Confronting the coral reef crisis

D. R. Bellwood[1], T. P. Hughes[1,2], C. Folke[3,4] & M. Nyström[3]

[1]Centre for Coral Reef Biodiversity, Dept. of Marine Biology, James Cook University, Townsville, Queensland 4811, Australia
[2]Ecole Pratique des Hautes Etudes, UMR CNRS 8046, Universite de Perpignan, 66860 Perpignan Cedex, France
[3]Department of Systems Ecology, Stockholm University, SE-106 91 Stockholm, Sweden
[4]Beijer International Institute of Ecological Economics, Royal Swedish Academy of Sciences, Stockholm, Sweden

The worldwide decline of coral reefs calls for an urgent reassessment of current management practices. Confronting large-scale crises requires a major scaling-up of management efforts based on an improved understanding of the ecological processes that underlie reef resilience. Managing for improved resilience, incorporating the role of human activity in shaping ecosystems, provides a basis for coping with uncertainty, future changes and ecological surprises. Here we review the ecological roles of critical functional groups (for both corals and reef fishes) that are fundamental to understanding resilience and avoiding phase shifts from coral dominance to less desirable, degraded ecosystems. We identify striking biogeographic differences in the species richness and composition of functional groups, which highlight the vulnerability of Caribbean reef ecosystems. These findings have profound implications for restoration of degraded reefs, management of fisheries, and the focus on marine protected areas and biodiversity hotspots as priorities for conservation.

The overall goal of coral reef management is to sustain the ability of tropical reefs to provide the ecosystem goods and services (for example, fisheries, tourism, aesthetic and cultural values), upon which human welfare depends[1]. Although there have been some local successes, current management of reefs has failed to achieve this goal at a regional or global scale. Instead, coral reefs worldwide are in serious decline, owing primarily to over-harvesting[2,3], pollution[4,5], disease[6] and climate change[7–9]. Even the Great Barrier Reef, widely regarded as one of the most 'pristine' coral reefs in the world, shows system-wide decline (Fig. 1). In many locations around the world, man-made stresses to coral reefs have exceeded their regenerative capacity, causing dramatic shifts in species composition and resulting in severe economic loss.

In a changing world, one must expect and learn to manage uncertainty[10]. In this review, we argue that the acceleration of human impacts on reef ecosystems requires a radical reassessment of the way these important marine resources are monitored and managed. We propose that the resilience of reef ecosystems—that is, their ability to absorb shocks, resist phase shifts and regenerate after natural and human-induced disturbances[11]—needs to be more directly assessed and actively managed. Achieving this outcome requires an improved understanding of the dynamics of coral reef ecosystems, of the processes that support or undermine resilience, and of the socio-economic drivers and governance systems that regulate water quality and rates of extraction of reef resources. Here, we begin this reassessment by focusing on one important aspect of resilience, the role of critical functional groups[12,13]. In this context, we document profound temporal and geographic variation in the ability of coral reefs to cope with accelerating human impacts.

Loss of resilience

Coral reefs, by definition, are three-dimensional shallow-water structures dominated by scleractinian corals. In the absence of severe human impacts, reefs readily reassemble after routine disturbances such as tropical hurricanes[14]. However, many contemporary coral reefs increasingly fail to regenerate after natural and human impacts, and instead have undergone a rapid shift to an alternate state[15–18]. The most familiar of these transitions is from dominance by corals to dominance by fleshy seaweed, although several other transitions have been documented (Fig. 2). The extent to which alternate states are stable or reversible is poorly understood[19] and represents a major challenge for research and management of reefs.

Until now there has been little success in predicting such regime or phase shifts, because the increased instability of coral reef ecosystems before their collapse has often been unrecognized, even on reefs that are relatively well studied. This cryptic loss of coral reef resilience can be manifested in numerous ways. For example, the collapse of many Caribbean coral reefs was long preceded by dwindling stocks of fishes and increased nutrient and sediment runoff from land[2,16]. By the 1950s, when modern studies of reef ecology began, the prevention of macroalgal blooms was increasingly due to a single species of sea urchin, *Diadema antillarum*. In the 1970s, recorded densities of *Diadema* on overfished reefs were extraordinarily high, averaging more than ten individuals per square metre in shallow waters[20–23]. The magnitude and crowded conditions of *Diadema* populations[24] may have contrib-
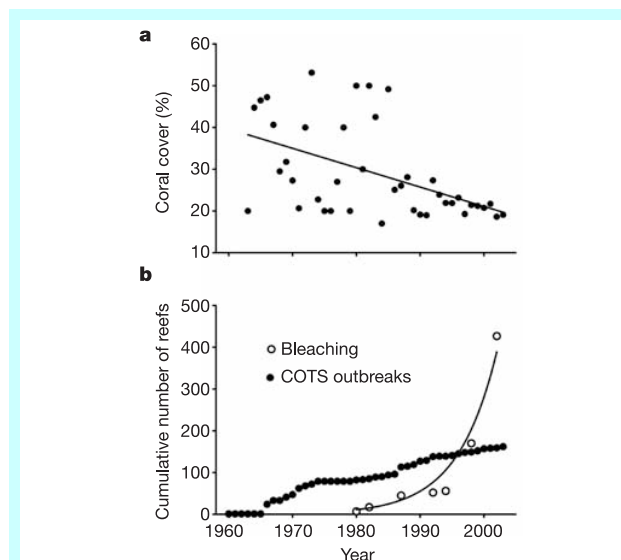
Figure 1 Degradation of coral reefs. a, Results of a meta-analysis of the literature, showing a decline in coral cover on the Great Barrier Reef. Each point represents the mean cover of up to 241 reefs sampled in each year. b, The recorded number of reefs on the Great Barrier Reef, Australia, substantially damaged over the past 40 yr by outbreaks of crown-of-thorns starfish (COTS) and episodes of coral bleaching.

uted to their eventual demise in 1983/4, when a disease outbreak spread throughout the Caribbean, reducing their numbers by two orders of magnitude[25] and precipitating macro-algal blooms that still persist. Today, remnant coral populations are further affected by increasingly prevalent coral disease and climatically induced coral bleaching[6,9].

