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the Department of Natural Resources and Mines

Global Climate Change and Coral Bleaching on the Great Barrier Reef

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ABOUT THIS DOCUMENT

This document is the third and final report produced in accordance with a contract for 'Climate change and coral bleaching on the Great Barrier Reef' developed between the Queensland Department of Natural Resources and Mines and the Australian Institute of Marine Science in May 1999. The forward projections included here are not definitive scenarios for the future. Rather, they are a representation of outcomes that are a consequence of the assumptions we made in our models, some of which are strongly supported by data, others only weakly. In particular, the analysis relied on assumptions about likely future ecological impacts, adaptation and recovery rates that are currently unverified. Other parts of the report relied on the use of data and the development of models derived from a number of other studies involving the authors. Details of methods and large data sets are omitted from this report for the sake of brevity and clarity. Readers are referred to publications in the Reference list for more details.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the assistance of Craig Steinberg and Mary Wakeford of the Australian Institute of Marine Science and John Guinotte of James Cook University. Barrie Pittock (CSIRO) and Paul Marshall (Great Barrier Reef Marine Park Authority) provided very useful suggestions leading to improvements in this final draft of April 2003.

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Executive Summary

The waters of the Great Barrier Reef are warming and are predicted to continue to do so at an accelerating rate throughout the 21st Century. The increasing temperatures will lead to increased levels of coral bleaching, coral mortality and biodiversity depletion that could have serious consequences for the Reef's biodiversity, ecology, appearance and dependent recreational use and economic activity. Coral bleaching, some leading to death of corals, has been observed sporadically on the Great Barrier Reef since 1982, and most notably, widespread and seriously, in 1998 and 2002. .

We explored the implications for reef appearance and ecology of one pessimistic and one optimistic IPCC scenario for climate change at one inshore, one mid-shelf and one outer-shelf reef in the Townsville area. Based on plausible assumptions on the relationships between increasing heat stress and impacts, we produced scenarios for the reefs that suggested retrogression or at least a retarded rate of progression in the reefs. Interestingly, due to a lower sensitivity to temperature stress, the inshore reef fared best in our scenarios, perhaps because its corals are acclimatized to warmer waters than are those living on mid- and outer-shelf reefs.

Our scenarios suggest that if society achieves lower rates of regional warming, it will be beneficial to reef appearance and ecology. Moreover, if mooted Great Barrier Reef management plans are successful in both enhancing biodiversity and abundance of reef species, and in improving water quality generally, these should enhance the key ecological property of 'resilience' in the reef systems, i.e. the ability to recover following natural and human disturbances.

As an aid to planning for management, enjoyment and sustainable use of the Great Barrier Reef, we recommend that further efforts be made to understand this complex and important pressure of climate change.

Introduction

The Intergovernmental Panel on Climate Change (IPCC 2001) foreshadows a gloomy future for the Earth's coral reefs, including those of the Great Barrier Reef World Heritage Area. By 2025, the IPCC projects that global temperatures will warm by 0.4 to 1.1°C, sea level will rise by 3 – 14 cm and that there will be an 'increase in frequency of coral bleaching and death of corals'. By 2100, as sea-temperatures rise by up to 5.8°C and sea levels by up to 88 cm, IPCC suggests there will be 'more extensive coral bleaching and death', and 'reduced species biodiversity and fish yield from reefs'. These general statements clearly have specific implications for the world's largest coral reef system - the Great Barrier Reef. One recent report suggests that the Reef is likely to be severely set back or even transformed to a non-coral dominated state by as early as 2030 (Hoegh-Guldberg 1999).

Episodic disturbance and population turnover in corals and associated communities are normal aspects of ecological dynamics in coral reefs. There can be little doubt, however, that global climate change has made the previously infrequent 'coral bleaching' disturbance commonplace. The relationship between climate change, coral bleaching and resultant coral death on the Great Barrier Reef is, therefore, a significant issue with potentially major environmental and economic consequences for Queensland and Australia. While the scientific record indicates that loss of colour by corals – or coral bleaching – is a natural phenomenon (Brown 1997), observations in the last two decades suggest its extent, severity and rates of consequent coral mortality are increasing (Glynn 1996; Hoegh-Guldberg 1999). The appearance of coral reefs and thus their amenity for tourism may be seriously compromised, and their productivity and biodiversity decimated.

The implications of this risk need to be considered within the context of other known influences on reef ecology and reef-based enterprises. These include adverse effects of crown-of-thorns starfish; runoff of pollutants, freshwater, silts and nutrients; diseases; fishing and other harvesting, and likewise the beneficial ecological effects of the Queensland Government and Great Barrier Reef Marine Park Authority's management of the World Heritage Area that provides protection from coastal runoff, pollution, over fishing and over harvesting. The Great Barrier Reef is very heterogeneous in relation to all these influences.

Collectively, the various zones and depths of the reefs of the Great Barrier Reef are colonized by diverse local assemblages of corals. Those on reefs in the central Great Barrier Reef, for example, have been classified into 17 coral 'community types' (Done 1982), each comprised of subsets of around 30 to 100 of the 400 or so coral species recognised on the Great Barrier Reef (Veron 2000). These communities have significant differences in their coral species compositions, and in localized spatial arrangements and interaction of coral colonies and their dynamic properties over years to decades (Done 1997). Understanding the differences in responses and outlooks for different coral communities is central to any consideration of the current health and future outlook for the Great Barrier Reef, and it is the subject of ongoing research by the authors. For this study, we needed to stand back from that level of detail while still producing a report that captures our current assessment of how overarching properties of 'ecological well-being and 'appearance' may unfold in coming years to decades. Because projected future conditions on the Great Barrier Reef are outside past or current conditions, we have had to make various assumptions about the severity of their ecological impacts. It is important for readers to be aware that what we present as future trajectories for reef 'ecology' and 'appearance' are totally determined by these assumed impacts, that we express as 'years of setback' relative to the ways the coral communities would have progressed in the absence of the extra episodic disturbance that is the subject of this report: coral bleaching. Coral bleaching is important, not only as an immediate indicator of environmental stress, but also, as a state that is sometimes the precursor to the death of the bleached coral. These distinctions are considered in more detail below.

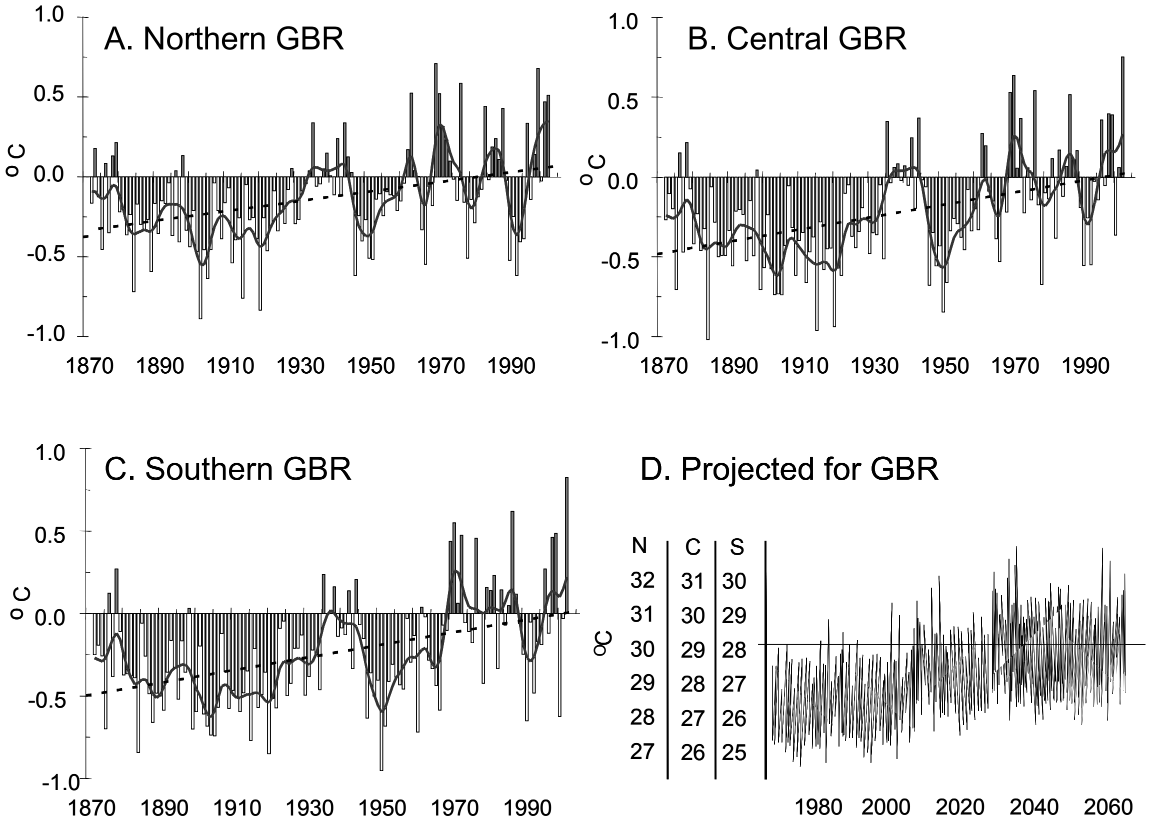

Figure 1. Records and projections of rising sea temperatures in the Great Barrier Reef. A to C show deviations from the long-term average sea temperatures for the northern, central and southern sections of the Great Barrier Reef, respectively. D. Projected sea temperature warming for Great Barrier Reef waters (after Hoegh-Guldberg 1999). The horizontal line indicates a notional threshold for coral bleaching that remains constant (i.e. no adaptation). Recent studies indicate the thresholds depend on duration of exposure and vary regionally.

Recent increases in the incidence of coral bleaching on the Great Barrier Reef have been correlated with warming sea temperatures. During the 20th Century, the annual maximum monthly mean seawater temperatures increased by 0.3 – 0.4°C in the Great Barrier Reef (Lough 2000; 2001 - Fig. 1). By the 1980s and 1990s, this increase was manifest in some parts of the Great Barrier Reef as blocks of consecutive summer days and weeks of high air temperatures and low winds – i.e. when sea temperatures were > 1°C above the mean summer maximum temperatures to which the corals are normally exposed (AIMS weather station data – www.aims.gov.au/pages/facilities/weather-stations). These conditions cause corals to bleach (Berkelmans 2002) and in the Great Barrier Reef, the year of 1998 was the hottest of the Century (Lough 2000), and witnessed the greatest level of coral bleaching on record (Berkelmans and Oliver 1999; Baird and Marshall 2002). A bleaching that appears to have caused even more coral death than the 1998 event occurred in the Great Barrier Reef in the first half of 2002 (GBRMPA 2002, Done et al. 2003).

In neither 1998 nor 2002 was coral bleaching or mortality uniformly distributed across the Great Barrier Reef's coral reefs. In 1998, mortality was high on some near-shore reefs, possibly exacerbated by osmotic stress caused by floodwaters (Berkelmans and Oliver 1999). But in 2002, the pattern of bleaching and mortality largely corresponded with, and can be attributed to, the pattern of maximum heat stress alone (Berkelmans et al. submitted). In general, the non-uniformity appears to reflect a number of factors: the diverse heat stress regime (Skirving et al. 2002) over the 14 degrees of latitude, 200 km width and 10 to 200 m depth spanned by Great Barrier Reef (Lewis 2001); diversity of physical environments within each of the 3000 separate reefs (afforded by complex reef shapes, depth profiles and interactions with the currents and waves – Hopley 1982); differences in local reef microenvironments, and thus individual coral communities (Done 1982) and their histories of acclimatization; differences in vulnerability of different combinations of corals and zooxanthellae (c.f. Rowan et al. 1997)

Patchiness in impact of coral bleaching and death across the Great Barrier Reef has the same implications for tourism as does patchiness and impact of bushfires across an entire Australian state. Public perceptions about location and extent of an impact, and prospects for future impacts, are vague in each case. The regenerative capacities and recovery times of the affected ecological systems – such as they may be – receive little attention. In both cases, a tourist's decision not to visit an area may be misinformed, if the reality is a patchy, localized and short-lived perturbation, but the broad public perception is uniform and permanent devastation. In each case, there is a need for good communication of the geographic extent and pattern of the disturbance, and the expectations for the time that will be required restoration of the pre-disturbance state.

Here, we address aspects of this general issue in relation to bleaching impacts and the Great Barrier Reef. We make an assessment on the seriousness of the hazard posed by warming seas, it's time frame, the vulnerability of the ecological systems, and the consequences in terms of the future amenity of Great Barrier Reef coral reefs for tourism i.e. as coral-dominated system with ongoing reef-building capacity. Our projections are based on models and assumptions as well as data. They are thus not definitive scenarios for the future, but a representation of outcomes that are a consequence of the assumptions we made in our models. In particular, our scenarios relied on assumptions about likely future ecological impacts, adaptation and recovery rates that are judgements based on experience, but not supportable by hard data.

