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Viewpoint

The coral reef crisis: The critical importance of <math><350\text{ ppm CO}_2</math>

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ABSTRACT

Temperature-induced mass coral bleaching causing mortality on a wide geographic scale started when atmospheric CO₂ levels exceeded ~320 ppm. When CO₂ levels reached ~340 ppm, sporadic but highly destructive mass bleaching occurred in most reefs world-wide, often associated with El Niño events. Recovery was dependent on the vulnerability of individual reef areas and on the reef's previous history and resilience. At today's level of ~387 ppm, allowing a lag-time of 10 years for sea temperatures to respond, most reefs world-wide are committed to an irreversible decline. Mass bleaching will in future become annual, departing from the 4 to 7 years return-time of El Niño events. Bleaching will be exacerbated by the effects of degraded water-quality and increased severe weather events. In addition, the progressive onset of ocean acidification will cause reduction of coral growth and retardation of the growth of high magnesium calcite-secreting coralline algae. If CO₂ levels are allowed to reach 450 ppm (due to occur by 2030–2040 at the current rates), reefs will be in rapid and terminal decline world-wide from multiple synergies arising from mass bleaching, ocean acidification, and other environmental impacts. Damage to shallow reef communities will become extensive with consequent reduction of biodiversity followed by extinctions. Reefs will cease to be large-scale nursery grounds for fish and will cease to have most of their current value to humanity. There will be knock-on effects to ecosystems associated with reefs, and to other pelagic and benthic ecosystems. Should CO₂ levels reach 600 ppm reefs will be eroding geological structures with populations of surviving biota restricted to refuges. Domino effects will follow, affecting many other marine ecosystems. This is likely to have been the path of great mass extinctions of the past, adding to the case that anthropogenic CO₂ emissions could trigger the Earth's sixth mass extinction.

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1. Introduction

Temperature-related effects of global warming on coral reefs are highly visible, well-defined and extensively documented. Cor-

relations between rising CO₂ levels, rising ocean temperature and the biological responses of reefs are therefore known in detail, providing a particularly well-grounded basis for future prediction. The more recently recognised effects of atmospheric CO₂ on ocean acidification will have even more profoundly detrimental long term effects on reefs but the full range of biological responses is, as yet, incompletely understood.

1.1. The importance of coral reefs

Although they make up only 0.2% in area of the marine environment, coral reefs are the most biodiverse ecosystems of the ocean, estimated to harbour around one third of all described marine species (Reaka-Kudla, 1997, 2001), most of which are found nowhere

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else. Their intricate three-dimensional landscapes promote elaborate adaptation, richly complex species interdependencies, and a fertile source of medically active compounds (Fenical, 2002; Bruckner, 2007). The extensive ramparts formed by reefs shield thousands of kilometres of coastline from wave erosion, protecting essential lagoon and mangrove habitat for vulnerable life stages of a wide range of commercial and non-commercial species (Johnson and Marshall, 2007).

More than 100 countries have coastlines with coral reefs (Moberg and Folke, 1999) and almost 500 million people (8% of the world's population) live within 100 km of a reef (Bryant et al., 1998). Consequently, tens of millions of people depend on reef ecosystems for protein and other services (Costanza et al., 1997). Resulting exploitation, combined with lack of regulation, has resulted in severe depletion of many reef resources and has caused widespread reef degradation particularly in highly populated regions (Pet-Soede et al., 1999). Despite these impacts, human dependence on reefs continues to increase. The values of goods and services provided by reefs have not been accurately determined, but estimates range from \$172 billion to \$375 billion per year (Moore and Best, 2001; Wilkinson, 2002; Fischlin et al., 2007; Martínez et al., 2007). This is probably underestimated given that many of the benefits of coral reefs pass through non-market economies (Donner and Potere, 2007) or involve intangible ecosystem services such as sand production and gas exchange.

Importantly, the consequences of coral reef destruction would not be limited to the loss of the value of these goods and services, for the demise of reefs would also mean the extinction of a large part of the Earth's total biodiversity – something never experienced before in human history.