With the benefit of hindsight, it is clear that long before the widespread loss of coral cover, many Caribbean reefs were on an unrecognized trajectory to collapse. The ecological symptoms included loss of macro-fauna[2,16], reduced fish stocks[26], a shift from fish-dominated to echinoid-dominated herbivory as the ecological role of herbivorous fishes was increasingly replaced by a single species of echinoid[22], destructive overgrazing and bioerosion by food-limited sea urchins[24,27], and reduced coral recruitment[21]. Yet, although all of these features were exceptionally well documented, nobody put the pieces together in time to forecast their eventual consequence. We need to do better at recognizing and responding to these warnings.

A similar sequence of events is occurring on the Great Barrier Reef, where terrestrial runoff, over-harvesting and climate change are changing the dynamics and stability of the region[2–5]. Inputs of sediment and nutrients from land have increased fourfold since European settlement[4,5], while the numbers of turtles, dugongs and other macrofauna have greatly decreased[28,29]. Modern management of the Great Barrier Reef began in 1975 with the establishment of the Great Barrier Reef Marine Park Authority, which protected 5% of the park from fishing. Comparisons of adjacent reefs open and closed to fishing today indicate that the biomass of targeted reef fishes has been reduced by up to 60%, causing substantial changes in the abundance of their prey[30]. Coral cover has significantly declined over the last 40 years (Fig. 1a), reflecting the impacts of three successive major outbreaks of crown-of-thorns starfish since the 1960s and two large-scale bleaching events in 1998 and 2000. In 2003, more than half the reefs sampled had 10% cover[31]. The low coral cover is likely to reflect marked demographic changes, reduced reproductive output of brood stocks, lower rates of recruitment, impaired connectivity, and species-level changes in coral composition (for example, in favour of short-lived, weedy taxa that re-colonize more quickly). All of these dynamic features contribute to increased instability, yet none of them has been systematically tracked.

A functional group approach to coral reef dynamics

There are striking and profoundly important regional differences in the species richness, functional composition, dynamics and resilience of reef systems (Fig. 3). For example, Caribbean reefs have only a fraction of the number of species found on the Great Barrier Reef, approximately 28% for fishes and 14% for corals. We define a functional group as a collection of species that perform a similar function, irrespective of their taxonomic affinities[12]. Although the Caribbean and Great Barrier Reef broadly share the same suite of functional groups, the species richness and taxonomic composition among functional groups is markedly different in the two regions. This difference is largely a biogeographic legacy of the evolutionary history of isolation and loss of taxa in the Caribbean basin[32,33]. The result is a functionally compromised assemblage that is more
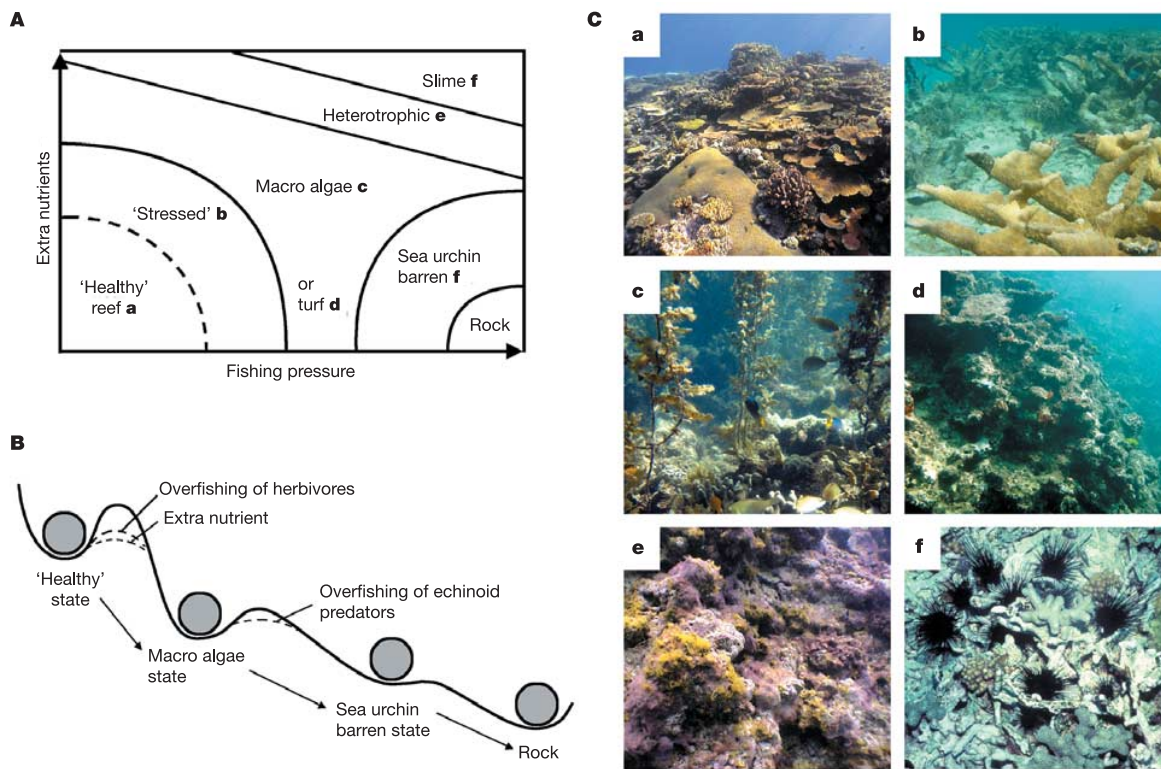

