

Richard B. Aronson · William F. Precht

Conservation, precaution, and Caribbean reefs

Received: 29 November 2005 / Accepted: 24 April 2006 / Published online: 1 June 2006
© Springer-Verlag 2006

Abstract Some authors argue that overfishing is an important reason that reef corals have declined in recent decades. Their reasoning is that overfishing removes herbivores, releasing macroalgae to overgrow and kill the corals. The evidence suggests, however, that global climate change and emergent marine diseases make a far greater contribution to coral mortality, and that macroalgae generally grow on the exposed skeletal surfaces of corals that are already dead. Macroalgal dominance, therefore, is an effect rather than a cause of coral mortality. Marine protected areas (MPAs), which are usually established to protect stocks of reef fish, foster populations of herbivorous fish under at least some circumstances. Increased herbivory can reduce algal cover, potentially accelerating the recovery of coral populations inside MPAs; however, establishing MPAs will have only a limited impact on coral recovery unless policymakers confront the accelerating negative effects of the global-scale sources of coral mortality.

Keywords Coral reef · Coral disease · Global climate change · Marine protected area · Overfishing · Precautionary principle

Communicated by Ecology Editor P.J. Mumby

R. B. Aronson (✉)
Dauphin Island Sea Lab, 101 Bienville Boulevard,
Dauphin Island, AL 36528, USA
E-mail: raronson@disl.org
Tel.: +1-251-8617567
Fax: +1-251-8617540

R. B. Aronson
Department of Marine Sciences,
University of South Alabama,
Mobile, AL 36688, USA

W. F. Precht
Ecological Sciences Division, PBS&J,
2001 NW 107th Avenue, Miami, FL 33172, USA
E-mail: bprecht@pbsj.com

Introduction

No coral reef scientist can credibly deny that reef ecosystems around the world are in jeopardy (Wilkinson 2000, 2004). The Caribbean region has been hit particularly hard, with an average loss of 40% absolute coral cover since the late 1970s (Gardner et al. 2003). Some authors attribute these losses primarily to decades or centuries of overfishing, coupled with the disease-induced, regional mass mortality of the echinoid *Diadema antillarum* in 1983–1984 (Jackson 2001; Jackson et al. 2001; Pandolfi et al. 2005). In their “herbivory scenario,” sharply reduced herbivory was the principal driver of coral mortality, because the loss of herbivores released fleshy and filamentous macroalgae, especially the brown algae *Lobophora variegata*, *Dictyota* spp., and *Sargassum* spp., to overgrow the corals. Regional-scale collapse of Caribbean reef ecosystems ensued. These authors contend that coral assemblages of the Caribbean have lost their resilience—their capacity to recover following perturbation. Macroalgal dominance thus constitutes an alternative community state, which may or may not be stable (Knowlton 1992; Scheffer et al. 2001; Petraitis and Dudgeon 2004). Many Indo-Pacific reefs are now losing their resilience as well, also purportedly due to overfishing (e.g., Bellwood et al. 2004).

The principal recommendation emerging from the herbivory scenario is that large, networked marine protected areas (MPAs) are the key to coral recovery, based on the assumption that cascading food-web effects will resume after no-take regulations are established and enforced (Nyström et al. 2000; Nyström and Folke 2001; Pandolfi et al. 2003, 2005; Bellwood et al. 2004; Hughes et al. 2005). In the absence of grazing by *Diadema*, larger, protected populations of herbivorous parrotfish (Labridae: Scarinae) and surgeonfish (Acanthuridae) should exert top-down control on algal growth and help corals recruit and recover. The corals should in turn provide the physical structure the herbivores require,

and the resultant positive feedback should benefit both corals and reef fish.

Given that MPAs protect predators, an alternative prediction is that cascading effects should reduce herbivory and increase, rather than decrease, macroalgal abundance inside reserves (e.g., Gibson et al. 2004). This prediction fails in most cases, for two reasons. First, it tacitly and incorrectly assumes only one predatory trophic level (cf. Bascompte et al. 2005). If MPAs protect the predators of herbivorous fish, then the latter should decline and macroalgae should increase; however, because MPAs are also designed to protect the predators of those predators, and because many predatory species feed at multiple trophic levels, herbivorous fish should actually increase and macroalgae should decline. Second, populations of herbivorous fish are often exploited on unprotected reefs (Hughes et al. 1987; Gibson et al. 2004; Mumby 2006; and many others), so the protections afforded by MPAs tend to have a direct positive impact on herbivorous fish as well. For both of these reasons, MPAs generally do not decrease herbivory. In some cases MPAs increase the abundance of large, herbivorous reef fish and the intensity of herbivory (Hawkins and Roberts 2003; Mumby et al. 2006), but this effect is by no means universal (Mosquera et al. 2000; Graham et al. 2003; Micheli et al. 2004; Robertson et al. 2005).

The idea of cascading effects is appealing because it is simple, makes intuitive sense, and can be addressed on a local level through sound fisheries management. Even if herbivory is not the only important factor, MPAs could at least help corals persist in the short term while we search for longer term solutions (Palumbi 2005). Are these interpretations correct? Will MPAs make reef assemblages more resilient by decreasing macroalgal cover, increasing coral cover, and helping restore coral assemblages to a desirable, coral-dominated state? What else should we do about coral populations and coral reefs that will make a difference?

Here we dissect the herbivory scenario into its component assertions: (1) that macroalgal overgrowth stemming from the loss of herbivores was the primary cause of coral mortality; and (2) that establishing MPAs will promote the recovery of coral populations. We then evaluate in scientific and ethical terms the rationale for applying the precautionary principle to MPAs in the face of incomplete evidence for the herbivory scenario. Finally, we propose a new agenda for promoting the recovery of coral reefs. Our agenda is based on accepting the idea of multiple, interactive causality [Quinn and Dunham 1983; Holling and Allen 2002; see Hoegh-Guldberg (2006) for application of these ideas to coral reefs]. We depart from previous discussions by emphasizing the urgent task of confronting environmental globalization at the same time we act to solve problems at a local scale, including the preservation and enhancement of stocks of reef fish.

