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Phase shifts and resilience of coral reefs

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Review

Rising to the challenge of sustaining coral reef resilience

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Phase-shifts from one persistent assemblage of species to another have become increasingly commonplace on coral reefs and in many other ecosystems due to escalating human impacts. Coral reef science, monitoring and global assessments have focused mainly on producing detailed descriptions of reef decline, and continue to pay insufficient attention to the underlying processes causing degradation. A more productive way forward is to harness new theoretical insights and empirical information on why some reefs degrade and others do not. Learning how to avoid undesirable phase-shifts, and how to reverse them when they occur, requires an urgent reform of scientific approaches, policies, governance structures and coral reef management.

The coral reef crisis

The world's coral reefs are important economic, social and environmental assets, and they are in deep trouble. How much trouble, and why, are critical research questions that have obvious implications for formulating policy and improving the governance and management of these tropical maritime resources. In particular, a better understanding of why some reefs rapidly degrade and others do not is critical for identifying management options for sustaining coral reefs [1,2]. On many reefs, the combination of overfishing of herbivorous fishes and added nutrients from land-based activities, elevated coral mortality and recruitment failure, have caused persistent shifts from the original dominance by corals to a preponderance of fleshy seaweed or other weedy assemblages [3–6], with flow-on effects to other species that are dependent on the habitat afforded by corals [7–9]. We focus here on reefs that have lost their capacity to remain in or return to a coral-dominated state, a world-wide phenomenon that is variously referred to as phase-shifts [2–5], regime-shifts [10,11] or movement between alternate stable states or basins of attraction [12,13].

Importantly, the scale of disturbances to reefs is increasing [1,14]. The chronic impacts of overfishing and coastal pollution, which can be managed successfully at a local scale, are increasingly compounded by the more recent, superimposed impacts of global warming, ocean acidification, introduced species, and by emerging diseases [2,8]. Global warming causes thermal stress leading to bleaching and higher rates of mortality of corals, even on reefs that are well managed or remote from other human impacts [15]. The term phase-shift was first used in the coral reef literature to describe slow or fast transitions from a coral-dominated assemblage to another alternative set of species [4]. Early examples included shifts to macroalgae recorded in Hawaii, Jamaica, Reunion Island, and on the Great Barrier Reef [4]. More recently, long-lasting shifts from corals to assemblages other than macroalgae (e.g. bivalves, sponges, tunicates, zooanthids) have also been widely reported [2,16]. A critical issue, explored below, is whether these shifts in species composition are transitory or permanent (at least at the scale of decades), and how they can be avoided or reversed. Under some circumstances, both coral-dominated and alternative phases can be highly persistent [17,18]. For example, over the past century many near-shore reefs on the inner Great Barrier Reef have become covered with sediment and macroalgae, and show little or no capacity to return to their former coral-dominated condition (Figure 1).

Some recent reviews have questioned the generality of phase-shifts on coral reefs, arguing that the best-known examples are unrepresentative, and that regional changes to date have been smaller than generally presented in the literature [19,20]. Our goals here are to address these controversies, clarify the theoretical framework of phase-shifts and ecosystem resilience, provide an outline of gaps in knowledge and novel areas of research that are in most urgent need of attention, and to highlight that the solutions to coral reef degradation will depend on an overdue overhaul of policies, governance structures and science-based management.

Phase-shifts and resilience

The resilience of a complex system (e.g. an ecosystem, society or economy) is its capacity to absorb recurrent disturbances or shocks and adapt to change without fundamentally switching to an alternative stable state [21–24]. Increasingly, the resilience of coral reefs has been eroded to the extent that they are unable to recover after recurrent disturbances, as they have done successfully

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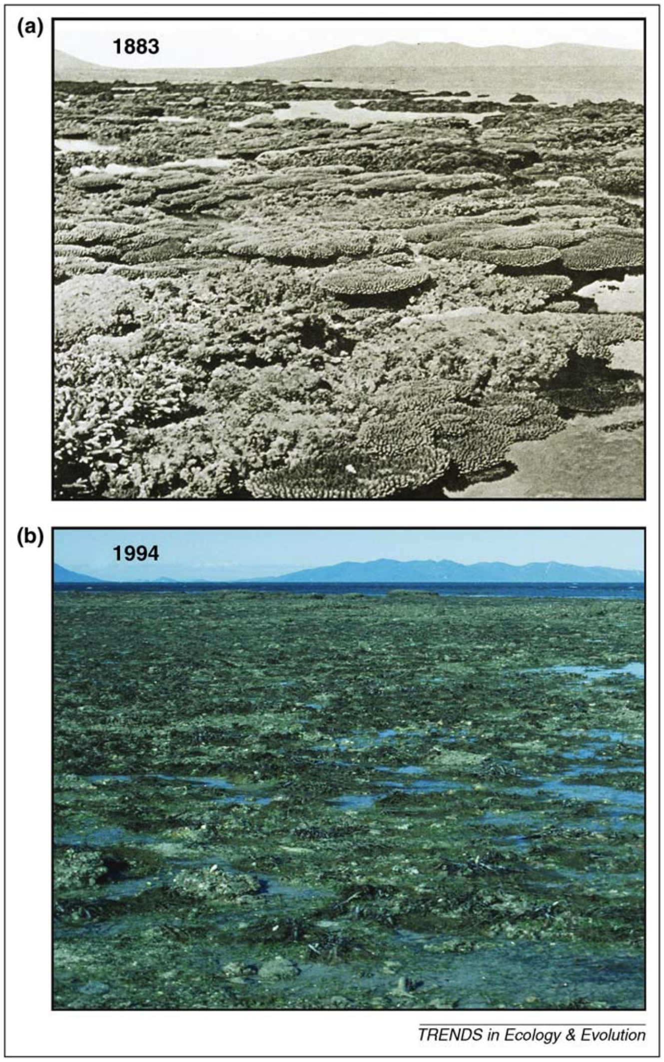

Figure 1. A phase shift from a coral-dominated seascape to a sediment-laden system dominated by macroalgae. Both photographs are from the same site on the inner central Great Barrier Reef, indicated by the hilly backdrop. The location of this site can be viewed with the Google Earth mapping system. The *Acropora*-dominated coral assemblage of the late 1800s is now greatly diminished on many coastal areas following changes in land-use in the 19th and 20th centuries [53].