The results are from a collaborative study by AIMS, CRC Reef and CSIRO Atmospheric Research. We examine two trajectories that Great Barrier Reef regional climate may take in coming decades, and the implications for the appearance and ecological structure of coral communities on inshore, mid-shelf and offshore reefs. The 'A1' scenarios (Fig. 2) assume rapid economic growth and a global population that peaks in the middle of the 21st Century with rapid introduction of new and efficient technologies Within 'A1' scenarios, we chose one 'pessimistic' and one 'optimistic' scenario, which are towards the upper and lower end of the envelope of climate change (Fig. 2). We believed, and confirmed with hindsight, that the assumptions and uncertainties in the ecological component of our modelling did not warrant more exhaustive exploration of the many climate scenarios available (Swart et al. 2002) The A1FI scenario (pessimistic) is one of rapid climate change that places the greater and more immediate demands for accommodation and adaptation in natural systems and humanity) compared to the more optimistic scenario A1T. Scenario A1FI assumes a fossil-fuel intensive future; A1T assumes transition to non-fossil alternative energy sources over the coming century. While there are uncertainties with both climate scenarios and the response of coral communities, the analysis has nevertheless allowed us to identify a range of plausible futures for the Great Barrier Reef as it is confronted by climate change. The authors gratefully acknowledge the Queensland Department of Natural Resources and Mines for their support of this study.

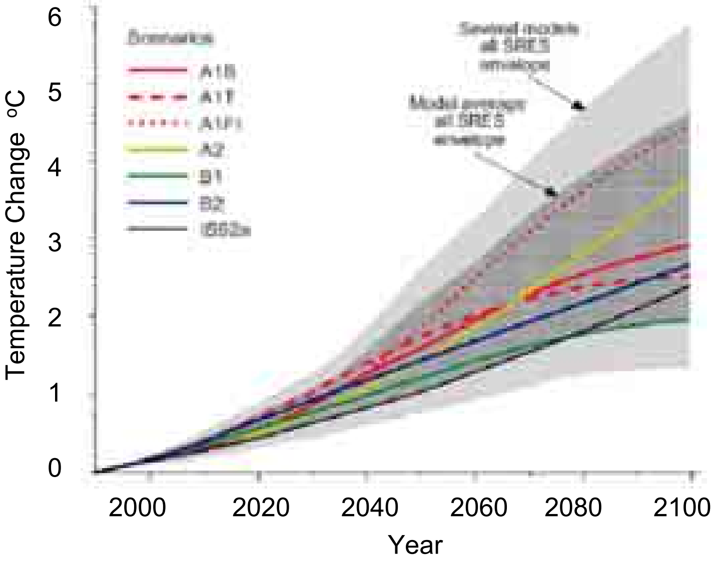

Figure 2. Projected global increase in temperature according to different scenarios for world carbon emissions. Curves are averages of several Global Climate Models, and assume a 2.5^{O}C rise for a doubling of atmospheric CO_2 . Source: IPCC (2001)

Corals, coral bleaching, ecology and appearance

Both living and dead corals have critical roles in coral reef structure and function. Nevertheless, the sudden and untimely bleaching and deaths of corals across large areas is a cause for concern. Living corals are fundamental to the Great Barrier Reef: they build and maintain its coral reef ecosystems; living corals provide habitat for reef biodiversity and are a primary attractor for tourists. But corals have finite life expectancies, most measured in decades to centuries. Dead coral, along with fragmented skeletons of thousands of other species of limestone-secreting plants and animals, is the raw material for reef framework, and the sand and rubble that builds beaches, coral islands and lagoon floors. Thus, it is not the death of corals *per se* that is of concern, but how its extent and timing influence the normal ecological diversity and functioning of affected reefs, and the ecological services they provide, such as fisheries habitats and destinations for tourism and recreational use.

Bleached corals lose their normal colours – most commonly creams, greens, browns mauves and blues. They take on a paler, sometimes pastel toning, and can eventually turn stark white (Appendix 1). The whiteness or paleness is a result of the coral animal shedding its resident symbiotic partner populations of millions of symbiotic microscopic algae (zooxanthellae). These algae normally give the coral much of its colour and a supply of energy-rich sugars that the algae have produced through photosynthesis. The much-reduced density of zooxanthellae in bleached corals deprives the coral of a major part of its daily nutrition, and allows the pure white skeleton to become visible through the now transparent coral tissues.

A major trigger for coral bleaching is an extended period of excessively hot, calm and clear conditions that damages the photosynthetic pathways of the zooxanthellae and causes their expulsion *en masse*. The bleached coral's capacity to build new skeleton is compromised, its tissues are damaged, and its reproduction is reduced, if not suspended (Michalek-Wagner and Willis 2000, Brown et al. 2000, Baird and Marshall 2002; Ward et al. 2002). A bleached coral may die, in part, or entirely (Baird and Marshall 2002). Alternatively, a bleached coral may fully recover its colour and the energy contribution of its zooxanthellae within months.

Dive tourism and island resorts are scattered throughout much of the length of the Great Barrier Reef (Zell 1999), and day-tourism facilities are located within 1-2 hours fast boat access from ports along the coast. At the scale of a local dive or reef tourism site (many thousands of colonies over hundreds to thousands of square metres), one measure of the ecological and visual impacts of a particular bleaching event is the proportion of corals that die. While the death of a small percentage of corals in any area may be considered as a minor setback with only transient consequences for that place's appearance and ecology, death of a large percentage is a major setback, especially where many of the victims are many decades or centuries old. The drab appearance of a seriously damaged tourism or diving site represents a loss of amenity to the business that can be translated to its economic bottom line.

Here we look at the likelihood of the amenity loss itself, as mean sea temperatures rise over coming decades, causing increased frequencies of the heat wave conditions that cause corals to bleach and die. In the long term, functional ecological systems, processes and cycles are the foundation of sustainable uses of reef resources. However, in the short term, 'appearance', notably high bottom cover of corals, and a variety of shapes, and large colony sizes, are prime attributes for attractive tourism and diving sites. 'Ecology' and 'appearance' are linked, but they are not the same, and so we identify them separately in our analysis. For our principal analysis, we assume there is no adaptive capacity in the coral communities. We then consider the consequences of some adaptive capacity within the coral community, and discuss management options that can support such a capacity.

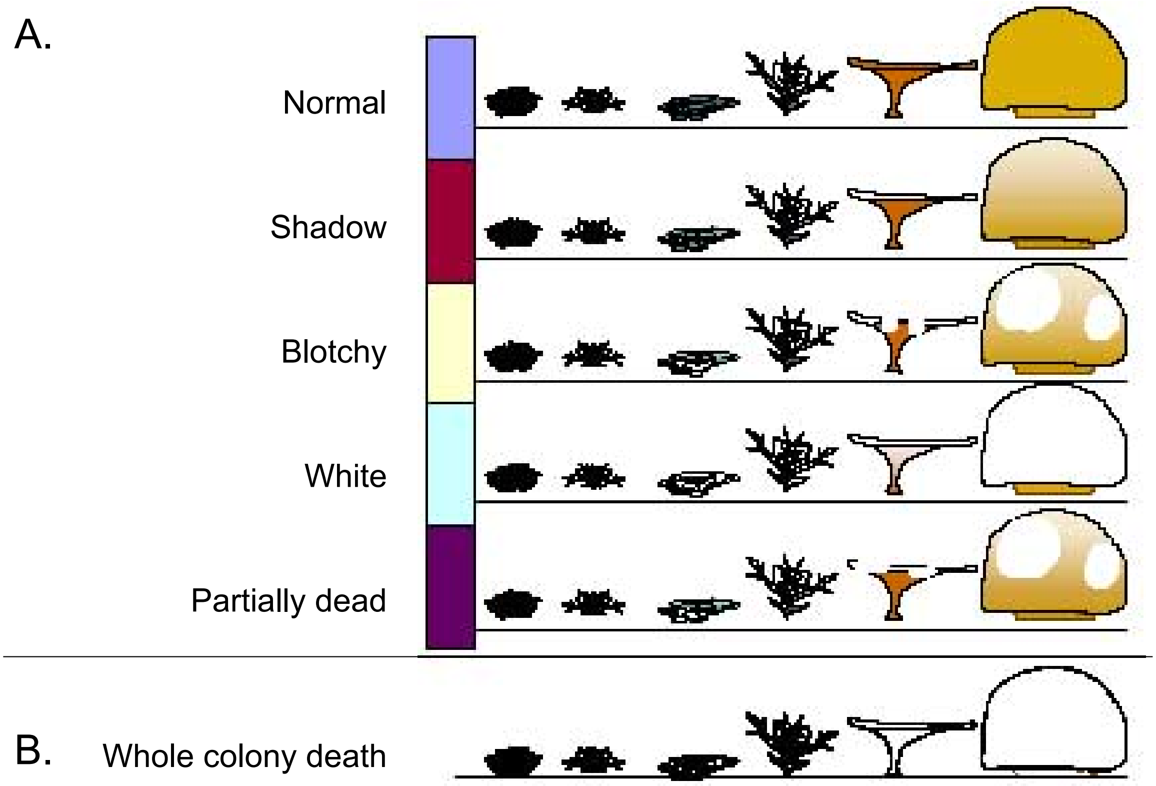

Figure 3. Four stages of coral bleaching, contrasted to normal coral colour (A) and dead coral (B). See also Appendix 1.

Levels of bleaching of coral reefs and their consequences: appearance, ecology and amenity

Coral bleaching can totally whiten most corals over reef areas that are occupied entirely by susceptible coral species. Alternatively, it can temporarily intersperse a normal toned reef with white patches, where vulnerable individuals are uncommon. Transient and minor events may have no long-term detrimental affect on reef appearance, nor, therefore, on diving and tourism that depend on an attractive site. By contrast, where there is high mortality, impacts on appearance and ecology could conceivably leave their mark for years to decades. We use the term 'setback' to describe and define a range of impacts (Table 1).

Table 1. A terminology for bleaching impacts on coral reefs. The levels are described in more detail in Table 2.

Level	Description	Appearance setback (years)	Ecology setback (years)
1	Sub-lethal impact	0	0
2	Very low level impact	0.5	3
3	Low level impact	1	5
4	Medium level impact	5	10
5	High level impact	10	20
6	Catastrophic impact	10	50

According to this scale, the rather transitory levels 1, 2 and possibly 3 would have little detrimental effect on tourism amenity. Levels 4 to 6 would constitute serious impacts and resultant site 'down times' of drab appearance. During down times, the reefs would have little appeal for discriminating divers and tourists and poor 'word of mouth' value for that particular operation, and likely the reputation of the whole Great Barrier Reef, warranted or not. The local ecological effects will include change in coral species diversity and abundances and poorly understood, but potentially serious, effects on other reef species that depend on live coral. Additional effects include reduction in local architectural complexity and rate of reef accretion, as well as reduction of the reef's reproductive output for the year in which the event occurred.

To date, no hard data exist that allow us to equate the levels of impact in Table 1 with particular levels of environmental stress, past or present. However the Table's development has been informed by quantitative modelling studies of coral impacts and recovery associated with crown-of-thorns starfish (Done 1988), and by field observations of changes in coral cover and composition during 'bleaching' years (Fisk and Done 1985; Baird and Marshall 2002; Marshall and Baird 2000; Done et al. 2003). The suggested setbacks for 'appearance' are guided by rates of post-disturbance increases in coral cover reported in Ninio and Meekan (2002), who showed how a particular group of corals (family Acroporidae) tends to contribute most to increases in total coral cover following disturbance. Analyses in Done (1988) guided the setting of the suggested setbacks for 'ecology', which takes longer to re-constitute than 'appearance', being more related to the time to re-establish the age structure of the slower growing and longer lived corals. Acroporids may relatively quickly occupy vacated spaces, but it takes longer for slower growing corals (all other families of hard corals) to re-establish coral communities with species richness, morphological composition, spatial pattern and age structure equivalent to the pre-disturbance state.

At the lower end of the scale in Table 1, then, we refer to a state in which the proportion of corals injured or killed is small, and whose replacement with a new cohort of corals of equivalent number and age could be completed in a few years, given everything else in favour of settlement, recruitment and growth of new corals. (In reality, that cannot be assumed to be a given in all cases). Done et al. (2003) observed many places in 2002 that would rate as levels 2 and 3, and a few at level 4 and 5, based on sizes and species of corals most affected. In the modelling of appearance and ecology that follows, the frequency of the higher-level impacts in Table 1 increases as temperature increases.

Table 2. Detailed description of coral bleaching impact levels on coral communities, and the associated 'setbacks' in appearance and ecology that are assumed in modelling of bleaching impact using a simple model called 'ReefState'.

Level 1: Sub-lethal impact
Sub-lethal impact bleaching describes the case when whitening occurs, but no coral tissue is killed. Detrimental effects are, thus, limited to tissue injury, and reduced skeletogenesis, colony growth rate and reproductive output of individuals. It has no effect on the percentage of the reefscape covered in live coral, nor on species composition, relative abundance, or size frequency distribution of corals present. In ReefState, it is modelled as a zero-year setback (ecology and appearance).

Level 2: Very low level impact
Very low-level impact bleaching describes the case when whitening occurs, and some corals are injured and when ubiquitous, but locally sparse, fast growing vulnerable species die. Ecologically, it may take several years for these species to recruit and grow to the same size as those that died.In terms of visual impact, however, their loss is quickly obscured by growth of survivors, which are in the majority. In ReefState, it is modelled as a 3.0-year setback (ecology) and 0.5 year (appearance).

Level 3: Low level impact
Low level impact bleaching is when the same ubiquitous corals are in high relative abundance locally, but their loss is obscured by growth of surviving corals, which are still in the majority. In ReefState, it is modelled as a 5.0-year setback (ecology) and 1.0 year (appearance).

This term and these model parameters also describe the case when there is conspicuous injury to many of the more visually dominant organisms, but little whole colony mortality among this group. Injuries may take several years to be occluded through the colony's own repair mechanisms, and net reproductive output and live surface will take some years to be reinstated. On the other hand, the relatively minor visual impact will be obscured by growth of surviving corals, which are still in the majority.

