

The image is a vertical composition. The top half shows a school of small, blue, oval-shaped fish swimming in clear, deep blue water. The bottom half shows a vibrant coral reef with various types of coral, including branching and table corals, in shades of green, yellow, and purple. The text is centered in the upper half of the image.

Part I: Introduction

Chapter 4

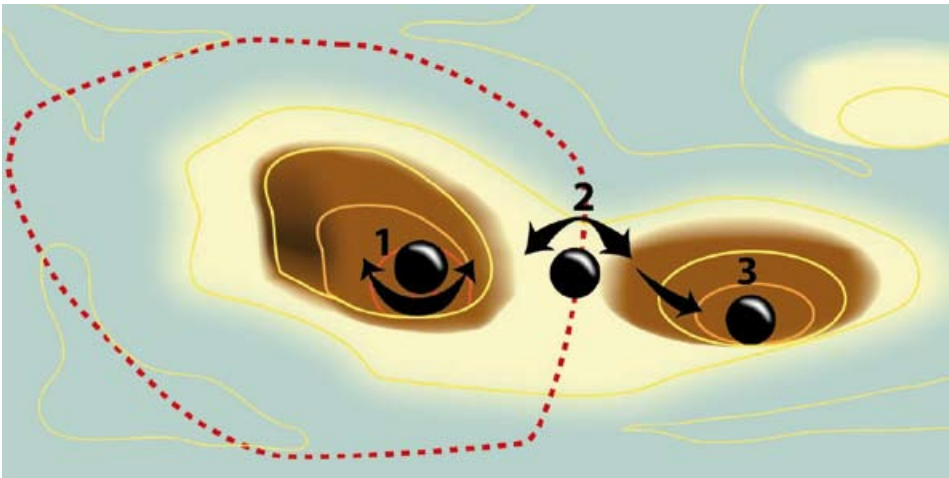
Ecological resilience, climate change
and the Great Barrier Reef

Laurence J McCook, Carl Folke, Terry Hughes, Magnus Nyström,
David Obura and Rod Salm

4.1 The concept of resilience in social-ecological systems

The vulnerability assessments in this volume frequently refer to the resilience of various ecosystem elements in the face of climate change. This chapter provides an introduction to the concept of ecological resilience, and its application as part of a management response to climate change threats. As defined in the glossary, *resilience refers to the capacity of a system to absorb shocks, resist dramatic changes in condition, and maintain or recover key functions and processes, without undergoing “phase shifts” to a qualitatively different state (Figure 4.1)^{32, 72}*. For example, people who are physically and mentally fit and strong will have good prospect of recovery from disease, injury or trauma: they are resilient.

Figure 4.1 Resilience, dynamic stability and alternate stable states (redrawn from Walker et al. 2004⁷³)



In Figure 4.1, a ball placed at position 1 is dynamically stable: not only will it remain in position, but if pushed in any direction, it will return to its original position; thus the ball in this state is resilient, in that it can absorb shocks and return to a similar condition or state. In contrast, a ball placed at position 2 may be initially stable (it will remain in position if undisturbed) but not dynamically stable: if disturbed, it will move away. Thus the ball at position 2 is not resilient, and disturbances will result in a shift in state. If the ball at position 1 is disturbed to anywhere within the red circle, the ball will return to position 1; however, if disturbed further, the ball may not return, but may move to a new, alternate stable state (eg position 3). This system is resilient to disturbances that push it within the red boundary. However, if external factors decreased the depth of position 1, or lowered the saddle at point 2, then the system’s resilience would be reduced. By analogy to coral reef ecosystems, position 1 might be a coral-dominated reef, and position 3 algal dominated. A disturbance such as killing coral that is overgrown by algae would move the reef toward an algal-dominated state; if the reef is resilient, this change would be temporary and natural processes would allow coral to re-establish and recover. If not, the algal dominance might be sufficient to preclude coral regrowth or recruitment, and the reef would change trajectory, moving toward algal dominance.

Ecological resilience refers to the capacity of an ecosystem, habitat, population or taxon to withstand, recover from or adapt to impacts and stressors, such as climate change, and retain the same structure, processes and functions³². For example, coral reefs are naturally very dynamic, undergoing constant change and disturbances, but, under natural conditions, they have considerable capacity to recover or maintain key processes and functions in the face of such disturbances or pressures. Tropical storms may cause dramatic damage to coral populations, and hence to the physical habitat structure, with dead coral being overgrown by various forms of algae. This will result in a temporarily changed state, and changes in ecological functions. On a resilient reef, over a period of five to 20 years, the altered state is unstable: coral fragments will regrow, and new corals will settle, grow and gradually replace the algae, restoring the reef to coral dominance, and restoring ecological structure and processes. In contrast, however, if human impacts have undermined that resilience, algal growth may be exacerbated, coral regrowth and colonisation may be suppressed, and the altered state and processes may become stable, causing a long-term “phase shift”, or change, to algal dominance^{33, 50, 37}.

For ecosystems to persist in the long term, successful reorganisation (recovery) after disturbance is fundamental. However, coral reefs are facing pressures at local, regional and global scales that challenge their capacity to reorganise following disturbance and thus challenge their existence^{31, 34, 78}. Coral reefs exposed to gradual change are often assumed to respond gradually and smoothly. However, like most other ecosystems, they are dynamic, complex and adaptive⁵⁷. Put simply, this means that they are characterised by environmental thresholds that, if crossed, may lead to large-scale and relatively abrupt shifts in state, including changes in ecosystem processes and structure (eg coral-dominated reefs shifting to algal dominance) and in their capacity for self-organisation^{44, 24}. Ecological resilience also embraces adaptability, in the sense that an ecosystem may maintain characteristic structures and processes by developing new and innovative organisation or attributes. For example, in the Caribbean, sea urchin populations increased in response to overfishing of herbivorous fishes; in effect, the ecosystem reorganised to maintain the process of herbivory^{30, 33}. Importantly, once a threshold is crossed and a shift in state or key processes occurs, it may be difficult, or even impossible, to reverse the shift, due to changes in feedback mechanisms that stabilise the new state. Such reinforcing mechanisms may, for example, involve algae that prevent corals from establishing by occupying substratum, trapping sediments, releasing allelopathic chemicals, and overgrowing juvenile and low-relief adult coral colonies^{51, 7, 67}. Reversing such a shift may require a different path, and restoring conditions to previous levels may not be sufficient (an effect known as “hysteresis”)³⁵. For example, the numbers and species of herbivorous fishes required to prevent algal overgrowth of corals may not be enough to remove an algal bloom once it has occurred. Reversal of such shifts may not only be difficult, but is likely to be significantly more expensive than prevention.

The concept of resilience provides a valuable integrating theme or perspective for both the science and management of natural environments, in particular because it addresses two of the most difficult challenges in understanding and managing human impacts on natural ecosystems: first, that different natural or anthropogenic (human-derived) stressors can interact, and synergise to cause more damage than either stressor alone^{33, 52}; and second, that stressors and their impacts and interactions can be difficult or even impossible to predict. Individual human-derived stressors rarely occur in isolation: for example, for example, terrestrial runoff to reef waters, usually contains increased levels of several pollutants, such as sediments, nutrients and pesticides. Several studies have shown much higher impacts in response to combinations of pollutants than to individual pollutants²². If, as human

populations grow, increased runoff co-occurs with overfishing, algal growth, enhanced by nutrients, may pass a threshold level, beyond which herbivorous fishes may fail to control algal abundance if their numbers have been reduced⁵⁰. The result may be a sudden overgrowth of algae that is well beyond that accounted for by the nutrient runoff.

