Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs

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Abstract. Many marine scientists have concluded that coral reefs are moving toward or are locked into a seaweed-dominated state. However, because there have been no regional- or global-scale analyses of such coral reef "phase shifts," the magnitude of this phenomenon was unknown. We analyzed 3581 quantitative surveys of 1851 reefs performed between 1996 and 2006 to determine the frequency, geographical extent, and degree of macroalgal dominance of coral reefs and of coral to macroalgal phase shifts around the world. Our results indicate that the replacement of corals by macroalgae as the dominant benthic functional group is less common and less geographically extensive than assumed. Although we found evidence of moderate local increases in macroalgal cover, particularly in the Caribbean, only 4% of reefs were dominated by macroalgae (i.e., >50% cover). Across the Indo-Pacific, where regional averages of macroalgal cover were 9–12%, macroalgae only dominated 1% of the surveyed reefs. Between 1996 and 2006, phase shift severity decreased in the Caribbean, did not change in the Florida Keys and Indo-Pacific, and increased slightly on the Great Barrier Reef due to moderate coral loss. Coral reef ecosystems appear to be more resistant to macroalgal blooms than assumed, which has important implications for reef management.

Key words: Caribbean; coral reefs; Florida Keys; Great Barrier Reef; Indo-Pacific; macroalgae; phase shifts; reef management.

INTRODUCTION

Natural and anthropogenic disturbances can cause the replacement of one group of dominant organisms by another (Petraitis and Dudgeon 2004). Such ecosystem-level transformations of natural communities can affect flows of energy and materials, the abundance and diversity of community inhabitants and valuable services for human societies (Sousa 1984, Pickett and White 1985). A topical example is the "phase shift" of coral reefs from coral to macroalgal dominance (McManus and Polsenberg 2004; Fig. 1).

Coral abundance on reefs around the world began to decline several decades ago (Gardner et al. 2003, Bruno and Selig 2007) due to a variety of factors including predator and disease outbreaks, poor land use practices, destructive fishing techniques, and ocean warming (Glynn 1993, McManus et al. 1997, Aronson and Precht 2001, Hughes et al. 2003). In some locations, the cover and biomass of benthic macroalgae increased concurrently with coral loss, resulting in community phase shifts to reefs dominated by macroalgae (Done 1992,

Knowlton 1992, McManus and Polsenberg 2004; Fig. 1). A widely cited and striking example occurred on nine reefs in Jamaica during the 1980s (Hughes 1994). In the 1970s, and presumably historically (but see Woodley 1992), coral cover on Jamaican reefs ranged from 40% to 70% and macroalgal cover was typically <10% (Hughes 1994). Following several disturbances including a major hurricane (Woodley et al. 1981), coral predator and coral disease outbreaks (Knowlton et al. 1990), the regional loss of the keystone grazer *Diadema antillarum* in 1983–1984 to a Caribbean-wide epizootic (Hughes et al. 1985), a second major hurricane (Woodley 1992), and a series of coral bleaching events in the late 1980s (Goreau 1992), coral cover on these reefs plummeted to <10% and macroalgae became the dominant benthic functional group (Liddell and Ohlhorst 1992, Hughes 1994).

The Jamaican case study is assumed to be illustrative of a widespread and ongoing phenomenon (Szmant 2001, Bellwood et al. 2004, McManus and Polsenberg 2004, Precht and Aronson 2006). While there are several case reports of decreased coral cover and increased macroalgal cover on other individual reefs (Endean and Stablum 1973, Smith et al. 1981, Done 1992, Rogers and Miller 2006), there have been no regional- or global-scale analyses of coral reef phase shifts. Therefore, the ecological generality of these observations and the

applicability of the Jamaican archetype to reefs around the world (Bellwood et al. 2004) are unknown.

Epidemiologists perform randomized population sampling to determine the generality of case reports in the medical literature (Rothman and Greenland 1998). Likewise, ecologists can apply various macro-ecological and meta-analytical techniques to understand the spatial dynamics, severity and impacts of major disturbances, community phase shifts, and other ecological phenomena (Brown 1999). Such basic pattern quantification over large spatial scales can put more detailed, local studies into a broader context (Côté et al. 2005). The purpose of this study was to assess the frequency, geographical extent, and degree of macroalgal dominance of coral reef communities and of coral to macroalgal phase shifts around the world. Specifically, we used data from quantitative reef surveys to determine the proportion of reefs in four geographic regions (Greater Caribbean, Florida Keys, Indo-Pacific, and Great Barrier Reef [GBR]; see Appendix A: Fig. A1) that were dominated by macroalgae (>50% absolute macroalgae cover). We determined the state of each reef along a continuum ranging from coral to macroalgal dominance by developing a "phase shift index" based on principal components analysis of the two benthic categories (coral and macroalgal cover) included in the meta-analysis. We also asked whether phase shift severity changed between 1996 and 2006.

