

Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean

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Abstract

The impact of climate change through thermal stress-related coral bleaching on coral reefs of the Western Indian Ocean has been well documented and is caused by rising sea water temperatures associated with background warming trends and extreme climate events. Recent studies have identified a number of factors that may reduce the impact of coral bleaching and mortality at a reef or sub-reef level. However, there is little scientific consensus as yet, and it is unclear how well current science supports the immediate needs of management responses to climate change. This paper provides evidence from the Western Indian Ocean in support of recent hypotheses on coral and reef vulnerability to thermal stress that have been loosely termed 'resistance and resilience to bleaching'. The paper argues for a more explicit definition of terms, and identifies three concepts affecting coral-zooxanthellae holobiont and reef vulnerability to thermal stress previously termed 'resistance to bleaching': 'thermal protection', where some reefs are protected from the thermal conditions that induce bleaching and/or where local physical conditions reduce bleaching and mortality levels; 'thermal resistance', where individual corals bleach to differing degrees to the same thermal stress; and 'thermal tolerance', where individual corals suffer differing levels of mortality when exposed to the same thermal stress. 'Resilience to bleaching' is a special case of ecological resilience, where recovery following large-scale bleaching mortality varies according to ecological and other processes. These concepts apply across multiple levels of biological organization and temporal and spatial scales. Thermal resistance and tolerance are genetic properties and may interact with environmental protection properties resulting in phenotypic variation in bleaching and mortality of corals. The presence or absence of human threats and varying levels of reef management may alter the influence of the above factors, particularly through their impacts on resilience, offering the opportunity for management interventions to mitigate the impacts of thermal stress and recovery on coral reefs. These concepts are compiled within an overarching framework of spatial resilience theory. This provides a framework for developing linked scientific and management questions relating to the larger scale impacts of climate change on coral reefs, their management needs and prospects for their future.

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1. Introduction

The impact of climate change on coral reefs of the Western Indian Ocean (WIO, Fig. 1), as well as other parts of the world, has been well documented and is related primarily to rising sea water temperatures and

associated intensification of the El Niño Southern Oscillation (ENSO) phenomenon (Wilkinson et al., 1999; Linden and Sporrang, 1999; Stone et al., 1999; Goreau et al., 2000). During the 1997–1998 ENSO event, the most significant coral bleaching ever recorded in the WIO resulted in 90–95% mortality of corals at the most heavily impacted sites, with 30% mortality on a regional scale (Wilkinson et al., 1999; Wilkinson, 2000). In East Africa, bleaching occurred when summer

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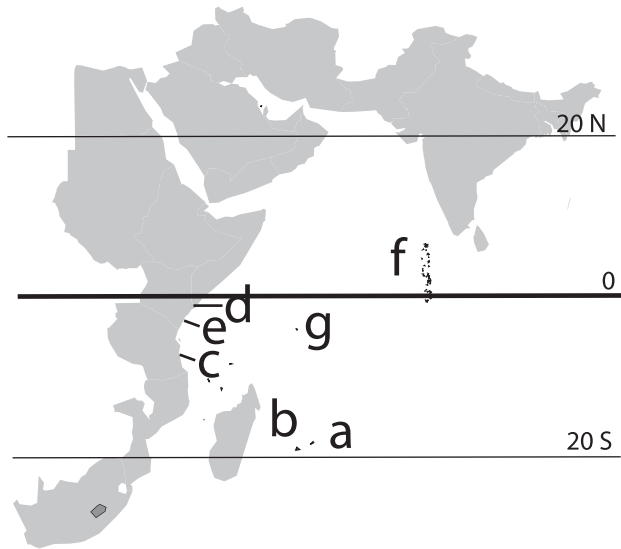


Fig. 1. Map of the western Indian Ocean showing the study sites discussed here: (a) Mauritius, (b) Reunion, (c) Songo Songo Archipelago, central Tanzania, (d) Kiunga Marine Reserve, northern Kenya, (e) Mombasa Marine Park, Kenya, (f) Maldive Archipelago and (g) Seychelles granitic islands.

sea surface temperature (SST) maxima were elevated in February–May by 1–2 °C above normal for over 2 months, causing expulsion of zooxanthellae from coral tissue and the subsequent mortality of corals. Since 1998, minor to moderate coral bleaching events have been reported for a number of areas within the WIO (e.g. Mauritius/Reunion in 1999: Turner et al., 2000; East Africa: Obura et al., 2002), with lower levels of bleaching and mortality than recorded in 1998.

Increasing global temperatures are predicted of 1.4–5.8 °C by 2100 for surface air temperatures globally (IPCC, 2001) and 1–3 °C by 2050 for sea surface waters in coral reef regions (Hoegh-Guldberg, 1999). As a result of this warming trend, the frequency and severity of temperature-induced coral bleaching and mortality events is expected to increase. Historically, mass bleaching events are thought to have occurred on decadal to century-scale frequencies prior to the 1980s, have been documented at a near-decadal frequency from 1982 to present, and are expected to increase to near-annual frequency in the next 20 to 50 years, depending on geographic location (Williams and Bunckley-Williams, 1990; Glynn, 1993; Brown, 1997; Hoegh-Guldberg, 1999). For the Indian Ocean, temperature conditions that were catastrophic in 1998 are predicted to be repeated 1 in 5 years by about the year 2020 within the most vulnerable latitudes in the Indian Ocean (about 10–15° S, Sheppard, 2003), and within a further 10–20 years, farther north and south. Climate change-associated coral bleaching and mortality now represent the greatest threats to coral reefs in the WIO, over and above the

many local threats affecting coral reefs in the region (McClanahan et al., 2000).

The threat of coral bleaching to the future of coral reefs is very real, but the expected impact is largely unknown due to the unprecedented spatial scale of the threat and its novelty to science. Current knowledge is insufficient to predict whether the impacts of climate change on coral reefs will be catastrophic, because corals and zooxanthellae may be unable to adapt fast enough to changing conditions (Hoegh-Guldberg, 1999), or milder, because of yet unquantified adaptive capacities and biogeographic opportunities available to corals and zooxanthellae (Coles and Brown, 2003; Hughes et al., 2003). A core problem in this debate is the likelihood that coral reefs have already changed in unknown ways as a result of human impacts as well as climate changes in the last several hundred years (Sheppard, 1995; Pandolfi et al., 2003), complicating the assessment of their current status and adaptive capacity.

The lack of a coherent set of hypotheses spanning all scales of the coral bleaching phenomenon is a barrier to the advancement of its study and management in a holistic sense, and this paper attempts to rectify this in broad terms within a heuristic framework. This has been done by building on existing work on coral bleaching resistance and resilience (Salm and Coles, 2001; West and Salm, 2003) by combining it with spatial resilience theory (Holling, 2001; Nyström and Folke, 2001).

1.1. Coral bleaching, mortality and recovery

Coral bleaching occurs as a stress response by symbiotic corals to a variety of environmental stressors that cause internal physiological imbalance (Brown, 1990). This paper focuses only on coral bleaching that results from thermal stress caused by positive temperature anomalies (Coles and Jokiel, 1978; Jokiel and Coles, 1990; Coles and Brown, 2003) and recently most commonly related to climate change-induced sea surface temperature warming and intensification of ENSO cycles (see Glynn, 1993; Brown, 1997; Hoegh-Guldberg, 1999; Stone et al., 1999). The bleaching response is a complex phenomenon with many environmental, ecosystem and physiological correlates and components, and is summarized for the purposes of this paper in Fig. 2. Bleaching of the coral colony is a late stage of a variety of physiological responses to thermal stress, including host cell detachment (Gates et al., 1992), oxidative stress (Downs et al., 2002), damage to photosystem II kinetics (Jones et al., 1998; Takahashi et al., 2004) and other mechanisms (see review by Coles and Brown, 2003). The specific bleaching mechanism induced by stress will have different implications for the survival and recovery of corals depending on repair processes associated with it, the bleached condition

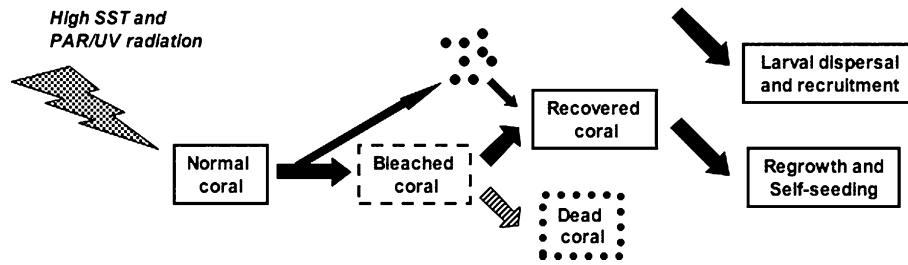


Fig. 2. Bleaching of corals in response to thermal (and/or radiation) stress occurs by expulsion of zooxanthellae. Bleached corals may recover or die depending on the nature and severity of the stress and other mitigating factors. Recovery of individual colonies from bleaching occurs by repopulation by residual zooxanthellae within the tissue, and/or by colonization of free-living zooxanthellae. Following mortality of corals, recovery of the coral population or community occurs by growth and self-seeding through reproduction of surviving colonies and recruitment of larvae dispersed from distant sources.

being already indicative of significant physiological and cellular damage. Bleaching may or may not be followed by mortality of the coral depending on the severity of stress and ability of the organism to withstand it. Thus it is critical to distinguish between bleaching and mortality in discussions of the severity and consequences of coral bleaching (Brown, 1997). The bleaching response is characterized by considerable variation in all stages of the process, and the literature reveals that there is variation across spatial (regional to micro-habitat) and temporal (between repeated thermal stress events) scales, and across levels of biological organization (from species to inter- and intra-colony levels) with interactions among these (see reviews by Glynn, 1993; Coles and Brown, 2003).

