Measuring, Interpreting, and Responding to Changes in Coral Reefs: A Challenge for Biologists, Geologists, and Managers

Caroline S. Rogers and Jeff Miller

Abstract

What, exactly, is a coral reef? And how have the world's reefs changed in the last several decades? What are the stressors undermining reef structure and function? Given the predicted effects of climate change, do reefs have a future? Is it possible to "manage" coral reefs for resilience? What can coral reef scientists contribute to improve protection and management of coral reefs? What insights can biologists and geologists provide regarding the persistence of coral reefs on a human timescale? What is reef change to a biologist... to a geologist?

Clearly, there are many challenging questions. In this chapter, we present some of our thoughts on monitoring and management of coral reefs in US national parks in the Caribbean and western Atlantic based on our experience as members of monitoring teams. We reflect on the need to characterize and evaluate reefs, on how to conduct high- quality monitoring programs, and on what we can learn from biological and geological experiments and investigations. We explore the possibility that specific steps can be taken to "manage" coral reefs for greater resilience.

Keywords

Monitoring · Random sampling · Marine protected areas · Biodiversity · Connectivity

12.1 Current State of Coral Reefs[1]

For the purposes of this paper, we define "true" coral reefs as rigid, topographically complex structures developed from carbonate accretion by corals and other cementing and calcifying organisms and the product of biological and geo- logical processes. This definition reflects comprehensive discussions in Buddemeier and Hopley (1988), Hubbard (1997), Hubbard et al. (1998) and Kleypas et al. (2001).

There is not complete agreement on which "hardbottom" habitats constitute coral reefs. Some would include communities with corals growing on boulders or other non-carbonate pavement, as well as low-relief habitats dominated by gorgonians as reefs, while others would not. However, the lack of consensus among scientists over what constitutes a coral reef, and the total areal extent of reefs in the world, should not interfere with the primary message that coral reefs are important and imperiled, and every effort should be made to reduce the stressors affecting them.

Coral reefs are changing rapidly, and scientists can play a role in communicating with the general public about these changes and what they mean. Coral reefs extend over less than 0.01 % of the marine environment, approximately

---

[1] C.S. Rogers
Wetland and Aquatic Research Center, Caribbean Field Station, US Geological Survey, 1300 Cruz Bay Creek, St. John, VI 00830, USA e-mail: caroline_rogers@usgs.gov
J. Miller
South Florida/Caribbean Inventory and Monitoring Network, US National Park Service, 1300 Cruz Bay Creek, St. John, VI 00830, USA

250,000 km2 (Burke et al. 2011). However, they provide many goods and services such as coastal protection, and support for tourism and fisheries (Burke et al. 2011) as well as non-economic benefits. Their significance to humans needs to be conveyed more broadly (Burns et al. 2003).

Even though surveys and monitoring have not been conducted everywhere (and using identical methods based on random sampling), there is compelling evidence that reefs worldwide are increasingly stressed (Wilkinson 2008; Burke et al. 2011; Jackson et al. 2014). For obvious reasons, many long-term monitoring programs have focused on reefs that are close to marine field stations or within national parks and other marine protected areas. Has this biased our characterization of the world's coral reefs? If biological monitoring had taken place randomly on reefs distributed throughout the world's oceans, would our assessment of the status of the world's reefs be different? If geologists had cored through randomly selected reefs, would their interpretation of Holocene reef history be different? Conversely, has coral reef degradation been so substantial and pervasive that the lack of random selection of sites for monitoring is not a problem? While we cannot be certain, and we support truly random sampling of coral reefs, we doubt that the prevailing view of the overall degraded condition of the world's reefs would be different if surveys had been done truly randomly--this reflects the seriousness of the current degradation of coral reefs worldwide.

With the genesis of modern scuba diving in the 1940s the ability to document long-term trends on reefs is relatively new. Yet changes in reefs over the past 50 years are quite dramatic, especially given that corals are such slow-growing organisms. While large-scale sample designs increase the ability to detect trends over vast areas, it is best when they are used in combination with smaller, reef-scale monitoring. Our recent access to mesophotic reefs (i.e., those in 30–150 m of water), some of which are less stressed and have coral-cover values similar to nearshore reefs 40 years ago, does not suggest that current threats to reefs overall are any less, or that dramatic declines in nearshore reefs are any less significant. If anything, the increasing knowledge of these "twilight" reefs should heighten the awareness for the need to better understand the connectivity between mesophotic and shallower systems. The Intergovernmental Panel on Climate Change (2007) concluded that 18 % of the world's coral reefs will likely be "lost" by 2030, but what is meant when we say a reef has been lost? What does this word mean to scientists or to the general public? We can all agree that a coral reef buried by an airport runway is lost. Some people describe reefs as lost if there has been a significant decline in coral cover and an increase in macroalgal cover. However, it would be preferable to be more exact as we consider the spectrum or progression from "threatened" to "lost" in less obvious situations. In general, high coral cover and low algal cover are thought of as desirable.

Perhaps it is more useful to think in terms of the current threats to coral reefs. Burke et al. (2011) estimated that over 90 % of the reefs in the world are already or will be threatened by increasing temperatures, ocean acidification, and local activities and stressors such as fishing, marine- based pollution, physical damage, coastal development, and watershed-based pollution, with about 60 % experiencing high to critical levels of threat. With global stressors such as climate change now added to the mix, it is critical to attempt to mitigate the damage and reverse some of the declines before it is too late. The ultimate goal is to provide rigorous scientific data from monitoring and experimental research that can lead to better management actions that might promote reef recovery, especially given the anticipated effects of global climate change.

12.2 Characterizing Reefs

How should we characterize and describe coral reefs? What are the attributes of degraded, healthy, resistant, resilient or recovering coral reefs? If a group of geologists and biologists were air-lifted to a remote coral reef that they had never seen before, and of which they had no prior knowledge, their assessments of the reef's condition would likely differ. If the reef had 100 % coral cover of several different coral species, and supported numerous large fishes, the scientists would likely agree the reef was in good condition. Similarly, if the reef had no corals, few fishes, and was carpeted by slimy algae, they would agree it was in bad shape. However, if the reef had 25 % coral cover, 25 % cover by macroalgae, and a few large fishes, the biologists might disagree on its current state. Such a snapshot of a coral reef is usually not sufficient to characterize its status. Knowledge of its "ecological history" (sensu Hughes 1989), such as changes in coral and algal cover, changes in fish assemblages, and past disturbances is essential to provide a better sense of its present, and possible future, condition. In addition, the geologists might want to examine several cores from the reef to determine if reef accretion was taking place or whether the reef community differed from that in the more distant past. Whatever the perspective, a baseline is necessary to provide context.

Even when we have the luxury of historical data, we can still argue about what an observed change means or how important it might be in the long run. If there were any documented decreases in coral cover and increases in macroalgal cover, some might conclude that a "phase shift" had occurred (e.g., Dudgeon et al. 2010). Although much discussed, this concept may not be particularly helpful, at least as previously applied. For a shift to occur, coral dominance must give way to algal dominance. However, dominance is too often not defined and not always apparent. Not all losses of coral and increases in algae are shifts that will irrevocably tip the balance from net accretion to losses in calcification, or from calcifying organisms, such as corals and coralline algae, to non-calcifying organisms such as many macroalgal species. It is important to consider if significant losses in coral cover can be reversed. Can a reef that has gone from 80 % coral cover to 80 % algal cover ever return to its initial coral cover? The question is not whether or not a phase shift has occurred—we want to find out if *recovery* is possible and define what that recovery might look like. Although "recovery" is sometimes used in a limited way to refer to a return to an initial level of coral cover, full recovery would also involve the restitution of the preexisting community composition (e.g., relative abundance of coral species) and framework complexity (Johannes 1975; Done 1992).

If our objective is to decide what attributes would indicate a recovering or resilient reef, we need to think in terms of both reef structure and reef function. When biologists speak of structure they are often referring to the composition of the coral reef (the relative abundance of different coral species, algal species, etc.) but, like geologists, they can also be referring to the actual physical structure of the reef—the topographically complex architecture that is the result of deposition of calcium carbonate and cementation. Reef function, on the other hand, refers to processes like coral growth, recruitment, nutrient cycling, and calcification.

The most fundamental unit of a coral reef is a coral polyp depositing a limestone (rock) corallite and surviving to grow. Whatever adversely affects this recruitment and calcification process endangers the coral reef. Ultimately, characterizing the status of a reef would require comprehensive knowledge of processes that are more difficult to monitor than just changes in benthic cover. How can we adequately measure changes in the balance of calcification versus bioerosion? Interestingly, Perry et al. (2012) are using basic monitoring data on cover by corals and calcifying algae as well as abundance of substrate-eroding organisms to estimate carbonate budgets that could provide clues to changes in reef structure.