METHODS

Hughes' classic study (Hughes 1994) of the degradation of Jamaican reefs demonstrates the power of repeated surveys of particular sites in detecting phase shifts across broad spatial scales. Unfortunately, very few such longitudinal studies were implemented until the early 1990s, years to decades (or longer) after reefs began to be altered by human activities (Pandolfi et al. 2003). Therefore, localized monitoring studies alone cannot be used to quantify the regional-to-global generality and severity of coral reef phase shifts. As an alternative approach, we used the extensive data from more recent reef surveys to make inferences about regional patterns (e.g., magnitude and spatial extent) of shifts in coral reef benthic communities. We assumed that most reefs were historically coral dominated and that macroalgae were relatively scarce. Therefore, the current state (in terms of coral and macroalgal cover) of reefs across a region can be used as a measure of regional-scale degradation or phase shift degree.

Our database included 3581 quantitative surveys of 1851 coral reefs (or sites) performed between 1996 and 2006 (see Appendix A). Our analysis was based on quantitative surveys that measured the percentage of the substratum covered by living coral and fleshy or calcareous macroalgae between 1 and 15 m depth (mean depth; 7.1 m). The abundance of macroalgae is considered a key metric of reef health (Steneck and Sala 2005). Most surveys used in our meta-analysis employed the line-transect technique, in which a transect (typically a 10–30 m measuring tape or chain) was placed on the reef. The coverage of coral and macroalgae was then estimated either in situ by recording the number of points along each transect that overlaid corals, macroalgae, and so forth, or by taking images of the reef substrate at these points, which were then analyzed in the laboratory. We only used surveys that differentiated macroalgae from other algal groups. Following Steneck (1988) and others, we defined macroalgae (i.e., seaweed) as "larger (canopy heights usually >10 mm), more rigid and anatomically complex algal forms." This functional group includes erect calcifying species (e.g., *Halimeda* spp.) but does not include microalgae and filamentous algae (i.e., turfs) or crustose algae (Steneck 1988).

Coral reef degradation and phase shifts are complex, multivariate phenomena (Sebens 1994, Graham et al. 2006) and can involve various combinations of coral loss and seaweed gain. To address this issue and to facilitate graphical and statistical comparisons among regions and years, we developed a coral reef phase shift index (PSI), a quantitative, one-dimensional measure of the degree to which a reef has changed from a pristine (high coral, low macroalgal cover) state to a low coral, high macroalgal cover state. PSI is the first component (PCA1) from a principal components analysis (eigenvalue, 1.25; variance explained, 62%) on the correlation matrix between macroalgal cover and the inverse of coral cover. The analysis essentially combines the two variables (coral and macroalgal cover) into a single value, which simplifies analysis and discussion of what would otherwise be a bivariate phenomenon by reducing the dimensionality of the data set. PSI values were derived from single site–year combinations and are measures of current reef state at the time of the survey, i.e., they are not a measure of the degree to which a particular reef has changed over time. By pooling large numbers of single site-year PSI values, we were able to describe population-level variation in PSI among years and regions. In this analysis, pristine reefs have a PSI of −2 to −3 and reefs with low coral and high macroalgal cover have a PSI of 2 to 3 (Fig. 1). The PSI on reefs that have undergone a severe phase shift was 3 to 5 (Fig. 1). The principal components analysis was performed on the most recent survey performed on each reef (i.e., we did not include multiple surveys of individual reefs through time) and included cover values from Hughes' 1994 study of Jamaican reefs in the 1970s and early 1990s (Fig. 2).