The literature outlines a number of factors that may affect patterns of coral bleaching and mortality in response to thermal stress that include physical factors and a range of biological attributes from genetic to ecological levels of organization (Table 1; Salm et al., 2001; Salm and Coles, 2001; West and Salm, 2003; Obura and Mangubhai, 2003). These factors may act at differing stages in the bleaching process. Fig. 3 summarizes this process in a cascade of responses. First, different regions, reefs or sites may be subject to differing levels of thermal stress, second, different corals may show differing degrees of bleaching when exposed to the same thermal stress, and third, different corals may show differing degrees of mortality when exposed to the thermal stress while displaying the same level of bleaching.

Lastly, different reefs may show differing recovery rates following mortality of corals (Fig. 3). Reefs that show robust recovery after severe mortality are said to be resilient to bleaching (West and Salm, 2003). However, the processes that confer resilience to bleaching (Table 1) are not specific to bleaching and fall under the general scope of the term 'ecological resilience' (see further discussion below). Recovery of a coral population following mortality after bleaching occurs as a result of re-growth by surviving colonies which may have suffered no or partial mortality, recruitment of new

individuals from sexual reproduction of local corals, and recruitment from sexual reproduction of distant corals. Partial mortality of coral colonies is common on reefs impacted by severe bleaching (Marshall and Baird, 2000; Obura, 2001; McClanahan et al., 2002) as well as by other factors and threats (Sheppard, 1982), and re-growth of surviving fragments can be rapid in the years following mortality. This does not add new genetic material to a population, but the population may have higher resistance to repeated bleaching as a result of mortality of the weaker genotypes and acclimation of the surviving ones.

The scale of connectivity and contributions to recruitment by larvae from local or distant sources is a critical factor in recovery of a reef. Studies to date have shown a full range of genetic variation among reefs from high differentiation at local scales (e.g. Planes et al., 1998) to high uniformity of various coral reef taxa over scales of thousands of kilometres (e.g. Stoddart, 1984) and intermediates between these (Ayre and Hughes, 2004). The view of marine systems being open with widely dispersing propagules (Roughgarden et al., 1988; Sale, 1991) promoted the paradigm of long distance dispersal of larvae along networks of habitat connected by currents. In contrast to this, direct studies on both recruitment (Jones et al., 1999; Taylor and Hellberg, 2003) and hydrodynamics and modelling (Sammarco and Andrews, 1989) have shown that self-seeding from locally produced larvae may be dominant over recruitment from widely dispersed larvae (Swearer et al., 2002; Thorrold et al., 2002). Reconciling these opposing results is a challenge in current theories on connectivity and their resolution will probably cover a full range of scenarios in which local or distant recruitment predominates. In the case of reefs recovering from large-scale coral mortality, the relative contributions of locally self-seeded propagules of corals and other taxa versus those from a greater distance will have profound implications on both recruitment rates, in the short to medium term (where local reproduction may be depressed by stress and low densities of

Table 1
Environmental, ecological and human factors that are hypothesized to affect coral bleaching avoidance, resistance and resilience

<i>Physical factors that reduce temperature stress</i>		<i>Ecological factors that aid recovery</i>	
Exchange (warm water replaced with cooler oceanic water)	A	Broad size and species distributions	L
Upwelling	A	Areas of considerable residual coral cover	L
Areas adjacent to deep water	A	Availability and abundance of local larvae	L
Wind-driven mixing	A	Recruitment success	L
		Low abundance of bio-eroders, corallivores, diseases	L
		Diverse, well-balanced community (e.g., herbivorous fishes)	L
<i>Physical factors that enhance water movement/flush toxins</i>		<i>Large-scale factors that aid recovery</i>	
Fast currents (eddies, tidal and ocean currents, gyres)	AR	Connectivity by currents (from larval source reefs)	L
Topography (peninsulas, points, narrow channels)	A	Strong and reliable source of larval supply	L
High wave energy	AR		
Tidal range	AR		
Wind	AR		
<i>Physical factors that decrease light stress</i>		<i>Human/management factors</i>	
Shade (high island shadow, reef structural complexity)	AR	Over-fishing	LM
Aspect relative to the sun	AR	Destructive fishing	LM
Steep reef slope	AR	Pollution	RLM
Turbidity	AR	Nutrients/sewage input	RLM
Absorption, e.g. by coloured dissolved organic matter (CDOM)	AR	Siltation/erosion	RLM
Cloud cover	AR	Tourism	LM
		Habitat destruction	LM
		ICM Management Plan in use	RLM
		MPA Management Plan in use	RLM
<i>Physical factors that increase resistance</i>			
Temperature fluctuations	AR	Fisheries management in operation	LM
Emergence at low tide	AR	Overall management effectiveness	RLM
<i>Population factors of adaptation/acclimation</i>			
Genetic variation in bleaching traits	RL		
Sexual reproduction (recombination)	RL		
Acclimation history at local site	RL		
Resistance to other stresses	RL		

Adapted from Salm and Coles, 2001; West and Salm, 2003; Obura and Mangubhai, 2003. Factors may influence one or a combination of (A)voidance, (R)esistance, resi(L)ience, or (M)anagement interactions (sensu West and Salm, 2003).

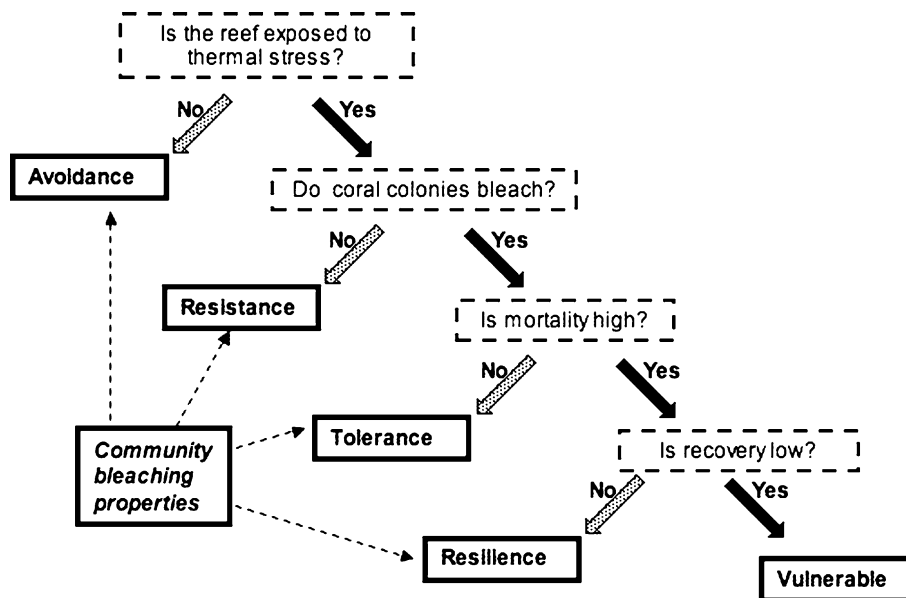


Fig. 3. Cascade of the stages proposed in applying resilience concepts to coral bleaching. The stages extend from whether a reef is exposed to thermal stress or not, through bleaching and mortality responses to recovery following mortality. The properties of bleaching avoidance, resistance, resilience (sensu West and Salm, 2003) and tolerance (this paper) are shown at their respective loci in the cascade.

Table 2
Bleaching protection, resistance, tolerance and resilience properties

Property	Protection	Resistance/Tolerance	Resilience
Description	Some reef areas appear to ‘avoid’ or be protected from the oceanographic conditions (e.g. high temperatures, high radiation and still waters) that induce coral bleaching (e.g. by oceanographic and climatic features such as upwelling zones, current systems, storm and cyclone belts). At local scales, some corals and habitats appear to be protected from the worst thermal conditions by local features, microenvironmental variation, or fluctuating conditions	Some reef areas, zones, patches and individual coral heads appear to be resistant to thermal stress and manifest lower bleaching and/or mortality, while adjacent areas and corals manifest greater bleaching and mortality. Resistance to bleaching and resistance to mortality (tolerance, see later sections) are different. Resistance and tolerance may be related to intrinsic (genetic) or extrinsic (environmental) factors	In the context of coral bleaching, resilience is the ability for coral communities and reefs to return to their initial state following significant mortality. Resilience can be differentiated into intrinsic (local ecological factors) and extrinsic (larger scale connectivity and larval supply) components
Scale			
Subcellular		+	
Organismal	+	+	
Local/ population	+	+	+
Regional/large	+		+

Adapted from Done, 2001; Salm et al., 2001; West and Salm, 2003. The approximate scales of influence (biological, spatial and temporal) are indicated, from subcellular to regional.

surviving adults), and on the genetic structure of populations and their ability to respond to future bleaching events.

The four stages identified in Fig. 3 have previously been grouped under three types of responses termed avoidance, resistance and resilience to thermal stress (Table 2; Done, 2001; West and Salm, 2003). They are presented here, with adaptations to the terminology, as working hypotheses of properties that determine the outcome of thermal stress on a given reef. They may be based on one or a combination of factors that affect the degree of bleaching, mortality and subsequent recovery (Table 1). They may operate at different levels of spatial, temporal and biological organization. Hypotheses on their influence can be tested by investigating and measuring the contributions of the environmental and biological factors (Table 1) to the bleaching response at the organismal level (Fig. 2) and the population and community level consequences at a given site (Fig. 3).

Table 2 summarizes the terminology and concepts used in this paper. The term ‘protection’ is preferred in this paper to ‘avoidance’ (Done, 2001), describing the protection offered by a range of physical factors to corals and reefs from thermal stress. ‘Avoidance’ is an active noun implying reaction and is thus inappropriate to fixed locations. ‘Protection’ from thermal stress is parallel in usage to, for example, ‘protection’ or ‘shelter’ from waves or predation, with greater established use in ecology. Resistance (sensu West and Salm, 2003) will be differentiated between (a) ‘intrinsic’ and ‘extrinsic’ components, corresponding to genetic versus environmental components respectively, and (b) in relation to bleaching versus mortality. Distinctions between these dichotomies are further explored in the Discussion.