It is challenging to look at changes in structure (including coral composition) but even harder to look at the mix of bioerosion, productivity, recruitment, calcification and the myriad processes that reorganize and redistribute carbonate within the reef over a large spatial scale. Also, we need to understand how these processes can change over time as environmental conditions change.

12.3 Monitoring

Although we acknowledge that reefs were in trouble before most long-term monitoring began (e.g., Jackson 1997), these programs evolved out of a need to quantify the magnitude and rates of change in coral reefs. In this section we discuss the different components of an effective monitoring pro- gram, specifically addressing why, where, and how we should monitor coral reefs, and finally what should be done with the results (So what?). We need to carefully consider each of these elements to design effective monitoring strategies.

12.3.1 Why Monitor?

Monitoring has been defined as “the collection and analysis of repeated observations or measurements to evaluate changes in condition and progress toward meeting a management objective” (Elzinga et al. 1998, page 1). Most people value monitoring (and the products, data, results, identified trends) but hope someone else will do it—it is the “Rodney Dangerfeld” of coral reef science! Well- designed and carefully implemented monitoring programs are essential for quantifying changes on coral reefs. While the characterization of reefs is important, repeated characterization is not monitoring. Monitoring should systematically and consistently measure changes in abundances of organisms, determine ranges in environmental factors, help to reveal possible cause-and-effect relationships, help mea- sure and differentiate the effects of both natural and human- induced stresses, and determine if a specific management action is working. It is essential to state the question you are hoping to answer before you begin your monitoring pro- gram. In some cases, the objective of monitoring may not be explicitly stated, but the implicit goal is usually to provide information that can be used to better manage coral reefs. Ideally, the monitoring will be driven by a particular hypothesis. It is possible to “miss the point”, that is, to get the right answer to the wrong question, by establishing a monitoring program that is statistically rigorous but ill-conceived. Conversely, challenges arise when comparing or combining reef monitoring data obtained with varying techniques collected in widely different “coral reefs” or coral reef zones to pro- duce regional trends (Jackson et al. 2014).

12.3.2 Where to Monitor?

It has been noted that, “when you are on the wrong train, every stop is the wrong stop” (Stein 1983). Having rigorous, peer-reviewed protocols is critical, but if the monitoring takes place in the wrong locations we are not going to reach our goal.

It is very important to make a distinction between coral monitoring and coral reef monitoring. The failure to differentiate between these two can lead to confusion and wasted effort. If the question is “What is the percent of coral cover in the Caribbean (or around an island or within a particular national park)?" that is very different from "What are the ecological changes over time on 'true' coral reefs?" Corals can be found growing in seagrass beds, on boulders and in other areas that we would not think of as reefs. If the interest is in documenting coral cover wherever corals occur, then a wider geographic approach (over a larger spatial area) is warranted. However, this broad approach will not provide the necessary ecological data or context for evaluating changes on actual coral reefs that cover a much smaller percent of the overall area.

For example, it is not too helpful for the manager of a marine protected area to learn that coral cover throughout the entire hardbottom area has dropped from 5 % to 4 % or even gone up from 5 % to 7 % over the course of a year. What management action might this provoke? How can one visualize this change and where does one go with this information? However, learning that there were losses of greater than 50 % of the living coral cover on true coral reefs is of great interest to park managers.

Well-developed reefs often will cover a small percent of the bottom, but they are of disproportionate ecological importance as habitats for organisms as well as sinks and sources of the larvae of fishes, corals, and other reef organisms (e.g., Sale 1991). These reefs should be the focus of study, especially within national parks and marine reserves. They are "special places" within "special places" that have been set aside precisely because of their ecological significance. At this spatial scale, the selection of which reefs to study is not and should not be random. Here we focus on monitoring true coral reefs (as defined earlier), not on monitoring of corals in any hardbottom community.

A rigorous statistical approach to sample design is optimal. Until recently few coral-reef monitoring programs used a random approach to sampling (Lewis 2004), but we now have the tools (e.g., GPS, georeferenced maps) and knowledge to do this. Recall, it was only recently, in 1998, that Executive Order 13089 by President Clinton identified—"comprehensive mapping, assessment and monitoring"—as priorities within the Coral Reef Initiative. When monitoring coral reefs, sampling units (i.e., transects or quadrats) should be randomly selected from within the boundaries of the reef or reef zone of interest. Some of these sampling units might not meet the predefined criteria, e.g., they may fall in sand or seagrass beds. In this case, they can be rejected and the next randomly selected unit can be chosen.

Caution must be used in extrapolating the results of monitoring to the appropriate area of inference. With random, unbiased selection of a sufficient number of sampling units, the results can be applied to larger spatial areas. The scientific literature is full of the results of monitoring based on haphazard (non-random) sampling in which conclusions are presented as if they applied to an entire reef zone or reef when they are only representative of a few quadrats or transects. The following quote from the 2008 Status of the Reefs report compiled by Wilkinson (2008) is instructive:

These status assessments and predictions are based on consider- able monitoring data using a range of methods, varying from very detailed species level monitoring to rapid monitoring by trained volunteers. However, it is recognized that monitoring in many countries only covers a small and unrepresentative pro- portion of the reefs, such that the monitoring data are inadequate for a quantitative assessment. In these cases we have relied on qualitative assessments based on the expert opinion of national and visiting scientists, complemented by information from professional dive guides.

Although the focus has been on corals primarily as the major architects of coral reefs, one of the biggest unanswered questions (there are many!) is “What effects will these coral declines have on reef biodiversity, on the reef fishes and other organisms?” [We do not know what happened to fishes when there were extreme losses of elkhorn (*Acropora palmata*) and staghorn (*A. cervicornis*) corals beginning over 25 years ago!] Monitoring fish populations at randomly selected points across a variety of habitats for example, will not help us answer this question. Serious consideration should be given to co-location of sites for monitoring coral cover and reef fish diversity/ abundance. Another important question is: “Is coral cover or structural complexity (shelter) a more significant driver of reef fish diversity and abundance?” However, it is also essential to look beyond the boundaries of a particular reef of interest to better understand the *connectivity* among the reef and associated habitats that serve as sources of larvae (see below).

12.3.3 How and How Often?

Monitoring must occur not only in the correct locations but also with appropriate protocols that outline exactly how measurements or samples will be taken and how often. Many different methods are now readily available (e.g., see Rogers et al. 1994; English et al. 1997; Patterson et al. 2008) and will not be reviewed here. In the last two decades, photography (still and video) has become increasingly affordable and valuable. Video provides a permanent visual record, but requires substantial time for processing. Conversely, quadrats, chain transects and line-intercept transects require much less processing after data collection to deter- mine percent cover of organisms, but are time-intensive in the field and provide no permanent visual record. Chain transects and LIDAR provide data on 3-dimensionality/ rugosity. LIDAR and other types of remote sensing can cover a much larger spatial scale but lose effectiveness with increasing depth. Remote sensing is not always effective at identifying benthic cover and is most useful for documenting relatively large changes in structure (e.g., Scopoletis et al. 2011). Taking sequential photographs can provide very useful information but it may be difficult to quantify change, depending on the scale (e.g.; aerial vs. in situ). In some cases, the degradation of a reef is so extreme that in situ photographs taken over time are sufficient to indicate that substantial change has occurred. Whatever the method, the critical objective is to reveal problems while there is still time to correct them.

One area where better technology has made a significant difference is in the production of increasingly accurate benthic habitat maps. For example, the progression of maps from Dry Tortugas National Park in Florida (Fig. 12.1) shows the shifting (and better definition) of boundaries as well as greater differentiation and delineation of habitats from the earliest map in 1881 to the most recent in 2010, based on satellite imagery. The new, georeferenced maps provide a basis for both identification of habitats or zones of the greatest interest and selection of appropriate monitoring locations.

Monitoring must also be done at an appropriate frequency. Annual monitoring is often not sufficient. More frequent monitoring has been shown to be essential in revealing the causes of some coral decline. In the absence of major disturbances, coral cover typically changes more slowly than algal cover. Surprisingly, however, many people present single, annual values for macroalgae ignoring the fact that macroalgal cover can vary substantially over short periods of time (days). When major disturbances occur over several months, infrequent monitoring can lead to misinterpretations of the timing and causes of change. For example, someone monitoring permanent transects in August 2005 in the US Virgin Islands and then again in August 2006 could mistakenly conclude that the severe bleaching event which began in

September 2005 caused extensive mortality, when, in fact, the coral disease outbreak that began later in 2005 was the actual cause of most of the coral decline (Miller et al. 2009).