Macroalgal overgrowth of Caribbean corals

To claim that overfishing has driven reef degradation in the Caribbean via the herbivory scenario is to invert the causal link between macroalgal growth and coral mortality. In the vast majority of cases, corals have not been killed by macroalgal overgrowth. Corals have been and are being killed by large-scale, external perturbations, and growth of macroalgae on the newly vacated substratum is a secondary, collateral effect (Aronson and Precht 2001a; McCook et al. 2001; McManus and Polsenberg 2004).

The popular conception that Caribbean corals have been killed primarily by macroalgal overgrowth has its roots in papers by Sammarco (1980, 1982) and Littler and Littler (1985), and especially in the recent reinterpretation of a paper by Hughes (1989). Hughes (1989) monitored permanent quadrats at three depths at Rio Bueno on the north coast of Jamaica from 1983 to 1987. Following the mass mortality of *Diadema*, two coral species that grow as small, low-relief colonies, *Agaricia agaricites* and *Madracis mirabilis*, were susceptible to overgrowth by macroalgae and declined (see also de Ruyter van Steveninck and Bak 1986). Other coral species were less strongly affected. The least affected species were *Colpophyllia natans*, which is a large brain coral, and the *Montastraea annularis* species complex, which produces massive, mound-shaped colonies. *Colpophyllia* declined at one depth and increased at another, while *Montastraea*, which is one of the three important framework-building corals of the region, significantly increased at the one depth for which it was reported (Hughes 1989, table 1). Hughes et al. (1987) explicitly stated that coral species producing high-relief colonies, such as *Colpophyllia* and *Montastraea*, were “relatively safe from algal overgrowth.” Hughes (1989) also pointed out that macroalgal dominance was pre-empting space and, therefore, sharply reducing coral recruitment and the potential for recovery.

Hughes (1994), citing his own 1989 paper, stated that after the *Diadema* dieoff “most adult colonies” that had survived Hurricane Allen in 1980 had been “killed by algal overgrowth, especially low-lying species...” In the same paragraph, Hughes (1994) discussed additional coral mortality from bleaching events. He went on to state in that paragraph that *Montastraea* declined sharply, but he did not explicitly link this mortality to either macroalgal overgrowth or bleaching.

Jackson et al. (2001) stated, “Large species of branching *Acropora* corals dominated shallow reefs in the tropical western Atlantic...until the 1980s when they declined dramatically.” The first sentence of the following paragraph then cited Hughes (1994) for the statement, “Western Atlantic reef corals suffered sudden, catastrophic mortality in the 1980s due to overgrowth by macroalgae that exploded after mass mortality of the superabundant sea urchin *D. antillarum* that [because of overfishing] was the last remaining

grazer of macroalgae.” These two sentences clearly imply that macroalgae overgrew not just low-lying colonies but also living colonies of the two framework-building *Acropora* species: *Ac. palmata* (elkhorn coral) and *Ac. cervicornis* (staghorn coral). Moreover, Jackson (2001), again citing Hughes (1994), explicitly stated that the principal cause of coral mortality across the Caribbean region, including mortality of *Montastraea* spp. and *Acropora* spp., was macroalgal overgrowth resulting from overfishing and the mass mortality of *Diadema*. Neither *Acropora* species was reported from the study quadrats in the original paper by Hughes (1989), and as mentioned above *Montastraea* had actually increased.

Subsequently, Pandolfi et al. (2003) stated that overfishing is the only reasonable explanation for the historical degradation of coral reefs. These authors did not propose a mechanism, but they cited Jackson et al. (2001). Bellwood et al. (2004) stated that overexploitation of herbivorous fish can increase algal overgrowth of corals, citing Hughes (1994) and McCook et al. (2001). Finally, Pandolfi et al. (2005) said essentially the same thing, but without attribution. The shifting baseline of emphasis in this sequence of papers brings to mind previous warnings against accepting unsupported claims about ecological effects (Elner and Vadas 1990; Hilborn 2004).

In reviewing the literature, Nyström et al. (2000), Nyström and Folke (2001), and Scheffer et al. (2001) recognized the importance of coral mortality to the subsequent growth and dominance of macroalgae, but they emphasized macroalgal overgrowth of living corals as well. Nyström and colleagues stressed that “even large old coral colonies” were overgrown by macroalgae on Jamaican reefs. We also made this mistake (Aronson and Precht 2001a).

Lirman (2001) showed that macroalgae could overgrow the living tissue of *Montastraea faveolata* colonies on heavily disturbed reefs in the Florida Keys. Although he did not assess the ecological impact on coral assemblages, Lirman demonstrated experimentally that overgrowth was more extensive when herbivores were excluded. Algal overgrowth, however, was predicated on morbidity or partial mortality of the *Montastraea* colonies. The degree to which macroalgae are able to overgrow healthy coral tissue and, conversely, the degree to which established coral colonies monopolize space and exclude algae remain equivocal in the context of community-level dynamics (de Ruyter van Steveninck et al. 1988; Umar et al. 1998; Lirman 2001; Jompa and McCook 2002; Nugues et al. 2004a; Mumby 2006).

There is only one experimental example from the Caribbean in which macroalgae, when released from the pressures of herbivory by fish, overgrew healthy corals to an ecologically significant extent. Lewis (1986) removed herbivorous fish from large enclosures in the back reef at Carrie Bow Cay, Belize and observed increased macroalgal cover and decreased cover of the dominant coral, *Porites astreoides*. *Diadema* were not important herbivores in her study. In all

other well-documented cases, widespread coral mortality has been the essential precondition for macroalgal dominance of reefs, and coral mortality has been decoupled from fishing pressure and herbivory (Aronson and Precht 2001a; Williams et al. 2001; Mumby et al. 2005).