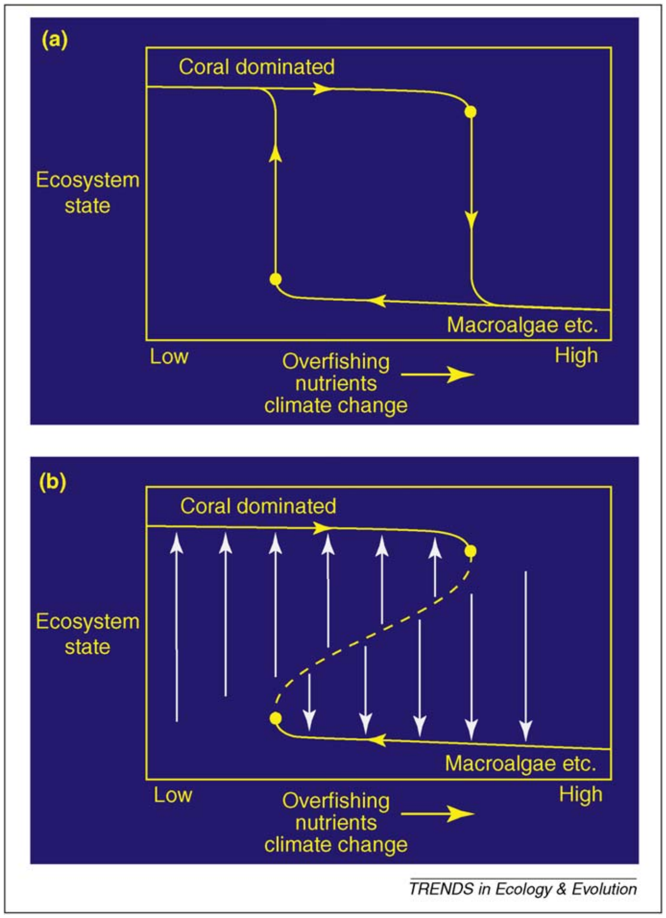

Figure 2. The non-linear response of coral reefs to slow drivers of change such as overfishing, added nutrients and climate change. **(a)** Two trajectories are indicated. One illustrates a tipping point between a coral-dominated system and an alternative degraded ecosystem dominated at equilibrium by macroalgae or other weedy species. The other, reverse trajectory has a different tipping point at a lower threshold. **(b)** Fast drivers of change such as cyclones or bleaching episodes, indicated by the arrows, displace alternative systems from their equilibral state. Once displaced, they quickly return to the same equilibrium provided they do not cross the dotted line separating the two alternative states. Resilience, the capacity to absorb acute disturbance without flipping, diminishes as either threshold is approached, indicated by the vertical arrows. Coral cover returns from low to high levels following a sudden disturbance in the coral-dominated phase. Coral cover can also be high during the initial transitory period following a phase-shift to a low-coral state.

throughout their evolutionary history [17]. We distinguish here between fast and slow drivers that change ecosystems over different timescales. Typically, ecosystems exhibit threshold, rather than linear, responses to slowly building drivers of change such as fishing pressure, added nutrients and rising global temperatures [10]. These slow, chronic drivers occur simultaneously and are highly interactive with each other. Fast drivers, in contrast, are episodic disturbances or shocks that quickly push the system away from its equilibrium state (Figure 2).

When chronic human stressors (slow drivers of change) are at a low level, reefs can be displaced far from their coral-dominated equilibrium by an acute, fast-acting disturbance and still recover (Figure 2). These short-term disturbance-recovery trends do not constitute a phase-shift, and are a normal part of the dynamics of functional coral reefs. For example, local sites on exposed reef crests on Heron Island on the Great Barrier Reef routinely lose almost all of their coral cover every decade or so because of cyclones, yet they have retained their ability to recover quickly and show no propensity to undergo a long-term shift to an alternative assemblage [18]. In contrast, many coral reefs have been slowly pushed close to a threshold by chronic human impacts, and now commonly fail to recover from pulses of coral mortality [25–28].

The stability of each alternative phase or regime arises from contrasting sets of feedbacks that reinforce and maintain them. For example, high coral cover and grazing of macroalgae promotes the production and successful recruitment of juvenile corals, maintaining coral-dominance [5,29,30]. Similarly, when herbivores are depleted, dense stands of macroalgae can also be resilient, preventing the return of corals by shading and overgrowing juveniles, destabilizing microbial communities, and promoting coral disease [6,31–35]. In theory, two sets of strongly reinforcing feedbacks mean that the tipping point away from the coral-dominated state is different from the threshold moving backwards, a phenomenon known as hysteresis

(Figure 2b). For instance, a mature stand of corals might be able to withstand high levels of chronic sedimentation from terrestrial runoff, but once cover is lost (e.g. because of a cyclone), a much lower level of sediments could prevent successful recruitment of juveniles.

We caution that the resilience concept outlined here (Figure 2) does not just focus on short-term recovery to a single, static equilibrium [21–23]. However, many people have adopted this much simpler concept, where resilience simply means a healthy individual, population or ecosystem that can recover from anthropogenic stress. In sum, the essential elements of the resilience concept are non-linear (threshold) dynamics in response to slow and fast drivers of change, alternate persistent phases, reinforcing feedbacks, and hysteresis (Figure 2).

The evidence-base for phase-shifts and global coral reef degradation

The temporal and spatial variances in the abundance of corals, macroalgae and other benthic organisms are very large, complicating the detection of phase-shifts (Box 1). Generally, at the spatial and temporal scales favored by ecologists, corals are suppressed quickly by acute natural disturbances such as hurricanes, and, on resilient reefs, coral cover rises comparatively slowly between these recurrent events. Similarly, when a threshold away from the coral-state is first transgressed, coral cover can be initially high as it declines towards a new low-cover equilibrium. The shift to macroalgal dominance can occur quickly if it is precipitated by a sudden acute event that kills most of the corals [5,26,36], or it can take decades or longer to unwind [25,37]. A gradual decline in coral cover occurs when slow drivers of change accumulate enough to tip a coral-dominated reef across a threshold into an alternate phase, without it being pushed there by a fast-acting disturbance. For example, in parts of the Caribbean, deep reefs have avoided catastrophic loss of corals from hurricanes and disease, but have nonetheless been slowly and incrementally overwhelmed by macroalgal blooms (Figure 3).

Coral and macroalgal cover also vary geographically and along gradients of exposure, light and depth [38,39]. For example, on Heron Island on the Great Barrier Reef, coral cover within square meter quadrats ranged from zero to 80% over a period of 30 years [18]. Most of the variation was attributable to five cyclones and to habitat, and there were no phase-shifts recorded during this time. Inner reef flats had lower and less variable coral cover, with a mean over time of 9%, whereas reef crests and slopes averaged close to 40% cover. Macroalgae were virtually absent on crests and slopes due to heavy grazing by herbivorous fishes, but were seasonally abundant on near-shore reef flats. This spatial variation, coupled with the temporal dynamics described above, means that there is no definitive cutoff in coral or macroalgal abundance or characteristic ratio of the two that defines a reef as being ‘healthy’ (Box 2).

