

The near future of coral reefs

TIMOTHY R. McCLANAHAN*

The Wildlife Conservation Society, PO Box 99470, Mombasa, Kenya

Date submitted: 3 August 2001 Date accepted: 11 June 2002

SUMMARY

In this paper the current status of coral reefs, predictions concerning the ecological state of coral reefs to the 2025 time horizon and the research needs that can help understanding and management activities that might alleviate detrimental ecological changes are evaluated and discussed. The present rate of CO₂ emissions will produce an atmospheric concentration in 100 years not experienced during the past 20 million years and water temperatures above those of the past interglacial 130 000 years before present. Human influences on water temperatures, seawater chemistry (toxic substances, nutrients and aragonite saturation), the spread of diseases, removal of species and food web alterations are presently changing reef ecology. A significant ecological reorganization is underway and changes include a reduction in calcifying and zooxanthellae-hosting organisms, their obligate symbionts, and species at higher trophic levels, with an increase in generalist species of low trophic level that are adapted to variable environments. Late-successional fleshy brown algae of low net productivity or non-commercial invertebrates such as sea urchins, starfish and coral-eating snails will dominate many reefs. These changes will be associated with a loss of both net benthic and fisheries production and inorganic carbonate deposition; this will reduce reef complexity, species richness, reef growth and increase shoreline erosion. To avert these changes management is needed at both global and local levels. Both levels need to reduce greenhouse gases and other waste emissions and renew efforts to improve resource management including restrictions on the use of resources and globalization of resource trade, run-off and waste production, and balancing potential reef production and resource consumption.

Keywords: carbon dioxide, fishing, global change, human influences, management, pollution, sea level

INTRODUCTION

Coral reefs are shallow subtidal ecosystems of the tropical

oceans formed at the edge of the land and sea that provide numerous resources to millions of people. They are a unique marine ecosystem in being characterized by a geologic component, the deposition of calcium carbonate by corals, molluscs, foraminifera and algae (Kleypas *et al.* 2001). These geologic structures leave good fossils that have allowed scientists to track evolutionary change over millions of years (Veron 1995; Wood 1999). Relative to many other ecosystems, evolutionary change on coral reefs is well documented and ancient reefs have been a focus for numerous studies of past global change (Pandolfi 1999; Budd 2000). Reefs as an ecosystem and geologic structure have been remarkably persistent over time, but the species composition of reefs has changed over time with most of the present reef species originating about 1–10 million years before the present (BP) (Veron 1995; Budd 2000). The Scleractinia, or modern stony corals, have, however, undergone a major radiation since the Cretaceous 65 million years BP with their species numbers increasing until the present (Veron 1995). With an estimated 22 ice ages over the past 1.8 million years (Muller & MacDonald 1997), there has been sufficient time for multiple cycles of global climate change. Past glacial cycles have been driven by changes in the Earth's eccentricity and obliquity, or Milankovitch frequencies, with atmospheric CO₂ concentrations lagging around 600 years behind temperature rises (Fischer *et al.* 1999; Zachos *et al.* 2001). An unprecedented experiment involving raising atmospheric CO₂ independently of the Earth's natural orbital cycles is now being undertaken and the initial ecological responses to this change are now being seen.

Coral reefs have persisted through changes in water temperature and sea level that have accompanied glacial and other cycles (Pandolfi 1996), but species extinction has occurred over these cycles and has been associated with synergistic losses in habitat and climate change (Pandolfi 1999; Budd 2000). The present atmosphere is one of the most CO₂-rich in recent geologic history with the current level being greater than at any time in the last 420 000 years. The level projected for the year 2100 is greater than that seen in the last 20 million years (Fischer *et al.* 1999; Albritton *et al.* 2001; Sandalow & Bowles 2001). Carbon dioxide and other greenhouse gases are reversing (Barnett *et al.* 2001; Levitus *et al.* 2001) the slow cooling that has been occurring over the past 50 million years (Lear *et al.* 2000). The warmest temperatures of the last 150 000 years were only about 1°C

* Correspondence: Dr Timothy R. McClanahan Tel: +254 11 485570 Fax: +254 11 472215 e-mail: crcp@users.africaonline.co.ke

Table 1 Environmental variables, the minimum (Min), maximum (Max), mean and standard deviation of sites (SD) for 1000 coral reef sites on ReefBase (taken from Kleypas *et al.* 1999a). PSU = ?.

<i>Variable</i>	<i>Min</i>	<i>Max</i>	<i>Mean</i>	<i>SD</i>
<i>Temperature (°C)</i>				
mean	21.0	29.5	27.6	1.1
minimum	16.0	28.2	24.8	1.8
maximum	24.7	34.4	30.2	0.6
<i>Salinity (PSU)</i>				
minimum	23.3	40	34.3	1.2
maximum	31.2	41.8	35.3	0.9
<i>Nutrients ($\mu\text{mol l}^{-1}$)</i>				
NO ₃	0	3.3	0.25	0.28
PO ₄	0	0.54	0.1	0.08
<i>Aragonite saturation (Ω_{arag})</i>				
mean	3.28	4.06	3.83	0.09
<i>Max depth of light penetration (m)</i>				
mean	-9	-81	-53	13.5
minimum	-7	-72	-40	13.5
maximum	-10	-91	-65	13.4

above today's and by the year 2100 temperatures are predicted, by global climate models, to increase by an average of a 3°C (range 1.4–5.8°C) (Albritton *et al.* 2001). In addition, the rate of environmental change is likely to be considerably accelerated in the near future. Multiple synergistic environmental disturbances are likely to interact to create stressful conditions unique to the current epoch (for example, human population growth and resource use, warm water and the dissolution of CaCO₃ in seawater).

Coral reefs are formed under conditions of warm water (>18°C), high light, high aragonite seawater saturation, stable full salinity and low dissolved seawater nutrients (Table 1). Corals and calcifying algae are often found in conditions that differ somewhat from these conditions (Kleypas *et al.* 1999a; Sheppard 2000a), but these communities do not form massive structures, such as barrier and atoll reefs, that survive over geologic periods of sea-level change. Determining the most important of these environmental factors has been difficult because they often vary together, making their influence on reefs difficult to tease apart (Kleypas *et al.* 1999a). Understanding the influence of these factors is important for their management as the future of coral reef organisms and reef distribution may depend on how these environmental factors vary over the current age of global climate change. Global climate change, through the accumulation of greenhouse gases, is most likely to influence water temperatures, monsoon and El Niño Southern Oscillation (ENSO) climate systems and the aragonite saturation concentrations of sea water. These changes, although currently changing the climate and oceans, are forced by the more immediate influences on coral reefs, human population growth and resource use. Below I will briefly discuss these environmental and human forcing factors, their current trends and likely influence on coral reef ecology by the time

horizon of the year 2025 (Foundation for Environmental Conservation 2001) and conclude by recommending areas for future research and management.

ENVIRONMENTAL FORCING FACTORS

Physicochemical factors

Physicochemical factors influence coral reefs organisms, and their abundance and distributions are influenced by their tolerance to variation in these factors. A summary of environmental factors collected from 1000 reefs indicates that there is a significant range for each variable, but there is also relatively minor variation around the means (Kleypas *et al.* 1999a; Table 1). For example, temperatures in both space and time range from 16 to 34°C, but standard deviations are quite low. This suggests that some extremes are tolerated or adapted to but the condition is one of minor variations around the means of temperature, salinity, phosphorus and aragonite saturation relative to temperate, intertidal and estuarine ecosystems. With increasing variability in physicochemical factors, such as temperature, coral communities persist but often with reduced species richness (Veron & Minchin 1992; T.R. McClanahan & J. Maina, unpublished data 2002) and changed ecological functions such as calcification and reef growth (Cortes 1993). Seawater nitrogen concentrations and light penetration are more variable and high variation in these factors is, therefore, likely to be tolerated more than that of environmental factors with low variation. Dependent on the factor that is changing, environmental variation will have variable consequences for reef ecology.

A few environmental factors vary together, for example temperature and aragonite are strongly ($r^2 = 0.76$) and nitrogen and phosphorus weakly ($r^2 = 0.30$) correlated (Kleypas *et al.* 1999a). In contrast, temperature, salinity and light do not vary together across the measured sites (Table 1) suggesting tolerance to variation between these environmental variables. Aragonite becomes increasingly saturated with increasing temperature but, importantly, aragonite saturation decreases with increasing atmospheric CO₂ concentration (Langdon *et al.* 2000). Light penetration and turbidity may greatly influence the depth to which calcification occurs, but are less likely to influence calcification in shallow waters of less than 7 m (Bosscher 1993). Consequently, factors that are generally abundant may become limiting at another depth or place.

Phosphorus and nitrogen concentrations may be an example where high variation in one factor can have little consequence, whereas small variation in the other can produce larger changes in reef ecology. The weak relationship between phosphorus and nitrogen concentrations may be due to the high temporal and spatial variation in nitrogen compared to phosphorus along a gradient of eutrophication. Phosphorus is often the more limiting of the nutrients, particularly in carbonate environments, where carbonate

sediments can adsorb phosphorus (Littler *et al.* 1991; Delgado & Lapointe 1994). Therefore, small increases in phosphorus are likely to cause a number of changes to reef calcification and ecology (Ferrier-Pagès *et al.* 2000; McClanahan *et al.* 2002?). Nitrogen is often fixed by algae and hard corals (Shashar *et al.* 1994a) and exported from reefs (Pilson & Betzer 1973; Wilkinson *et al.* 1984; Shashar *et al.* 1994b). It has also produced variable responses in coral and algal growth (Williams & Carpenter 1988; Delgado & Lapointe 1994; Miller *et al.* 1999; Koop *et al.* 2001). Nitrogen and phosphorus may increase photosynthesis in corals but can inhibit calcification and coral skeletal growth, inhibition occurring at only 2 µm for phosphorus and 20 µm for nitrogen (Ferrier-Pagès *et al.* 2000). High nutrient levels are expected to increase organic carbon and decrease inorganic carbon production on coral reefs. Phosphorus is more likely than nitrogen to cause this change.

Temperature is often a good indicator of the latitudinal limits of reefs, but it is poorer at predicting reef distributions within those limits. Differences in light and aragonite saturation state (Ω_{arag}) may be more important within the latitudinal range of corals (Kleypas *et al.* 1999a). Aragonite saturation is a significant limitation on reef growth as both corals and calcifying algae require supersaturated sea water and, at least from short-term experiments, calcification is often proportional to the level of saturation (Gattuso *et al.* 1998; Langdon *et al.* 2000). Many of the large-scale regional differences in the distribution of reef communities may be influenced by the spatial variability of temperature and aragonite saturation, where reefs in low aragonite-saturation or upwelling conditions grow slowly and are poorly cemented (Cortes 1993; Kleypas *et al.* 1999a). For example, the eastern Pacific and high latitude reefs have low aragonite saturation levels that reduce the production of CaCO_3 and reef formation.

One hundred years ago mean (± 1 SD) Ω_{arag} was 4.6 ± 0.2 , is presently 4.0 ± 0.2 and is predicted to be 3.1 ± 0.2 by 2065 ($\Omega_{\text{arag}} = 1$ indicates chemical equilibrium and numbers >1 indicate supersaturation; Kleypas *et al.* 1999b). These values indicate that aragonite and calcite precipitation on reefs have already decreased by around 8% from pre-industrial levels, and are likely to decrease by another 13% under doubled CO_2 conditions, resulting in an estimated 25% decrease in calcification by the end of this century (Fig. 1a). There is some evidence to support this hypothesis from the Florida Keys, USA (Helmle *et al.* 2000), but most multi-decadal studies of coral cores indicate that calcification is unchanged or increasing with increased seawater temperatures (Lough & Barnes 1997; Carricart-Ganivet & Beltran-Torres 2000). Given that there is only a predicted 8% change to the present, the methods for detecting this change must be accurate and there are differences expected among the Earth's hemispheres and ocean basins. Most reef organisms deposit aragonite but others such as red coralline algae secrete a matrix high in magnesium calcite and these algae are affected more than corals by increased seawater acidity (Langdon

2002?). Coralline algae are important for cementing reefs and corals and their loss or low calcification can lead to brittle and poorly-cemented reef structures (Cortes 1993).

Documented by a number of measures, including ship-board measurements and oxygen isotope chemistry taken from coral cores, seawater temperature has increased by about 1.5°C over the last 100 years (Parker *et al.* 1995; Cole *et al.* 2000; Barnett *et al.* 2001), most of this warming occurring since the mid-1970s (Fig. 1b). This indicates an accelerating temperature trend, but further field data are required to test this possibility, as most models do not predict an exponential rise (Albritton *et al.* 2001). Seawater temperature is quite cyclical on different time scales (Tudhope *et al.* 2001; Zachos *et al.* 2001). For example, during the last century, the ENSO in the Indian Ocean appeared to oscillate between 3.5 and 5.3 year periods, with the shorter cycle dominant before the 1920s and after the 1960s, and the longer cycle dominant in the interim. Both cycles are contained within a decadal cycle of 11.8–12.3 years driven by the Asian monsoon system (Charles *et al.* 1997); therefore the most extreme warming may occur when decadal and ENSO oscillations are temporarily in phase. An even lower frequency oscillation that can influence global temperatures is called the North Atlantic Oscillation (NAO; Hurrell 1995) and, depending on the phase of this oscillation, it can influence the direction of the warming in the near future. These oscillations will influence the ability to detect directional trends.

The apparent predictability of ENSO-associated patterns is contradicted by evidence that both ENSO events and bleaching are spatially patchy and sometimes show surprising relationships. A number of recent 150–200 year temperature records from coral cores found strong connections between Indian Ocean and Pacific oscillations. There were, however, occasional diversions from this association (Fig. 1b; Charles *et al.* 1997; Cole *et al.* 2000) and differences between the locations within ocean basins (Kuhnert *et al.* 1999). Despite the spatial and temporal variability, century-scale temperature records from the Indian Ocean are showing the predicted rise in water temperatures. Measured rises include 0.8°C in a Seychelles core and approximately 1.2–1.4°C in both western Australia and East African coral cores (Charles *et al.* 1997; Kuhnert *et al.* 1999; Cole *et al.* 2000). There are, however, differences to be expected in the different regions, latitudinal position and hemispheres as discussed below.