12.3.4 So What?

A primary objective of monitoring is to differentiate natural from anthropogenic change to allow identification of actions that can be taken to reduce reef damage. However, this is often not an easy task (Hughes et al. 2011; Sweatman and Syms 2011; Sweatman et al. 2011). Even with several years of monitoring, it can be hard to determine the normal variation in the abundance (cover) of different organisms. Monitoring results will not always be directly applicable (or useful) for local management. To illustrate, the manager of a Marine Protected Area (MPA) should know that over half of the coral within the MPA has succumbed to diseases but will not be able to take specific action to quickly reverse coral cover decline. As seen in the definition of monitoring above, progress towards a management goal is often considered an integral objective. The scales for management actions need to be aligned with the scale of the monitoring and *vice versa*. Regional monitoring may provide regional baseline data, yet regional management actions are rare. Local protective measures within a bay or watershed are more likely to gain public support and produce discrete, measurable results. Public opinion cannot be overlooked with respect to management actions. Whether it is the listing of threatened or endangered species, such as the National Oceanic and Atmospheric Administration's recent listing of 20 additional coral species, limits on anchoring, designation of boating/swimming access, or fishing closures, the success of these actions depends on public compliance.

Stressors differ in their essential characteristics, and not all can be categorized as purely natural or anthropogenic. Anchor damage or destruction from a vessel running aground on a reef is very different from chemical or sediment contamination, for example. Stressors that remove living tissue but leave coral skeletons intact differ substantially from those that destroy the physical structure and even the underlying framework of a reef. The effects of some stressors are easier to measure. Bleaching and diseases are much harder to quantify and address than damage from boat anchors and groundings.

Because coral diseases are not clearly either natural or anthropogenic and vary greatly in their temporal and spatial distribution, their global significance can be hard to evaluate. In their report "Reefs at Risk", Burke et al. (2011) compile data on local human-related stressors (the primary focus of the document) and on past thermal stress (bleaching). They address coral disease as a "compounding threat" and include a map showing the global distribution of disease incidence from 1970 through 2011. However, they note that this map is based on an incomplete database. Also, the map does not show disease prevalence or trends in disease occurrence over time.

Coral diseases have had the greatest adverse effects on Caribbean coral reefs in the last 50 years, and they are of increasing concern in the Indo-Pacific (Willis et al. 2004; Raymundo et al. 2008; Weil and Rogers 2011). They are found in all ecosystems, but increased prevalence in some cases can be attributed to release of sewage or other human activities (Bruno et al. 2003). Diseases may also be linked to bleaching which in turn is linked to high seawater temperatures. Given the anticipated increase in seawater temperature associated with climate change, we need to learn more about the relationship among thermal stress, bleaching and disease. Increases in temperatures that lead to bleaching may have both a natural and human component (e.g., Donner et al. 2007).

Often reefs are subjected to several natural and human- related stressors simultaneously, making attempts to manage them even more problematic. For example, a heavily overfished reef can be damaged by a hurricane. Explosions of Crown-of-Thorns starfish may reflect natural cycles but also increases in nutrients from agricultural runoff (Brodie et al. 2005; De'ath et al. 2012). The loss of Diadema antillarum in the Caribbean (Lessios 1988) is likewise complex regarding both cause and subsequent impact to reef processes. A combination of well-designed long-term monitoring programs and hypothesis-driven experimental research is needed to make progress in sorting out the effects of single and multiple stressors on coral reef organisms and reef processes.

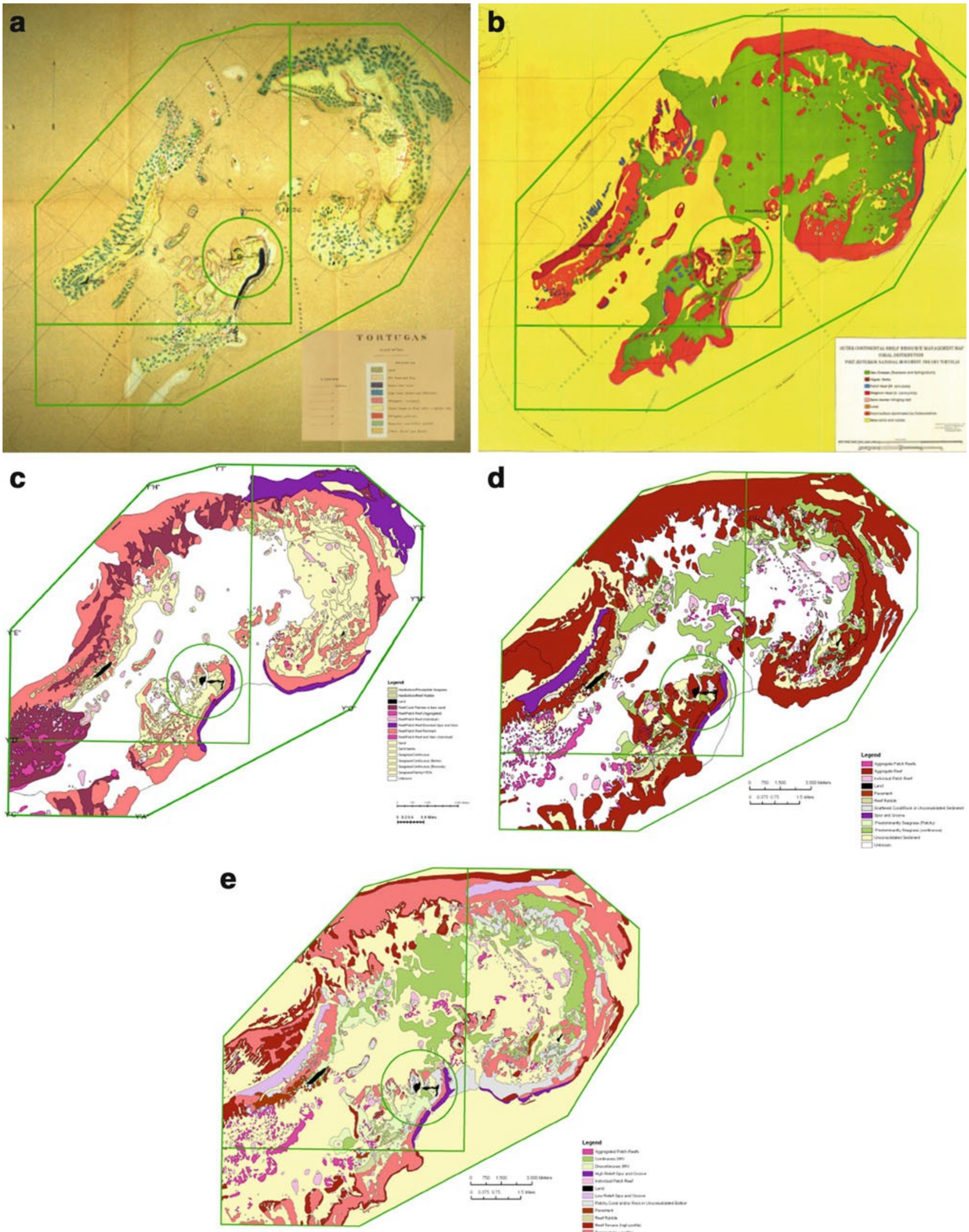

Figure. 12.1 A progression of maps of benthic habitats in Dry Tortugas National Park showing greater accuracy and finer detail with improved mapping technology (see Waara et al. 2011) [Sources for maps a Agassiz (1882); b Davis (1979); c FMRI and NOAA (1998); d Avineon (2008); Waara et al. (2011)]

12.3.5 Monitoring: A Few Concluding Thoughts

A primary objective of monitoring programs is to turn data or results into information for better management of reefs. This depends on effective communication among scientists and managers. Many groups have made a strong commit- ment to high-quality monitoring programs, including but not limited to: The Australian Institute of Marine Science, the Global Coral Reef Monitoring Network, the US National Park Service Inventory & Monitoring Program, the US Geo- logical Survey, the National Oceanic and Atmospheric Administration, the Caribbean Coastal Marine Productivity Program, the Atlantic and Gulf Rapid Reef Assessment program, Reef Check, and the Reef Environmental Education Foundation (Miloslavich et al. 2010; Burke et al. 2011).

