. Context and Goals

The International Coral Reef Initiative (ICRI) was founded in 1995 to organize an international response to the newly recognized crisis of the degradation of coral reefs (International Coral Reef Initiative 1995). The Global Coral Reef Monitoring Network (GCRMN) was established at the same time to document the status and trends of coral reefs around the world (International Coral Reef Initiative 1995). GCRMN was highly successful in drawing global attention to the ongoing degradation of coral reefs due to overfishing, pollution, and climate change. However, the degradation of reefs continues to accelerate, and there are increasing demands for a more systematically rigorous quantitative assessment of the status and trends of reef ecosystems. The International Union for the Conservation of Nature (IUCN) assumed coordination of the GCRMN in 2010 with the primary objective of strengthening the scientific program while at the same time maintaining and strengthening interactions and communication among the far flung members of the network and making data available for member nations and management in a timely fashion. More specifically, we aim to:

1. Document quantitatively the global status and trends for all routinely monitored components of coral reef ecosystems including corals, macroalgae, other sessile benthos, sea urchins, and fishes based on available data from individual scientists as well as the peer reviewed scientific literature, monitoring programs, and reports;
2. Bring together the people who have collected the scientific data in addition to representative GCRMN members of the regions for a series of regional workshops to directly involve local people in data analysis and synthesis;
3. Integrate coral reef status and trends with independent environmental, management, and socioeconomic data to better understand what are the primary factors responsible for coral reef decline, the possible synergies among factors that may further magnify their impacts, and how these stresses may be more effectively alleviated;
4. Continue to work with GCRMN partners to build a more effective, standardized, and practical protocol and infrastructure for future routine monitoring and assessment of reefs; and
5. Disseminate information and results promptly and effectively to help guide member state policy and actions.

II. Agenda and Desired Outcomes of the Panama Workshop

The IUCN team assembled by the time of the workshop about 250 varying complete quantitative datasets from more than 58 contributors in 29 countries, plus more than 100 papers from the peer reviewed scientific literature and government reports when original data were not available. These represent well under half the studies that will be obtained for the final Caribbean synthesis report. Data include surveys of reef corals, other sessile animals, algae, sea urchins, and fishes as well as habitat information on reef type, depth, exposure, etc. Additional environmental data and information on human impacts have not yet been incorporated into the database but will be later in the year. Variability in survey techniques, data formats, scientific names, and precision is extreme. This lack of a widely accepted and standardized set of methodologies for surveying reefs and archiving of data is a major impediment to effective synthesis that became a recurrent theme during workshop discussions.

We presented our initial exploratory analyses of these data at the start of the workshop and posed five questions:

1. What new contributions to science and management of Caribbean coral reefs can emerge from the data we are accumulating?
2. What questions can we most appropriately ask of the data and what are the statistical limitations?
3. What are the most appropriate analytical approaches we should employ?
4. What important data sets were still missing that could be readily obtained, especially from the CARICOMP and AGRRA Programs?
5. What are the most important products we should strive to produce over the 2012 time frame on the GCRMN Caribbean effort, including scientific papers and GCRMN/ICRI reports?

Products proposed to begin discussions included:

1. A research article for *Science* that examines variation in trajectories of reef conditions throughout the Caribbean and their most likely explanations to be co-authored by all workshop participants plus others contributors who could not attend the workshop.
2. Other scientific papers depending on the initiative of subsets of participants, including but not limited to: (i) synthesis of changes in reef coral and fish communities; (ii) modeling of the data to predict future outcomes for reefs in specific regions in relation to alternative management actions and events; (iii) qualitative historical ecological analysis for the century preceding the start of quantitative data; and (iv) assessment of the relative importance of different physical and socioeconomic drivers.

3. GCRMN/ICRI Caribbean Synthesis Report to be submitted in draft form in December 2012 and published by March 2013. This synthesis report should include an overview and assessment of the quantitative analyses in addition to synopses of reports to be solicited from all Caribbean GCRMN member states. This report will be a short (approximately 50 page) printed and web-based document with more detailed reference materials and accompanying online data to the extent the providers wish to make their data publicly available. We will also complete a comparable tropical eastern Pacific synthesis report by the end of 2013.

The detailed agenda and list of participants are attached as appendices to this report. What follows is a summary of the major items of discussion and major points to emerge from the workshop.

III. Data and Database Considerations

We attempted to contact people in all the countries of the Caribbean via over 2000 emails, requests for data posted on relevant websites, and attendance at the 64th Gulf and Caribbean Fisheries Institute (GCFI) annual conference in Puerto Morelos, Mexico. We also corresponded with managers of large communal 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 (AGGRA), 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). In spite of these efforts, we missed several important sources, many of which we were able to track down at the Panama workshop, the International Coral Reef Symposium (ICRS) and ICRI meetings in Cairns. We have since made arrangements to acquire these data for inclusion in our database.

Compilation of the great majority of existing ecological time series data for Caribbean coral reefs presented substantial challenges for data organization and management. We compiled 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. Each of these datasets was presented in a unique format, were collected using various sampling designs and methodologies, reported widely variable ecological and environmental parameters, and utilized differing codes and groupings for reported variables. Consequently, we had to convert each database into a standardized, uniform format with accompanying crucial meta-data on sampling methodology, reef environmental parameters, and reef management history and status. To accomplish this, we developed a data template by soliciting input from study collaborators at the workshop in Panama. Compiling and organizing this information required a coordinated and extremely time-consuming effort to edit and reformat each dataset individually. Often, this effort required consulting data contributors and scientific literature to extract necessary information.