Interactions between chronic and acute disturbances are particularly significant. For example, on coral reefs, considerable evidence has emerged that while some chronic human-derived stressors, such as over-fishing or eutrophication (nutrient and sediment pollution), may have relatively small direct effects on established corals, they may severely limit the capacity of coral populations to recover after acute disturbances such as storm damage or mass bleaching due to sea warming. In this scenario, the chronic stressor may be of little immediate and direct threat to undisturbed reefs, but may reduce the resilience of the habitat, so that failure to recover from frequent, repeated disturbances may result in a gradual, piecemeal degradation or “ratchetting down” of reef health (Figure 4.2)^{33, 52}.

Figure 4.2 Modelling the effects of chronic stressors, such as eutrophication, and repeated disturbance, such as mass bleaching, showing the potential importance of interactions (redrawn from McCook et al 2001⁵²). Individual graphs represent the changes in coral (blue lines) and algae (brown lines) through time, for computer simulations of reef dynamics.

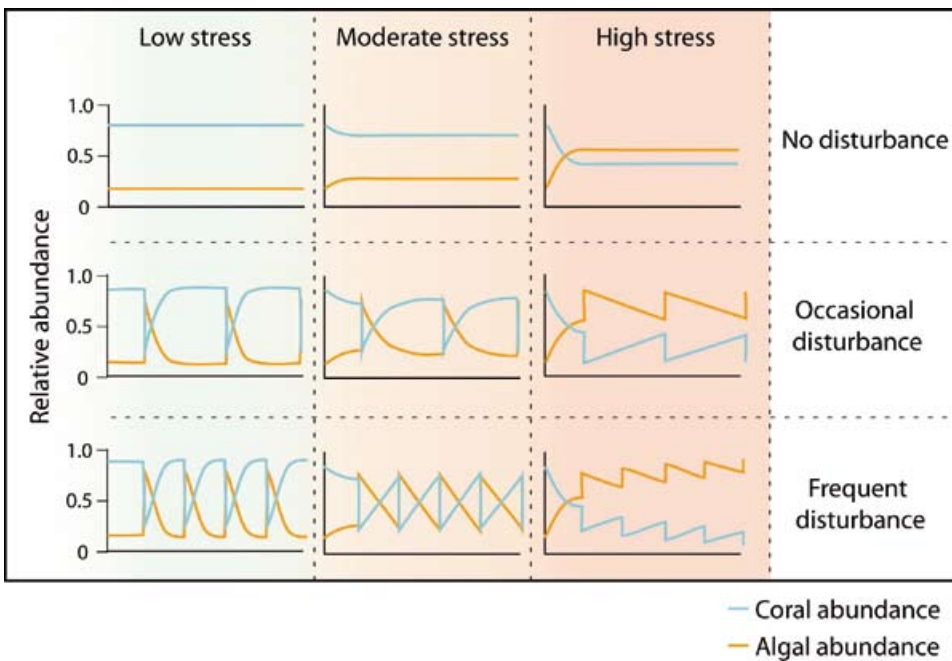


Figure 4.2 simulates the effects of increasingly frequent disturbances⁵². The graphs on the left show that the “virtual reef” is relatively resilient and coral populations recover after each disturbance, so that even with relatively frequent disturbances overall reef condition is maintained in the long term. The three graphs along the top row indicate potential effects of increasing stresses, such as overfishing or eutrophication. Reef condition declines with increased stress, but coral populations can persist at moderate levels: reef condition is moderate, but resilience is reduced by the stresses. However, when chronic stress is combined with frequent disturbance (bottom right graph), the reduced resilience means the reef cannot fully recover before the next disturbance, damage accumulates and there is a serious long-term decline in condition. Thus, this model reef community can persist with either frequent disturbances or chronic stresses, but becomes degraded if subjected to both impacts. This model illustrates two important points. Firstly, the chronic stresses do not appear to cause the coral declines in the bottom right panel; simple monitoring of this system would suggest the declines are caused by the disturbances. Only by understanding the processes that engender recovery and resilience do we recognise the critical role of the chronic stresses. Secondly, management strategies that seek to both reduce the frequency of disturbance (eg by mitigating climate change) and enhance the resilience (eg by reducing overfishing or runoff of pollutants) may be much more effective than either action alone.

The risk with this situation is that management actions that address stressors in isolation may fail if they do not address the potential interactions. In addition, they may fail to engender public support; for example, addressing pollutant runoff might be seen as wasted effort because the perception is that climate change will damage the reef anyway. By understanding these interactions, scientists, managers and the public will be able to see the value of specific management actions not only in addressing the specific risk, such as pollutant impacts, but also in maintaining the overall resilience of the ecosystem to resist or recover from other impacts.

The second benefit of managing for overall resilience, as well as for specific threats or impacts, is that it provides the best insurance against future unforeseen or unpredictable threats^{42,26}. Several of the most significant threats to coral reefs in recent decades have emerged unexpectedly. The decline of Caribbean reefs was significantly increased by the completely unforeseen, wide-scale disease-induced mortality of herbivorous *Diadema* sea urchins in the 1980s. These herbivorous sea urchins had previously prevented algal exclusion of corals, and the impact of this die-off was much more severe because of the wide-spread depletion of herbivorous fish^{33,8}. Similarly, the now wide recognition of the impact of climate change on coral reefs through increased mass bleaching was unforeseen 10 years ago³¹. It is likely that other currently unrecognised threats will emerge for reefs and other habitats within the Great Barrier Reef (GBR) until science identifies new threats, the best management strategy is to aim for a system with the resilience to recover from a wide range of possible challenges.

The concept of resilience is not limited to ecosystems in isolation from humans, but also applies to social and economic systems and it has been recognised for some time that social, economic and ecological resilience are strongly intertwined. Management actions aimed at protecting ecological resilience that also take account of the social and economic wellbeing of the community will generally be more sustainable and effective in the long-term. For example, marine protected areas that generate increased tourism revenue for local communities from the improved condition of ecological resources, or increase sustainability of fisheries, generate support in those communities,

in turn generating improved compliance and enforcement^{77,2}. Management that ignores or overruns the social or economic context will often be less effective, or fail, owing to a lack of local support or political intervention. Importantly, social, economic and ecological resilience are not inconsistent goals, and can be effectively integrated²⁷.

Resilience also provides a basis for integration of management strategies and responses to different issues, and for adaptive management approaches. Thus, management action to reduce terrestrial runoff may be markedly more or less effective, depending on the management of pressures on herbivorous fish populations^{48,41}. It may be most beneficial to manage fishing pressure in areas with the highest runoff. Adaptive management requires that the effectiveness of current management practices be periodically reviewed as conditions and circumstances change, and as new threats emerge. The concept of resilience suggests that any review should include not only the apparent state of the ecosystem (or social-ecological system), but also the key processes and functions which confer resilience, and that management actions should respond or adapt to changes in those processes and functions³⁷.

4.2 Ecological resilience in the context of climate change

Human-induced climate change is a major threat to many ecosystems, including the GBR^{31,34} (see chapters 5–22). In simple terms, two management approaches can be taken to minimise these impacts: reduce the extent of the changes; and maximise the capacity of the system to resist, adapt to, or recover from, those impacts (Figure 4.3). Overall, addressing the cause of the problem (for example, by abatement of greenhouse gas emissions) is critically important and likely to be the most effective approach. It is also likely to be the most cost-effective strategy overall, because it will ameliorate impacts on a vast range of systems, both human and natural. However, such measures are beyond the scope of marine management agencies, and will not be sufficient alone. Because there will be long lag times in the reversal of current climate trends (decades to centuries), ongoing change is inevitable for the next several decades (Lough chapter 2).