1.2. Coral reefs and resilience

Resilience concepts are being increasingly applied to coral reefs from both theoretical (e.g. Nyström and Folke, 2001) and empirical perspectives (e.g. McClanahan et al., 2002; Bellwood et al., 2004). Resilience is a systems concept, addressing the ability of a system to undergo change but retain the same functions and general structure (Holling et al., 1995). This requires some sort of memory within the system that stores information and makes it available for innovation and maintaining the system in a stable state (Holling, 2001; Nyström and Folke, 2001). Systems may have multiple stable states, to which they may trend after perturbations away from one of the states (Holling, 2001). Depending on the scale of the perturbation away from a stable state, the system may return to it, or it may gravitate towards a different one. A system that tends to return to the same state even after major perturbations has high resilience, while one that shifts into another state has low resilience. Thus resilience of a system requires some capacity for memory, which enables it to be self-organizing and return to a stable state. This can, at least in principle, be quantified on a measurable scale. Resilience can be applied to social as well as ecological systems (Folke et al., 2003; Holling, 2001), the common property being the capacity for self-reorganization, i.e. some sort of memory and mechanisms for reorganization.

In biological systems, the system or ecological memory that prescribes the stable states and enables movement of the system towards one of them is held in genes and the genetic diversity of the community. Broadly and operationally, this is indicated by the structure and function of species in the system, their

interactions within the environment and their evolutionary history. This broader concept of the genetic basis of a system or ecological memory is generally captured in the term ‘biodiversity’.

The concept of ‘spatial resilience’ is differentiated from that of ecological resilience by recent authors (Nyström and Folke, 2001; Bengtsson et al., 2003), most importantly in terms of the spatial scale over which it is applied. Ecological resilience generally applies to properties within the spatial boundaries of an ecosystem. In coral reef studies, this is generally considered to extend up to tens and sometimes hundreds of kilometres. Spatial resilience extends beyond this to include large-scale functions and processes beyond the boundaries of an ecosystem unit. For a coral reef, this would include the processes of connectivity to other reefs by currents and larval dispersal, large-scale oceanographic phenomena such as upwelling in adjacent systems and other features that may occur over hundreds to thousands of kilometres.

Ecological resilience has traditionally been discussed in terms of species diversity and relative abundance (e.g. Holling, 1973), that is, the components of ecological memory, though it is not always clear that high species diversity confers high resilience (see early theoretical studies, May, 1982). However, the mechanisms of reorganization are increasingly considered to be as important as, and perhaps more relevant than species diversity. These new ideas focus on the roles of functional processes (such as herbivory, recruitment, connectivity) and the functional overlap (or replaceability, or redundancy) of multiple species in a system (Nyström and Folke, 2001; Bellwood et al., 2004). Functional diversity contributes to resilience in multiple ways: multiple species can replace one another; slight differentials in their traits mean their functional roles do not perfectly overlap; and differences in their vulnerabilities to different disturbances mean they are not affected equally by all disturbances (Elmqvist et al., 2003; Bellwood et al., 2004). Importantly, the components of ecological memory and the functional diversity and replaceability in ecosystems are all coded in genes, and captured in the term ‘biodiversity’ as indicated above.

1.3. Management of coral bleaching

In terms of management of coral reefs, current science offers limited guidance on how to mitigate the impacts of climate change (Westmacott et al., 2000; Obura et al., *in review*), and on how to manage impacts with appropriate responses to minimize losses and suffering to human populations dependent on coral reefs. Given that the immediate threat of climate change is beyond the geographic scope of management, that its

outcome is affected by multiple interactions with many other threats and that regional degradation may severely limit opportunities for recovery locally, the prospects of managing the impacts of climate change seem remote. If climate change and the issue of coral bleaching are not addressed the investments made in managing other threats through site-specific management in Marine Protected Areas (MPAs) may be undermined. This is because coral communities at sites with historically high-priority for protection may degrade with changing climate while other sites may require higher relative status or prioritization.

Numerous management tools and guidelines for mitigating the impacts of climate change are being developed as conservation agencies try to address the serious threat that coral reef managers are facing from climate change (Hansen, 2003; TNC, 2004; Marshall and Schuttenberg, 2004). These are based on the precautionary principle and maintenance of the adaptive capacity of ecosystems and their components to resist extant threats or even augment their adaptive capacity to resist future threats and changing environmental conditions. Their theoretical framework framed in the phrase ‘coral and reef resistance and resilience’ draws on a diverse range of ecological concepts (Salm and Coles, 2001; West and Salm, 2003), but is yet at early stages of scientific enquiry.

This paper will explore the application of spatial resilience theory as applied to coral reefs (Nyström and Folke, 2001; Nyström et al., 2000) to the properties of thermal stress on corals (Table 2) using evidence from the WIO (Fig. 1). Examples from other parts of the world will further illustrate this. The concept of resilience has been criticized for inclusion of too many parameters such that in the end it explains little. A primary goal of this paper is to present a framework of testable hypotheses relevant to coral bleaching. It is hoped that this will assist both the scientific investigation of the medium to large-scale implications of coral bleaching (at the scales of ecosystems and connected regions), and the further development of a framework for the conservation of coral reef environments in the context of climate change and coral bleaching, in individual and/or networks of MPAs. Drawing on the strengths of resilience as a concept, this may be applicable to other ecosystems, their larger scale ‘bioregions’ and their management.

2. Results

This section presents recent evidence and developments from the Western Indian Ocean from a variety of sources, including published work, grey literature and some original results.

2.1. Thermal protection

While most of the Indian Ocean suffered severe coral bleaching and mortality in 1998 (Linden and Sporrang, 1999; Wilkinson et al., 1999), the reefs of Mauritius, and to some extent Reunion, suffered lower impacts (Fig. 1a,b; Turner, 1999; Quod, 1999; Quod and Bigot, 2000). Turner (1999) reported that Mauritius, in particular, suffered low levels of bleaching and near-zero mortality in spite of a 1–1.5 °C positive temperature anomaly in the region during February and March 1998 on a scale they report to have caused bleaching in aquarium and field experiments. In early February, cyclone Anacelle passed 60 km east of Mauritius causing massive rainfall on both islands with a high cloud cover and low sunshine hours for the month of February. Bleaching of corals on Mauritian reefs was reported for most sites (85%), but at low levels (<15%; Quod, 1999; Turner et al., 2000), with many colonies becoming pale rather than fully white. Only one site, 5 km offshore of the main island on a barrier reef and therefore probably beyond the cloud cover associated with the main island, showed high levels of coral mortality one year after the bleaching event (at >50%, Turner et al., 2000). In Reunion, bleaching in 1998 was reported as moderate and recovery good, and only affected corals in reef zones stressed by other factors, such as pollution and eutrophication (Quod, 1999).

Low levels of bleaching on Mauritius and Reunion did not appear to result from their high latitude, as other sites at similar latitudes in the Indian Ocean reported high levels of bleaching and mortality during the same months in 1998 (Table 3). At these other sites, high SST anomalies occurred without the moderating factors of reduced irradiance, increased cloud cover, water-column mixing and rainfall associated with a cyclone. Observations from

these sites included ‘high’ levels of bleaching at 4 out of 6 sites, ‘high’ mortality at 2 of 6, and ‘moderate’ or 20% mortality at 2 of 6 sites (Table 3).

The reefs of the Songo Songo archipelago in southern Tanzania (Fig. 1c) were first surveyed in the mid-1990s and reported to have largely undamaged coral reefs, with 50–60% hard coral cover on patch reefs and the outer fringing reef slope (Darwall and Guard, 2000). The reefs were reported to have escaped the main impacts of coral bleaching in 1998 (Muhando, 1999; M. Nur, pers. comm.), and surveys in early 2003 confirmed the high coral cover and diversity on the reefs from the surface to >20 m in the archipelago (Obura and Richmond, 2005). In 2003, the coral cover was as high as 60–90% in patches, the reefs being dominated by monotypic stands of *Galaxea astreata* and staghorn *Acropora* spp. Such coral communities were typical of mainland East African reefs before 1998 (Hamilton and Brakel, 1984; Obura et al., 2000). However, both *G. astreata* and *Acropora* spp. showed the highest susceptibility to bleaching and mortality (Obura, 2001; McClanahan et al., 2001), shifting these communities to dominance by turf algae and/or sub-dominant coral species.

The Songo Songo Archipelago is located offshore of the Rufiji River delta in southern Tanzania where the continental shelf widens from 8–10 km to 35 km wide (Darwall and Guard, 2000) and covers a basin area of some 1600 km². The outer fringing reef is relatively continuous with the Mafia island reef system to the north, forming a partial barrier that traps outflow from the river and delta in the large basin of the archipelago. Turbidity in the archipelago is reported to be higher than on other reefs in East Africa (Darwall and Guard, 2000; Obura, pers. obs.), though no measurements have been reported in the literature. The persistently high

Table 3
Summary of 1998 bleaching and mortality reports from high-latitude locations in the western Indian Ocean