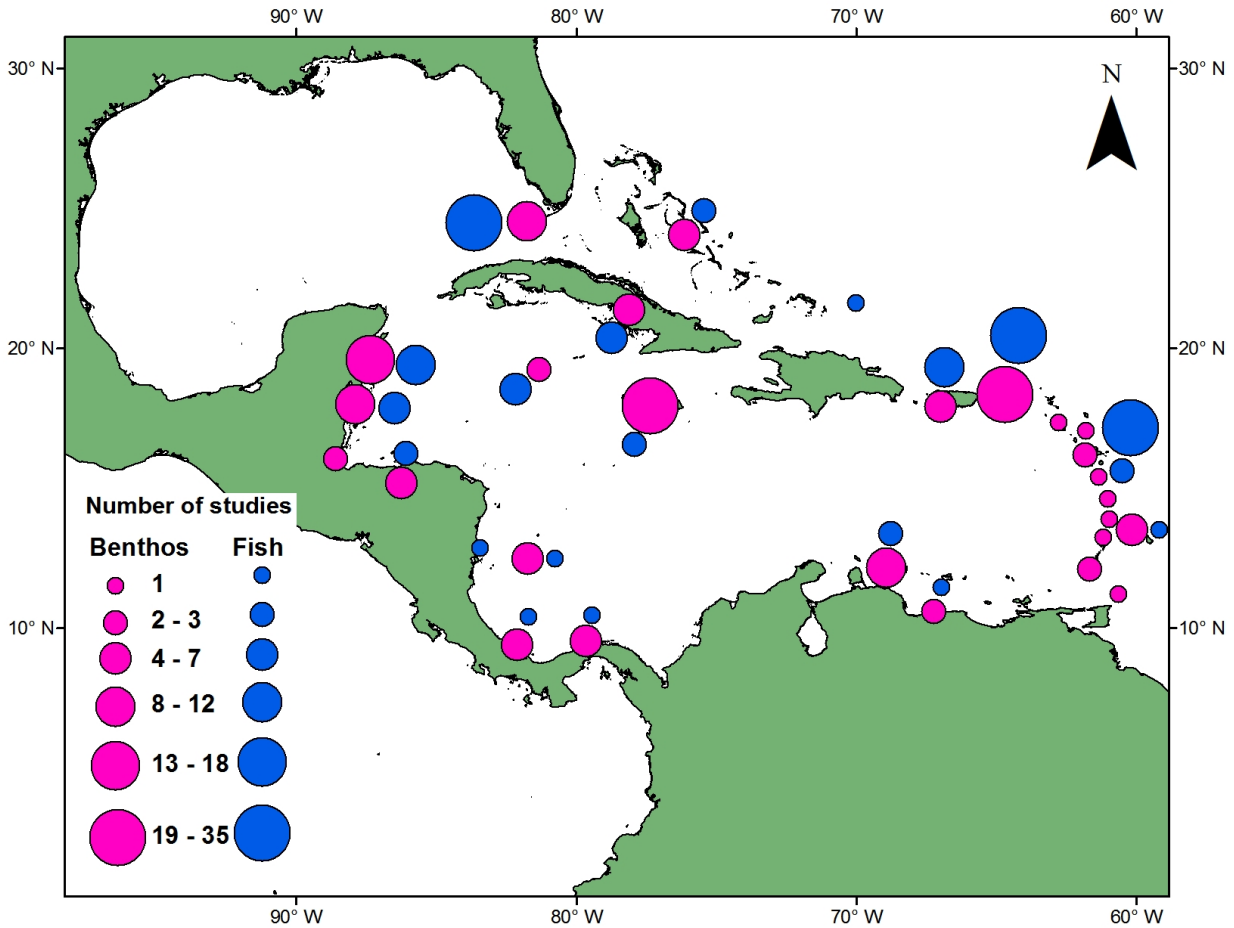


FIGURE 1. Geographical coverage by country of data; sizes of circles are proportional to the number of data sets for benthos (pink) and fish (blue).

After data were formatted in the template, exploratory analyses of temporal trends in reef community components by coarsely defined subregions (island, coast, country, etc.) were conducted using the software program R.

Within each region, trends in percent cover were assessed for all stony corals, dominant coral taxa, macroalgae, octocorals, sponges, and zoanthids, while trends in density were assessed for *Diadema antillarum* and fishes. Multivariate analyses were also conducted to investigate trends in the composition of the stony coral and overall reef benthic community within a region and to compare the magnitude and timing of ecological change among regions.

IV. Preliminary Analysis of Benthic Data

These first analyses were based upon 178 data sets from 58 contributors from 29 countries spanning 40 years. A “data set” is defined as the information provided by a particular contributor or monitoring program for a particular place or set of places (Fig. 1). Examples include the remarkable nearly 40-year data set provided by Rolf Bak for fixed quadrats in Curacao and Bonaire, larger scale transect surveys for particular reefs by individual

scientists, and large monitoring programs such as NOAA, CARICOMP, AGGRA, CREMP, FWC, and the I&M Program of the US NPS/SFCN. The great majority of data sets are for fringing fore-reef environments shallower than 10 to 15 meters depth. However, metadata for depth and habitat were unavailable for many reef sites until after the workshop, so we were unable to control for depth and habitat in these initial exploratory analyses.

Among the initial 178 data sets, 168 contain data for corals, 136 for algae, 94 for other sessile benthos, and 90 for sea urchins (mostly only *Diadema antillarum*). About 60% of the coral data sets identified corals to species and 40% of the algal data sets identified algae to genus. Data sets from Bonaire, Curacao, Jamaica, the US Virgin Islands (USVI), and Florida Keys extend for > 20 years, and this list will grow considerably when we have incorporated all the data from the Bahamas, Barbados, Belize, Bermuda, Colombia, Costa Rica, Flower Garden Banks, Mexico, Panama, Venezuela, etc. An additional surge of data collection started in the late 1990s, resulting in numerous 10- to 20-year data sets from another dozen countries (Fig. 2).

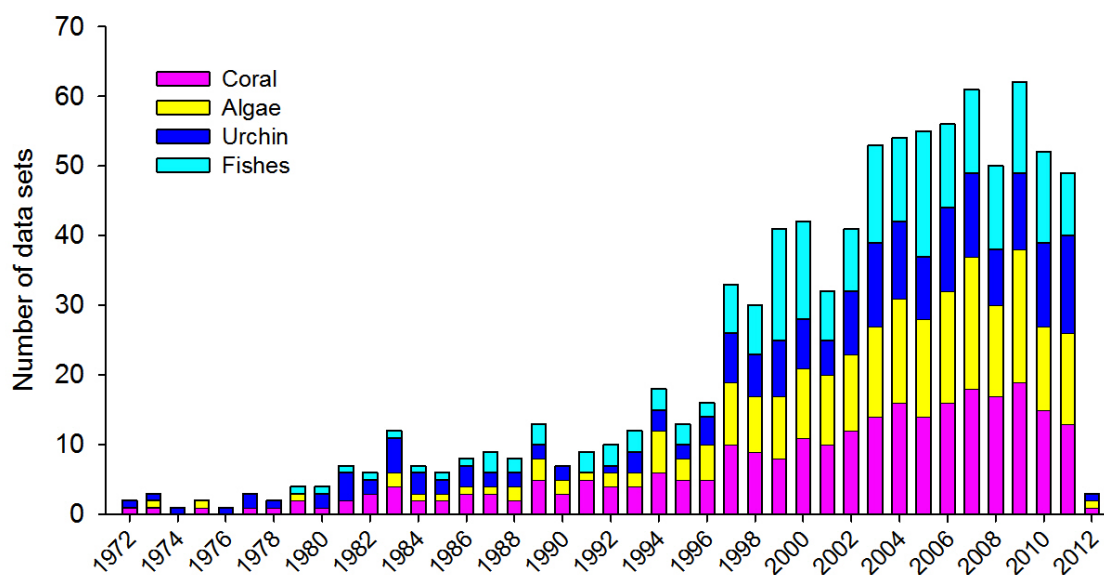


FIGURE 2. Number of data sets by year for coral (pink), algae (yellow), urchin (blue), and fishes (cyan).

We were able to analyze only a subset of the data at the workshop and in the subsequent two months leading up to our presentations of initial results at the International Coral Reef Symposium and ICRI meeting in Cairns in July 2012. These analyses were based upon data from seven subregions of varying size, including Bonaire, Cayman Islands, Curacao, Florida Keys, Jamaica, Puerto Rico, and the USVI. Biological parameters analyzed included percent cover of total stony corals, major coral taxa, and macroalgae, as well as density of the sea urchin *Diadema antillarum*.

We first examined trends for all the data combined, as has been standard practice for earlier regional analyses. Total coral cover from all subregions combined exhibited progressive decline comparable to that reported earlier (Gardner et al. 2003) (Fig. 3). However, there are very large fluctuations in the early years of the time series due to fewer samples across the Caribbean. For example, the sharp drop in total coral cover in the mid 1970s is an artifact due to lack of data from Curacao where coral cover was high. Consequently, total cover was driven by data from the Florida Keys that were already severely degraded in the early 1970s. The combined data also clearly documents the catastrophic decline in the sea urchin *Diadema antillarum* due to disease, and the consequent rise in the abundance of macroalgae that were on average more abundant than live corals on Caribbean reefs by the mid-1980s (Hughes 1994; Lessios 1988; Lessios et al. 1983; Hughes et al. 2010; Fig. 4).

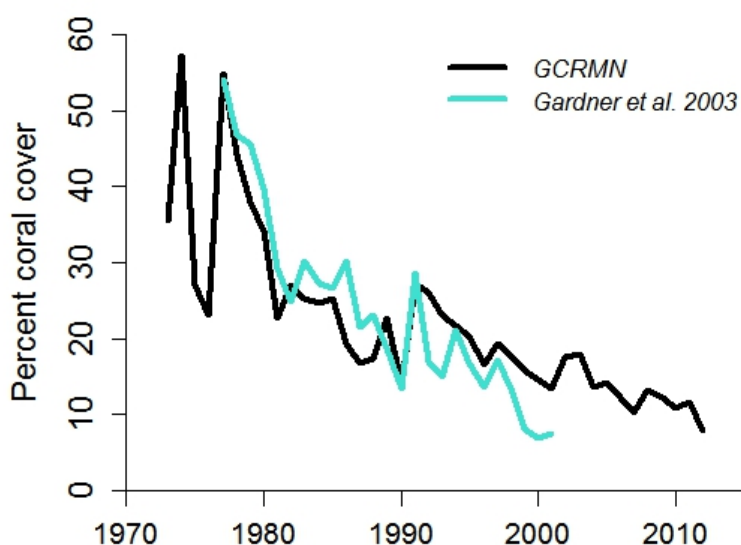


FIGURE 3. Decline in percent coral cover on Caribbean coral reefs from 1963 to present based on data compiled for this report (yearly averages weighted by the area surveyed per study) compared to Gardner *et al.* 2003 (yearly averages weighted by the inverse of a study's sample variance).