Level 4: Medium level impact
Medium level impact bleaching is when fast growing visually dominant organisms suffer moderate to serious death and injury, but there are substantial viable living remnants with high prospects for re-growth. The affected area does not depend on the vagaries of coral recruitment, which may or may not be reliable at that place. In ReefState, it is modelled as a 10-year setback (ecology) and a 5-year setback (appearance).

Level 5: High level impact
High level impact bleaching is when fast growing visually dominant organisms die en masse, and there are few viable living remnants to initiate re-growth. This area does rely on the vagaries of coral recruitment. In ReefState, it is modelled as a 20-year setback (ecology) and a 10-year setback (appearance).

Level 6: Catastrophic impact
Catastrophic bleaching is when ancient visually dominant organisms die en masse, regardless of whether there are viable living remnants to initiate re-growth. All else in its favour (water quality, larval replenishment, optimal grazing rates), it can become dominated by corals in a decade. In ReefState, it is modelled as a 10-year setback (appearance) and a 50-year setback (ecology - although total restoration of a coral community of equivalent ages structure may taken even longer).

Thresholds and coping ranges

Berkelmans (2002) has shown that the initiation of bleaching among the most vulnerable coral species on a particular reef can be predicted by a curve of temperature versus duration above a bleaching threshold (Fig. 4). The sub-lethal bleaching threshold (Fig. 4) is defined by temperature and duration, above which the most vulnerable coral species at that reef will bleach. The coping range is the range of temperatures and times above the bleaching threshold within which those corals will bleach but not die. If the dose of temperature is higher, corals will die. There are presently no data to define dose-mortality response relationships for impacts (Table 1). We therefore use a simpler measure of 'days above the threshold' for illustrative purposes of potential impacts under the two chosen climate change scenarios.

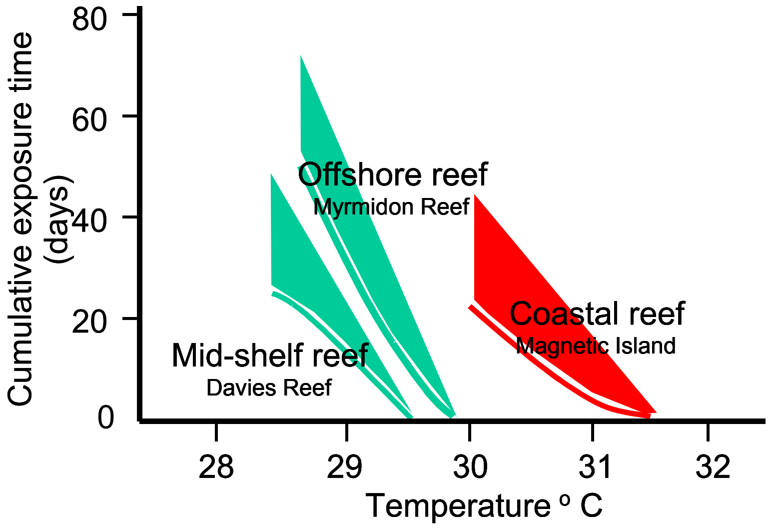

Figure 4. Sub-lethal bleaching threshold curves and indicative coping ranges (shaded areas) for a coastal, a mid-shelf and an offshore reef in the Townsville sector. Curves are from Berkelmans (2002). Temperature and exposure time combinations in the shaded areas to the right of each curve will result in bleaching of the more vulnerable coral species (e.g. 1 day at 29.6°C will cause bleaching at Davies Reef, whereas Myrmidon Reef would need about 20 days at that temperature. At Magnetic Island, bleaching would be caused by a one-day exposure of 31.5°C or 20 days at 30.3°C. Still warmer and longer exposures beyond the coping range kill corals progressively, from more vulnerable to more robust species).

Projected sea-temperatures for the Great Barrier Reef

Projections of sea temperatures for the Great Barrier Reef under global emission scenarios A1FI (high climate sensitivity) and A1T (low climate sensitivity - Fig. 5) suggest that increasing mean summer sea temperatures in coming decades will tend to increase the frequency of exceedence of bleaching thresholds (Fig. 4). Differences among the sub-lethal bleaching thresholds at the three reefs (Fig. 4) reflect the major variability in the Great Barrier Reef's thermal environment (Fig. 6, 7). This variability has a latitudinal hot-cold gradient at its base, overlaid by complex interactions among local weather, tides, currents and bathymetry. Only the latitudinal element is well captured any of seven regional climate models available to us. - Fig. 5).

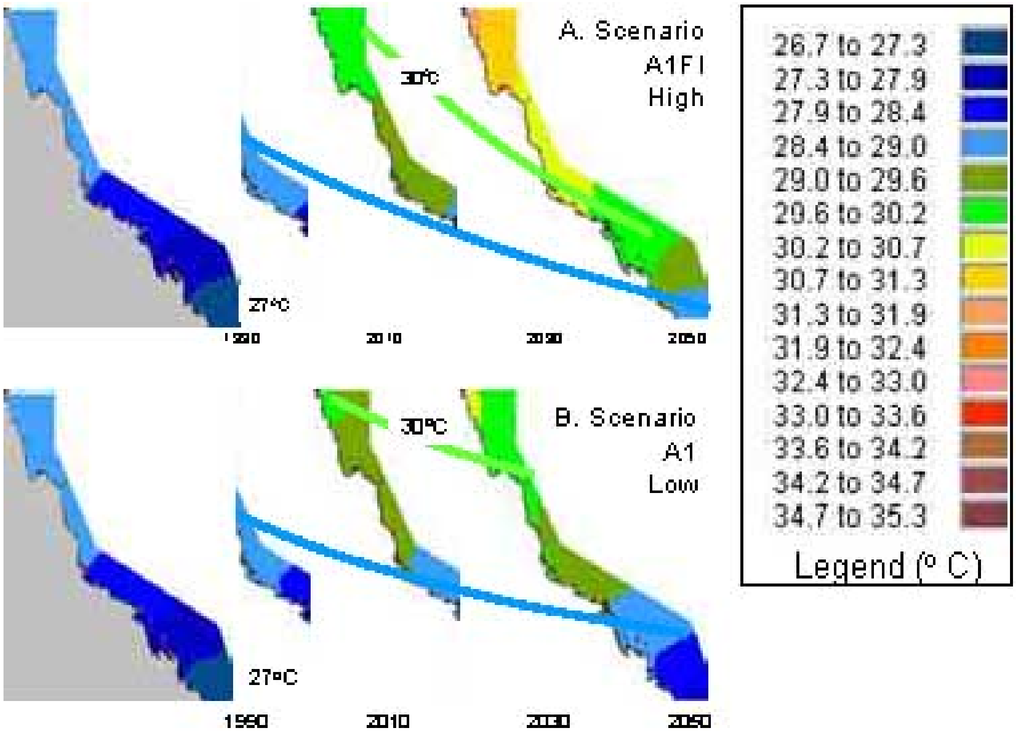

Figure 5. Projected warming of Great Barrier Reef mean summer (Dec-Jan-Feb) sea surface temperature 1990-2050. A. Scenario A1FI High climate sensitivity projects Cape York temperatures at the southern end of the Great Barrier Reef by 2050. B. Scenario A1T Low climate sensitivity projects Cape York temperatures at the southern end of the Great Barrier Reef by 2100. Model: Canadian Climate Centre Global Climate Model.

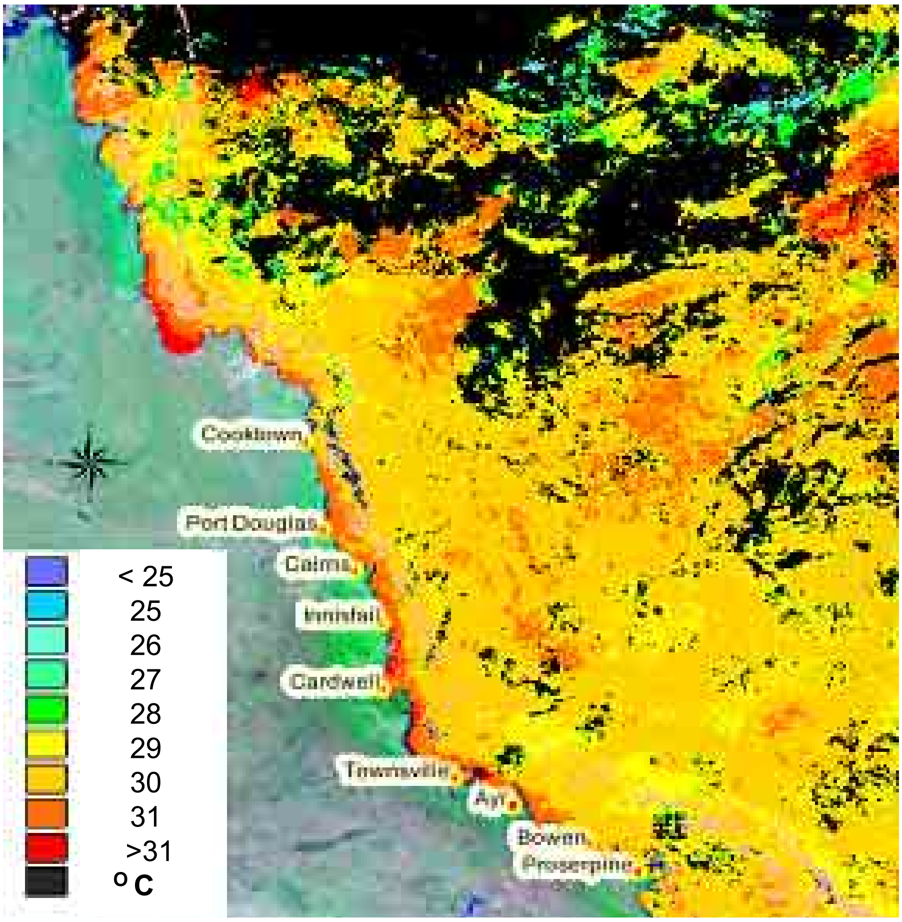

Figure 6. Regional and local variability in the thermal climate of the Great Barrier Reef. Sea surface temperatures (SSTs) Feb 23 2002, from AIMS SST archive. Black areas represent missing data (caused by cloud cover).

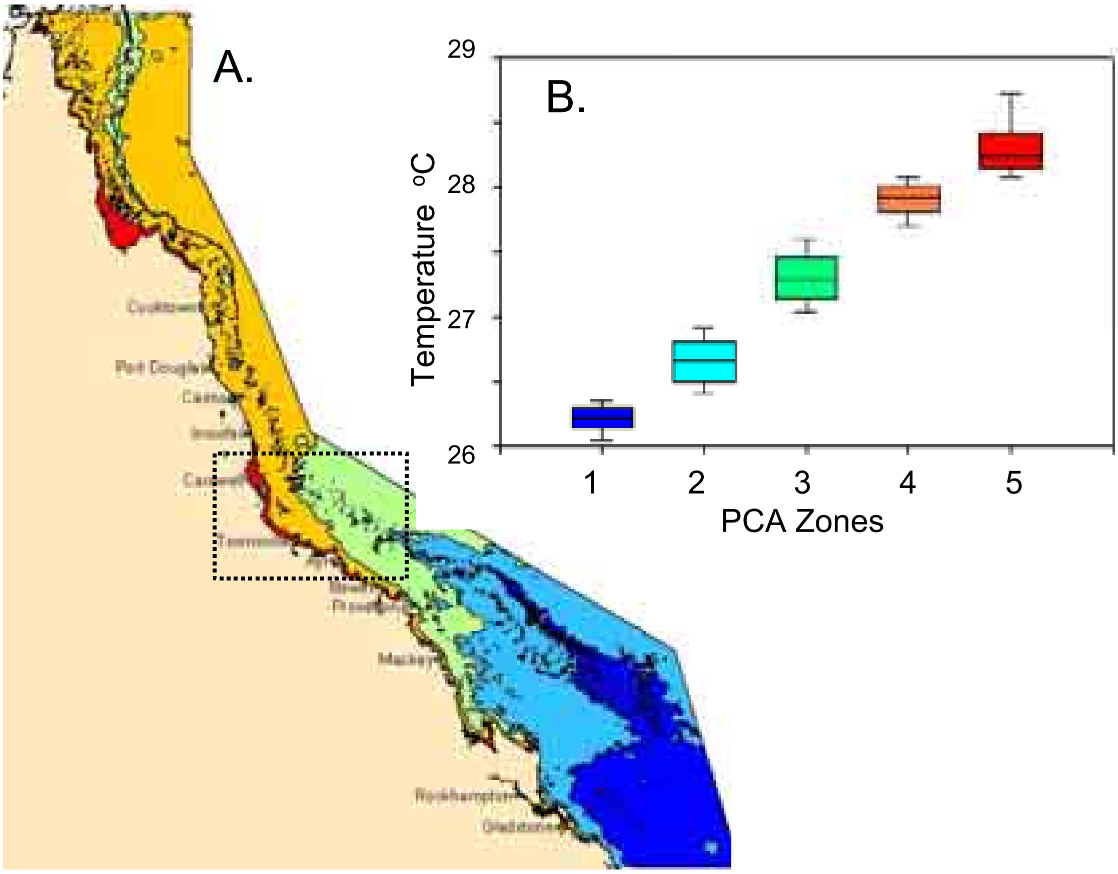

Figure 7. Variability in the 'normal' thermal climate of the Great Barrier Reef. A. Five classes of water ('PCA Zones') based on hottest monthly mean SST. The hottest monthly mean SST for each pixel was selected from the months of December, January and February for each year in the period 1990-2000 but excluding 1998, which was an exceptionally hot year. A Principal components analysis was conducted. The PCA zones represent equal intervals of the first principal component.. B. Summary statistics of the PCA Zones, indicative of the normal warmest summer average in which reefs existed during the 1990s. The boundaries of the boxes represent the 25th and 75th percentiles respectively. The line within the box marks the median, whilst the whiskers above and below the box indicate the 90th and 10th percentiles.

