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Coral reef management and conservation in light of rapidly evolving ecological paradigms

Peter J. Mumby[1] and Robert S. Steneck[2]

[1] Marine Spatial Ecology Lab, Hatherly Laboratory, University of Exeter, Prince of Wales Road, Exeter EX4 4PS, UK
[2] School of Marine Sciences, University of Maine, Darling Marine Center, 193 Clarks Cove Road, Walpole, ME 04573, USA

The decline of many coral reef ecosystems in recent decades surprised experienced managers and researchers. It shattered old paradigms that these diverse ecosystems are spatially uniform and temporally stable on the scale of millennia. We now see reefs as heterogeneous, fragile, globally stressed ecosystems structured by strong positive or negative feedback processes. We review the causes and consequences of reef decline and ask whether management practices are addressing the problem at appropriate scales. We conclude that both science and management are currently failing to address the comanagement of extractive activities and ecological processes that drive ecosystems (e.g. productivity and herbivory). Most reef conservation efforts are directed toward reserve implementation, but new approaches are needed to sustain ecosystem function in exploited areas.

The challenge for science and management

Coral reefs are among the most diverse and productive ecosystems on Earth. They are the world's largest biogenic structures and the only such structure visible from space. Coral reefs are also perhaps the most globally endangered of ecosystems.

With no shortage of unpreventable insults to coral reefs (Table 1) [1], agencies, managers and policymakers charged with protecting them need effective ways to minimise the decline and aid their recovery. Ultimately, such solutions must integrate social perspectives of people who depend on and use these ecosystems together with the biological aspects that drive coral reef ecosystems [2]. Without a better understanding of such drivers, it will be difficult to determine the best practices and goals for management, which usually aims to sustain fisheries production, maintain biodiversity and ensure conflict-free use of coastal resources [3]. However, managers have limited resources and a limited toolbox for interventions such as fisheries regulations, multiple-use zoning, protection of coastal habitat, reductions in sewage or agricultural run-off, and direct restorative activities (Table 1).

For management to move forward, it must assimilate the ever-growing body of scientifically relevant information, and adapt efforts toward the evolving best practices. We begin by briefly reviewing the trend of coral reef research over the past several decades, to illustrate how the paradigms have shifted and what these changes might mean for management. For space considerations, we only touch on the burgeoning topic of reef restoration (see Box 1).

Evolving paradigms and scientific approaches

No marine ecosystem has received more scientific attention than coral reefs over the past half-century. Although we have learned much about the ecological structure and functioning of reef ecosystems, we are often surprised by their response to stress and continue to struggle (largely without success) with ways to manage human impact on them.

During the late 1970s and early 1980s, armies of reef scientists developed 'worldviews' explaining how, apparently stable, coral reefs were structured and functioned. Endean [4] asserted that coral reefs had 'a particularly stable or predictable organisation because they are biologically accommodated.' The focus then was on documenting this stability by measuring patterns of distribution and abundance and on 'biologically accommodating' ecological processes such as competition and predation. For example, manipulative experiments identified herbivory as a key driver maintaining the then low algal abundance of the Caribbean [5]. New population dynamics models developed for clonal corals concluded that 'once [coral] colonies reached moderate size, the probability of their being killed falls almost to zero' [6]. Others concluded that the most unpredictable event in the lives of large coral might be so rare that they would include millennial-scale changes in sea level [7]. Mortality of large reef-building corals was thought to be confined to intense and localised, but infrequent, storms [6]. Ecological theory used the frequency and

Glossary

Acroporids: Collective name for species of coral in the genus *Acropora*.
Demersal: Describes the habitat of organisms living near the sea bed (reef).
Ecosystem services: The quantifiable services that an ecosystem provides to humans, including consumables and nonconsumables. Resource economists assign monetary values to these services to estimate the economic value of a healthy ecosystem.
Management: The planning and the responsible use of the coastal zone, generally overseen by government departments but increasingly involving partnerships with local communities and nongovernment organisations.
Multiple-use zoning: Segregation of human activities in the coastal zone through delineation of specific zones, each with their own restrictions.

Corresponding author: Mumby, P.J. (p.j.mumby@ex.ac.uk).