Figure 2 Alternate states in coral reef ecosystems. A, A conceptual model showing human-induced transitions between alternate ecosystem states based on empirical evidence of the effects from fishing and excess nutrients[15–17]. The 'stressed' state illustrates loss of resilience and increased vulnerability to phase-shifts. B, A graphic model depicting transitions between ecosystem states. 'Healthy' resilient coral-dominated reefs become progressively more vulnerable owing to fishing pressure, pollution, disease and coral bleaching. The dotted lines illustrate the loss of resilience that becomes evident when reefs fail to recover from disturbance and slide into less desirable states. C, Six characteristic reef states (as in A) from sites on the Great Barrier Reef (a, c, d, e) and in the Caribbean (b, f).

vulnerable to catastrophic phase shifts, particularly when subject to human exploitation and impacts.

Fish functional groups are generally synonymous with guilds of species from different trophic levels within a food chain (for example, predators and herbivores)[34], reflecting their role as a major conduit for the flow of energy on reefs. In this study, however, functional groupings are also identified by their roles in ecosystem processes. In contrast to fishes, the greatest contribution of corals is in the accumulation of carbonate and provision of structure. For corals, we can classify functional groups on the basis of the shape of their colonies, reflecting their role in reef processes. These include the creation of three-dimensional habitats for fishes and other organisms and their contribution to reef growth as either primary or secondary framework builders[34]. Corals, like fishes, often play multiple functional roles and thus support several different reef processes. These functional groups also have strikingly divergent ecologies and life histories, and exhibit marked differences in their susceptibility to hurricanes, sedimentation and other disturbances[35].

In the Caribbean, several critical functional groups are missing or represented by only a handful of species (Fig. 3). There are, for example, no three-dimensional bottlebrush species and just one staghorn (Acropora cervicornis) and one tall, tabular coral (Acropora palmata). Importantly, these are the dominant habitat-creating functional groups on healthy reefs in both the Indo-Pacific and Caribbean. Until recently, the two Caribbean species were abundant and widespread, commonly comprising more than 30–50% of the total coral cover down to a depth[36–38] of 20 m. Today, many areas have effectively lost not only these two species, but also two critical functional groups and two major shallow-water reef habitats: the

elkhorn 'palmata zone' and the staghorn 'cervicornis zone'[36]. Both species were added in 1999 to the Candidate Species List of the US Endangered Species Act[37], a sad reflection of our inability to implement regional-scale management of Caribbean reefs.

For fishes, the composition of functional groups on Caribbean reefs is also markedly different from that of the Great Barrier Reef (Fig. 3). Nocturnal and diurnal planktivores, in particular, are greatly under-represented in the Caribbean. For both fishes and corals, the Great Barrier Reef fauna has more species than the Caribbean in all functional groups (Fig. 3). This may confer a higher degree of functional redundancy within groups on the Great Barrier Reef, where the loss of any one species is potentially compensated for by the actions of another.

But does high species richness confer a degree of ecological insurance for ecosystem performance, as suggested by some small-scale experimental studies of biodiversity and ecosystem function[39]? The available evidence for coral reefs is equivocal. High diversity undoubtedly provides the potential for functional redundancy. However, even in high-diversity systems redundancy in critical functional groups can be limited[40]. Conversely, low diversity reefs at some isolated locations, such as Clipperton Atoll, survive with minimal representation in major functional groups[41].

Figure 4 Three critical functional groups and their roles in facilitating reef recovery. a, The jaws of a bioeroding parrotfish (Bolbometopon muricatum); each individual ingests five tonnes of coral annually. Scale 1 cm. b, An extensive stand of dead coral in Samoa, killed by coral bleaching, remains intact because of reduced bioerosion by depleted fish populations. c, A scraping herbivore, the parrotfish (Scarus flavipectoralis) removes epilithic algae and sediment. d, A juvenile coral overwhelmed by algae and trapped sediment. e, A grazing parrotfish (Sparisoma rubripinne) reduces overgrowth of corals by competing macroalgae. f, An adult coral shaded and overgrown by fleshy macro-algae.
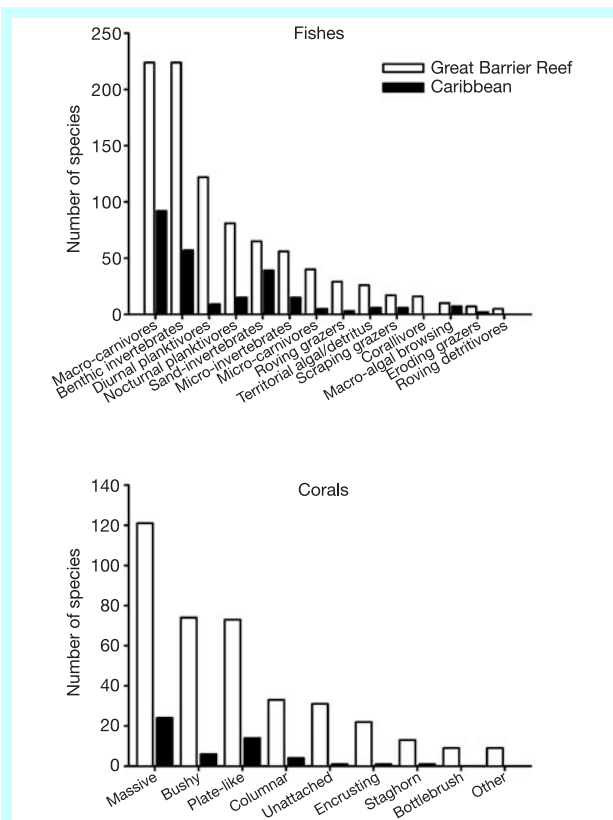