To determine whether the degree to which reefs are dominated by macroalgae has changed over time (i.e., to test the null hypothesis that PSI did not change between 1996 and 2006), we performed two types of regression analysis. For one analysis we used the entire data set to calculate annual regional mean PSI values and for the other we only used data from monitoring
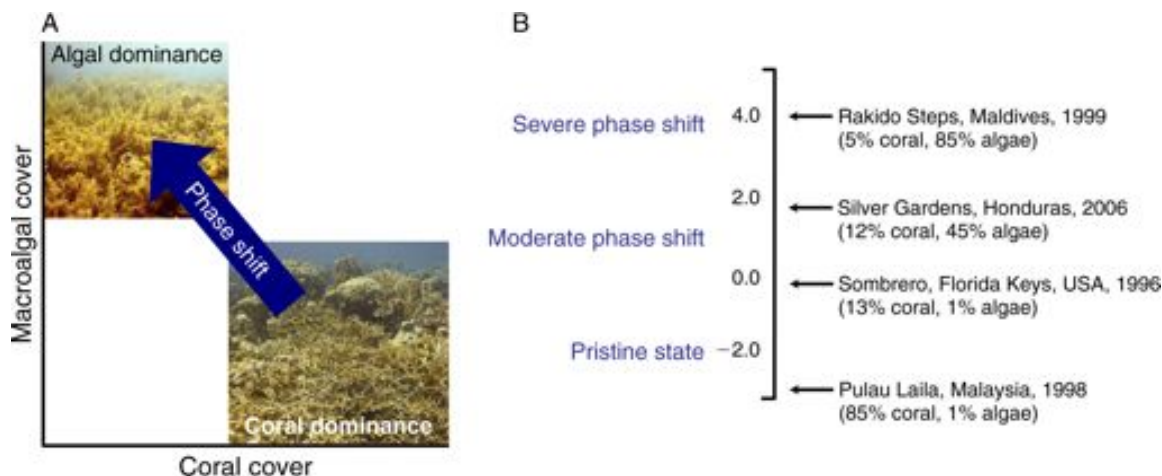
FIG. 1. The coral reef "phase shift" concept. (A) Images are from neighboring reefs near Discovery Bay Jamaica, in January 2003 (photos by J. Bruno). (B) Examples of different degrees of coral reef degradation around the world, based on the phase shift index used in this analysis.

studies. Data from each of the four regions were analyzed separately. Time (year) and PSI were treated as continuous variables and data were transformed when necessary to meet basic statistical assumptions. The first analysis was a simple linear regression between year and the annual mean PSI (i.e., the replicate PSI measures within each region for each year were pooled into a single value). A strength of this analysis, in contrast to one based on monitoring studies, is that the sampled reefs were more or less randomly selected, which allows for greater generalization. However, a significant weakness of this approach is that observed temporal changes in PSI could be due solely to changes in the population of reefs that were surveyed each year. For the second temporal analysis, we used only the subset of 458 reefs that were surveyed in two or more years. These data were analyzed with linear repeated measures regression analysis (using Stata version 9.1, Stata Corporation, College Station, Texas, USA). This test accounted for the longitudinal structure of the survey data, particularly for the GBR, which was largely based on monitoring data from the Australian Institute of Marine Science's Long Term Monitoring Program.
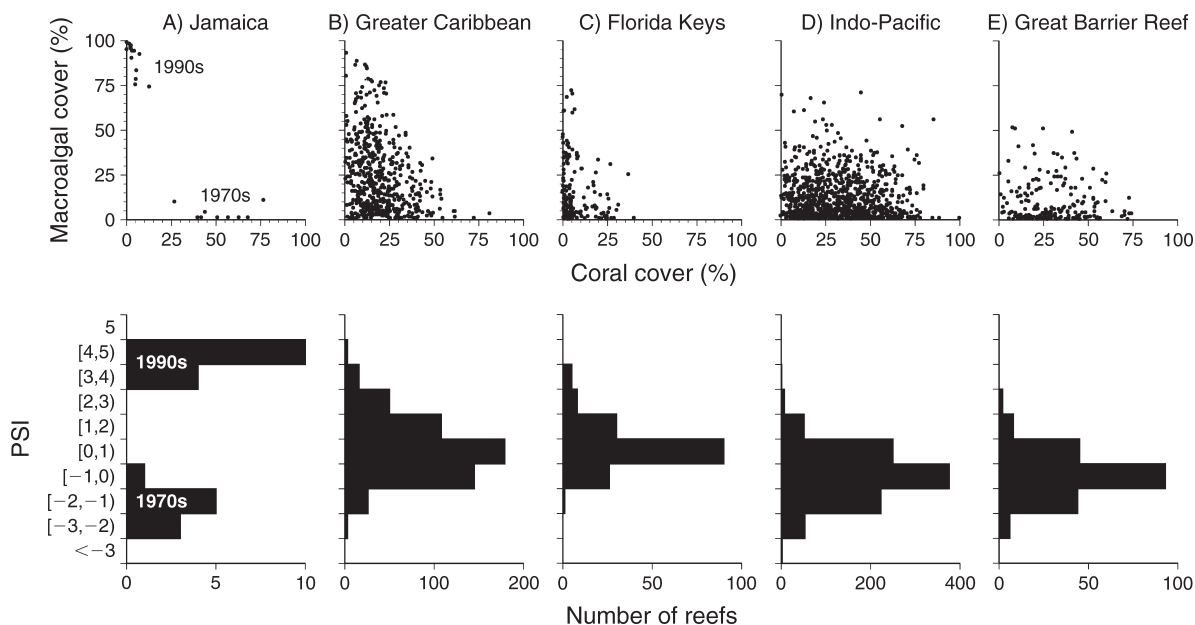