Table 1. Matching management problems on coral reefs to the available toolbox

Documented problem and cause	Expected consequences	Management tools	Refs
Global			
Ocean acidification (rising carbon dioxide concentration)	↑ Disease and fragility in calcifying organisms; ↓ growth rate of calcifying organisms; ↓ reduced coral-based services[a]	No direct, short-term solution (NS); facilitate coral recovery by managing herbivores and water quality (RECOVERY[b])[c]	[1]
Coral bleaching (global warming)	↑ Disease in calcifying organisms; ↓ reduced coral-based services[a]	NS; RECOVERY; place MRs in areas of low thermal stress[d]	[1]
Sea-level rise (global warming)	↑ Flooding; ↑ coastal erosion; ↓ freshwater; ↓ land area	NS; RECOVERY; sea defences[e]	[65]
Low fisheries yield (overfishing)	↑ Economic hardship for fishers; ↓ biodiversity and ecosystem function	↓ Fishing effort (EFFORT); MRs; ↓ loss of mangrove nursery habitats; ↑ alternative livelihoods; ↓ international export of reef fishes	[45]
Local			
Crown-of-thorns starfish outbreaks (agricultural runoff and/or fishing of predators)	↓ Reduced coral-based services[a]	Watershed management (WATER[b]); EFFORT	[15]
Algal blooms (fishing of herbivores, eutrophication)	↓ Reduced coral-based services[a]; ↓ public health	WATER; EFFORT; RECOVERY	[10]
Rising number and prevalence of diseases (high physiological stress; nutrient runoff[f])	↓ Reduced coral-based services[a]	NS; WATER; RECOVERY	[11]
Tropical cyclone damage[g] (warm oceans)	Areas of extensive coral mortality; reduced resilience of reefs locally	NS; RECOVERY	[12]
Invasive species (release of ballast; aquarium discharge)	Disease (e.g. loss of Caribbean *Diadema*); disrupt trophic pathways (e.g. novel predator *Pterois volitans* in Bahamas)	Enforce and implement controls to ballast water treatment	[9]

↑ and ↓ denote increasing and decreasing, respectively. Management tools are described once and given a code (in capitals) which is used thereafter. MR = marine reserves.
[a]Coral-based services include diversity and density of invertebrates and vertebrates (particularly small reef fishes), coastal defence from storms, reduced beach erosion, sediment production, fisheries production, aquarium-trade industry, diving and fishing tourism.
[b]RECOVERY includes reduce fishing effort (EFFORT) and watershed management of agrichemicals, sewage and sediment runoff (WATER).
[c]Much uncertainty about consequences and efficacy of tools in this context.
[d]Appropriate design of MRs unknown.
[e]Defences are expensive, and so are restricted to affluent areas.
[f]Causative agents and treatments are often unknown.
[g]Only a problem when combined with overfishing and poor watershed management.

intensity of such storms and resulted in the 'intermediate disturbance hypothesis' [8], which took hold because it compellingly integrated ecological processes of competition and disturbance with observed patterns of biodiversity. Arguably, much of the science at that time helped explain why highly diverse coral-dominated systems were so stable.

The 1980s marked a turning point in ecological paradigms for coral reefs because by then it was evident to even casual observers that these ecosystems were not stable. In 1983 and 1984, the dominant herbivore of most Caribbean reefs, the long-spined urchin *Diadema antillarum*, suffered a pathogen-induced mass mortality. Within a year, >90% of the population of this species had died and algal biomass increased rapidly throughout Caribbean reefs [9,10]. This 'phase-shift' [9] from coral to algal dominance was a complete surprise. No one had predicted or suggested that the

reefs of Jamaica or elsewhere in the Caribbean could change so radically due to the mortality of a single species. The early 1980s also heralded an initially less conspicuous, but possibly more damaging, disease that killed the dominant reef-building coral of the Caribbean. White-band disease of acroporid corals was slower to kill its hosts than the disease affecting *Diadema*, but within a decade it had spread throughout the Caribbean [11].

Ecosystem surprises such as these stimulated new research, but they also created new paradigms with new goals for managers. To better understand recent scientific trends, we used the search engine Google Scholar (www.scholar.google.com) with the keyword phrase 'coral reefs' to quantify trends in citations since 1970. We focused on the most influential papers (i.e. those cited ≥100 times). There were 41 such papers garnering 7695 citations. Whereas the majority of the important papers during

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Box 1. Active reef restoration: Great Expectations or Field of Dreams?

When a forest is lost to fire or clear cutting, we often take action to restore it by replanting trees. Similar principles have been applied to coral reefs that have experienced acute local disturbance such as ship groundings. At small scales, it is possible to collect scattered coral fragments and either fix them directly to the reef (or concrete structures) or use laboratory culture to generate hundreds of clones for use in replanting. From an ecological standpoint, we raise two issues concerning reef restoration.

Scale

To date, the largest active restoration project treated an area of 0.07 km², which is six orders of magnitude less than the estimated global area of damaged coral [72]. However, new low-technology propagation and culturing methods are improving the cost-effectiveness of the approach, such that thousands of individual fragments can be reared at a cost of around $1 each [72]. Although it remains unlikely that active restoration will become a feasible means of restoring vast areas of damaged reef, local interventions might at least become cost-effective in the future.