Abundance of staghorn and elkhorn *Acropora* corals sharply declined after the mid-1970s due primarily to white band disease (Gladfelter 1982; Aronson and Precht 2001; Bruckner 2002), but there are again extreme fluctuations in the time series because of the small sample size in earlier years and the combination of data from different sites that varied greatly in the relative abundance of the two *Acropora* species, as well as the extent and timing of mortality from disease, hurricanes, pollution, etc. (Fig. 5). There are also strong historical and paleontological data that demonstrate massive loss of *Acropora* in the early 1900s (Lewis 1984; Jackson and Johnson 2001; Pandolfi 2002; Cramer et al. 2012), implying that land clearing for intensive agriculture and other local human impacts in addition to coral disease may have played an important role in the *Acropora* decline. When data are combined across regions, all other major groups of corals declined to differing extent so that the relative abundance of taxa shifted strongly (Fig. 5).

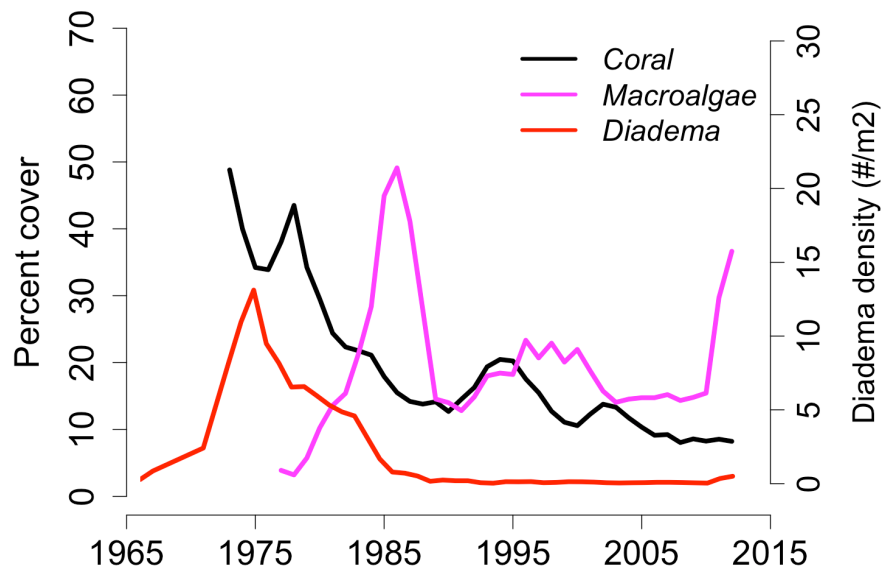


FIGURE 4. Time series of percent cover of coral, and macroalgae with density of *Diadema antillarum* averaged over data sets collected from Bonaire, Curacao, Cayman Islands, Jamaica, Puerto Rico, Florida Keys and USVI. Bold lines are three-year running averages weighted by area surveyed.

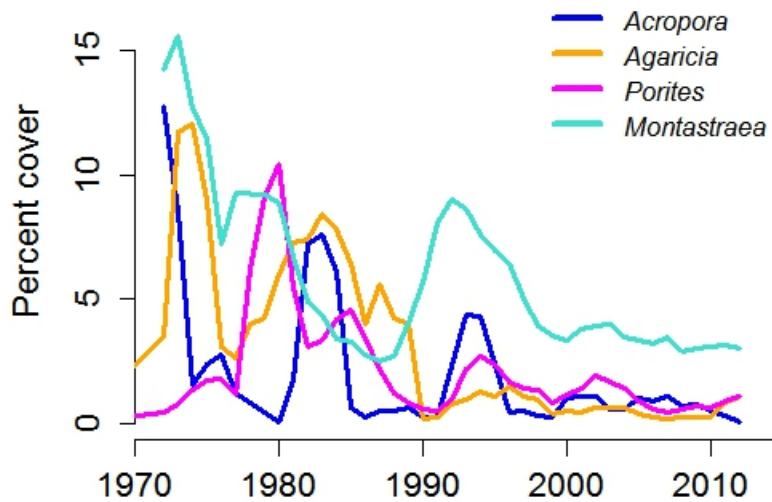


FIGURE 5. Percent cover over time of major coral genera: *Acropora*, *Agaricia*, *Porites*, and *Montastraea* “annularis” species complex. Lines are three-year running averages weighted by area surveyed.

The obvious problem with such analyses is that they combine data from very different kinds of reefs, depths, environmental conditions, and human impacts, which confounds results and greatly diminishes their practical utility. We therefore repeated the analyses

separately for each of the seven subregional data sets as a first step towards assessing differences in status and trends among different reef sites. Subsequent analyses for the complete Caribbean data set will break down sites by specific reef sites, depth, and habitat.

Total coral cover varied greatly among sites (Fig. 6). Corals declined precipitously on the Jamaican north coast in the 1980s after the *Diadema* die-off (Hughes 1994), but not at Curacao and Bonaire where coral cover has more gently declined to about 25-30 % today (Bak et al. 2005, Fig. 6). In contrast, total coral cover in the Florida Keys; USVI; and Puerto Rico has progressively declined from 25 to 35% in the 1970s to less than 15% today. Coral cover in the Cayman Islands appears to have held steady since the mid 1990s at about 20 to 25%.

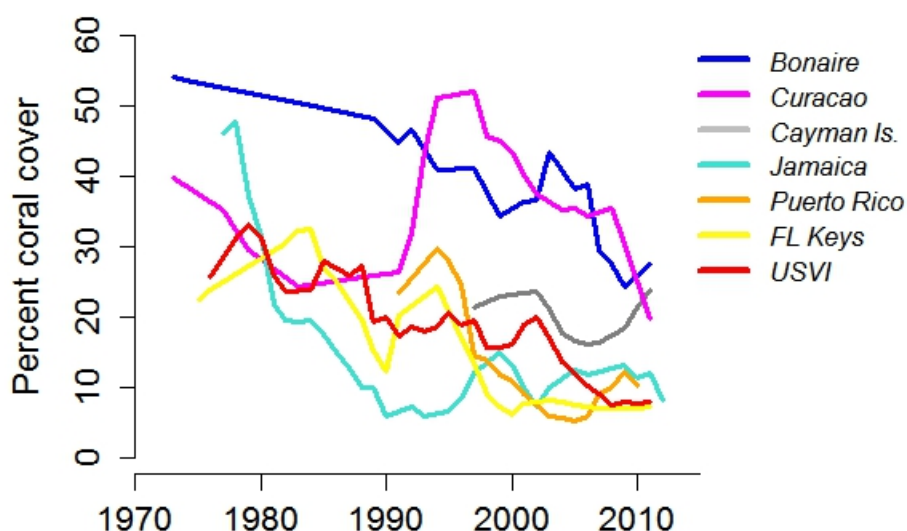


FIGURE 6. Percent total coral cover over time by region. Lines are three-year running averages of yearly averages weighted by area surveyed.

Strong regional differences in coral trajectories also occur within and among individual coral taxa (Fig. 7). The collapse of *Acropora* in Jamaica was due to Hurricane Allen in 1980 (Woodley et al. 1981). *Acropora* was also severely reduced in the USVI during the 1970s but showed a brief modest recovery from near zero to 8% in the early 2000s. In contrast, *Acropora* declined much later in the Florida Keys due largely to disease. *Acropora* cover was consistently very low in Bonaire and Curacao where *Agaricia* and the *Montastraea annularis* species complex [henceforth *M. "annularis"*] are dominant (Fig 7c,d). *Montastraea "annularis"* cover in Bonaire fluctuates greatly over the study period, but remains dominant compared to other taxa (Fig. 7d). Similar regional differences exist for the rise of macroalgae that rapidly increased to nearly 70% cover in Jamaica (Hughes 1994), where it still exceeds 40% cover, but has remained below 10% cover at Curacao (Fig. 8). In contrast, the collapse of *Diadema* populations was effectively synchronous throughout the wider Caribbean (Lessios et al. 1983; Lessios 1988; Fig. 8).