Evidence of phase-shifts from the primary literature

Peer-reviewed studies of changes in coral reef ecosystems provide the most detailed accounts of shifts from corals to alternative assemblages, and of the underlying processes and mechanisms. The largest clusters of published studies conducted over the past 50 years are from the Caribbean and Florida, the Great Barrier Reef, Japan, Kenya, Israel, Hawaii, French Polynesia, and the Eastern Pacific. Among the more intensively studied regions, Caribbean coral reefs have been the most extensively degraded in recent decades, owing to a complex sequence of chronic and acute disturbances and to widespread recruitment failure of corals [37,40–44]. Coral cover has declined by about 80–90% since the late 1970 s or 1980 s at most Caribbean locations [27], whereas the abundance of macroalgae and other weedy species has sharply increased [20,45].

Box 1. Metrics of reef status or ‘health’

The status of coral reef ecosystems is routinely measured and monitored using a small number of metrics, usually abundances of important taxonomic groups, especially corals. However, coral cover is not a reliable metric of resilience, because a healthy reef that is recovering towards a coral-dominated equilibrium can have substantially less coral than one that is locked into a downward trajectory to dominance by macroalgae. Coral cover only becomes a definitive indicator of phase-shifts if the same site is monitored for many years, and if the mechanisms and feedbacks have been identified. The spectacular decline of corals in many parts the Caribbean in the 1980s came as an ecological surprise because people then and now commonly mistake high coral abundance as an indicator of resilience.

To date, most overviews and meta-analyses of coral reef status have focused on death of corals, rather than why they have lost their capacity to recover from recurrent shocks. In a demographic context, mortality is only one side of the coin. Changes in fecundity, fertilization success, larval dispersal, and recruitment have played a major role in promoting shifts in abundances and species composition [25,90–92], but replenishment processes have been virtually ignored in comparison to the attention lavished on death and destruction. For example, the recent meta-analyses of coral cover across the Caribbean and Indo-Pacific (supplemental material A) invoke storms, sedimentation, fishing, predator outbreaks, bleaching and disease as the probable causes of coral loss, but none of the meta-analyses mention the importance of widespread recruitment-failure. New metrics of resilience could focus on recruitment processes, and on monitoring critical functional groups and processes that build or erode resilience to alternative ecosystem states [2,93].

Lumping species obscures the consequences

Resilience approaches highlight the importance of functional groups, ecosystem processes and feedbacks. The species composition and functional dynamics of corals invariably change whenever cover increases or decreases. For example, major mortality agents for corals are all highly selective: storms affect tabular and staghorn species disproportionately [94], bleaching and disease affect physiologically resistant ‘winners’ less than susceptible ‘losers’ [51,95], algal overgrowth impacts on encrusting species more than three-dimensional ones [5], corallivores select their preferred prey [96], and so on. Similarly, short-lived coral species are more vulnerable to recruitment failure compared to longer-lived ones [25,89]. Weedier groups such as bushy acroporids and pocilloporids re-colonize faster, whereas some former spatial dominants that are long-lived could take centuries to regain their abundance. This two-step filter, differential mortality and replenishment, is changing the face of reefs worldwide [15,44,50,94,97]. The convenient practice of measuring total coral and macroalgal cover obscures these important shifts in composition. Importantly, these changes show that at least some coral reefs have a considerable capacity to absorb recurrent bleaching events and retain functional, albeit different, assemblages of corals, without undergoing a phase-shift to a completely different coral-depleted system.

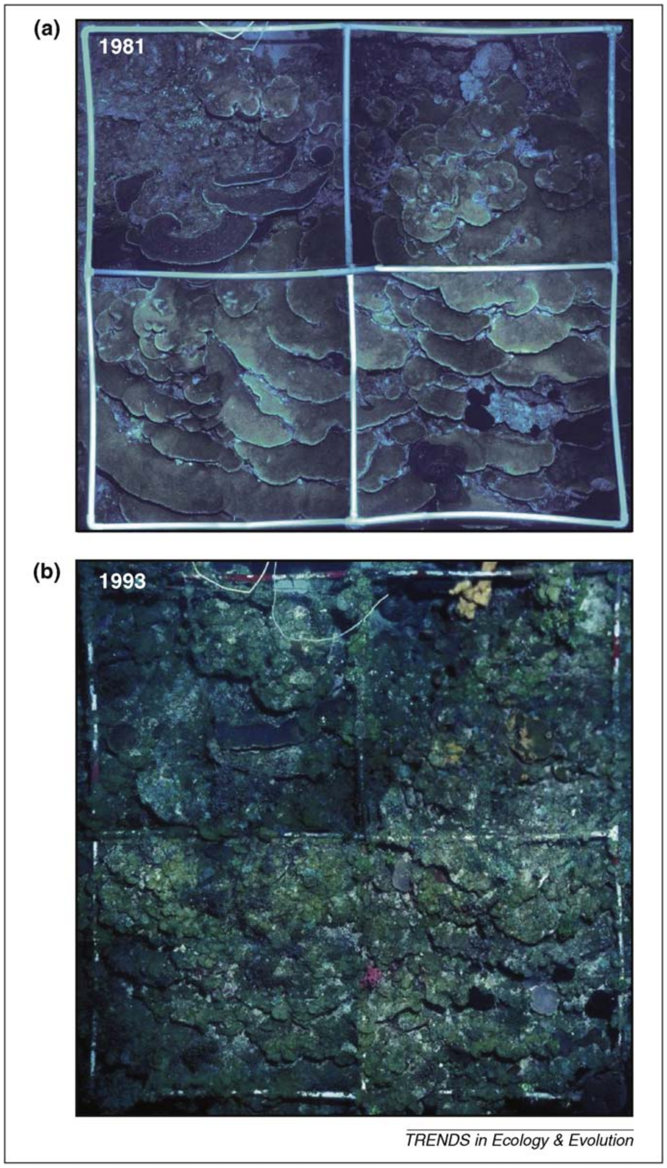

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Figure 3. A phase-shift from corals to macro-algal dominance in Jamaica. These photographs show the same 4m^2 quadrat at a depth of 35m, which was censused annually from 1981 to 1993. Coral cover at this deep site declined by small amounts each year, and was not significantly affected by hurricanes (in 1980 and 1987), or by any other sudden events. Despite the low impacts from acute disturbances, macroalgae increased steadily over time, preventing new coral recruitment and gradually overgrowing low-lying adult corals. The most likely driver of this change is diminished herbivory due to overfishing and recruitment failure of corals. This example illustrates that phase shifts from corals to macro-algae are often gradual, and not necessarily precipitated by catastrophic loss of corals.

The die-off of the abundant Caribbean sea urchin, *Diadema antillarum*, from a disease epidemic in 1983–1984 [46] was a critical event in the ensuing phase-shifts that occurred at overfished locations, from coral-dominated reefs to today's degraded systems, in which fleshy macro-algae typically predominate [5,36,40]. Coral mortality rates have increased across the region from disease, coral bleaching and runoff from coastal development [14,47]. Phase-shifts have been quantified from many Caribbean locations, including Barbados, Belize, Columbia, the Dutch Antilles, Florida, Jamaica, Panama, Puerto Rico, Tobago, and the Virgin Islands [3,5,36,37,40–44].