Causal connections

Coral mortality cannot in general be attributed to macroalgal overgrowth, but once macroalgae are established, they can suppress coral recruitment (Hughes 1989; Hughes and Tanner 2000; McCook et al. 2001). The question is whether we can manage for ecosystem resilience by promoting the process of herbivory if we do not simultaneously and directly confront the as-yet uncontrolled global pressures causing coral mortality (e.g., McClanahan et al. 2002). Chief among these are (1) climatic warming, increased cyclone intensity, and changes in ocean chemistry, all of which stem from greenhouse-gas emissions (Done 1999; Hoegh-Guldberg 1999; Kleypas et al. 1999; Pittock 1999; Walther et al. 2002; Emanuel 2005; McWilliams et al. 2005; Webster et al. 2005); and (2) the spread of infectious marine diseases, which could be related to global warming and may be exacerbated locally by nutrient loading (Aronson and Precht 2001b; Harvell et al. 2002; Rosenberg and Ben-Haim 2002; Bruno et al. 2003; Sutherland et al. 2004). Nugues et al. (2004b) showed that macroalgae could be acting as reservoirs for coral disease, raising the possibility of positive feedback in which coral mortality leads to increased macroalgal cover, which in turn leads to more disease-induced coral mortality.

Most of the 40% decline in coral cover on Caribbean reefs reported by Gardner et al. (2003) resulted from the catastrophic mortality of *Acropora palmata* and *Ac. cervicornis*, which were the dominant space occupants at shallow and intermediate depths, respectively. The primary cause was a regional outbreak of white-band disease (WBD), which began in the late 1970s and continued through the early 1990s (Aronson and Precht 2001b). The Caribbean-wide *Acropora* kill overwhelmed the capacity of herbivores to respond behaviorally or numerically to the vast expanses of newly opened space, and macroalgal abundance increased enormously (Knowlton 1992; Aronson and Precht 2001a). Although the mass mortality of *Diadema* in 1983–1984 has been promoted in the literature as the pivotal event that drove Caribbean reefs in the direction of macroalgal overgrowth and increased coral mortality (Jackson et al. 2001; Bellwood et al. 2004), fully half the decline of coral cover reported by Gardner et al. (2003) occurred prior to that event. This is clearly evident from one of their graphs, which shows the regional loss of coral cover from 1977 to 2002 as a step-function rather than a gradual decline (Fig. 1). Interestingly, there was no decline of coral cover immediately following the loss of *Diadema*. Subsequent declines were related to losses of

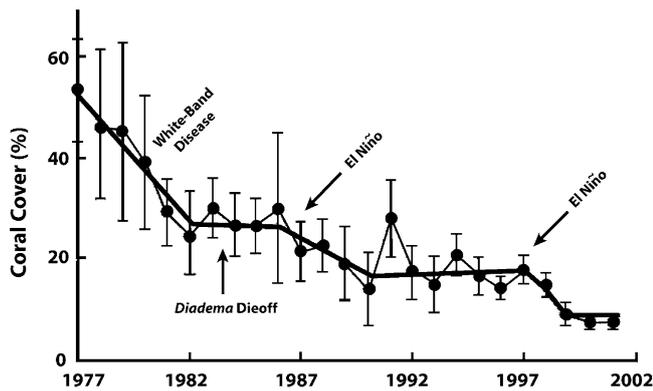


Fig. 1 Long-term trajectory of coral cover on Caribbean reefs, based on a meta-analysis of ecological studies. *Solid circles* are means, and *error bars* are 95% bootstrapped confidence intervals. The *thin, solid line* connects the means; the *thick, solid line* displays the overall trend in the data. The initial decline in 1977–1982, representing a decrease in absolute coral cover from approximately 50 to 25%, corresponds to the regional loss of *Acropora palmata* and *Acropora cervicornis* caused by white-band disease. The declines in 1987–1990 and 1998–1999 are associated with major, El Niño-induced bleaching events. The latter two declines primarily represent the loss of non-acroporid corals, because much of the damage to acroporids was already done by 1987. Redrawn from Gardner et al. (2003)

Montastraea spp. and other non-acroporid corals, due to bleaching and disease (e.g., McClanahan and Muthiga 1998; Ostrander et al. 2000; Burke et al. 2004).

The recent ecological history of the Belizean barrier reef highlights the importance of coral mortality as the prerequisite for macroalgal dominance. Hurricane Hattie severely damaged coral populations within a section of the barrier reef in 1961, more than two decades before the mass mortality of *Diadema*. The salient consequence was macroalgal dominance for more than a decade despite the abundant, unexploited state of reef-fish populations (Stoddart 1963, 1965, 1969, 1974). Twenty years later, reef-crest populations of *Ac. palmata* (0–3 m depth) were wiped out by WBD and replaced by macroalgae along the length of the barrier reef. *Ac. cervicornis* populations in the deep spur-and-groove zone of the fore reef (9–15 m) suffered a similar fate, and that zone also shifted to macroalgal dominance (Littler et al. 1987; Aronson et al. 1994). Coral cover remained high, however, in the intervening shallow spur-and-groove zone (3–6 m), which was dominated by *Agaricia tenuifolia* (Aronson and Precht 1995). *Ag. tenuifolia* is not susceptible to WBD, which apparently affects only the genus *Acropora*. *Ag. tenuifolia* persisted at high levels of percent cover, and macroalgae did not have the opportunity to become dominant in the shallow spur-and-groove. Herbivorous fish were not exploited and were more abundant, not less abundant, in the deep spur-and-groove than in the shallow spur-and-groove; *Diadema* was not a significant herbivore in either zone; and consumption rates of experimentally tethered algae were higher, not lower, in the deep zone (Lewis and Wainwright 1985).