The history of sea level has been critical in the development of reefs. Sea-level rise is associated with the global warming phenomenon through both the thermal expansion of surface sea water and melting of the Antarctic ice cap. Sea level has risen around 0.15 m over the past one hundred years and is predicted to increase between 0.09 and 0.88 m by the year 2100 (Albritton *et al.* 2001). The maximum rate of reef growth is about 10 mm yr⁻¹ (Buddemeier & Smith 1988) and should be sufficient if this high level can be maintained and reef growth is stimulated by

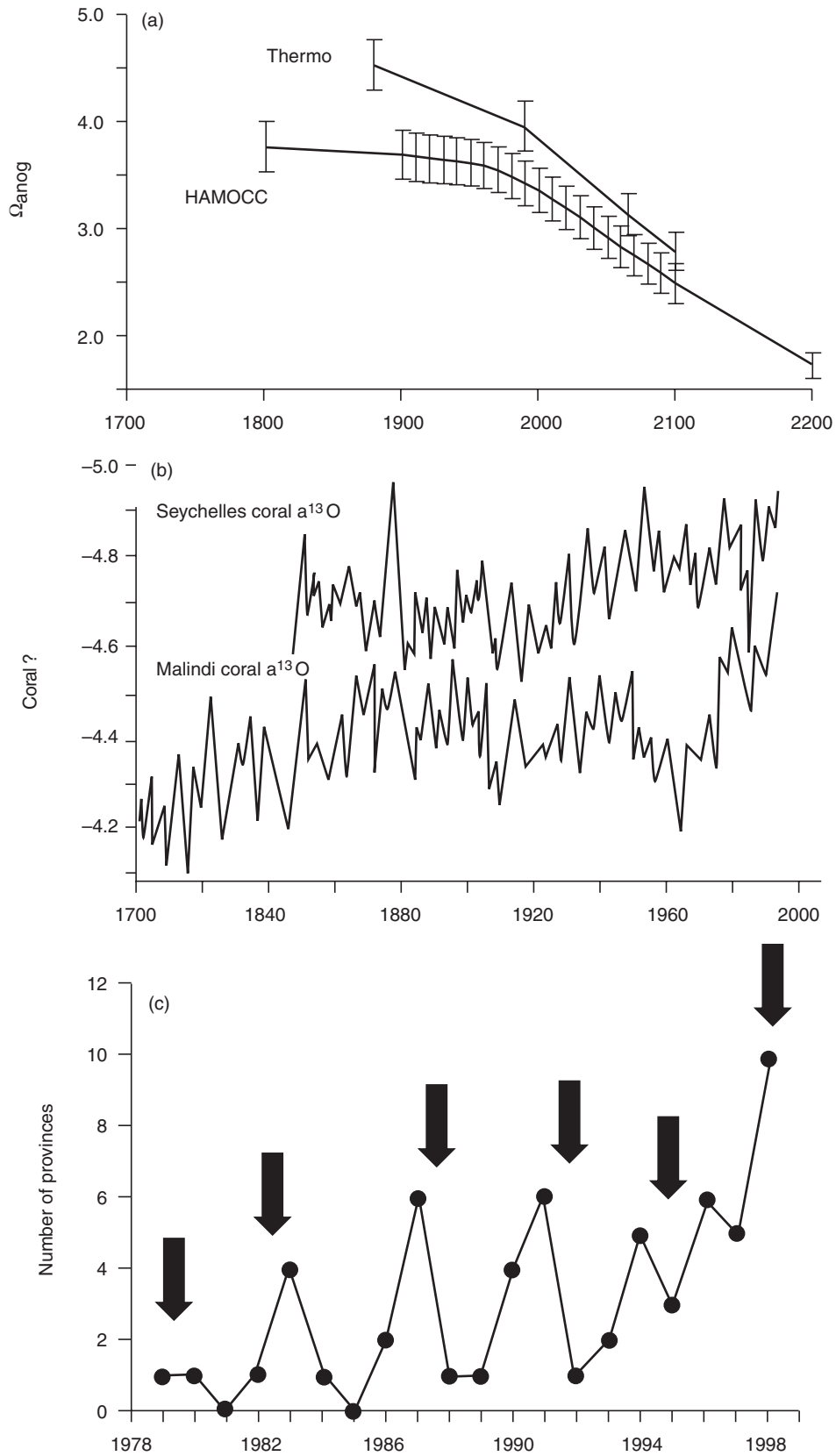


Figure 1 Time series graphs of (a) estimated global aragonite saturation concentration (mean \pm SD) of seawater (reproduced with permission of Kleypas *et al.* 1999b), (b) mean and running averages of seawater temperature trends in the Seychelles and Malindi, Kenya indicated by $\delta^{13}O$ (oxygen isotope) data (reproduced with permission of Cole *et al.* 2000), and (c) the number of reef provinces reporting severe incidences of coral bleaching (adapted from Hoegh-Guldberg 1999 with permission).

sea-level rise. There is considerable variation around the proposed mean values, however, and if calcification is reduced and erosion increases there may be some problems in maintaining this net growth rate. Historically, sea-level rise has been good for corals, because it expands the area that they can colonize (Pandolfi 1999). Nonetheless, reefs at high latitudes, such as Hawaii, have drowned during periods of rapid sea-level rise (Grigg 1997). Sea-level rise is an opportunity for the expansion of corals and calcifying organisms. If sea level was the major factor influencing reef calcification, then calcification could double from 900 to 1800 million tonnes per year in the next 100 years (Kinsey & Hopley 1991). This assumes that the conditions for coral growth are good, but current conditions of multiple and synergistically-additive nearshore stresses are likely to undermine this prediction.

Human development of tropical coasts combined with changed land and water use, associated river discharge and sediments, and changed seawater salinity can cause ecological changes in coral reefs. Sudden and large drops in salinity (to 15–20‰ for 24 h) associated with heavy rains and discharge have caused coral bleaching and death (Jokiel *et al.* 1993), as can very heavy deposition of sediments (Cortes & Risk 1985; Acevedo *et al.* 1989; Rogers 1990; Stafford-Smith & Ormond 1992). More modest and gradual changes in these factors are more common, and corals appear to have a greater ability to tolerate and recover from modest changes (Muthiga & Szmant 1987; Hoegh-Guldberg & Smith 1989; Brown & Suharsono 1990; McClanahan & Obura 1997; Möberg *et al.* 1997). For example, a study in marine parks that excluded fishing for >20 years found only modest changes in taxonomic composition of reef biota and these were attributed to the pulsed nature of the disturbance and lack of other interactive effects such as fishing (McClanahan & Obura 1997). Warming from the mid-1970s evaporative flux in the tropics has increased by about 5% (Graham 1995) and global warming has increased and is expected to further increase the tropical hydrologic cycle (Chen *et al.* 2002).

Associated with run-off from land are a variety of chemical pollutants, some of which are important for organism growth, such as phosphorus, iron and nitrogen (Dubinsky & Stambler 1996). The concern with inorganic nutrients is that they improve conditions for fast-growing algae with high organic but low inorganic carbon or CaCO₃ production (Littler *et al.* 1991; Lapointe 1997, 1999; Ferrier-Pagès *et al.* 2000). Some algae can competitively exclude the slower-growing corals that produce more inorganic carbon (Hughes & Tanner 2000) and this may lead to reefs that no longer appreciably accrete CaCO₃. The third concern is that nutrients improve conditions for infaunal organisms that erode reef substratum and often become more abundant in reefs in nutrient-rich waters (Highsmith 1980; Rose & Risk 1985; Risk *et al.* 1995; Holmes *et al.* 2000). Experiments with increased nutrients suggest that phosphorus and nitrogen alone may not increase the abundance of microboring organisms (Kiene 1997; Koop *et al.* 2001), but may interact with herbivory (Chazottes *et al.* 1995; T.R. McClanahan & W.

Kiene, unpublished data 2002). A poorly explored, but likely possibility is that nutrients and bioeroder abundance are influenced by high levels of organic matter associated with planktonic productivity (Highsmith 1980) and water column carbon that are often associated with inorganic nutrients. Reefs in plankton and organic matter-rich waters are, therefore, likely to have high erosion rates and lower net reef accretion.

Chemicals detrimental to growth and reproduction are many and have not been well studied, with the exception of oil spills (Loya & Rinkevich 1980; Jackson *et al.* 1989). Many coral reefs are found along the major oil shipping routes and are, therefore, likely to be exposed to oil during tank cleaning procedures and accidental spills. Spilled oil causes both lethal and sublethal effects on reef organisms as well as indirect ecological effects (Jackson *et al.* 1989). Corals exposed to sublethal oil spills often have reduced levels of reproduction and larval recruitment (Loya & Rinkevich 1980; Guzman & Holst 1993). Pesticides and other chemicals may bind with soil particles and when exposed to the pH of sea water may be released and influence reef organisms; for instance, the pesticide chlorpyrifos at <1 ppm decreased larval settlement and metamorphosis (Connell & Miller 1984; Acevedo 1991). Corals near areas of urban and agricultural run-off often have high incidences of diseases and other blemishes and dead patches (Glynn *et al.* 1988).

Biological factors

Although physico-chemical factors can determine the distribution, growth and success of coral reef organisms, there is a great deal of evidence to suggest that biological interactions on reefs determine species abundance and the production of both the organic and inorganic carbon. For example, the persistent grazing of algae by herbivorous fishes has been suggested to promote net algal production on coral reefs and is seen by some investigators as a greater influence on algal growth than nutrients or light (Hatcher 1983; Carpenter 1988; Miller *et al.* 1999). Grazing also encourages the most herbivore-resistant calcifying algae (Littler *et al.* 1983; Hay 1984; Lewis 1986), mediates competition between corals and erect fleshy algae (Tanner 1995) and herbivores therefore indirectly influence reef accretion. The balance between calcifying and eroding organisms is critical to the net growth of reefs and both of these are influenced by species interactions.

Reefs are characterized by a rich diversity of predator-prey relationships. In particular, fish often influence the abundance of invertebrates (McClanahan 1990; McClanahan *et al.* 1999a) and plant species (Hay *et al.* 1983). Therefore, fishing can influence these interactions, the reef community, ecological processes and production. The influences of predator-prey interactions and fishing have been studied in some detail in East African reefs (McClanahan *et al.* 1999a). Fishing tends to remove an important and slow-colonizing keystone predator, the red-lined triggerfish (*Balistapus*

undulatus), which primarily feeds on sea urchins (McClanahan 2000b). On heavily-fished East African reefs, sea urchins are typically found at levels of 4000 kg ha⁻¹, or around 100 times more abundant than in unfished marine parks (McClanahan *et al.* 1999a). Sea urchins graze intensely and erode reef substratum at high levels such that reefs dominated by sea urchins may have negative accretion or growth (McClanahan & Mutere 1994; McClanahan 1995; Carreiro-Silva & McClanahan 2001). Consequently, fishing, by decreasing herbivorous and invertebrate-eating fishes, can indirectly influence reef processes of production, calcification and erosion. More obvious forms of resource degradation are achieved through destructive fishing such as drag nets, explosives and poisons. These fishing methods are becoming increasingly common as fishers learn to use these methods and find them more profitable and competitive than traditional use of hook and line, set nets and various traps (Pauly *et al.* 1989; McClanahan *et al.* 1997; Muthiga *et al.* 2000).

Determining and ranking the importance of each of the above factors (Table 2) in coral reefs is difficult due to lack of research, lack of consensus among reef scientists, regional variation and the continually unfolding observations on reef dynamics in the current decades of rapid environmental change. Most reef scientists until recently agreed that heavy fishing and organic pollution were the two dominant environmental problems facing coral reefs (Ginsburg 1994). Recently, it has been becoming clear that diseases and warm water are having devastating effects on a regional to global scale (Aronson & Precht 2001; Goreau *et al.* 2000). Diseases appear to be increasing and their rapid spread can cause large changes to reef communities (Porter 2001). Two Caribbean diseases that have drastically changed reef ecology are the white-band disease that spread throughout most of the region in the mid-1980s (Aronson & Precht 2001) and the long-spined urchin (*Diadema antillarum*) disease that did most of its damage in 1983 (Lessios 1988).

IDENTIFIED TRENDS

During the past three decades rapid changes to coral reef ecosystems have taken place in many of the world's regions and on a large scale such that few regions could presently be claimed to have many 'pristine' coral reefs (Jackson 1997). The development of scuba, scientific diving and a heightened interest in the marine environment over this period have produced a number of insightful and decadal-length studies of coral reef ecology that give a view of the current trends in coral reef ecology and degradation. Unfortunately, the information prior to the 1960s is patchy and incomplete, making an historical time line difficult to convincingly piece together (Jackson 1997). Below I will briefly review the gross trends in each of the major regions based on the current literature. This will then be followed by an overview of global environmental trends with a view to making future projections to the year 2025.

Caribbean and Atlantic

The Caribbean and Atlantic contain only about 9% of the Earth's coral reefs (Bryant *et al.* 1998), but have among the best-studied coral reefs due to a number of permanent marine stations, a benign working environment and availability to many visiting scientists. The reefs are under moderate threat and have moderate coastal population densities of around 64 persons per km² (Bryant *et al.* 1998). One of the most obvious changes in Caribbean coral reefs is the shift in dominance from hard corals to turf and erect fleshy algae since the mid-1980s (Carpenter 1990a; Hughes 1994; Shulman & Robertson 1996; McClanahan & Muthiga 1998; Ostrander *et al.* 2000). Despite a good deal of investigation, the causes of this phase shift are not entirely clear and a number of hypotheses have been proposed (Shinn *et al.* 2000; Lessios *et al.* 2001).

- (1) A common hypothesis is that the shift was caused by a disease-induced pan-Caribbean loss of an important grazer, the sea urchin *Diadema antillarum*. *D. antillarum* may have naturally been an abundant grazer (Lessios *et al.* 2001), but some investigators believe it was unnaturally abundant (>5 m⁻²) due to heavy fishing that reduced its predators (Hughes 1994). Predators include species such as the queen and ocean triggerfish, porgies and large wrasses such as the hogfish that are commonly fished (McClanahan 1999a). Fishing intensity was also hypothesized to have reduced important herbivorous fishes, such as parrot and surgeonfishes, and when *D. antillarum* died there were few large herbivores to compensate for the loss of *D. antillarum*. The consequence was colonization of reefs by erect fleshy algae and few reefs have shown signs of coral recovery since this change (Connell 1997) unless *D. antillarum* has also recovered (Edmunds & Carpenter 2000).
- (2) Another hypothesis is that high levels of nutrients were largely or partially responsible for this change (Lapointe 1997, 1999).
- (3) A loss of the common coral *Acropora cervicornis* by the white-band disease may have affected many Caribbean reefs shortly after the *D. antillarum* disease and opened up space for colonization by algae (Aronson & Precht 2001).
- (4) Coral bleaching and mortality opened up space that was colonized by algae (Ostrander *et al.* 2000) and escaped intensive grazing (Williams *et al.* 2001).
- (5) A final hypothesis is that diseases and bleaching were putatively caused by dust and associated pathogenic microbes that were transported from west Africa and associated with drought and heavy grazing of the Sahel (Shinn *et al.* 2000).

Clearly, all the above factors could have contributed to the observed change and investigators frequently observed algal dominance in reefs that experienced change associated with each factor. When viewed on the larger scale of the whole Caribbean, however, it is clear that erect-algal dominance is

occurring in remote areas (McClanahan & Muthiga 1998; Ostrander *et al.* 2000). In these areas either *A. cervicornis* was not common or nutrients, unless supplied by dust (Shinn *et al.* 2000), were unlikely to have increased over time. Small-scale experiments designed to test the importance of lost herbivory, lost coral or increased phosphorus indicated that herbivory is the most likely explanation or at least the dominant force in promoting erect algae (McClanahan *et al.* 2002?). A loss of coral can lead to increases in algal dominance because, when additional space is created and herbivory is stable, algal biomass can accumulate until herbivory increases to compensate for this additional space and resource (Williams *et al.* 2001). The die-off of the long-spined urchin was associated with increased herbivorous fish abundance (Carpenter 1990b; Robertson 1991), but herbivory was still insufficient to control algal abundance (Carpenter 1990a; McClanahan *et al.* 2001c). Coral bleaching and mortality are often associated with warm calm periods, notably 1987–1988, 1995–1996 and 1997–1998 (Williams & Bunkley-Williams 1988; McGrath & Smith 1998; McField 1999; Goreau *et al.* 2000), and loss of coral opened space up for fast-colonizing organisms (Ostrander *et al.* 2000). The combination of continued loss of coral through bleaching and diseases (Richardson 1998) with low herbivory through fishing or sea urchin mortality, and nutrients sufficient to promote erect algal growth, appear to have interacted to promote erect algal dominance. It must be appreciated that these changes are not just restricted to a few reefs heavily influenced by humans; they have occurred on reefs with various levels of human influence throughout the region (Hughes 1994; McClanahan & Muthiga 1998; Ostrander *et al.* 2000; Williams & Polunin 2001).