Box 2. How much seaweed is too much?

Macro-algae affect corals by competing with them for space by overgrowth, allelopathy, shading and whiplash; inducing physiological stress, reducing growth and fecundity, increasing mortality by direct competition or indirectly via increased microbial contamination, and reducing coral recruitment [32–35]. Recruitment-failure of corals, following phase-shifts to macro-algae or other weedy species, plays a key role in maintaining the resilience of alternate assemblages on degraded reefs [25]. Increases in the amount of macro-algal can cause a disproportionate decline in coral recruitment, especially if corals or other occupiers of space (sponges, clonal anemones, zoanthids, etc.) are also abundant, leaving limited room for new recruits. For example, in Jamaica, coral recruitment decreased by more than 80% within two years of the die-off of the sea urchin *Diadema antillarum* (from an average of 31 to 5 recruits m^{-2} per year), when macro-algal abundance increased from 2 to 20% cover [98].

Bruno *et al.* [20] proposed that 50% cover by macroalgae represents a reasonable indicator of a phase-shift to dominance by macroalgae. Using this cutoff, they conclude that phase-shifts to macroalgae have occurred infrequently across the world's coral reefs, because the mean cover of macroalgae (pooled across all sampled sites, habitats, reefs and all years between 1996 and 2006) is typically less than 50%. A 50% cutoff for macro-algal is clearly exceptionally high compared to historic baselines [45]. Indeed, using this arbitrary abundance threshold would lead to the curious conclusion that coral reefs have never been dominated by corals either: mean coral cover in all regions of the world falls short of 50% since records began around 50 years ago [59].

Dramatic and destructive increases in macroalgae on coral reefs are clearly evident from the scientific literature. Côté *et al.* [45] established a 1970s baseline in the Caribbean of 2% average cover by macroalgae [27]. In comparison, the average cover of macroalgae on Caribbean reefs during 1996–2006 had increased by 20-fold, to 40% [20]. Estimates of average macroalgal cover are now substantially higher than for all corals combined across the Caribbean and in the Florida Keys (Figure I). This shift from coral- to algal-dominance represent a dramatic regional-scale degradation of reefs, with the majority of Atlantic reefs now subjugated by the dynamics of macroalgae, sponges and other alternative assemblages, rather than corals (Figure I).

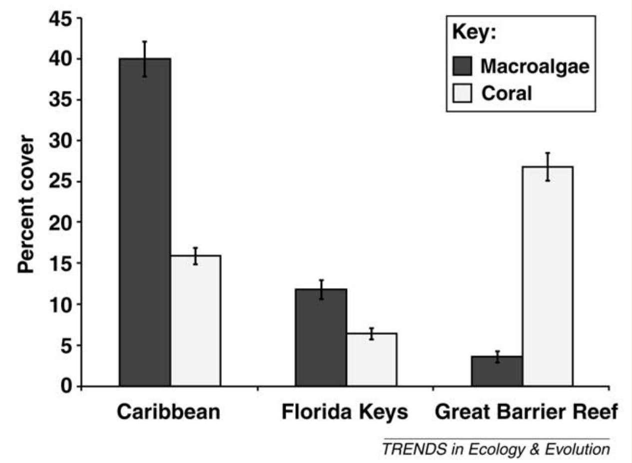

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Figure I. Estimates of average cover by corals and macroalgae in three tropical regions in 1996–2006, showing the contemporary prevalence of macroalgae in the Caribbean and Florida Keys, compared to the continuing dominance by corals on the Great Barrier Reef. Redrawn from Bruno *et al.* [20], excluding Reef Check surveys. Together, corals and macroalgae account for 19–55% of benthic cover. Other occupiers of space were not reported.

In the Indo-Pacific, declines in coral cover caused by population explosions of the pandemic crown-of-thorns starfish, have been widely documented in the primary literature for the past 40 years [48]. El Nino-driven bleaching events have also caused more recent damage, notably in 1982–1983 in the Eastern Pacific [44,49] and in 1998, when the largest bleaching event ever recorded killed many corals, especially in the Western Pacific and Indian Ocean [50,51]. For example, in parts of the Seychelles, coral cover after the 1998 El Nino bleaching declined to <1% by 2005, while macroalgal cover rose by up to 40% [6]. A similar decline in corals has occurred in the Galapagos Islands, driven by increasingly severe El Nino events and population explosions of sea urchins [49,52]. As in the Caribbean, Indo-Pacific locations with moderate or large human populations are usually overfished, and substantial degradation of fringing coastal reefs from terrestrial runoff began centuries ago [53] (Figure 1). Oceanic reefs in the Indo-Pacific, because of their exposure, lower nutrients and generally lower fishing-pressure, are much more resilient than Caribbean reefs [2]. On the other hand, isolated oceanic reefs and atolls in the Indo-Pacific have reduced larval connectivity, and the resultant reliance on self-seeding and long-distance replenishment increases their long-term vulnerability to the depletion of local adults stocks from coral bleaching and other disturbances [54–56].

Reef assessments

The Global Coral Reef Monitoring Network (GCRMN) compiles IPCC-like report cards for 17 coral reef regions [14]. Published every 2–4 years since 1998, the reports provide a worldwide compendium of reef condition from up to 97 countries based on local opinion, monitoring and assessment data. The latest GCRMN report from 2008 estimates that 19% of the world's reefs are effectively lost (i.e. unlikely to recover), another 15% are at a critical stage and likely to be lost within 10–20 years, and a further 20% are under threat from local human pressures (already experiencing 20–50% loss of corals). The remaining 46% of reefs are scored as being at low risk from human impacts, but even they are threatened by climate change and ocean acidification. These are imprecise figures: the reports stress that the estimates are notional for most regions and countries because of inadequate data. Nonetheless, these qualitative reports are politically useful in highlighting the need to respond to long-term declines in the global status of reefs.

Learning from the past

Pandolfi *et al.* [1] have taken a longer-term approach to documenting coral reef degradation, selecting reefs with a range of histories of human impacts from 14 regions in the Caribbean and Indo-Pacific, to reconstruct their ecological trajectories using paleontological, archaeological, historical and modern information. They showed that human impacts began centuries ago, and have followed a similar progression almost everywhere: the severe depletion and local extinction of megafauna preceded declines in fish and more recent widespread losses of corals, which have accelerated especially in the 1970s and 1980s. This long history of reef degradation is often overlooked by many contemporary studies [57], which often seek to explain current conditions by the most recent events only (Box 3).