Treating the symptoms versus the causes of an unhealthy reef

A reef is considered unhealthy if it lacks the resilience needed for natural processes of recovery. The cause of poor health often involves a combination of overharvesting of herbivores, low coral cover, high macroalgal cover, high sedimentation, and eutrophication. The system can be so hostile to coral that the transplants die rapidly or, at best, opportunities for the restoration activity to encourage natural processes of recovery might be limited. Thus, active restoration should occur once the causes of ill health have been treated (e.g. reduce eutrophication, allow recovery of herbivores). Further, restoration is unlikely to be cost-effective in a resilient system that has high recruitment potential (i.e. plenty of coralline algal nursery habitats and three-dimensional refugia for recruiting corals) because natural processes of recovery should suffice.

As Edwards points out [72], active restoration has the greatest potential to stimulate recovery in systems of intermediate health. Ecological theory can help design such interventions. Given the inverse dependence of grazing intensity on the area of grazable substrate, it would be appropriate to deploy corals in smaller patches of high cover, rather than dispersing corals more widely but at lower cover. The high-coral-cover approach can increase grazing levels around the coral patches sufficiently to help facilitate natural processes of recruitment, with the expectation that natural processes of recovery would extend outward from each coral patch. The low-coral-cover approach might cover a wider area to begin with but might fail to bolster natural coral recruitment because grazing intensity was not sufficiently enhanced.

the 1970s (i.e. 58%) focused on patterns of diversity and habitat use, most citations in the 1980s and 1990s focused on explanatory processes such as reproduction, recruitment, herbivory and predation. Disturbances of reef ecosystems (primarily due to disease and bleaching but also overfishing) became the hot new topics of the 1990s, garnering 35% of the citations in that decade. Since 2000, 85% of citations have focused on those disturbances, but with overfishing now leading the list. Publications on disease and management have also been steadily increasing. Clearly the scientific focus has shifted from small-scale, curiosity-driven basic research of a presumed stable system to larger-scale (even global) threats to coral reef ecosystems and how best to manage them.

We review this new scientific focus and what it might mean for future management of coral reefs. We divide the paper into three sections: (i) processes occurring on reefs

that are the cause or consequence of declining coral cover; (ii) drivers of recovery following a disturbance; and (iii) management and conservation consequences of reef degradation and no-take reserves. Our hope is that understanding of driving processes should guide policymakers toward the best management approaches.

Coral decline: causes and consequences

Causes of coral decline

Living coral plays a pivotal role in the structure and functioning of coral reef ecosystems [12]. Globally, average coral cover has been declining at an alarming rate over the past several decades. Meta-analyses, which combine the results of several independent studies to increase the statistical power, from the Caribbean [13] and Indo-Pacific [14] report declines of 20% to 5% per decade for the two oceans, respectively. Proximate versus ultimate drivers causing these declines in coral are still debated. Proximate drivers include several factors such as coral disease, bleaching and algal competition, whereas ultimate drivers likely include climate change (warming, ocean acidification and storms), trophic-level dysfunction, eutrophication and other factors related to human land use.

Diseases of corals have increased in number and spatial extent since 1980 [11], fuelling speculation that they result from larger environmental stresses such as ocean warming or acidification [1]. A variety of other factors caused significant widespread coral mortality in recent years. Among Indo-Pacific coral reefs, periodic outbreaks of the coral-devouring crown-of-thorns starfish, *Acanthaster planci*, create acute mortality events for a suite of reef-building coral species. Severe outbreaks can consume virtually all the corals on the infested reef. These spatially and temporally discrete events might be triggered by extrinsic factors such as eutrophication [15]. Other acute mortality events have also increased over the last two decades with a rise in the incidence of coral-bleaching events [16] and increases in severe tropical cyclones of categories 4 and 5 [17]. Critically, such sudden events can push reefs beyond their stable coral-dominated state [18], which can then trigger phase shifts in community structure toward algal domination (see Box 2). Macroalgae commonly, but not always, increase in abundance following major coral mortality, but the degree to which they contribute to, or result from, that mortality remains controversial [11]. For this reason, we single out macroalgae for further discussion.

### Macroalgae: a driver or passenger of ecosystem change?

The recent global mortality of corals is often attributable to the sudden events listed earlier but not to macroalgae *per se*. Nevertheless, macroalgal biomass interferes with coral recruitment (Figure 1c,d) [19], suppresses coral growth and fecundity [20] and can even cause direct, albeit localised, coral mortality to certain species [20,21]. Perhaps the most important net effect of such coral–algal interactions is that the recovery rate of coral populations is diminished by macroalgal blooms and forms feedbacks that drive reef decline further (see Box 2) [18]. So what determines the likelihood of an algal bloom?