These monitoring programs are all good examples of how to turn data into information for improved management of reefs. There is also the need to “monitor the monitoring”, to step back and see if adjustments should be made because of changes on the reefs, or monitoring technology. Although methods should be standardized whenever possible (especially when the objective is to compare reefs), and the same methods should be used over time, significant changes in reef structure or the appearance of new stressors may necessitate a shift in methods. For example, as coral cover continues to decline, it is becoming harder and harder to measure, particularly using visual estimates. One will be more accurate observing a decline from 80 % to 40 % coral cover than a decline from 4 % to 2 %, although both reflect a 50 % relative loss.

The support for using a common method and metric (e.g., quadrats to estimate coral cover) does not diminish the need to explore other reef indicators and processes. For example monitoring coral recruitment is necessary for assessing potential coral recovery (Hughes et al. 2000, 2011). Basic monitoring using quadrats and transects is not well suited to documenting trends in recruitment because by the time one can reliably identify recruits on the reef they can be several years old (Vermeij 2006). Conversely, settling plates provide convenient substrates for quantifying recruitment but may not be representative of what is happening on more complex natural reef surfaces. An overall picture of changes on coral reefs requires a combination of different approaches including monitoring and experimental field research.

12.4 Management

The definition of monitoring presented above includes the concept of measuring “progress” towards reaching a management goal. What are the explicit goals of management? Management for sustainable fisheries would presumably differ from management for maintenance of biodiversity. In many cases, the goal will be to conserve or restore a coral reef, i.e., to promote recovery.

There are a number of actions that managers can take locally to increase the likelihood that reefs will be able to persist in the face of local and global stressors. In the early 1990s, many scientists concluded that the most serious threats to reefs were associated with human activities: shore- line development, overfishing, and degraded water quality from sediments and sewage (Ginsburg 1994). Then, with severe bleaching episodes beginning in 1998, the focus shifted more to global stressors and climate change (Wilkinson 1999). In some ways we are back to where we started with an emphasis on managing human activities at a local level (e.g., reducing anchor damage, controlling release of sewage and sediments), while still hoping that international efforts to control greenhouse emissions will become more effective (Hughes et al. 2003; Aronson and Precht 2006; Hoegh-Guldberg et al. 2007; Maynard et al. 2008; Burke et al. 2011; Kelly et al. 2011). Managing local stressors is far more feasible than trying to control global stressors, but even this has not proven to be easy. In spite of all of the uncertainties, it only makes sense to move forward with controlling those stressors that we can control rather than waiting for an international response to climate change.

Monitoring can provide data for models that can be useful for reef management. For example, models have the potential to suggest reef-specific strategies to improve conditions (Wooldridge et al. 2005; Baskett et al. 2010; Mumby et al. 2010). Models can also help to identify the optimal locations for establishing MPAs, e.g., areas with a history of fewer bleaching events (Mumby et al. 2010). Many of the existing models focus on control of macroalgae, reflecting the importance of algae in restricting coral recruitment. Some models suggest that there are thresholds in the abundance of some reef organisms such as herbivorous fishes that must be exceeded if coral cover is to remain level or increase. Many models focus on abundance of herbivores because of their role in controlling macroalgae and some indicate that even small increases in herbivore numbers can have significant effects (Wooldridge et al. 2005). However, further research is needed to determine if thresholds can be identified for specific reef processes in ways that can inform management.

12.4.1 Marine Protected Areas

The establishment of MPAs is one of the most promising management actions that can be taken. When we say that an area is "protected" we are implying that it is less subject to human activities that adversely affect the organisms within it. Sometimes the goal of a monitoring program is to evaluate the effectiveness of an MPA. However, designing such a monitoring program can be challenging because perfect controls or even reference areas may not exist. The MPA and non-protected area may differ in several characteristics, such as distance from shore, depth, and reef zonation. Another complicating factor is that MPA boundaries are often politically rather than ecologically derived. They are often unmarked, further complicating results as users are often unaware of management restrictions. Public education regarding MPA regulations may be lacking or ineffective, and evaluation of user compliance with regulations, integral for an accurate "inside/outside" comparison, is often not done (Claudet and Guidetti 2010).

Marine protected areas, particularly no-take marine reserves, have been shown to increase the abundance of targeted species and sustain or, in a few cases, increase cover of corals and other non-harvested species (Lester et al. 2009; Selig and Bruno 2010). It is harder to find evidence of increases in coral cover than increases in abundance of previously harvested fishes. Protecting fish does not necessarily reduce macroalgal cover, increase coral abundance, or preserve or increase topographic heterogeneity that is critical to maintaining or increasing fish abundance (e.g., Aronson and Precht 2006; Alvarez-Filip et al. 2011; Huntington et al. 2011). Analyses of the effectiveness of MPAs may be misleading if they include areas where fishing and other extractive uses are allowed or areas with ineffective enforcement of strict regulations.

Selig and Bruno (2010) found no change in coral cover over time across all reefs within MPAs over about four decades (1969–2006) but a decline in cover on unprotected reefs. Their analysis did not conclude that MPAs (encompassing areas with different levels of enforcement and protection) would lead to increases in coral abundance. It is also important to note that their study did not incorporate significant losses in coral cover following the Caribbean bleaching event in 2005 and the subsequent disease outbreak (Miller et al. 2009).

Networks of MPAs, if well-designed, can result in more benefits than single protected areas—with the whole being greater than the sum of its parts. They can include sources of larvae to replenish reef organisms and areas with stronger currents and upwelling, bringing cooler temperatures. How- ever, variation in stressors as well as the heterogeneity of reefs even over short distances can make it difficult to predict where the greatest protection can be realized. Where it is feasible to design networks of marine reserves, every effort should be made to protect areas that are likely to survive future climate-driven changes, although this is certainly not very straightforward (McLeod et al. 2009).

12.5 Biodiversity as a Management Goal

Networks of marine reserves that protect the connections among coral reefs, seagrass beds, and mangroves have the potential to maintain biodiversity. There is an urgent need for more information on the biodiversity of coral reefs and on how different reef species will respond to the combination of local and global stressors.

It is estimated that over 90 % of the species inhabiting coral reefs have yet to be discovered (Reaka-Kudla 1997; Ausubel et al. 2010). We need to have a better understanding not only of how organisms might change in their distribution and abundance, but how they may or may not adapt to changes in climate. Also, the complex interactions among different organisms may themselves change over time (e.g., Harley 2011). Although Harley (2011) does not specifically mention corals or reefs, his conclusions on interactions among species and how these could react to climate change seem relevant. What happens to other reef organisms when coral cover or diversity is reduced?

Coral reef species differ in their responses to local stressors and to environmental factors that are anticipated to change with changing climate. For example, some coral species may not be as affected by increasing temperatures in terms of their physiology, larval development and survival. Weil and Vargas (2010) note the importance of learning more about the reproductive biology of major reef-building corals and how increasing water temperatures, whether or not they lead to bleaching, could affect fecundity and larval survival. Corals and other reef species also vary in their response to acidification (Pandolf et al. 2011). More information on the variation in responses of reef organisms to local and global stressors, only briefly referred to here, must come from experimental research.

It is possible that the complexity and biodiversity of coral reefs, one of their core characteristics, can help to ensure that they have a future. In other words, biodiversity, and effectively managing for biodiversity, may confer resilience. Because reefs are now so degraded, there has been considerable discussion about managing for “resilience”. Humans are clearly reducing the resilience of reefs (Nystrom et al. 2000).What is resilience and can we manage for it?

12.3 Coral Reef Resilience

Resilience has been defined as “a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables” (Holling 1973, page 14). In short, resilience is the ability to rebound. Although the word resilience is sometimes used to encompass “resistance,” greater clarity is achieved by making a distinction between the two (Tang 2001; West and Salm 2003). When applied to coral reefs, resistance can refer to the ability of the entire reef or of individual corals and other organisms to remain unaffected by a stress, and resilience can be thought of as the capacity for the reef to recover after disturbance or stress.

In general, few examples of significant recovery can be documented, although some reefs have seen increases in coral cover primarily after bleaching events (Diaz-Pulido et al. 2009; Graham et al. 2011). Reefs with faster-growing corals, cooler water temperatures, less macroalgae, and sources of larvae are more likely to be resilient (e.g., see McLeod et al. 2009). Some scientists have argued that it is better to manage for a reduced number of more resistant reef organisms than to try to restore original species assemblages (Cote and Darling 2010). However, given how little is known about the tolerances of different species and how difficult it is to predict future environmental conditions, managing for a resistant reef with less biodiversity rather than a resilient, diverse reef seems counterproductive. A major question is the degree to which human-caused changes on modern reefs are unprecedented, jeopardizing reef resilience (Hughes et al. 2003).