Systematic monitoring of reefs

Properly designed monitoring of coral reefs, for multiple years on replicate reefs across a region, is a modern invention that long post-dates much of the recent degradation experienced by reefs over the past half-century. For example, an international reef monitoring program, CARICOMP, was initiated in the Caribbean in 1990, involving up to 30 institutions from 23 countries. Systematic monitoring of the Great Barrier Reef by the Australian Institute of Marine Science (AIMS) began in 1992, decades after two major outbreaks of the crown-of-thorns starfish and the earlier degradation of near-shore reefs due to increased runoff of sediment and nutrients in the 19th and 20th centuries [53] (Figure 1). The largest international assessment program, Reef Check, was founded in 1996. It relies on volunteer recreational divers to survey reefs, usually only once. This global program targets reefs that have the highest percentage of living corals in each region, with lower than average human impacts [58]. Substantial differences in protocols between CARICOMP, AIMS and Reef Check programs hinder quantitative comparisons between them.

Synthesizing imperfect information: meta-analysis

An emerging approach, loosely termed meta-analyses, synthesizes information on the conditions of coral reefs from disparate data sources (the primary literature, unpublished reports, new monitoring programs, etc.), in order to reconstruct regional and global trends in the abundance of corals, macroalgae and fishes [20,27,45,59–63] (supplemental material A). However, the results so far are often inconsistent from one compilation to the next, pointing to the current limitations of this approach. For example, two meta-analyses of coral cover in the Caribbean between 1976 and 2001, deviated from each other each year by up to 17% in absolute terms (supplemental material A). Meta-analyses of macroalgal cover are even more divergent. One study calculated that the average cover of macroalgae in the Caribbean increased from 2% prior to 1983 to a peak of 43% in 1987, but then unaccountably fell to a mean of 10% by 2001 [45]. Another compilation prescribes a completely different trajectory with three times more macroalgal (6%) before 1983, rising to a steady average of 40% between 1996 and 2006 [20], which is more than four times the alternative estimate [45]. In addition to these inconsistencies, a major shortcoming of coral reef meta-analyses is that they cannot retrospectively identify the complex mechanisms or processes causing long-term change [64]. Fundamentally, they are desktop syntheses that rely entirely on patchy information provided by the original sources of data. Although they generally provide a useful summary of available information on reef status, meta-analyses cannot offer new insights into important elements of phase-shifts and resilience such as feedbacks, thresholds and hysteresis (Figure 2).

Much more could be done to harness the vast amounts of coral reef monitoring data collected by government agencies, NGOs, volunteers and scientists. An obvious improvement to meta-analyses would be to remove the unwanted variance among primary studies, to eliminate the effects of depth, habitat, and methodology [65], thereby focusing on

Box 3. Shifting base-lines blinker retrospection

Our short memories promote a tendency to focus on recent events that we have personally experienced. These shifting baselines [64,99,100] cloud our judgment in assessing the extent and pace of both decline and recovery of coral reefs. We present two examples from the Caribbean:

Regional decline of coral cover

Shifting baselines have obscured the timing and causes of decline of Caribbean reefs. The relatively smooth downward trajectories in coral cover averaged across many sites by meta-analyses have been misinterpreted as evidence that regional declines have been synchronous. For example, two meta-analyses of the loss of structural complexity of Caribbean reefs between 1969 and 2008 [63] and of coral cover from 1971 to 2006 [61] have proposed that an unreported epidemic of white band disease killed off most branching staghorn and elkhorn corals across the region in the 1970 s. In reality, the loss of coral cover has been highly asynchronous, and disease is only one of many causes of the decline. For instance, cold water killed >90% of staghorn corals in the Dry Tortugas, Florida in the winter of 1976–77 [101]. The collapse of branching acroporids in Jamaica was overwhelmingly because of Hurricane Allen in 1980 [102]. There is only one report of a significant outbreak of white band disease in the Caribbean before 1980, a localized die-off affecting 5 hectares of shallow reef in St. Croix, US Virgin Islands in 1976–1979 [103]. In contrast, hurricanes and coral disease were dismissed as causes of the steep decline in coral cover in the Dutch Antilles from 1973 to 1992 [37]. Even the Caribbean-wide die-off of the sea urchin *Diadema antillarum* elicited heterogeneous responses around the region [36]. A minority of reefs, where grazing fishes were plentiful, did not undergo phase-shifts to macroalgae in the 1980 s [36], and a few retain relatively high coral cover today [104].

Recovery of the sea urchin, *Diadema antillarum*

The historic densities of *Diadema* before its dramatic die-off in 1983–1984 have been mostly forgotten. Average densities of 20m^{-2} or more were widely reported in the 1970 s and early 1980 s from over-fished sites in Barbados, Cozumel, Curacao, Haiti, Jamaica and the US Virgin Islands (supplemental material B). Some recent reports have suggested the widespread recovery of *Diadema* in the past decade [29], but others have not [105–107]. Our analysis of sea urchin densities at 35 island nations and regions across the Caribbean indicates that recovery up to 25 years after the die-off is still very incomplete (Figure I). The average densities reported since 2000 are still less than 0.3m^{-2}, compared to a mean of 7.7m^{-2} from 1970 to 1983, representing more than a 25-fold difference. The modal density of *Diadema* densities across 1064 censuses for 2000–2008 remains zero, although there are a growing number of reports of higher densities.

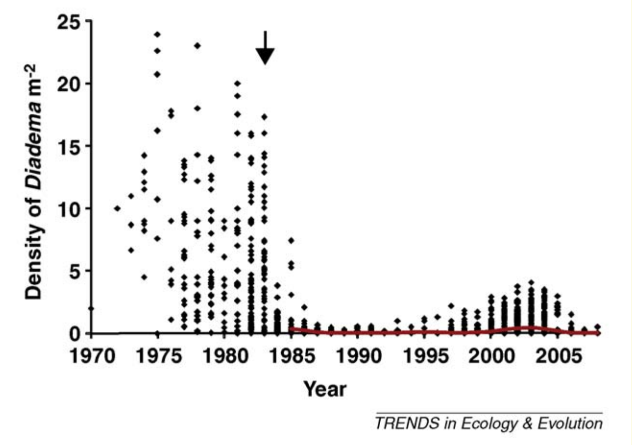

Figure I. A. Densities of *Diadema antillarum* from 1970 to 2008, based on a compilation of 3,496 records from 74 published and 3 unpublished sources (see supplemental material B). Twelve records of densities >25m^{-2} before 1983 are not shown. Each data point is the average density reported from one location. Three recent studies that specifically targeted aggregations of sea urchins are excluded. The fitted red line is a 3-year moving average across locations after 1983 (indicated by the vertical arrow), when the die-off occurred.

the variables of interest (e.g. time and geographic region). More sophisticated techniques for meta-analyses are also emerging that use hierarchical Bayesian models to deal with the inherent variability in these kinds of large-scale data compilations [66]. Rather than simply reaffirming environmental degradation, meta-analysis and monitoring data could be used much more productively in the future to assess the efficacy of management interventions, using before and after comparisons with appropriate controls [67].