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Box 2. Feedback mechanisms on coral reefs

The dynamics of coral reefs are characterised by ecological feedback mechanisms which we demonstrate here for both positive and negative trajectories (Figure I). Whether a reef follows a positive or negative trajectory depends primarily on whether grazing intensity is sufficiently high that macroalgal blooms are prevented from occurring. This is important because increases in macroalgae lead to reductions in the rates of coral recruitment, growth and fecundity. An algal bloom occurs if algae colonise and grow without being predated upon by herbivores. Thus, blooms are most likely to occur in a system that has rapid algal growth (high productivity) and much algal settlement space available, such as a reef that has recently experienced mass coral mortality. This type of reef would require the highest levels of grazing intensity to prevent an algal bloom from taking place. Ideally, reefs would be managed to ensure a surplus of grazing capacity such that even when the availability of algal settlement substratum is high (which dilutes grazing intensity), there is sufficiently high herbivorous fish biomass to overwhelm the ability of macroalgae to bloom [18].

The ecological feedback processes driving positive and negative trajectories are essentially the same, but their directions are reversed (Figure I). An example (negative) feedback might start with inadequate grazing intensity. This could be caused by a combination of depleted herbivorous fish biomass (because of excessive fishing), high algal productivity (high wave power or elevated nutrient concentration) and/or low coral cover (recent bleaching event). Macroalgal cover begins to increase (Figure I), which reduces the settlement space available for corals. Furthermore, the increase in macroalgal cover enhances the frequency and duration of competitive interactions with coral recruits, which serve to increase their postsettlement mortality rate. The combined effects of reduced settlement space and enhanced mortality reduce the density of recruits on the reef. If this impact on recruitment is large enough, a bottleneck forms in the coral population such that natural losses of adult corals are not replaced by new corals. This has the effect of reducing coral cover and liberating additional space for macroalgal colonisation (which is equivalent to diluting grazing intensity, as each patch of reef is now grazed less frequently). The increase in macroalgal colonisation space encourages faster colonisation of macroalgae. The resulting algal bloom further reduces the density of coral recruits, thereby intensifying the bottleneck in coral population dynamics and the weakening of grazing intensity. Moreover, the continued loss of corals reduces the structural complexity of the reef. Lower habitat complexity then exerts deleterious impacts on the recruitment of corals (reduced availability of refugia from algae) and the recruitment of herbivorous fishes (because of increased predator efficiency). These mechanisms exacerbate the failure of coral recruitment and reduce grazing intensity even more, thus reinforcing the feedback.
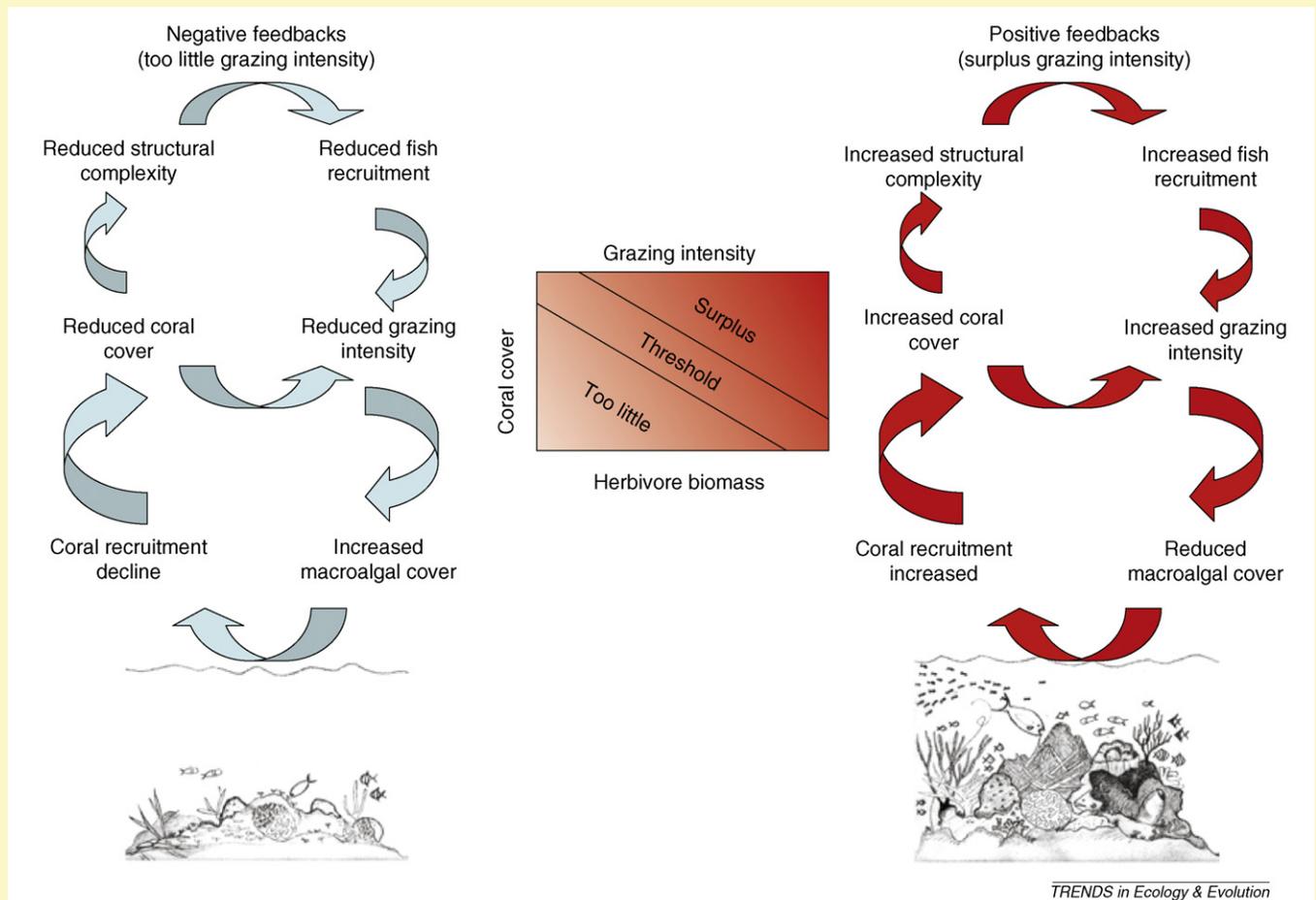
Figure I. Schematic representation showing positive and negative feedback processes driving a reef toward either an unhealthy system lacking coral and structural complexity or a healthy system dominated by corals with great structural complexity. Whether the feedback is positive or negative depends on whether grazing intensity is high enough to prevent the start of an algal bloom.