The ability of coral reefs to recover after disturbances could depend on their connectivity not only to other reefs but also to seagrass beds and mangroves, systems which are often neglected or understudied (Rogers 2013). Sources of larvae are needed to replenish depleted populations of corals, fish and other organisms. Mumby and Hastings (2008) used models to show that reefs near mangroves were better able to recover from intense storms than those that were not linked to mangroves. In addition, these systems (and the connections or linkages between and among them) may respond differently to stressors associated with global climate change. Sea level rise could be more of a threat to mangroves than to coral reefs, which could actually benefit (Cubit 1985; Hallock 1997). It is important to keep in mind that changing climate has many components (sea level rise, alterations of current patterns, ocean acidification, increasing temperatures) and marine ecosystems can respond differently to each of these.

12.7 Predicting Coral Reef Change: Back to the Future

Given the complexity of coral reefs, it is not surprising that an accurate evaluation of their potential for recovery or for persistence will require efforts by scientists in many different disciplines—including biology, geology, and physical oceanography. Biology and geology are more closely inter- related in studies of coral reef ecosystems than in any other ecosystems. What can biologists learn from geologists and vice versa? (see Box 12.1 for an example based on Caribbean *A. palmata*). Biologists can look to the fossil record and patterns therein to form hypotheses for experimental research. Geologists can learn from biologists about the environmental constraints to coral growth. Working more closely with each other could help advance our knowledge of reefs at this critical crossroads. One hundred years from now what will we find? Some scientists have predicted reefs could collapse into rubble as early as 2050 if CO2 concentrations reach 560 ppm (Silverman et al. 2009; Erez et al. 2011). Are reefs collapsing anywhere now? What can geologists tell us about this and where it is likely to happen? What is the time frame?

Box 12.1 The Evolving Story of *Acropora palmata*

An examination of the history of research on Acropora palmata provides interesting insights into the challenges involved in documenting reef change and predicting the future for coral reefs. Acropora palmata is without doubt one of the most significant corals on Caribbean reefs. With its large size and intricate, branching morphology, it creates a complex architecture for the shallow zones seaward of the reef crests of fringing and barrier reefs. Before the 2005 Caribbean bleaching event followed by a disease outbreak that led to an average loss of 60 % live coral cover (of primarily massive species) in the Northeastern Caribbean (Miller et al. 2009), white band disease (WBD) was probably the single greatest cause of coral mortality on shallow coral reefs in the Caribbean. White band disease and hurricanes are thought to have caused mortality of over 90 % of the *A. palmata* populations at several sites throughout the region beginning in the late 1970s and continuing through at least the 1980s. Evidence that WBD was the primary cause of this extensive mortality comes from a variety of sources, ranging from anecdotal observations to a few cases of well-documented research on the disease as it advanced through zones dominated by this species (Rogers 1985; Aronson and Precht 2001a, 2001b). Careful scrutiny of the literature reveals very few quantitative and/or definitive studies of declines in A. palmata, and these are from only a few locations (more data are available for *A. cervicornis*.) In some cases, scientists returned to sites they had visited 10 or more years previously and found piles of rubble and/or stands of dead *A. palmata* colonies but did not have direct proof that WBD was the cause of the losses (e.g., Panama: Ogden and Ogden 1994; Bahamas: Greenstein et al. 1998). Although it is likely that disease caused the observed mortality, few people have actually documented the disease progressing through a reef. The most definitive records come from St. Croix (Gladfelter 1982), Belize (Aronson and Precht 1997), and the British Virgin Islands (Davis et al. 1986; Bythell and Sheppard 1993). From 1976 to 1988, Gladfelter (1991) noted a drop from 85 % to 5 % at two sites at Buck Island, St. Croix, from WBD and Hurricanes David and Frederic (1979). There was a further loss from 5 % to less than 1 % attributable to Hurricane Hugo in 1989 (Gladfelter 1991). Data from monitoring along with anecdotal observations (see Bruckner 2003) documented the low population levels in the Carib- bean that eventually led to the listing of this species as threatened under the US Endangered Species Act in 2006 (Hogarth 2006) and as critically endangered on the International Union for Conservation of Nature Red List in 2008.

Surprisingly, data that would indicate the effects of the loss of *A. palmata* on fishes or other organisms are not available. Perhaps this is because some scientists focus more on corals and others focus more on fishes! Co-location of monitoring at permanent reference sites has the highest potential to provide useful ecological data. Fish abundance and diversity reflect the abundance (cover) of coral but also the presence of complex structure that provides habitat: even dead coral can provide shelter. Collapse of *A. palmata* from hurricanes fattens the topography and makes an area less likely to support large fish populations. In the absence of hurricanes, how long does it take for *A. palmata* to break down from boring sponges or other bioeroders?

Currently we lack sufficient quantitative data for the wider Caribbean to state whether *A. palmata* recovery is occurring substantially or to provide a baseline for future evaluation. Information on distribution and abundance comes from Aronson and Precht (2001a, 2001b), Bruckner (2003), Precht and Aronson (2006) and the Acropora Biological Status Review Team (2005), but there are few records since 2000. Given the species' status as threatened/endangered, the low number of current monitoring programs focused on this species is surprising. No studies document significant recovery to levels of abundances or densities characteristic of the 1970s, and only a few studies indicate limited recovery (Zubillaga et al. 2008; Rogers and Muller 2012). It is possible that *A. palmata* will recover more quickly than Orbicella annularis and O. faveolata which have been disproportionately affected by diseases in the last decade (Edmunds and Elahi 2007; Miller et al. 2009; Rogers et al. 2009; Bruckner 2012) although they continue to be the most abundant species on many reefs in the USVI (Fig. 12.2).

Disease continues to affect *A. palmata* populations, although white pox (white patch) disease is now more prevalent than the more virulent WBD, at least at some sites (Mayor et al. 2006; Rogers and Muller 2012). Problems in differentiating white pox from other "white" diseases make an accurate assessment difficult. Some *A. palmata* colonies exhibit signs of white pox, white band, and other un-described diseases simultaneously. Climate change is expected to increase the frequency of bleaching episodes, and these may be linked to disease outbreaks. In 2005, *A. palmata* bleached for the first time on record in the USVI, and bleached colonies in Hawksnest Bay, St. John, had more disease than unbleached ones (Muller et al. 2008). In 2010, there was moderate to severe bleaching of many coral species but not of A. palmata.

Some have questioned the value of monitoring, stating that there is little point in continuing to monitor declines in coral cover or abundance. However, monitoring provides a quantitative basis to determine if recovery is taking place, either as part of a natural cycle or in response to a specific management action. The best evidence of *A. palmata* recovery would come from multi-year studies showing all of the following: an increase in the overall amount of living tissue of this species, growth of existing colonies, and an increase in the number of small corals arising from sexual recruitment. Some *A. palmata* zones continue to have little to no *A. palmata* cover while others have high densities of the species (Fig. 12.3).

Although WBD was first noted over 30 years ago, no specific cause of the disease has been identified, partly because of the difficulty in culturing bacteria and because both the coral host and associated symbionts can be involved. Recently Kline and Vollmer (2011) have experimentally shown that the causative agent for WBD is probably pathogenic

Figure 12.2 An *A. palmata* colony growing on top of a dead *Orbicella annularis* colony

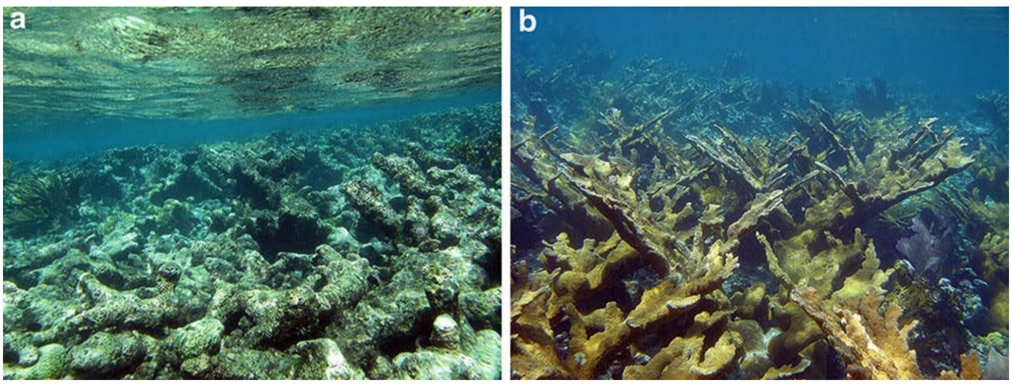

Figure. 12.3 Two *A. palmata* zones in St. John, US Virgin Islands: (a) Newfound Reef: Little live coral is present in this zone that was probably decimated by white band disease and storms. (b)Hawksnest Reef*:* *A. palmata* grows in high density here

bacteria. However, it is unlikely we will ever know why these bacteria triggered the disease beginning in the late 1970s. In 1977, Gladfelter observed that 5 ha of Tague Bay Reef, off the northeast coast of St. Croix, was affected by WBD and remarked that there was little evidence of any link with human disturbance (Gladfelter 1982).