Eastern Pacific

Eastern Pacific reefs occupy a small percentage of the Earth's total reef area, but represent an extreme environment for coral reefs. Reefs in this region are typically of low diversity, with small continental shelf space, seasonal coastal upwelling and isolation from centres of diversity, factors that hinder coral reef development (Glynn & Ault 2000). Modern reefs have an origin of <6000 years, occur patchily throughout the region and are considered to possess a relict fauna of the Tethyan species, most of which went extinct during subsequent glaciation (Glynn & Ault 2000). Nonetheless, 41 species of zooxanthellate scleractinian corals and hydrocorals inhabit this region and many coastlines have yet to be explored (Glynn & Ault 2000).

Corals that build the reef are usually restricted to one or a few species and skeletal growth rates can be comparable to reefs in other regions (Cortes *et al.* 1994). The structural integrity of these reefs is, however, low and submarine cementation is rare, crustose coralline algae produce poorly developed pavements and bioerosion is high (Cortes 1993). The low aragonite saturation of the seawater ($\Omega_{\text{arag}} = 3.0\text{--}4.0$) and abundance of bioeroding organisms associated

with cool and plankton-rich waters contribute to these factors. The present state of this region may reflect the future of many reefs as global aragonite saturation declines in the coming decades (Kleypas *et al.* 1999b). All the above factors make these reefs vulnerable to environmental change, the vulnerability corroborated by the small continental shelf, short life span and low species richness of these reefs (Glynn 2000). Many of these reefs were badly disturbed by the 1982–1983 El Niño. Reefs in areas such as the Galapagos have largely disappeared (Glynn 1994) due to extreme coral mortality and high erosion of the carbonate framework by sea urchins (Eakin 1996; Reaka-Kudla *et al.* 1996; Glynn 2000).

The 1982–1983 El Niño that devastated many reefs was considered a rare event, but was followed up by another extreme event in 1998 that produced less mortality, perhaps due to the poor recovery or some adaptation to the prior disturbance (Glynn 2000; Baker 2002). Some species that were nearly extirpated by the 1982–1983 El Niño were extirpated by the 1998 event. One site-restricted species, *Acropora valida*, and three species of *Millepora*, namely *M. platyphylla*, *M. boschmai* and *M. intricata*, are now either extinct or represented by only a few remaining colonies (Glynn & Ault 2000) while another six species have experienced devastating declines in abundance (Glynn 2000). These species were not the dominant reef-building corals and although the reef builders may persist they are still threatened by the crown-of-thorns starfish (*Acanthaster planci*) (Fong & Glynn 1998). The outcome of global climate change may be a complex interaction between El Niño frequency and predation by the crown-of-thorn starfish (Fong & Glynn 1998, 2000).

The Pacific, Asia and Australia

This region contains around 70% the Earth's reefs (Bryant *et al.* 1998), which are the most diverse in species and also in management institutions. Management ranges from traditional and localized tenure common in many Pacific Islands including Papua New Guinea to complex national zoning programmes, as currently used on Australia's Great Barrier Reef. Human population densities are variable but generally high in South-east Asia and some islands such as Fiji, and many people are highly dependent on marine resources. Pacific reefs are among the least threatened of the Earth's reefs with only 10% of the reef areas exposed to high levels of threat (Bryant *et al.* 1998). The opposite is true of South-east Asia where fishing and land use are intense.

A global overview of threats undertaken in the mid-1990s (Bryant *et al.* 1998) identified South-east Asia, an area with 68 100 km² or a quarter the Earth's reef area, as the region with the greatest frequency of high threats, with 56% of reefs in this high-threat category. Destructive fishing including dynamite, poisons, small mesh nets, and methods that break coral in order to chase out fish for the live fish food trade, are very common (Pauly *et al.* 1989; Pet-Soede & Erdmann 1998; McManus *et al.* 2000). Pollution and dredging of the seafloor are intense around major cities like Hong Kong, Jakarta and

Manila (Morton 1996; Tomascik *et al.* 1997). Extensive deforestation has led to high levels of sedimentation in many nearshore areas (Hodgson & Dixon 1992). Beyond deforestation of land, there has been a large-scale loss of coastal mangroves for wood pulp, aquaculture ponds, tidal agriculture and plantations. For example, since the 1980s mangrove cover has been reduced by 60% in Indonesia and by 90% along the coast of Java, mostly for the creation of aquaculture ponds (Tomascik *et al.* 1997). The net result is high levels of sediment and organic matter in the water column that reduces light penetration, coral diversity and the effective depth to which corals can survive (Edinger *et al.* 1998). A study overlaying patterns of species endemism with these threats identified the Philippines, Sunda Islands (Borneo, Sumatra, Java, Celebes and Timor) and Southern Japan as among the three top areas for conservation priorities based on threats to biodiversity (Roberts *et al.* 2002).

Australia, a subregion with 48 000 km² or 20% of the Earth's reef area, had 70% of its area in the low-threat category (Bryant *et al.* 1998). The difference is largely due to the coastal population density of Australia, which is 12 people per km² (compared to 128 people per km² in South-east Asia), and the area in marine protected areas, which is 374 967 km² (compared to 36 263 km² in South-east Asia). Nonetheless, the coral-eating starfish (*Acanthaster planci*) has gone through periodic population outbreaks in Australia and other reefs in this region (Moran 1986) and their feeding on corals greatly reduces coral cover (Colgan 1987; Done 1992). The frequency of outbreaks in the Great Barrier Reef, at 10 to 15 years, appears to occur at about the rate of coral recovery (Done 1987). Some suggest this is a natural predator-prey cycle (Bradbury *et al.* 1985) or a cycle influenced by the loss of predators (Ormond *et al.* 1988) or pulses of nutrients (Birkeland 1982) and the cycle is dampening and leading towards the loss of both coral and starfish abundance (Bradbury & Seymour 1997). The dampening cycle may be accelerated when other factors such as coral bleaching, pollution or dynamite fishing increase coral mortality or slow recovery. Coral bleaching has been reported over most of the region and much of the coral mortality reported on these reefs may be due to these warm-water events (Berkelmans & Oliver 1999; Hoegh-Guldberg 1999; Goreau *et al.* 2000). Similar to the eastern Pacific the interaction of multiple sources of coral mortality and predator-prey interaction is likely to produce complex responses to global climate change. There is hope that complexity of the island geography, associated oceanography and high species diversity in this region will give reefs higher resilience to ecological degradation.

Western Indian Ocean

Western Indian Ocean and Red Sea reefs contain around 14% of the Earth's reefs, which largely exist on the continental edges of Africa and Arabia and on the oceanic islands, notably the Maldives, Chagos, Seychelles and Mascarene

Islands (Bryant *et al.* 1998; McClanahan 2000a?). Fishing pressure is intense in many areas of Africa, notably southern Kenya to northern Tanzania, western Madagascar and some of the more populated islands of the Seychelles and Mascarenes (McClanahan 2000a?). Destructive fishing techniques such as drag nets with small mesh and dynamite fishing are common in these areas, often as a result of competition for dwindling fish resources (McClanahan *et al.* 1997; Muthiga *et al.* 2000; McClanahan & Mangi 2001). Fish catch in these areas rarely exceeds 4 kg person⁻¹ day⁻¹ (McClanahan & Mangi 2001). In contrast, a number of areas such as the Maldives, Chagos and some areas of Arabia have either highly selective fishing or no fishing pressure (Medio *et al.* 2000; Sheppard 2000b). Catches in the Chagos are typically around 50 kg person⁻¹ day⁻¹ indicating low fishing pressure and high fish biomass (Mees *et al.* 1999). Nonetheless, even the remotest reefs of the Chagos are showing effects of fishing in the most valuable resources such as sharks (Sheppard 2000b). Pollution is relatively low and focused on a few coastal cities of moderate size. In the Arabian and Red Sea region, oil spills such as those around oil depots (Loya & Rinkevich 1980) are a source of damage and the Gulf of Oman has among the highest reported beach tar concentrations (Coles & Al-Riyami 1996).

The largest source of damage to these reefs in recent time has, however, been coral bleaching associated with periods of warm and still water or warm El Niño conditions (Wilkinson *et al.* 1999; Goreau *et al.* 2000). Bleaching has occurred on these reefs in 1987–1988, 1994–1995, and the largest and most intense bleaching was in 1997–1998, affecting most of the region except for the northern Red Sea and South Africa. The 1997–1998 event produced coral mortality of 40–99 %; for many reefs coral was reduced to < 10 % of the benthic cover (Goreau *et al.* 2000). This mortality was most pronounced on some of the most pristine and undisturbed reefs that had a high abundance of bleaching-sensitive branching corals such as *Acropora*, *Stylophora*, *Pocillopora*, *Seriatopora* and branching *Millepora* (McClanahan 2000a; McClanahan *et al.* 2001a?). In addition, soft corals were greatly damaged and both turf and fleshy algae increased on many of these reefs (McClanahan *et al.* 2001a?). The initial effects on the fish were less detrimental with some increases in herbivorous fish (Lindahl *et al.* 2001) but a loss of butterflyfish, wrasses, and damselfish was recorded in Kenya over a 3-year period (McClanahan *et al.* 2002/3?). This extensive bleaching damage is arguably greater than all the other current sources of coral mortality and the future of these reefs may greatly depend on the rates of recovery relative to the frequency of these bleaching events.

TRAJECTORY OF CORAL REEFS TO 2025

An essential part of the scientific learning process is to make predictions that can be falsified (Popper 1972). Below are a series of predictions based on current coral reef science followed by a more detailed rationale, description and caveats

Table 2 Important environmental factors influencing coral reefs and their projected direction and relative rate of change in the next 25 years. + = positive, increased rate of change, - = negative, decreased rate of change.

<i>Environmental factor</i>	<i>Direction of change</i>	<i>Relative rate of change</i>	<i>Explanation</i>
Human population growth and movement	+	-	Expected to increase but at an increasingly slower rate for the next 50 years
Fishing (overfishing)	+	-	Should follow current population trends
Habitat destructive fishing	+	+	Competition for dwindling fish resources will increase destructive fishing
Coral mining and collection	-	-	Replacement of coral with cement and other synthetic materials
Tourism (anchoring and coral contact)	+	-	Expected to rise but level with the expendable income of developed nations
Vessel grounding	+	-	Increase with ship traffic but should decrease with improved navigation technology and law suits associated with grounding
Waste emissions	+	-	Expected to follow human population growth but may be reduced faster with limiting resources and improved recycling
Coastal development, run-off, sediments and changing salinity	+	-	Continued deforestation and high intensity agriculture and pastoralism, in some cases increased damming may reduce these factors
Herbicides and pesticides		-	Expected to follow increased intensification of land use
Industrial and urban pollution	+	-	Expected to follow human population growth
Oil pollution	-	-	Improved tanker design and public pressure
Greenhouse gases	+	-	Expected to follow energy consumption
Xenobiotics and diseases	+	+	Increased movement of people, boats and atmospheric circulation with increased soil erosion
Environmental education	+	+	Increased awareness of environmental problems and recognition of the importance of education and community support for conservation
Laws, regulations and enforcement	+	+	Increased recognition of the importance of restrictions on uncontrolled resource use
Pest populations (coral eating invertebrates and sea urchins)	+	-	Overfishing will change ecological state towards dominance by unused species with strong competitive ability
Algal overgrowth	+	-	Loss of higher trophic levels will improve conditions for fast-growing lower trophic levels
Erosion of reefs	+	+	Combination of increased organic pollution and reef-eroding pests
Warm water	+	-	Expected to follow greenhouse gas emissions
Seawater acidity	+	+	Expected to follow greenhouse gas emissions
Hurricane and storm damage	+	+	Expected to follow greenhouse gas emissions
Sea level	+	+	Expected to follow greenhouse gas emissions
Coral bleaching	+	+	Expected to follow greenhouse gas emissions
El Niño frequency	0	0	Presently at maximum frequency
El Niño intensity	+	+	Presently at maximum frequency

in the text. The predictions are ecologically conservative in that they are made to increase awareness and future monitoring of potentially detrimental ecological changes and to provoke the application of the precautionary principle (O'Riordan & Cameron 1994); many will, hopefully, be disproved from this monitoring. Table 2 presents a number of predictions focusing on external forcing factors and Table 3 lists the predictions for important components of the coral reef ecosystem. As I will point out, the effects of each factor

will greatly depend on the position of individual reefs in terms of the latitude, vicinity to shore and human populations and position in the ocean basin.

Physicochemical factors

Climatic oscillations and disturbances

Recognition of the importance of moderate-scale oscillations in climate and oceanographic conditions including the

Table 3 Ecologically conservative predictions for the coral reef environment, function and components in the year 2025. + = positive, increased rate of change, - = negative, decreased rate of change, 0 = unchanged.

<i>Ecological Variable</i>	<i>Direction of change</i>	<i>Explanation and caveats</i>
<i>Physicochemical environmental factors</i>		
Phosphorus	-/+	Reduced in offshore areas of the subtropics due to reduced winds and water-column mixing but increased in equatorial areas due to increased monsoons. Nearshore areas will experience increased water cycle, human and domestic animal waste production, soil erosion and water column mixing. Temporal variation will be high.
Nitrogen	+/-	Offshore water column mixing in subtropics will be reduced resulting in increased nitrogen fixation and may also increase in nearshore waters due to increased erosion and water cycle. Decrease in equatorial areas where monsoon conditions increase.
Trace elements	-/+	As for phosphorus
Seawater acidity	+	Increased atmospheric CO ₂
Currents and mixing	+/-	Increase in equatorial areas and decrease in subtropics.
Light penetration ?	?	Difficult to predict due to interactions between cloud cover, aerosols and phytoplankton concentrations but light at sea surface will increase in subtropics and decrease in equatorial areas as above
Ultraviolet light	++	A small increase
Dissolved and particulate organic matter	+	Increased plankton and fleshy algae
<i>Ecological functions</i>		
Gross organic production	+	Increased temperature and nutrient concentrations, lower hard coral cover but high erect algal production may reduce net compared to gross production
Inorganic production	-	Decreased calcifying coral and algae abundance due to increased acidity and loss of coral cover through bleaching
Organic/inorganic ratio	+	Increased non-calcifying algae and decreased calcifying algae and coral
<i>Reef components</i>		
<i>(i) Primary producers</i>		
Turf algae	-/0/+	Increased space and nutrients but increased competition with fleshy algae
Erect fleshy algae	+	Reduced herbivory
Coralline red algae	+	Increased seawater acidity high nutrients
Erect calcareous green algae	-/+	Increased phosphorus and decreased herbivory can increase but increased seawater acidity decrease abundance
Seagrass	+	Increased sand and nutrients
<i>Symbiodinium</i> in corals	-/0	Changes in taxonomic composition but will decrease with loss of coral
<i>(ii) Consumers</i>		
Soft corals	-	Increased bleaching mortality will reduce abundance unless increased organic matter can compensate by increasing growth
Sponge	-/+	Increased bleaching, diseases will cause losses, but increased organic matter, space and reduced predation will increase encrusting and endolithic species
Hard corals, the animal	-	Bleaching mortality and competition with erect algae
Hard corals, algae/animal	+	Higher nutrients will increase the density of <i>Symbiodinium</i> in the animal host
<i>(iii) Sessile invertebrates</i>		
Commercial invertebrates	-/0	Increased use by humans but decreased use by predatory fish
Non-commercial invertebrates	+	Ecological release from predatory fishes
<i>(iv) Fishes</i>		
Herbivorous/detritivorous fishes	-	Increased fishing
Invertebrate-eating fishes	-	Increased fishing
Piscivorous fishes	-	Increased fishing
Planktivorous fishes	-	Increased fishing
<i>(v) Detritivores</i>		
Epifaunal invertebrates	-/+	Commercial species decrease while non-commercial species increase
Infaunal bioeroders	+	Increased inorganic nutrients and organic matter

ENSO, Pacific and Indian Ocean Decadal Oscillations and the NAO and their influence on reefs is the basis for reasonable predictions up to the 2025 time horizon. The smallest-scale oscillations, such as the Indian Ocean biannual oscillations and the El Niño, are likely to be repeated frequently enough during the next two and a half decades that their effects will be averaged over time. Changes in their frequency and intensity will result in measurable changes in reef ecology. Therefore, the increasing intensity of the intra-annual monsoon oscillation (Chen *et al.* 2002) is likely to have one of the greatest and most predictable influences on reefs in equatorial areas during this time horizon.