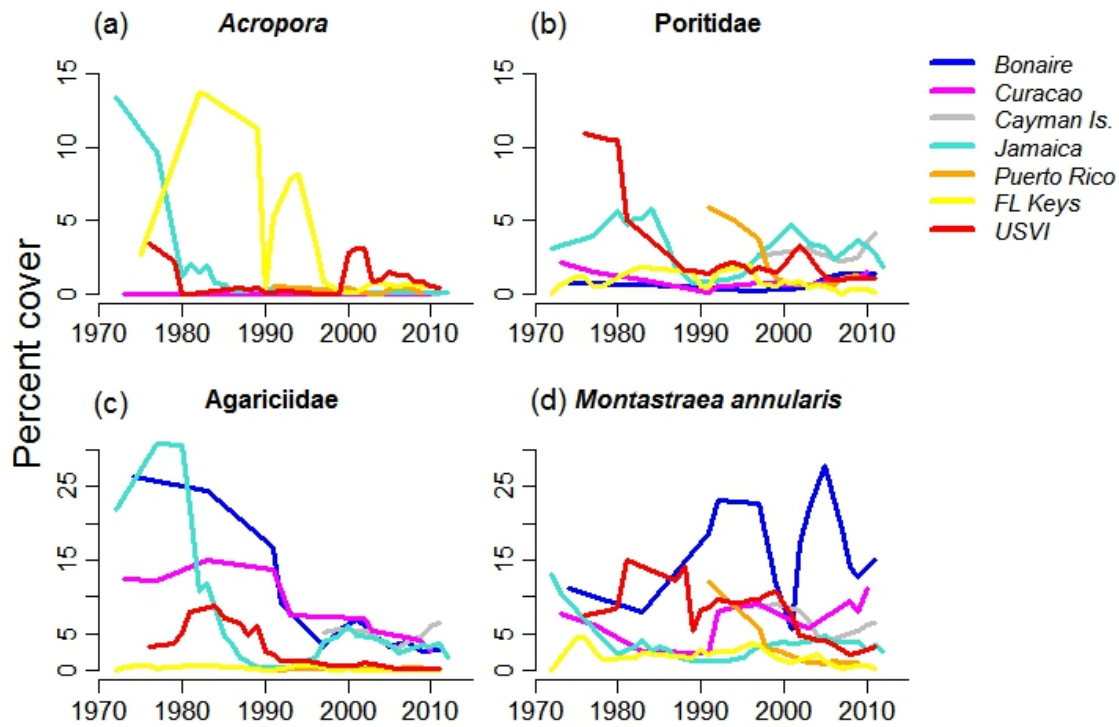


FIGURE 7. Percent cover by region for (a) *Acropora*, (b) *Poritidae*, (c) *Agariciidae*, and (d) the *Montastraea annularis* species complex. Lines are three-year running averages of yearly averages weighted by area surveyed.

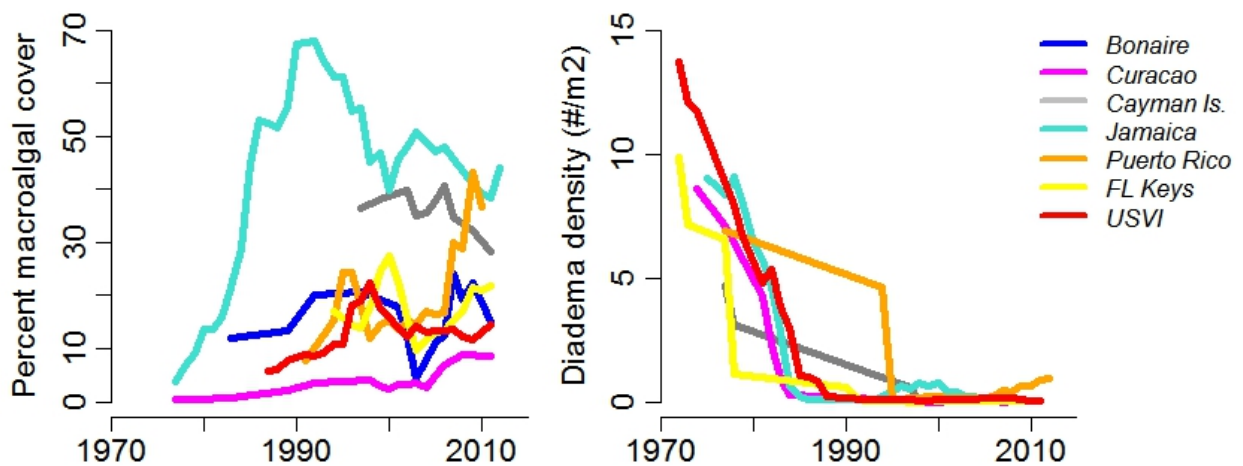


Figure 8. Percent cover of macroalgae and *Diadema* density by region. Lines are three-year running averages of yearly averages weighted by area surveyed. Lines are three-year running averages of yearly averages weighted by area surveyed. Three small surveys conducted in the Florida Keys, one each from 1965, 1966, and 1970, were excluded from this figure because of anomalously low *Diadema* density values.

V. Preliminary Analysis of Fish Data

A total of 60 fish data sets from 37 locations spanning 38 years have been obtained to date. These data come from 22 different contributors, including one large monitoring program (AGGRA) with more to come from Florida. Several long-term data sets (>20 years) exist, including from the USVI, Florida Keys, and French Antilles. A surge of data collection started in the late 1990s leading to 10-20 year data sets from several additional sites.

Initial exploratory analyses of fish included 60 data sets from 20 locations (Fig. 1). Species were grouped into four major trophic levels. Fish biomass varied about 30-fold among different subregions (Fig. 9). The greatest overall biomass of approximately 300 g·m⁻² was observed in Cuba before 2000. In contrast, Jamaica had the lowest reef fish biomass with values as small as 11 g·m⁻². Trophic structure also varied considerably among regions, with the biomass of apex predators (sharks, large snappers and groupers) almost zero in the USVI, French Antilles, Puerto Rico, and Jamaica (Fig. 9).

Varyingly long and detailed time series were constructed for seven subregions, including Belize, Cuba, Guadeloupe, Jamaica, Mexico, Puerto Rico, and the USVI (Fig. 10). Biomass was at or below 100 g·m⁻² everywhere except Cuba. Biomass has remained under 50 g·m⁻² around both St. John and St. Croix but appears to be increasing slightly in recent years (Fig. 10). Total fish biomass has remained constant under 40 g·m⁻² for the last 10 years at La Parguera, Puerto Rico. One data set from St. John, USVI is available beginning in 1989, and provides one on the longest time series of coral reef fish data globally. Total biomass has remained stable between 1990 and 2011 with small fluctuations from year to year. More comprehensive sampling began in the USVI in 1999 (e.g., wider range of habitats and depths), revealing that biomass can vary greatly throughout the archipelago but is still low compared to most other Caribbean regions.

The data from St. John were also used as a case study to highlight three specific trends in Caribbean fish assemblages. The first is the loss of large groupers, included here as three species from the genus *Mycteroperca*. Individuals of this genus were observed on multiple transects in 1989, 1990, and 1991 and then seldom, if at all, thereafter (Fig. 11). The loss of larger groupers coincides with an increase in smaller-bodied groupers of the genus *Cephalopholis*, which increase steadily in abundance from 1989-2011. This likely represents a case of predation release whereby meso-carnivores have increased as a result of the loss of larger predators. Second, large excavating parrotfishes (e.g., *Scarus coelestinus*, *S. coeruleus* and *S. guacamaia*) were occasionally observed around St. John into the 1990s but have not been seen since 2001. This guild plays an important role in coral reef resilience by removing dead coral and exposing hard substrate for coral recruitment as well as removing macroalgae and turfs (Mumby 2009). Their loss has likely contributed to the decline in reef health observed around the USVI. These two patterns contribute to the third finding that large-bodied fishes contribute less to the overall fish biomass over time around St. John, and presumably the rest of the USVI. Through size-spectra analysis we find the slope of the regression between density and size classes of all taxa pooled has decreased over time. Thus, smaller individuals are

more dominant in the fish assemblage around St. John today compared with 20 years ago.