Clearly, linking coral disease to human activities would be vitally important as it provides a basis for management action. White pox in Florida appears to be associated with human sewage (Sutherland et al. 2010, 2011), but that association has not been made for what appears to be the same disease in St. John (Polson et al. 2009; May et al. 2010). The listing of *A. palmata* and the closely related

A. cervicornis has focused more attention on these species. At Buck Island Reef National Monument, St. Croix, managers are proposing "boat free zones" to eliminate anchor damage and reduce the possibility of vessels running aground on shallow stands of these species.

What insights does the geological record provide? Van Woesik et al.(2012)explore the vulnerability of modern corals specifically to thermal stress by examining extinctions in the Plio-Pleistocene. They developed "resilience scores" based on biological traits such as type of symbionts, calcification rate, and colony size as well as on biological processes such as sexual recruitment and colony re-growth for several Caribbean taxa. On a scale of 5 to 6 (most to least resilient), *A. palmata* had a score of 2 and O. annularis complex a score of 4. Above we suggested that *A. palmata* might recover more quickly than O. annularis based on consideration of other stressors including susceptibility to diseases.

Hubbard (2009) describes how the perspective on *A. palmata* reefs in the Caribbean shifted with an increase in the number of cores that were drilled in reefs. This story underscores the importance of having sufficient data to provide a basis for extrapolating findings to larger spatial scales. He notes "For geologists, three cores from Lang Bank [St. Croix] described at the 1977 ISRS meeting in Miami, Florida set the direction of the coral-reef discussion for the next three decades." These cores indicated a gap in reef accretion at a time when *A. palmata* reefs would have been expected to keep up with sea level rise. Additional cores in

St. Croix, Puerto Rico and Florida suggested that reef accretion had continued during these time periods (Hubbard 2009). However, they also pointed out an absence of *A. palmata* reef accretion for unknown reasons between 7000 and 6000 Cal BP (calibrated years before present) and again at c. 3000 Cal PB. Hubbard (2009) asks if this regional decrease in reef accretion provides some clues into the more recent decline of this species. It is interesting to consider if other widespread disease epidemics led to the hiatus in coral growth during these two time periods. The dynamic between sea level rise and *A. palmata* reef accretion described in Hubbard (2009) may be pertinent to predicting the future of some reefs as sea level continues to rise.

Given how difficult it is to get cores from reefs and interpret them, have enough been taken to provide an adequate picture of reef changes and reef history? It would be interesting to look back in time to see what the geological record can (or can't) tell us about connectivity among reefs, seagrass beds and mangroves, and how these ecosystems have changed in spatial relationship to each other. Decades into the future, geological investigations may be able to tell us if our management actions have been successful. One hundred years from now, will we be able to tell from the brief geological signature if reefs were effectively protected within MPAs?

There are constraints and challenges in predicting what to expect with climate change (e.g., Kleypas 2007), and biologists and geologists can both contribute to reducing the uncertainty through monitoring and experimental research. Climate change is sometimes described as the greatest "single" threat to coral reefs. However, climate change is comprised of different components (e.g., sea level rise, ocean acidification, higher seawater temperatures, more frequent and intense storms), and these should be considered separately. Major bleaching episodes are likely to become more frequent (Hoegh-Gulberg 2011). Can the geological record provide different signatures for coral bleaching and disease, and indicate how the two are related? The greater precipitation expected with changing climate could increase runoff of sediment into waters overlying coral reefs, a pattern that can be discerned in geological cores.

One of the most fundamental questions is: What can the fossil record tell us about the past, present and future of corals reefs? Pandolf (2011) observed that paleo ecological studies can help put the current status of coral reefs into perspective and provide insights into the reefs of the future. For example, such studies can indicate how disturbances and environmental changes in the past have influenced processes that affect species diversity through time (Precht and Miller 2007). Variation in coral growth rates, the susceptibility of different coral species to extinction, and overall reef accretion can all be put into context. Even processes such as predation, herbivory and competition can be studied through the fossil record (see Chap. 10). Pandolf (2011) notes it has been challenging to answer a key question in ecology: How is biodiversity maintained in ecological communities? The geological record may help to explain why biodiversity "hotspots" form. The fossil record can tell us not only about corals but also about other reef organisms that contribute to the complexity of the reef.

There is the potential for the geological record to provide many clues into the future persistence of coral reefs. How- ever, this record will provide more information on some aspects of climate change (warming temperatures, sea-level rise) than others (rates and magnitude of CO_2 rise) [Pandolf and Greenstein 2007; Solomon et al. 2007].

12.8 Conclusions

Coral reefs are clearly more than just hazards to navigation (Columbus 1492). They enrich and protect human life. Geologists and biologists can provide evidence of the eco- system services that are associated with these beautiful and threatened ecosystems and make recommendations for more effective management. Understanding and predicting future changes and the very survival of coral reefs will require continued long-term monitoring as well as biological/geological experiments and investigations.

Interpretation of monitoring results needs to be done with full awareness of the context in which they were obtained. Meta-analysis combining numerous regional monitoring studies with disparate objectives and methods can identify large-scale trends, but often errantly extrapolate findings of monitoring studies beyond the areas of inference for which they were originally designed.

Considering the relatively recent advent of underwater exploration, we've learned much in a short period of time, but for a system that is the poster-child for "geologic time" we must acknowledge that this is a 'work in progress'. Changes in global climate, declines in coral cover from habitat loss/disease, and rearrangement of trophic assemblages due to overfishing are examples of manipulations currently taking place on coral reefs, for which the effects are still unknown. In many places we've moved from convincing managers that monitoring was necessary, to engaging managers in discussions on the merits of stratified random versus haphazard sampling and under- standing monitoring results.

Acknowledgements

We thank Dr. Dennis Hubbard for inviting us to submit this chapter and for stimulating exhausting but productive discussions and two USGS scientists for reviewing an earlier draft. Dr. Bill Precht's review was particularly insightful and constructive. We also wish to thank Julia Dileo and Lee Richter for their helpful comments.

References

Acropora Biological Status Review Team (2005) Atlantic *Acropora* Status Review Document. Report to National Marine Fisheries Service, Southeast Regional Office. March 3, 2005. 152 p + App.

Agassiz A (1882) Explorations of the surface fauna of the Gulf Stream, under the auspices of the United States Coast Survey. II. The Tortugas and Florida reefs. Mem Amer Acad Arts Sci Centennial, II: 107–134

Alvarez-Filip L, Cote IM, Gill JA, Watkinson AR, Dulvy NK (2011) Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? Global Change Biology 17: 2470–2477 doi: 2410.1111/j.1365-2486.2010.02385.x

Aronson RB, Precht WF (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. Paleobiology 23: 326–346

Aronson RB, Precht WF (2001a) White band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460: 25–38

Aronson RB, Precht WF (2001b) Evolutional paleoecology of Caribbean coral reefs. In: Allmon WD, Bottjer DJ (eds) Evolutionary paleoecology: The ecological context of macroevolutionary change. Columbia University Press, NY, pp 171–233

Aronson RB, Precht WF (2006) Conservation, precaution, and Caribbean reefs. Coral Reefs 25: 441–450

Ausubel, JH, Crist, DT, Waggoner, PE (eds) (2010) First Census of Marine Life 2010: Highlights of a decade of discovery. Census of Marine Life. Washington, D.C. 64 pp

Avineon, Inc (2008) DRTO_coral\crdublin\photo\FWRI\Tortugas\Final_Inspection\shapefles\ DRTO_coral.shp. Clearwater, FL

Baskett M, Nisbet R, Kappel C, Mumby P, Gaines S (2010) Conservation management approaches to protecting the capacity for corals to respond to climate change: a theoretical comparison. Global Change Biology 16: 1229–1246

Brodie J, Fabricius K, De'ath G, Okaji K (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. Mar Poll Bull 51: 266–278

Bruckner AW (ed) (2003) Proceedings of the Caribbean *Acropora* workshop: Potential application of the U.S. Endangered Species Act as a conservation strategy. NOAA Tech Memo NMFS-OPR- 24, Silver Spring, MD, 199 pp

Bruckner AW (2012) Factors contributing to the regional decline of *Montastraea annularis* (complex). Proc 12th International Coral Reef Symposium: 5p

Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. Ecol Lett 6: 1056–1061

Buddemeier RW, Hopley D (1988) Turn-ons and turn-offs: causes and mechanisms of the initiation and termination of coral reef growth, Proc. 6th Intl Coral Reef Symp. 1:253–261

Burke L, Reytar K, Spalding MD, Perry A (2011) Reefs at Risk Revisited. World Resources Institute, Washington, D.C. 114 pp

Burns TW, O'Connor DJ, Stocklmayer SM (2003) Science communication: a contemporary definition. Public Understanding Sci 12: 183–202.