Isotope studies of recent and ancient corals indicate that ENSO has existed for at least the past 130 000 years and that events of the past 120 years are among the most intense of the record (Tudhope *et al.* 2001). ENSO intensity and variability are correlated, and the weakest and least variable events are found during glacial periods. The ENSO during the past 100 years has oscillated between 3.5 and 5.3 year periodicities. Prior to 7000 years BP, ENSO frequency was around 15 years (Rodbell *et al.* 1999) and in the 19th century the oscillation was around a decade (Urban *et al.* 2000). Consequently, it seems likely that the current frequency of this oscillation is at its maximum and will stay at this historically-high frequency in the near future. Nevertheless, the intensity and variation of oscillations may increase as judged by the intensity of the 1983 and 1998 oscillations relative to the historical record (McPhaden 1999; Tudhope *et al.* 2001). It is important to recognize that the intensity of El Niño does not have to change for bleaching events to be associated with El Niño events if the underlying sea temperature continues to increase over time. The interaction of increasing El Niño frequency and rising temperatures will have an additive or multiplicative effect on the frequency of bleaching events (Hoegh-Guldberg 1999).

Oscillations equal to or greater than a decade will only repeat themselves once or twice in the coming quarter century and their effects may be less easy to predict or averaged over time. For example, the NAO showed a downward trend from the early 1940s to the 1970s, causing cool winters in the northern hemisphere during this time, but this trend has been reversed since the 1980s producing some of the highest temperature indices, particularly in the mid-1990s (Hurrell 1995). The time at which this oscillation will be reversed again is important for determining the trend of warming in the Northern Hemisphere up to the year 2025. A reversal in the near future would provide some temporary respite from the current rising temperature. However, the NAO may be caused by tropical temperature oscillations and warm tropical conditions may maintain the NAO in one of its extreme phases (Hoerling *et al.* 2001). Uncertainties confound the ability to make predictions but global warming may be overriding any of the cool phases of even the NAO (Hoerling *et al.* 2001). The Indian Ocean and Pacific Ocean near-decadal cycles are likely to produce two more warm periods in this coming quarter century that may coincide

with ENSO events and produce some of the warmest conditions experienced in the recent geologic record. These events are likely to be as intense as the 1982–1983 and 1997–1998 events, but reefs may have already experienced changes in species composition and dominance and this may lessen the ecological response to these events.

Disturbance frequency and reef recovery

The frequency and intensity of disturbances, whether caused by weather, predators or pollution, produce a regeneration niche that will be occupied by species that have regeneration times that fit within the period of disturbance. Because of the high species diversity in coral reefs there are a large number of associated regeneration times; ranging from days to decades (Hatcher *et al.* 1987; Nyström *et al.* 2000). An important example from coral reefs is the benthic production of algae and corals that have regeneration times ranging from tens of days to decades (Steneck & Deither 1994; Done 1997; McClanahan 1997; Ninio *et al.* 2000). Turf algae have the fastest regeneration times of the order of 20 days, following by fleshy and coralline algae and lastly corals. Corals have regeneration times ranging from a few years to decades depending on the species, depth, type of reef and growth form (Done 1997; Ninio *et al.* 2000). The fast-replacing organisms increase organic to inorganic carbon production ratios relative to the slow-replacing species. In addition to regeneration times, there are fundamental physicochemical limits or a fundamental niche that will restrict the success and recovery of species (Hutchinson 1965).

The high species richness in coral reefs assures that there are some species that will have fundamental and regeneration niches that will allow them to persist or thrive under different disturbance regimes. This variety and redundancy of species and functional groups may create ecological resilience (Naeem 1998). Nonetheless, the ecological organization of reefs under a new set of disturbance conditions can create ecosystems that may fundamentally differ from previous ecological states in terms of species composition and ecological processes, such as organic and inorganic carbon production (McClanahan *et al.* 2002b?). Additionally, the ecological services used by the human economy may be reduced or become unavailable. Below is a description of likely ecological changes associated with the predicted changes in the forcing functions (Table 2).

Oceanographic and environmental changes

The increased heating in the tropics is projected to increase the intensity of tropical atmospheric circulation, the annual monsoons and seawater mixing and produce more extreme hurricanes and ENSO events (Meehl 1992; Albritton *et al.* 2001). Reefs are most affected by monsoons largely between 0–10°, and tropical storms within 10–20° N and S of the equator. Equatorial convective areas are becoming cloudier and wetter and tropical and subtropical areas experiencing subsidence circulation less cloudy and dryer (Chen *et al.* 2002). In general, currently dry areas will continue to become

drier and wet areas wetter (Meehl 1992). Doubled CO₂ is predicted to increase the intensity of hurricanes by 5 to 12% (Knutson *et al.* 1998). These findings indicate very different environmental changes and associated ecological responses in tropical versus subtropical regions.

A problem with the general model predictions is that associated with greenhouse gases are increased aerosol concentrations above land, particularly Asia, that can decrease rather than increase the land-sea gradient and result in less intense monsoons and rainfall (Ramanathan *et al.* 2001). In fact, during the warm period between 1971 and 1990 there were less intense monsoons and rainfall in Asia (Meehl & Washington 1993), but more rainfall over the ocean (Graham 1995). Rainfall over Asia in the last century has been negatively influenced by warm ENSO periods, but since the mid-1970s it has become independent of ENSO events probably due to the higher winter and spring temperatures that override the ENSO influence (Kumar *et al.* 1999). This suggests further spatial heterogeneity in the changes associated with global climate change with some areas experiencing more and others less intense monsoons, ENSO and rainfall, depending on the balance between greenhouse gas warming, aerosol cooling and seasonal variability. This complicates simple predictions for any locality and the Earth as a whole and even for the subtropical-tropical dichotomy proposed above. Below I will discuss changes as they may effect areas with these different responses to global climate change, but will generally follow the Intergovernmental Panel on Climate Change (IPCC) predictions of intensified monsoons and ENSO events (Albritton *et al.* 2001).

The hydrologic cycling rate, human population density and associated land use and waste release are likely to enhance the concentration of nutrients and trace elements in nearshore waters of tropical countries near the equator (Wilkinson 1996; Tilman *et al.* 2001). The opposite is likely in subtropical and atmospheric-subsidence areas, except where human population densities and land use continue to increase. Subtropical areas will, however, experience more intense tropical storms that will result in greater interannual pulsed climatic disturbances. Increased nutrient levels are particularly likely in the tropics for elements that have terrestrial and deepwater sources and increase in sea water with better mixing and associated rains. Many of these elements are currently at high levels in nearshore waters and their concentrations may become partially saturated rather than increase monotonically with the projected increase in the hydrologic cycle and coastal erosion. Nitrogen comes from terrestrial run-off and upwelling, but fixation from the atmosphere is the largest source of offshore seawater nitrogen and this is greatly influenced by the amount of water-column mixing in tropical waters, the less mixing the more fixation (Smith 1984; McClanahan 1988). Consequently, the predictions for nitrogen and phosphorus can be quite different depending on a reef's distance from shore or whether global climate change will increase or decrease mixing (Smith 1984). During warm ENSO phases there were increases in

stratification of nitrogen and phosphorus concentrations, concentrations of nitrogen-fixing *Trichodesmium* and the N:P ratio in subtropical Hawaii (Karl 1999). In the subtropics or tropical areas where monsoon conditions are becoming less extreme, such as in areas with high aerosol concentrations, the trend found in Hawaii should continue with global warming.

Benthic ecosystems, such as coral reefs, will be influenced by changes in adjacent planktonic ecosystems that absorb light (Yentsch *et al.* 2002) and because nutrients and energy are transferred between ecosystems. The water column is presently seen as more limited by nitrogen and iron than phosphorus, and this is attributable to the high water movement in the open seas as compared to freshwater lakes and more isolated estuaries (Smith 1984; McClanahan 1988; Coale *et al.* 1996). In contrast, benthic and coral reef production are more limited by phosphorus (Delgado & Lapointe 1994). When nitrogen, iron and phosphorus are made available through coastal erosion, plankton blooms can be expected in nearshore waters, particularly in areas where seawater mixing is low. High water temperatures will increase not only gross production, but also metabolism, particularly of microbes that produce dissolved organic matter (DOM), and this could result in lower net and secondary production of species requiring flagellates, dinoflagellates and eukaryotic plankton as food (Karl 1999). In areas with reduced monsoon extremes there may be more stability in the water column and a greater frequency of N₂-fixing plankton blooms, more phosphorus limitation and greater metabolism and production of DOM. Depending on the plankton requirements of larvae, this could enhance or decrease recruitment rates to coral reefs. The effect of this stratification on nutrient-enhanced production of the reef benthos is likely to be small, however, as reef ecosystems produce and have a net export of nitrogen (Wilkinson *et al.* 1984; Shashar *et al.* 1994b).

Phosphorus is made available to shallow waters by mixing and run-off and is, therefore, likely to increase with increased winds, run-off, an increased hydrologic cycle and waste emissions. Inorganic elements from land are derived from land conversion (Dunne 1979) and the use of fertilizers (Tilman *et al.* 2001). Many tropical regions have already undergone a land conversion in the middle part of the 20th century. Fertilizer use has and is expected to increase (FAO 1990) along with the export of nitrogen to the sea which is closely associated with human population density and fertilizer use (Vitousek *et al.* 1997). The quantities of nitrogen reaching the sea are expected to increase, but the rate of increase may decline with improved knowledge (Matson *et al.* 1998) and the increased poverty of small-scale subsistence farmers, which are common to the tropics. Wet and dry cycles are probably critical in influencing soil erosion and the variability in these tropical cycles is projected to increase (Albritton *et al.* 2001). This suggests that while terrestrial-element and phosphorus concentrations in nearshore waters are and will be high relative to pre-agricultural conditions, the inputs will

be highly variable with the use of fertilizers and wet and dry cycles. I therefore suggest that in most tropical areas where agriculture has already developed that inputs of inorganic elements will continue to rise at a declining rate above the present but will be highly variable and influenced by periodic ENSO events, other large storms, and the wet and dry seasons. Near urban and intensified agricultural areas, where human populations, fertilizer use and poor waste treatment continue, phosphorus and nitrogen concentrations are likely to rise proportionally to human population size. In oceanic areas experiencing intensified monsoons, phosphorus levels are expected to increase due to increased seawater mixing. In non-upwelling and extra-tropical areas that depend on fixed nitrogen and water-column stability, phosphorus will decrease and nitrogen will increase. Because coral reef calcification is more sensitive to phosphorus than nitrogen (Ferrier-Pagès *et al.* 2000) those areas experiencing increased phosphorus are likely to experience reduced reef growth.

Water flow plays an important role in delivering nutrients and flushing waste products, particularly during warm periods (Charpy 2001; Hearn *et al.* 2001; Nakamura & van Woesik 2001). Where monsoons remain intense, the conditions for nutrient supply, flushing and coral reef growth will improve. One of the most notable effects of the 1998 warm ENSO was, however, a weakened north-east monsoon that caused massive coral bleaching and mortality (Goreau *et al.* 2000; McClanahan *et al.* 2001a?). The lack of stirring caused stratification of seawater temperatures and kept temperatures above 30°C for many months. Consequently, even the slow-growing massive coral species were affected (Mumby *et al.* 2001) and this was due to the synergistic effect of warm water and reduced water flow (Nakamura & van Woesik 2001). There is evidence that water motion can influence the effects of ultraviolet (UV) radiation; reduced currents can reduce the transfer of gases and waste products that can increase the stress associated with warm water and high light intensity (Kuffner 2001). The frequency of these weakened monsoons associated with warm ENSO events and rising water temperatures is likely to be one of the most detrimental forces of global change to coral reefs.

Water-column mixing can also influence light penetration, including UV light, depending on phytoplankton concentrations (Yentsch *et al.* 2002). If water-column phytoplankton concentrations increase in nearshore waters as predicted, then UV penetration to the bottom is likely to decrease in the coming decades. The opposite may occur in offshore areas influenced by intensified monsoons. UV light at sea level is, however, expected to increase slightly with reduced ozone levels in the coming decades, but reductions are expected to be least for the tropics and most for temperate regions. For a worst-case scenario of tropical ozone depletion, there will be a 2.3–3.2% increase in UV-B (308 nm) at 1 m depth per 10 years (Shick *et al.* 1996). Corals, like many other aquatic organisms, produce mycosporine-like amino acids (MAAs) that act as sunscreens that can vary with the intensity of UV and may act to shield corals from the effects of UV (Shick *et*

al. 1999; Kuffner 2001). In addition, the bright colours of many corals are produced from pigments that fluoresce under UV-A and blue light and further act to reduce excess light and bleaching and increase photosynthetic efficiency (Salih *et al.* 2000). There are interspecific differences in the susceptibility of corals to UV-B (Siebeck 1988); this suggests that in the future there could be selection for species more tolerant of UV.

Production

Processes of organic and inorganic production are likely to change with both changing seawater conditions and the biological community. There is good evidence that organic production on reefs is primarily influenced by herbivory and the species or functional composition of benthic algae (Larkum 1983). Similarly, calcium carbonate deposition results from the abundance and species composition of calcifying algae and corals that are also influenced by rates of disturbance such as herbivory and physicochemical conditions (Littler *et al.* 1991). Predictions, therefore, require a holistic view rather than one based on simple singular changes in physicochemical rates or species interactions. For many of the benthic primary producers there is an inverse relationship between organic and inorganic carbon production (Littler 1980). With increased bleaching, coral mortality and reduced saturation of calcium carbonate in seawater, organic production will increase and inorganic carbon production will decrease, particularly for organisms producing aragonite. The change in this organic/inorganic production ratio will also affect the production of CO₂ from coral reefs, most reefs with high coral cover changing from being net CO₂ producers to being net consumers. This could result in a negative feedback in global warming, although the contribution of coral reefs to the total CO₂ budget is <2 % (Ware *et al.* 1992; Frankignoulle *et al.* 1994; Gattuso *et al.* 1996; Kawahata *et al.* 1997).

Increased inorganic nutrients and organic matter in sea water and a reduction of calcifying algae, coral and predatory fishes will produce reefs with high levels of bioeroding organisms. These will include both infaunal species such as various microbes, worms, sponges and bivalves, and epifaunal organisms such as sea urchins (Glynn 1997; Holmes *et al.* 2000), and the increase will result in the loss of reef framework and an increase in sand production (Eakin 1996; McClanahan & Mutere 1994). Increased production of sand and reduced herbivory will improve conditions for colonization by seagrasses and many areas previously dominated by coral reef organisms are likely to be converted to seagrass ecosystems (McClanahan & Kurtis 1991). Seagrasses are an important tropical ecosystem but they support considerably lower diversity of species, particularly fishes, than coral reefs and do not produce the hard bottom substratum essential for the survival of reef-associated species (Duarte 2002).

Currently, the most obvious and damaging effect on coral

reefs is coral bleaching or the loss of the coral-symbiont dinoflagellate *Symbiodinium*. From the early 1980s the frequency and number of regions reporting bleaching and associated mortality has been increasing (Hoegh-Guldberg 1999; Fig. 1c) with most widespread bleaching and mortality occurring in 1998 (Goreau *et al.* 2000). The bleaching events are expected to be maintained at a frequency of about once every 3–5 years in the coming decades and significant ecological reorganization of reef communities is expected. Hoegh-Guldberg (1999) predicts that coral bleaching will become a nearly annual phenomenon by 2020, but this assumes that bleaching will continue at the current threshold temperatures and that the same species of coral and *Symbiodinium* will be dominant on reefs. Some bleaching events can result in low and others in high coral mortality (Goreau *et al.* 2000), and Baker (2002) argues that this may be partially due to a shift in dominance of *Symbiodinium* towards those taxa that are more tolerant of higher water temperatures over increasing warm-water periods.