Figure 3 Functional composition of Caribbean and Great Barrier Reef assemblages of fishes and corals. The fourteen fish and eleven coral functional groups are identified by their roles in ecosystem processes.
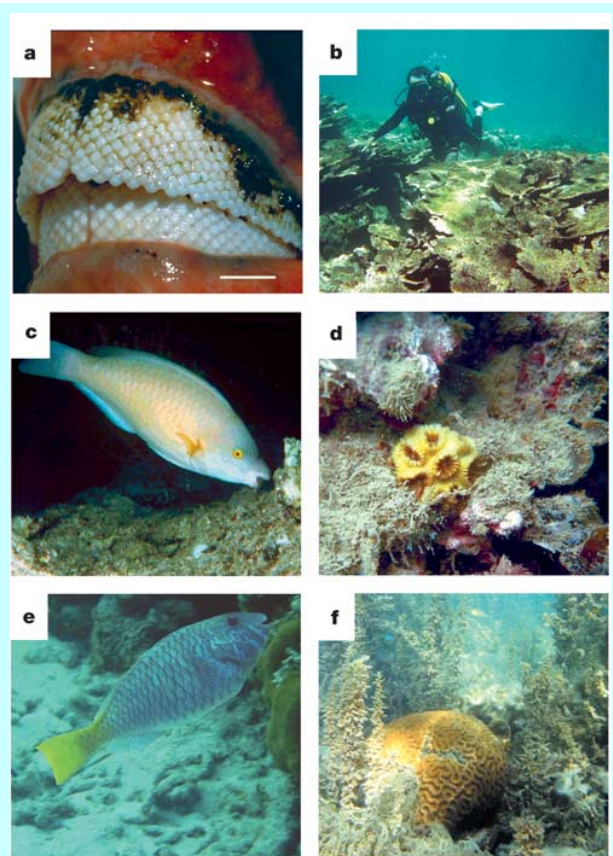
Nevertheless, the clearest examples available emphasize the impact of limited redundancy in relatively depauperate locations. For example, sea urchins became the principal herbivores on many Caribbean reefs following the depletion of fishes, and they prevented the rapid phase shift to dominance by macro-algae that was precipitated by the die-off of *Diadema*[16,17,23].

However, the changes to Caribbean reefs also demonstrate that the loss of functional redundancy can come at great cost, even when some members of a group compensate for others. Although fishes

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Box 1
Functional groups, fisheries and economic development

Overfishing is a major environmental and economic problem facing virtually all marine ecosystems[2,71]. Typically, overexploitation of a mixed reef fishery first depletes stocks of large predators (for example, sharks and groupers), and herbivorous fishes and planktivores subsequently become a more prevalent component of the total catch[26,71]. Consequently, it is increasingly difficult to evaluate the ecological effect of loss of predators because few places remain with relatively intact fish faunas to serve as experimental controls[72]. Nonetheless, comparisons of lightly and heavily fished sites provide evidence for top-down alterations to food webs after depletions of predators, on the Great Barrier Reef[30] and in Fiji[73]. These trophic cascades occur despite the potential functional redundancy of fish predators, which are represented by approximately 18 families and up to 200 species in a typical central Indo-Pacific reef system (Fig. 3). Importantly, in more species-impoverished bioregions, lower functional redundancy and response diversity may lead to substantially greater impacts from loss of predators. In parts of the Caribbean and Eastern Pacific, for example, depletion of fish predators of echinoids is likely to have played a key role in generating unsustainably high densities of sea urchins[22]. Similarly, the widespread declines of herbivorous and predatory turtles are likely to have increased the biomass of seagrasses and sponges[2].

Until recently, fishing on most coral reefs has been largely artisanal, providing a much-needed and cheap source of protein. Nevertheless, in many Pacific locations, traditional fishing has severely undermined major components of the bioeroding group and compromised ecosystem function[40]. Similarly, in Jamaica and elsewhere in the Caribbean, intense artisanal fishing focuses heavily on grazers[26]. In recent decades, however, there has been a dramatic increase in fishing effort on coral reefs, and export of both live and dead coral reef fishes is expanding rapidly. Parrotfishes from the Seychelles and Persian Gulf are now sold by fish retailers in London. The unprecedented demand for live reef fishes in China, Singapore and Taiwan is financed by the expanding disposable incomes of a large Asian hinterland, and exerts additional fishing pressure on reefs throughout vast areas of the Indo-Pacific[74,75]. With retail prices[76] of up to US$ 250 per kg, exploitation of remote reef systems has become financially viable for the first time, overcoming previous cost barriers. Herbivorous fishes are an increasingly significant component of the live fish trade, ranking currently as the second largest group targeted for exploitation (based on biomass) (Fig. 5). These new markets have greatly augmented both the intensity and scale of exploitation, and are set to increase as fish stocks elsewhere continue to decline[71]. The depletion of herbivorous fishes combined with increasingly frequent bleaching events is an ominous combination, but one faced by numerous reef systems around the globe[8].

The exploitation of reef fish, such as groupers and parrotfishes, clearly illustrates a mismatch between the global demand for reef fishes and the fundamental role of functional groups in ecosystem resilience. Phase-shifts of tropical reefs to less desirable states (Fig. 2) can have devastating economic effects on maritime developing nations[1]. Without healthy reef systems, future options for social and economic development will be constrained or lost.

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and echinoids both consume algae, and can substitute for each other in this role, echinoids are far more destructive bioeroders. Only a few species of parrotfish erode significant volumes of reef carbonate when feeding, and they feed primarily on dead corals and other protuberances, avoiding flat surfaces[33,42]. In marked contrast, grazing echinoids burrow into and erode the reef matrix[27]. In high densities they can undercut and dislodge massive corals. If unchecked, urchins have the capacity to destroy reefs, as documented in the Galapagos Islands and elsewhere in the East Pacific[43,44], where the reef structure has been eroded at rates of up to $10 \, \text{kg m}^{-2} \, \text{yr}^{-1}$.