FIG. 2. State of the world's coral reefs. The top row shows absolute living coral and macroalgal cover. The bottom row shows count histograms of the phase shift index (PSI) in the four regions; the y-axis shows the lower and upper ranges of PSI in each bin. Data in panel A are from Hughes (1994). Data in panels B–E are based on the most recent survey from each site.

TABLE 1.   Reef state in the four study regions.

Region	Number of sites	Years	Coral cover (%)	Macroalgal cover (%)	Macroalgae > 25%†	Macroalgae > 50%†
Caribbean	530	1996–2006	20.0 ± 0.5	23.6 ± 0.8	39%	10%
Florida Keys	160	1996–2005	8.1 ± 0.7	14.7 ± 1.3	23%	4%
Indo-Pacific	963	1996–2006	33.2 ± 0.6	11.7 ± 0.4	13%	1%
Great Barrier Reef	198	1996–2006	30.5 ± 1.2	9.1 ± 0.8	10%	1%

Notes: All summary statistics were based on the most recent survey performed at each site. Values for coral and macroalgal cover are means ± SE.

† Percentage of surveyed reefs.

RESULTS AND DISCUSSION

Presently, there are no defined or generally accepted thresholds of the degree of coral loss and macroalgal increase that constitutes a phase shift (Rogers and Miller 2006). This has led to substantial confusion about the causes, generality, severity, and management implications of phase shifts on reefs. Many authors appear implicitly to define coral reef phase shifts as cases where macroalgae dominate the reef benthos (Hughes et al. 2003, McManus and Polsenberg 2004, Knowlton 2008). Unfortunately, what is meant by "dominate" is rarely articulated. The use of "dominance" and similar terms such as "preponderance" and "seaweed reef" implies a threshold of 50% macroalgal cover. Based on this definition, only 4% of the 1851 reefs used in our primary analyses were dominated by macroalgae. Across the Indo-Pacific (including the GBR) macroalgae only dominated 1% of the surveyed reefs (Tables 1 and B1).

Species or functional groups do not necessarily need to occupy or control a majority (>50%) of a limiting resource to "dominate" or define a community, but even based on a much lower threshold of 25%, only 20% of surveyed reefs were seaweed dominated (Tables 1 and B1). Furthermore, more than half (53%) of these were in the Caribbean, which includes only ~8% of the world's reefs (Spalding and Grenfell 1997). This result confirms the common belief that phase shifts have been more severe in the Caribbean than elsewhere (Pandolfi et al. 2003, Bellwood et al. 2004). However, among-region comparisons should be made with caution because reef geomorphology, the types of reef habitats that are surveyed, and possibly even reef community baselines all vary among our study regions. Surprisingly, our results indicate that few of the world's reefs fall into either of the classically defined coral reef stable points of coral or macroalgal dominance (Petraitis and Dudgeon 2004). A large majority, including those in the Caribbean, are somewhere between these extremes; a pattern not concordant with the belief (Knowlton 1992, Bellwood et al. 2004) that coral reef communities switch between coral and macroalgal dominated stable states.

We quantified phase shift severity using a phase shift index (PSI) that combined the coral and macroalgal coverage of a reef into a single variable using principal components analysis (Figs. 2 and B1). A rough threshold for a severe phase shift based on the Jamaican archetype was a PSI > 3, which in our analysis corresponded to less than 10% coral cover and macroalgal cover >60 % (Figs. 1 and 2). Based on this threshold, only 25 of the 1851 reefs (<1%) could be classified as having undergone a complete coral to algal phase shift (Fig. 2B–E) and all except one of these reefs were in the Caribbean. Phase shift severity is a continuum, so categorical delineations of relative severity are subjective and may be not be ecologically relevant. Nevertheless, our results indicate that the severity of phase shifts on a majority of the world's reefs (Figs. 2 and B1) appear to be substantially less severe than those seen in a few well-known examples.