Bythell JC, Sheppard C (1993) Mass mortality of Caribbean shallow water corals. Marine Pollution Bulletin 26: 296–297

Claudet J, Guidetti P (2010) Improving assessments of marine protected areas. Aquatic Conservation: Marine and Freshwater Ecosystems 20: 239–242

Columbus C (1492) Journal of New World Pillage, Plunder and Exploitation 1: 1–21
Cote I, Darling E (2010) Rethinking ecosystem resilience in the face of climate change. PloS biology 8 (7): e1000438. doi:10.1371
Cubit JD (1985) Possible effects of recent changes in sea level on the biota of a Caribbean reef fat and predicted effects of rising sea levels. Proc 5th International Coral Reef Symposium 3: 111–118
Davis GE (1979) Outer continental shelf resource management map, coral distribution Fort Jefferson National Monument, the Dry Tortugas. US Dept of Interior, Bureau of Land Management, Outer Continental Shelf Office, 500 Camp Street, New Orleans, LA 70130
Davis M, Gladfelter E, Lund H, Anderson M (1986) Geographic range and research plan for monitoring white band disease. Biosphere Reserve Research Report No. 6. National Park Service. 28 pp
De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-yr decline of coral cover on the Great Barrier Reef and its causes. PNAS doi:10.1073/pnas.1215836109
Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O (2009) Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. PLoS ONE 4(4): e5239. doi:10. 1371/journal.pone.0005239
Done T (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247: 121–132
Donner S, Knutson T, Oppenheimer M (2007) Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. PNAS 104: 5483–5488
Dudgeon S, Aronson R, Bruno J, Precht W (2010) Phase shifts and stable states on coral reefs. Marine Ecology Progress Series 413: 201–216
Edmunds PJ, Elahi R (2007) The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. Ecological Monographs 77: 3–18
Elzinga C, Salzar D, Willoughby J (1998) Measuring and monitoring plant populations. Bureau of Land Management. Technical Ref 1730–1. 477 pp
English S, Wilkinson C, Baker V (1997) Survey Manual for Tropical Marine Resources. Townsville. 390 pp
Erez J, Reynaud S, Silverman J, Schneider K, Allemand D (2011) Coral calcification under ocean *Acidification* and global change. In: Dubinsky Z, Stambler N (eds.) Coral reefs: an ecosystem in transition. Springer, Dordrecht, pp 151–176
Florida Marine Research Institute (FMRI) and National Oceanic and Atmospheric Administration (NOAA) (1998) Benthic habitats of the Florida Keys. FMRI Technical Report TR-4. 59 pp.
Ginsburg RN (ed.) (1994) Proceedings of the colloquium on global aspects of coral reefs: health, hazards and history, 1993. Rosenstiel School of Marine and Atmospheric Science, University of Miami
Gladfelter WB (1982) White band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull Mar Sci 32: 639–643
Gladfelter WB (1991) Population structure of *Acropora palmata* on the windward forereef, Buck Island National Monument; seasonal and catastrophic changes 1988–1989. Chapter 5. Ecological studies of Buck Island Reef National Monument, St. Croix, US Virgin Islands: a quantitative assessment of selected components of the coral reef ecosystem and establishment of long term monitoring sites. Part 1. NPS Coral Reef Assessment Program. 22 pp
Graham NAJ, Nash KL, Kool JT (2011) Coral reef recovery dynamics in a changing world. Coral Reefs 30: 283–294
Greenstein BJ, Curran HA, Pandolf JM (1998) Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean province: a Pleistocene perspective. Coral Reefs 17: 249–261
Hallock P (1997) Reefs and reef limestones in earth history. In: Birkeland C (ed) Life and Death of Coral Reefs. pp 13–42.
Harley CDG (2011) Climate change, keystone predation, and biodiversity loss. Science 334: 1124–1127
Hoegh-Gulberg O (2011) The impact of climate change on coral reef ecosystems. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Dordrecht (pp 391–403)
Hoegh-Guldberg O, Mumby P, Hooten A, Steneck R, Greenfeld P, Gomez E, Harvell C, Sale P, Edwards A, Caldeira K, Knowlton N, Eakin C, Iglesias-Prieto R, Muthiga N, Bradbury R, Dubi A, Hatziolos M (2007) Coral Reefs Under Rapid Climate Change and Ocean *Acidification*. Science 318: 1737–1742
Hogarth WT (2006) Endangered and threatened species: fnal listing determinations for elkhorn coral and staghorn coral. Fed Regist 71: 26852–26861
Holling CS (1973) Resilience and stability of ecological systems. Ann Rev Ecol Syst 4: 1–23
Hubbard D (1997) Reefs as dynamic systems. In: Birkeland C (ed.) Life and Death of Coral Reefs. Chapman & Hall, pp 43–67
Hubbard DK (2009) A new Caribbean reef model: a view from ye shoulders of giants. Proc 11th Int Coral Reef Symp 1: 2–6
Hubbard DK, Burke RB, Gill IP (1998) Where's the reef: the role of framework in the Holocene. Carbonates and Evaporites 13: 3–9 Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. Ecology 70: 275–279
Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBS, Kleypas JA, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolf JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science: 929–933
Hughes TP, Baird AH, Dinsdale EA, N.A. M, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81: 2241–2249
Hughes TP, Bellwood DR, Baird AH, Brodie J, Bruno JF, Pandolf JM (2011) Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al. (2011). Coral Reefs 30: 653–660
Huntington BE, Karnauskas M, Lirman D (2011) Corals fail to recover at a Caribbean marine reserve despite ten years of reserve designation. Coral Reefs doi 10.1007/s00338-011-0809-4

IPCC (2007) Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (eds) Cambridge University Press, Cambridge, UK. 976 pp

Jackson JBC (1997) Reefs since Columbus. Coral Reefs 16, Suppl: S23-S32

Jackson JBC, Donovan MK, Cramer KL, Lam VV (eds) (2014) Status and trends of Caribbean coral reefs: 1970–2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland. 306 pp

Johannes RE (ed) (1975) Pollution and degradation of coral reef communities. Elsevier Scientific Publ, New York pp 1–12

Kelly RP, Foley MM, Fisher WS, Feely RA, Halpern BS, Waldbusser GG, Caldwell MR (2011) Mitigating local causes of ocean acidif- cation with existing laws. Science 332: 1036–1037

Kleypas JA (2007) Constraints on predicting coral reef response to climate change. In: Aronson RB (ed) Geological approaches to coral reef ecology. Ecological studies 192. Springer, New York, pp 386–424

Kleypas JA, Buddemeier RW, Gattuso J-P (2001) The future of coral reefs. Inst J Earth Sciences (Geol Rundsch) 90: 426–437

Kline D, Vollmer SV (2011) White band disease (type 1) of endangered Caribbean acroporid corals is caused by pathogenic bacteria. Scientifc Reports 1: doi:10.1038/srep00007

Lessios HA (1988) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Ann Rev Ecol Syst 19: 371–393

Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airam S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384: 33–46

Lewis JB (2004) Has random sampling been neglected in coral reef faunal surveys? Coral Reefs 23: 192–194

May LA, Avadanei AR, Rogers CS, Miller J, Woodley CM (2010) Microbial community analysis of *Acropora palmata* mucus swabs, water and sediment samples from Hawksnest Bay, St. John, U.S. Virgin Islands. NOAA Technical Memorandum NOS NCCOS 123 and NOAA Technical Memorandum Coral Reef Conservation Program 14

Maynard JA, Baird AH, Pratchett MS (2008) Revisiting the Cassandra syndrome: the changing climate of coral reef research. Coral Reefs 27: 745–749

Mayor PA, Rogers CS, Hillis-Starr ZM (2006) Distribution and abundance of elkhorn coral, *Acropora palmata*, and prevalence of white band disease at Buck Island Reef National Monument, St. Croix, US Virgin Islands. Coral Reefs 25:239–242

McLeod E, Salm R, Green A, Almany J (2009) Designing marine protected area networks to address the impacts of climate change. Front Ecol Environ doi: 10.1890/070211