Furthermore, resilience is critically dependent on the range of responses to environmental change by species within each functional group—that is, their response diversity[45]. Clearly, functional redundancy is ineffective if every species comprising a functional group always reacts to a disturbance in the same way and to the same extent. For example, the response of reef fishes to chronic overfishing leaves few species intact. In such cases, the insurance value of redundancy and of high species richness is negligible.

Resilience and functional groups

Three functional groups (conventionally combined as 'herbivores' and dominated by fishes), play different and complementary roles in preconditioning reefs to permit recovery of corals. These three groups—bioeroders, scrapers and grazers—are a critical source of both resilience and vulnerability to phase shifts. Bioeroding fishes remove dead corals[40,42], exposing the hard, reef matrix for settlement of coralline algae and corals. Scrapers directly remove algae and sediment by close cropping, facilitating settlement, growth and survival of coralline algae and corals[46,47]. Grazers remove seaweed, reducing coral overgrowth and shading by macro-algae[16,48] (Fig. 4).
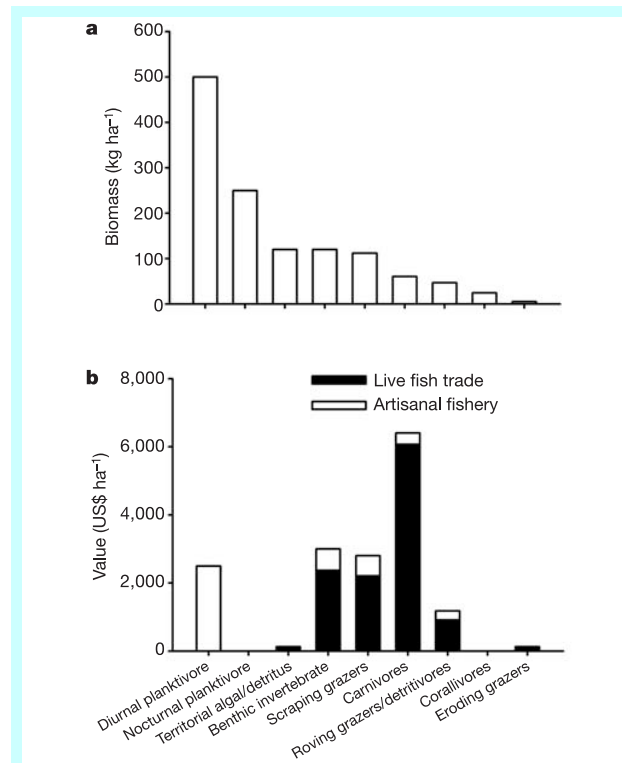

Figure 5 The mismatch between the economics of consumption and the ecological role of fishes on coral reefs. a, b, The biomass of functional groups of reef fishes in a central Indo-Pacific reef system (a), compared to the economic value of the fishes to an artisanal fishery or the international live fish trade (b).

The extent to which reefs possess these functional groups is central to their capacity to resist phase shifts, regenerate and retain critical functions in the face of disturbance.

A key element in resisting phase shifts to degraded alternate states is the maintenance of successful larval colonization by the full range of coral functional groups characteristic of the region. (Regrowth of residual corals can also be locally important, but they too must be replaced ultimately by new recruits). Degraded reefs exhibit declining rates of coral recruitment, through a poorly understood combination of reduced adult fecundities, lower settlement, and higher rates of early mortality (for example, due to smothering by algae and sediment)[46,49–51]. Reduced rates of fish bioerosion and increased mortality of corals have dramatically increased the prevalence of a relatively new phenomenon: large tracts of intact dead coral skeletons[7]. Coral settlement on such physically fragile or unstable foundations results in abbreviated recovery and a shift to weedy coral species. The scale of dispersal of coral larvae is also crucial to understanding coral reef reorganization after large-scale disturbances. The degree of connectivity and gene flow between local populations varies substantially among corals: some settle quickly and are largely self-seeded; others are more widely dispersed[52]. The isolation of oceanic reefs renders them particularly vulnerable to loss of local broodstocks[53]. On degraded reefs, the local loss of brood stocks is likely to select against self-seeding species and to shift the taxonomic composition of recruits in favour of those with longer planktonic durations, with potentially far-reaching consequences for community structure. Even if local conditions for settlement improve (for example, as a result of reduced overfishing, or a partial recovery of *Diadema antillarum*), it can no longer be assumed that coral recruitment will simply resume exactly as before.

Regenerative capacities need to be better understood and actively managed, so that human beings can become a more efficient and much less destructive component of coral reef ecosystems. If coral reefs are to resist phase shifts after disturbance it is imperative that critical functional groups of fishes, corals and other taxa are actively managed and sustained. Unfortunately, the critical groups that underpin the formation of three-dimensional coral growth and herbivory by fishes are increasingly threatened at precisely the time when the impacts of human disturbance to coral reefs make their functions as promoters of coral reef resilience all the more essential[8,11] (Box 1).

Shifting baselines and adaptive management

It is increasingly clear that the rapid decline of reef systems calls for a suite of more vigorous, innovative and adaptive management strategies. Responding to the global coral reef crisis requires active management of human activities that modify essential ecological processes. In particular, it requires an ability to scale up management and governance systems to secure the future of functional groups and their roles in supporting the resilience of coral reefs. There is a growing awareness of what has already been lost[2,3], and also a recognition that in a changing world, the resilience of coral reefs is increasingly uncertain[8].