1.2. Impacts of global warming

The fossil record of reefs provides an unparalleled window into the effects of climate change through geological time. In the broadest context, today's reef-forming corals have existed for 240 million years during which time they have been repeatedly decimated by climate changes from many different causes, most of which are linked to upheavals of the carbon cycle (Veron, 2008b). Although, on geological timescales reef ecosystems are clearly very persistent, the geological record offers crucial warnings that on human timescales reefs can indeed be lost, that a large proportion of coral and other calcifying species can go extinct and that once lost, reefs can take thousands to millions of years to re-establish. Perhaps most importantly, there is no evidence that reefs have ever experienced true parallels to today's anthropogenically-driven combination of stressors. At the rate at which these stressors are currently compounding we are going into uncharted waters (Veron, 2008a).

Already an estimated 19% of the world's coral reefs have been lost and a further 35% are seriously threatened (Wilkinson, 2008). As a result, one-third of all reef-building corals are considered to be at risk of extinction (Carpenter et al., 2008). To date, there have been a range of principal causes: predation by the coral-eating crown-of-thorns starfish, sedimentation from urban development and deforestation, over-fishing, destructive fishing practices, eutrophication from agriculture and sewage, pollution from herbicides and pesticides, diseases, and global warming. However, global warming has now overtaken all other impacts in importance because it is the cause of increasingly destructive and extremely widespread mass bleaching events (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Veron, 2008a).

The multiple nature of stressors on reefs associated with climate change is unprecedented in human history and studies of its synergisms are still in their infancy (for example, De'ath et al., 2009). It is however, virtually certain that the likely consequences

of multiple impacts will be synergistic, and far more severe than indicated from studies of individual stressors.

2. Mass bleaching and mortality: the current crisis

Regionally significant mass bleaching of corals (bleaching of multiple species on an ecologically significant scale) was first observed in the late 1970s and was soon correlated with abnormally high sea temperatures, especially pulses naturally induced by El Niño events, which currently recur every 4–7 years (Glynn, 1984, 1990, 1991) superimposed on generally elevated sea temperatures due to global warming (Hoegh-Guldberg, 1999). Detailed surveys of mass bleaching were first conducted in 1979/1980 in the Caribbean and surrounding seas (Hughes, 1994) (notably in Jamaica and the Bahamas), the far eastern Pacific (Panama and the Galápagos Islands), in isolated instances in the Pacific (notably French Polynesia and Thailand) (Brown, 1997; Brown et al., 2000) and on the Great Barrier Reef (Berkelmans and Oliver, 1999; Berkelmans et al., 2004).

Although there are many other causes of more restricted bleaching in corals, the worldwide phenomenon colloquially known as 'mass bleaching' has been shown to require a combination of both sunlight and abnormally high water temperature (Hoegh-Guldberg, 1999). Small increases (1–2 °C) in sea temperature above the long-term summer maxima destabilises the relationship between host corals and their symbiotic dinoflagellate algae (zooxanthellae), on which they rely for energy and growth (Muscatine, 1973; Trench, 1979). In high light conditions, there is a breakdown of the photosymbiotic system which causes a toxic buildup of reactive oxygen derivatives and results in a loss of the brown algae from the tissues leaving them white or 'bleached'. If the effect is short-lived, corals may recover, otherwise they become prone to disease and death. This dependence on both light and temperature has been confirmed in corals kept in shaded aquaria (Jones et al., 1998 and many subsequent studies) as well as those growing naturally on reefs (Mumby et al., 2001).

Unlike most ecosystems where the effects of climate change are matters of future prediction, mass bleaching of corals has been studied for 30 years and is understood in considerable detail (Glynn, 1993; Buddemeier et al., 2004; van Oppen and Lough, 2008).

2.1. Carbon dioxide levels

When the mass bleaching of coral was first recorded (1978/79), the CO₂ level in the atmosphere was ~336 ppm (NOAA/ESRL, 2009). On the basis of an optimistic lag-time of 10 years,² this event may be considered the outcome of a CO₂ level of ~320 ppm. Since that time there have been seven major world-wide bleaching events. It was the 1982/83 mass bleaching that drew attention to the association between bleaching, CO₂ level, and ocean temperature (Glynn, 1984, 1990, 1991; Hoegh-Guldberg, 1999; Buddemeier et al., 2004). That summer, about two-thirds of all inshore reefs and about 14% of offshore reefs of the Great Barrier Reef had moderate to high levels of bleaching. CO₂ then was at a level of 340 ppm, with water temperatures reflecting a 10-year time-lagged response to <~326 ppm (NOAA/ESRL, 2009).