The dotted box around Townsville is enlarged in Fig. 8.

Case study using an inshore, a mid-shelf and an offshore reef

Middle Reef at Magnetic Island, Davies Reef and Myrmidon Reef (Fig. 8) are examples of coastal, mid-shelf and offshore reefs, respectively. Magnetic Island is five km from the coast, and its fringing coral reef extends from the surface to the sea floor at about 5 – 10 m depth. Davies Reef is about 70 km from shore in approximately 80 m of water, and its living corals extend to a depth of around 30 m. Myrmidon Reef is 105 km from the coast, has live coral down to 100 m depth on the edge of the continental slope, that extends down to over 2000 m in the adjacent Coral Sea.

Each of these reefs is special in having two essential requirements for this study: viz., an 8-10 y record of daily sea-temperatures (www.aims.gov.au/pages/facilities/weather-stations/) and an estimate of a temperature- bleaching dose-response relationship (Berkelmans 2002). No other reefs on the Great Barrier Reef meet these requirements, and thus we have no replicates within the three reef tracts. Analysis of these reefs thus provides insights that are indicative of the types of changes that have and might occur more widely, but we have no direct way of saying here how representative they are. But we do note that they are typical, in several respects, of coastal, mid-shelf and outer-shelf reefs in the Townsville area: relative proximity to shore and the Coral Sea; depth of surrounding sea-floor; composition and zonation of coral communities (Done 1982) and regimes summertime maximum temperatures (Fig. 7). Sweatman et al. (2001) and Ninio and Meekan (2002) have demonstrated that replicate reefs within reef tracts at given latitude have followed similar trajectories of hard coral cover over much of the 1990s, so it is not unreasonable to expect our projections will be representative of many reefs in similar environments.

This study projects changes in synoptic indicators of progression of the state of the three reefs' coral communities. However the detailed responses at the level of coral populations are not considered, nor would they, or the indicator of progression, necessarily be uniform across all inner, mid and offshore reefs in the region. To the contrary, we consider the heterogeneity in the environment and in bleaching impacts between and within the coastal, mid-shelf and outer reef tracts to be one of the key issues for further study (Fisk and Done 1985; Marshall and Baird 2000; Done et al. 2003) and for factoring into conservation management of coral reefs (Done 2001; Salm et al. 2001). This work on heterogeneity and application to management issues is the focus of ongoing research (e.g. Wooldridge and Done submitted).

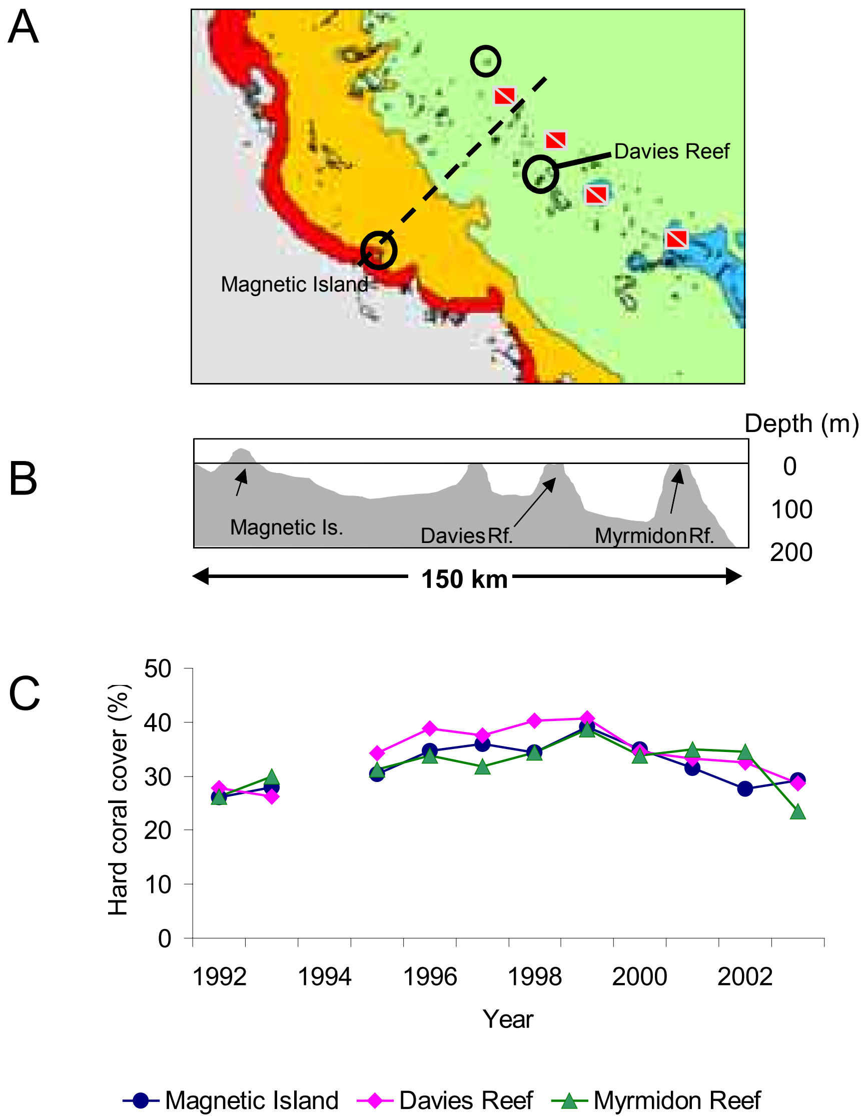

Figure 8. The study reefs Magnetic Island, Davies Reef and Myrmidon Reef. A. Map showing reef locations and four of the five thermal water types in Fig. 7. B, as well as dives sites mentioned in Zell (1999). Dotted line indicates notional location of cross-section in B. B. Schematic cross sectional diagram of continental shelf off Townsville showing location of reefs. C. Map of percent coral cover 1992 – 2002. Source of data for C. AIMS Long Term Monitoring Program..

Observed changes – 1990s

Each of these reefs has been monitored for coral cover since 1992 using fifteen 50 m long fixed transects along their NE slopes at a depth of around 6-9 m (Sweatman et al. 2001). Coral bleaching was recorded in the region, and on these reefs, in the early months of 1994, 1998 and 2002. Overall, there was little resulting coral mortality following the 1994 and 1998 bleaching episodes (Fig. 8C). The data are not yet available post-2002. However it is clear, and important to the development of Tables 1 and 2, that the bleaching events in our study reefs in the 1990s did not progress to be major coral mortality events even at Magnetic Island in 1997-8, where high levels of bleaching were likely a consequence of the combined effects of heat stress and runoff of freshwater from rivers and the island (Berkelmans and Oliver 2000). In none of the three reefs were there net setbacks in hard coral cover over the 1990s. Marshall and Baird (2000) emphasised that different bleaching impacts on reefs exposed to apparently similar stresses may be in large part a consequence of differences in coral community composition and acclimatization regime. Recent work by Done et al. (2003) supports this view.

Modelled changes – 1990 - 2050

We used 8-10 years of AIMS daily water temperature records on Myrmidon and Davies Reef and near Magnetic Island to statistically characterize the summertime variability in their sea temperatures with bleaching threshold curves for the corals at these places by Berkelmans (2002). We (RJ and PW) created the ReefClim model and use it to model two 'bleaching indicators' for those reefs for each year of the 21st Century as the temperature rises.

We used a four-step procedure to model the progression of reef appearance and ecological status of coral communities at these three reefs.

1. ReefClim was used to model daily summertime SSTs under global climate scenarios A1FI and A1T. The increase in mean summer (December-March temperatures) for the three reefs is shown in Fig. 9. Any model that generated high-end and low-end temperatures at our study reefs would suit our purpose. (It was beyond the scope of the study to evaluate the performances of the CMs themselves). We used the Canadian Climate Centre model in ReefClim because it did that, having captured some coastal influence. Moreover, it was 'average' in its projections (mostly < 1.0° C change in GBR sea temperatures per 1° C change in global air temperatures. Of seven models available to us, only CSIRO's DALARM

predicts substantially greater temperatures. These would bring forward a number of the ecological impacts discussed below.

2. For each year until 2100, ReefClim accumulated the number of days at temperatures exceeding the Berkelmans' bleaching threshold curve (Fig. 10 A) for the reef in question, and computed two indices (Fig. 10B):
    - A count of days per year that exceeded the bleaching threshold.
    - A coral bleaching index that added 1.0 for each day degree above the threshold curve, and subtracted 0.25 day degree for temporary deviations below the curve until the episode ended. (This assumes it would take four times as many days below the curve to undo damage caused by one day above. The idea – similar in concept to NOAA's degree heating week index (Lui et al. 2003) seems plausible, but there are no data to support the specific figures of 1.0 and 0.25. The two indices were loosely correlated (Fig. 10C), and given the other uncertainties, we chose to explore further only the simpler index 'number of bleaching days'.
3. For selected years (2000, 2010, 2030, 2050) ReefClim generated the probability distribution function for number of bleaching days. These distributions were smoothed using a three point running mean, and overlaid on six 'coral bleaching impact' categories (Fig. 10D: See also Fig. 11 and Table 1).
4. We (SW and TD) developed a simple new model called 'ReefState' (described in more detail below) to simulate indicators of 'appearance' and 'ecology' through the 21st Century, given the bleaching day probabilities in step 3. We assumed that bleaching impact (Table 1) advanced by one level for each additional 20 days exceedance of the bleaching threshold (Fig. 10D). Hence, any less than 20 bleaching days per year is assumed to have 'sub-lethal' impact, as defined in Table 1, while any more than 100 bleaching days per year is assumed to have 'catastrophic' impact.

Magnetic Island waters during summer months are on average somewhat cooler than those at Davies and Myrmidon Reefs. Satellite records downloaded at AIMS since the early 1990s provided an insight into temperatures throughout the study area since that time (Skirving et al. 2002). The Principal Component Analysis (Fig. 7) allowed us to divide Reef waters into five water zones based on the warmest mean summertime temperature of each pixel in each year. Our three case study reefs (Figs 7 and 8) occupy two of these. This means that Magnetic Island corals have been routinely exposed, and potentially acclimatized, to waters whose warmest summer months averaged around 28.3 °C compared to around 27.3 °C for both Davies and Myrmidon Reefs.

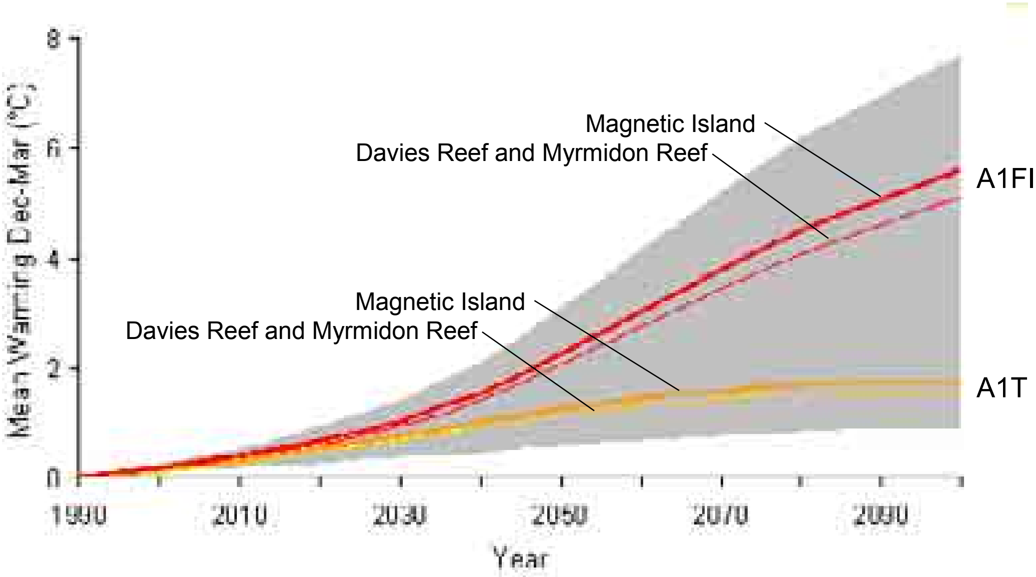

Figure 9. Projections for increase in mean summer sea surface temperatures (December-March) for the three reefs and two scenarios A1F1 (high sensitivity – or a 4.5 °C increase in temperature for doubling of CO_2) and A1T (low sensitivity – or a 1.5 °C increase in temperature for doubling of CO_2) used in this study. These scenarios are based on the Canadian Climate Centre Global Climate Model (GCM). The grey envelope represents the range of warming at these reefs based on the eight GCMs considered by the Intergovernmental Panel on Climate Change (IPCC 2001).