The relative importance of nutrients versus herbivory in driving phase shifts in coral community structure has been one of the most divisive issues in reef science [22]. Clearly, interest in the issue has not abated, because when short-listing 190 ecological papers of relevance to management since 2005, the largest group (26%) addressed nutrient and/or herbivory impacts on coral reefs.
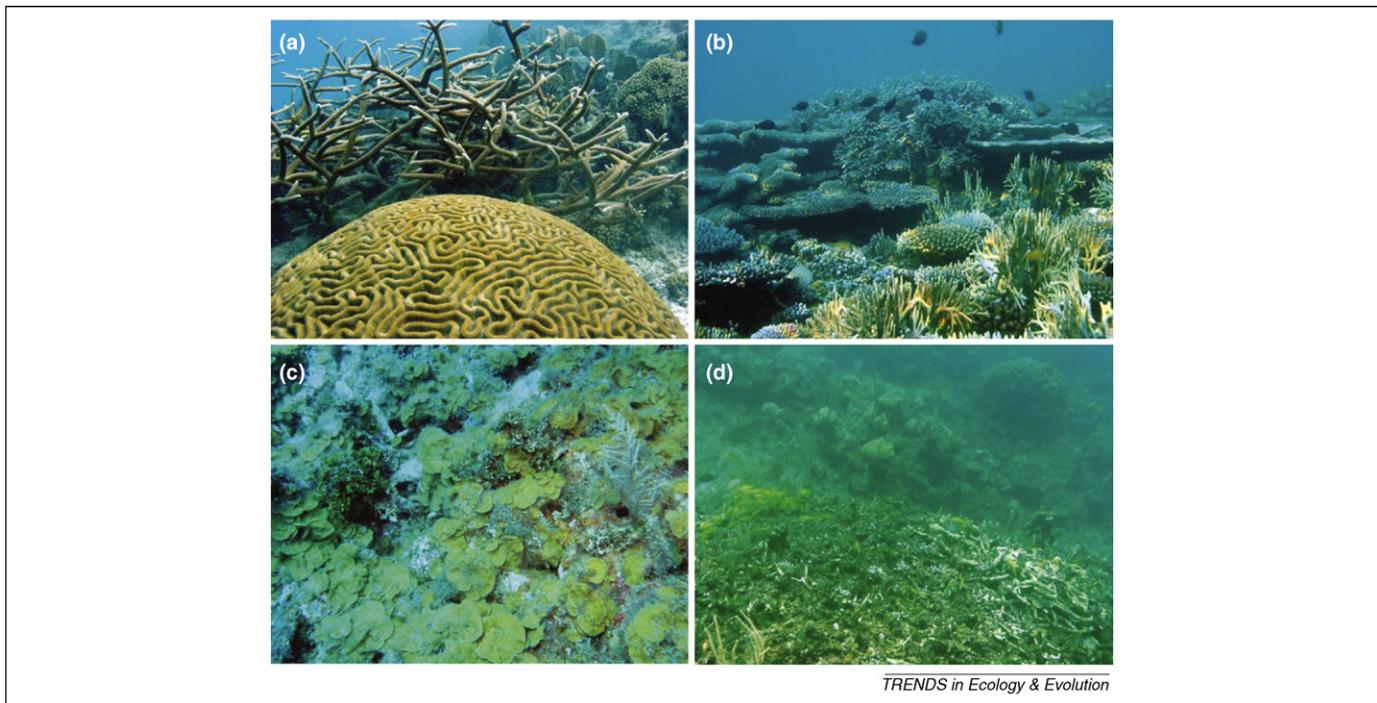
Figure 1. The changing fortunes of coral reefs. Healthy coral reefs in **(a)** the Caribbean and **(b)** the Pacific characterised by great structural complexity from branching and table acroporid corals. **(c)** Rising macroalgal cover, such as *Lobophora variegata*, limits the settlement space available to coral recruits and their subsequent survival and **(d)** causes prolific algal blooms with low coral cover. (Photos from the Caribbean.).