Figure 4.3 Management responses to increasing pressure on coral reefs

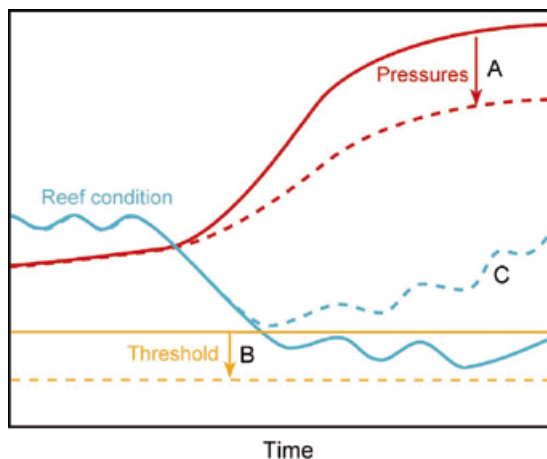


Figure 4.3 shows that the effect of pressures on reefs (solid red line) is predicted to increase dramatically over the next century, due to climate change and other human impacts. As a result, ecosystem condition is likely to decline, along with the capacity to recover from those impacts. If the loss of resilience is sufficient, reefs may pass a threshold beyond which they do not recover, but remain in an alternate, degraded state (solid green line). There are two complementary strategies available to managers. First, and paramount, is to reduce climate change and other human pressures on reefs (dashed red line); in the case of climate change, this requires action at global scales, and is beyond the scope of marine management agencies. Second is to manage other sources of stresses or pressures on the reefs, so that the decline in resilience is reduced and the ecosystem has enhanced capacity to maintain itself or to recover, rather than pass the threshold. Action on this strategy – managing for resilience – is challenging but possible for marine management agencies.

In this context, it is critical to maximise the capacity of the GBR ecosystem, and the communities and industries that depend on it, to adapt to climate change. However, as numerous chapters in the current volume illustrate, for many taxa and ecosystems there is a lack of detailed scientific understanding of the impacts, and an even greater ignorance of how to address those impacts directly. This makes it very difficult to develop specific management strategies for climate change adaptation. It thus becomes increasingly critical to maximise the resilience or capacity of the ecosystem to cope with changes generally. Management for resilience is therefore not only a general strategy for protection, but an important part of responding to the impending threat of climate change³⁴.

It is important to emphasise that abatement and adaptation are necessarily complementary strategies. Managing for resilience is unlikely to provide sufficient protection for the biodiversity of the GBR; rather, it aims to slow and reduce the impacts sufficiently to allow natural adaptation and abatement of climate change to occur. Good management of marine ecosystems must not be seen as reducing the need for strong and urgent attention on a global scale to a problem of global magnitude.

4.3 Aspects of the ecological resilience of the Great Barrier Reef

Of the numerous and varied habitats found in the GBR, the factors contributing to the resilience of coral reefs are best understood^{57,46,34,5}. The following section provides a brief overview of some of these factors, although the discussion is intended to be illustrative, rather than exhaustive. Unfortunately, there is relatively little or no specific information available on the factors contributing to resilience of most other GBR habitats. This section therefore focuses primarily on coral reefs, as an example of the approach, and then only very briefly considers how the approach might apply to other habitats, and to species of particular conservation concern (such as dugong and other megafauna).

4.3.1 Factors contributing to ecological resilience of coral reefs

4.3.1.1 Population condition and dynamics of reef-building corals

The population condition and dynamics of corals, as the major contributors to reef construction, are fundamental to the capacity of reefs to absorb and recover from disturbances. Abundance of corals is an important factor, since disturbance to a reef with abundant coral will generally still leave some coral alive that can be a basis for population recovery. However, other key aspects include

the diversity, fecundity, settlement and post-settlement survival rates and general metabolic and immunological condition of the corals³. It is important to recognise that a reef dominated by large but fragile corals may have a lower capacity to recover from a disturbance than a reef with less coral but more diversity of forms and higher recruitment rates. Similarly, low abundance of coral may simply reflect recent disturbance history, rather than overall low resilience. If coral recruitment and growth is high, reef condition may recover relatively quickly⁴⁷.

Coral population dynamics can have important indirect significance for resilience. For example, a reef with abundant and diverse corals is likely to have a complex, topographic structure that provides important habitat for other groups of organisms, thereby increasing biodiversity and potentially strengthening critical functions such as herbivory^{71,50}.

4.3.1.2 Benthic algal assemblages and herbivory

Competition between corals and benthic algae is fundamental to the abundance of corals on reefs. Algae may directly overgrow coral tissue, reduce the amount of light available for photosynthesis, abrade tissue, or produce chemicals that damage or kill coral tissue⁵¹. All of these effects will have significant metabolic costs to the coral, even if it is able to resist or defend itself.

Recent work has highlighted a particular, chemically mediated, mechanism of algal competition related to the microbial community on reefs. Plants release organic carbon into the water column and this has been found to increase microbial activity, which can result in coral tissue mortality^{45,43,67}. Additionally, increasingly complex and long-living algal assemblages may accumulate larger microbial populations. Again, even if the coral tissue is not killed, these microbial stresses will have significant metabolic costs, reducing the capacity of corals to respond to other stresses.

Perhaps more significantly, algae may pre-empt space, inhibiting or preventing coral recruitment. Coral mortality is almost universally followed by colonisation by benthic algae of various forms (Figure 4.4)^{15,17}. After wide-scale coral mortality, such as results from climate change-induced mass coral bleaching^{31,78}, the majority of substrate will be covered in various forms of algae, and recovery of coral populations will generally require recruitment on substrates dominated by algae (rather than on live coral, for example).⁷ The nature of this algal assemblage will be fundamentally important to the success of subsequent coral settlement and growth. Substrate dominated by crustose coralline algae, with a sparse covering of short (less than 1 mm), fine filamentous turf algae, is likely to be highly favourable for coral settlement and growth. In contrast, a dense algal mat or thick growth of upright foliose or fleshy algae may severely inhibit coral settlement and survival, especially as such mats will often trap large amounts of sediment^{7,37}.

Under expected climate change scenarios, mass bleaching events are expected to occur with increasing frequency and severity³¹. Under these scenarios, algal overgrowth of dead corals and consequent algal dominance will become the norm, and coral populations are unlikely to recover sufficiently in between bleaching events. In such circumstances, the effects of different algal assemblages on coral recruitment, and on the recovery of surviving coral fragments, will become critical to the resilience of the reef, as will the effects of climate change on algal assemblages (Diaz-Pulido et al. chapter 7). It is likely that algal impacts on coral populations will become a real “bottleneck” for reef recovery.

Figure 4.4 Algal overgrowth of bleached corals in the Keppel Islands, Great Barrier Reef (August 2006). Severe bleaching of corals in the summer of 2006 resulted in extensive coral mortality and overgrowth by the alga *Lobophora variegata*. Previous work has shown *L. variegata* to be a highly effective competitor with corals^{40,41}. The fate of these reefs will depend on factors such as herbivory, which influence the persistence of alga, and its impact on coral regrowth and recruitment.

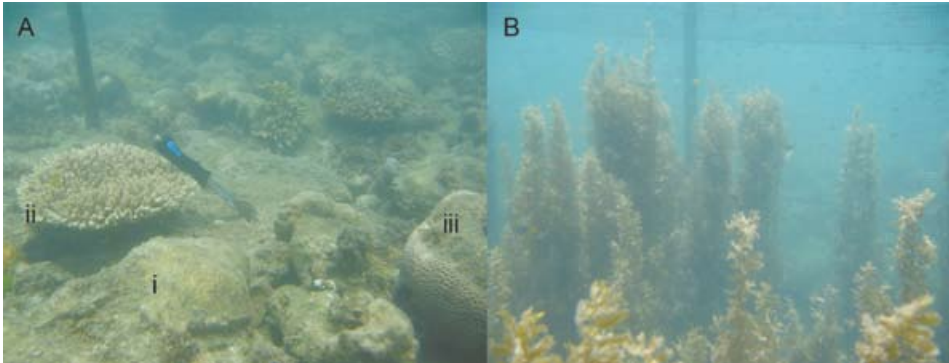


Given the importance of benthic algae to coral populations, controls on the abundance and type of algae are critically important to reef condition. The primary controls on algal abundance and type on coral reefs are substrate availability and grazing by herbivores, usually fish or invertebrates such as sea urchins. The abundance and diversity of herbivores have been shown to be critical to long-term reef condition around the world. In the Caribbean, overfishing of herbivorous fishes resulted in a low-diversity herbivore community dominated by *Diadema* sea urchins. The sudden, regional scale die-off of sea urchins due to disease resulted in rapid increases in algal abundance, with subsequent declines in coral populations and failure to recover from disturbances^{33,8}. Studies on the GBR have shown that herbivores are equally critical to algal distributions (Figure 4.5)^{16,37,40,41,48,49,6}. Fortunately, pressure on herbivorous fishes is currently minimal, so this important element of reef resilience remains largely intact.