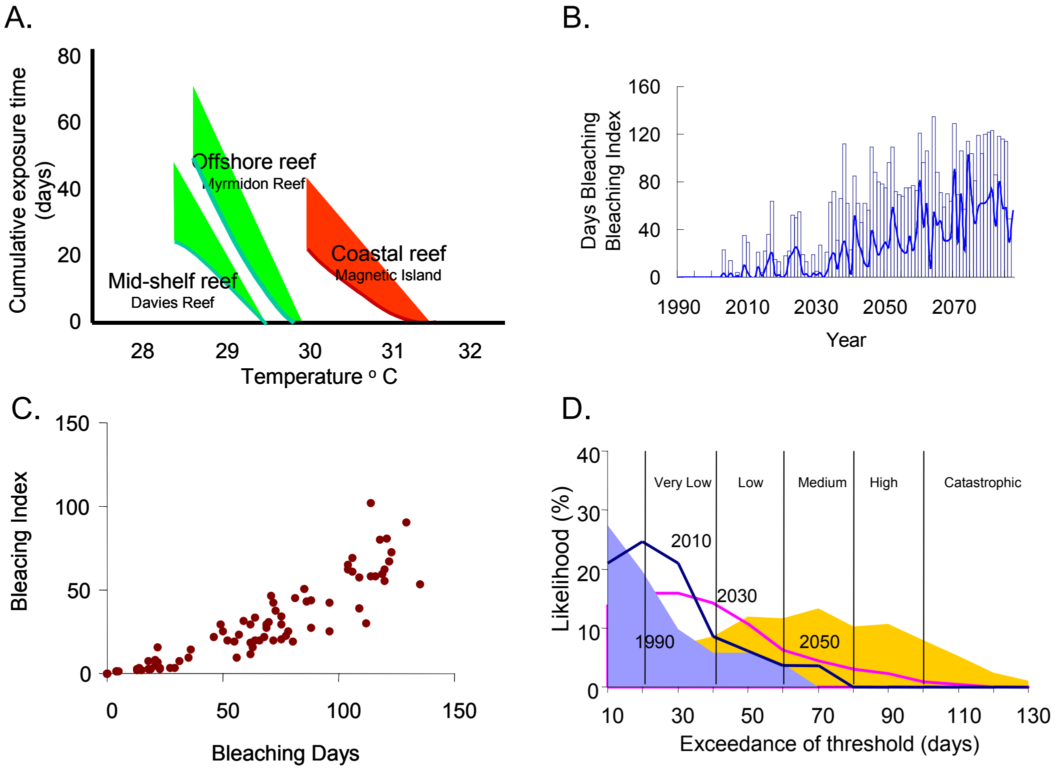

Figure 10. The ReefClim model: inputs and outputs. A. Berkelmans' bleaching curves (solid lines - determined empirically), and coping ranges (shaded areas to the right of each curve -indicative only). B. ReefClim projections for number of days above the bleaching curve (bars), and a beaching index (line) that accumulates degrees above and below the bleaching curve. C. Relationship between bleaching days and bleaching index. D. Predicted bleaching days per annum (under scenario A1T - low climate sensitivity) for Myrmidon Reef in 1990, 2010, 2030 and 2050, plotted as probability distribution functions and indicating impact levels as defined in Tables 1 and 2 and used as input for the ReefState model.

Modelling the likelihood of increasing bleaching impacts

Under the high climate change scenario A1FI (Fig. 11A,C, E), ReefClim predicted that bleaching exposures of medium and above (> 60 bleaching days in a summer) are inevitable in coming decades. By 2050, 'catastrophic' exposure (> 100 days) is probable at all three reefs. By contrast, under the low climate change scenario A1T (Fig. 11, B, D, F), 'catastrophic' exposure is much less likely at nearshore Magnetic Island by 2050, although it would still be possible at the mid-shelf Davies Reef and the outer Myrmidon Reef.

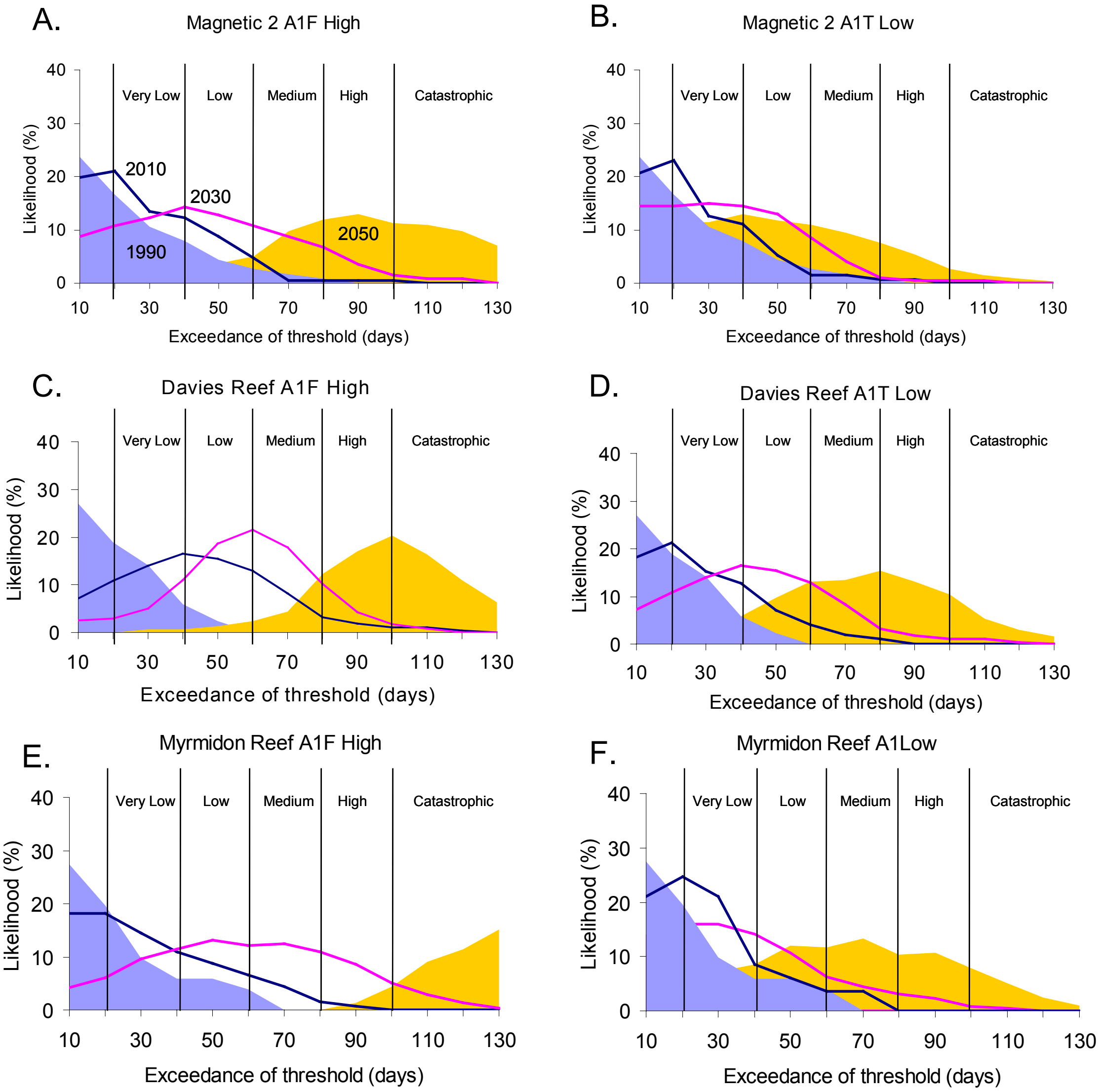

Figure 11. Magnetic Island, Davies Reef and Myrmidon Reef. ReefClim projections of likelihood of days above 'very low' to 'catastrophic' bleaching thresholds (Table 1) for years 1990 (baseline), 2010, 2030 and 2050 under two climate scenarios: A1FI and A1T. In this and following figures, the terms 'high' and 'low' in the headings refer to climate sensitivities of 4.5 and 1.5 degrees warming per doubling of CO_2, respectively.

Scenarios for appearance and ecology of the reefs: additive impacts of bleaching; no adaptation

The 'ReefState' model produced visualizations of likely trajectories for 'generalized' coral communities at Magnetic Island, Davies Reef and Myrmidon Reef (Figs. 12 – 15). ReefState codifies what the exposures in Fig. 11 may mean for the appearance and ecological state of the coral communities at these reefs based on our assumptions (Table 2) about the severity of bleaching impacts in terms of 'progression' and 'set back': how long it will take 'appearance', and 'ecology' to be restored to pre-disturbance states. Conceptually, set back in 'appearance' equates with the time needed to restore 'coral cover', whereas the usually longer setback in 'ecology' refers to the time needed to restore pre-disturbance coral diversity and age frequency distribution as well as coral cover. For the sake of simplicity, we exclude consideration of impacts other than bleaching that can set back coral communities, such as flood plumes, predatory snails, predatory sea-stars and cyclones (but see Discussion).

ReefState accumulates a 'Progression Index' for each year, defined as follows:

$$\textbf{Progression Index in year '}\boldsymbol{n}\textbf{' (PI}_n\textbf{) =}$$
$$\textbf{Calendar Year (CY) – Baseline Year (BY) - } \sum_{1-n} \textbf{ Setbacks (S)}$$

In other words, the coral community 'progresses' year by year (Fig. 12A), in 'appearance' (e.g. % coral cover), and 'ecology' (e.g. % coral cover, mean colony size, changes in level of monopolization by individual species). Without any set backs (by any disturbance – not just a bleaching impact), a community monitored from 1990 would attain a progression index of +60 years by 2050. In 'bleaching years', the community is 'set back' a number of years (Fig. 12B and Table 1), depending on the number of days above the threshold curve that summer (Fig. 11). 'Ecology' is always set back more than 'appearance'. This convention reflects our assumption that ecological parameters such as an old age frequency distribution and high associated biodiversity take longer to be restored than simple percentage coral cover, the key indicator for 'appearance' (Fig. 12A).

Over a period of decades, the community undergoes a net progression or a net retrogression, depending on the interval between bleaching years, and the number of years it is set back in each bleaching year. We thought it important to allow scope for net improvement in indicators of coral 'progress' relative to the 1990 baseline (more and larger corals, higher diversity), as can occur during periods between disturbances (e.g. Fig. 8C for coral cover). This circumvents the need to assume coral communities were 'pristine' in 1990, or that the only way available is down.

In any calendar year, a site's current status may be related to either the 'no setbacks' trajectory or the 1990 baseline (Fig. 12). For example, after the second impact in 2046 (Fig. 12A), the site's appearance (e.g. percent coral cover) has advanced about 15 years relative to its 1990 baseline, but the ecology has been setback about 20 years (e.g. it would take 20 years for natural processes of recruitment, growth and repair to restore the 1990 age frequency distribution for the coral community, and 76 years to take it to the 'no setback' line). The envelopes in Fig. 12C indicate the variability about the long-term trends in the progression indices. These were forecast by ReefState as the 25th to 75th percentile of 10,000 simulated trajectories, using as input, ReefClim's simulated probability distributions of bleaching days per summer (e.g. Fig. 11D), the associated impact levels (Table 1), and setbacks for ecology and appearance (Fig. 12B).

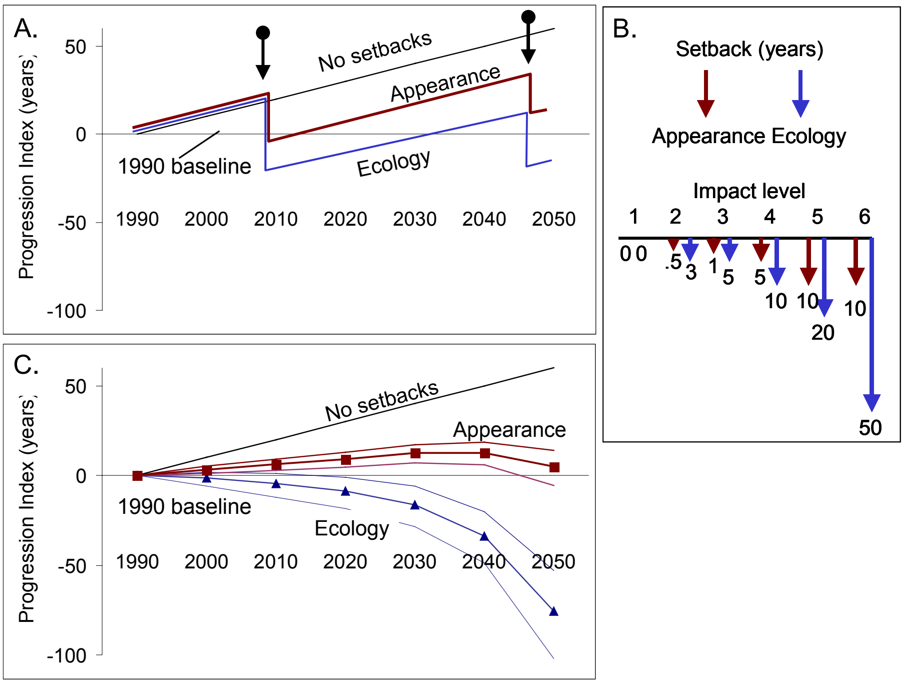

Figure12. The ReefState model tracks a 'progression index' for coral communities. The progression index is the difference between the number of calendar years in a period, minus the number of years the coral community has been 'set back' by bleaching during that period. A. A hypothetical trajectory of a coral community set back by two bleaching events (arrows). B. The six levels of setback, which we equate to thresholds of numbers of bleaching days exposure. C. An example of projected trends in appearance and ecology, based on 10,000 simulations with exposure levels increasing according to our two climate scenarios. Lines represent 25th, 50th, and 75th percentile of reef state, expressed as its progression index at 10-year intervals from 1990 to 2050. A site may be said to have either progressed or have been set back relative to the 1990 baseline (horizontal line) or the 'no setbacks' line. Example used in C is Myrmidon A1FI (high climate sensitivity).