Decades ago, most coral reefs were said to be devoid of macroalgae (Figure 1a,b) [23]. Sudden phase shifts to macroalgae are best documented for reductions in herbivory such as the mass mortality of the urchin *Diadema* in the Caribbean [9,10]. Indeed, experimental evidence that algal blooms can occur if herbivory is reduced is unequivocal, even though specific algal responses vary among studies [20]. Herbivory is an area-specific rate (i.e. proportion of grazable substrate grazed per unit time) and therefore sudden changes to the area of grazable substrate will strongly impact grazing intensity (at least until herbivores can respond by altering their population density). This is a critical concept, because the rapid die-off of coral or other algal-suppressing substrates can greatly increase substrate availability to grazers and therefore facilitate algal blooms by inadvertently reducing the intensity of herbivory and providing new opportunities for macroalgae to escape predation [24]. Whether or not this occurs depends on the balance between rates of herbivory and those of algal colonisation and growth [25] (Box 2). For example, the reefs of Palau have a diverse and abundant herbivore community and although corals suffered mass mortality in the 1998 bleaching event, the reefs never phase shifted to macroalgae and many are now in full recovery (Figure 1b) [26].

Two meta-analyses [27,28] and a major review [29] of the relative importance of top-down (herbivore-controlled) versus bottom-up (nutrient-controlled) causes of algal blooms concluded that herbivory exerts the dominant impact. So does this mean that bottom-up processes are unimportant? Certainly not. The hugely variable outcomes of nutrient manipulations on reefs [30–32] probably reflect the *ad hoc* geographic distribution of the research and the preoccupation with nutrient concentration as a driver of

algal blooms. Nutrient concentration *per se* is arguably a relatively minor driver of algal production; it is the overall flux of nutrients to the alga (together with light) that drives production, and this is largely controlled by the flow rate and turbulence of water [33,34]. Large variations in productivity would, therefore, be expected along a gradient of wave exposure (which influences water turbulence) even if the general habitat type and depth were constant. In other words, it is quite feasible to expect contrasting impacts of nutrient enrichment within a single reef system, and a holistic analysis of the interactions between wave exposure, nutrient concentration and herbivory is lacking. In principle, a given reduction in herbivory is more likely to cause an algal phase shift if the reef has high productivity (e.g. an open-ocean-facing reef) than if productivity and algal growth rates are low (e.g. a tranquil leeward system). It follows that management efforts to maintain the process of herbivory are likely to be more urgent on open-ocean-facing reefs than on leeward reefs [25].

Consequences of coral decline
The 1998 bleaching event caused worldwide coral mortality and was particularly severe in the Indian and Pacific Oceans [35]. Such sudden and extensive declines in living coral cover, which exceeded 95% in many locations, formed an unprecedented natural experiment on the response of reefs to large-scale disturbance. Now, a decade later, we can summarise the first lessons learned.

Reductions in coral cover, as a result of bleaching, have strongly reduced the abundance and diversity of fishes that have a direct obligate dependence on live coral for settlement habitat or food [36,37]. In some cases, the reduction in living coral has precipitated a shift in fish communities from trophic and habitat specialists to generalists [38].

However, in areas where coral recovery has been slow, such as the inner Seychelles Islands, processes of storm damage and bioerosion have significantly reduced the structural complexity of the habitat with concomitant deleterious consequences for the density of many fish species [39]. Indeed, studies of the general relationship between structural complexity and fish community structure have proliferated rapidly, with 23 papers published in the last 2 years. Loss of habitat complexity, which can increase the foraging efficiency of predators [40], influences the density of small-bodied fishes disproportionately [39]. Meta-analyses of fish-monitoring studies indicate that 62% of fish species declined within 3 years of a reduction of at least 10% coral cover [41].

Declines in the structural complexity of coral habitats have also been found to reduce the diversity of invertebrate taxa [42] and the density of commercially important invertebrates such as the spotted spiny lobster, *Panulirus guttatus* [43].

Losses of fish and invertebrate habitat have always been of concern, but until recently the problem has been largely local in scale, resulting from cyclones or destructive fishing practices [44]. Today, however, the phenomenon of habitat loss is occurring at such large scales (thousands of kilometres) that it might encompass most subpopulations of a metapopulation and therefore reduce population stability. At best, this will exacerbate the ongoing concerns over overexploitation of fisheries [45] and at worst, threaten the very persistence of some species.