² Lag time is defined here as the time it takes for the temperature of the surface ocean and hence the atmosphere to equilibrate with any particular CO₂ level. It is generally estimated to be in the order of several decades. There can be no precise measurement of lag times when CO₂ levels are changing; however, it is at least a single decade, the time interval factored-in here. Note that if the lag time is assumed to be longer than 10 years, the equivalent forcing CO₂ level would be lower (i.e. worse). Deep ocean temperatures equilibrate with surface forcing over timescales approaching a millennium hence increasing the eventual surface temperature change for a given change in CO₂.

The 1997/1998 mass bleaching event killed approximately 16% of coral communities globally (Berkelmans and Oliver, 1999; Wilkinson, 2004). It was also the start of a decline from which there has been no significant long-term recovery. By then, the CO₂ level was ~365 ppm, with water temperatures reflecting a 10-year time-lagged response to a level of <350 ppm (NOAA/ESRL, 2009).

The 2002 mass bleaching event was particularly serious for Asia and the Great Barrier Reef (Berkelmans et al., 2004) and the 2005 event commenced a new phase of decline characterised by a diminishing habitat complexity in reefs of the Caribbean and a deterioration of species diversity (Alvarez-Filip et al., 2009).

It is now clear that the vulnerability of coral reefs to bleaching varies geographically (Cook et al., 1990; Jokiel and Coles, 1990; Aeby et al., 2003) according to resilience (Coles and Brown, 2003) (see below) which, in turn is dependent on the frequency and severity of bleaching (McClanahan et al., 2007; Sheppard et al., 2008), the thermal history of the location (Brown et al., 2000; Brown et al., 2002) and levels of other stressors, notably sedimentation, over-fishing and water quality (Hutchings et al., 2005; Johnson and Marshall, 2007). Significantly, although there are some taxonomic differences in susceptibility of both corals and algae to bleaching, it is virtually certain that all shallow-water zooxanthellate corals will ultimately succumb to bleaching if summer sea temperatures increase by 1–3 °C above their present long-term values, or if high sea temperature pulses become increasingly sustained.

2.1.1. The time-line

Apart from isolated occurrences of bleaching in severely stressed environments (for example, Yonge and Nicholls, 1931), there are no substantiated records of mass bleaching before the late 1970s. Further evidence that mass bleaching is a recent phenomenon is seen in long-lived corals, especially large colonies of *Porites* which can be over 600 years old and which have been dying en masse from bleaching since 1970.

Further back in time the potential existence of mass bleaching can only be inferred from possible temperature consequences of CO₂ highs. It is possible that clades of zooxanthellae not seen today may have occurred in past intervals of high temperature, the most recent being the temperature peaks of the Pliocene (5–2.6 million years ago), especially if temperature increase occurred sufficiently slowly for evolutionary adaptation to occur. Since the Pliocene peaks, global temperatures, though variable, have been only marginally higher than at present (Haywood and Williams, 2005) and there is no evidence that rates of global temperature increase relevant to the thermal thresholds of corals were anywhere near as rapid as they are today (Robinson et al., 2008). There is thus no reason to believe that mass bleaching would have been a major stress on reefs at any time since the temperature peaks of the Pliocene.

In contrast, the future path of mass bleaching events is only too clear. Rising sea surface temperatures will lead to increased severity of El Niño-associated thermal anomalies and consequently mass bleaching (Sheppard, 2003; Hoegh-Guldberg et al., 2007; Veron, 2008a; Baker et al., 2008). Current models predict an increase in the amplitude of the El Niño Southern Oscillation with no change in frequency (Guilyardi, 2006). However, incidence of mass bleaching is now likely to de-couple from El Niño cycles in many parts of the world as indicated by the observation that damaging temperatures are already starting to occur during non-El Niño years. This will put affected reefs at increasing annual risk, greatly shortening event return times and decreasing resilience (Sheppard, 2003).