4.3.1.3 Biological diversity

Marine ecosystems with high biological diversity will generally be relatively resilient, largely because they will have more diverse responses and capacities available to them, which can provide the basis for adaptation to new threats such as climate change⁴⁷. This diversity may be at a range of levels, including genetic diversity within species, diversity of species within guilds (functional groups, such as corals or herbivores), trophic diversity, and complexity and diversity of habitats. For example, genetic diversity within a coral species, or diversity of the symbiotic zooxanthellae within a coral population, may provide greater capacity for the coral population to survive diverse stresses, and increase the likelihood of some individuals surviving a particular bleaching event⁴. Different species

Figure 4.5 Effects of herbivory on resilience of a coral reef.³⁷ A. The reef crest at Orpheus Island, Great Barrier Reef, was severely damaged by mass bleaching in 1998,³⁷ resulting in overgrowth by fine, filamentous turf algae (i). Over the next few years, coral populations recovered by recruitment of new corals (ii) and by regrowth of surviving fragments (iii), with little impact from the filamentous turfs. B. In contrast, when large fishes were excluded to simulate the effects of overfishing, there was a dramatic overgrowth of Sargassum and other large, fleshy seaweeds, which reduced the growth and recruitment of corals and inhibited recovery of the community.



and morphologies of coral have different susceptibilities to temperature-induced bleaching and to other threats; a reef dominated by a few coral types may be more vulnerable to widespread damage than a more diverse reef⁴⁶. A reef with a diverse range of herbivores will have greater capacity to remove or prevent outbreaks of different types of algae⁶, and will be less vulnerable to events such as the disease outbreak that killed *Diadema* sea urchins in the Caribbean. Diversity of habitats within an ecosystem increases the likelihood of some habitats being less severely impacted by particular stresses or disturbances⁴⁷. For example, shallow reefs are often more vulnerable to storm damage and to coral bleaching. Deeper reef areas or areas with more complex topography may provide refuges that can be a source population for repopulating damaged areas.

Diversity within guilds has two aspects that underpin resilience: *redundancy* and *response diversity*. *Redundancy*^{74,70,6} describes the capacity of one species to functionally compensate for the loss of another within a functional group. Some species that seem unimportant may become critical for reorganisation when conditions change, whether slowly (eg increasing seawater temperature, accumulation of nutrients) or abruptly (eg crown-of-thorns or disease out-breaks, hurricanes, bleaching events). Thus, in the Caribbean herbivore example, the presence of sea urchins suppressed algal overgrowth, even when herbivorous fishes were overexploited. The critical importance of herbivorous fishes only became apparent when disease wiped out the sea urchins^{33, 8}. However, if all species are affected by a disturbance in the same way, even having a large number of species in a functional group may not contribute to resilience. *Response diversity*²⁰ describes the variability of responses within functional groups to disturbance¹⁰. A wide range of responses enables some species to compensate for others, which facilitates regeneration after a disturbance. Although it is not clear to what extent aspects of biodiversity contribute to resilience, it is clear that different aspects will be important under different circumstances.

4.3.1.4 Connectivity

The capacity of reefs to recover after disturbances, or reorganise in the face of new stresses, depends critically on the supply of larvae or propagules available to reseed populations of key organisms, such as fish and corals^{38,63}. Most marine organisms have a planktonic larval phase, in which larvae are dispersed by a combination of active behaviour, such as swimming, and passive transport by ocean currents. Connectivity refers to the extent of the connections between reefs and source populations, which may be other reefs or other habitats, such as coastal mangroves (for many fish), inter-reef seafloor, or seagrass beds^{19,55}. Patterns of connectivity depend strongly on ocean currents, the length of time that larvae remain viable in the plankton, and the existence of upstream habitats with refuge source populations. Even if a reef is well protected and soundly managed, alterations in the surrounding seascape may erode resilience if the supply of critical processes and functions, such as coral recruitment, is cut off⁴⁷.

Over short spatial and temporal scales, connectivity provides for the dispersal of both larvae, enabling recolonisation of sites, and adult organisms, potentially supporting ecological functions such as herbivory. Recent studies indicate that reef populations are overwhelmingly self-seeding^{69,13}, due to a combination of hydrographic and biological properties that retain larvae and/or strongly dilute a larval pool as it disperses from its source. When disturbances or stresses reduce the capacity for self-seeding, connectivity plays a critical role.

At larger spatial and longer temporal scales, connectivity provides the means of exchange of genetic material, and thus the currency of diversity, in space and time. Over multiple generations, connectivity maintains genetic continuity within populations and species, and defines the biogeographic spread of species. Resilience operates at many scales, and connectivity provides a mechanism for spreading and sharing resilience properties among locations. Thus 'connected' locations influence one another to varying extents in terms of resilience. Different ecosystem properties may operate across different scales, and degradation in multiple parts of a seascape may be masked by overall connectivity and sharing of resilience. Fragmentation of a seascape by the erosion of resilience in different locations may make the overall ecosystem vulnerable. For example, if the connectivity of a critical process is undermined by a disturbance event, the ecosystem may be pushed beyond a previously hidden threshold.⁵⁷

Connectivity may also reduce resilience, if it facilitates dispersal of undesirable factors, such as disturbance, pollutants (eg nutrients) or organisms (eg diseases, algae, exotic species). The success of undesirable, invasive species will depend on the resilience of individual reefs within the seascape mosaic. Erosion of resilience at local scales may create dispersal refuges for undesirable organisms.

4.3.1.5 Refugia

Refugia are areas where ecosystems are unaffected by, or protected from, stressors or disturbances that reduce resilience. Refugia help to maintain diversity and abundance by serving as sources for replenishing the disturbed populations that underpin connectivity, and serve as stepping stones for maintaining connectivity across larger scales. Important features of refugia include sufficient location and separation distances to ensure connectivity, adequate extent to provide sufficient source populations, and inclusion of comprehensive and representative examples of the different habitats within a region^{34,36,54}.

A primary tool in marine protected area management is establishing no-take zones that aim to provide refuges from human stressors. They thus maintain the resilience of local sites, and of the overall system, through connectivity with each other and with adjacent zones open to human uses^{54,36}. While it is clear that a higher proportion of a seascape maintained within refugia will provide greater protection on the whole, the nature of the relationship is as yet only approximately estimated. However, the irreversibility and threshold behaviour discussed above suggest that insufficient refugia will likely have serious long-term consequences⁵.

4.3.1.6 Water pollution and environmental quality

The quality of the chemical and physical environment is a strong determinant of resilience. A poor-quality environment exacts significant costs to organisms in maintaining physiological health and integrity and in maintaining ecosystem function. In particular, good water quality is critical to the health of corals, and to ecological processes such as the recruitment of corals and coral-algal competition, both of which are important for ecosystem resilience^{68,50,29}. In most nearshore tropical marine ecosystems, poor water quality is manifested as a long-term chronic increase in anthropogenic inputs of nutrients, sediments and other pollutants³⁹. Recent work has particularly emphasised the role of excess organic carbon in reducing the resilience of coral populations^{43,45}.