Management of tropical fisheries, where it exists, has almost always been instigated long after exploitation has peaked, with the goal of sustainably harvesting whatever little remains. Typically, the stocks continue to decline even further, and over time management targets slip lower and lower, a scenario known as "the shifting baseline"[54]. Today, for example, a new generation of Caribbean researchers and managers may never have seen a decent stand of Caribbean *Acropora* coral, a manatee or a large shark, nor can they remember the destruction wrought in the 1970s by a million sea urchins per kilometre of coastline. Shifting baselines such as these pervade coral reef science and management[55]. Recent descriptions of purported recovery of degraded reefs in the Caribbean and Hawaii[51,56], and well-meaning efforts to culture and reintroduce *Diadema* dramatically illustrate the issue. Similarly, there is a

common tendency to attribute reef condition solely to more recent and better-studied impacts, underplaying the importance of historical disturbances[2,3,8]. Much has been lost, and some of it forever.

Management of functional groups represents a radical departure from current management philosophy. The fundamental difference is that management of functional groups recognizes that the cost of failure extends beyond the immediate impacts of depletion of overexploited fish stocks or reductions in coral cover. Thus, the management of herbivorous fishes can facilitate the regeneration of reefs after large-scale disturbances such as bouts of bleaching or disease that are impossible to regulate locally. Critically, a functional approach provides the basis for managing uncertainty by maintaining the functional groups that support dynamic ecological processes (for example, herbivory and provision of habitat), in contrast to the conventional goals of maintaining the status quo (high coral cover and sustainable fisheries yields).

Today, 'no-take' areas (NTAs), where fishing and other human activities are prohibited, are an increasingly prevalent approach to coral reef management[55,57,58]. If they are adequately enforced, NTAs provide a spatial refuge from harvesting. Importantly, such protection may also permit critical functional groups to persist, and thus contribute to local ecosystem resilience. However, even the largest NTAs in the world are not self-sustaining, because they are too small relative to the scale of natural and human disturbances, and to the dispersal distances of many larvae and migrating adults[59]. Currently, most NTAs are a few square kilometres or less in size, and they are invariably surrounded by vastly larger areas that are often already badly degraded. Although one of the main benefits of NTAs is the export of propagules and adults, on coral reefs the initial success of existing NTAs can often be attributed to an influx of larvae[57]. It is crucial, therefore, that NTAs are viewed more realistically in the context of the whole seascape. There is a distinct danger in overselling the benefits of establishing a few highly protected areas at specific locations, whose purported role is to remain or once more become "pristine"[60]. Indeed, as human impacts continue, recruitment from degrading reefs into NTAs is not only likely to decline but also may include a growing component of undesirable species (for example, algal spores, pathogens and introduced species). Ultimately, the long-term success of NTAs and the status of surrounding areas should be evaluated in terms of the processes and mechanisms that contribute to the resilience of reefs, not just estimates of abundance or counts of selected species. This caveat applies equally to another current issue for contemporary management of coral reefs—the focus on biodiversity hotspots.

Hotspots, areas of exceptional species richness[61], are one of the most frequently identified targets for the protection of marine ecosystems[62]. However, there are several lines of evidence to suggest that 'cool spots', areas of low species richness, are more vulnerable[63–65]. Low-diversity reefs, such as in the Caribbean Basin, the Eastern Pacific, and many high-latitude or remote locations in the Indo-Pacific have low functional redundancy, where functional groups may be represented by a single species. In these systems, as noted above, minor changes in biodiversity can have a major impact on ecosystem processes and consequently on the people whose livelihoods depend on the services that ecosystems generate.

A blueprint for the future

We conclude with four major recommendations for managing human activities in coral reef ecosystems. First, the rate of establishment and size of NTAs, as a tool for resilience management, needs to be hugely increased. In Australia, the expansion of NTAs in 2004 from , 5% to 33% of the Great Barrier Reef Marine Park, with a parallel focus on improving water quality, provides a good model[66]. In the United States, in comparison, there are more modest plans[67] to increase NTAs to incorporate 20% of reefs by 2010, a clear case of too little, too late. Currently, these two affluent nations are responsible for over two-thirds of the world's coral reef Protected Areas[68].

Elsewhere, developing countries are faced with a serious lack of resources, which limits the number, size and efficacy of NTAs and increases the likelihood of 'paper parks'. International efforts in support of marine parks for promoting resilience need to be substantially expanded. Second, the focus on NTAs and hotspots must not be allowed to detract from the provision of improved management measures for the vast majority of reefs that are heavily affected by people[69]. Unless we can achieve regional-scale active management of critical functional groups to support reef resilience, any small-scale successes within NTAs or by individual countries may be unable to stem the decline of reef systems as a whole. Third, reef management needs to be more inclusive, proactive and responsive. Governance systems should support ownership and empowerment of users as stewards of reef resilience, provide incentives for herbivore protection before—not after—stocks collapse, and implement flexible restrictions (for example, to enhance the protection of critical broodstocks during the vulnerable spawning period). Fourth, markets for reef resources must be reformed to incorporate economic incentives that prevent exploitation of species in critical functional groups (Box 1). Such action is unlikely to emerge from uninformed human preferences. Markets for reef resources urgently need to be framed by norms and rules (institutions), operating from local to global scales, that secure coral reef resilience and thereby promote a greater diversity of options for economic development[70].