Miller J, Muller E, Rogers C, Waara R, Atkinson A, Whelan KRT, Patterson M, Witcher B (2009) Coral disease following massive bleaching in 2005 causes 60 % decline in coral cover on reefs in the US Virgin Islands. Coral Reefs 28: 925–937

Miloslavich P, Diaz JM, Klein E, Alvarado JJ, D{az C, Gobin J, Escobar-Briones E, Cruz-Motta JJ, Weil E, Cortes J, Bastidas AC, Robertson R, Zapata F, Mart{n A, Castillo J, Kazandjian A, Ortiz M (2010) Marine Biodiversity in the Caribbean: Regional Estimates and Distribution Patterns . PLoS One 5: e11916

Muller EM, Rogers CS, Spitzack AS, van Woesik R (2008) Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St John, US Virgin Islands. Coral Reefs 27:191–195

Mumby PJ, Elliott IA, Eakin CM, Skirving W, Paris CB, Edwards HJ, Enriquez S, Iglesias-Prieto R, Cherubin LM, Stevens JR (2010)Reserve design for uncertain responses of coral reefs to climate change. Ecology Letters doi: 10.1111/j.1461-0248.2010.01562

Mumby PJ, Hastings A (2008) The impact of ecosystem connectivity on coral reef resilience. J Applied Ecology 45: 854–862

Nystrom M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. TREE 15: 413–417 Ogden JC, Ogden NB (1994) The coral reefs of the San Blas islands; revisited after 20 years. In: Ginsburg, RN (compiler) Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History, 1993. RSMAS, University of Miami. pp 267–272 Pandolf JM (2011) The Paleoecology of coral reefs. In: Dubinsky Z,

Stambler N (eds.) Coral Reefs: an Ecosystem in Transition. Springer, Dordrecht, pp 13–24

Pandolf JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333: 418–422

Pandolf JM, Greenstein B (2007) Using the past to understand the future: palaeoecology of coral reefs. In: Johnson JE, Marshall PA (eds) Climate change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority and the Australian Greenhouse Offce, Townsville, Australia, pp 717–744

Patterson ME, Atkinson AJ, Witcher BD, Whelan KRT, Miller WJ, Waara RJ, Patterson JM, Ruttenberg BI, Davis AD, Urgelles R, Shamblin RB (2008) South Florida/Caribbean Network vital signs monitoring plan. Natural Resource Report NPS/SFCN/NRR-2008/

063. National Park Service, Fort Collins, Colorado

Perry C, Edinger EN, Kench PS, Murphy G, Steneck RS, Smithers SG, Mumby PJ (2012) Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. Coral Reefs 31: 853–868

Polson SW, Higgins JL, Woodley CM (2009) PCR-based assay for detection of four coral pathogens. Proc 11th Int Coral Reef Symp 1:251–255

Precht WF, Aronson R (2006) Death and resurrection of Caribbean coral reefs: a paleoecological perspective. Conservation Biology Series-Cambridge 13: 40–77

Precht WF, Miller SL (2007) Ecological shifts along the Florida Reef Tract: the past as a key to the future. In: Aronson RB (ed) Chapter 9: 237–312

Raymundo LJ, Couch CS, Harvell CD (eds) (2008) Coral disease handbook. Guidelines for assessment, monitoring and management.

GEF-CRTR program. Australia, 121 pp
Reaka-Kudla M (1997) Chapter 7. The global biodiversity of coral reefs: a comparison with rain forests. In: Reaka-Kudla M, Wilson D, Wilson E (eds) Biodiversity II: Understanding and protecting our biological resources. Joseph Henry Press, Washington, DC pp 83–108
Rogers CS (1985) Degradation of Caribbean and Western Atlantic coral reefs and decline of associated fisheries. Proc 5th Intl Coral Reef Symp 6:491–496
Rogers CS (2013) Coral reef resilience through biodiversity. ISRN Oceanography 2013: article ID 739034.
Rogers CS, Garrison G, Grober R, Hillis Z-M, Franke MA (1994) Coral reef monitoring manual for the Caribbean and Western Atlantic, 107 pp
Rogers CS, Muller E, Spitzack T, Miller J (2009) Extensive coral mortality in the US Virgin Islands in 2005/2006: A review of the evidence for synergy among thermal stress, coral bleaching and disease. Caribb J of Sci 45: 204–214
Rogers CS, Muller EM (2012) Bleaching, disease and recovery in the threatened scleractinian coral *Acropora palmata* in St. John, US Virgin Islands: 2003–2010. Coral Reefs 31: 807–819
Sale PF (ed) (1991) The ecology of *fishes* on coral reefs. Academic Press, Inc, New York (754)
Scopoletis J, Andrefouet S, Phinn S, Done T, Chabanet P (2011) Coral colonisation of a shallow reef fat in response to rising sea level: quantification from 35 years of remote sensing data at Heron Island, Australia. Coral Reefs 30: 951–965
Selig ER, Bruno JF (2010) A global analysis of the effectiveness of marine protected areas in preventing coral loss. PLoS ONE 5(2): e9278. doi:10.1371/journal.pone.0009278
Silverman J, Lazar B, Cao L, Caldeira K, Erez J (2009) Coral reefs may start dissolving when atmospheric CO_2 doubles. Geophysical Research Letters 36. doi:10.1029/2008GL036282
Solomon S, Qin D, Manning M, Chen Z, Marquis J, Averyt KB, Tignor M, Miller HL (eds) (2007) IPCC, 2007. Climate change 2007: the physical science basis, contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press
Stein, Benjamin (1983) Ludes: A Ballad of the Drug & the Dream.
New York: St. Martin's/Marek. pp 248.
Sutherland KP, Porter JW, Turner JW, Thomas BJ, Looney EE, Luna TP, Meyers MK, Futch JC, Lipp EK (2010) Human sewage identified as likely source of white pox disease of the threatened Caribbean elkhorn coral, *Acropora palmata*. Environ Microbiol 12: 1122–1131
Sutherland KP, Shaban S, Joyner JL, Porter JW, Lipp EK (2011) Human pathogen shown to cause disease in the threatened elkhorn coral *Acropora palmata*. PLoS ONE 6(8): e23468. doi:10.1371/ journal.pone.0023468
Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. Coral Reefs 30: 521–531
Sweatman H, Syms C (2011) Assessing loss of coral cover on the Great Barrier Reef: A response to Hughes et al. (2011). Coral Reefs 30: 661–664
Tang C (2001) Chapter 5. Stability in ecological and paleoecological systems: variability at both short and long timescales. In: Allmon W, Bottjer D (eds) Evolutionary paleoecology: The ecological context of macroevolutionary change. Columbia University Press, New York, pp 63–81
van Woesik R, Franklin EC, O'Leary J, McClanahan T, Klaus JS, Budd AF (2012) Hosts of the Plio-Pleistocene past reflect modern-day coral vulnerability. Proc Royal Society B doi: 10.1098/rspb.2011.2621
Vermeij MJA (2006) Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. Coral Reefs 25: 59–71 Waara, RJ, Patterson JM, Atkinson AJ, Estep AJ (2011) Development and policy applications of the 2010 benthic habitat map for Dry Tortugas National Park. Natural Resource Technical Report.
NPS/SFCN/NRTR—2011/474. National Park Service, Fort Collins, Colorado
Weil E, Rogers CS (2011) Coral reef diseases in the Atlantic- Caribbean. In: Dubinsky Z, Stambler N (eds) Coral reefs: an eco- system in transition. Springer, Dordrecht, pp 465–491

Weil E, Vargas WL (2010) Comparative aspects of sexual reproduction in the Caribbean coral genus *Diploria* (Scleractinia: Faviidae). Mar Biol 157: 413–426

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Cons Biol 17:956–967

Wilkinson C (1999) Global and local threats to coral reef functioning and existence: review and predictions. Mar Freshwater Research 50: 867–878

Wilkinson CR (2008) Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre, Townsville, 296 pp

Willis BL, Page CA, Dinsdale EA (2004) Coral disease on the Great Barrier Reef. In: E. Rosenberg E, Loya Y (eds) Coral Health and Disease. Springer-Verlag. Berlin, pp 69–104

Wooldridge SA, Done TJ, Berkelmans R, Jones R, Marshall P (2005) Precursors for resilience in coral communities in a warming cli- mate: a belief network approach. Mar Ecol Prog Ser 295: 157–169

Zubillaga AL, Marquez LM, Croquer A, Bastidas C (2008) Ecological and genetic data indicate recovery of the endangered coral *Acropora palmata* in Los Roques, Southern Caribbean. Coral Reefs 27: 63–72