Coral reefs of the Flower Garden Banks (FGB) in the northwestern Gulf of Mexico provide an interesting counterpoint to what has happened in the Caribbean. The FGB are too far north for the cold-sensitive acroporids to have established populations prior to the warming conditions of the past few decades (Precht and Aronson 2004). The cover of living hard corals has remained stable at 40–60% from at least as early as the 1970s to the present, in large part because in the 1980s there were no acroporids available to die of WBD and thereby open large areas of reef surface for algal colonization (Aronson et al. 2005). As was the case in Belize, herbivorous fish are abundant on the FGB and historically have not been exploited (Pattengill-Semmens and Gittings 2003). Following the decline of *Diadema* in the early 1980s from an initial density of less than 2 ind/m² to essentially zero (S.R. Gittings, unpublished data), macroalgae increased by approximately 10% absolute cover (from 2.5 to 13%) within 2 years; however, coral cover did not decline and the macroalgae were only able to grow in the patches of open substratum between living coral colonies (Gittings 1998).

A logical prediction of the herbivory scenario is that reefs in closer proximity to people, or in proximity to people for a longer time, are more likely to be degraded (Jackson et al. 2001; Pandolfi et al. 2003, 2005; Bellwood et al. 2004; Palumbi 2005). Evidence from throughout the Caribbean shows this not to be the case (Gardner et al. 2003, 2005; Lang 2003). For instance, acroporid corals died from WBD at the same rate both near and far from centers of fishing activity and other anthropogenic stressors (Aronson and Precht 2001a, b). Even the most remote, least fished areas of the Pacific have been affected by coral bleaching, resulting in mass coral mortality (Walther et al. 2002; Alling et al. 2006). Large-scale perturbations continue to cause significant coral decline in the world's largest and best-managed reef system, Australia's Great Barrier Reef (Bellwood et al. 2004; Pandolfi et al. 2005). No form of local stewardship, including large MPAs, could have prevented the large-scale disturbances responsible for the worldwide increase in coral mortality over the past few decades.

The cause-and-effect relationship between fishing and coral mortality is tenuous at best. The instances in which such connections have been clearly established are almost entirely limited to the Indo-Pacific and include: (1) blasting, *muro ami*, cyanide poisoning, and other destructive fishing techniques, in which corals are killed as part of the extraction process (McManus et al. 1997); and (2) a positive relationship in Fiji between fishing pressure and density of the corallivorous seastar *Acanthaster planci*, and, possibly as a cascading consequence, a negative relationship between fishing pressure and coral cover (Dulvy et al. 2004). Conversely, Jones et al. (2004) observed that declining fish abundance and diversity were direct consequences of catastrophic coral mortality in Papua New Guinea, again regardless of protection status.

Marine protected areas and coral recovery

There is no doubt that reef resources must be better managed, and we support efforts in that direction. Establishing new MPAs, enlarging the existing ones, and pursuing adaptive management and co-management strategies surely have positive impacts on species that are the targets of exploitation (Dayton et al. 2000; Mosquera et al. 2000; NRC 2001; Russ and Alcala 2003; Sobel and Dahlgren 2004; Granek and Brown 2005). Common sense and modeling results (Mumby 2006) suggest that using MPAs to increase herbivory by fish should have positive effects on corals and other living structural components (i.e., ecosystem impacts), but those effects have not been established empirically (Jameson et al. 2002; Graham et al. 2003; Sale et al. 2005). A further complication is that some species of parrotfish in the Caribbean eat corals as well as algae (Littler et al. 1989; Miller and Hay 1998; Rotjan and Lewis 2005). On a positive note, Mumby et al. (2006) showed that increased densities of herbivorous fish in a MPA in the Bahamas controlled macroalgal growth in the wake of widespread coral mortality from bleaching in 1998 (see also Williams and Polunin 2001). In the Florida Keys, however, Miller et al. (2003) found no difference in macroalgal abundance between no-take reserves and reference sites.

If the largest-scale sources of disturbance are not addressed, they will continue to kill remnant coral populations and suppress recruitment. Judging from recent observations of the extent of coral mortality from disease and bleaching, there is every reason to suspect that under such circumstances higher levels of herbivory will have little or no influence on coral recovery. The same can be said for hurricane damage: Mumby's (2006) modeling results predict that enhanced herbivory by parrotfish inside MPAs could promote coral recovery in subregions of the Caribbean with a low incidence of hurricanes, but not where hurricanes frequently damage the reefs. We know of only one case from St. Croix, US Virgin Islands in which the trophic control exerted by herbivorous fish not only suppressed macroalgal growth following an outbreak of WBD and subsequent hurricanes, but also promoted the recruitment and growth of corals (Bythell et al. 2000). Other recent studies in both the Caribbean and the Indo-Pacific have found that coral decline was not ameliorated, nor was recovery enhanced, in MPAs (McClanahan et al. 2001, 2005; Jones et al. 2004).

Sufficient densities of *Diadema* and another herbivorous echinoid, *Echinometra viridis*, can control macroalgal growth and promote coral recruitment and growth in the Caribbean on both small and large spatial scales (Sammarco 1982; Hughes et al. 1987; Aronson and Precht 1997, 2000). Whether or not *Diadema* populations in the Caribbean were artificially inflated by overfishing prior to the mass mortality is debatable (Hay 1984; Levitan 1992; Lessios et al. 2001; Precht and

Aronson 2006), but their ongoing recovery is having a positive impact on coral populations (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006). At very high densities, however, *Diadema* populations tend to overgraze reef substrata, to the detriment of coral populations (Bak and van Eys 1975; Sammarco 1980; Carpenter 1981). The analogous effect occurs in the western Indian Ocean, where overfishing increases echinoid populations, leading to complex ecosystem effects. These include lower algal cover, but also lower coral cover from overgrazing (McClanahan and Muthiga 1989; McClanahan et al. 1994, 1999; McClanahan and Shafir 1990).

Populations of *Acropora* spp. are now recovering at localities dispersed throughout the Caribbean (Precht and Aronson 2006). Increases in the abundance of acroporids bear no relation to protection status or fish abundance, and they could be related to the recovery of *Diadema*. *Acropora* spp. are even increasing dramatically on some reefs along the heavily fished north coast of Jamaica (Idjadi et al. 2006; Precht and Aronson 2006). A question of critical importance is whether the recovery of these coral populations will outpace future damage from hurricanes, bleaching events, and disease outbreaks.