A considerable body of recent research suggests that a major impact of poor water quality is not in direct effects on corals or coral-algal competition, but in the inhibition of recovery from other stresses and disturbances^{50,79}. For example, after mass bleaching events, excess sediments and nutrients may inhibit coral recruitment synergistically with increased algal growth, with the result that coral populations re-establish too slowly to recover between disturbances²¹. Suppressed physiological health may also increase susceptibility to thermal stress and coral bleaching, given the metabolic costs of bleaching (the loss of the photosynthetic zooxanthellae). Modelling work has shown that an ecosystem able to cope with either frequent disturbances or eutrophication may show serious long-term degradation if the two occur in combination, amounting to a critical loss of resilience (Figure 4.2)⁵².

From a management perspective, however, improving environmental quality provides one of the most accessible tools for maximising resilience to many other threats, from chronic fishing pressure to acute disturbances. In the classic case study of Kaneohe Bay in Hawaii, reductions in pollution delivered to the relatively enclosed bay were followed by partial recovery of reefs from a degraded, eutrophic state to a healthier condition⁶⁸. On the GBR, water quality is being addressed proactively through the Reef Water Quality Protection Plan (see Section 4.6).

4.3.1.7 Aspects of resilience specific to climate change

As well as the general resilience factors discussed above, there are a number of environmental, ecological and physiological factors that relate directly to climate change-specific threats^{75,59}. Most work to date has focused on thermal stress due to climate change; other impacts, especially acidification, are likely to be important (Fabricius et al. Chapter 17). The factors listed below have been shown to reduce thermal stress, coral bleaching or mortality in some cases. However, it is important to recognise that these factors are not always sufficient, and that they do not act independently. Addressing one in isolation of others, and of other processes that affect coral health and resilience, is likely to be ineffective.

Thermal protection

Some reef areas appear to avoid or be protected from the oceanographic conditions that induce coral bleaching. This may be due to reduced water temperature, reduced light levels, and/or increased flushing. At large scales, these conditions may be induced by oceanographic and climatic features such as upwelling zones, current systems or regional climates that increase cloud cover, storms or cyclones⁶⁶. At local scales, some corals and habitats appear to be protected from the worst thermal conditions by local topographic features that provide shading, screening or other micro-environmental variation³.

Thermal resistance

Some reef areas, zones, patches and individual corals appear to be resistant to thermal stress and show less bleaching and/or mortality than other areas or corals under similar conditions. Resistance may be related to intrinsic (genetic) or extrinsic (environmental) factors. Genetic factors include the identity of the coral species and of the symbiotic zooxanthellae, and individual variation. In particular, some clades (genetic groups) of zooxanthellae have been found to be more resistant to bleaching than others⁴. Environmental factors include conditions that allow corals to acclimate to higher temperatures or to variability in temperatures^{53,18}.

Bleaching tolerance

Some reef areas, zones, patches or individual corals appear to be more tolerant to bleaching and suffer less mortality after bleaching than other areas or corals. Tolerance may also be related to intrinsic or extrinsic factors, but appears to be distinct from resistance to thermal stress⁶⁵.

These factors may be useful to reef managers in identifying and protecting areas of potential resistance and resilience of coral reefs to climate change. For example, areas that appear to have survived or recovered rapidly from previous bleaching might, in principle, be suitable sites for protection. However, to date no two mass bleaching and mortality episodes at a site have followed very similar patterns, so caution is needed and a range of resilience factors must be considered simultaneously, including the predictability and regularity of their occurrence⁷⁵.

4.3.1.8 Minimising bleaching impacts at local scales

There can be no doubt that the most effective strategy to reduce bleaching impacts on coral reefs is to minimise climate change drivers. However, given that significant change is now unavoidable, it is also necessary to take every possible step to minimise the impacts of that change at local scales by addressing the various factors outlined above. It is likely that the two strategies, proceeding in tandem, may have synergistic benefits for reefs. Thus, in general terms Salm et al.⁶⁴ recommend that managers (a) identify and protect from direct anthropogenic impacts, specific patches of reef where local conditions are highly favourable for survival generally, and that also may be at reduced risk of temperature-related bleaching and mortality and (b) locate such protected sites in places that maximise their potential contribution to the recovery of damaged or vulnerable reefs that are connected through larval dispersal.

Table 4.1 Summary of local management approaches for mitigating climate change impacts on coral reefs

R2—Reef Resilience Toolkit ⁵⁶	A Global Protocol for Assessment and Monitoring of Coral Bleaching ⁶¹ , A Reef Manager’s Guide to Coral Bleaching ⁵³ and other approaches ^{9,60}
<ol style="list-style-type: none"> 1. Managing for risk: representation and replication—protecting multiple examples of a full range of reef types helps to ensure inclusion of representatives of the area’s total reef biodiversity. Replication of each reef type reduces the chance of any one type being completely compromised by an unmanageable impact such as a major bleaching event. 2. Refugia—Identifying and fully protecting coral communities that demonstrate bleaching resistance and that can thus serve as refugia is an effective way to facilitate reseeding and recovery of other areas that are seriously damaged by bleaching. 3. Connectivity—Identifying patterns of connectivity among source and sink reefs, so that these can be used to inform reef selection in the design of marine protected area networks and provide stepping stones for larval dispersal over longer time frames, is an important step in building resilience into networks. 4. Effective management—Managing reefs for both health and resilience and monitoring multiple indicators of the effectiveness of current actions are the bases for adaptive management. Effective management is fundamental to the success of any conservation effort and the daily business of managers’ work. 	<ol style="list-style-type: none"> 1. Use the ability to predict bleaching events to enhance coral reef monitoring programs; try to obtain pre- and post-bleaching data. 2. Establish monitoring protocols to answer specific questions about the causes and effects of bleaching events. 3. Use remote sensing tools to increase the level of predictability. 4. Use the ability to predict bleaching events to gain the attention of the public and to solicit their assistance in coral reef conservation. 5. Use the severe impacts of coral bleaching as a way to leverage other conservation measures such as reducing point and non-point sources of pollution. 6. Use coral bleaching events as a way to increase the public’s awareness and peer pressure as to the need to cease destructive fishing practices. 7. Contact coral reef users and encourage them to lessen their direct impact on coral reefs during these stressful periods. 8. Engage divers in providing education and outreach messages about coral reefs so they can take direct action to lessen their physical impacts on the corals during stressful periods. 9. Communicate the long-term impacts of coral bleaching to reef users and solicit help in communicating to decision-makers the kinds of appropriate actions that need to be taken regarding climate change. 10. Identify coral reefs that are resistant to bleaching and develop criteria that will aid in the design of marine protected areas. 11. Establish fully protected reserves in areas resistant to coral bleaching. 12. Enlist the scientific community to assist in communicating the long-term trends that can be expected if current trends of climate change continue. 13. Integrate the geological and biological sciences in such a way as to hindcast our observations into geological times in order to forecast the long-term expectations for coral reefs.

More specifically with respect to mitigating climate change impacts, The Nature Conservancy's R2 toolkit: building resilience into coral reef conservation⁵⁶ recommends a four-level approach (see Table 4.1) that condenses practical application of lessons learned by marine protected area managers during past bleaching events, such as those developed in the Florida Keys National Marine Sanctuary^{9,60} and the GBR^{61,53}. The development of management approaches that emphasise resilience and its application to mitigating the effects of climate change has accelerated with the recognition of the potential for a resilience approach. Management approaches have advanced from making general recommendations^{76,64} to providing increasingly technical and specific ones^{28, 53}, and are turning towards specific recommendations for monitoring and assessment protocols for protected areas that focus on climate-related and resilience indicators⁶¹.