Location	Positive SST anomaly, 1998	Other conditions, 1998	Bleaching	Mortality	Ref.
Mauritius (21° S)	+1–1.5 °C for >1 month	Cyclone Anacelle. High rainfall, cloud cover, waves. Low sun hours	Low (<10%), observed at many sites (85%).	Not noticeable. One offshore site with >50% mortality 1 year later	Turner et al., 1999, 2000
Reunion (21° S)	High anomaly observed	High rainfall	Moderate, at ‘pre-stressed’ sites	Recovery reported as good	Quod, 1999; Quod and Bigot, 2000
Madagascar, northeast (15° S)	High anomaly observed	None	High, inferred from high mortality observations	High, >30%	Obura (pers. obs.); McClanahan and Obura, 1997
Madagascar, southwest (23° S)	High anomaly observed	None	High	10–20%	Quod and Bigot, 2000
Mozambique, northern (12–17° S)	High anomaly observed	None	High, inferred from mortality observations	Moderate/variable: 20–30%	Schleyer et al., 1999
Mozambique, southern (21° S)	High anomaly observed	None	High, inferred from mortality observations	High/variable: 20–80%	Schleyer et al., 1999
Maputaland, South Africa (22° S)	5-year trend of +0.25 °C yr ⁻¹	High water movement, deep reefs	Limited partial bleaching	None	Schleyer and Celliers, 2000

turbidity probably results from the combined effects of the high river input and long residence time of water in the area. Other parts of southern and northern Tanzania and the Kenyan coast have narrow fringing reef systems (1–5 km wide) along the mainland or island shores on narrow continental shelves (8–10 km wide; Darwall and Guard, 2000; Horrill et al., 2000; Obura et al., 2000). While many of these fringing reef systems have inner lagoons and patch reefs with high levels of turbidity from local rivers and mangrove estuaries (e.g. Malindi: van Katwijk et al., 1993; McClanahan and Obura, 1997), the spatial scale is smaller with correspondingly higher flushing rates and lower water residence times. Turbidity has been found to reduce the synergistic effects of high heat and light stress on corals (Coles and Jokiel, 1978; Table 1). The greater extent of the waters in the Songo Songo Archipelago may have persistently high-turbidity that is not maintained in smaller systems where flushing is higher, thus protecting the former from bleaching and mortality in a way that is not experienced by the smaller systems on the East African coast.

2.2. Thermal resistance and tolerance

In Kenya (Fig. 1d,e), inter- and intra-specific differences in resistance of corals to thermal stress were shown during bleaching events in 1998 and 2003. Data for the 1998 event were obtained from a wide range of reefs spread over 500 km of coastline such that site-specific differences in environmental parameters that might affect bleaching were averaged out by aggregating the sites together (Obura, 2001). Additionally, highly uniform bleaching and mortality were reported at widely differing sites (Obura, 2001; McClanahan et al., 2001), suggesting a uniform environmental threat. Data for the 2003 event were from two shallow back reef coral communities in Mombasa, each covering approximately 500 m² and separated by about 7 km. The small size and uniform habitat within and between the two sites suggests variation in environmental parameters between them would be minimal.

The severe bleaching event of 1998 revealed widely different bleaching responses between coral species, which could be separated into three basic patterns (Fig. 4; Obura, 2001): (a) high bleaching and mortality; (b) low bleaching and mortality; and (c) high bleaching but low mortality. These three strategies show that (a) coral species bleach to different degrees in response to different stress levels, and (b) the degree of mortality following bleaching is not uniform between species, and that some species appear to show high mortality with low levels of bleaching (Obura, 2001).

Inter-specific differences in bleaching and mortality responses were also demonstrated during a milder bleaching event in 2003, when bleaching and mortality rates were lower (Fig. 5). Bleaching was noted shortly

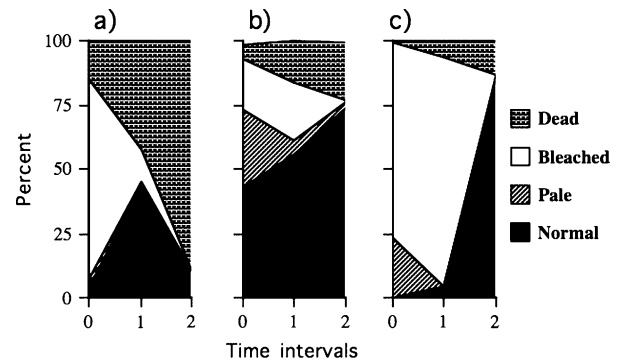


Fig. 4. Interspecific bleaching resistance strategies of corals on Kenyan reefs in response to the El Niño Southern Oscillation of 1998 during (time 0), 6 months after (time 1) and 12 months (time 2) after the event. Resistance strategies are described as (a) high vulnerability, (b) low bleaching, high survival, and (c) high bleaching, high survival. These strategies were derived from 14 species bleaching patterns sampled using random population sampling methods. From Obura, 2001.

after 20 April, 2003, and observations were recorded on permanently marked colonies on 1 and 18 May, and after all bleaching had ceased on 11 August, 2003. Of three abundant species with high levels of sampling, *Pocillopora eydouxi* showed the highest bleaching and mortality rates, *P. damicornis* showed low to moderate bleaching and mortality, and *Porites lutea* showed low bleaching and no mortality.

Intra-specific differences in coral bleaching and mortality patterns were also shown in 2003. *Pocillopora damicornis* showed average bleaching levels of 21% by 18 May, which declined to zero on 11 August (Fig. 6). Average mortality of *P. damicornis* on 18 May was ≈16%, increasing to 25% by August. There were strong differences in individual colony responses, however, with both bleaching and mortality levels varying from 0 to 100% (Fig. 7a). All colonies that underwent

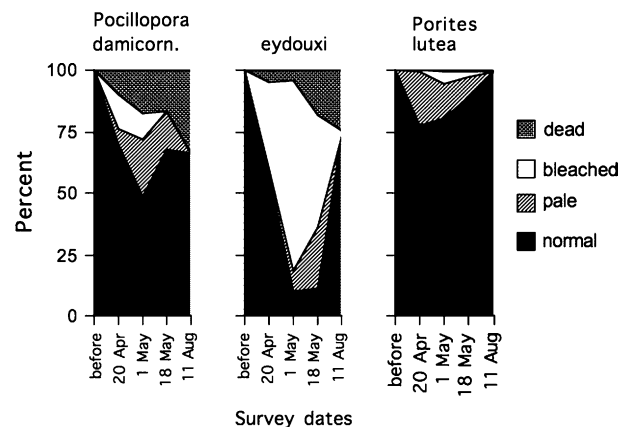


Fig. 5. Interspecific bleaching resistance differences between two species of *Pocillopora* (left, *P. damicornis* and *P. eydouxi*) compared to *Porites lutea* (right) in April–August 2003. Y axis shows the percentage of colonies manifesting normal, pale and bleached condition, and mortality.

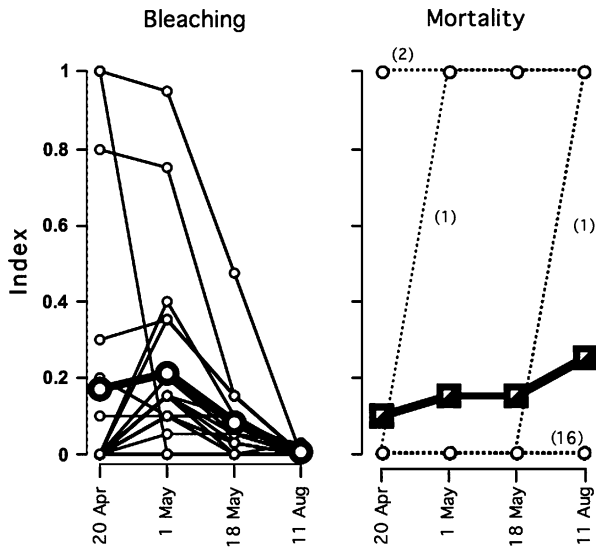


Fig. 6. Individual colony bleaching and mortality trajectories in 2003, showing individual colonies in light lines ($n=20$), and the mean in heavy lines with symbols. The index quantifies bleaching and mortality between 0 to 1. Bleaching index = (%bleaching + half of %pale) \times proportion of colony alive. Individual colony trajectories for mortality overlap, the numbers in brackets indicate the number of colonies following the four different lines shown.

bleaching levels $\geq 20\%$ showed full recovery, and all colonies ($n=3$) that were recorded with zero bleaching levels in May suffered 100% mortality by August (Fig. 7b). Thus bleaching level and mortality were inversely correlated (Spearman's coefficient of rank correlation, $\rho = -0.516$, $P < 0.05$). Two colonies were already dead by the first survey of 1 May, so it is not known if they bleached between 20 April and the beginning of May, or died without having bleached.

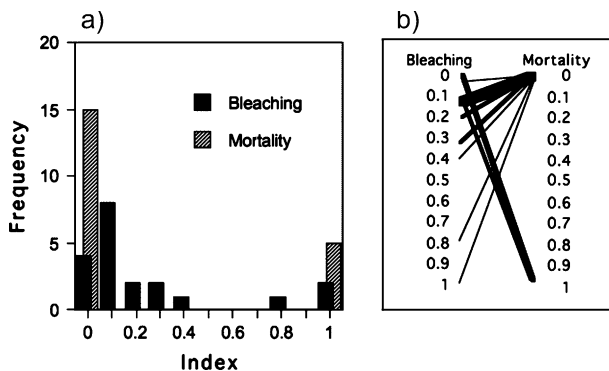


Fig. 7. Maximum bleaching and mortality levels documented for individual colonies of *Pocillopora damicornis* in Mombasa Marine National Park in 2003 (from Fig. 6). Maximum bleaching was generally recorded around 1 May, 2003, and maximum mortality was recorded on the last sample day, 11 August, 2003. (a) Frequency distributions and (b) pairwise comparison by colony. Spearman's rank correlation of maximum bleaching and mortality $\rho = -0.516$, $P < 0.05$.