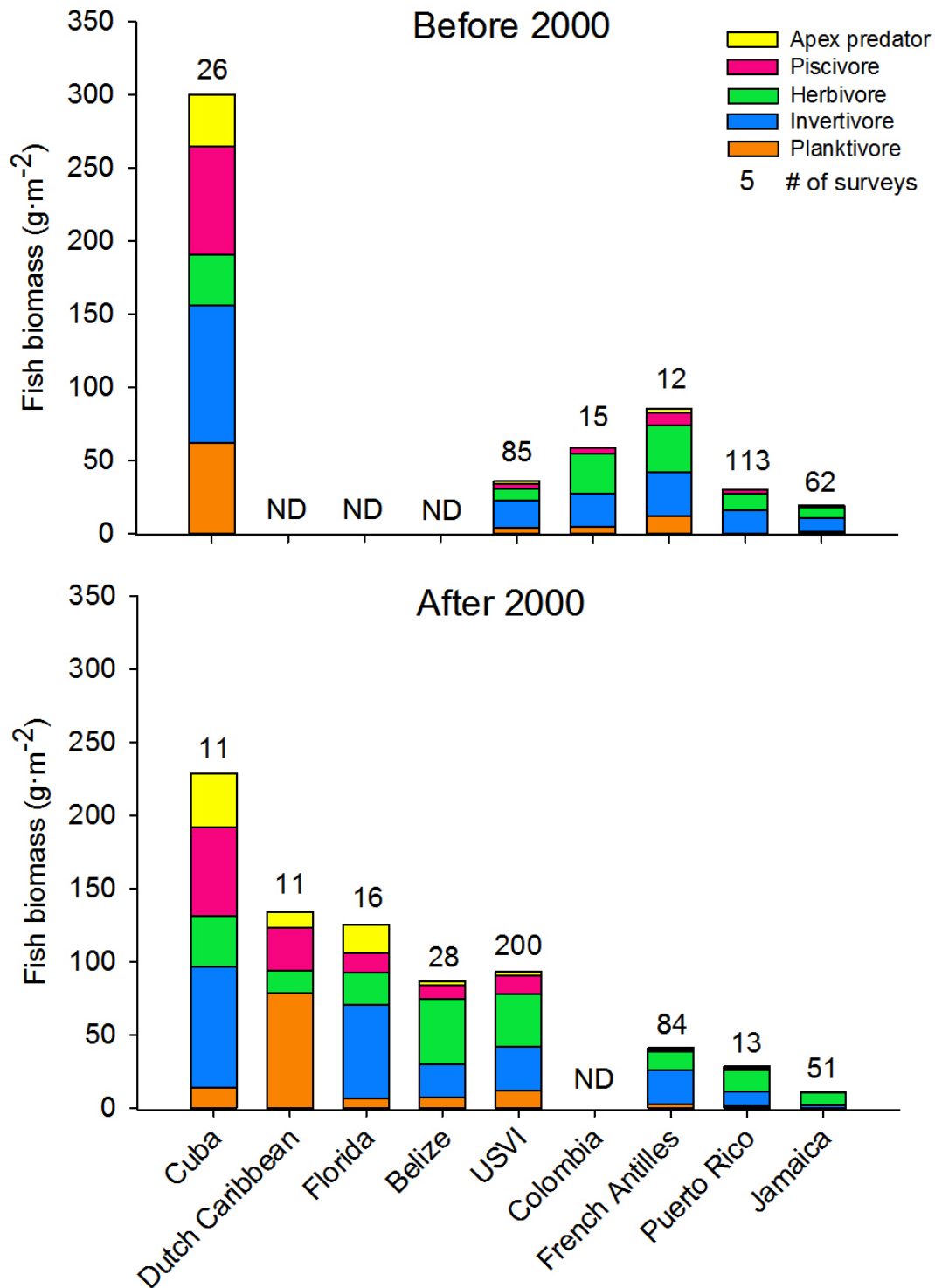


FIGURE 9. Total fish biomass by trophic level ($\text{g}\cdot\text{m}^{-2}$) and region for (a) period before 2000 and (b) period after 2000. Numbers above bars are number of surveys. ND indicates regions with no data.

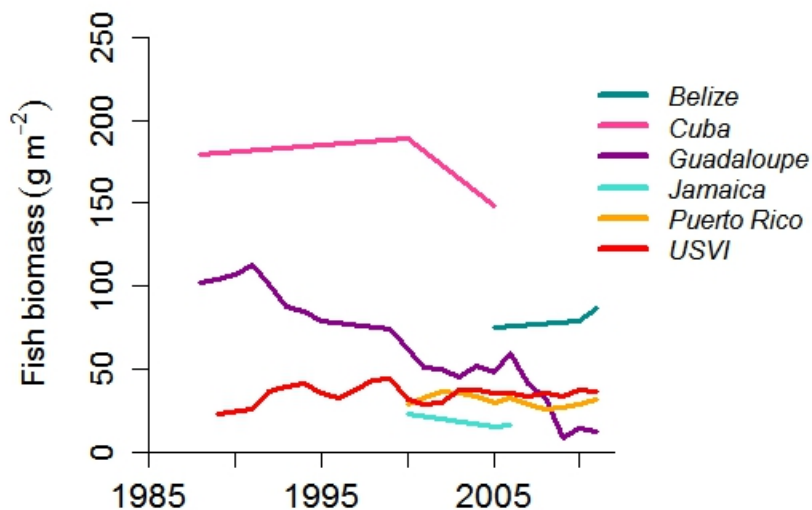


FIGURE 10. Trends in total fish biomass for Belize, Cuba, Guadeloupe, Jamaica, Puerto Rico and the USVI

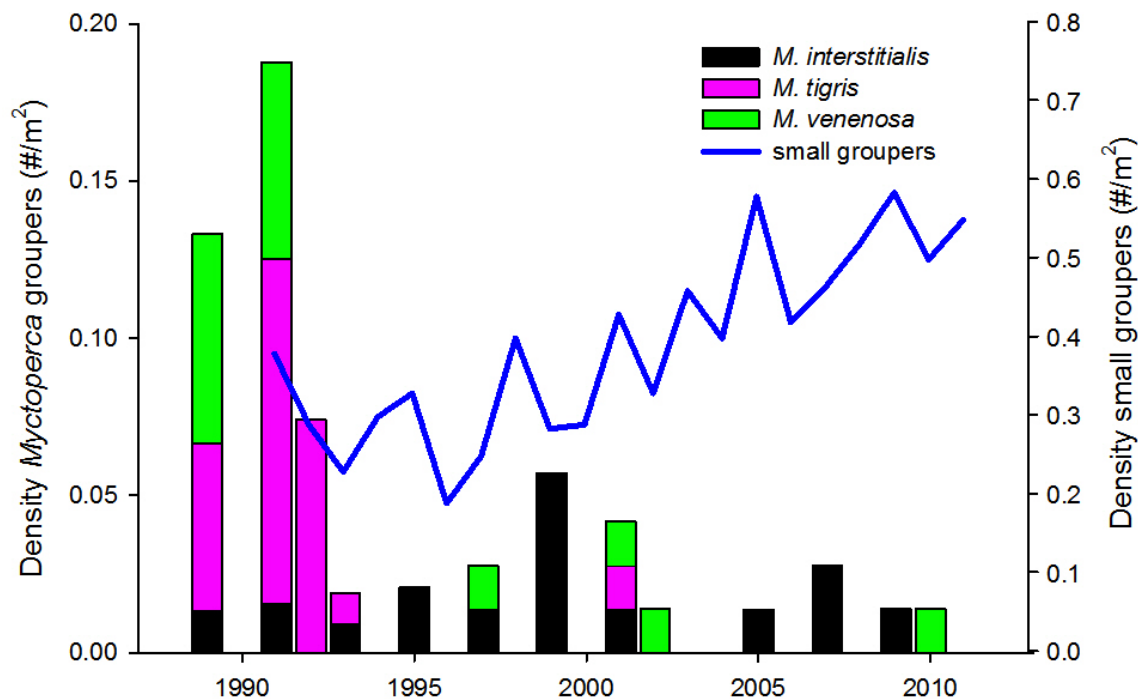


FIGURE 11. Comparison of trends in density of grouper species at St. John, USVI between large *Myctoperca* species and smaller-bodied groupers.