It is not possible to equate precise ecological community states with the envelopes in Figs. 12 to 16. However the following 'community states' reflect the likely consequences for coral communities, as the envelopes move from high positive towards high negative progression index (after Done 1999; see also Marshall and Baird 2000; Loya et al. 2001).

COMMUNITY STATE 1: UNCHANGED CORALS

This is the 'status quo' outcome, where collectively, the coral populations at a site have resisted bleaching impacts in terms of their population sizes and long-term vigour because the stresses were slight and infrequent, the corals were physiologically tolerant, or both. It describes the situation when the impacts have been mainly sub-lethal, and there has been no deviation from the trajectory that would have taken place in the absence of impacts. Longer-lived corals will have continued to occupy the site, and shorter-lived populations would have turned over at the same or similar rates to those in the absence of bleaching years. Some species turnover may occur due to vagaries in coral settlement and recruitment, and to displacements of some colonies by others in competition for space. Any established tendency for some coral species to increase their relative dominance of areas at the expense of others would continue unabated. But the overall compositional and successional characteristics of the site would remain the same.

COMMUNITY STATE 2: MORE EPHEMERAL VERSION OF THE SAME CORAL COMMUNITY

This describes the situation where, over a period of years to decades, there has been substantial decrease in the life expectancy of most coral colonies at a site, caused by increasing frequency of lethal heat stress or other impacts. The overall compositional character of the site would remain the same, albeit more often dominated by younger individuals. This outcome would be brought about by a favourable local environmental setting (e.g. good quality water and substrata), a location that is well connected to a strong source of replenishment of the same suite of coral species, and a favourable ecological structure. 'Favourable ecological structure' refers in particular to 1) sufficiently high levels of grazing (that prevents accumulation of algal biomass to levels that preclude or seriously interfere with coral settlement, recruitment and/or growth – McCook 1999) and 2) sufficiently low levels of physical and biological erosion (to allow net bioconstruction of reef framework by calcifying organisms – Van Woesik and Done 1999). Given these circumstances, we would also expect to see an increased incidence of the skeletons of today's large head corals becoming the substratum for new coral.

Despite the increased coral mortality caused by bleaching, over the space of a decade, such places could be described as resilient reef areas.

COMMUNITY STATE 3: DIFFERENT CORAL SPECIES

In this case, the frequency and severity of bleaching and/or changed environment or ecological structure make the site uninhabitable for a significant proportion of the coral species that previously sustained populations. More resistant species of today's assemblage may persist and in due course monopolise the area. Other immigrating coral species may or may not be able to occupy spaces left by the more susceptible species. Such a reef could still have the quintessential reef characteristic of net accretion of reef framework, and could indeed be equally as diverse as the coral assemblage it replaces. But equally, it may be of much reduced biodiversity compared to the original state, and its net rate of accretion reduced or indeed, negative. The site may be relatively starved of settlers of the original suite of species, due to decimation of their reproductive coral populations at its usual source reefs, and despite all conditions at the site being favourable.

COMMUNITY STATE 4: PHASE SHIFT

The phase-shifted reef is the persistent 'seaweed covered rubble bank' for which the quintessential 'reef' property of accretion of reef framework is no longer possible (Done 1992). Here, sea-weed (macro-algae), that can sometimes be a transitory stage colonizing standing coral skeletons or fallen coral rubble following major natural disturbance, endures for decades and prevents establishment of coral communities of any type (Hughes 1999). Prostate fleshy algae that continuously carpet large areas are particularly effective in preventing coral settlement (Hughes 1999). This state may be perpetuated by lack of sufficient grazing pressure, and may be exacerbated by increased nutrients from land runoff that fertilize the macro-algae (McCook 1999). To prevent or reverse phase shift, management actions need to both reduce the fertilization effect and maintain or restore grazing pressure (McCook 1999; McClanahan et al. 2002).

Scenarios for the three reefs

The scenarios for both 'appearance' and 'ecology' all track the 1990 baseline for some years to decades (Figs. 13 – 15), indicating mainly level 1-2 simulated impacts early in the simulated period, and higher impact levels in coming decades. The level, to slightly rising, envelopes for 'appearance' of all reefs for the 1990s is consistent with the observed changes in coral cover at the study reefs (Fig. 8C). The simulated downturns in all trajectories for appearance and ecology (assuming no adaptation) suggest an increasing likelihood that the coral communities will become transformed from their current state (state 1) to states 2, 3 or 4. The simulations suggest the reefs will differ in the extent to which a lower rate of global warming would delay the downturn in the trajectory, and are discussed in turn here. (Please note that in spite of any apparent certainty implied in the language of the following section, these trajectories are not 'hard' predictions based on detailed climatic and ecological analysis. Rather, they are graphic representations of the consequences of our assumptions about the relationships between temperature and impacts on corals that are 'hard wired' into the simulations (Table 1 and Fig. 11). We believe the assumptions are well founded, but as in any attempts to predict the future, we are prepared to be shown to be wrong).

A coastal reef - Magnetic Island

On the shallow coastal reef at Magnetic Island, the high climate change scenario A1FI brings a marked increase in the likelihood of medium to high bleaching exposures in the coming one to two decades (Fig. 13B). Compared to a non-bleaching future, the reef scenarios suggest both the appearance (Fig. 13D) and the ecology (Fig. 13E) will be substantially set back. 'Appearance' is projected to advance more slowly from its 1990 baseline than it would in the absence of bleaching events, but 'ecology' is projected to decline relative to 1990 immediately. Achieving the low climate change A1T carbon emissions (Fig. 13F) would buy some time. Bleaching exposures will remain 'sub-lethal' to 'low' until 2030 (Fig. 13G), and only then followed by a rapid increase in the likelihood of 'medium' and 'high' level exposures by 2050. These are reflected in a longer period of improvement in 'appearance' (Fig. 13I), (albeit still at a reduced rate), and a delay in the steep decline in 'ecology' (Fig. 13J).

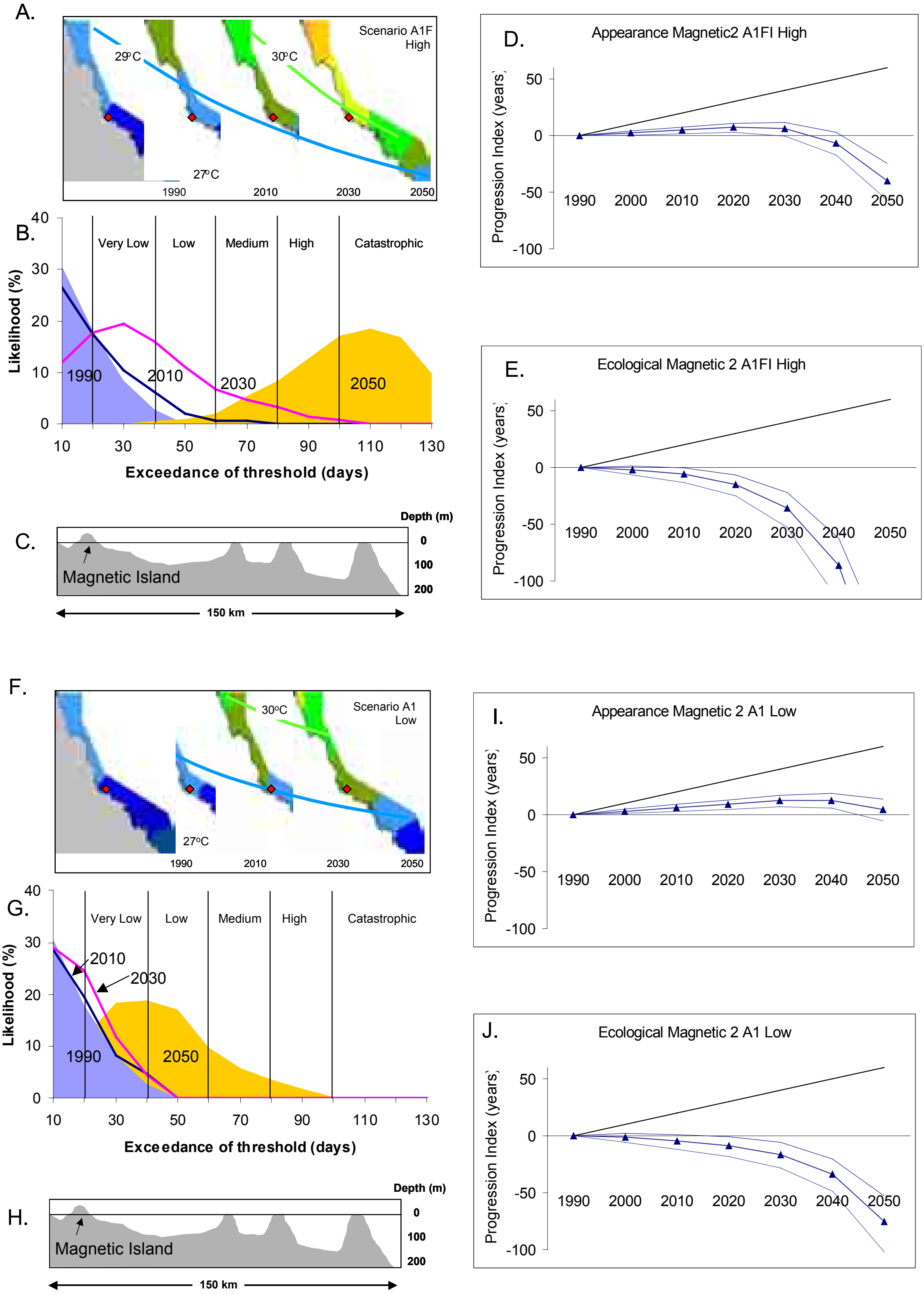

Figure 13. Magnetic Island. Projected implications of warming sea temperatures for appearance and ecology of coral reefs using high climate change scenario A1FI (A – E), and low climate change scenario A1T (F-J).

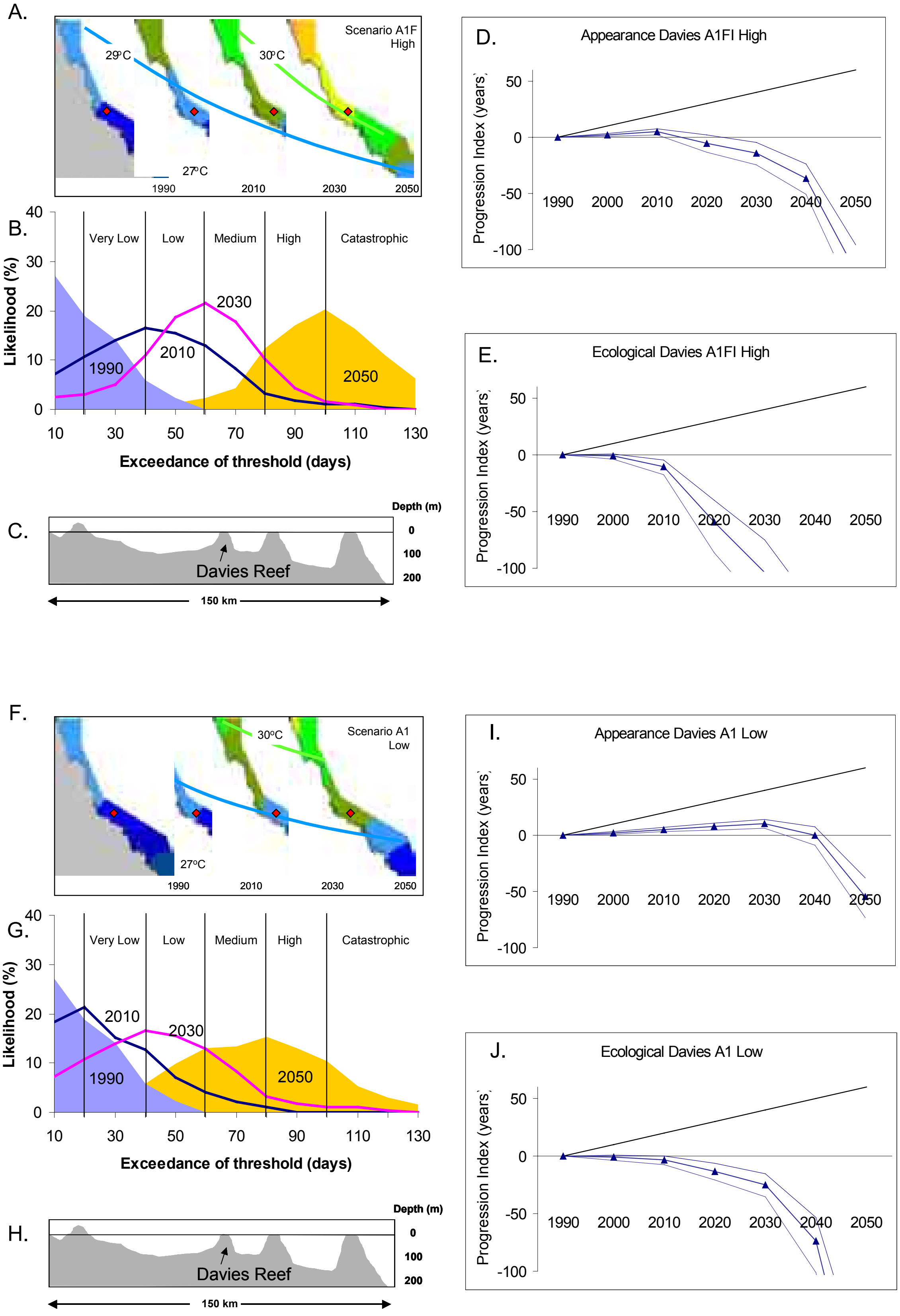

Figure 14. Davies Reef. Projected implications of warming sea temperatures for appearance and ecology of coral reefs using high climate change scenario A1FI (A–E), and low climate change scenario A1T (F-J).