The reorganization of the coral–algae symbiosis with the different *Symbiodinium* clades combined with a change in dominance of coral species towards those that are less affected by warm water, may confound this disturbing prediction (Ware *et al.* 1995; Rowan *et al.* 1997; Baker 2001). Evidence to support this ‘adaptive bleaching hypothesis’ (Buddemeier & Fautin 1993) is still largely circumstantial, with previous experiments and models not controlling well for natural variability in the symbiont abundance and in environmental factors other than temperature (Hoegh-Guldberg *et al.* 2002). The western Indian Ocean experienced coral mortality of between 40 and 99% in 1998 with a number of rapidly-growing branching taxa including *Acropora*, *Seriatopora*, *Stylophora*, *Millepora* and *Pocillopora* experiencing >90% mortality (Sheppard 1999; Goreau *et al.* 2000; Edwards *et al.* 2001; McClanahan *et al.* 2001a?). Some localized extirpation of species was reported from the Maldives and the eastern Pacific (McClanahan 2000a; Glynn *et al.* 2001). There is likely to be a trade-off between skeletal growth and respiration in corals (Gates & Edmunds 1999). High respiration is associated with high metabolism of protein and this activity is likely to produce greater resilience to environmental stresses such as warm water. Consequently, there is likely to be greater relative dominance of the slow growing, high respiration taxa in the future. Some massive and slow-growing taxa that have been reported to be tolerant were, nonetheless, reported to bleach and die in French Polynesia in 1998 (Mumby *et al.* 2001). McClanahan *et al.* (2001c?) also reported high mortality for some coral species that did not bleach significantly and this implies that they did not change their *Symbiodinium* with fatal consequences. Much remains to be learnt about the adaptability and potential resilience of corals to warm water and these lessons will greatly enhance the ability to make future predictions about coral reef ecology. Clearly bleaching frequency and intensity will be important factors for predicting the ecology of coral reefs in the near future.

Consumption

Fishes

Primary production and the transfer of organic production into the consumer food web will depend on rates of herbivory, which can be partially controlled by fishing. Herbivore populations may be reduced or possibly enhanced by a loss of carnivores through fishing; carnivorous fish often being the target of fishing in lightly fished reefs but herbivorous fishes increasing in importance as fishing intensifies (T.R. McClanahan & J. Maina, unpublished data 2002). Coral reefs exhibit complex food webs composed of a variety of commercial and non-commercial species. There are a number of non-commercial herbivores, notably sea urchins, which can compensate for the loss of commercial herbivorous fishes (McClanahan 1992, 1995). From my studies on East African reefs I have suggested that fishing of invertebrate-eating fish, such as some triggerfish (McClanahan 2000b), results in a proliferation of sea urchins that reduce algae to levels lower than maintained by herbivorous fishes (McClanahan 1992, 1995; McClanahan *et al.* 1999a). In this system, fishing and competition with sea urchins results in a reduction of both herbivorous fish and species of erect algae. A similar pattern has been suggested for Caribbean reefs (Hughes 1994; Williams & Polunin 2001), with the exception that a pathogen largely eliminated the dominant sea urchin *Diadema antillarum* in most of this basin in 1983 resulting in a proliferation of erect algae (Lessios *et al.* 1984). Similarly, extensive mortality of the dominant sea urchin on Kenyan reefs, *Echinometra mathaei*, occurred in 1994 and this loss, followed by slow recovery, continued fishing, and coral bleaching and mortality has resulted in an increase in erect algae on Kenyan reefs (McClanahan *et al.* 2001a, 2002?). These studies indicate that fishing, diseases of both corals (Aronson & Precht 2001) and herbivorous sea urchins, and other sources of mortality to herbivores and competitors of algae are likely to continue and result in the continued dominance of many reefs by late successional fleshy algae (Szmant 2001).

Among the consequences of fleshy algal dominance are losses of both net primary production (Carpenter 1988) and the abundance of fish (McClanahan *et al.* 1999b, 2001c?), and a further loss of hard coral (Hughes & Tanner 2000). Increases in erect algae are likely to improve conditions for some small invertebrates such as amphipods (Duffy & Hay 1994), but most species at high trophic levels appear to be detrimentally influenced by these unpalatable and late successional algae (McClanahan *et al.* 1999b, 2001c?). Curiously, even some invertebrate-eating species such as wrasses experienced reduced numbers on reefs dominated by erect algae (McClanahan *et al.* 1999b, 2001c?). The response of the fish and benthic algae appeared to depend on the history of fishing on these reefs; the oldest area protected from exploitation had the largest response to the erect algal reduction and the slowest recovery of erect algae (McClanahan *et al.* 2001c?, 2002?). These studies suggest that

erect-algal dominance will further degrade reefs through the loss of fish, and that the condition is difficult to reverse (Connell 1997) without long periods of recovery from fishing (McClanahan *et al.* 2002?).

Without effective fisheries restrictions, fishes will continue to be influenced primarily by heavy fishing in nearshore waters (Munro 1996). In many regions where the coastal population exceeds 50 people per km², notably the Caribbean, South-east Asia and East Africa, fishing is already intense and competition for fishes and the desire for profits have promoted the use of destructive fishing techniques (Pauly *et al.* 1989; Muthiga *et al.* 2000). Additionally, fishing for high-value species, such as for the live fish trade and shark fins, will continue to expand into more remote reef areas (Sheppard 2000*b*). The lack of refuge from fishing and habitat destruction will jeopardize the sustainability of these fisheries. Some species with restricted ranges may be threatened with extinction (Hawkins *et al.* 2000; Roberts *et al.* 2002). The consequences of the loss of these consumers will include trophic changes in reef ecosystems as described above for algae, sea urchins, snails and starfish. In some cases the ecological role of the commercial species can be replaced by non-commercial or less-targeted species (Shpigel & Fishelson 1991), but in many cases there are limits to the effectiveness of these species (McClanahan 2000*b*). Recovery of coral reef fishes and biomass as a whole may take only of 3–10 years (McClanahan & Kaunda-Arara 1996; McClanahan & Arthur 2001; Halpern 2002), but for many top-predators the recovery rates can be considerably slower (McClanahan 2000*b*).

Invertebrates

The response of sessile reef invertebrates to resource use is likely to be complex as well due to the interactions between collection by humans, losses of their predators through fishing (McClanahan 1990; McClanahan 2002) and changes in the physicochemical conditions of sea water and its effect on recruitment and growth. There may be fundamentally different responses depending on the commercial value of the species, but even this categorization does not insure the direction of change. Many of the highly valuable commercial invertebrate species with slow growth, such as sea cucumbers and large-bodied molluscs, are likely to experience continued unsustainable collection resulting in large population declines (Uthicke & Benzie 2001; McClanahan 2002). Many valuable giant clams, large-bodied gastropods and sea cucumber populations are presently at such low levels in many regions that there is a need to develop protected areas and aquaculture to specifically protect populations from local extirpation (Munro 1989). Some smaller fast-growing invertebrates may, however, benefit from the current overfishing of finfish which appears to reduce mortality through reduced predation (Aronson 1990; McClanahan 1990, 2002). On Kenyan reefs, only a small portion of the commercial snails show signs of excessive collection and some commercial and many non-commercial species were significantly more

abundant in reef lagoons with both shell collection and heavy fishing (McClanahan 1990, 2002). In general, populations of large-bodied commercial species are most likely to be influenced by direct collection while small-bodied species may be most influenced by the indirect effects caused by fishing.

A number of non-commercial sessile invertebrates, such as some reef-eroding sea urchins and coral-eating starfish and snails, are likely to continue to be reef pests. As described above, the loss of predatory fish can result in increased populations of species that are detrimental to the ecological processes and ecological services of coral reefs (McClanahan 1995; Bradbury & Seymour 1997). Diseases that reduce these pest species or the loss of their prey such as coral, as in the case of the crown-of-thorns (Bradbury & Seymour 1997), may ultimately limit the success of pest populations. In some cases, however, pests are tolerant of the loss of their prey and persist by their low metabolic demands or ability to rely on alternate prey (McClanahan 1992). In these cases their presence on the reef can significantly suppress the recovery of their prey. Coral-eating snails, such as *Drupella cornus* in the Indo-Pacific and *Coralliophila abbreviata* in the Caribbean, may benefit from a loss of predatory fishes, and in turn suppress the recovery of corals damaged through bleaching, pollution or overfishing (Knowlton *et al.* 1988; Hayes 1990*a,b*).

Diseases

Coral reef ecologists are increasingly recognizing the importance of diseases (Porter 2001). Devastating diseases in coral reefs have been commonly reported for coralline algae, sponges, hard and soft corals, sea urchins and fishes (Peters 1997; Richardson 1998). Diseases require a virulent pathogen, susceptible host and an environment stressful to the host in order to thrive. Future conditions of warm water, high nutrients, poor land use and increased dust and sediments, toxic chemicals, low flushing or water movement, and increased connectivity of marine environments are likely to increase the present list of coral reef diseases. The effects of these diseases can be great, as exemplified by the case of the white-band disease, a microbe affecting *Acropora* species in the Caribbean (Aronson & Precht 2001). This disease has caused a large-scale demise of these once-common species over a 10-year period and geologic evidence suggests that this is unique to the past 4000 years. In many cases the loss of these corals has been associated with increased algal cover, but in some cases there has been replacement by the corals *Agaricia* or branching forms of *Porites* (Aronson & Precht 1997; Greenstein *et al.* 1998). The loss of this coral by disease and the sea urchin *Diadema antillarum* (Lessios *et al.* 1984) has shifted dominance of many Caribbean reefs from corals to erect algae (Szmant 2001). It is difficult to predict diseases and their influences on reef ecology, but recent cases suggest that they will continue to infect reef organisms and cause surprising ecological changes to coral reefs.

CONCLUSIONS

The above discussion and cited literature make it clear that coral reefs are currently undergoing a global-scale change in their ecology associated with a number of synergistic disturbances. Many of these changes began before the time of most of the cited ecological studies (Jackson 1997; Jackson *et al.* 2001). The current trajectory is from localized small-scale disturbances such as fishing, river discharge and pollution towards regional and global-level disturbances associated with warm water, diseases and changes in seawater chemistry. There has also been a temporal pattern with regional-level ecological change occurring first in the Atlantic and Eastern Pacific beginning in the early 1980s followed by the Indo-Pacific and Indian Oceans. Changes in the future will depend on the location of reefs as described above, but we can generally expect to see a shift in benthic dominance from late-successional coral to algal taxa with higher organic but lower inorganic production and a consequent loss of reef growth and substratum complexity. Losses in coral species at the local level and possible extinction in regions with small shelf size are likely to continue. The consumer community will shift from large-bodied, edible, slow-growing and ornamental species to various unused invertebrates and some fast-growing and colonizing generalist fishes. In many places reefs will be replaced or colonized by seagrass, rubble and sand ecosystems (McClanahan & Kurtis 1991; Cortes *et al.* 1994).

Recommendations for research

Identifying reefs that will or will not be extirpated in the current age of global change will help prioritize conservation within the financial limits of support for coral reef research and conservation (Salm & Coles 2001). It is important to identify the environmental, ecological and biological properties of coral reef communities and organisms that will allow them to persist into the future. Perhaps the most obvious distinguishing environmental factor is to identify diverse coral reefs in stable cool water and low light conditions that are projected to persist in the future. Factors likely to mitigate global climate change effects include those that (1) reduce temperature stress, such as depth, upwelling and mixing, (2) enhance water movement, such as tides, winds and waves, (3) decrease light intensity, such as reef slope, depth and turbidity, and (4) correlate with reduced bleaching, including temperature variability and salinity stability (Vermeij 1986; West 2001). It is also possible that some of these factors will result in lower tolerance to rare variation or result in poorer recovery potential from disturbances and, therefore, research on the short- and moderate-term responses of reef taxa to these factors is needed. Factors likely to influence the recovery potential include (1) the connectivity and currents among reefs, (2) spatial heterogeneity and availability of refuge from disturbance, (3) recruitment availability and success, (4)

diversity, keystone species and associated ecological redundancy of species, (5) the persistence of herbivores and higher trophic levels through isolation from resource use or successful management, (6) physicochemical environmental conditions that promote coral growth, and (7) disease-causing species such as microbes, corallivores or bioeroders (Nyström *et al.* 2000; McClanahan *et al.* 2002b?). Interaction between the above factors may be as important as the single factors alone.

The above hypotheses tested under different biogeographic regions, environmental regimes and patterns of diversity and reef ecology are among the leading research foci required to identify the properties that maintain diversity, reef function and the ability of reef ecosystems to resist and recover from disturbance. It is important that the ecological measures used to define the success or resilience of reefs are defined, as the selected measures will influence conclusions. For example, a recent study of reefs with different temperature regimes found that ENSO temperature extremes resulted in lower loss of coral cover but a greater loss of taxa on reefs with high compared to low background temperature variation (T.R. McClanahan & J. Maina, unpublished data 2002). It is, therefore, important to select a variety of measures of success, including measures of taxonomic diversity and ecological function. It is further important when testing these hypotheses to distinguish correlation from causation in order to insure that causative factors are distinguished from associated factors. A surprising example of this problem is exemplified by the relationship between bleaching and distance from shore during the 1997–1998 ENSO. In the eastern Pacific, nearshore reefs were less influenced than offshore reefs (Glynn *et al.* 2001) but the opposite was found in eastern Australia (Berkelmans & Oliver 1999). The putative reason that requires further investigation is that nearshore turbidity reduced bleaching in the eastern Pacific, but nearshore salinity variation increased it in eastern Australia. Finally, multiple scales of study and their interaction, from the subcellular to the biogeographic region, are needed, as findings at one level may not be supported or relevant at another.

Improved measurement of seawater temperatures from *in situ* gauges and global satellite data and analysis of the historical data set will greatly enhance the ability to predict future changes in seawater temperatures around coral reefs and prioritize areas for conservation. There is a continued need to relate these temperature and environmental regimes to on-the-ground studies of reef ecology and diversity in order to link environmental regimes with reef condition. Additionally, region-specific models of the future global climate are needed to help prioritize those regions, latitudes and reefs of global concern for increased management. Additionally, models that link environmental processes to reef ecology are needed in order to improve future predictions and to link ecological with global-change and management models. More detailed measurements on seawater alkalinity, temperature, reef calcification and their

interaction are needed from more regions to assist in determining environments that will be affected by the increasing atmospheric CO₂. Finally, we need to study the interaction between the physicochemical and human-resource environments to determine what patterns of resource use will or will not result in sustainable resource extraction in the coming age of global climate change.

Recommendations for management

The management of coral reefs is no longer an environmental issue restricted to tropical countries and their donors; global climate change and globalization of trade have made their management a global concern and responsibility. Management is also no longer a simple issue of managing local pollution and maintaining sustainability of fisheries, but must also consider the global context when making local decisions. Management efforts are, therefore, needed from the local to the global levels. At the global level, efforts to reduce greenhouse gases now will have little effect on coral reefs in the next 25 years, but there is a need to support ongoing efforts to reduce greenhouse gases (Sandalow & Bowles 2001) in order to reduce climate change effects in the coming centuries. Restrictions on the global trade of reef resources such as sharks, ornamentals and the live-fish trade are, however, one area where immediate action at the global level can reduce further degradation. Management of watersheds and water quality is an important issue at the regional level, where greater effort to reduce the influx of inorganic and organic nutrients and sediments should promote reef resistance to and recovery after disturbances.