VI. Analytical Considerations

Sean Connolly was invited to the workshop to provide analytical advice and guidance for the statistical treatment of the inevitably unbalanced and poorly behaved data derived from so many disparate sources and based on a wide variety of sampling procedures. Professor Connolly leads the Coral Reef Biodiversity Program in the ARC Centre for Coral Reef Studies in Townsville, and is a recognized authority in modeling and analysis of complex ecological data. Professor Connolly gave a formal presentation in plenary on the second afternoon of the workshop. The underlying message of his presentation, and the extensive discussion that followed, helped to set guidelines for the remainder of the workshop. The main points are as follows:

1. Off-the-shelf statistical models for nicely behaved data that have been used in all such previous analyses are inappropriate. This extends even to non-parametric methods such as NMDS ordination.
2. Instead, we need to take responsibility for model formulation, asking what causes the response variables (coral and macroalgal cover, *Diadema* and herbivorous fish abundance, etc.) to vary. Causes will include the drivers of the patterns that we care about (decline of reef corals and fish, rise of macroalgae, loss of topographic complexity, etc.) as well as drivers that obscure the patterns we care about (other biological variability, measurement errors, and “nuisance parameters”).
 - a. Parameters of interest include:
 - Habitat effects (depth, wave exposure, geomorphology, etc.)
 - Local management (MPAs, land use, etc.)
 - Regional regime (local economy, climate, etc.).
 - b. Nuisance parameters include:
 - Temporal and spatial autocorrelation
 - Varying sampling intensities
 - Varying sample areas
 - Methodological effects (biases)
 - Researcher effects
3. Since all observations are model-dependent, we need to translate our prejudices about what may be going on into assumptions of the models we use and let the data speak for itself. To this end, we need reasonable alternative models that lead to good estimates of patterns of response variables, and rigorously inspect model fit to the data.
4. The preliminary analysis of lumping data from all places together (described above) made a long list of assumptions that are clearly invalid. For example:
 - All groups and methods are equally (un) biased

- All habitats and locations within regions or subregions have the same mean cover in any given year, and/or sampling is equally distributed in all years
 - Data values are not correlated spatially or temporally
 - All observations have the same sampling variance, regardless of sampling intensity or method
 - Change is slow, justifying the smoothing of lines with multi-year running averages.
5. What we should ideally do (but is impractical):
- Write down a “loss function” (e.g., likelihood) including our sub-models for both the “real” variation in the response variables and the filtering of observational biases.
 - Fit the model, probably using Markov chain Monte Carlo analysis. This would require bringing on someone with a very high level of statistical knowledge and experience for sophisticated statistical programming, and about six months full time.
6. What we can do (that would be a major advance over previous meta-analyses of coral reef decline):
- Assume that the biological signals of interest are strong enough to allow ad hoc estimation of “measurement” errors
 - Use the appropriate parameters to explain temporal biological patterns based on the parameters of interest (ecological “drivers”) identified above
 - Employ some sort of Generalized Least Squares type of analysis (heterogeneous variances, correlation structure, random effects, etc.)
 - Do a sensitivity analysis by Monte Carlo simulation.

All this will require us to focus on the best well-resolved case studies and may require re-consideration as we move on to other regions.

Several major points emerged from the subsequent discussion:

1. Our data are much more extensive and complete than any such previous analysis and will allow us to move away from simplistic analyses of total coral cover to dissection of changes in benthic community composition. However, most of the big changes in fish assemblage composition occurred long before any quantitative surveys. Addressing past fish abundance will therefore require a space-for-time substitution that relies upon comparisons among regions with varying degree of exploitation (e.g., Newman et al. 2006; Sandin et al. 2008).
2. We need to decide what we want to measure and ask what is the demographic meaning of rates of change?

3. The most interesting approach will be to analyze changes in community composition for specific reef sites with adequate documentation of depth, reef type, and other associated environmental data. We can then fit an appropriate model to each site and note known episodic disturbances and chronic change.

We then discussed at length what sites or subregions were the best candidates for detailed analysis, as well as how to treat the great majority of studies with shorter time series.

VII. Quality of Data Among Major Taxa and Sites

The great differences among surveys in terms of the numbers and kinds of taxa observed and numbers of years of observations limits the extent to which we can compare trajectories over time among different taxa and reef sites. Comparisons between fish and benthos are possible for 18 locations, but most of these have data for only one to a few years. Time series for fish of more than 20 years duration are available for only three sites (Florida Keys, USVI, and the French Antilles) and more than 10 years for another 3 (Belize, Cayman Islands, and western Puerto Rico).

The situation is considerably better for comparisons among different benthic taxa, thanks especially to the CARICOMP Program that collected data on corals, all other major groups of animal benthos, and algae for more than ten years from 15 sites all around the Caribbean. We had data from about half of these by the time of the workshop that were provided by the people who originally collected the data. Four subregions have more than 20 years of varyingly continuous or episodic data on corals and algae (Florida Keys, Jamaica, USVI, Dutch Caribbean) and at least 4 more with > 10 years (Panama, Belize, Cayman Islands, and western Puerto Rico). The latter do not include the complete CARICOMP data that are now available.

The longest continuous time series with consistent data are Rolf Bak's data set beginning in 1973 for large fixed photo quadrats at 4 stations and 4 depths at Curacao 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 to date for 5-year intervals. An additional site in east Curacao was added in 1994 to present. Bob Steneck also began monitoring reefs at Bonaire in 1999 (Steneck and Arnold 2003). Comparably long time series extending back into the early 1970s to early 1980s are available from the Florida Keys (Dustan 1977, 1985; Porter and Meier 1992), Jamaica (Liddell and Ohlhorst 1986, 1992; Hughes 1994), the USVI (Rogers et al. 1984, 1991; Edmunds 2002), and Panama (Guzman et al. 1991; Shulman and Robertson 1996; Guzman 2003), but the records were compiled by different workers at different times and are not as consistent or complete as data from the Dutch Caribbean.

Taking into account all of these factors, we have tentatively identified several dozen reef locations (e.g., Discovery Bay, Bocas del Toro, St. Croix, etc.) and several hundred specific reef sites for which we will be able to construct ecologically meaningful time series for two or more of the major groups of greatest interest (corals broken down to species or genera, other benthic animals (which are generally recorded only to major

group such as gorgonians, sponges, and ascidians), benthic algae, *Diadema*, and fish species or genera).

VIII. Major Outcomes and Emergent Themes

The unprecedented amount, diversity, and detail of quantitative data we have amassed greatly exceed any previous compilation and will allow us to do three new and important things that have not been attempted before:

1. Describe detailed trajectories of change for specific reef sites: We can document and compare for the first time the trajectories of change for large numbers of individual reef sites (e.g., each of Bak's quadrats in Curacao and Bonaire analyzed separately) or for similar types of reefs from the same depth at a single narrowly defined subregion (e.g., fringing reefs at 15 m depth at Discovery Bay, Jamaica). This is an important new approach from previous syntheses of Caribbean coral reef degradation [Schutte et al (2010) examined much larger subregions and combined data from different reef types and depths] that is fundamental to understanding cause and effect. Focus on individual sites is necessary because most of the factors affecting coral reefs, including fishing, land-based pollution, coral bleaching, many forms of coral disease, and hurricanes have affected populations and communities to varying degrees at different times in different places. Combining all of the data into a single analysis, as in previous studies, obscures the insights possible from analyzing different trajectories independently.
2. Describe changes in all major components of reef ecosystems: We are looking at most of the major visible taxa on reefs instead of only corals, and analyzing changes in the taxonomic and functional composition of coral assemblages and other major components of reef communities, instead of merely total coral cover. This approach allows us to document changes in entire coral reef ecosystems, which should provide clues to the relative importance of different processes driving reef change.
3. Standardize all analyses to data from similar reef environments: Previous studies have combined data from widely varying depths, reef types, and exposure. The environmental data we have compiled for our very large ecological data set will allow us to standardize comparison of trajectories from different reef sites to the same depth, reef type, etc. Most of our data come from shallow fore reefs between roughly 2 to 15 m depth so that most geographic comparisons will be restricted to these environments. Variations in depth within even this narrow range are correlated with strong differences in community composition, and we will control for this by subdividing the shallow fore reef zone. We also have considerable data from depths down to 40 meters for a smaller number of localities that will permit comparison of changes in trajectories over a wide depth range.