4.3.1.9 Social and economic resilience and governance effects on ecological resilience

There are key points at which the ecological resilience of coral reef can be influenced by socio-economic and governance factors (and vice versa)^{24,21,12}. This discussion does not aim to fully explore these aspects, or to discuss social, economic or governance issues generally (Fenton et al. chapter 23), but rather to illustrate their relevance to ecological significance. Social and economic conditions influence patterns of reef use and impacts, such as fishing practices and terrestrial land management²¹. Fishing practices may be carefully managed, as on the GBR, or may include destructive fishing techniques such as the use of explosives, nets or cyanide. This will have major consequences for the abundance, diversity and connectivity of key fish populations, as well as corals (through direct damage from explosives, etc). Similarly, social and economic contexts are critical to the nature of land management practices, such as land clearing and intensive use of chemical fertilisers and pesticides in farming, and to the capacity of local communities to modify those practices to reduce impacts on reefs or other habitats. Indeed, social and economic factors are the basis of threats to ecosystem resilience, and effective management of those threats requires strategies that are socially and economically sustainable^{14,25,58}.

In this context, the significance of governance arrangements is receiving increasing recognition. Governance relates to the community's capacity to make choices that impact on environmental quality, biodiversity conservation and the like, and the efficacy of implementing those choices. Although governance includes political will and the role of governments, it also includes broader aspects, such as the engagement of various community sectors with reefs and their management. Again, because all local threats to resilience relate to the activities of people, governance and its efficacy directly influence whether resilience is undermined, preserved or strengthened^{12, 62, 27}.

4.4 Resilience of non-reef tropical habitats, ecosystems and processes

Although most scientific attention focuses on the coral reefs of the GBR, an estimated 94 percent of the area of the Marine Park consists of habitats other than coral reefs. This area includes deep seabed, shoals, sponge gardens, sand and mud bottom, deep water seagrass beds, beds and mounds of the calcifying green seaweed *Halimeda*, continental shelf slopes and intertidal mudflats and seagrass beds. Not surprisingly, little is known about the factors that contribute to the resilience of most of these habitats; subsequent chapters in this volume assess the vulnerability of these habitats to

climate change (Diaz-Pulido et al. chapter 7, Waycott et al. chapter 8, Kingsford and Welch chapter 18). However, the general principles of maintaining physical, ecological and chemical processes and structures provide a strong starting point. The major pressures on these habitats are likely to include trawling and line-fishing for top predator fishes, and effects of terrestrial runoff, principally in inshore areas¹¹. Trawling can dramatically disrupt the physical structure of sea bottom habitats, such as sponge gardens and seagrass beds, and also alter ecological structure by removal of target and bycatch species. The major impact of line-fishing is on food-web structure through the removal of top predators, many of which are highly mobile and provide a basis for connectivity between habitat areas and types. Terrestrial runoff contains increased loads of sediments, nutrients and pesticide pollutants (including herbicides), which can interfere with the ecological functions of inshore habitats such as seagrass beds^{39,11}.

In the absence of better information, potential management responses to these pressures can initially only focus on ensuring that sufficient proportions of the ecosystem are protected from the known and likely pressures. These responses include establishing comprehensive, adequate, representative and replicated refuges in spatial arrangements that provide a basis for connectivity, and seeking to reduce excess runoff of sediments, nutrients and pesticides. Reduction of herbicide pollution is particularly important for preserving the resilience of the extensive inshore intertidal seagrass beds¹¹. Similarly, mangrove forests face potential negative impacts from a range of climate related factors, with a range of management measures to mitigate these climate related impacts possible.

4.5 Resilience in the context of species conservation

Many species of particular conservation interest, such as dugongs, turtles, sharks, dolphins and whales, are highly vulnerable to human impacts. This is often due to the nature of their life cycles; they may have low rates of reproduction, even under ideal conditions, or 'bottlenecks' that are particularly vulnerable to disruption, such as turtle nesting sites. Although populations of these species may be resilient when abundant, many are already strongly depressed due to intensive hunting or fishing, or other causes. Under such circumstances, even with strong protection, rates of population recovery are unavoidably slow, and show little capacity for improving resilience. This suggests that reducing or even completely removing pressures and stresses on these species, and managing for resilience, is not likely to be sufficient to regenerate populations within a few decades. This is a particular concern in the context of climate change, which is likely to exert significant additional pressures (Chin and Kyne chapter 13, Hamann et al. chapter 15, Lawler et al. chapter 16) that populations will have little capacity to absorb, adapt to, or recover from.

4.6 Management approaches to maintain resilience of the Great Barrier Reef

On the GBR, management approaches have focused on critical issues considered to be threats to the ecosystem, such as water quality, sustainability of fishing, and tourism activities³. However, it is important to recognise that these management issues are not independent. For example, on coral reefs, it is known that herbivorous fish can graze down enhanced growth of algae due to nutrient increases, providing protection against algal exclusion of corals⁴¹. Protecting fish populations thus provides additional protection against terrestrial runoff of nutrients. Similarly, minimising pollution of reef waters may maintain habitat for herbivorous fishes⁵⁰.

a http://www.gbrmpa.gov.au/corp_site/info_services/publications/brochures/index.html

The Great Barrier Reef Marine Park is jointly managed by the Australian Government and the Queensland Government. The Great Barrier Reef Marine Park Authority focuses on protection of the ecosystems and maintenance of the World Heritage values of the Marine Park, and the Queensland State Government is responsible for day-to-day management, fisheries management and most catchment management activities.

The Great Barrier Reef Marine Park Authority and the Queensland State Government have jointly implemented the Reef Water Quality Protection Plan^b, aimed at directly addressing terrestrial runoff into the GBR. The Great Barrier Reef Marine Park Authority has also implemented a new Zoning Plan, which increases protection of biodiversity^c. Because this Zoning Plan provides increased protection for fishes, it will also provide indirect support for the aims of the Reef Water Quality Protection Plan. The integration of these and other measures will enhance the overall resilience of the ecosystem to deal with a range of threats, not limited to the original issues, and in turn protect the sustainability of reef-dependent industries and communities. Importantly, these threats include the impending impacts of climate change (see subsequent chapters).

The Great Barrier Reef Marine Park Zoning Plan 2004

Aims to provide comprehensive, adequate, representative and replicated protection of biodiversity in no-take areas, with 33 percent of the total area of the Marine Park in highly protected areas, and more significantly, a minimum of 20 percent of each of the 70 bioregions^{23d}. The main activities that are regulated by the Zoning Plan include fishing, collecting, research, tourism, boating and shipping. Allocating a relatively high proportion of refuge areas aims to maintain natural biodiversity, and, through careful design of the Zoning Plan, ensure connectivity between relevant areas (eg fish spawning areas and habitats).

Reef Water Quality Protection Plan

A joint initiative by the Australian and Queensland Governments, the Reef Water Quality Protection Plan aims to halt and reverse the decline in the quality of water entering the reef within ten years. This initiative addresses a major component of ecosystem resilience, and importantly, requires most changes to take place in the catchment upstream of the GBR. The GBR catchment lies outside the jurisdiction of the Great Barrier Reef Marine Park Authority, and therefore implementation is largely the responsibility of communities, rural industries and local governments.

Tourism and recreational use

Tourism and recreation are carefully managed and monitored by the Great Barrier Reef Marine Park Authority through the Zoning Plan, Plans of Management in high use areas such as Cairns and the Whitsunday Islands, limits on use (aimed at addressing carrying capacities), permits and environmental impact assessment requirements for significant developments.