Precaution, metaphor, and the politics of conservation

Managers are watching corals die for reasons having nothing to do with the abundance of fish; the location, size, or connectivity of MPAs; or the presence or absence of fishers. Should we play it safe, invoke the precautionary principle, and manage fisheries for reef resilience just in case it has some value in the end? For most conservation-minded people, a positive response to this question hinges on the metaphorical comparison of reef degradation to human illness (e.g., Palumbi 2005). There are two types of errors in medical testing: false positives and false negatives. A false positive is a case in which the test result indicates a disease that is not present. In a false negative, the disease is present but the test fails to detect it. A false positive can be very upsetting but a false negative is far more dangerous, and this latter aspect of the medical analogy has dictated attitudes toward the conservation and management of coral reefs.

In statistical testing, false positives (false alarms) correspond to type I statistical errors and false negatives (defective alarms) correspond to type II errors (e.g., Gonick and Smith 1993). Until recently, ecologists have been obsessed with avoiding type I error: falsely concluding that there is an effect when in fact there is none. Fear of type I error has led to ultraconservative testing, which has come at the cost of equally problematic type II error: falsely concluding that there is no effect when in fact there is one. The rationale for the precautionary principle is to avoid type II errors in conservation and management by easing the requirement of an excessively

low rate of type I errors; in other words, the burden of proof is shifted from those who would protect the environment onto those who would damage it (Buhl-Mortensen 1996; Dayton 1998). Cast in terms of coral reefs, some aspects of reef degradation and recovery may not be completely understood or fully detectable right now, but the risks to (metaphorical) reef health are potentially so severe that precaution is the only reasonable option.

In our view, reefs should not be construed as sick superorganisms, with overfishing as etiology and MPAs as therapy. Neither the metaphor of human illness nor the statistical rationale for the precautionary principle applies to the idea that maintaining abundant stocks of reef fish will necessarily promote coral recovery in the Caribbean. Without substantial sacrifice from the rest of the world on global environmental issues, MPAs will not fix the problem of globally declining coral populations.

Facile application of the precautionary principle is a rich man's game. As Cooney (2004) pointed out, "For precaution to contribute to, rather than conflict with, sustainable development, the burden of the precautionary principle must be borne by those most able to afford it." In the case of industrial-scale fishing operations, mandated precautionary actions are affordable and appropriate, but for the sake of subsistence fishers on Caribbean reefs, our goals must be compassion and accuracy rather than reflexive conservatism in either direction. In other words, we should not insist on unrealistically low error rates of either type (Dayton et al. 1995; Gray 1996; Holm and Harris 1999), and meta-analysis may be capable of providing the desired balance (Côté et al. 2005). From a practical standpoint, conserving populations of Caribbean reef fish and sustaining fisheries for the benefit of local people are worthy and attainable goals in their own right, so why complicate the issue with premature promises about coral recovery that promote fishing restrictions of questionable efficacy (see McClanahan 1999; Agardy et al. 2003; Hilborn 2004)?

A new agenda

Pandolfi et al. (2003) characterized coral mortality from disease and bleaching as distractions from the main effect, which they perceived to be overfishing. In a follow-up paper, Pandolfi et al. (2005) evidently reversed themselves and stated that all identified causes of degradation are important and should be addressed. They recommended, furthermore, that "...scientists should stop arguing about the relative importance of different causes of reef decline." Quite to the contrary, scientific debate and discussion are essential if we are to determine the most effective courses of action. We all know how limited the resources are that can be brought to bear on reef conservation, especially in developing countries. If we attempt to address all issues simultaneously, we

simply will not make progress rapidly enough to deflect the downward trajectory of coral reefs.

Attending to the most workable issues—herbivory and other local problems such as nutrient loading and pollution—could be salutary but in the long term may not be sufficient to reverse the decline of coral populations in the Caribbean. There is already an abundance of creative thought on more effective, ecosystem-based approaches (Allison et al. 2003; Roberts et al. 2003; Pikitch et al. 2004; Guerry 2005; Fernandes et al. 2005; McClanahan et al. 2006). One promising idea is to locate MPAs in areas where physical conditions are less conducive to bleaching and other physical damage (Done 1999; West and Salm 2003; but see Kim et al. 2005 on marine diseases). Managing for socio-ecological resilience (Adger et al. 2005) is also a step in the right direction. There is wisdom in integrated planning for environmental-economic-cultural disasters; however, only by addressing the root causes of those catastrophes at the highest levels of government and society will we be able to find lasting solutions (McClanahan et al. 2002; Ehrlich and Kennedy 2005).

The central agenda item of a new conservation ethic for all of us as coral reef scientists must be direct action on the global problems that now overshadow all local issues, transcending even the largest conceivable marine reserves. It goes without saying that the situation is considerably more dire than when Glynn (1991), Smith and Buddemeier (1992) and others sounded the alarm about global change and coral reefs. Knowing what we already know about climate change, it would be disingenuous to argue that such legislation is required on purely precautionary grounds; the type I error rate is already low for predicted and observed effects. Hopefully, even the most recalcitrant of developed nations can be convinced to help bear the costs of prevention, by taking such actions as adopting the Kyoto Protocol and then adhering to it.

At the same time, single-taxon management remains a powerful and relatively inexpensive approach to achieving certain goals of conservation (Power et al. 1996; Simberloff 1998; Hilborn 2004). Conserving and enhancing populations of *Diadema* in tandem with action on global change could be the most direct route to coral recovery, provided their densities are not elevated to the point that they graze juvenile corals. Echinoids appear to be more effective than fish at reducing macroalgae and enhancing coral recruitment in the Caribbean (Sammarco 1980, 1982; Carpenter 1986; Aronson and Precht 1997; Carpenter and Edmunds 2006), so they could be our best hope for increasing herbivory rapidly and effectively in an overfished world. An unresolved question is whether MPAs, by protecting the predators of *Diadema*, will diminish the resilience of coral assemblages (McClanahan et al. 2001). In the absence of *Diadema*, no-take restrictions on parrotfish populations, such as those currently in place in Florida and Bermuda, could limit macroalgal overgrowth and promote coral recovery on at least some Caribbean reefs (Mumby 2006).