2.3. Resilience

Intrinsic or ecological resilience of sites following high levels of bleaching and mortality is suggested by evidence from protected areas in Kenya (Fig. 1e). Following mortality of corals in 1998, hard and soft coral cover decreased on shallow Kenyan reefs by 50–80%, macroalgal cover rose by 222% on unprotected reefs and 115% in MPAs, and algal turf rose by 3% on unprotected reefs and 88% in MPAs (Fig. 8; McClanahan et al., 2001). Past studies have demonstrated the interactions between fishing, predation on sea urchins, herbivory and coral cover in shallow backreef coral communities in Kenya (McClanahan, 1992). On protected reefs, algal turf and fleshy algae increased by approximately similar levels (Fig. 8), while on unprotected reefs, rapid colonization and growth by fleshy algae occurred. In protected areas, high rates of herbivory control rapid growth and dominance by fleshy algae, maintaining algal populations in turf forms (Littler et al., 1989), which provides a suitable substratum for coral recruitment (Tamelander, 2002). On unprotected reefs, however, the absence of fish herbivores leads to rapid growth of algal turf forms into fleshy macroalgae (McClanahan et al., 1996), which eventually dominate the substratum. Dominance by fleshy algae inhibits both coral recruitment and growth of adult colonies. It is thus expected to retard the return of unprotected reefs that are affected by bleaching to a state of high dominance and diversity of corals, their state prior to heavy fishing. The smaller increase in fleshy algae following coral mortality on protected reefs should allow greater coral recruitment and recovery

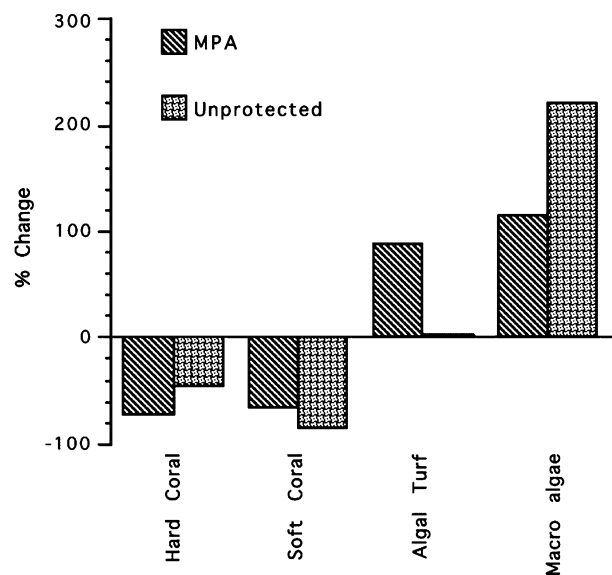


Fig. 8. Changes in benthic cover categories in the year following mass coral mortality in 1998–1999, in unprotected and protected sites. Source: McClanahan et al., 2001.

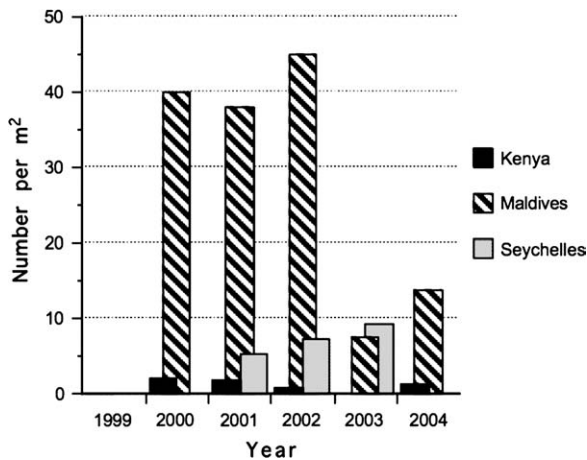


Fig. 9. Recruitment of coral <50 mm diameter onto natural substrata in Kiunga, Kenya; North Male Atoll, Maldives; and the granitic islands, Seychelles (colonies per m²). Sampling in Maldives started in 2000, and Seychelles in 2001. No data were collected in Kenya in 2003. Sources: Zahir et al., 2002; Obura et al., in review; unpublished data: F. Benzoni, N. Bianci, A. Cargnano, U. Engelhardt.

than would be possible on unprotected reefs, a consequence of the greater ecological resilience attributed to protected reefs by the presence of herbivores (Bellwood et al., 2004).

Larger-scale contributions to resilience were suggested by reported recovery rates of reefs in the Maldivian Archipelago and the Seychelles granitic islands, compared to the mainland coast of Kenya (Fig. 1e–g). In 1998, all three areas suffered severe mortality levels of ≥ 50 –80% (Wilkinson, 2000). In 2001–2002, coral recruitment rates and coral cover differed markedly between the Maldives on the one hand and Kenya and Seychelles on the other (Fig. 9). The Maldives experienced high recruitment within two years following coral mass mortality in 1998 (Loch et al., 2002; Zahir et al., 2002). Recruitment was low in Kenya (Obura et al., 2002; Obura et al., in review) and in the Seychelles granitic islands up to 2001 (Engelhardt, unpublished data). Recruitment in Kenya has stayed at similar low rates of ≤ 2 m⁻² to date but stabilized at ≥ 10 m⁻² in the Seychelles and Maldives from 2003. The precise sources of high recruitment in the Maldives and Seychelles are not known; no published reports from either island system noted unimpacted reefs.

2.4. Vulnerability

Finally, reef areas that do not exhibit any of the above properties are vulnerable to thermal stress. Following mortality, they persist at lower states of coral cover and diversity, or even switch to alternate states. In the six years of monitoring in the Kiunga Marine National Reserve in Kenya since 1998, three groups of sites were distinguished by their response to bleaching

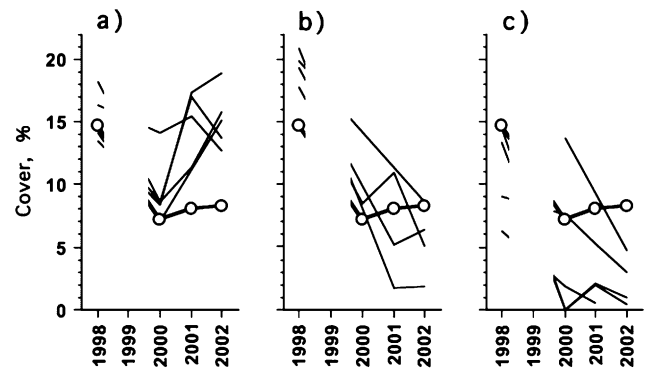


Fig. 10. Vulnerability to coral bleaching, Kiunga Marine National Reserve, Kenya. (a) Sites with initially high coral cover and good recovery, (b) sites with initially high coral cover but low to no recovery, (c) sites with initially low coral cover and low to no recovery. The latter two show high vulnerability due to their low avoidance, resistance and resilience to coral bleaching. Data were not collected in 1999.

(Fig. 1d; Obura, 2002). Approximately one third of sites had high levels of coral cover and diversity before the El Niño event and, following mortality, have shown reasonable levels of recovery (Fig. 10a). Another third started with low levels of coral cover and diversity, suffered mortality, and remained at comparably low levels (Fig. 10c). The final third had moderate to high levels of coral cover and diversity before bleaching, but following mortality have not recovered, and some have even declined further (Fig. 10b). This last category are the vulnerable reefs.

3. Discussion

The discussion will explore some difficulties in the evidence presented in this paper. It will highlight some areas of ambiguity in the conceptual framework that require better framing and will conclude with its relevance to management.

3.1. Bleaching protection

The list of protection factors (Table 1) can be segregated into three major classes of variables: oceanographic and climatic features that are variable in nature (upwelling, cyclones, temperature variability, etc.), topographic and bathymetric factors that are fixed (proximity to deep water, steepness of island and reef slopes, proximity to breaking waves, aerial exposure at low tide), and physical microhabitat features that change or are biogenically derived (shading by corals, mixing caused by microtopography of coral heads, etc.). Done (2001) identifies the larger-scale oceanographic features as site-specific properties that achieve 'avoidance' of thermal stress. West and Salm (2003) include these in their broader list of resistance factors, which at

the smaller end of the scale include some biologically derived physical properties such as the influence of coral heads and the reef framework on water mixing and shading. The broad range of spatial (and temporal) scales, and the mixing of purely physical and biogenic factors complicate a simple classification of protection factors.

For example, water cooling can occur in multiple ways on different scales. It can be caused by cyclone and storm belts, as in the example of Mauritius and Reunion in 1998 (see earlier sections), which may extend across hundreds to thousands of kilometres causing water-column mixing and decreased heating. It may also be caused by topographic and bathymetric features that cause upwelling and mixing which may extend from continental shelf and archipelago scales of hundreds of kilometres to reef zone and organismal scales of hundreds to tens of metres. The larger-scale processes can be clearly be said to offer protection from thermal stress as they protect a reef system or area from a broader signal affecting other parts of the surrounding region. On smaller scales, upwelling around a promontory may be constant (in a coastal current) or may fluctuate (due to tidal currents and eddies), or may cause a constant or fluctuating depression in the thermal stress. These may confer protection by reducing the thermal stress signal or they may promote ‘resistance’ by creating a fluctuating environment that promotes acclimation of individual organisms. Thus depending on the scale, protection factors may also contribute to environmental components of variation in an organism’s phenotype, i.e. as extrinsic resistance mechanisms. Important to this will be the scale of variation in the factor relative to aspects of the coral’s life history, such as size, lifespan and larval dispersal distance. In addition, secondary factors may confer protection

through interaction with the primary signal (thermal stress), such as the effects of PAR and UV radiation. These different aspects of protection factors, and examples, are summarized in Table 4. It should be explicit that even for the larger-scale protection factors, the degree of protection may vary from one time to another resulting in different exposure of a site to thermal stress conditions in different years.

3.2. Bleaching versus mortality: resistance and tolerance

There is often inadequate distinction between bleaching and mortality in the literature, particularly in the context of large-scale bleaching events. While low level bleaching of corals without mortality has been noted for many years by researchers (Douglas, 2003), the language associated with large-scale bleaching events followed by mass mortality—whether caused by thermal stress (Glynn, 1993) or other threats (e.g. floods, Goreau, 1964)—has dominated the conceptualization of coral bleaching. Nevertheless, there is a large and increasing body of literature documenting the distinction between a coral colony’s susceptibility to bleaching and, following that, mortality (Glynn, 1993; Berkelmans and Oliver, 1999; Marshall and Baird, 2000; Obura, 2001; Coles and Brown, 2003; McClanahan et al., 2002) and other stresses (e.g. sedimentation; Rogers, 1990; McClanahan and Obura, 1997).