Moving beyond the gloom and doom

The global decline of coral reefs begs the question: what are we going to do about it? Most of the loss of coral cover, about 125,000 km^2 so far, has occurred in the past 50 years [1–5,14]. Indisputably, this ongoing global decline represents a failure of policy, governance and implementation at multiple levels [2,30,68,69] (Box 4). Here we explore how a focus on resilience-based science could guide improvements in coral reef governance and management.

The coral reef science and management communities have widely adopted the resilience concept because of the extensive evidence for phase-shifts to persistent alternative ecosystem configurations. Reef management agencies and NGOs around the world have learned from the lessons of Hawaii, the Caribbean, the Indian Ocean, the Galapagos Islands and elsewhere about the potential for phase-shifts and the vulnerability of reefs to overfishing, declining water quality, and climate change. One clear warning from both resilience theory and practical experience is that prevention is better than cure. The empirical evidence is unambiguous: the trajectory of reef condition is declining globally; because once a reef is degraded it usually stays that way (but see below). Interventions need to focus (a) on reversing interacting slow drivers, particularly overfishing, pollution and greenhouse gas emissions, to avoid transgressing thresholds leading to phase-shifts, and (b) on promoting processes like coral recruitment and herbivory that maintain the coral-dominated states of healthy reefs. A resilience-based approach to coral reef management is a logical extension of current ecosystem-based management practices, building on an improved understanding of the dynamics of thresholds, reinforcing feedbacks, hysteresis and the reversibility of phase-shifts [2,15,22,23,70]. Enabling resilience-based management will require a major refocus of coral reef research (Box 5).

To date, the scientific focus has been on the widespread transition away from a coral-dominated system. We know far less about how to actively navigate the reverse trajectory away from a stable degraded state. The main reason of course is that slow drivers of change are ongoing and generally increasing almost everywhere, and there are only a handful of cases where they have actually been

Box 4. Coral reef governance

A common approach by many agencies is to construct a list of current threats to reefs, prioritize them and tackle them individually. This reactive approach (which invariably focuses on changes that have already occurred) needs to be replaced by more proactive, integrative and flexible styles of governance and management that can deal with uncertainty and the risk of ecological surprises leading to phase-shifts. Legislation and policy need to focus on rebuilding ecosystem functions and bolstering ecosystem resilience to future disturbances, rather than maintaining the status quo. We make the following recommendations as a pathway towards integrated, resilience-based management of coral reefs:

(i) Empower and educate local people to improve protection of reefs. In many developing countries, this will require a radical change in governance structures, away from top-down centralized systems to multi-scale institutional arrangements that promote greater local participation and ownership [71,108]. For example, without strong local support, no-take marine reserves inevitably fail to reach their objective of repairing distorted food webs, rejuvenating depleted stocks [86,109], and rebuilding resilience. Similarly, changes in land-use, which are critical for managing runoff of sediment and pollutants, require sustained local involvement and support [110].

(ii) Augment the traditional focus on regulating harvesting with more controls on the marketplace [111]. For example, existing CITES provisions for international trade in corals need to be properly enforced, and extended to include additional species such as macro-herbivores and top predators that play critical ecological roles [2].

(iii) Integrate the science of coral reef resilience with decision-making and management by improving access to international networks of expertise, and by providing financial assistance, particularly for small developing countries that are highly dependent on coral reef resources.

(iv) Create new legal frameworks, policies and agencies that are specifically focused on managing coral reefs. In particular, wealthier countries such as the USA could improve their system of coral reef governance to one that is less redundant, more focused and efficient, and better funded.

(v) Confront climate change as the single most important issue for coral reef management and conservation by sharply reducing greenhouse gas emissions. Without urgent action, unchecked global warming and ocean acidification promise to be the ultimate policy failures for coral reefs [15,112]. Although it is possible to promote the recovery of reefs following bouts of bleaching via local actions such as improving water-quality and protecting herbivores, these interventions alone cannot climate-proof reefs.

reduced. We tend to make a societal, value-laden judgment about which types of ecosystems are desirable [71], and so management today often focuses on bolstering the resilience of the desired coral-dominated phase [72]. An equally valid management approach, which has scarcely been considered, is to apply resilience-based concepts to navigate a transition away from an undesirable phase. If hysteresis is weak, it might be easier to re-build functional reefs than we commonly assume.

Reversing unwanted phase-shifts

We present four sets of case studies to illustrate the prospect of reversibility of degraded regimes, pointing towards potential interventions for confronting the global decline of reefs. The first example is Kaneohe Bay in Hawaii, a land-locked shallow coral reef system that receives inflowing freshwater and nutrients from the surrounding catchment, and in the 1970's also bore the brunt of sewage discharge and heavy recreational fishing pressure [73]. Higher nutrients and particulates caused phytoplankton blooms, while corals were overgrown by macroalgae, sponges and filter-feeders. When the sewage was diverted further offshore, the water quality improved and a phase-shift back to corals ensued (until more recent years when invasive species took their toll [74]).

Secondly, small-scale herbivore exclusion experiments [75–78] commonly create algal blooms that are reversible once herbivory resumes. For example, the exclusion of grazing fishes on the inner Great Barrier Reef for 30 months generated 2m-tall stands of *Sargassum* that reduced coral recruitment by two-thirds. The seaweed was subsequently devoured in a few weeks once grazers were reinstated. Importantly, the suite of fishes responsible for maintaining low algal abundances on these heavily grazed reefs did not consume the mature *Sargassum*. Rather, a previously overlooked batfish species that was incorrectly assumed to be a planktivore was responsible for most of the reversal [79]. This unexpected result highlights the importance of identifying critical species and functional groups that can help to undermine the resilience of undesirable regimes.

A third example is the dynamic that is unfolding today in the Caribbean, due to the slow and patchy recovery of the sea urchin, *Diadema antillarum* (Box 3). Its recovery is not caused by human intervention, but nonetheless provides a clear example of the importance of herbivory as a slow driver of change. Most Caribbean reefs today are algal-dominated, because of overfishing of herbivorous fishes and the continuing low densities of *Diadema* (Box 2). One exception is a narrow shallow band at locations where *Diadema* has returned; where macroalgae are once more heavily grazed and coral recruitment is underway [29,80,81].

A fourth line of evidence for reversibility comes from some studies of no-take fishing reserves, where higher abundances of herbivorous fishes (compared to adjoining fished areas) have coincided with lower amounts of macroalgae and more coral recruits. For example, in the Bahamas, grazing intensity by large parrotfishes was six-times higher inside no-take reserves compared to fished areas, and the cover of seaweed was 14% compared to 75% on adjoining reefs [82]. Similarly, in the Philippines, the biomass of herbivorous fishes was 8-times lower outside no-fishing reserves, whereas macroalgal cover was 25-times higher [83].