We cannot lapse into paralytic nihilism and assume that global environmental issues—greenhouse-gas emissions in this case—and their ultimate cause, the human population (Birkeland 2004), are intractable problems. If predictions of escalating coral mortality from bleaching and related causes are realized, then local management in vacuo will amount to little more than a series of rear-guard actions, which will at best delay the demise of coral populations and the dissolution of reef ecosystems. Reversing the global-scale causes of coral mortality will be critical to saving coral reefs.

Acknowledgements We are grateful to N.D. Bood, G.F. Crozier, M.R. Dardeau, K.J.P. Deslarzes, K.L. Heck Jr., N.L. Hilbun, L.S. Kaufman, S.L. Miller, R.M. Moody, P.S. Petratis, C.S. Rogers, and J.F. Valentine for advice and discussion, and to S.R. Gittings for access to his unpublished data from the Flower Garden Banks. Comments from J.F. Bruno, T.R. McClanahan, T.J.T. Murdoch, R.T. Paine, M.L. Robbart, R. van Woeseik and an anonymous reviewer improved the manuscript. We thank R.M. Moody and R.P. Dunne for help in drafting Fig. 1. Financial support was provided by the Dauphin Island Sea Lab (DISL) and PBS&J. This is DISL Contribution 376.

References

- Adger N, Hughes TP, Folke C, Carpenter SR, Rockström J (2005) Social-ecological resilience to coastal disasters. *Science* 309:1036–1039
- Agardy T, Bridgewater P, Crosby MP, Day J, Dayton PK, Kenchington R, Laffoley D, McConney P, Murray PA, Parks JE, Peau L (2003) Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquat Conserv* 13:353–367
- Alling A, Doherty O, Logan H, Feldman L, Dustan P (2006) Catastrophic coral mortality in the remote Central Pacific Ocean: Kiribati, Phoenix Islands. *Atoll Res Bull* (in press)
- Allison GW, Gaines SD, Lubchenco J, Possingham HP (2003) Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecol Appl* 13:S8–S24
- Aronson RB, Precht WF (1995) Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. *J Exp Mar Biol Ecol* 192:1–14
- Aronson RB, Precht WF (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23:326–346
- Aronson RB, Precht WF (2000) Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Limnol Oceanogr* 45:251–255
- Aronson RB, Precht WF (2001a) Evolutionary paleoecology of Caribbean coral reefs. In: Allmon WD, Bottjer DJ (eds) *Evolutionary paleoecology: the ecological context of macro-evolutionary change*. Columbia University Press, New York, pp 171–233
- Aronson RB, Precht WF (2001b) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38
- Aronson RB, Edmunds PJ, Precht WF, Swanson DW, Levitan DR (1994) Large-scale, long-term monitoring of Caribbean coral reefs: simple, quick, inexpensive techniques. *Atoll Res Bull* 42:1–19
- Aronson RB, Precht WF, Murdoch TJJ, Robbart ML (2005) Long-term persistence of coral assemblages on the Flower Garden Banks, northwestern Gulf of Mexico: implications for science and management. *Gulf Mex Sci* 23:84–94
- Bak RPM, van Eys G (1975) Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia* 20:111–115
- Bascompte J, Melián CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. *Proc Natl Acad Sci USA* 102:5443–5447
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Birkeland C (2004) Ratcheting down the coral reefs. *BioScience* 54:1021–1027
- Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. *Ecol Lett* 6:1056–1061
- Buhl-Mortensen L (1996) Type-II statistical errors in environmental science and the precautionary principle. *Mar Pollut Bull* 32:528–531
- Burke CD, McHenry TM, Bischoff WD, Huttig ES, Yang W, Thorndyke L (2004) Coral mortality, recovery and reef degradation at Mexico Rocks Patch Reef Complex, Northern Belize, Central America: 1995–1997. *Hydrobiologia* 530/531:481–487
- Bythell JC, Hillis-Starr Z, Rogers CS (2000) Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Mar Ecol Prog Ser* 204:93–100
- Carpenter RC (1981) Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *J Mar Res* 39:749–765
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56:345–363
- Carpenter RC, Edmunds PJ (2006) Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. *Ecol Lett* 9:271–280
- Cooney R (2004) The precautionary principle in biodiversity conservation and natural resource management: an issues paper for policy-makers, researchers and practitioners. IUCN, Gland
- Côté IM, Gill JA, Gardner TA, Watkinson AR (2005) Measuring coral reef decline through meta-analyses. *Philos Trans R Soc Lond B* 360:385–395
- Dayton PK (1998) Reversal of the burden of proof in fisheries management. *Science* 279:821–822
- Dayton PK, Thrush SF, Agardy MT, Hofman RJ (1995) Environmental effects of marine fishing. *Aquat Conserv* 5:205–232
- Dayton PK, Sala E, Tegner MJ, Thrush S (2000) Marine reserves: parks, baselines, and fishery management. *Bull Mar Sci* 66:617–634
- de Ruyter van Steveninck ED, Bak RPM (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*. *Mar Ecol Prog Ser* 34:87–94
- de Ruyter van Steveninck ED, van Mulekom LL, Breeman AM (1988) Growth inhibition of *Lobophora variegata* (Lamouroux) Womersley by scleractinian corals. *J Exp Mar Biol Ecol* 115:169–178
- Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *Am Zool* 39:66–79
- Dulvy NKD, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol Lett* 7:410–416
- Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc Natl Acad Sci USA* 98:5067–5071
- Ehrlich PR, Kennedy D (2005) Millennium assessment of human behavior. *Science* 309:562–563
- Elnor RW, Vadas RL Sr (1990) Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. *Am Nat* 136:108–125
- Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436:686–688
- Fernandes L, Day J, Lewis A, Slegers G, Kerrigan B, Breen D, Cameron D, Jago B, Hall J, Lowe D, Innes J, Tanzer J, Chadwick V, Thompson L, Gorman K, Simmons M, Barnett B, Sampson K, De'Ath G, Mapstone B, Marsh H, Possingham H, Ball I, Ward T, Dobbs K, Aumend J, Slater D, Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. *Conserv Biol* 19:1733–1744

- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology* 86:174–184
- Gibson J, McField M, Heyman W, Wells S, Carter J, Sedberry G (2004) Belize's evolving system of marine reserves. In: Sobel J, Dahlgren C (eds) *Marine reserves: a guide to science, design, and use*. Island Press, Washington, DC, pp 287–315
- Gittings SR (1998) Reef community stability on the Flower Garden Banks, northwest Gulf of Mexico. *Gulf Mex Sci* 16:161–169
- Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol Evol* 6:175–179
- Gonick L, Smith W (1993) *The cartoon guide to statistics*. HarperCollins, New York
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30:200–208
- Granek E, Brown MA (2005) Co-management approach to marine conservation in Mohéli, Comoros Islands. *Conserv Biol* 19:1724–1732
- Gray JS (1996) Environmental science and a precautionary approach revisited. *Mar Pollut Bull* 32:532–534
- Guerry AD (2005) Icarus and Daedalus: conceptual and tactical lessons for marine ecosystem-based management. *Front Ecol Environ* 3:202–211
- Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, Ostfeld RS, Samuel MD (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158–2162
- Hawkins JP, Roberts CM (2003) Effects of fishing on sex-changing Caribbean parrotfishes. *Biol Conserv* 115:213–226
- Hay ME (1984) Patterns of fish and urchin grazing on coral reefs: are previous results typical? *Ecology* 65:446–454
- Hilborn R (2004) Ecosystem-based fisheries management: the carrot or the stick? *Mar Ecol Prog Ser* 274:275–278
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O (2006) Complexities of coral reef recovery. *Science* 311:42–43
- Holling CS, Allen CR (2002) Adaptive inference for distinguishing credible from incredible patterns in nature. *Ecosystems* 5:319–328
- Holm S, Harris J (1999) Precautionary principle stifles discovery. *Nature* 400:398
- Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. *Ecology* 70:275–279
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81:2250–2263
- Hughes TP, Reed DC, Boyle M-J (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *J Exp Mar Biol Ecol* 113:39–59
- Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol Evol* 20:380–386
- Idjadi JA, Lee SC, Bruno JF, Precht WF, Allen-Requa L, Edmunds PJ (2006) Rapid phase-shift reversal on a Jamaican coral reef. *Coral Reefs* 25:209–211
- Jackson JBC (2001) What was natural in the coastal oceans? *Proc Natl Acad Sci USA* 98:5411–5418
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jameson SC, Tupper MH, Ridley JM (2002) The three screen doors: can marine “protected” areas be effective. *Mar Pollut Bull* 44:1177–1183
- Jompa J, McCook LJ (2002) The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnol Oceanogr* 47:527–534
- Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Kim K, Dobson AP, Gulland FMD, Harvell CD (2005) Diseases and the conservation of marine biodiversity. In: Norse EA, Soule ME (eds) *Marine conservation biology: the science of maintaining the sea's biodiversity*. Island Press, Washington, DC, pp 149–166
- Kleypas JA, Buddemeier RW, Archer D, Gattuso J-P, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284:118–120
- Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. *Am Zool* 32:674–682
- Lang JC (ed) (2003) *Status of coral reefs in the western Atlantic: results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRRA) program*. *Atoll Res Bull* 496:1–630
- Lessios HA, Garrido MJ, Kessing BD (2001) Demographic history of *Diadema antillarum*, a keystone herbivore on Caribbean reefs. *Proc R Soc Lond B Biol Sci* 268:2347–2353
- Levitan DR (1992) Community structure in times past: influence of human fishing pressure on algal-urchin interactions. *Ecology* 73:1597–1605
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56:183–200
- Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. *J Exp Mar Biol Ecol* 87:215–228
- Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392–399
- Littler MM, Littler DS (1985) Factors controlling relative dominance of primary producers on biotic reefs. *Proc 5th Int Coral Reef Cong* 4:35–39
- Littler MM, Taylor PR, Littler DS, Sims RH, Norris JN (1987) Dominant macrophyte standing stocks, productivity and community structure on a Belizean barrier reef. *Atoll Res Bull* 302:1–24
- Littler MM, Taylor PR, Littler DS (1989) Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80:331–340
- McClanahan TR (1999) Is there a future for coral reef parks in poor tropical countries? *Coral Reefs* 18:321–325
- McClanahan TR, Muthiga NA (1989) Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *J Exp Mar Biol Ecol* 126:77–94
- McClanahan TR, Muthiga NA (1998) An ecological shift in a remote coral atoll of Belize over 25 years. *Environ Conserv* 25:122–130
- McClanahan TR, Shafir SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83:362–370
- McClanahan TR, Nugues M, Mwachireya S (1994) Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *J Exp Mar Biol Ecol* 184:237–254
- McClanahan TR, Muthiga NA, Kamukuru AT, Machano H, Kiambo RW (1999) The effects of marine parks and fishing on coral reefs of Northern Tanzania. *Biol Conserv* 89:161–182
- McClanahan TR, McField M, Huitric M, Bergman K, Sala E, Nyström M, Nordemar I, Elfving T, Muthiga NA (2001) Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* 19:367–379
- McClanahan TR, Polunin NVC, Done TJ (2002) Resilience of coral reefs. In: Gunderson LH, Pritchard L Jr (eds) *Resilience and the behavior of large-scale systems*. SCOPE Series, vol 60, Island Press, Washington, DC, pp 111–163
- McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E (2005) Detriments to post-bleaching recovery of corals. *Coral Reefs* 24:230–246