Drivers of recovery: the roles of organism, habitat and ecosystem connectivity

Recruitment is essential for reefs to recover from disturbance. Connectivity links reproductive populations to their recruiting offspring but does so in several different ways at distinctly different spatial scales. For recruitment at any location, each reef-dwelling organism requires propagules such as competent larvae to reach nursery habitats, defined as areas where postsettlement mortality is relatively low. Some organisms cue into the location of nursery habitats using light, sound or chemistry, and this field has gained considerable importance in recent years. Not all nursery habitats for reef organisms are on or even in close proximity to coral reefs. Such ontogenetic 'ecosystem connectivity' has recently been shown to have demographic consequences for important reef-dwelling organisms. Here we provide a brief review of some important developments in larval and ontogenetic dispersal, because this reflects where much of the research activity lies and the outcomes have a bearing on management.

Demographic connectivity: more local than expected
New studies of the dispersal of corals and fish argue for an increasingly localised paradigm with relatively high larval retention and limited downstream connectivity of larvae. Models of demographically relevant reef fish dispersal in the Caribbean identified relatively short dispersal distances of 10–100 km [46]. These predictions are consistent with new surveys of reef fish larval dispersal in French Polynesia which were mostly found within 300 km [47]. In some cases, demersal reef fish appear to have extremely fine, subkilometre, scales of larval retention [48]. Studies of genetic structure in branching corals are generally consistent with the local-dispersal paradigm in that limited genetic exchange has been detected on scales as small as 2 km [49].

The limited dispersal distance of many reef organisms is potentially consistent with the goal of protecting intact populations within reserves but is also likely to limit one of the putative fisheries benefits of reserves: larval spillover to support harvested populations nearby [50]. In principle, the formation of reserve networks with a spacing of tens of kilometres might improve the likelihood that reserves can support fisheries. However, this would require a major upscaling of current management efforts [51], requiring integrated governance of factors affecting reefs (e.g. fisheries, environment, development, agriculture, tourism), the strengthening of community-based enforcement of regulations, scaling up community harvesting reserves, investment in alternative livelihoods and social protection for those displaced because of habitat protection [52].

Ecosystem connectivity: larger and more important than expected
Many reef fish undertake developmental migrations from lagoonal habitats (mangroves and seagrass beds) where they settle as larvae to coral reefs where they live as adults. Studies in the Caribbean evaluating the impact of losing significant areas of mangrove found demonstrable negative demographic effects on adult fishes such as some species of snappers, grunts and parrotfish [53,54]. Fringing red mangroves (*Rhizophora mangle*) might be particularly important in the Caribbean because the region's low tidal range allows mangrove prop-roots to remain permanently inundated, providing a predictable nursery habitat for juvenile fishes. By contrast, many mangrove systems in the Indo-Pacific only provide a temporary habitat at high tide, which might be expected to decrease the importance of these nurseries relative to those in the Atlantic. Perhaps surprisingly, then, recent studies in Australia and Thailand found compelling evidence of a positive relationship between the availability of mangroves and fisheries production [55,56]. However, it is still premature to draw generalisations about the importance of specific nursery habitats for fishes in the Indo-Pacific. Overall, seagrass beds might be a more important nursery habitat than mangroves for several reef species [57], although specific coral reef habitats in the lagoon also appear to be important for many commercially important species such as the humphead wrasse (*Cheilinus undulatus*) and squaretail coral grouper (*Plectropomus areolatus*) [58].

Mangroves are currently being deforested at a faster rate than rain forests [59]. However, the effective maintenance of seagrass and mangrove habitats by controlling land reclamation, sediment dredging, boat anchoring, aquaculture development and coastal development should have indirect benefits to reef fisheries because the number of fishes reaching the adult reef habitat should be ensured. Moreover, the maintenance of mangroves, together with appropriate land management, can help prevent the runoff of sediments which can interfere with coral recruitment and growth [60].

Table 2. Status of knowledge about the effects of fully protected marine reserves in coral reef areas

Reserve impact	Status of science	Refs
Increased fish and invertebrate biomass within borders	Confirmed and widely reported	[66]
Adult spillover to support adjacent fishery	Confirmed by a few studies but not others	[67]
Larval spillover to provide demographic support to nearby fished reefs	Expected but not demonstrated	[68]
Facilitation of trophic cascades that prevent urchin plagues (Indo-Pacific)	Confirmed by few studies so far	[69]
Facilitation of trophic cascades that increase fish grazing and reduce macroalgal cover (Caribbean)	Confirmed by few studies so far	[70]
Increased coral recruitment (Caribbean)	Confirmed by few studies so far	[63]
Increased recovery rate of coral populations	Expected but not demonstrated	[18]
Enhanced biodiversity	Mixed results (positive, negative and no impact reported)	[71]
Reduced direct impact of hurricanes or coral bleaching	Unlikely to occur	[36]
Reduced incidence of coral disease	Unknown	