Having established these three points, the final discussion at the workshop focused on two big questions:

1. What are the most interesting regional contrasts?
2. Has coral survival and reef degradation varied significantly with depth?

To help guide the discussion, we first drew a graph representing the trajectories of coral cover at a small number of subregions for which we were already confident of the pattern from our preliminary analyses and previous detailed studies. These sites that exhibit three very different patterns of change in coral cover (Figs. 6-8):

1. Catastrophic collapse in the 1970s and 1980s in Jamaica and the Florida Keys
2. Initial gradual decline in the 1970s and 1980s followed by catastrophic collapse in the 1980s and 1990s in the USVI and Belize
3. Unrelenting slow and gradual decline in the Dutch Caribbean.

We then reviewed what we know about processes known to be responsible for coral decline in one way or another. The point is to develop a list of testable hypotheses to better understand the trajectories of reef ecosystems within individual subregions, and ultimately to explain the great differences in trajectories among subregions. We began with the most obvious, well-documented factors and moved on to the more difficult and less well understood:

1. Mass mortality of *Diadema* due to disease
Mass mortality of 95-99% of *Diadema* occurred throughout the wider Caribbean in 1983 and possibly again later in Florida (Lessios 1988). This loss of herbivores resulted in rapid explosions of algae on many reefs but not on others (Hughes 1994; Edmunds 2002; Schutte et al. 2010), a difference generally attributed to extreme overfishing in places such as Jamaica (Hughes 1994; Schutte et al. 2010). In all cases, the virtual disappearance of *Diadema* caused a massive change in the role of herbivory on reefs (Hughes et al. 2010). We then asked where and why has *Diadema* begun to make a modest recovery on some reefs (Ruyter van Steveninck and Bak 1986; Edmunds and Carpenter 2001; Carpenter and Edmunds 2006; Vermeij et al. 2010). This is especially interesting in relation to the absence of predators on *Diadema* in places like Jamaica that are apparently witnessing the strongest recovery (Newman et al. 2006, Hughes et al. 2010, Vardi 2011).
2. Mass mortality of *Acropora*
Both *Acropora palmata* and *A. cervicornis* declined primarily due to white band disease and to a lesser extent due to hurricanes and bleaching. But the timing of events varied greatly among regions (Fig. 7). In Jamaica, for example, the initial decline was due to Hurricane Allen in 1980 (Woodley et al. 1981) followed by an

imbalance in the great abundance of snail predators compared to the few surviving fragments of their *A. palmata* and *A. cervicornis* prey (Knowlton et al. 1981; Knowlton et al. 1990). Recruitment and apparent recovery began soon afterwards until a devastating outbreak of coral disease (Hughes and Connell 1999; Aronson and Precht 2001). In contrast, > 90% of *A. cervicornis* were lost within two years in the early 1980s in the Dutch Caribbean, whereas *A. palmata* has shown a more heterogeneous response in both space and time. The big question here is how synchronous were the outbreaks of white band disease in different subregions (Bruckner 2002).

3. Macroalgal explosion

The rise of macroalgae occurred immediately after the *Diadema* die-off in Jamaica because of a virtual lack of herbivorous fishes to take up the slack (Hughes 1994). But the rise in macroalgae elsewhere was much more varied in timing and extent and is likely related to the composition and abundance of herbivores at different sites, the amount of available “bare space” for macroalgal growth, and the overall productivity of the environment (Lessios 1988; Edmunds 2002; Carpenter and Williams 2007; Schutte et al. 2010; Vermeij et al. 2010).

There was considerable discussion of the relative importance of “top-down” versus “bottom-up” effects, with general agreement that their relative importance is primarily a function of the “intactness” of the herbivore assemblage (Hughes and Connell 1999; Aronson and Precht 2001; Burkepile and Hay 2008; McClanahan et al. 2011). For example, bite rates of herbivorous fishes on algal substrates vary over orders of magnitude (Steneck 1983; Steneck et al. 2011). However, striking differences between Caribbean versus Pacific reefs suggests oceanographic processes are also important (Roff and Mumby 2012). Thus, it will be essential for us to document nutrient levels at different locations to see whether there is a rigorous case for the role of bottom-up processes (Lapointe 1997; Burkepile and Hay 2006).

4. Decline of non-acroporid corals

The decline of the remainder of the coral community is considerably more complex than for acroporids, involving large increases in mortality and severe decline in numbers of recruits into the coral population. The major causes of mortality are (i) various coral diseases, particularly black and yellow-band disease in *Montastrea*, (ii) macroalgae and sediments encroaching at colony borders, and (iii) coral bleaching, and (iv) increased abundance and distribution of cyanobacterial mats that affect coral larval recruitment and survival (Edmunds 1991; Glynn 1996; Goreau et al. 1998; Bak and Meesters 1999; Paul et al. 2005; Kuffner et al. 2006; Box and Mumby 2007). The importance and timing of these different factors has varied greatly among sites. Jeff Miller (Virgin Islands National Park) has been collecting monthly data on sea surface temperature, bleaching, and disease in the USVI to try to disentangle cause and effect.

Larval recruitment of corals on Caribbean reefs was historically dominated by species of *Porites* and *Agaricia* that brood their larvae before release from the parent (Bak and Engel 1979; Rylaarsdam 1983; Green and Edmunds 2011; Hughes and Tanner 2000; Irizarry-Soto and Weil 2009). But since the 1970s there has been a sharp decline in both “adult” colonies and new recruits of these brooding species. New recruits declined 44% in Curacao (Vermeij et al. 2011) and 80% in Jamaica (Hughes 1994; Hughes and Tanner 2000). The data are very variable, but the apparent cause is some combination of a decline in adult (parental) colonies, the decline in *Diadema*, and increased abundance of macroalgae. However, there are no experimental data. The result is a coral community increasingly dominated by relict colonies of *Montastrea “annularis”* and a mixed bag of other free-spawning species (Hughes 1994; Hughes and Tanner 2000). This dramatic shift in species composition is referred to as a “storage effect” that reflects differences in the life histories of coral species.

5. Rise of other major groups of sessile animals?

There was a general feeling among many participants that other sessile animal groups may be increasing in relative or absolute abundance in response to the sharp decline in reef corals. Suspension feeding invertebrates have increased at one site in the USVI (Colvard and Edmunds 2011). In contrast, abundance of sponges on deep Jamaican reefs was stable for at least a decade in the face of a sharp decline in corals and explosion of macroalgae (Hughes 1996). Other possible examples include increases in gorgonians in Florida, zoanthids in Tobago, colonial ascidians in Curacao (Bak et al. 1981, 1986) and Grenada, the fire coral *Millepora*, and possibly crustose reef corals. We have extensive data still to be analyzed on the abundance of these groups. We should also be able to determine whether any increases are dominated by mixototrophs (animals that feed but also harbor photosynthetic symbionts) or heterotrophs, or by brooding or broadcasting species.

6. Decline of 3-dimensional reef structure

There have been scattered studies of the collapse in 3-dimensional reef structure due to coral death and bioerosion of their remnant skeletons (Alvarez-Filip et al. 2009). This flattening of the reef is associated with a loss in critical fish habitat and reduction in fish abundance (Paddack et al. 2009). It is unclear whether we will have sufficient data to further explore this.