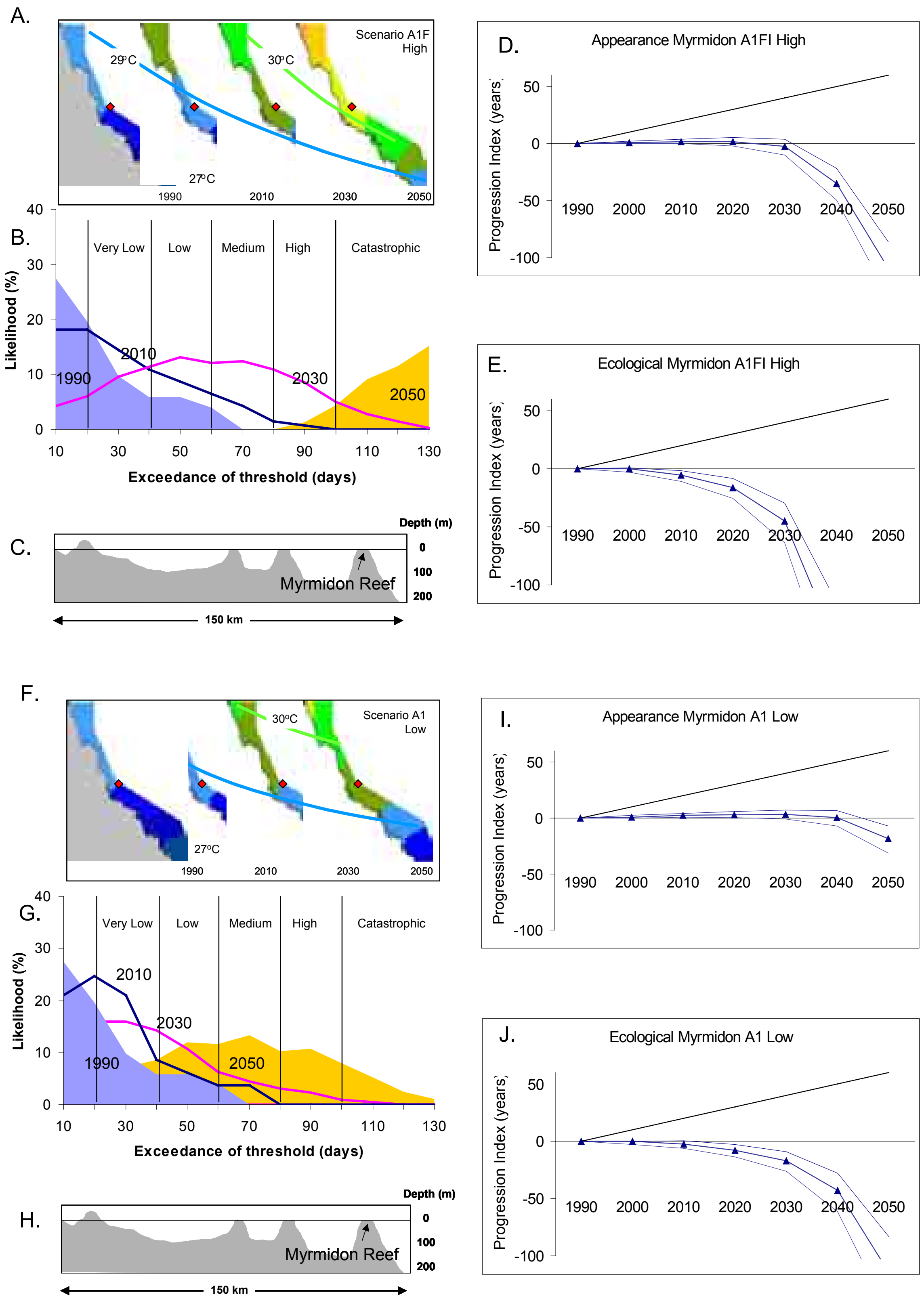

Figure 15. Myrmidon Reef. Projected implications of warming sea temperatures for appearance and ecology of coral reefs at using high climate change scenario A1FI (A–E), and low climate change scenario A1T (F-J).

A mid-shelf reef – Davies Reef

Davies Reef has the worst outlook of the three reefs. Under A1FI, it is the most likely to exceed medium to high bleaching thresholds in the coming one or two decades (Fig. 14B). Its appearance will be set back relative to 1990 by 2015 (Fig. 14D) and its ecology (Fig. 14E) by 2005. The low climate change scenario A1T (Fig. 14F) buys about two decades for appearance (Fig. 14I) but only a few years for ecology (Fig. 14J). Until 2030, the major ecological changes may be masked by maintenance of high coral cover, but by 2050, appearance too is predicted to be greatly set back.

An offshore reef – Myrmidon Reef

For Myrmidon Reef (150 km offshore - Fig. 15), the future looks similar to Davies Reef. For the high climate change scenario A1FI (Fig. 15A), there is some chance of high exposure as early as 2030 and probable catastrophic exposure by 2050 (Fig. 15B). Neither appearance (Fig. 15D) nor ecology (Fig. 15E) would improve relative to their 1990 levels. With the low climate change scenario A1T (Fig. 15F), the setback in appearance is delayed by about one decade (Figs. 15I), but ecology (Fig. 15J) receives little respite.

Adaptation effects and non-additivity of impacts

The results above assumed that no biological or ecological adaptation would take place in the period 1990 to 2050, and that effects on appearance and ecology would be additive (i.e. setbacks of 10 years in two consecutive years would give a net setback of 20 years). It also assumes there will be cumulative negative effects on the resistance of individual corals such that the second event may 'finish off' any individual that had had a previous exposure.

An alternative assumption is that the coral community 'adapts' or 'adjusts'. Community states 2 and 3, for example, represent outcomes that, though changed, may nonetheless be functional and even attractive coral reefs. State 4, by contrast, is neither. New trajectories for 'appearance' and 'ecology' are indicated in Fig. 16 for a 0.1 degree per decade rate of adaptation. This was modelled by increasing the bleaching thresholds at that rate. Adaptation 'buys time' for the communities. Although in the example given, reef 'appearance' still falls behind the 'no setbacks' line, 0.1 degree per decade adaptation allows it to improve in appearance relative to the 1990 baseline for both climate scenarios. This purpose of this example is to demonstrate the idea that coral communities may have some capacity to adapt to the changing conditions (e.g. transform from State 1 to State 2 or 3). This issue is contentious (Hoegh-Guldberg 1999), and is considered again in the Discussion.

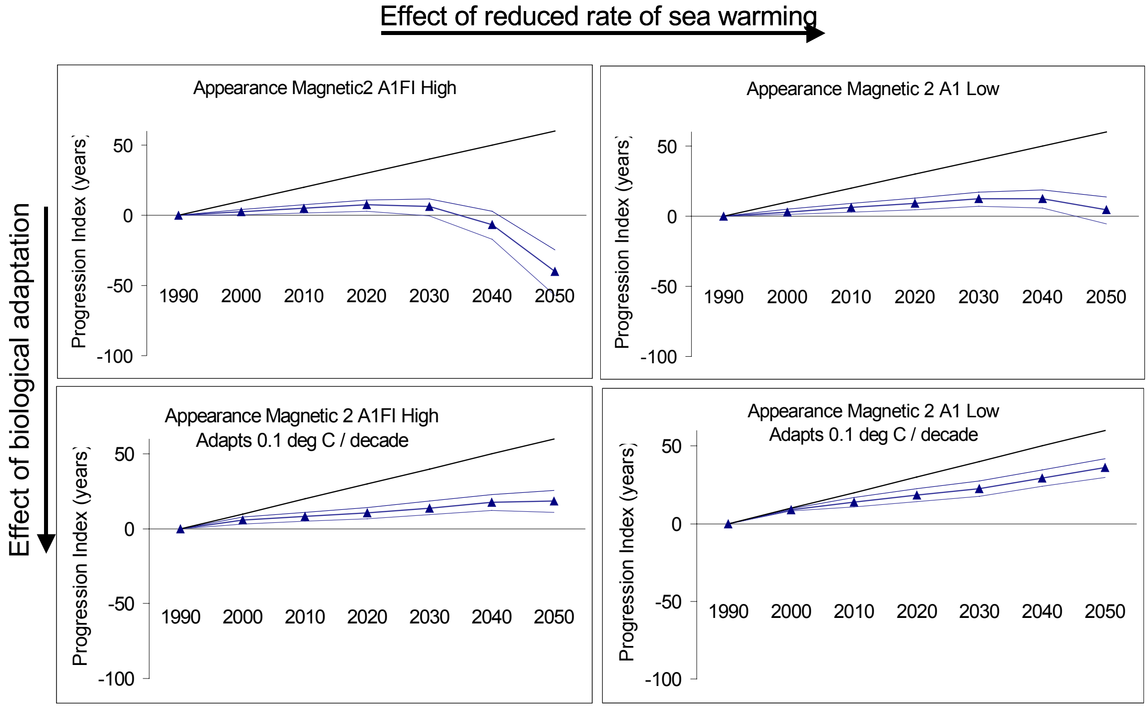

Figure 16. Effects of adaptation. The upper panels assume that there is no adaptation within the coral reef community. The lower panel assumes the coral reef system adapts at a rate of 0.1°C per decade. Complete adaptive compensation (i.e. no bleaching setbacks) would require adaptation at a rate of 0.45°C per decade (A1FI) or 0.2°C per decade (A1T).

Extrapolating to other coral reefs

Magnetic Island, Davies Reef and Myrmidon Reef are just three out of more than three thousand coral reefs in the Great Barrier Reef World Heritage Area. The present analysis of these three reefs was possible due to the existence at or near these reefs of two important inputs: Berkelman's bleaching threshold curves (Fig. 4) and 8-10 year daily sea temperature records from AIMS' automatic weather stations. At present, we are very limited in the extent to which we can extrapolate the scenarios to other reefs in the region. To do so, we would need to establish those reefs across the region whose coral communities were equivalent in both risk of exposure, and susceptibility to, increased temperature stress associated with the IPCC scenarios, and to know the spatial characteristics such increases. As mentioned earlier, we consider the heterogeneity in the environment and in bleaching impacts between and within the coastal, mid-shelf and outer reef tracts to be one of the key issues for further study (Marshall and Baird 2000; Done et al. 2003) and for factoring into conservation management of coral reefs (Done 2001; Salm et al. 2001).

Given these caveats, we suggest that the logical first steps in dividing up the region into areas containing reefs that may respond similarly would be to a) develop and map an appropriate index of the sea's normal summer temperature regimes (e.g. Fig. 7), and b) identify and map differences in susceptibilities among different types of coral communities. Our first serious attempts at this were made after this study concluded, and are described in Done et al. (2003) and Wooldridge and Done (submitted). We found that our ability to predict observed impacts of the 2002 bleaching event was best when we used a Bayesian Belief Network to combine a classification of water bodies into thermal types like Fig. 7, with information on habitats, coral community types and proxies both summer 2002 heat stress and the geographic and environmental settings of different reefs.

Discussion

Our scenarios for climate change impacts on coral communities suggest that there will be setbacks in a simple 'progression index' for both ecological structure and appearance relative to a 'no setbacks' future. They also suggest an improved mid-term (years to decades) outlook for Great Barrier Reef coral reefs as a dividend of lower rates of global warming. However we need to provide further explanation and add a number of caveats.

Likely climate change

We believe these outlooks for the reefs are plausible, in spite of any uncertainties in the water temperature scenarios related to future greenhouse gas emissions and climate sensitivity. Of the two scenarios used in this report (Fig. 9), the lower scenario, A1T, was taken at the low end of climate sensitivity (1.5 ° C change per doubling of CO_2), with regional warming of sea temperatures at just below global mean warming. This warming scenario is fairly likely to be exceeded, especially if emissions over the coming century are not contained. The warmer A1FI scenario and high climate sensitivity (4.5 ° C change per doubling of CO_2), is much less likely to be reached, but underlines the risk of combining high emissions which we do have control of, with high climate sensitivity, which we do not.

The regional warming on the Great Barrier Reef at 0.3–0.4°C over the 20th Century is less than the average warming over the Australian landmass in the same period. However, data from both land and sea indicate the rate of warming has increased over the past 50 years, with increases in water temperatures lagging behind those on land. Further work will be needed to relate the likelihood of given warming scenarios with mortality rates of corals in more detailed risk assessments. But even at this time, it has been instructive to examine future scenarios for the reefs based on our current judgments about environmental thresholds and ecological responses.