At the regional to global level, efforts to identify and manage species that are prone to extinction are needed. The present global scale of disturbance suggests the possibility of larger-scale species extirpations and possibly extinction (Roberts & Hawkins 1999; Glynn 2000; Roberts *et al.* 2002). Consequently, one priority of the next 25 years is to identify specific reef ecosystems and species that will require special protection in order to persist through the coming age of global warming and the intense resource use driven by the poverty of tropical countries (Salm & Coles 2001). Species that are likely to be extinction prone generally include those that (1) have narrow environmental limits, common to many coral reef organisms, (2) are endemic or with restricted ranges, (3) have small population sizes often caused by restricted habitat requirements or high trophic level, (4) low dispersal capabilities, (5) slow growth and (6) species endemic to biogeographic regions with small continental shelves (Roberts & Hawkins 1999; Glynn 2000; Bellwood & Hughes 2001). In coral reefs, however, all species hosting *Symbiodinium* (Cnidaria, Foraminifera, Porifera, Mollusca), calcifying organisms (i.e. Corallinaceae, Halimedaceae) and their obligate hosts are of special concern as they are all potentially sensitive to warm water and changes in the seawater carbonate system. As part of the cataloguing of coral reef species, the above details need to be collected to assist the

identification of these extinction-prone species and to preserve them and their habitats. It is not too early to consider the global prohibition on extractive use and the *ex situ* preservation of sensitive taxa in public or scientific aquaria. This is currently being done to preserve the remaining few colonies of recently-recognized species, *Siderastrea glynni* (Fenner 2001). Transplanting and cultivation of corals tolerant of high or variable temperatures are other alternatives. This will, however, be expensive if applied to large areas and the success can be highly variable, often depending on the coral species and the abundance of coral-eating organisms at the recipient site (T.R. McClanahan, J. Maina, C.J. Starger, P. Herron-Perez & E. Dusek, unpublished data 2002).

At the regional to local level there is a need to renew efforts for sustainable fisheries management through restrictions on space, species, size, gear and effort. Restrictions on space include the establishment of more protected areas and marine fisheries reserves, but more importantly there is a need to find ways to finance the already existing network (Kelleher *et al.* 1995; McClanahan 1999b). Some ecologists believe that traditional fisheries management in the tropics has failed and this requires a new approach to management (Roberts & Polunin 1993; Bohnsack 1998), but the failure rate is equally high for MPAs and this management dichotomy is not well justified (McClanahan *et al.* 1997; McClanahan 1999b; Polunin 2002). Different management methods will work depending on cultural and economic factors that influence coastal economies and fishing. Closed areas may be the best alternative where tourism and taxes can finance them (McClanahan 1999b). Where national fisheries programmes are strong, improved efforts to sustain and adapt them should continue; where they are weak, alternatives such as community-based management or co-management should be encouraged (McClanahan *et al.* 1997; Cooke *et al.* 2000).

Restriction on fishing space should not include just MPAs, but also the elimination of national or donor programmes that extend fisheries into previous unfished areas. Many tropical nations have nearshore areas that are overfished but they are fished sustainably because there are sources of recruits coming from areas that are too distant or dangerous to be fished by artisanal fishers. In areas where this is not the case, such as many Caribbean islands, there is loss of breeding stock and associated fisheries collapse (Berkes 1987). Unfished source areas act as refuges for breeding populations and the spillover of vagile adults and larvae into nearshore fisheries (McClanahan & Mangi 2000). It may be short-sighted to increase the capacity of fishers to exploit these populations as this could lead to large-scale collapse of both near and offshore fisheries. Programmes to increase fishing capacity may, however, be justified if closed areas near to shore are successfully established simultaneously.

Restrictions on destructive gear and effort will provide challenges to conservation as human numbers increase in tropical countries and competition for dwindling resources accelerates. In addition to legislation and enforcement to

eliminate destructive fishing methods, there is a growing need to alleviate poverty such that fishing is not one of a very few major economic options for tropical people. This requires economic planning and implementation and improved attempts to realistically balance populations, resources and economic growth. The responsibility for balancing ecological and economic production and the control of carbon, toxic and nutrient wastes from both tropical and temperate nations are needed to provide an improved future for coral reefs and their economic services.

ACKNOWLEDGEMENTS

This paper benefited greatly from discussions and comments by R.W. Buddemeier, J. Cole, K.P. Helmle, O. Hoegh-Guldberg, J. Kleypas, C. Langdon, N. Polunin, M. Risk and P. Swart.

References

- Acevedo, R. (1991) Preliminary observations on effects of the pesticides, carbaryl, naphthol, and chloropyrifos on the planulae of the hermatypic coral *Pocillopora damicornis*. *Pacific Science* **45**: 287–289.
- Acevedo, R., Morelock, J. & Olivieri, R.A. (1989) Modification of coral reef zonation by terrigenous sediment stress. *Palaios* **4**: 92–100.
- Albritton, D.L. and others (2001) *Summary for Policy Makers: A Report of Working Group I of the Intergovernmental Panel on Climate Change*. Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.
- Aronson, R.B. (1990) Onshore-offshore patterns of human fishing activities. *Palaios* **5**: 88–93.
- Aronson, R.B. & Precht, W.F. (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* **23**: 336–346.
- Aronson, R.B. & Precht, W.F. (2001) Evolutionary paleoecology of Caribbean coral reefs. In: *Evolutionary Paleoecology: The Ecological Context of Macroevolutionary Change*, ed. W.D. Allmon & D.J. Bottjer, pp. 171–233. New York, USA: Columbia University Press.
- Baker, A.C. (2001) Reef corals bleach to survive change. *Nature* **411**: 765–766.
- Baker, A.C. (2002) Is coral bleaching really adaptive? *Nature* **415**: 601–602.
- Barnett, T.P., Pierce, D.W. & Schnur, R. (2001) Detection of anthropogenic climate change in the world's oceans. *Science* **292**: 270–274.
- Bellwood, D.R. & Hughes, T.P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**: 1532–1534.
- Berkelmans, R. & Oliver, J.K. (1999) Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs* **18**: 55–60.
- Berkes, F. (1987) The common property resource problem and the fisheries of Barbados and Jamaica. *Environmental Management* **11**: 225–235.
- Birkeland, C. (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Marine Biology* **69**: 175–185.
- Bohnsack, J.A. (1998) Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* **23**: 298–304.
- Bosscher, H. (1993) Computerized tomography and skeletal density of coral skeletons. *Coral Reefs* **12**: 97–103.
- Bradbury, R. & Seymour, R. (1997) Waiting for COTS. In: *Proceedings of the 8th International Coral Reef Symposium*, volume 2, ed. ?, pp. 1357–1362.
- Bradbury, R.H., Hammond, L.S., Moran, P.J. & Reichelt, R.E. (1985) Coral reef communities and the crown-of-thorns starfish: Evidence for qualitatively stable cycles. *Journal of Theoretical Biology* **113**: 69–80.
- Brown, B.E. & Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* **8**: 163–170.
- Bryant, D., Burke, L., McManus, J. & Spalding, M. (1998) *Reefs at Risk*. Washington, DC, USA: World Resource Institute.
- Budd, A.F. (2000) Diversity and extinction in the Cenozoic history of Caribbean reefs. *Coral Reefs* **19**: 25–35.
- Buddemeier, R.W. & Fautin, D.G. (1993) Coral bleaching as an adaptive mechanism: a testable hypothesis. *Bioscience* **43**: 320–326.
- Buddemeier, R.W. & Smith, S.V. (1988) Coral reef growth in an era of rapidly rising sea level: predictions and suggestions for long-term research. *Coral Reefs* **7**: 51–56.
- Carpenter, R.C. (1988) Mass-mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proceedings of the National Academy of Sciences* **85**: 511–514.
- Carpenter, R.C. (1990a) Mass mortality of *Diadema antillarum*: I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology* **104**: 67–77.
- Carpenter, R.C. (1990b) Mass mortality of *Diadema antillarum*: II Effects on population densities and grazing intensities of parrotfishes and surgeonfishes. *Marine Biology* **104**: 79–86.
- Carreiro-Silva, M. & McClanahan, T.R. (2001) Echinoid bioerosion and herbivory on Kenyan coral reefs: The role of protection from fishing. *Journal of Experimental Marine Biology and Ecology* **262**: 133–153.
- Carricart-Ganivet, J.P. & Beltran-Torres, A.U. (2000) Skeletal extension, density and calcification rate of the reef building coral *Montastraea annularis* (Ellis and Solander) in the Mexican Caribbean. *Bulletin of Marine Science* **66**: 215–224.
- Charles, C.D., Hunter, D.E. & Fairbanks, R.D. (1997) Interaction between the ENSO and the Asian Monsoon in a coral record of tropical climate. *Science* **277**: 925–928.
- Charpy, L. (2001) Phosphorus supply for atoll biological productivity. *Coral Reefs* **20**: 357–360.
- Chazottes V., Le Campion-Alsumard, T. & Peyrot-Clausade, M. (1995) Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia). *Paleogeography, Paleoclimatology and Paleoecology* **113**: 189–198.
- Chen, J., Carlson, B.E. & Del Genio, A.D. (2002) Evidence for strengthening of the tropical general circulation in the 1990s. *Science* **295**: 838–841.
- Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, M.R., Tanner, S., Chavez, F.P., Ferioli, L., Sakamoto, C., Rogers, P., Millero, F., Steinberg, P., Nightingale, P., Cooper, D., Cochlan, W.P., Landry, M.R., Constantinou, J., Rollwagen, G., Trasvina, A. & Kudela, R. (1996) A massive phytoplankton bloom induced

- by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* 383: 495–501.
- Cole, J., Dunbar, R., McClanahan, T. & Muthiga, N. (2000) Tropical Pacific forcing of decadal variability in SST in the western Indian Ocean. *Science* 287: 617–619.
- Coles, S.L. & Al-Riyami, K.A. (1996) Beach tar concentrations on the Muscat coastline, Gulf of Oman, Indian Ocean, 1993–1995. *Marine Pollution Bulletin* 32: 609–614.
- Colgan, M.W. (1987) Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* 68: 1592–1605.
- Connell, J.H. (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16: S101–S113.
- Connell, D.W. & Miller, G.J. (1984) *Chemistry and Ecotoxicology of Pollution*. New York, USA: Wiley: 444 pp.
- Cooke, A., Polunin, N.V.C. & Moce, K. (2000) Comparative assessment of stakeholder management in traditional Fijian fishing-grounds. *Environmental Conservation* 27: 291–299.
- Cortes, J. (1993) Comparison between Caribbean and eastern Pacific coral reefs. *Revista Biologica Tropical* 41(supplement 1): 19–21.
- Cortes, J.N. & Risk, M.J. (1985) A reef under siltation stress: Cahuita, Costa Rica. *Bulletin of Marine Science* 36: 339–356.
- Cortes, J., Macintyre, I.G. & Glynn, P.W. (1994) Holocene growth history of an eastern Pacific fringing reef, Punta Isletes, Costa Rica. *Coral Reefs* 13: 65–73.
- Delgado, O. & Lapointe, B.E. (1994) Nutrient-limited productivity of calcareous versus fleshy macroalgae in a eutrophic, carbonate-rich tropical marine environment. *Coral Reefs* 13: 151–159.
- Done, T.J. (1987) Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: evidence of population resilience? *Coral Reefs* 6: 75–90.
- Done, T. (1992) Constancy and change in some Great Barrier Reef coral communities: 1980–1990. *American Zoology* 32: 655–662.
- Done, T.J. (1997) Decadal changes in reef-building communities: implications for reef growth and monitoring programs. In: *Proceedings of Eight International Coral Reef Symposium*, volume 1, pp. 411–416.
- Duarte, C.M. (2002) The future of seagrass meadows. *Environmental Conservation* 29: 00–00.
- Dubinsky, Z. & Stambler, N. (1996) Marine pollution and coral reefs. *Global Change Biology* 2: 511–526.
- Duffy, J.E. & Hay, M.E. (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology* 75: 1304–1319.
- Dunne, T. (1979) Sediment yield and land use in tropical catchments. *Journal of Hydrology* 42: 281–300.
- Eakin, C.M. (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral Reef* 15: 109–119.
- Edinger, E.N., Jompa, J., Limmon, G.V. & Risk, M.J. (1998) Reef degradation and coral biodiversity in Indonesia: effects of land-based sources of pollution, destructive fishing practices, and changes over time. *Marine Pollution Bulletin* 37: 617–630.
- Edmunds, P.J. & Carpenter, R.C. (2000) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Science (USA)*: 00–00.
- Edwards, A.J., Clark, S., Zahir, H., Rajasuriya, A., Naseer, A. & Rubens, J. (2001) Coral bleaching and mortality on artificial and natural reefs in Maldives in 1998, sea surface temperature anomalies and initial recovery. *Marine Pollution Bulletin* 42: 7–15.
- FAO (1990) *Fertilizer Yearbook*. New York, USA: United Nations.
- Fenner, D. (2001) Mass bleaching threatens two coral species with extinction. *Reef Encounters* 29: 9–10.
- Ferrier-Pagès, C., Gattuso, J.-P., Dallot, S. & Jaubert, J. (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19: 103–113.
- Fischer, H., Wahlen, M., Smith, J., Mastroianni, D. & Deck, B. (1999) Ice core records of atmospheric CO₂ around the last three glacial terminations. *Science* 283: 1712–1714.
- Fong, P. & Glynn, P.W. (1998) A dynamic size-structured population model: does disturbance control size structure of a population of the massive coral *Gardineroseris panulata* in the Eastern Pacific? *Marine Biology* 130: 663–674.
- Fong, P. & Glynn, P.W. (2000) A regional model to predict coral population dynamics in response to El Niño-Southern Oscillation. *Ecological Applications* 10: 842–854.
- Foundation for Environmental Conservation (2001) An introduction to long-term environmental trends [www document]. URL <http://www.ncl.ac.uk/icef>
- Frankignoulle, M., Canon, C. & Gattuso, J.-P. (1994) Marine calcification as a source of carbon dioxide: positive feedback of increasing atmospheric CO₂. *Limnology and Oceanography* 39: 458–462.
- Gates, R.D. & Edmunds, P.J. (1999) The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* 39: 30–43.
- Gattuso, J.P., Frankignoulle, M. & Wollast, R. (1998) Carbon and carbonate metabolism in coastal aquatic ecosystems. In: *Annual Review of Ecology and Systematics*, ed. D.G. Fautin, D.J. Futuyma & F.C. James, pp. 405–434. Palo Alto, California, USA: Annual Reviews Inc.
- Gattuso, J.-P., Frankignoulle, M., Smith, S.V., Ware, J.R., Wollast, R., Buddemeier, R.W. & Kayanne, H. (1996) Coral reefs and carbon dioxide. *Science* 271: 1298–1300.
- Ginsburg, R.N., ed. (1994) *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History, 1993*. Miami, USA: Rosenstiel School of Marine and Atmospheric Science, University of Miami: 420 pp.
- Glynn, P.W. (1994) State of coral reefs in the Galapagos Island: natural vs anthropogenic impacts. *Marine Pollution Bulletin* 29: 131–140.
- Glynn, P.W. (1997) Bioerosion and coral-reef growth: a dynamic balance. In: *Life and Death of Coral Reefs*, ed. C. Birkeland, pp. 68–113. New York, USA: Chapman & Hall.
- Glynn, P.W. (2000) El Niño-Southern Oscillation mass mortalities of reef corals: a model of high temperature marine extinctions? In: *Carbonate Platform Systems: Components and Interactions*, ed. E. Insalaco, P.W. Skelton & T.J. Palmer, pp. 117–133. London, UK: Geological Society of London.
- Glynn, P.W. & Ault, J.S. (2000) A biogeographic analysis and review of the far eastern Pacific coral reef region. *Coral Reefs* 19: 1–23.
- Glynn, P.W., Mate, J.L., Baker, A.C. & Calderon, M.O. (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997–98 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69: 79–109.
- Glynn, P.W., Szmant, A.M., Corcoran, E.F. & Cofer-Shabica, S.V.