IX. Summary and Conclusions

The workshop confirmed that the new GCRMN is working effectively to gather the essential data for a significant advance in understanding of the patterns and processes in the progressive degradation of Caribbean coral reef ecosystems. The extent and quality of data are unprecedented in allowing detailed analysis of the status and trends of reef organisms from individual countries, subregions, and specific sites of the Caribbean in the context of known processes and events at those places. In contrast, most previous studies have combined all of the Caribbean data together, assuming that

local differences are unimportant; an assumption that is clearly false. Earlier syntheses have also focused almost exclusively on total coral cover ignoring changes in community composition that we are addressing through analysis of coral species composition as well as other benthic animals, algae, and fish. Our preliminary results were presented at the July 2012 International Coral Reef Symposium and ICRI Meeting in Cairns, and will be submitted for publication in scientific journals in late 2012. The draft Caribbean Synthesis Report will be submitted for internal review by December 2012.

Looking forward, there is a desperate need for coral reef ecologists and managers to develop a universal standard for monitoring the ecological status and trends of coral reefs (Knowlton and Jackson 2008). The failure of the coral reef community to rise above petty differences and regional prejudice to achieve a universal standard is the greatest impediment to coral reef conservation and management. The situation is especially appalling in comparison to the extraordinary advances that have been made in the documentation for the status and trends of tropical forest ecosystems around the world under the auspices of the Center for Tropical Forest Science (www.ctfs.si.edu). CTFS maintains a global network of 47 plots in primarily tropical but also temperate forests in 21 countries with 75 partner institutions to monitor the growth and survival of approximately 4.5 million trees and 8,500 species. The results have revolutionized tropical forest science and conservation (Losos and Leigh 2004). Achieving a comparable network of high quality monitoring and exchange of information should be the ultimate goal of the GCRMN in the coming decade.

To this end, we are planning to extend the Caribbean model of data acquisition and analysis step by step to all of the regional seas where coral reefs occur. This work will be done in conjunction with major regional research institutions, existing monitoring programs, and various nodes of the GCRMN. The tentative schedule is to begin work on Australia and Melanesia in 2013, the core Coral Triangle and East Asia in 2014, and the North Pacific, South Pacific, and Indian Ocean/Red Sea in 2015. We have greatly streamlined the efficiency of our approach based on our Caribbean analysis and expect to complete all of the regional analyses prior to the 13th International Coral Reef Symposium in 2016 where we will conduct a global synthesis workshop. The global synthesis will be published by late 2017. In so doing, we will have compiled in standard format the results of the vast majority of all previous quantitative surveys of coral reefs in a single freely accessible website, thereby providing the definitive scientific baseline for all further reef surveys, policy, and management.

X. References

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Tropical Americas Coral Reef Resilience Workshop (29th April – 5th May 2012, STRI Tupper Center, Panama City)

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TROPICAL AMERICAS CORAL REEF RESILIENCE WORKSHOP (29th April – 5th May 2012, STRI Tupper Center, Panama City)

29 April (Sunday)

Whole Day Arrival of participants and transport to hotel

17:00-19:00 Informal reception at hotel

30 April (Monday) TUPPER AUDITORIUM

National Holiday in Panama

08:00 Buses to STRI Tupper Center

09:00 Welcome Remarks (*Anthony Coates*)

09:15 Introduction and goals of workshop including scientific papers, a detailed ICRI Report, and potential tools and information for reef managers (*Jeremy Jackson*)

09:45 History and purpose of ICRI/GCRMN (*Andy Hooten*)

10:15 *BREAK*

10:45 Overview of benthic data (*Jeremy Jackson and Katie Cramer*)

11:15 Overview of fish data (*Alan Friedlander and Mary Donovan*)

11:45 Questions and Discussion

12:30 *LUNCH*

14:00 Coverage and gaps in database (*Vivian Lam*)

14:30 Problems of diverse data sets and database structure (*Andy Hooten*)

15:00 Preliminary analytical framework (*Katie Cramer and Mary Donovan*)

15:30 *BREAK*

16:00 Plenary discussion of the challenges ahead and desired products of the workshop (*Jeremy Jackson*)

18:00 Buses to hotel

1 May (Tuesday) EXHIBIT HALL

08:15 Buses to STRI Tupper Center

09:00 Overview for the day: Break into subgroups by different geographic subregions, and major taxa. Physical environmental variability and human impacts (*Jeremy Jackson*)

09:15 Subregions: Discussion of data already obtained, other available data, histories and outstanding unique features of each subregion that require consideration

10:45 *BREAK*

11:15 Subregional discussions in plenary

12:30 *LUNCH*

13:30 Taxa: Benthic and fish plus sea urchin data to evaluate data quality, gaps, opportunities, etc.

15:00 *BREAK*

15:30 Major taxa discussions in plenary

- 16:30 Cause and effect 1? Overview of variations in physical environmental conditions throughout the wider Caribbean (*Iliana Chollett and Peter Mumby*)
- 17:15 Cause and effect 2? Brief overview of variations in human activities and protection efforts throughout the region (*Rolf Bak and Peter Mumby*)
- 18:00 Buses to Hotel

2 May (Wednesday) EXHIBIT HALL

- 08:15 Buses to STRI Tupper Center
- 09:00 Plenary discussion: What are the most important scientific questions to ask for a major synthesis paper for *Science*? What can we contribute that's new compared to previous meta-analysis efforts, such as Gardner et al 2003, Cote et al 2005, and Paddock et al. (*Jeremy Jackson*)
- 10:30 *BREAK*
- 11:00 Statistical and database considerations for moving forward on a *Science* paper (*Sean Connolly, Katie Cramer, Alan Friedlander, Mary Donovan, and Andy Hooten*)
- 12:00 Plenary discussion: Goals and structure of a *Science* paper (*Jeremy Jackson*)
- 12:30 *LUNCH*
- 13:30 Plenary discussion: What other scientific papers should we consider and who realistically would lead such efforts? For example, modeling future trajectories, historical ecology, corals versus macroalgae, is *Diadema* really recovering, comparisons and evaluation of data from previous coordinated efforts (Caricomp, AGGRA, Reef Check), etc. (*Jeremy Jackson*)
- 14:15 Contributions to the ICRI Report (*Andy Hooten*)
- 15:00 ARC Centre of Excellence for Coral Reef Studies Seminars at Tupper Auditorium (*Sean Connolly, Terry Hughes, Peter Mumby, & John Pandolfi*)
- 17:00 *STRI RECEPTION AND BARBEQUE*
- 19:30 Buses to hotel

3 May (Thursday) EXHIBIT HALL

- 08:15 Buses to STRI Tupper Center
- 09:00 Plenary discussion: Outline for a Science paper and the kinds of figures and tables required
- 10:30 *BREAK*
- 11:00 Breakout groups: 1) Core *Science* paper team to develop mock-up figures, run exploratory data analyses, etc.; 2) Regional syntheses: leaders for each sub-region develop historical narratives and data summaries for their sub-region (e.g., Florida Keys, USVI, Netherland Antilles, etc.) and a standard format for comparisons among sub-regions; 3) Historical ecology 4) Modeling; 5) Particular taxa; 6) Others?
- 12:30 *LUNCH*
- 13:30 Reports from breakout groups in plenary and general discussion
- 15:00 *BREAK*

15:30 Breakout groups continue
18:00 Buses to hotel
EVENING Breakout groups continue working at hotel to prepare reports to the group for Friday morning

4 May (Friday) EXHIBIT HALL

08:15 Buses to STRI Tupper Center
09:00 Leaders of breakout groups present plans for papers and reports
10:30 BREAK
11:00 Continue breakout group reports
12:30 LUNCH
13:30 Plenary discussion
15:00 BREAK
15:30 Closeout of workshop: Where we stand, logistics for the coordination of future efforts for completion of papers and reports including a data drop-box for everyone who wants to participate. Anticipated production schedule until completion in December 2012
17:00 Buses to hotel

5 May (Saturday)

Transportation of participants to Tocumen Airport for departure



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