Developing new metrics for stewardship of coral reef resilience is vital for coping with uncertainty and surprise in a biosphere increasingly shaped by human action. In this context the focus, both within and outside NTAs, should shift from conservation of species to active management of critical functional groups that support important processes and sustain ecosystem services. Current aspirations towards sustaining fisheries need to fundamentally change their metrics from stock assessments to capturing the ecosystem performance and resilience that support long-term fisheries production[71]. Ecosystem metrics for monitoring the status of coral reefs need to move beyond coral cover and counts of targeted species to include functional groups, functional redundancy and response diversity. In all of these endeavours, we are faced with a critical lack of knowledge. Our ability to continue to exploit coral reef resources will depend on an effective combination of science-based management, public support and political will. Clearly, successful management of coral reef ecosystems will also require courage, creativity and a willingness to move beyond traditional metrics, models and perceptions. A

1. Moberg, F. & Folke, C. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233 (1999).
2. Jackson, J. B. C. et al. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638 (2001).
3. Pandolfi, J. M. et al. Global trajectories of the long-term decline of coral reef ecosystems. Science 301, 955–958 (2003).
4. Williams, D., McB. et al. The Current Level of Scientific Understanding on Impacts of Terrestrial Run-Off on the Great Barrier Reef World Heritage Area. khttp://www.reef.crc.org.au/aboutreef/coastal/waterquality_consensus.htmll (2002).
5. McCulloch, M. et al. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421, 727–730 (2003).
6. Harvell, C. D. et al. Climate warming and disease risks for terrestrial and marine biota. Science 296, 2158–2162 (2002).
7. Wilkinson, C. (ed.) Status of Coral Reefs of the World (Australian Institute of Marine Science, Townsville, Australia, 2002).
8. Hughes, T. P. et al. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933 (2003).
9. Gardener, T. A., Cote, I., Gill, J. A., Grant, A. & Watkinson, A. R. Long-term region-wide declines in Caribbean corals. Science 301, 958–960 (2003).
10. Kinzig, A. P. et al. Coping with uncertainty: A call for a new science-policy forum. Ambio 32, 330–335 (2003).
11. Nyström, M., Folke, C. & Moberg, F. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol. Evol. 15, 413–417 (2000).
12. Steneck, R. S. & Dethier, M. N. A functional group approach to the structure of algal-dominated communities. Oikos 69, 476–498 (1994).
13. Walker, B. H. in Plant Functional Types (eds Smith, T. M., Shugart, H. H. & Woodward, F. I.) 91–103 (Cambridge Univ. Press, UK, 1997).
14. Connell, J. H., Hughes, T. P. & Wallace, C. C. A 30-years study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol. Monogr. 67, 461–488 (1997).
15. Done, T. J. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247, 121–132 (1992).
16. Hughes, T. P. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551 (1994).
17. Knowlton, N. Thresholds and multiple stable states in coral reef community dynamics. Am. Zool. 32, 674–682 (1992).
18. Scheffer, M. et al. Catastrophic shifts in ecosystems. Nature 413, 591–596 (2001).
19. Scheffer, M. & Carpenter, S. R. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18, 648–656 (2003).
20. Ogden, J. C., Brown, R. A. & Salesky, N. Grazing by the echinoid Diadema antillarum Philippi: Formation of halos around West Indian patch reefs. Science 182, 715–717 (1973).
21. Sammarco, P. W. Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. Exp. Mar. Biol. Ecol. 45, 245–272 (1980).
22. Hay, M. E. Patterns of fish and urchins grazing on Caribbean coral reefs: are previous results typical? Ecology 65, 446–454 (1984).
23. Lessios, H. A. Mass mortality of Diadema antillarum in the Caribbean: what have we learned? Annu. Rev. Ecol. Syst. 19, 371–393 (1988).
24. Levitan, D. R. Density-dependent size regulation and negative growth in the sea urchin Diadema antillarum Philippi. Oecologia 76, 627–629 (1988).
25. Lessios, H. A., Robertson, D. R. & Cubit, J. D. Spread of Diadema mass mortality through the Caribbean. Science 226, 335–337 (1984).
26. Munro, J. L. (ed.) Caribbean Coral Reef Fisheries 2nd edn, Vol. 7, 1–276 (ICLARM Stud. Rev., ICLARM, Makati, 1983).
27. Ogden, J. C. in Reefs and Related Carbonates—Ecology and Sedimentology (eds Frost, S. H., Weiss, M. P. & Saunders, J. B.) Stud. Geol. 4 281–288 (Am. Assoc. Petrol. Geol., USA, 1977).
28. Heppell, S. S. et al. Population model analysis for the loggerhead sea turtle, Caretta caretta, in Queensland. Wildl. Res. 23, 143–159 (1996).
29. Great Barrier Reef Marine Park Authority. Overview: the current status of the Great Barrier Reef. khttp://www.gbrmpa/corp_site/info_services/publications/sotr/downloads/SPRR_Overview2.pdfl (2003: cited December 2003).
30. Graham, N. A. J., Evans, R. D. & Russ, G. R. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environ. Conserv. 30, 200–208 (2003).
31. AIMS. Australian Institute of Marine Science. Reef Monitoring http://www.aims.gov.au/pages/research/reef-monitoring/reef-monitoring-index.html. (2003: cited December 2003)
32. Johnson, K. G., Budd, A. F. & Steemann, T. A. Extinction selectivity and ecology of Neogene Caribbean reef corals. Paleobiology 21, 52–73 (1995).
33. Bellwood, D. R. & Wainwright, P. C. in Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem (ed. Sale, P. F.) 5–32 (Academic, San Diego, 2002).
34. Done, T. J., Ogden, J. C., Wiebe, W. J. & Rosen, B. R. in Functional Roles of Biodiversity: a Global Perspective (eds Mooney, J. H., Cushman, E., Medina, E., Sala, O. E. & Schulze, E.-D.) 393–429 (John Wiley, Sons, New York, 1996).
35. Hughes, T. P. & Connell, J. H. Multiple stressors on coral reefs: A long-term perspective. Limnol. Oceanogr. 44, 932–940 (1999).
36. Goreau, T. F. The ecology of Jamaican coral reefs. 1. Species composition and zonation. Ecology 40, 67–89 (1959).
37. NOAA Fisheries. Candidate Corals: Acropora palmata (Elkhorn Coral) and Acropora cervicornis (Staghorn Coral) khttp://www.nmfs.noaa.gov/habitat/ecosystem/AcroporaWorkshop.html.
38. Aronson, R. B., McIntyre, I. G., Precht, W. F., Murdoch, T. J. T. & Wapnick, C. M. The expanding scale of species turnover events on coral reefs in Belize. Ecol. Monogr. 72, 233–249 (2002).
39. Loreau, M., Naeem, S. & Inchausti, P. (eds) Biodiversity and Ecosystem Functioning: Synthesis and Perspectives 1–306 (Oxford Univ. Press, Oxford, 2002).
40. Bellwood, D. R., Hoey, A. S. & Choat, J. H. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol. Lett. 6, 281–285 (2003).
41. Glynn, P. W. & Ault, J. S. A biogeographic analysis and review of the far eastern Pacific coral reef region. Coral Reefs 19, 1–23 (2000).
42. Bellwood, D. R. & Choat, J. H. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ. Biol. Fishes 28, 189–214 (1990).
43. Eakin, C. M. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific. Coral Reefs 15, 109–119 (1996).
44. Glynn, P. W. El Nino warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. Galaxea 7, 129–160 (1988).
45. Elmqvist, T. et al. Response diversity, ecosystem change and resilience. Front. Ecol. 1, 488–494 (2003).
46. Hunte, W. & Wittenberg, M. Effects of eutrophication and sedimentation on juvenile corals. II. Settlement. Mar. Biol. 114, 625–631 (1992).
47. Steneck, R. S., in 6th International Coral Reef Symposium (eds Choat, J. H. C. et al.) Vol. 1 37–49 (6th International Coral Reef Symposium Executive Committee, Townsville, 1988).
48. McCook, L. J., Jompa, J. & Diaz-Pulido, G. Competition between corals and algae on coral reefs: a review of available evidence and mechanisms. Coral Reefs 19, 400–417 (2001).
49. Richmond, R. H. Coral reefs: present problems and future concerns resulting from anthropogenic disturbances. Am. Zool. 33, 524–536 (1993).
50. Hughes, T. P. & Tanner, J. E. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81, 2250–2264 (2000).
51. Edmunds, P. J. & Carpenter, R. C. Recovery of Diadema antillarum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc. Natl Acad. Sci. USA 98, 5067–5073 (2001).
52. Ayre, D. J. & Hughes, T. P. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. Evolution 54, 1590–1605 (2000).
53. Ayre, D. J. & Hughes, T. P. Climate change, genotypic diversity and gene flow in reef-building corals. Ecol. Lett. 7, 273–278 (2004).
54. Pauly, D. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol. Evol. 10, 430 (1995).
55. Bohnsack, J. A. Shifting baselines, marine reserves, and Leopold's biotic ethic. Gulf Caribb. Res. 14, 1–7 (2003).
56. Scully, E. P. & Ostrander, G. K. Corals and phase shifts. Trends Ecol. Evol. 16, 126–127 (2001).