Fishery Management Plans

Primarily the responsibility of the Queensland State Government, these include Plans for Fin Fish and Coral Reef Fisheries, with an Inshore Fisheries Management Plan currently in development. These plans focus on fisheries, rather than ecosystem health, and the Great Barrier Reef Marine Park Authority works closely with the State Government to ensure the plans are consistent with the need to protect the values of the GBR.

b http://www.gbrmpa.gov.au/corp_site/key_issues/water_quality/rwqpp.pdf

c http://www.gbrmpa.gov.au/corp_site/management/zoning

d http://www.gbrmpa.gov.au/corp_site/management/zoning/rap/rap/pdf/rap_overview_brochure.pdf

Importantly, these various management initiatives are not implemented in isolation, but rather as an integrated, ecosystem-based package of complementary measures. They seek to address the *cumulative* impacts and interactions between impacts, and not just individual issues. As outlined above, there are potentially powerful synergies in, for example, simultaneously minimising inputs of sediments, nutrients and pesticides, and ensuring fish biodiversity and abundance is sufficient to maintain processes such as herbivory. Inshore areas are especially vulnerable to over-use, and to impacts of water quality, and so are carefully considered in both Plans of Management and Fisheries Management Plans. Importantly, the broader community increasingly recognise the value of this complementary and integrative approach over single-issue initiatives. In combination, these measures enhance the resilience of the ecosystem to other stresses and enhance the links to social systems. Thus, where previously managers were criticised for addressing water quality while climate change was of even greater concern, it is increasingly understood that the best protection against current and emerging threats, including climate change, is to ensure the ecosystem is as resilient as possible.

Also significant is the incorporation of adaptive management approaches into the management of the GBR. Thus, both the Reef Water Quality Protection Plan and the new Zoning Plan were developed in response to emerging scientific evidence that existing management activities were insufficient to ensure the long-term resilience of the ecosystem. Emerging understanding of the biodiversity of the GBR showed that previous zoning did not provide sufficient coverage of many bioregions. New research and monitoring suggested that degradation of inshore habitats was the most likely outcome of previous land-use practices³⁹. Management is continuing this adaptive approach, developing monitoring and research programs to assess the adequacy and impacts of management actions and strategies, as a basis for future policy development, refinement and adaptation. Included are programs that focus on specific management initiatives, such as the Zoning Plan and the Reef Water Quality Protection Plan, and programs that assess the overall status of the ecosystem, and the related industries and communities.

4.7 Outlook: resilience in the face of changing climate

A key aspect of an adaptive management approach is the realisation of the emerging but urgent need to prepare for the effects of global climate change on the GBR and its habitats. Effective measures to achieve this will require the best possible information about the likely vulnerability to climate change of the various ecosystems and taxa. The present volume is intended to make a start in compiling that information, and clearly demonstrates that impacts are likely to be not only dramatic, but also very difficult to predict with any precision. There is, and is likely to remain, considerable uncertainty about the nature and extent of direct effects and of their interactions with other stressors. As an emerging area of science, assessment of vulnerability to climate change tends to focus on direct effects of climate change on systems and processes, perhaps considering interactions between impacts or stressors (eg climate change and overfishing or eutrophication). However, climate change stressors will also affect the ability of these systems and processes to respond to other stressors. This means that the resilience of the various ecosystems and taxa is likely to be threatened to an unprecedented extent. This, along with the considerable inherent uncertainty about these changes, will significantly increase the challenge of adaptively managing and maintaining ecosystem integrity. Chapter 24 of this volume (Marshall and Johnson) aims to take up this challenge.

References

- 1 Alcala AC and Russ GR (2002) Role of socioeconomic factors in coral reef protection and management. In *Proceedings of the Ninth International Coral Reef Symposium*, vol. 1, Bali, Indonesia, 29–32 .
- 2 Alcala AC and Russ GR (2006) No-take marine reserves and reef fisheries management in the Philippines: a new people power revolution. *Ambio*, 35, 245–254.
- 3 Anthony KRN, Connolly SR and Hoegh-Guldberg O (2007) Bleaching, energetics and coral mortality risk: effects of temperature, light and sediment regime. *Limnology and Oceanography*, 52, 716–726.
- 4 Baker AC (2004) Diversity, distribution and ecology of Symbiodinium on coral reefs and its relationship to bleaching resistance and resilience. In E Rosenberg and Y Loya (eds) *Coral health and disease*. Springer-Verlag, Heidelberg, Berlin, pp. 177–194 .
- 5 Bellwood DR, Hughes TP, Folke C and Nyström M (2004) Confronting the coral reef crisis. *Nature*, 429, 827–833.
- 6 Bellwood DR, Hughes TP and Hoey AS (2006) Sleeping functional group drives coral-reef recovery, *Current Biology*, 16, 2434–2439.
- 7 Birrell CL, McCook LJ and Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Marine Pollution Bulletin*, 51, 408–414.
- 8 Carpenter RC (1990) Mass mortality of *Diadema antillarum* : I. Long term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology*, 104, 67–77.
- 9 Causey, BD (2001) In RV Salm and SL Coles (eds) *Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design*, Bishop Museum, Honolulu, Hawaii, 29–31 May 2001. Asia Pacific Coastal Marine Program Report No. 0102. The Nature Conservancy, Honolulu, Hawaii.
- 10 Chapin FS, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE and Tilman D (1997) Biotic control over the functioning of ecosystems. *Science*, 277, 500–504.
- 11 Chin A (2003) Inter-reefal and lagoonal benthos. In A Chin (ed.) *State of the Great Barrier Reef on-line*. Great Barrier Reef Marine Park Authority, Townsville, viewed 2 February 2007.
- 12 Courtney CA and White AT (2000) Integrated coastal management in the Philippines: testing new paradigms. *Coastal Management*, 28, 39–53.
- 13 Cowen RK, Paris CB and Srinivasan A (2006) Scaling of connectivity in marine populations. *Science*, 311, 522–527.
- 14 DeVantier L, Alcala A and Wilkinson C (2004) The Sulu-Sulawesi Sea: environmental and socioeconomic status, future prognosis and ameliorative policy options. *Ambio*, 33, 88–97.
- 15 Diaz-Pulido G and McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. *Marine Ecology Progress Series*, 232, 115–128.
- 16 Diaz-Pulido G and McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. *Ecology*, 84, 2026–2033.
- 17 Diaz-Pulido G and McCook LJ (2004) Effects of live coral, epilithic algal communities and substrate type on algal recruitment. *Coral Reefs*, 23, 225–233.
- 18 Done TJ (2001) In RV Salm and SL Coles (eds) *Coral bleaching and marine protected areas. Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design*, Bishop Museum, Honolulu, Hawaii, 29–31 May 2001. Asia Pacific Coastal Marine Program Report No. 0102. The Nature Conservancy, Honolulu, Hawaii, pp. 53–59.
- 19 Done TJ, Ogden JC, Wiebe WJ and Rosen BR (1996) Biodiversity and ecosystem function of coral reefs. In HA Mooney, JH Cushman, E Medina, OE Sala and E-D Schulze (eds) *Functional roles of biodiversity: a global perspective*. John Wiley & Sons, pp. 393–429.
- 20 Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B and Norberg J (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1, 488–494.
- 21 Fabricius K, De'ath G, McCook L, Turak E and Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin*, 51, 384–398.
- 22 Fabricius KE, Wild C, Wolanski E and Abele D (2003) Effects of transparent exopolymer particles (TEP) and muddy terrigenous sediments on the survival of hard coral recruits. *Estuarine, Coastal and Shelf Science*, 57, 613–621.
- 23 Fernandes L, Day J, Lewis A, Slegers S, 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 and Stapleton K (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. *Conservation Biology*, 19, 1733–1744.