- (1988) Condition of coral reef cnidarians from the northern Florida tract: pesticides, heavy metals, and histopathological examination. *Marine Pollution Bulletin* 20: 568–576.
- Goreau, T., McClanahan, T., Hayes, R. & Strong, A. (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* 14: 5–15.
- Graham, N.E. (1995) Simulation of recent global temperature trends. *Science* 267: 666–671.
- Greenstein, B.J., Curran, H.A. & Pondolfi, J.M. (1998) Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective. *Coral Reefs* 17: 249–261.
- Grigg, R.W. (1997) Paleooceanography of coral reefs in the Hawaiian-Emperor Chain - revisited. *Coral Reefs* 16: S33–S38.
- Guzman, H.M. & Holst, I. (1993) Effects of chronic oil-sediment pollution on the reproduction of the Caribbean reef coral *Siderastrea siderea*. *Marine Pollution Bulletin* 26: 276–282.
- Halpern, B. (2002) The impact of marine reserves: a review of key ideas. *Ecological Applications* (in press).
- Hatcher, B.G. (1983) Grazing in coral reef ecosystems. In: *Perspectives on Coral Reefs*, ed. D.J. Barnes, pp. 164–179. Manuka, ? : Brian Clouster Publishers.
- Hatcher, B.G., Imberger, J. & Smith, S.V. (1987) Scaling analysis of coral reef systems: an approach to problems of scale. *Coral Reefs* 5: 171–181.
- Hawkins, J.P., Roberts, C.M. & Clark, V. (2000) The threatened status of restricted-range coral reef fish species. *Animal Conservation* 3: 81–88.
- Hay, M.E. (1984) Predictable spatial escapes from herbivory: how to do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64: 396–407.
- Hay, M.E., Colburn, T. & Downing, D. (1983) Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* 58: 299–308.
- Hayes, J.A. (1990a) Distribution, movement and impact of the corallivorous gastropod *Coralliophila abbreviata* (Lamarck) on a Panamanian patch reef. *Journal of Experimental Marine Biology and Ecology* 142: 25–42.
- Hayes, J.A. (1990b) Prey preference in a Caribbean corallivore, *Coralliophila abbreviata* (Lamarck) (Gastropoda, Coralliophilidae). *Bulletin Marine Science* 47: 557–560.
- Hearn, C.J., Atkinson, M.J. & Falter, J.L. (2001) A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. *Coral Reefs* 20: 347–356.
- Helmle, K.P., Wellington, G.M., Dodge, R.E. & Swart, P.K. (2000) Decline in coral calcification rate over the last century: preliminary evidence. Abstract: 9th International Coral Reef Symposium, Bali, Indonesia, 23–27 October 2000.
- Highsmith, R.C. (1980) Geographic patterns of coral bioerosion: a productivity hypothesis. *Journal of Experimental Marine Biology and Ecology* 46: 55–67.
- Hodgson, G. & Dixon, J.A. (1992) Sedimentation damage to marine resources: environmental and economic analysis. In: *Resources and Environment in Asia's Marine Sector*, ed. J.B. March, pp. 421–426. Washington, DC, USA: Taylor and Francis.
- Hoegh-Guldberg, O. (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50: 839–866.
- Hoegh-Guldberg, O. & Smith, G.J. (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *Journal of Experimental Marine Biology and Ecology* 129: 279–303.
- Hoegh-Guldberg, O., Jones, R.J., Ward, S. & Loh, W.K. (2002) Is coral bleaching really adaptive? *Nature* 415: 601–602.
- Hoerling, M.P., Hurrell, J.W. & Xu, T. (2001) Tropical origins for recent North Atlantic climate change. *Science* 292: 90–?.
- Holmes, K., Edinger, E., Limmon, H. & Risk, M. (2000) Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. *Marine Pollution Bulletin* 40: 606–617.
- Hughes, T.P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551.
- Hughes, T.P. & Tanner, J.E. (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81: 2250–2263.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* 269: 676–679.
- Hutchinson, G.E. (1965) *The Ecological Theater and Evolutionary Play*. New Haven, CT, USA: Yale University Press: 255 pp.
- Jackson, J.B.C. (1997) Reefs since Columbus. *Coral Reefs* 16: S23–S32.
- Jackson, J.B.C., Cubit, J.D., Keller, B.D., Batista, V., Burns, K., Caffey, H.M., Caldwell, R.L., Garrity, S.D., Getter, C.D., Gonzalez, C., Guzman, E.M., Kaufmann, K.W., Knap, A.H., Levings, S.C., Marshall, M.J., Steger, R., Thompson, R.C. & Weil, E. (1989) Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science* 243: 37–44.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndahl, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlanson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629–638.
- Jokiel, P.L., Hunter, C.L., Taguchi, S. & Watarai, L. (1993) Ecological impact of a fresh-water 'reef kill' in Kaneohe bay, Oahu, Hawaii. *Coral Reefs* 12: 177–184.
- Karl, D.M. (1999) A sea of change: biogeochemical variability in the North Pacific Subtropical Gyre. *Ecosystems* 2: 181–214.
- Kawahata, H., A., Suzuki, ? & Goto, K. (1997) Coral reef ecosystems as a source of atmospheric CO₂: evidence from PCO₂ measurements of surface waters. *Coral Reefs* 16: 261–268.
- Kelleher, G., Bleakley, C. & Wells, S. (1995) *A Global Representative System of Marine Protected Areas*. Washington, DC, USA: The World Bank: 219 pp.
- Kiene, W.E. (1997) Enriched nutrients and their impact on bioerosion: results from ENCORE. *Proceedings of Eight International Coral Reef Symposium*, volume 1, pp. 897–902.
- Kinsey, D.W. & Hopley, D. (1991) The significance of coral reefs as global carbon sinks - response to greenhouse. *Palaeogeography, Palaeoclimatology & Palaeoecology* 89: 363–377.
- Kleypas, J.A., Buddemeier, R.W. & Smith, S.V. (2001) Defining 'coral reef' for the age of global change. *International Journal of Earth Sciences* 90: 426–437.
- Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J.P., Langdon, C. & Opdyke, B.N. (1999b) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284: 118–120.
- Kleypas, J.A., McManus, J.W. & Menez, L.A.B. (1999a) Environmental limits to coral reef development: where do we draw the line? *American Zoologist* 39: 146–159.

- Knowlton, N., Lang, J.C. & Keller, B.D. (1988) Fates of staghorn coral fragments on hurricane-damaged reefs in Jamaica: The role of predators. In: *6th International Coral Reef Symposium*, Volume 2, ed. ?, pp. 83–88. Townsville, Australia: ?.
- Knutson, T.R., Tuleya, R.E. & Kurihara, Y. (1998) Simulated increase of hurricane intensities in a CO₂-warmed climate. *Science* **279**: 1018–1020.
- Koop, K., Booth, D., Broadbent, A., Brodie, J., Bucher, D., Capone, D., Coll, J., Dennison, W., Erdmann, M., Harrison, P., Hoegh-Guldberg, O., Hutchings, P., Jones, G.B., Larkum, A.W.D., O'Neil, J., Steven, A., Tentori, E., Ward, S., Williamson, J. & Yellowlees, D. (2001) ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. *Marine Pollution Bulletin* **42**: 91–120.
- Kuffner, I.B. (2001) Effects of ultraviolet radiation and water motion on the reef coral *Porites compressa* Dana: a flume experiment. *Marine Biology* **138**: 467–476.
- Kuhnert, H., Patzold, J., Hatcher, B.G., Wyrwoll, K.-H., Eisenhauer, A., Collins, L.B., Zhu, Z.R. & Wefer, G. (1999) A 200-year coral stable oxygen isotope record from a high-latitude reef off Western Australia. *Coral Reefs* **18**: 1–12.
- Kumar, K.K., Rajagopalan, B. & Cane, M.A. (1999) On the weakening relationship between the Indian monsoon and ENSO. *Science* **284**: 2156–2159.
- Langdon, C. (2002) Overview of experimental evidence for effects of CO₂ on calcification of reef builders. In: *Proceedings of the 9th International Coral Reef Symposium*, ed.?, pp.?.
- Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H. & Atkinson, M.J. (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* **14**: 639–654.
- Lapointe, B.E. (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on corals reefs in Jamaica and Southeast Florida. *Limnology and Oceanography* **42**: 1119–1131.
- Lapointe, B.E. (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. *Limnology and Oceanography* **44**: 1586–1592.
- Larkum, A.W.D. (1983) The primary productivity of plant communities on coral reefs. In: *Perspectives on Coral Reefs*, ed. D.J. Barnes, pp. 221–230. Manuka, ? : Brian Clouston Publisher.
- Lear, C.H., Elderfield, H. & Wilson, P.A. (2000) Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite. *Science* **287**: 269–272.
- Lessios, H.A. (1988) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Review of Ecology and Systematics* **19**: 371–393.
- Lessios, H.A., Garrido, M.J. & Kessing, B.D. (2001) Demographic history of *Diadema antillarum*, a keystone herbivore on Caribbean reefs. *Proceedings of the Royal Society of London B* **268**: 1–7.
- Lessios, H.A., Robertson, D.R. & Cubit, J.D. (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**: 335–337.
- Lewis, S.A. (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* **56**: 183–200.
- Levitus, S., Antonov, J.I., Wang, J., Delworth, T.L., Dixon, K.W. & Broccoli, A.J. (2001) Anthropogenic warming of Earth's climate systems. *Science* **292**: 267–270.
- Lindahl, U., Ohman, C.O. & Schelten, C.K. (2001) The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin* **42**: 127–131.
- Littler, M.M. (1980) Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypotheses. *Botanica Marina* **22**: 161–165.
- Littler, M.M., Littler, D.S. & Titlyanov, E.A. (1991) Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: A test of the relative-dominance paradigm. *Coral Reefs* **10**: 199–209.
- Littler, M.M., Taylor, P.R. & Littler, D.S. (1983) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* **2**: 111–118.
- Lough, J. & Barnes, D. (1997) Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: a proxy for seawater temperature and a background of natural variability against which to identify unnatural change. *Journal of Experimental Marine Biology and Ecology* **211**: 29–67.
- Loya, Y. & Rinkevich, B. (1980) Effects of oil pollution on coral reef communities. *Marine Ecology Progress Series* **3**: 167–180.
- Matson, P.A., Naylor, R. & Ortiz-Monasterio, I. (1998) Integration of environmental, agronomic, and economic aspects of fertilizer management. *Science* **280**: 112–115.
- McClanahan, T.R. (1988) Seasonality in East Africa's coastal waters. *Marine Ecology Progress Series* **44**: 191–199.
- McClanahan, T.R. (1990) Kenyan coral reef-associated gastropod assemblages: distribution and diversity patterns. *Coral Reefs* **9**: 63–74.
- McClanahan, T.R. (1992) Resource utilization, competition and predation: a model and example from coral reef grazers. *Ecological Modelling* **61**: 195–215.
- McClanahan, T.R. (1995) A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecological Modelling* **80**: 1–19.
- McClanahan, T.R. (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* **218**: 77–102.
- McClanahan, T.R. (1999a) Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems* **2**: 511–523.
- McClanahan, T.R. (1999b) Is there a future for coral reef parks in poor tropical countries? *Coral Reefs* **18**: 321–325.
- McClanahan, T.R. (2000a) Bleaching damage and recovery potential of Maldivian coral reefs. *Marine Pollution Bulletin* **40**: 587–597.
- McClanahan, T.R. (2000b) Recovery of the coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation* **94**: 191–198.
- McClanahan, T.R. (2002) The effects of time, habitat and fisheries management on Kenyan coral-reef associated gastropods. *Ecological Applications* (in press)
- McClanahan, T.R. & Arthur, R. (2001) The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecological Applications* **11**: 559–569.
- McClanahan, T.R. & Kaunda-Arara, B. (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* **10**: 1187–1199.
- McClanahan, T.R. & Kurtis, J.D. (1991) Population regulation of the rock-boring sea urchin *Echinometra mathaei* (de Blainville). *Journal of Experimental Marine Biology and Ecology* **147**: 121–146.
- McClanahan, T.R. & Mangi, S. (2000) Spillover of exploitable

- fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* **10**: 1792–1805.
- McClanahan, T.R. & Mangi, S. (2001) The effect of closed area and beach seine exclusion on coral reef fish catches. *Fisheries Management and Ecology* **8**: 107–121.
- McClanahan, T.R. & Mutere, J.C. (1994) Coral and sea urchin assemblage structure and interrelationships in Kenyan reef lagoons. *Hydrobiologia* **286**: 109–124.
- McClanahan, T.R. & Muthiga, N.A. (1998) An ecological shift in a remote coral atoll of Belize over 25 years. *Environmental Conservation* **25**: 122–130.
- McClanahan, T.R. & Obura, D. (1997) Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* **209**: 103–122.
- McClanahan, T.R., Cokos, B. & Sala, E. (2002a) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. *Marine Pollution Bulletin* **44**: 441–451.
- McClanahan, T.R., Done, T.J. & Polunin, N.V.C. (2002bc?) Resilience in coral reef ecosystems. In: *Resilience and Sustainability in Large-Scale Ecosystems*, ed. L. Gunderson, B.-O. Jansson, C.S. Hollings & C. Folke, pp. (in press). ? : Island Press.
- McClanahan, T.R., Glaesel, H., Rubens, J. & Kiambo, R. (1997) The effects of traditional fisheries management on fisheries yields and the coral-reef ecosystems of southern Kenya. *Environmental Conservation* **24**: 105–120.
- McClanahan, T.R., Hendrick, V., Rodrigues, M.J. & Polunin, N.V.C. (1999b) Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. *Coral Reefs* **18**: 195–203.
- McClanahan, T.R., Maina, J. & Pet-Soede, L. (2003?) Effects of the 1998 coral mortality event on Kenyan coral reefs and fisheries. *Ambio* (in press).
- McClanahan, T.R., McField, M., Huitric, M., Bergman, K., Sala, E., Nyström, M., Nordemer, I., Elfving, T. & Muthiga, N.A. (2001a) Responses of algae, corals and fish to the reduction of macro algae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* **19**: 367–379.
- McClanahan, T.R., Muthiga, N.A. & Mangi, S. (2001b) Coral and algal response to the 1998 coral bleaching and mortality: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* **19**: 380–391.
- McClanahan, T.R., Muthiga, N.A., Kamukuru, A.T., Machano, H. & Kiambo, R. (1999a) The effects of marine parks and fishing on the coral reefs of northern Tanzania. *Biological Conservation* **89**: 161–182.
- McClanahan, T.R., Uku, J.N. & Machano, H. (2002bc?) Effect of macroalgal reduction on coral-reef fish in the Watamu Marine National park, Kenya. *Journal of Marine and Freshwater Research* **53**: 223–231.
- McField, M.D. (1999) Coral response during and after mass bleaching in Belize. *Bulletin of Marine Science* **64**: 155–172.
- McGrath, T.A. & Smith, G.W. (1998) The effects of the 1995/1996 Western Atlantic coral bleaching event on the patch reefs around San Salvador Island, Bahamas. *Revista Biologie Tropicale* **46** (Supplement 5): 91–99.
- McManus, J.W., Menez, L.A.B., Kesner-Reyes, K.N., Vergara, S.G. & Ablan, M.C. (2000) Coral reef fishing and coral-algal phase shifts: implications for global reef status. *Journal of Marine Science* **57**: 572–578.
- McPhaden, M.J. (1999) Genesis and evolution of the 1997–98 El Niño. *Science* **283**: 950–954.
- Medio, D., Sheppard, C.R.C. & Gasgoine, J. (2000) The Red Sea. In: *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, ed. T.R. McClanahan, C.R.C. Sheppard & D.O. Obura, pp. 231–255. New York, USA: Oxford University Press.
- Meehl, G.A. (1992) Effect of tropical topography on global climate. *Annual Review of Earth Planet Science* **20**: 85–112.
- Meehl, G.A. & Washington, W.M. (1993) South Asian summer monsoon variability in a model with doubled atmospheric carbon dioxide concentration. *Science* **260**: 1101–1104.
- Mees, C.C., Pilling, G.M. & Barry, C.J. (1999) Commercial inshore fishing activity in the British Indian Ocean Territory. In: *Ecology of the Chagos Archipelago*, ed. C.R.C. Sheppard & M.R.D. Seaward, pp. 327–345. London, UK: The Linnean Society of London.
- Miller, M.W., Hay, M.E., Miller, S.L., Malone, D., Sotka, E.E. & Szmant, A.M. (1999) Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnology and Oceanography* **44**: 1847–1861.
- Möberg, F., Nyström, M., Kautsky, N., Tedengren, M. & Jarayabhand, P. (1997) Effects of reduced salinity on the rates of photosynthesis and respiration in the hermatypic corals *Porites lutea* and *Pocillopora damicornis*. *Marine Ecology Progress Series* **157**: 53–59.
- Moran, P.J. (1986) The *Acanthaster* phenomenon. *Oceanography and Marine Biology Annual Review* **24**: 379–480.
- Morton, B. (1996) Protecting Hong Kong's marine biodiversity: present proposals, future challenges. *Environmental Conservation* **23**: 55–65.
- Muller, R.A. & MacDonald, G.J. (1997) Glacial cycles and astronomical forcing. *Science* **277**: 215–218.
- Mumby, P.J., Chisholm, J.R.M., Edwards, A.J., Clark, C.D., Roark, E.B., Andrefouet, S. & Jaubert, J. (2001) Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia. *Marine Biology* **139**: 183–189.
- Munro, J.L. (1989) Fisheries for giant clams (Tridacnidae: Bivalvia) and prospects for stock enhancement. In: *Marine Invertebrate Fisheries: Their Assessment and Management*, ed. J.F. Caddy, pp. 541–558. New York, USA: Wiley.
- Munro, J.L. (1996) The scope of tropical reef fisheries and their management. In: *Reef Fisheries*, ed. N.V.C. Polunin & C.M. Roberts, pp. 1–14. London, UK: Chapman & Hall.
- Muthiga, N.A. & Szmant, A.M. (1987) The effects of salinity stress on the rates of aerobic respiration and photosynthesis in the hermatypic coral *Siderastrea siderea*. *Biological Bulletin* **173**: 539–551.
- Muthiga, N.A., Riedmiller, S., Carter, E., van der Elst, R., Mann-Lang, J., Horrill, C. & McClanahan, T.R. (2000) Management status and case studies. In: *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, ed. T.R. McClanahan, C.S. Sheppard & D. Obura, pp. 473–505. New York, USA: Oxford University Press.
- Naeem, S. (1998) Species redundancy and ecosystem reliability. *Conservation Biology* **12**: 39–45.
- Nakamura, T. & van Woesik, R. (2001) Differential survival of corals during the 1998 bleaching event is partially explained by water-flow rates and passive diffusion. *Marine Ecology Progress Series* **212**: 301–304.
- Ninio, R., Meekan, M., Done, T. & Sweatman, H. (2000) Temporal

- patterns in coral assemblages on the Great Barrier Reef from local to large spatial scales. *Marine Ecology Progress Series* **194**: 65–74.
- Nyström, M., Folke, C. & Möberg, F. (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution* **15**: 413–417.
- O’Riordan, T. & Cameron, J. (1994) The history and contemporary significance of the precautionary principle. In: *Interpreting the Precautionary Principle*, ed. T. O’Riordan & J. Cameron, pp. ?–?. London, UK: Earthscan.
- Ormond, R., Bradbury, R., Bainbridge, S., Fabricus, K., Keesing, J., DeVantier, L., Medley, P. & Steven, A. (1988) Test of a model of regulation of Crown-of-Thorns starfish by fish predators. In: *Acanthaster and the Coral Reef: a Theoretical Perspective*, ed. R.H. Bradbury, pp. 190–207. Townsville, Australia: Springer-Verlag.
- Ostrander, G.K., Armstrong, K.M., Knobbe, E.T., Gerace, D. & Scully, E.P. (2000) Rapid transition in the structure of a coral reef community: The effects of coral bleaching and physical disturbance. *Proceedings of the National Academy of Science* **97**: 5297–5302.
- Pandolfi, J.M. (1996) Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global changes. *Paleobiology* **22**: 152–176.
- Pandolfi, J.M. (1999) Response of Pleistocene coral reefs to environmental change over long temporal scales. *American Zoologist* **39**: 113–130.
- Parker, D., Folland, C.K. & Jackson, M. (1995) Marine surface temperature: observed variations and data requirements. *Climatic Change* **31**: 5559–5600.
- Pauly, D., Silvestre, G. & Smith, I. (1989) On development, fisheries and dynamite: a brief review of tropical fisheries management. *Natural Resource Modeling* **3**: 307–329.
- Peters, E.C. (1997) Diseases of coral-reef organisms. In: *Life and Death of Coral Reefs*, ed. C. Birkeland, pp. 114–139. New York, USA: Chapman & Hall.
- Pet-Soede, L. & Erdmann, M.V. (1998) Blast fishing in SW Sulawesi, Indonesia. *Naga* **21**: 4–9.
- Pilson, M.E.Q. & Betzer, S.B. (1973) Phosphorus flux across a coral reef. *Ecology* **54**: 581–584.
- Polunin, N.V.C. (2002) Marine protected areas, fish and fisheries. In: *Handbook of Fish and Fisheries*, ed. P.J.B. Hart & J.C. Reynolds, pp. ?. Oxford, UK: Blackwell.
- Popper, K.R. (1972) *Objective Knowledge*. New York, USA: Oxford University Press: ? pp.
- Porter, J. (2001) *Ecology and Etiology of Newly Emerging Marine Diseases*. Dordrecht, the Netherlands: Kluwer: ? pp.
- Ramanathan, V., Crutzen, P.J., Kiehl, J.T. & Rosenfeld, D. (2001) Aerosols, climate, and the hydrological cycle. *Science* **294**: 2119–2124.
- Reaka-Kudla, M.L., Feingold, J.S. & Glynn, P.W. (1996) Experimental studies of rapid bioerosion of coral reefs in the Galapagos Islands. *Coral Reefs* **15**: 101–109.
- Richardson, L.L. (1998) Coral diseases: what is really known? *Trends in Ecology and Evolution* **13**: 438–443.
- Risk, M.J., Sammarco, P.W. & Edinger, E.N. (1995) Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. *Coral Reefs* **14**: 79–86.
- Roberts, C.M. & Hawkins, J.P. (1999) Extinction risk in the sea. *Trends in Ecology and Evolution* **14**: 241–246.
- Roberts, C.M. & Polunin, N.V.C. (1993) Marine reserves: simple solutions to managing complex fisheries? *Ambio* **22**: 363–368.
- Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C. & Werner, T.B. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**: 1280–1284.
- Robertson, D.R. (1991) Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Marine Biology* **111**: 437–444.
- Rodbell, D.T., Seltzer, G.O., Anderson, D.M., Abbott, M.B., Enfield, D.B. & Newman, J.H. (1999) An ~15,000-year record of El Niño-driven alluviation in Southwestern Ecuador. *Science* **283**: 516–520.
- Rogers, C.S. (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**: 185–202.
- Rose, C.S. & Risk, M.J. (1985) Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. *Marine Ecology* **6**: 345–363.
- Rowan, R., Knowlton, N., Baker, A. & Jara, J. (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* **388**: 265–269.
- Salih, A., Larkum, A., Cox, G., Kuhl, M. & Hoegh-Guldberg, O. (2000) Fluorescent pigments in corals are photoprotective. *Nature* **408**: 850–853.
- Salm, R.V. & Coles, S.L. (2001) Coral bleaching and marine protected areas. Honolulu, Hawaii, USA: The Nature Conservancy, Asia Pacific Coastal Marine Program: 107 pp.
- Sandalow, D.B. & Bowles, I.A. (2001) Fundamentals of treaty-making on climate change. *Science* **292**: 1839–1840.
- Shashar, N., Cohen, Y., Loya, Y. & Sar, N. (1994a) Nitrogen fixation (acetylene reduction) in stony corals: evidence for coral-bacteria interactions. *Marine Ecology Progress Series* **111**: 259–264.
- Shashar, N., Feldstein, T., Cohen, Y. & Loya, Y. (1994b) Nitrogen fixation (acetylene reduction) on a coral reef. *Coral Reefs* **13**: 171–174.
- Sheppard, C.R.C. (1999) Coral decline and weather patterns over 20 years in the Chagos Archipelago, Central Indian Ocean. *Ambio* **28**: 472–478.
- Sheppard, C.R.C. (2000a) Coral reefs of the western Indian Ocean: An overview. In: *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, ed. T.R. McClanahan, C.R.C. Sheppard & D.O. Obura, pp. 3–38. New York, USA: Oxford University Press.
- Sheppard, C.R.C. (2000b) The Chagos Archipelago. In: *Coral Reefs of the Indian Ocean: Their Ecology and Conservation*, ed. T.R. McClanahan, C.R.C. Sheppard & D.O. Obura, pp. 445–470. New York, USA: Oxford University Press.
- Shick, J.M., Lesser, M.P. & Jokiel, P.L. (1996) Effects of ultraviolet radiation on corals and other coral reef organisms. *Global Change Biology* **2**: 527–545.
- Shick, J.M., Romaine-Lioud, S., Ferrier-Pages, C. & Gattuso, J.P. (1999) Ultraviolet-B radiation stimulates shikimate pathway-dependent accumulation of mycosporine-like amino acids in the coral *Stylophora pistillata* despite decreases in its population of symbiotic dinoflagellates. *Limnology and Oceanography* **44**: 1667–1682.
- Shinn, E.A., Smith, G.W., Prospero, J.M., Betzer, P., Hayes, M.L., Garrison, V. & Barber, R.T. (2000) African dust and the demise of Caribbean coral reefs. *Geophysical Research Letters* **27**: 3029–3032.
- Shpigel, M. & Fishelson, L. (1991) Experimental removal of piscivorous groupers of the genus *Cephalopholis* (Serranidae) from coral

- habitats in the Gulf of Aqaba (Red-Sea). *Environmental Biology of Fishes* 31: 131–138.
- Shulman, M.J. & Robertson, D.R. (1996) Changes in the coral reef of San Blas, Caribbean Panama: 1983 to 1990. *Coral Reefs* 15: 231–236.
- Siebeck, O. (1988) Experimental investigations of UV tolerance in hermatypic corals (Scleractinia). *Marine Ecology Progress Series* 43: 95–103.
- Smith, S.V. (1984) Phosphorus versus nitrogen limitation in the marine environment. *Limnology and Oceanography* 29: 1149–1160.
- Stafford-Smith, M.G. & Ormond, R.F.G. (1992) Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Australian Journal of Marine Freshwater Resource* 43: 683–705.
- Steneck, R.S. & Dethier, M.N. (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69: 476–498.
- Szmant, A.M. (2001) Why are coral reefs world-wide becoming overgrown by algae? Algae, algae everywhere, and nowhere a bite to eat! *Coral Reefs* 19: 299–302.
- Tanner, J.E. (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* 190: 151–168.
- Tilman, D., Fargione, J., Wolff, B. & others (2001) Forecasting agriculturally driven global environmental change. *Science* 292: 281–284.
- Tomaschik, T., Mah, A.J., Nontji, A. & Moosa, M.K. (1997) *The Ecology of the Indonesian Seas*. Hong Kong, China: Periplus: 1388 pp.
- Tudhope, A.W., Chilcott, C.P., McCulloch, M.T., Cook, E.R., Chappell, J., Ellam, R.M., Lea, D.W., Lough, J.M. & Shimmield, G.B. (2001) Variability in the El Niño–Southern Oscillation through a glacial-interglacial cycle. *Science* 291: 1511–1517.
- Urban, F.E., Cole, J.E. & Overpeck, J.T. (2000) Influence of mean climate change on climate variability from a 155-year tropical Pacific coral record. *Nature* 407: 989–990.
- Uthicke, S. & Benzie, J.A.H. (2001) Effect of beche-de-mer fishing on densities and size structure of *Holothuria nobilis* (Echinodermata: Holothuroidea) populations on the Great Barrier Reef. *Coral Reefs* 3: 271–276.
- Vermeij, G.J. (1986) Survival during biotic crises: the properties and evolutionary significance of refuges. In: *Dynamics of Extinction*, ed. D.K. Elliott, pp. 231–246. New York, USA: Wiley.
- Veron, J.E.N. (1995) *Corals in Space and Time: The Biogeography & Evolution of the Scleractinia*. ?, Australia: University of New South Wales Press: 321 pp.
- Veron, J.E.N. & Minchin, P.R. (1992) Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan. *Continental Shelf Research* 12: 835–857.
- Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. & Tilman, D.G. (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7: 737–750.
- Ware, J.R., Smith, S.V. & Reaka-Kudla. (1992) Coral reefs: sources or sinks of atmospheric CO₂? *Coral Reefs* 11: 127–130.
- Ware, J.R., Fautin, D.G. & Buddemeier, R.W. (1995) Modeling the adaptive bleaching hypothesis: insights into patterns of coral bleaching. *Ecological Modelling* 84: 199–214.
- West, J.M. (2001) Environmental determinants of resistance to coral bleaching: implications for management of marine protected areas. In: *Proceedings of the Workshop on Mitigating Coral Bleaching Impact through MPA Design*, ed. R.V. Salm, & S. L. Coles, pp. 40–52. Asia Pacific Coastal Marine Program Report No. 0102. Honolulu, Hawaii, USA: The Nature Conservancy.
- Wilkinson, C. (1996) Global change and coral reefs: impacts on reefs, economies and human cultures. *Global Change Biology* 2: 547–558.
- Wilkinson, C.R., Williams, D.M., Sammarco, P.W., Hogg, R.W. & Trott, L.A. (1984) Rates of nitrogen fixation on coral reefs across the continental shelf of the central Great Barrier Reef. *Marine Biology* 80: 255–262.
- Wilkinson, C., Linden, O., Cesar, H., Hodgson, G., Rubens, J. & Strong, A.E. (1999) Ecological and socioeconomic impacts of 1998 coral mortality in the Indian ocean: an ENSO impact and a warning of future change? *Ambio* 28: 188–199.
- Williams, E.H. & Bunkley-Williams, L. (1988) Circumtropical coral reef bleaching in 1987–1988. In: *Proceedings of the 6th International Coral Reef Symposium*, ed. ?, pp. 313–318. Townsville, Australia: ?.
- Williams, I.D. & Polunin, N.V.C. (2001) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19: 358–366.
- Williams, I.D., Polunin, V.C. & Hendrick, V.J. (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222: 187–196.
- Williams, S.L. (1990) Experimental studies of Caribbean seagrass bed development. *Ecological Monographs* 60: 449–469.
- Williams, S.L. & Carpenter, R.C. (1988) Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. *Marine Ecology Progress Series* 47: 145–152.
- Wood, R. (1999) *Reef Evolution*. New York, USA: Oxford University Press: 414 pp.
- Yentsch, C.S., Yentsch, C.M., Cullen, J.J., Lapointe, B., Phinney, D.A. & Yentsch, S.W. (2002) Sunlight and water transparency: cornerstones in coral research. *Journal of Experimental Marine Biology and Ecology* 268: 171–183.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.