Results presented here from Kenya show an inverse correlation between bleaching and mortality, in individual colonies of the branching coral *Pocillopora damicornis* (Figs. 6, 7). Colonies that showed high bleaching levels suffered no mortality while those that showed no, or little bleaching, died. This result runs counter to the general sense that bleaching is an

Table 4

Environmental (physical) factors that confer protection from thermal stress, and that contribute environmental (extrinsic) controls on coral and/or zooxanthellae phenotypic expression of resistance and tolerance

Property	Scales (general)	Action	Examples
Thermal protection	Larger than the local scale (e.g. regional and seasonal factors) and/or highly regular and reliable	Alter the local thermal stress signal away from its level in the surrounding geographic area	Cyclones and storms reduce the magnitude of elevated sea surface temperatures Upwelling induced by tidal and current patterns and shelf or reef topography
Environmental (extrinsic) factors affecting resistance and/or tolerance	On the scale of the local to microenvironment and organism, fluctuating and less predictable	Interact with the organism’s genotype affecting phenotypic expression and natural selection	Fluctuating temperature regimes in shallow reef environments raise tolerance to thermal stress Other fluctuating environmental factors (e.g. tidal exposure) may also confer general tolerance to thermal stress
Interacting or secondary physical factors	Variable	Alter the impact of the thermal stress signal	Turbidity and CDOM reduce light stress, reducing thermal stress Tidal currents enhance water exchange that clear toxins and metabolites from coral boundary layers reducing stress, and can reduce temperatures

equivalent, or early indicator, of mortality. This result also argues against combining bleaching and mortality results into a single index, though at coarse taxonomic and geographic resolutions this does yield useful comparisons (e.g. McClanahan et al., 2002). In keeping with recent proposals (Marshall and Schuttenberg, 2004), it is proposed that the term bleaching resistance related to the first property, i.e. the degree of bleaching experienced by a coral, and tolerance to the second property, i.e. the degree of mortality experienced. A coral that shows a high predilection to bleach under a given thermal stress would show low resistance to bleaching, and vice versa. A coral that shows a low predilection to mortality under the same stress would have a high tolerance. Thus, all four combinations of low versus high thermal resistance and tolerance should theoretically be possible (Table 5).

Thermal resistance and tolerance will probably vary depending on the mechanism(s) of bleaching damage (Coles and Brown, 2003). For example, resistance and tolerance to thermal stress mediated through damage of the photosystem II repair capability at the molecular level (e.g. Takahashi et al., 2004) will probably differ from resistance and tolerance to thermal stress mediated through damage of cellular repair mechanisms following host cell detachment (Gates et al., 1992). The implications of either of these mechanisms of damage may include molecular damage to photosynthetic machinery within zooxanthellae, oxygen toxicity in host cells and cellular damage in host cells and tissues. These occur across a range of levels of biological organization, and thereby also of a range of spatial and temporal scales. High variability in coral species' induction thresholds of these different mechanisms of thermal stress resistance and tolerance should therefore be expected.

This separation between bleaching resistance and tolerance offers an empirical avenue into testing the physiological role of bleaching. While it may not yet be possible to address the evolutionary claims and consequences of the Adaptive Bleaching Hypothesis (Buddemeier and Fautin, 1993; Buddemeier et al., 1997), it may be that at the organismal and ecological level, bleaching serves a homeostatic function (*sensu* Stebbing,

1981) to reduce the greater stress that would result to the coral and/or zooxanthellae from not bleaching under high (thermal) stress. In this model, acclimation and adaptation of the bleaching mechanism (Coles and Brown, 2003; Hughes et al., 2003) should be expected as in any other physiological homeostatic response, and their limits or counteractive capacity will vary with the bleaching mechanism involved (Douglas, 2003). Thus, mortality following bleaching would vary among species and levels of stress, according to the counteractive capacity or reaction norm of the induced homeostatic bleaching mechanism, and the acclimation and adaptation history of the holobiont. However, mortality is in no way 'caused by' bleaching. Thus resistance and tolerance to thermal stress should be separated in any model on coral bleaching (Figs. 2, 3), the latter being tested only when the genotypic- and species-specific limits of the former are exceeded.

Terminologically, resistance and tolerance mechanisms relate to thermal stress, not to bleaching. Bleaching is simply an indication of the induction of a resistance mechanism that results in visual bleaching of the coral colony, and mortality is an indication of conditions exceeding the resistance and tolerance thresholds of the organism. While it may be desirable to continue to use 'bleaching' as a primary reference for communication purposes (as in 'coral mortality due to bleaching' or 'resistance and resilience to bleaching'), this is mechanistically misleading. A primary focus of investigation should be to identify mechanisms and thresholds of resistance and tolerance mechanisms, their interdependence and potential for change through acclimation, adaptation and recombination. While initially presented as linear sequential processes (Fig. 3) this is not predicted by the arguments here. It should be possible, for example by using metabolic blockers, to block the resistance and/or tolerance mechanisms to determine their effects on survival of the coral.

The differences in bleaching and mortality responses among coral individuals, populations, species and higher taxa reflect genetic and environmental differences in thresholds of their resistance and tolerance mechanisms. At the genus level variation in bleaching-mortality

Table 5
Resistance and tolerance to thermal stress

Tolerance	Resistance	
	Low (high bleaching)	High (low bleaching)
Low (high mortality)	High bleaching/high mortality—species that show high levels of bleaching and mortality to moderate or high thermal stress. Strategy (a), Fig. 4	Low bleaching/high mortality—species show little bleaching but suffer high mortality under high thermal stress
High (low mortality)	High bleaching/low mortality—species that show moderate to high levels of bleaching but low mortality. Strategy (c), Fig. 4	Low bleaching/low mortality—species that show little bleaching and persist through bleaching events. Strategy (b), Fig. 4

Resistance is indicated by bleaching, a set of homeostatic responses to reduce thermal stress. Tolerance is indicated by mortality, the failure of bleaching (and potentially other) mechanisms to reduce thermal stress to non-lethal levels.

relationships between the Great Barrier Reef and East Africa has been shown (McClanahan et al., 2002), demonstrating divergence in resistance and tolerance characteristics of reproductively isolated populations. Hard coral genera and species cluster into ‘bleaching strategies’ which show different susceptibility towards bleaching and mortality; the most susceptible corals to bleaching show rapid and total mortality in a severe stress event (e.g. the genera *Acropora*, *Pocillopora*, *Stylophora*) and other taxa show high bleaching levels but no or low mortality (e.g. the genera *Porites*, *Astreopora*, *Turbinaria*; Berkelmans and Oliver, 1999; Marshall and Baird, 2000; McClanahan et al., 2001; Obura, 2001). Within species, susceptibility to bleaching and mortality can be different even under the same environmental conditions (Figs. 6, 7), suggesting the possibility of individual genetic variation in resistance and tolerance.

3.3. Intrinsic versus extrinsic components of thermal resistance and tolerance

There are intrinsic and extrinsic components affecting coral and zooxanthellae resistance and tolerance to thermal stress, equivalent to genotypic and environmental components of variation, respectively. The phenotype and survival of a coral colony are an expression of resistance and tolerance as a result of acclimation and adaptation. Intrinsic factors, related to physiological properties, are by definition genetically determined, and therefore vary among individuals, populations and species according to variation in the relevant genes. With respect to thermal stress, such variation may be due to coral and/or zooxanthellae genotypes, and to interactions and synergies between the two (Baker, 2001; Lajeunesse, 2002; Baker et al., 2004).

Variation in intrinsic resistance and tolerance to thermal stress has been reported for many reef areas, both between coral species and between populations of the same species on different reefs and in different reef zones (Berkelmans and Oliver, 1999; Obura, 2001; Marshall and Baird, 2000). In coming years, with repeated thermal stress, increased resistance and tolerance may emerge in new recruits and through an increase in the abundance of resistant and tolerant genotypes. One of the challenges in research on the subject will be to distinguish between genetic and environmental components of increasing resistance and tolerance, as they offer different opportunities for mitigating the impacts of bleaching.

3.4. Bleaching resistance and resilience

West and Salm (2003) cemented the terminology ‘resistance and resilience to bleaching’, synthesizing a series of workshops and contributions (Salm and

Coles, 2001; Salm et al., 2001). This usefully distinguishes direct factors involved in the bleaching and mortality of corals (resistance) from both recovery processes following mortality and secondary factors that may influence bleaching (resilience). However it still masks considerable variation within these categories, which this paper has attempted to address. Synthesizing the foregoing discussions, the following can be proposed as hypotheses for the 3 major components within West and Salm’s ‘resistance’ category.

3.4.1. Thermal protection factors

Thermal protection factors are physical factors that alter the thermal stress signal and that may interact with thermal response mechanisms at the organismal level. Done (2001) differentiated water mixing at regional scales as an ‘avoidance factor’, different from water mixing at a local level within reefs zones and habitats, as the former putatively prevents corals from experiencing the stress signal, while the latter exposes corals to fluctuating conditions (though even large-scale mixing processes do vary within seasons and among years, resulting in interaction with individual corals). West and Salm (2003) grouped both under the heading ‘resistance factors’, with other physical factors (Table 1). They are grouped here as they are physical (though some may be biogenic in origin, such as shading by canopy corals) and occur across sliding scales of space and time.

3.4.2. Thermal resistance factors

Thermal resistance factors are genetically determined properties of corals and/or zooxanthellae that affect their ability to withstand thermal stress. The ones that have been of primary interest result in visually observable bleaching (see Coles and Brown, 2003; Douglas, 2003), but there may be others that do not. Depending on environmental variation, these may interact with thermal protection factors resulting in the phenotypic properties of individual coral-zooxanthellae holobionts. Given the focus of West and Salm (2003) on environmental factors that could be used in management planning, thermal resistance factors (as defined here) were only listed as a single category.