These four examples all involve reducing the drivers of change and weakening reinforcing feedback to erode the resilience of the low-coral, high-macroalgal phase (e.g. by enhancing herbivory or reducing nutrients). They illustrate that changes in the structure of food webs and in the inputs of pollutants and larval recruits (of both desirable and undesirable species) play a critical role in determining the resilience of coral reefs, pointing to opportunities for interventions. For example, the top-down role of herbivorous fishes in maintaining low algal biomass provides support for establishing no-take fishing reserves, restricting gear that targets herbivorous fishes, and establishing market-based instruments that regulate their sale and export.

Box 5. Future research

An improved understanding of the processes and mechanisms that build or erode resilience is urgently required, in order to predict and avoid undesirable phase-shifts (or to regain a coral-dominated phase). Building the empirical evidence for feedbacks, thresholds and hysteresis needs to be a key focus. Reducing fast and slow drivers of change, where feasible, is a major research and policy challenge.

Meta-analyses of reef status could play a more important role in synthesizing data and in measuring ecosystem responses to management interventions, building stronger links between monitoring and adaptive governance. Research on meta-analysis should focus on separating unwanted variance (e.g. because of methodology and habitat) from regional and long-term trends, coping with apples and oranges data, and with gaps in information.

Currently, monitoring focuses on changes in reef status rather than changes in processes or mechanisms underlying resilience. New research should explore the development of novel metrics for monitoring important processes, such as rates of herbivory, coral recruitment, and connectivity.

Connectivity is critical for replenishment of corals, fishes and other species that comprise functional reefs. There is also a dark side to connectivity: the spread of pollution and diseases, introduced species, and population explosions of other species that undermine the resilience of healthy reefs (e.g. macro-algae, sea urchins, corallivores). The scale of stock-recruitment relationships for important species and functional groups remains poorly understood.

Many management interventions are based on sound scientific knowledge but nonetheless fail, because of a poor understanding of social and economic contexts and constraints, and inadequate governance. Research needs to focus more on the human dimension of coral reefs, recognizing the importance of reef ecosystem services to societal well being, and the impacts of people on reef resilience. Critical issues include how levels of economic development, social capital, local history and culture influence resource use and governance systems. To date these issues have typically been the subjects of unreplicated anecdotal case studies or comparative studies with only limited geographic, social, and economic scope. To make significant progress, the disciplinary constraints of biologists, social scientists and economists need to be broken down to focus on the resilience of coral reefs as linked social-ecological systems.

Marine reserves and resilience

To date, much of the effort in conserving coral reefs by national governments and NGOs has been directed at the establishment of networks of marine parks, including no-take fishing reserves. Reserves can help to re-build the biomass of targeted fish species, and therefore contribute to the rebuilding of distorted food webs [67,84]. Larger, more fecund fish within reserves can potentially lead to higher levels of connectivity to surrounding areas [85]. Whereas marine reserves provide no direct protection from pollution or the impacts of climate change, an increase in the stocks of herbivorous fishes inside them should help to reduce the likelihood of macroalgal dominance [15,82,83]. However, many reserves have failed to prevent ongoing overfishing because of a lack of support from impoverished local people, poor compliance and inadequate resources for education and enforcement [86,87].

Even the most successful and intensively managed marine parks are vulnerable to degradation outside their boundaries that cause shifts in external sources of larvae [12]. Whereas most of the research focus has been on the potential for export of fish larvae from marine parks to the surrounding seascape or to and from other parks in a network, in reality most parks are far too small and too far apart to be self-sustaining or resilient in their own right [88,89]. The reliance of marine parks on the influx of larvae into them from outside is a two edged sword that in some cases can undermine resilience, as exemplified by population explosions of coral predators and the spread of introduced species and diseases. From a resilience perspective, protecting small parks is only one approach that needs to be combined much more vigorously with other interventions. Efforts to tackle coastal pollution, climate change, and the decline of roaming megafauna (e.g. dugongs, sharks and turtles) all need to be intensified.

Finally, we need to recognize that the coral reef crisis is a crisis of governance (Box 4). Scientists can help by undertaking solution-focused research, by participating more vigorously in policy debates to improve coral reef legislation and implementation, and by sending the clear message that reefs can still be saved if we try harder.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2010.07.011.

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Supplemental Material:

A. Coral Reef Meta-analysis: Supplemental Text, Supplemental Table 1 and Supplemental Figures 1,2

B. Bibliography of source studies on densities of *Diadema antillarum* for Figure I in Box 3.

A. Coral reef meta-analysis

The first and most comprehensive meta-analyses of coral reef status have come from the Caribbean, a relatively small region where reefs have been the most intensively studied (Supplemental Table 1). Gardner et al. [27] compiled data on coral cover from 65 of the primary studies describing changes between 1977 and 2001, and their analysis indicated a near-continuous decline in average cover, from a mean of 50% to 11%. Subsequent meta-analyses have also summarized information on the proliferation of macroalgae following the die-off of the sea urchin *Diadema* [45] and the declining rugosity of Caribbean reefs due to the loss of corals [63]. Meta-analyses of corals and macroalagae in the vast Indo-Pacific [20, 59], home to 92% of the world's coral reefs, rely on a much sparser evidence base, with little or no information available for many countries, especially before about 1990.

There are three limitations to these meta-analyses that account for the disparities between them (Supplemental Figure 1). Firstly, the number of records available to undertake them reliably is often inadequate, especially for the Indo-Pacific and before the recent proliferation of systematic monitoring programs. Even in the data-rich Caribbean, there are no estimates of coral cover prior to 1990 from half of the 21 islands and regions used in a meta-analysis of trends from 1976 to 2001 [27]. In the Indo-Pacific, one-third of the records of coral cover used in an analysis spanning from 1968 to 2004 come from one habitat in one region (mid-depth reef slopes in Australia) after 1997 [59]. For Caribbean fishes, just four of the 48 studies included in a meta-analysis from 1955-2007 were conducted in the 25 years before 1980 [62]. This sparseness of data for the first half of the 52 year census period undermines the study’s main conclusion that declines in fish abundance in the Caribbean have occurred only in the past decade.

Secondly, the coral reef meta-analyses undertaken so far (Supplemental Table 1) vary substantially in their choice of which existing information to include. Some use all of the relevant peer-reviewed literature, but others rely heavily on data collected by CARICOMP and Reef Check from a biased subset of reefs that are in better than average condition. The mix of source data used in each meta-analysis makes a huge difference. For example, the inclusion of Reef Check data raises the estimated mean coral cover of Indo-Pacific reefs between 1996 and 2006 from 20% to 33% [20]. Similarly, if the Reef Check volunteer surveys from “near-pristine” reefs are included, the Caribbean-wide average cover of macro-algae reported between 1996 to 2006 drops substantially from 40 to 24%, reflecting a two-fold disparity between the volunteer data and other sources of information [20].