Certainty and uncertainty about future ecological states and reef appearance

Our scenarios (Figs. 13 – 15) suggest worrying outlooks for coastal, mid-shelf and outer reefs in terms of 'progression indices' for appearance and ecology. The curves are similar for all three reefs, with the greatest difference being between coastal Magnetic Island and the other two. Part of the explanation of Magnetic Island's higher bleaching thresholds and slightly better outlook is that its corals may have been selected for and acclimatized to somewhat warmer coastal waters (Done 1982 and Fig. 7, Fig. 8A).

However the precise situation corresponding to these indices some decades into the future is uncertain, as it depends on ecological rates and processes that are impossible to know at this time. We assume that a high positive progression index reflects a 'good' outcome within any given decade: some sort of steady growth of colonies and a dynamic equilibrium or ordered succession in species composition, within any given decade, local mortality and injury approximately compensated by growth and replacement of colonies (Community state 1). A not quite so high index signifies a demographically changed coral community (Community state 2) comprising some surviving originals and a faster population turnover of those heat-sensitive coral species that are periodically decimated by bleaching events. The three study reefs have remained in the domain of States 1-2 over the last 10 years: although each has been disturbed periodically, there has been recovery of coral cover with no transformation in the suites of dominant corals (Done 1997; Fig. 8C; Sweatman et al. 2001).

There are at least two potential outcomes we associate with a high negative index: Community state 3 – where only the tough survivors of current bleaching episodes persist, where future hot years may have little additional impact on a site of probably greatly reduced coral cover and diversity, and where heat-sensitive corals (or corals harbouring heat-sensitive zooxanthellae) will be unable to establish local populations in the face of very frequent and severe warm events. Or Community state 4, where the site is transformed to an algal covered rubble bank, devoid of all or most hard corals, including the toughest species. With limitations to the supply of larvae of heat-resistant corals, unsuitable local conditions, or both, the site no longer has the capacity to rebuild wave-resistant reef structures characterized by complex and stratified microhabitats for other coral-dependent biodiversity. It will have undergone a phase shift to a state that effectively lacks any capacity to maintain these features of structure, biodiversity, function and productivity that epitomize healthy coral reefs (Done et al. 1996).

It clearly matters a great deal which of these scenarios unfolds in the future. States 2 and 3 may be functionally adequate and aesthetically appealing as coral communities, but state 4 would be neither. All outcomes are plausible, given our current lack of understanding of key thresholds and the rates of adjustment that may be possible.

Uncertainties about adaptation

Among the key uncertainties is the capacity of local coral communities to adjust or adapt. Hoegh-Guldberg (1999) considered that rate of adaptation will be limited by cellular mutation rates, and will be too slow to compensate for the rapidly increasing sea surface temperature in the next few decades. When we assumed some capacity for 'adaptation', our models demonstrated better outcomes for reef appearance and ecology.

Adaptation could also work at the scale of the coral community. Indeed, the transitions from Community states 1 through 3 could be argued as ones that would allow reefs to retain their essential functions and productivity. But such changes would likely be accompanied by a rapid decline in the species diversity of corals at many sites, with potential flow-on effects to any coral-dependant biodiversity. For example, certain species of fish or invertebrates that have obligate relationships with a limited number of coral species that are no longer supported at a site will themselves no longer be supported (Munday 2002).

In the years following a severe bleaching impact, replenishment of corals and their associated biological diversity is a chancy process of larval arrival, settlement, post-settlement survival, and growth. If, and where, as Hoegh-Guldberg (1999) maintains, bleaching thresholds are exceeded annually by the middle of this Century, there should by then be strong selection in favour of any heat-resistant propagules (coral larvae and zooxanthellae partnerships) that do arrive at such places. The numbers of such propagules in a given year will ultimately be limited by the abundance and fecundity of those species at source areas for that site – upstream reefs that are well populated by healthy corals and well connected to the damaged reef by reliable currents. If these source areas are themselves seriously depleted by heat stress or other regionally widespread impact such as crown-of-thorns starfish or fresh-water impacts, the process of recolonisation of the original damaged site may be greatly protracted, relying on a stepping-stone process of successive colonization of reefs at increasing distances down-stream from the original viable source reef.

Other disturbances

In addition to bleaching impacts, it is almost certain that the reefs in our case study will be subject to other major disturbances in the 60-year horizon of our analysis. In particular, Magnetic Island reefs are the closest reefs to the mouth of Queensland's largest river (the Burdekin), and exposed to minor or major flood plume impacts most decades (King et al. 2002). As a mid-shelf reef, Davies Reef is prone to periodic outbreaks of crown-of-thorns starfish that reduce coral cover drastically (Sweatman et al. 2001). Should these impacts be simply additive on bleaching impacts, their omission will have biased our already pessimistic projections towards over-optimism. However over medium (decadal) time scale, impacts are unlikely to be simply additive. For example, a coral community with its *Acorpora* coral already reduced by a recent outbreak of crown-of-thorns starfish may be little affected by bleaching, which also can preferentially affect *Acropora* species.

Other effects of climate change

Other aspects of global climate change that will impinge on coral reefs include the frequency and intensity of cyclones and floods, the height of mean sea level, and the chemistry of surface waters (Pittock 1999). In the Great Barrier Reef region, cyclone frequency seems likely to remain the same, but with increased intensity of extreme events, the severity of destruction of reef communities and the breadth of the destructive swathe may be increased (Pittock 1999). An increase in the magnitude of extreme floods may cause coral death by hypo-osmotic stress (Coles and Jokiel 1992) at ever increasing distances into the tract of coral reefs (King et al. 2002). Increased sea level will allow growth of some reef top benthic communities currently limited by sea level, but also lead to the smothering of others, as a result of redistribution of reef-top sediments (Wilkinson 1996). Increased atmospheric CO_2 will marginally reduce the alkalinity of reef waters, causing an increase in the rate of chemical dissolution of existing reef limestone, and a decrease in deposition rate and/or strength of new limestone deposited by reef organisms (Kleypas et al. 1999).

It is apparent that the very settings in the Great Barrier Reef that are attractive for tourism may also amplify their vulnerability to some or all of these pressures. For example, the narrowness and shallowness of the continental shelf may make reefs in the Cairns region more vulnerable than those in deeper and more exposed parts of the GBR. The proportion of the shelf area covered by coral reefs in the Cairns region is about average for the entire GBR (~10%), whereas the volume of water in which they are bathed is low compared to other regions (Lewis 2001). The reefs to the south lie in deeper waters and are in many cases exposed to open ocean swells and strong tidal currents that tend to reduce their propensity to overheat. The intensive farming of coastal plains and extensive grazing of upland areas have elevated the rates of nutrients entering poorly flushed sections of the Great Barrier Reef (Furnas and Mitchell 2001). Under global climate change, extreme flood events are likely to be less frequent (Pittock 1999), but to have increased reach into the reef tract (King et al. 2002).

Implications for management and policy

Our scenarios have implications for management and policy responses in relation to coral reef use and conservation in a changing climate. Ideally, policies and management should seek to have at worst neutral, and at best, beneficial effects on conditions for recovery of corals and associated biodiversity following disturbances. They should promote the ecological attribute of 'resilience' at many scales across the Great Barrier Reef (Done 1994). 'Resilience' (capacity of a degraded site to recover rapidly to a former desired ecological state) relies on adequate rates of larval and/or asexual replenishment of depleted reef populations, accompanied by adequate on-site survival and growth rates of the 'correct' reef species.

'Good' resilience should be a consequence of successful implementation of a number of current initiatives of GBRMPA. Protection of a network of reefs from fishing should allow them to revert to more natural reef-fish compositions and size structures, with flow on effects through the food web to the diverse fish, invertebrate and plant populations (McClanahan et al. 2002). Improvements in water quality (reduced nutrients and sediments) should work in favour of corals, and against the faster growing plants that can out-compete corals in high nutrient areas (McCook 1999). A dispersed network of protected sites will have the potential to improve their efficacy as source areas for replenishment of surrounding and distant reefs through larval export. At local scales and high value sites such as tourist pontoons, there may be opportunities to manage the abundance of herbivorous organisms as key facilitators of coral recruitment and growth and to strengthen of coral recruitment through transplantation and/or the seeding of reefs with coral larvae and/or fragments transported from warmer areas, should these be considered acceptable interventions.

Coral bleaching, coral mortality and tourism

There are potentially major effects of coral bleaching on Australia's tourism visitation and revenue. In the short term, there is potential for media reports of coral bleaching on the Great Barrier Reef to be construed by some potential overseas visitors as reason to cancel a planned visit to Australia, or for domestic visitors to cancel a visit to the Great Barrier Reef. For both sectors, the cancellation would be misguided if in reality the section of the Great Barrier Reef they would have otherwise visited had not been affected by coral bleaching, of if the effect had been minor, leading only to a paling of colour and an enhancement of some pastel colours of corals that many people find more attractive than their darker phase colours. They could also be misguided if their decision to cancel was based on an incorrect belief that a particular area that was starkly bleached in one summer would of necessity still be bleached or worse, the majority of coral died, by the following winter, spring or summer.

Patchy and transitory ecological bleaching impacts may have a relatively small impact on a tourism operation such as a ship or resort, in which the appearance of the coral is one of many elements of the product (e.g. water sports; land based activities and scenery). On a scuba-diving operation where reef appearance is paramount, even a localized and transitory impacts seen by a client can lead to damaging word-of mouth accounts being propagated through global dive-tourism networks. In both businesses – resort and diving – improved assessment, monitoring and media reporting are all part of providing an informed basis for the decision to visit or not. For medium to longer term planning in the tourism industry – researchers could assist by identifying places that are at relatively lower risk of exposure to damaging high temperatures, and/or have coral and associated reef communities with a relatively greater capacity to resist, adapt or adjust to the changing environment.

Priority research questions

There are many unknowns and many research questions that could be addressed. We believe the following questions are of fundamental importance to understanding the ecological and geographic dimensions of climate change and coral bleaching on the Great Barrier Reef in coming decades. They are also highly relevant to society's goals and aspirations for the Reef:

1. Are some reefs of the Great Barrier Reef more at risk of exposure than others to the conditions that promote coral bleaching?
2. If so, will all places at risk of exposure respond equivalently, or will there be some places where the impact is merely cosmetic, others, catastrophic?
3. Can we identify reefs that will systematically escape exposure to bleaching conditions, as a function of their local environmental settings (in relation to currents and surrounding sea floor depths)?
4. What roles do coral-community composition, history and other stresses play in determining risk of bleaching, risk of mortality from bleaching, and probability of recovery?
5. Can existing and emerging methods and tools be developed with appropriate certainty and resolution for management, and applied over relevant spatial scales?

Answers to the biophysical aspects of these questions will require integration of studies of reef ecology, adaptation and acclimatization, regional climate change, local weather, population genetics of corals and their symbiotic algae, physical oceanography and satellite remote sensing.

Summary and recommendations

To the extent that our scenarios reflect ‘real’ futures, they suggest that societal measures that reduce rates of greenhouse emissions should have demonstrable benefits for the Great Barrier Reef’s coral reefs. We base this conclusion on our scenarios that suggest lower rates of regional warming will ‘buy time’ for two key indicators of reef health and amenity. It also suggests that policies and management actions for use and protection of the Great Barrier Reef are relevant to its capacity to cope with climate change. They will be beneficial in so far as they are successful in protecting or enhancing the ecological and environmental underpinnings of resilience and coral community adaptation in the ecological system.

We believe that current initiatives of federal and state governments in relation to protected areas, fishing and water quality should all work to promote ecological resilience in coral communities. Their success will depend on where, how and how much, appropriate levels of use and protection of Great Barrier Reef habitats and resources are implemented. Warming waters are only one of the many pressures faced by the Reef’s ecological systems, and no future zonal system of use and protection could or should be based on an analysis of this single pressure. Geographically explicit advice to governments and other decision makers on reefs most and least at risk of a bleaching-related impact is unavailable at this time, least of all in the context of other pressures such as flood plumes, crown-or-thorns starfish, diseases, cyclone impacts, and water quality that affect reef quality and amenity. However research in progress should improve our capacity to factor effects of climate change stresses into future management initiatives.

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Appendix 1

Stage 1: Paling: Only a small proportion of zooxanthellae are expelled, the coral becomes paler, but the remaining thousands of zooxanthellae in each polyp continue to feed it with the excess sugars that their photosynthesis creates.

Stage 2: Partial colony bleaching: Parts of the colony retain high zooxanthellae densities and normal colour, whereas other parts lose the great majority of their zooxanthellae, and thus become paler or turn pure white (bleached). These bleached polyps, lacking an autonomous daily supply of photosynthetic sugars, can be sustained by sugars translocated from the healthy section of the colony.

Stage 3: Whole colony bleaching: All zooxanthellae are expelled from every polyp, the coral can only survive so long as it can meet its energy demands using stored foods (typically lipids) and ingested food (zooplankton, organic detritus).

Stage 4: Partial colony death: An area of contiguous polyps dies, exposing the bare coral skeleton beneath to invasion by fouling organisms and grazing by herbivorous fishes. Initially, the fouling organisms are usually fine filamentous algae, but the fouling succession varies greatly according to location, local environmental factors, the available species of fouling organisms, and the rate of grazing.

Stage 5: Whole colony death: The entire colony dies and is fouled and grazed as above. A dead colony that becomes fouled by encrusting coralline algae can persist in the reef's framework indefinitely. A dead colony that becomes heavily infested with boring algae, sponges, worms, and molluscs can within a few years to decades be transformed to rubble, sand and silt.