3.4.3. Thermal tolerance factors

Thermal tolerance factors are genetically determined properties of corals and/or zooxanthellae that affect their ability to withstand mortality under thermal stress. These are likely affected by the action of thermal resistance factors but may be distinct processes. Depending on environmental variation, these may interact with thermal protection factors resulting in the phenotypic properties of individual coral-zooxanthellae holobionts. In general, these have not been given large consideration in the literature as research has focused on visual bleaching mechanisms (i.e. resistance) and

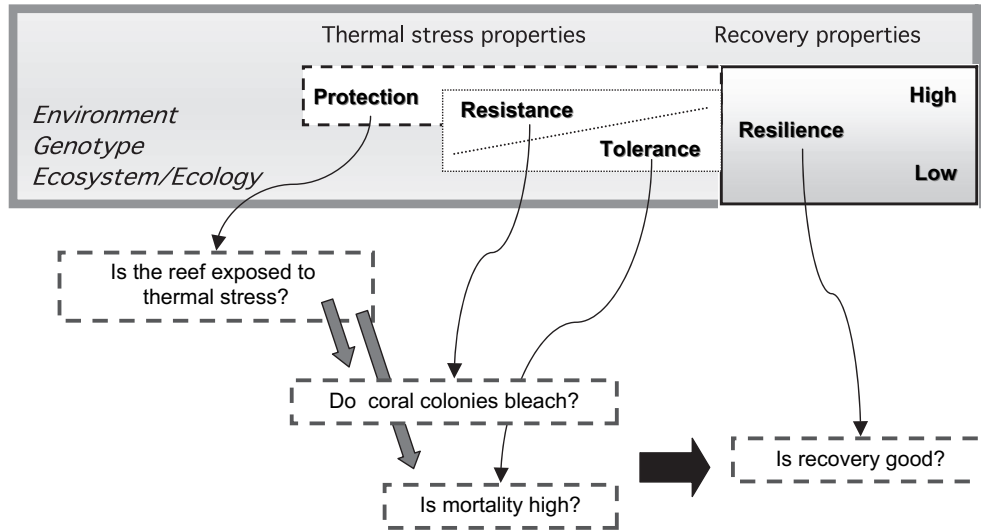


Fig. 11. Revised relationships between thermal stress protection, resistance and tolerance properties and ecological resilience or recovery potential (from Fig. 3). Physical protection factors extend from large to microenvironmental scales, at the latter end interacting with resistance and tolerance properties of individual coral genomes. Following coral bleaching and mortality, resilience and recovery are influenced by the selective survival of corals and the full range of ecological, ecosystem and environmental factors from small to large scales.

physical environmental factors (West and Salm, 2003), and generally confounded bleaching and mortality (Douglas, 2003).

Fig. 11 synthesizes the foregoing discussions of factors that confer thermal protection, resistance and tolerance of corals. In particular, it shows the prior action of large-scale protection factors followed by overlap of some protection factors with genetic resistance and tolerance properties, and the non-sequential nature of resistance and tolerance.

3.5. Resilience and scaling

Three resilience concepts are alluded to in the preceding sections and in presentations to date on 'resilience to bleaching' (West and Salm, 2003): resilience specific to coral bleaching, generalized ecological resilience (McClanahan et al., 2002), and large-scale or spatial resilience (Nyström and Folke, 2001). While this may be partially due to over-use of the term resilience and its increasing popularity in recent years, it is also an indicator of gravitation towards a new ecological paradigm and ongoing testing of its scope and limitations. Of the two examples presented in this paper, one is based on the general factors of predation, herbivory and benthic competition, interacting with the human interventions of fishing and MPA management (see McClanahan et al., 2002), i.e. ecological resilience. The other is based on the intermediate to large-scale processes of larval dispersal and recruitment across archipelagos and along continental coastlines, i.e. spatial resilience. In both examples, the smaller scale processes of genetic resistance, physiological tolerance and differential survival of corals operate, simultaneously,

with all the other species and ecological interactions within the reef community, linked with influences from external systems.

Ecological resilience and its contribution to reef recovery after bleaching is perhaps the most well understood of the three resilience concepts and is discussed by Knowlton (1992) and McClanahan et al. (2002), and termed 'bleaching recovery' or 'recoverability' by Marshall and Schuttenberg (2004). Bleaching resilience can be considered a special case of ecological resilience, bounded by the selective mortality of corals defined by their bleaching resistance and tolerance. The mortality of vulnerable coral species (as well as of zooxanthellae taxa, Baker, 2001; Baker et al., 2004) in a bleaching event destroys the ecological memory codified in their genes, and the system cannot recover its historic diversity of species and functional processes without the externally sourced replacement of the relevant genes. For example, if the lost species are the fast-growing, spatial dominants (such as the acroporids) that contribute to most of the shallow reef community structure, shallow coral reefs may not fully regain their previous function, and long term changes in community structure and ecosystem dynamics may occur (e.g. reef growth or erosion, Sheppard, 2003). Bleaching resilience therefore relates specifically to those components of ecological resilience that are codified in coral genomes and are thereby vulnerable to selective loss determined by resistance and tolerance properties within the same genome. This is different to genetic loss due to coral mortality caused by other threats, such as a storm, hurricane or pollution event, as coral mortality in these cases may either be arbitrary, or bounded by other traits, such as pollution resistance, codified within the coral genome.

Spatial resilience by definition includes the larger-scale processes of connectivity and linkages between ecosystems (Holling, 2001; Nyström and Folke, 2001). While this scaling-up in space, to hundreds or even thousands of kilometres, may seem unmanageable from a local ecosystem perspective, it is widely recognized as being integral to marine systems (e.g. Roughgarden et al., 1988) and is the foundation of large-scale bio-regional approaches such as ‘ecoregions’ (Olson and Dinerstein, 1998) or Large Marine Ecosystems (Sherman and Laughlin, 1992). When the boundaries of a given reef system are extended to include the larger scale of reefs with which it is connected by ocean currents and potential sources of larvae, then sites with different thermal protection, resistance and tolerance properties enter the spatial ‘neighbourhood’ of the reef in question. As a result, these additional reefs with different properties become part of the ‘resilience portfolio’ of the reef and thereby contribute to the spatial resilience of the reef. The properties of distantly connected sites are introduced through the contributions of larval recruitment; protection by the presence and quantity of recruitment, resistance and tolerance by the genetic makeup of the coral larvae introduced from beyond the local scale of bleaching and mortality, and resilience by the presence of other taxa, both larval and adult, from distant sources.

In the examples presented here, the high coral recruitment rates documented first in the Maldives, then in the Seychelles, suggest that there were refuge populations of corals in these island systems, and that within a few years these served as larval sources for the impacted reefs. Conversely, in the Kenyan example, either refuge populations or the necessary level of connectivity, or both, were absent. It is possible that the varied spatial and hydrographic nature of the island systems increased the large-scale (spatial) resilience of reefs in the system, by enabling a complex mix of locations with different thermal protection, resistance and tolerance properties connected by complex current systems.

Thus the study of the impacts of coral bleaching on reef communities, and the properties of thermal protection, resistance, tolerance and resilience, can be framed in broader theories of spatial resilience. This will provide better-formulated hypotheses for testing aspects of protection, resistance, tolerance and resilience (Table 1, Fig. 2) which to date have only been investigated as general factors (Salm et al., 2001; Obura and Mangubhai, 2003). Spatial resilience theory provides tools to analyse processes across multiple scales, including spatial, temporal and biological levels of organization (Fig. 12). In the broader context, coral reefs offer opportunities to investigate applications of spatial resilience theory relevant to climate change,

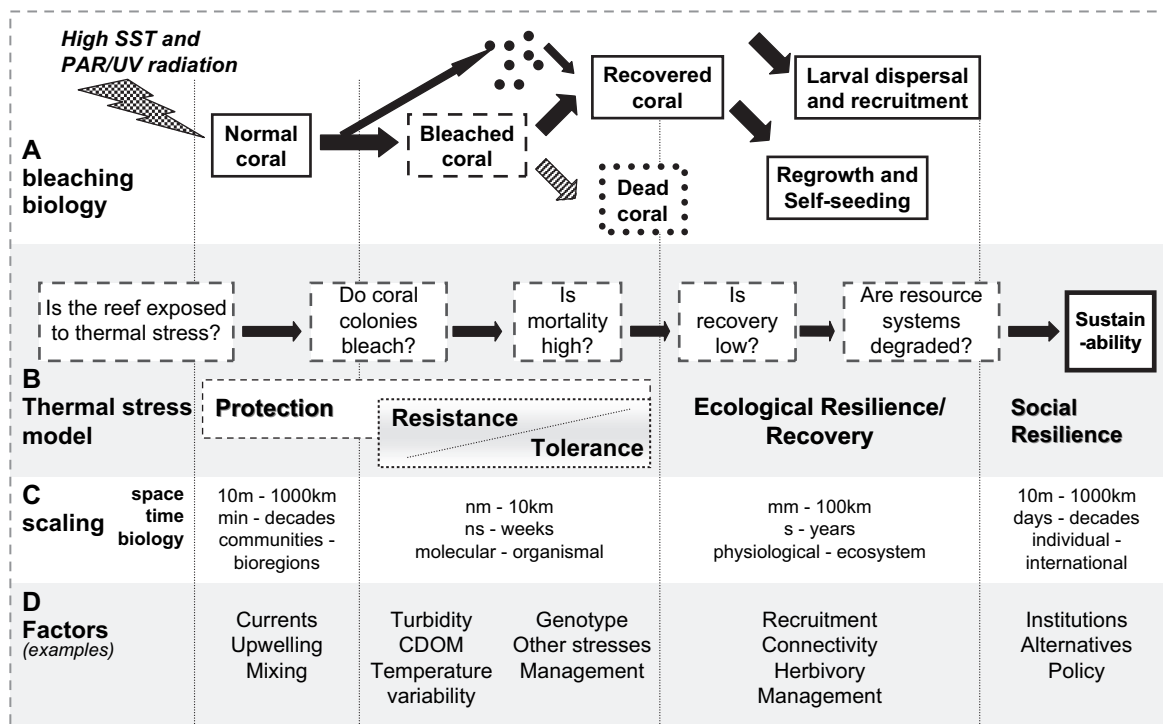


Fig. 12. Synthesis figure illustrating the proposed spatial resilience framework for hypotheses on climate change impacts on coral reefs. (A) Coral bleaching biology (Fig. 2), (B) thermal stress cascade of protection, resistance and tolerance properties, and ecological resilience (Fig. 3), with a component for social resilience added (following Marshall and Schuttenberg, 2004), (C) scaling of spatial, temporal and biological levels of organization and (D) examples of parameters that influence thermal properties and resilience of coral reefs, that may have value in management and mitigation of thermal stress impacts (from Table 1; West and Salm, 2003).

offering a combination of fixed and often small sites hosting adult communities for intensive study, these being linked by larval dispersal and recruitment over varying spatial scales, connected by increasingly well-understood currents.