Thirdly, problems of interpretation arise when there are consistent methodological differences among primary studies undertaken in different regions or at different time scales. Côté et al. [45] found that photoquadrats reveal large increases in macroalgal cover in the Caribbean, whereas monitoring based on video transects show no change, and line-intercept transects are intermediate (Supplemental Figure 2). Importantly, the prevalence of video transects has grown dramatically in recent years, so that methodology and time are confounded. Similarly, estimates of regional differences in coral and macroalgal abundances are confounded by large discrepancies in the habitats and depths targeted by large monitoring programs in different parts of the world.

Supplemental Table 1. Recent coral reef compilations and meta-analyses.

Metric	**Geographic Focus**	**Time-line**[1*]	**No. of Observations**	**Major data sources**	**Authors**
Coral cover	Caribbean	1977-2001	263	65 studies, CARICOMP, Florida Keys Monitoring Project	[27]
Coral cover	Indo-Pacific	1968-2004	6001	50 studies, AIMS/Reef Check monitoring programs	[59]
Coral cover (inside marine parks)	Global	1969-2008	5170	AIMS/Reef Check monitoring programs	[60]
Coral cover (outside marine parks)			3364		
Coral cover	Caribbean	1977-2001	294	51 studies	[45]
Macroalgal cover			174	34 studies	
Coral cover	Caribbean	1971-2006	3777	Monitoring programs	[61]
Macroalgal cover			2247		
Coral cover	Global	1996-2006	3581	AIMS/Reef Check monitoring programs	[20]
Macroalgal cover					
Fish abundance	Caribbean	1955-2007	318	48 studies	[62]
Reef rugosity	Caribbean	1969-2008	464	49 studies	[63]
Diadema abundance	Caribbean	1970-2008	3496	74 studies, monitoring programs	Box 3

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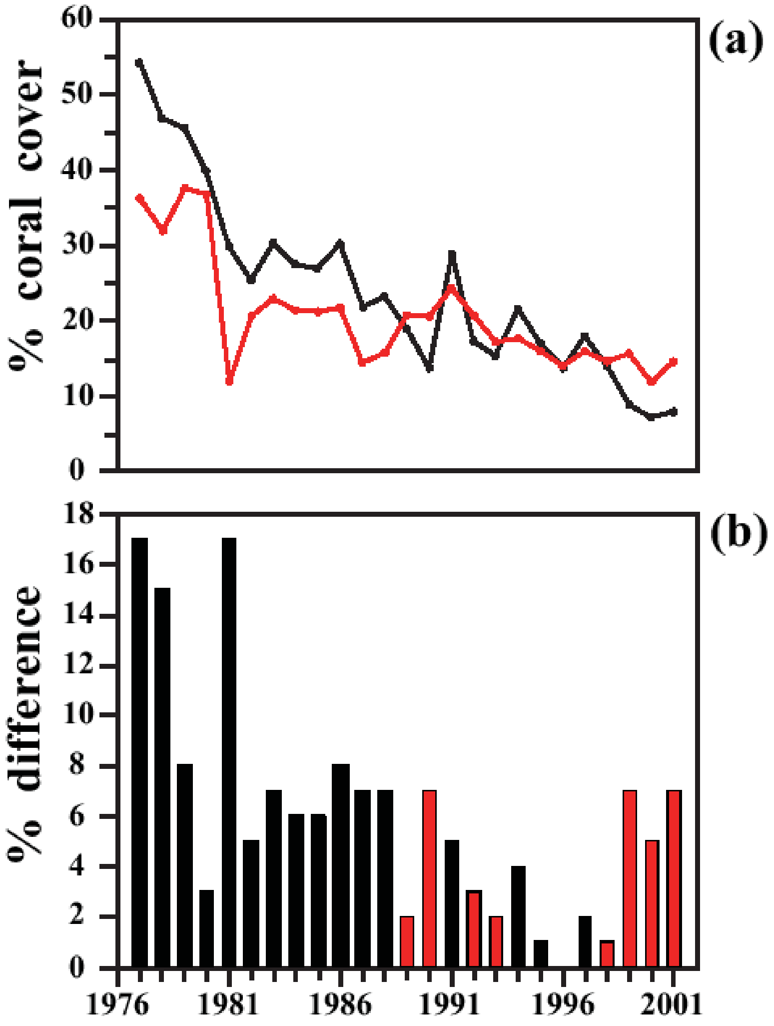
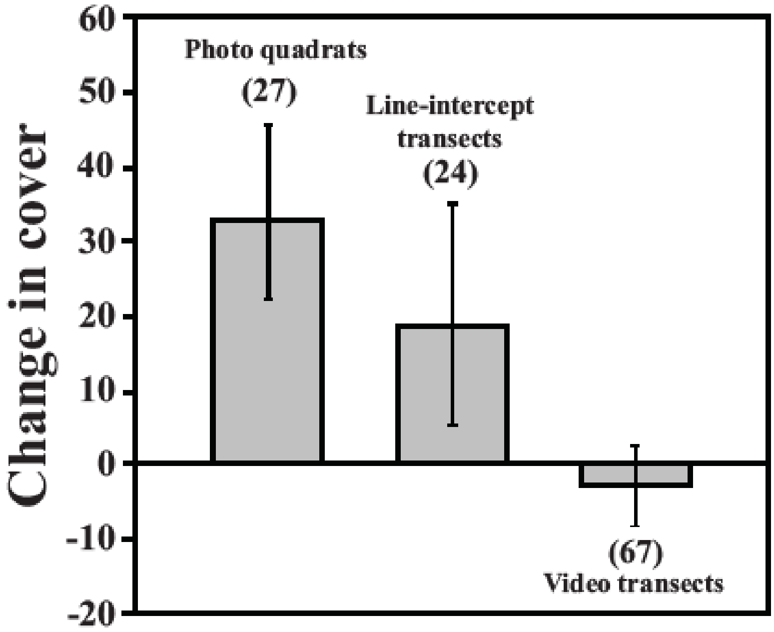
[*] Note that sample sizes for the first half of these periods are invariably very small.



Supplemental Figure 1. Comparison of two recent meta-analyses of coral cover in the Caribbean, from 1976 to 2001. A. Trajectories of coral cover, redrawn from Gardner et al. [27], in black, and Schutte et al. [61], in red. B. Disparities in coral cover between these two meta-analyses. The bar color indicates which study calculated the higher amount. One analysis was consistently higher for the first 12 years, but then ended with an estimate of half the cover of the other study. Consequently, one indicates that mean coral cover in the Caribbean declined by four-fifths in 25 years [27], while the other proposes it declined by only half [61].



Supplemental Figure 2. Mean annual change in cover of macroalgae in the Caribbean, according to studies using three different techniques: photoquadrats, line-intercept transects and video transects. The error bars indicate 95% confidence limits. Re-drawn from Côté et al. [45]. This disparity reflects the difficulty of distinguishing macroalgae in underwater hand-held videos, which have lower resolution than close-up photographs or in situ measurements along line intercept transects.

B. Bibliography of source studies on densities of *Diadema antillarum* for Figure 1 in Box 3.

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