Management tools for maintaining ecosystem services

Most ecosystem services, such as coastal protection from storms, generation of high-quality fisheries habitat and provision of sand beaches, depend on living coral and therefore many management tasks, including fisheries and coastal erosion, should not be divorced from that of corals. But how should living corals be managed? The largest-scale and arguably most severe problems facing corals relate to climate change, which has no direct local or short-term management solution (Table 1). Thus, management tools should be selected that at least minimise impacts at local scales by having a demonstrable means of improving coral health and recovery. To date, the vast majority of efforts have focused on the implementation of marine reserves (Table 1). Reserves do indeed play important roles (Table 2), but reserves alone are inadequate for 'confronting the coral reef crisis' [61] at an appropriate scale.

The role of marine reserves

Much effort is being invested in extending the global network of marine reserves on coral reefs [51]. With appropriate compliance, marine reserves are able to restore ecosystem structure and trophic processes although evidence for a demographically detectable effect of larval spillover is lacking (Table 2). However, to avoid misguided decision making, it is critical that realistic expectations are set for reserves. Investments in marine reserves have been criticised because coral health appears to be unaffected by the reduction in fishing when sampled within a few years of a major coral-bleaching event [11]. Arguably, however, this is an unrealistic expectation. Coral bleaching is an acute radiative stress caused by elevated temperature, and it is unreasonable to expect that a cessation in fishing will influence such physical stress, particularly when thermal climatologies have never been incorporated explicitly into reserve design. The role of reserves is usually to reduce biological stress rather than physical stress (although pollution is more likely to be controlled within reserves than elsewhere). Experimental studies of coral–algal inter-

actions and herbivore manipulations predict that an accumulation of herbivorous fish in marine reserves could drive local trophic cascades and increase the resilience of coral populations [62]. So far, there is partial support for this hypothesis from a well-managed reserve in the Bahamas in which algal cover has declined and been accompanied by an increase in coral recruitment [63] (Table 2). At this point, the final link to enhanced recovery of the entire coral population has not been shown. Whether reserves can impact upon other sources of biological stress, such as diseases, is unknown. If reef fish are found to act as vectors of coral disease, then the outcomes could be either positive or negative depending on the response of particular fish to a cessation in fishing and subsequent trophic cascades.

The latest developments in reserve design explicitly recognise that physical stress is a critical driver of coral health. As a result, efforts to locate reserves in less stressful physical environments, such as relatively cool environments that experience high levels of mixing with cooler, deeper water, are now being considered [64].

Scaling up the management of ecosystem processes

Reef fisheries management has focused on the sustainability of harvested species and usually ignored the impacts of harvesting on the ecological processes that drive the ecosystem (including providing habitat for various fisheries species). With a few exceptions, such as Bermuda where fish traps were banned to help support parrotfish populations, the vast majority of reefs lack any formal protection of ecosystem processes, and those that do (those in reserves where all harvest is banned) constitute a tiny proportion of the coastal zone [51]. For example, fished reefs are the most likely to exhibit rapid habitat degradation for either of two reasons: (i) reduced fish grazing as herbivorous fish are depleted and/or (ii) urchin plagues as their fish predators are removed. If reef habitat quality declines then fisheries production will also decline, as prey and habitat availability is lost. Arguably, it is not enough to rely on marine reserves to manage coral communities;

'coral-friendly' fisheries policies are also needed that explicitly consider the impacts of harvesting on herbivory. Unfortunately, developments in fisheries policy receive much less attention than the study and implementation of marine reserves. Although not exhaustive, a search of coral reef literature from 2005 to 2007 using the terms 'fisheries' and 'marine reserve/protected area' located 24 papers on reserves but only 10 papers on fisheries, of which only 1 modelled policy options. Thus, the paucity of research on fisheries policy is at odds with the crisis facing managers of coral reefs. Ideally, new fisheries policies will become available that can be integrated with other efforts to scale up coastal protection such as establishing truly integrated governance structures for coastal management that extend from the watershed throughout the reef system [52].

Concluding remarks

The paradigm of widespread healthy, stable coral reef ecosystems has evolved to one that views them as patchy, unstable and fragile. Coral reefs suffer from global and climate stresses that local managers and policymakers are powerless to reverse. However, recent research suggests that exploitation-related degradation and the seeds of recovery can and should be managed locally. Additional research will be required to quantify the efficacy of management tools and the spatial scale of effect and to identify means of managing ecosystem processes alongside harvesting activities. Studies of this type, together with bolstering governance and local participation in management, are essential to be effective under the chronic challenges imposed by climate change.

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