3.6. Management

The driving question behind many investigations of coral bleaching protection, resistance and resilience is one of management (Westmacott et al., 2000; Salm et al., 2001; Hansen, 2003; Obura et al., in review). This is because regional losses due to coral bleaching may fundamentally erode any potential for the recovery of impacted sites—and thereby undermine all the current efforts at Marine Protected Area (MPA) management. This is also recognized in other marine and terrestrial environments, where landscape-level losses in ecosystem diversity, processes and functions undermine attempts at local or small-site management (Bengtsson et al., 2003; Hansen et al., 2003). Recommendations for management responses to coral bleaching (Westmacott et al., 2000) are essentially precautionary, and based on resilience concepts; in the absence of better knowledge the manager is advised to focus on how to reduce the impacts of other threats, thus maintaining functional diversity and ecological memory to maximize bleaching resistance and resilience. At the larger scale, spatial resilience concepts are invoked through the recognition of the need for networks of MPAs to deal with protection (Done, 2001) and the source-sink dynamics of larval pools for resettlement of impacted reefs (Salm et al., 2000). Resilience thus offers a practical framework for the development of management responses to coral bleaching (Bellwood et al., 2004; Obura et al., in review), drawing on the larger literature on terrestrial and landscape management systems (Bengtsson et al., 2003).

The management of coral reefs needs essentially to be site-specific, accomplished within identifiable boundaries or management zones in MPAs, or within coastal zone management frameworks. This delimits the foundation for a Resilience model incorporating coral bleaching components, for sites with a range of thermal protection, resistance, tolerance and resilience properties (Table 6). Earlier recommendations called for the selection of resistant, tolerant and resilient sites for inclusion in MPAs, as these have properties needed to locally counteract the threat of coral bleaching (Done, 2001; West and Salm, 2003). Sites with resistance and tolerance properties serve as refuges and sources for genes selected for intrinsic resistance and tolerance to thermal stress, and these may provide the primary mechanism for the long-term survival of corals in the face of increasing ocean temperatures. Sites with high resilience properties may suffer high levels of mortality due to low resistance and tolerance, and thus may not necessarily serve as refuges or larval sources in the short term. However, they show high recovery rates and this may provide them with some capacity for adaptation and the fixing of resistant and/or tolerant genes; over medium time frames (e.g. 5–10 years), their rapidly recovering coral populations may serve as refuges and larval sources for sites with lower levels of resilience.

A broader spatial resilience model also ascribes value to sites with protection properties and even to vulnerable sites, as these may make significant contributions to connectivity and patch dynamics at larger scales (Table 6). Sites protected from thermal stress have coral communities that are not depleted by mortality, and thus provide genetic material for reseeding of impacted sites, making them important refuges and larval sources. Genes from these sites may or may not have any resistance or tolerance to bleaching, but they do provide material for recombination through sexual reproduction,

Table 6
Application of thermal stress and spatial resilience concepts to conservation of sites in a network of Marine Protected Areas (MPA)

Site properties:	Protection	Resistance	Tolerance	Resilience	Vulnerable
<i>Thermal stress</i>					
Refuge populations	++	+	+		
Larval supply to impacted sites	++	++	++		
Adaptation/evolution to cope with climate change	+	++	++	+	
Recovery promoted by management	++			++	++
<i>Spatial resilience</i>					
Nodes in the network/stepping stones	++	++	++	++	++
Sites with other values (e.g. recreation, fisheries reserves)	+	+	+	+	+

This assumes real connectivity of sites within the MPA network by larval supply and migration of mobile species. ++, direct significance of corals at a site; +, indirect significance, e.g. by providing genetic variation for recombination during sexual reproduction.

which may provide novel resistance and tolerance capacities. Vulnerable sites (i.e. with low protection, resistance, tolerance and resilience properties, Fig. 3) may support ecosystem processes important for large-scale spatial resilience unrelated to bleaching. For example, they may have regionally important populations of other functional taxonomic groups, such as of key fish or invertebrates of importance in the recovery of vulnerable sites, or in maintaining regional populations. Lastly, sites with high protection and low resilience may play an important geographic role in a network of local and regional stepping stones for the successful dispersal and recruitment of corals and other taxa. In the language of spatial resilience theory, these vulnerable sites may be significant repositories of functional diversity and ecological memory for resilience in the larger scale system, and therefore also for smaller sites within the system (Bengtsson et al., 2003).

The spatial and temporal predictability of environmental factors that confer bleaching protection and extrinsic resistance is important for the manager (Done, 2001; West and Salm, 2003). For example, seasonal local upwelling that occurs at a time of thermal stress may confer protection properties to a site, while water-column mixing driven by unpredictable storm and climate factors may not. At small scales, fluctuating environmental conditions, such as variation in temperature on shallow reef flats in response to tidal, diel and seasonal factors, may result in acclimation of corals to different temperatures. To be useful for management, these factors need to be predictable, so that management plans can be based on their occurrence at specific times and places. However, as in all natural processes, the occurrence of a property under one set of conditions does not guarantee its presence under slightly different conditions, particularly in this case with the uncertainty imposed by incremental climate change.

Management can nevertheless harness resilience by using and enhancing natural properties of protection, resistance, tolerance and resilience (Table 1). Management based on spatial resilience theory is consistent with existing concepts of Integrated Coastal Zone Management (ICZM) where the land- and seascape matrix is fully assigned differing levels of management interventions. It is also approached by recent trends in planning MPA networks to embrace large-scale and 'ecoregional' areas for conservation (Salm et al., 2000) as opposed to single-site management. It is also at the core of increasing global consensus to plan Protected Areas within a landscape matrix, recognizing that biodiversity and ecosystem health within protected areas is intimately connected with the surrounding areas, even in highly altered rural and urban landscapes (Bengtsson et al., 2003; WPC, 2004).

The network approach thus emphasizes the management of sites with varied properties as nodes in a

connected network (Table 6). Each type of management area can be viewed as a potential refuge for some aspect of system resilience, with adequate replication of the refuges to ensure a sufficiently connected system. The replication of the managed sites must be related to both stepping-stone (i.e. spatial) issues as well as ecological and biodiversity (species and functional group representation, habitat representation, size) considerations. The specific inclusion of sites with high vulnerability to thermal stress (i.e. low protection, resistance, tolerance and resilience) in this management framework is a necessary component within this theory, and is encapsulated in the notion of risk spreading (Done, 2001; Day et al., 2002; Hansen, 2003).

Management of coral reefs occurs within a broader context of social and environmental issues other than coral bleaching. Resilience theory provides a way to plan for these in the same framework as bleaching, incorporating their impacts on and contributions to functional diversity and ecological memory. Sites possessing values or threats other than those related to coral bleaching have their own sets of values (Table 6), which can be modelled in terms of resilience in a similar fashion as has been done here for bleaching. These can include fisheries, tourism, conservation and other socioeconomic activities currently associated with coral reefs (McClanahan et al., 2002). This will be of great value for the management of coral reefs as they are intensively used by people, and concern for the welfare of communities dependent on coral reefs is among the prime factors motivating increasing research and interest in their fate (Wilkinson et al., 1999). Resilience equals sustainability (as used in social and economic development contexts) in ecological terms (see Folke et al., 2003; Bengtsson et al., 2003), and is thus central to human welfare. Social resilience issues can be included in the bleaching model proposed here as a final step, relating the social vulnerability to the resilience of the reefs and resources on which they depend (Marshall and Schuttenberg, 2004). Finally, spatial resilience theory explicitly provides for scaling up from local to regional and even global scales, and for traversing across ecological and social boundaries to enable the cross-linking of actions that will be necessary to deal with the threats of climate change to ecosystems (Payet and Obura, 2003).

4. Conclusions

Spatial resilience theory provides a unifying conceptual framework for research on natural and threat-induced changes on coral reefs, developing management responses from local to regional scales, and understanding social consequences and drivers of change on coral reefs. The fledgling model developed here explores

spatial resilience pertaining to coral bleaching and climate change. To be useful, it needs to serve two general purposes: to be (a) specific enough to determine hypotheses on coral bleaching for scientific testing, and (b) general and heuristic enough to enable managers to develop interventions to mitigate bleaching impacts and design networks of MPAs. Meanwhile, it needs sufficient flexibility to allow iterative improvement as hypotheses are proven, rejected or modified over time. The more speculative aspects of the model deal with larger-scale issues (such as connectivity, genetic adaptation, larval supply) that are as yet beyond the scope of most current coral reef management projects, but are beginning to receive attention in large-scale conservation planning initiatives. The utility of the protection-resistance-tolerance framework (Fig. 11) will be tested over time. Greater confidence can be placed in the more local-level aspects of the model, particularly those related to ecological resilience that are more accessible to management intervention through, for example, zoning and direct interventions with respect to resource use.

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