- 24 Folke C (2006) Resilience: the emergence of a perspective for social-ecological systems analyses. *Global Environmental Change*, 16, 253–267.
- 25 Folke C, Carpenter S, Elmqvist T, Gunderson L, Holling CS and Walker B (2002) Resilience and sustainable development: building adaptive capacity in a world of transformations. *Ambio*, 31, 437–440.
- 26 Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L and Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, 35, 557–581.
- 27 Folke C, Hahn T, Olsson P and Norberg J (2005) Adaptive governance of social-ecological systems. *Annual Review of Environmental Resources*, 30, 441–73.
- 28 Hansen L (2003) Increasing the resistance and resilience of tropical marine ecosystems to climate change. In L Hansen, J Biringer and J Hoffman (eds) *Buying time: a user's manual for building resistance and resilience to climate change in natural systems*. WWF, Washington DC, pp. 157–176.
- 29 Harrison P and Ward S (2001) Elevated levels of nitrogen and phosphorus reduce fertilization success of gametes from scleractinian reef corals. *Marine Biology*, 139, 1057–1068.
- 30 Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology*, 65, 446–454.
- 31 Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, 50, 839–866.
- 32 Holling CS (1973) Resilience and stability of ecological systems. *Annual Review of Ecological Systems*, 4, 1–23.
- 33 Hughes TP (1994) Catastrophes, phase-shifts and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1–23.
- 34 Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Gosberg R, Hoegh-Guldberg O, Jackson JBC, Kleyvas JA, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B and Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933.
- 35 Hughes TP, Bellwood DR, Folke C, Steeneck RS and Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, 20, 380–386.
- 36 Hughes TP, Bellwood DR, Folke CS, McCook LJ and Pandolfi JM (2007) No-take areas, herbivory and coral reef resilience. *Trends in Ecology & Evolution*, 22, 1–3.
- 37 Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook LJ, Moltschanivskyj N, Pratchett MS, Steeneck RS and Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, 17, 1–6.
- 38 Hughes TP and Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology*, 81, 2250–2264.
- 39 Hutchings P, Haynes D, Goudkamp K and McCook L (2005) Catchment to reef: water quality issues in the Great Barrier Reef region – an overview of papers. *Marine Pollution Bulletin*, 3–8.
- 40 Jompa J and McCook LJ (2002) Effects of herbivory and competition on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology*, 271, 25–39.
- 41 Jompa J and McCook LJ (2002) The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnology and Oceanography*, 47, 527–534.
- 42 Kinzig A and Starrett D (2003) Coping with uncertainty: a call for a new science-policy forum. *AMBIO: A Journal of the Human Environment*, 32, 330–335.
- 43 Kline DI, Kuntz NM, Breitbart M, Knowlton N and Rohwer F (2006) Role of elevated organic carbon levels and microbial activity in coral mortality. *Marine Ecology Progress Series*, 314, 119–125.
- 44 Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist*, 32, 674–682.
- 45 Kuntz NM, Kline DI, Sandin SA and Rohwer F (2005) Pathologies and mortality rates caused by organic carbon and nutrient stressors in three Caribbean coral species. *Marine Ecology Progress Series*, 294, 173–180.
- 46 McClanahan TR, Baird AH, Marshall PA and Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, 48, 327–335.
- 47 McClanahan TR, Polunin N and Done TJ (2002) Ecological states and the resilience of coral reefs. *Conservation Ecology*, 6, 18.
- 48 McCook LJ (1996) Effects of herbivores and water quality on the distribution of *Sargassum* on the central Great Barrier Reef: cross-shelf transplants. *Marine Ecology Progress Series*, 139, 179–192.

- 49 McCook LJ (1997) Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Marine Biology*, 129, 713–722.
- 50 McCook LJ (1999) Macroalgae nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs*, 18, 357–367.
- 51 McCook LJ, Jompa J and Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*, 17 Special Issue on Algal Dynamics on Coral Reefs, 400–417.
- 52 McCook LJ, Wolanski E and Spagnol S (2001) Modelling and visualizing interactions between natural disturbances and eutrophication as causes of coral reef degradation. In E Wolanski (ed.) *Physics biology links in the GBR*. CRC Press, Boca Raton, Florida, pp. 113–125.
- 53 Marshall P and Schuttenberg HZ (2006) *A reef manager's guide to coral bleaching*. Great Barrier Reef Marine Park Authority, Townsville.
- 54 Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW and Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*, 311, 98–101.
- 55 Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczyńska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CC and Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, 427, 533–536.
- 56 The Nature Conservancy (2004) *R2 – Reef resilience toolkit, version 2.0*.
- 57 Nyström M and Folke C (2001) Spatial resilience of coral reefs. *Ecosystems*, 4, 406–417.
- 58 Nyström M, Folke C and Moberg F (2000) Coral reef disturbance and resilience in a human dominated environment. *Trends in Ecology & Evolution*, 15, 413–417.
- 59 Obura D (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine and Coastal Marine Science*, 63, 353–372.
- 60 Obura DO, Causey B and Church JC (2006) Management response to a bleaching event. In J Phinney, O Hoegh-Guldberg, J Kleypas, W Skirving and A Strong (eds) *Coral reefs and climate change*. American Geophysical Union.
- 61 Oliver J, Marshall P, Setiasih N and Hansen, L (2004) *A global protocol for assessment and monitoring of coral bleaching*. WWF, Washington DC.
- 62 Olsson P, Folke C and Berkes F (2004) Adaptive comanagement for building resilience in social-ecological systems. *Environmental Management*, 34, 75–90.
- 63 Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science*, 278, 1454–1457.
- 64 Salm R, Clark J and Siirila E (2000) *Marine and coastal protected areas: a guide for planners and managers*. IUCN, Washington DC.
- 65 Salm R, Coles SL, West JM, Llewellyn G and Done T (2001) In R Salm and SL Coles (eds) *Proceedings of the Workshop on Mitigating Coral Bleaching Impact Through MPA Design*, Bishop Museum, Honolulu, Hawaii, 29–31 May 2001. Asia Pacific Coastal Marine Program Report No. 0102. The Nature Conservancy, Honolulu, Hawaii, pp. 1–107.
- 66 Skirving WJ and Guinotte J (2001) The sea surface temperature story on the Great Barrier Reef during the coral bleaching event of 1998. In E Wolanski (ed.) *Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef*. CRC Press, Boca Raton, Florida, pp. 301–313.
- 67 Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M and Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe induced coral mortality. *Ecology Letters*, 9, 835–845.
- 68 Smith SV, Kimmerer WJ, Laws EA, Brock RE and Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science*, 35, 279–385.
- 69 Steneck R (2006) Staying connected in a turbulent world. *Science*, 311, 480–481.
- 70 Steneck RS (2001) Functional groups. In SA Levin (ed.) *Encyclopedia of biodiversity*, vol. 3. Academic Press, pp. 121–139.
- 71 Szmant AM (1997) In *Proceedings of the Eighth International Coral Reef Symposium*, vol. 2, Panama, pp. 1527–1532.
- 72 Walker B, Carpenter S, Anderies J, Abel N, Cumming G, Janssen M, Lebel L, Norberg J, Peterson G and Pritchard R (2002) Resilience management in social-ecological systems: a working hypothesis for a participatory approach. *Conservation Ecology*, 6, 14.
- 73 Walker B, Holling CS, Carpenter SR, Kinzig A (2004) Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society*, 9(2), 5.
- 74 Walker BH (1992) Biodiversity and ecological redundancy. *Conservation Biology*, 6, 18–23.

- 75 West JM and Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology*, 17, 956–967.
- 76 Westmacott S, Teleki K, Wells S and West J (2000) *Management of bleached and severely damaged coral reefs*. International Union for the Conservation of Nature, Gland, Switzerland and Cambridge, UK.
- 77 White AT, Courtney CA and Salamanca A (2002) Experience with marine protected area planning and management in the Philippines. *Coastal Management*, 30, 1–26.
- 78 Wilkinson C (ed.) (2004) *Status of coral reefs of the world: 2004*. Australian Institute of Marine Science, Townsville.
- 79 Wolanski E, Richmond R, McCook LJ and Sweatman H (2003) Mud, marine snow and coral reefs: the survival of coral reefs requires integrated watershed-based management activities and marine conservation. *American Scientist*, 91, 44–51.