Overall, our results indicate that there is no general recent trend (i.e., post-1995) toward macroalgal dominance (see Appendix C). PSI did not change during 1996 to 2006 in the Florida Keys or Indo-Pacific (Fig. C1, Table C1). Many of the changes in these regions and in the Caribbean presumably took place before broad-scale surveying began. Based on one of our two temporal analyses, PSI marginally increased ($P = 0.07$) on the GBR between 1996 and 2006, presumably due to a 3–4% decline in coral cover (there was no concurrent change in macroalgae) caused primarily by outbreaks of the corallivorous seastar *Acanthaster planci* (Miller 2002). In contrast, PSI decreased slightly in the Caribbean (Fig. C1, Table C1) due to a modest decrease in macroalgal cover from 34.0% ± 2.9% to 21.4% ± 1.3% (values are mean ± 1 SE) and even smaller increases in coral cover from 19.9% ± 1.5% to 21.8% ± 0.7%, through 2005. Our results indicate there was a small increase in PSI and a ~5% decrease in mean regional coral cover between 2005 and 2006 (from ~22% to 17%), possibly caused by the mass coral bleaching and mortality event in late 2005 in the northern and eastern Caribbean (Donner et al. 2007).

Coral reef baselines and recent changes in macroalgal abundance

Macroalgae play an important ecological role on shallow reefs (Vroom et al. 2006). Tropical macroalgae are highly diverse and countless species have evolved adaptations to consume and utilize them (e.g., fishes whose camouflage mimics macroalgae). But what was the historical baseline of macroalgal cover and how much has macroalgae increased? Nearly all surveys of Caribbean reefs during the 1970s and early 1980s

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reported absolute macroalgal cover values between 0% and 10%. The mean of 19 surveys of 16 sites performed between 1977 and 1982 is 6.6% (see Appendix D; Table D1). However, one survey reported macroalgal cover as high as 20.5% (Liddell and Ohlhorst 1992), and only a small number of locations were surveyed (primarily in St. Croix, U.S. Virgin Islands and along the north coast of Jamaica). Additionally, there is speculation that macroalgal cover was unnaturally low during this period due to anomalously high densities of the urchin *Diadema antillarum* caused by the overfishing of its predators (Hay 1984, Levitan 1992).

If the regional baseline was indeed roughly 3–10%, averaging ~6%, then macroalgal cover in the Caribbean has increased fourfold. Although this increase may be ecologically significant, it is much smaller than generally assumed. Additionally, most evidence of negative effects of macroalgae on the growth and survival of juvenile corals comes from studies in which macroalgal cover was far higher, typically 50–70% (Carpenter and Edmunds 2006, Hughes et al. 2007). However, one recent study found that macroalgal cover as low as 20–30% was negatively correlated with coral recruit density (Mumby et al. 2007).

Another approach to estimating reef baselines of the past is to study modern "quasi-pristine" reefs that are substantially less affected by human activities, due mainly to their isolation but also to legal protections (Knowlton and Jackson 2008). Two recent expeditions (Vroom et al. 2006, Sandin et al. 2008) surveyed 10 such remote reefs in the central Pacific in part to establish a regional baseline. They found that macroalgal cover averaged 13.1% ± 2.0% (mean ± 1 SE) and ranged from 3% to 28% (Table D2). With minimal or no fishing, these reefs have intact food webs with plentiful top predators (Vroom et al. 2006, Sandin et al. 2008) and are probably our best window into the past (Knowlton and Jackson 2008). If so, macroalgae were substantially more abundant than we think, at least on some reefs and in some regions (Vroom et al. 2006). Macroalgal cover on these "pristine" reefs is similar to the regional averages for three of our four study regions, suggesting that macroalgal cover may currently be close to the historical baseline across most the world.