57. Russ, G. R. in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P. F.) 421–443 (Academic, San Diego, 2002).

58. Halpern, B. S. & Warner, R. R. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5, 361–366 (2002).

59. Nyström, M. & Folke, C. Spatial resilience of coral reefs. *Ecosystems* 4, 406–417 (2001).

60. Folke, C., Holling, C. S. & Perrings, C. Biological diversity, ecosystems, and the human scale. *Ecol. Appl.* 4, 1018–1024 (1996).

61. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. & Kent, J. Biodiversity hotspots and conservation priorities. *Nature* 403, 853–858 (2000).

62. Roberts, C. M. *et al.* Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295, 1280–1284 (2002).

63. Bellwood, D. R. & Hughes, T. P. Regional-scale assembly rules and biodiversity of coral reefs. *Science* 292, 1532–1534 (2001).

64. Hughes, T. P., Bellwood, D. R. & Connolly, S. R. Biodiversity hotspots, centers of endemicity, and the conservation of coral reefs. *Ecol. Lett.* 5, 775–784 (2002).

65. Kareiva, P. & Marvier, M. Conserving biodiversity coldspots. *Am. Sci.* 91, 344–351 (2003).

66. Great Barrier Reef Marine Park Authority Representative Areas Program ⟨http://www.reefed.edu.au/rap/pdf/rap_overview_brochure.pdf⟩ (2003).

67. USCRTF The National Action Plan to Conserve Coral Reefs ⟨http://coralreef.gov⟩ (US Coral Reef Task Force, Washington, DC, 25 December 2003).

68. Spalding, M. D., Ravilious, C. & Green, E. P. *World Atlas of Coral Reefs* (Univ. California Press, Berkeley, 2001).

69. Folke, C. *et al.* Regime shifts, resilience and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* (in the press).

70. Dietz, T., Ostrom, E. & Stern, P. C. The struggle to govern the commons. *Science* 302, 1907–1912 (2003).

71. Pauly, D. *et al.* Towards sustainability in world fisheries. *Nature* 418, 689–695 (2002).

72. Steneck, R. S. Human influences on coastal ecosystems: does overfishing create trophic cascades? *Trends Ecol. Evol.* 13, 429–430 (1998).

73. Jennings, S. & Polunin, N. V. C. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16, 71–82 (1997).

74. Birkeland, C. Symbiosis, fisheries and economic development on coral reefs. *Trends Ecol. Evol.* 12, 364–367 (1997).

75. Sadovy, Y. J. & Vincent, A. C. J. in *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P. F.) 391–420 (Academic, San Diego, 2002).

76. McGilvray, F. & Chan, T. T. C. The trade in live reef foodfish: a Hong Kong perspective. *Aquaculture Asia* 7, 21–26 (2002).

Correspondence and requests for materials should be addressed to D.R.B. (david.bellwood@jcu.edu.au).