- McClanahan TR, Verheij E, Maina J (2006) Comparing the management effectiveness of a marine park and a multiple-use collaborative fisheries management area in East Africa. *Aquat Conserv* 16:147–165
- McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417
- McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Prog Oceanogr* 60:263–279
- McManus JW, Reyes RB Jr, Nanola CL Jr (1997) Effects of some destructive fishing methods on coral cover and potential rates of recovery. *Environ Manage* 21:69–78
- McWilliams JP, Côté IM, Gill JA, Sutherland WJ, Watkinson AR (2005) Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology* 86:2055–2060
- Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecol Appl* 14:1709–1723
- Miller MW, Hay ME (1998) Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* 113:231–238
- Miller MW, Aronson RB, Murdoch TJT (2003) Monitoring coral reef macroalgae: different pictures from different methods. *Bull Mar Sci* 72:199–206
- Mosquera I, Côté IM, Jennings S, Reynolds JD (2000) Conservation benefits of marine reserves for fish populations. *Anim Conserv* 4:321–332
- Mumby P (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol Appl* 16:747–769
- Mumby PJ, Foster NL, Glynn Fahy EA (2005) Patch dynamics of coral reef macroalgae under chronic and acute disturbance. *Coral Reefs* 24:681–692
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffer RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- NRC (2001) Marine protected areas: tools for sustaining ocean ecosystems. National Research Council, National Academy Press, Washington, DC
- Nugues MM, Delvoye L, Bak RPM (2004a) Coral defense against macroalgae: differential effects of mesenterial filaments on the green alga *Halimeda opuntia*. *Mar Ecol Prog Ser* 278:103–114
- Nugues MM, Smith GW, van Hooijdonk RJ, Seabra MI, Bak RPM (2004b) Algal contact as a trigger for coral disease. *Ecol Lett* 7:919–923
- Nyström M, Folke C (2001) Spatial resilience of coral reefs. *Ecosystems* 4:406–417
- Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP (2000) Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. *Proc Natl Acad Sci USA* 97:5297–5302
- Palumbi SR (2005) Germ theory for ailing corals. *Nature* 434:713–714
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) Are U.S. coral reefs on the slippery slope to slime? *Science* 307:1725–1726
- Pattengill-Semmens CV, Gittings SR (2003) A rapid assessment of the Flower Garden Banks National Marine Sanctuary (stony corals, algae and fishes). *Atoll Res Bull* 496:500–510
- Petratis PS, Dudgeon SR (2004) Detection of alternative states in marine communities. *J Exp Mar Biol Ecol* 300:343–371
- Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ (2004) Ecosystem-based fishery management. *Science* 305:346–347
- Pittock AB (1999) Coral reefs and environmental change: adaptation to what? *Am Zool* 39:10–29
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *BioScience* 46:609–620
- Precht WF, Aronson RB (2004) Climate flickers and range shifts of reef corals. *Front Ecol Environ* 2:307–314
- Precht WF, Aronson RB (2006) Death and resurrection of Caribbean reefs: a palaeoecological perspective. In: Côté I, Reynolds J (eds) *Coral reef conservation*. Cambridge University Press, Cambridge, pp 40–77
- Quinn JF, Dunham AE (1983) On hypothesis testing in ecology and evolution. *Am Nat* 122:602–617
- Roberts CM, Andelman S, Branch G, Bustamante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KS, Leslie H, Lubchenco J, McArdle D, Possingham HP, Ruckelshaus M, Warner RR (2003) Ecological criteria for evaluating candidate sites for marine reserves. *Ecol Appl* 13:S199–S214
- Robertson DR, Choat JH, Posada JM, Pitt J, Ackerman JL (2005) Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance? *Mar Ecol Prog Ser* 295:245–256
- Rosenberg E, Ben-Haim Y (2002) Microbial diseases of corals and global warming. *Environ Microbiol* 4:318–326
- Rotjan RD, Lewis SM (2005) Selective predation by parrotfishes on the reef coral *Porites astreoides*. *Mar Ecol Prog Ser* 305:193–201
- Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983–2000. *Ecol Appl* 13:1553–1565
- Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol* 20:74–80
- Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J Exp Mar Biol Ecol* 45:245–272
- Sammarco PW (1982) Echinoid grazing as a structuring force in coral communities: whole-reef manipulations. *J Exp Mar Biol Ecol* 61:31–55
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596
- Simberloff D (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol Conserv* 83:247–257
- Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. *Annu Rev Ecol Syst* 23:89–118
- Sobel J, Dahlgren C (eds) (2004) *Marine reserves: a guide to science, design, and use*. Island Press, Washington, DC
- Stoddart DR (1963) Effects of Hurricane Hattie on the British Honduras reefs and cays, October 30–31, 1961. *Atoll Res Bull* 95:1–142
- Stoddart DR (1965) Re-survey of hurricane effects on the British Honduras reefs and cays. *Nature* 207:589–592
- Stoddart DR (1969) Post-hurricane changes on the British Honduras reefs and cays: re-survey of 1965. *Atoll Res Bull* 131:1–25
- Stoddart DR (1974) Post-hurricane changes on the British Honduras reefs: re-survey of 1972. *Proc 2nd Int Coral Reef Symp* 2:473–483
- Sutherland KP, Porter JW, Torres C (2004) Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. *Mar Ecol Prog Ser* 266:273–302
- Umar MJ, McCook LJ, Price IR (1998) Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. *Coral Reefs* 17:169–177
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395

- Webster PJ, Holland GJ, Curry JA, Chang H-R (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309:1844–1846
- West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv Biol* 17:956–967
- Wilkinson C (ed) (2000) Status of coral reefs of the world: 2000. Australian Institute of Marine Science, Cape Ferguson and Dampier
- Wilkinson C (ed) (2004) Status of coral reefs of the world: 2004. (vols 1 and 2). Australian Institute of Marine Science, Cape Ferguson and Dampier
- Williams ID, Polunin NVC (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19:358–366
- Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Mar Ecol Prog Ser* 222:187–196