Macroalgal blooms, coral decline, and reef management

Macroalgal blooms on coral reefs are generally understood to be caused by reduced herbivory (resulting from fishing and also from urchin die-offs in the Caribbean) and coral loss, which allows macroalgae to colonize open substrate, thereby increasing primary production and overwhelming grazers (Knowlton 1992, Hughes et al. 1999, Williams et al. 2001). Thus, macroalgal cover and coral cover are widely assumed to be causally linked and inversely related. Yet we found only weak negative relationships between coral and macroalgal cover (linear regression analyses based on the most recent survey of each site; Greater Caribbean $P = 0.0001$,

$R^2 = 0.09$; Florida Keys $P = 0.008$, $R^2 = 0.04$; Indo-Pacific $P = 0.02$, $R^2 = 0.01$; Great Barrier Reef $P = 0.28$). Surprisingly, macroalgal cover has not increased appreciably on most of the world's reefs that have very low coral cover. For example, 379 of the 1851 reefs had ≤10% coral cover, but macroalgal cover was also low (≤20%) on nearly two thirds of these reefs. In fact, more than half the benthic cover on reefs in the Caribbean, Pacific and Indian Oceans consists of organisms other than hard corals and macroalgae, possibly because other taxa, such as sponges and gorgonians, have been the primary beneficiaries of coral loss (Aronson et al. 2002, Norström et al. 2009). The degree of macroalgal dominance is widely considered a key measure of reef health. For instance, Steneck and Sala (2005) argued that "macroalgal abundance is the single best indicator of poor conditions for coral reefs." However, since the cover of coral and macroalgae are only weakly related, macroalgal abundance may not be a good indicator of either coral loss or habitat quality.

The absence of evidence for expected widespread increases in macroalgae could be due to the limited extent of nutrient pollution on most reefs (Szmant 2002, Greenaway and Gordon-Smith 2006), especially isolated offshore reef systems. Herbivores can clearly regulate reef macroalgae (Lewis 1986, Steneck 1988, Williams and Polunin 2001, Carpenter and Edmunds 2006) and overfishing has reduced the densities of herbivorous fishes on many reefs (Pandolfi et al. 2003, Bellwood et al. 2004). But compensatory increases in the abundance of other herbivores may have partially filled this function (Aronson and Precht 2000). One explanation for the low macroalgal cover in the Florida Keys and Great Barrier Reef is that local management has been effective in preventing herbivore populations from being depleted (Aronson and Precht 2006). Another is that commercial and recreational fishers in these relatively affluent parts of the world target piscivores. Thus, herbivorous fish are both released from predator control and largely unaffected by direct fishing pressure (Graham et al. 2003). Additionally, the recovery of populations of the keystone grazer *Diadema antillarum* on some Caribbean reefs has reduced seaweed cover close to recent historical levels at shallow sites and has also increased coral recruitment (Carpenter and Edmunds 2006).

Conclusions

The mismatch between descriptions of reef degradation in the literature and patterns in nature was caused by the generalization of a relatively small number of examples. Case reports of local phase shifts were not intended to be representations of the state and dynamics of reefs in general. They were instead published as notable quantitative observations. Although in retrospect atypical, case studies such as the degradation of Jamaican reefs have been invaluable warnings of the consequences of subjecting reef communities to multiple natural and anthropogenic disturbances.

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Since the Jamaica story was an anomaly, it makes a poor foundation for general models of reef ecology (e.g., Knowlton 1992, Bellwood et al. 2004). The current paradigm of reef management and "resilience" is based in large part on the perception that most of the world's reefs are being overrun by seaweed (Szmant 2001, Precht and Aronson 2006, Knowlton 2008). This belief led to the argument that reef managers should focus primarily on conserving herbivores or water quality (Szmant 2002, Pandolfi et al. 2003, Bellwood et al. 2004). While these are clearly important objectives of management, our analysis suggests that the macroalgae problem has been exaggerated. Overfishing and poor land use practices may trigger widespread coral to macroalgal phase shifts in the future, but to date, the principal form of coral reef degradation has been the loss of reef-building corals, with only limited and localized increases in macroalgae. Therefore, the primary goal for reef managers and policy makers should be the conservation of coral populations, without which the entire system would collapse.

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APPENDIX A

A description of procedures and sources of data used in the meta-analysis (*Ecological Archives* E090-100-A1).

APPENDIX B

Basic analyses performed without data from Reef Check (*Ecological Archives* E090-100-A2).

APPENDIX C

Analyses of the relationship between time and phase shift index (PSI) values between 1996 and 2006 (*Ecological Archives* E090-100-A3).

APPENDIX D

Reported macroalgal cover from early Caribbean reef surveys (1976–1982) and on remote Pacific reefs (*Ecological Archives* E090-100-A4).