Some reefs, notably those of the southern Red Sea (which has naturally high temperature) and parts of the 'Coral Triangle' (Roberts et al., 2002; Hoegh-Guldberg et al., 2009; Veron et al., 2009) (which has natural refugia) are likely to be relatively less vulnerable to mass bleaching as are other locations which could benefit

from temporary changes in water circulation. Nevertheless, such effects can only offer a short-term reprieve: at the current rate of increase in global CO₂ emissions (now exceeding 3% per year) a level of 450 ppm, which far exceeds the most optimistic outlook for the viability of almost all reefs, will be reached in the 2030s (Meehl et al., 2007; Raupach et al., 2007). The result will be widespread destruction of coral communities, with a few persisting in shaded, turbid waters or at depth (generally below 20 m in clear water). The major issue here is that reef-building corals will become rare members of tropical reef assemblages, threatening the ecological services provided by coral reefs to tens of thousands of other dependent species as well as coastal human societies.

In the very long term (centuries to millennia) mass bleaching alone is unlikely to cause widespread extinctions of corals because the complexities of reef topographies provide refuges from which re-seeding could occur. Such refuges, however, may not provide protection for other taxa restricted to shallow-water reef habitats and will not provide protection for corals from ocean acidification which looms as an even more serious threat.

3. Ocean acidification

Prior to the industrial revolution, absorption and release of CO₂ by the oceans was in approximate equilibrium (Watson and Orr, 2003). Since then, atmospheric CO₂ has risen from ~280 ppm to today's level of ~387 ppm (NOAA/ESRL, 2009) and is estimated to be increasing at a rate at least 100 times faster than has occurred naturally for at least the past 650,000 years (Siegenthaler et al., 2005). About half of all CO₂ from anthropogenic sources still remains in the atmosphere (Houghton, 2007). A further 20% has been taken up by terrestrial life and the remaining 30% has been taken up by the oceans, a process that has now used up about one-third of the storage capacity of the ocean surface (Sabine et al., 2004). This uptake by the oceans is causing acidification of surface waters because dissolved CO₂ forms carbonic acid which alters the ratio of the pH-maintaining carbonate/bicarbonate buffers which in turn decreases pH (Feely et al., 2004; Raven et al., 2005). These changes are now clearly observable in cold high latitude oceans where CO₂ is relatively soluble (Mayewski et al., 2009). On current trajectories of atmospheric CO₂ levels, the acidification process, already underway in high latitudes, will severely impact the tropics by 2030–2050 at which time all reefs of the world will be under increasing acidification stress (Cao et al., 2007; Meehl et al., 2007).

Although correlations between CO₂ levels, depth changes in ocean chemistry and geographic patterns of acidification that result are imperfectly known, the process itself is not in doubt (Bud-demeier et al., 2004; Orr et al., 2005). Historically, studies of carbonate compensation depths have been based on calcite, the dominant form of calcium carbonate, but coral skeletons are made of aragonite, which is more soluble.

3.1. Aragonite saturation

Shallow tropical seawater is supersaturated with respect to aragonite ($\Omega_{\text{aragonite}} > 4$), but saturation levels have fallen significantly over the past century (from 4.6 to 4.0) and will continue to fall as atmospheric CO₂ rises (Kleypas and Langdon, 2006). Although field confirmation is in its early stages there is growing evidence of sub-lethal changes on tropical reefs that are consistent with predicted responses to acidification (see below). It is therefore probable that most sub-tropical reefs are already in sub-optimal condition, although more research is needed to verify this. When atmospheric CO₂ reaches 560 ppm, most ocean surface waters will be adversely undersaturated with respect to aragonite and the pH will have reduced by about 0.24 units – from almost 8.2 today to just over 7.9.

At this point (sometime in the third quarter of this century at current rates of increase) only a few parts of the Pacific will have levels of aragonite saturation adequate for coral growth (Guinotte et al., 2003) and all will be stressed by climate-related synergies (see below). If CO₂ levels are allowed to reach 800 ppm, the pH decrease will be 0.4 units (Riebesell et al., 2000; Orr et al., 2005) and total dissolved carbonate ion concentration will have decreased by at least 60%. At this point it is almost certain that all reefs of the world will be in erosional states (Veron, 2008a; Hoegh-Guldberg et al., 2009). Impacts will be further exacerbated in coastal areas from atmospheric pollutants forming nitric and sulphuric acids (Doney et al., 2007).

The levels of CO₂ and pH predicted around the end of this century may not have occurred since the Middle Eocene (Caldeira and Wickett, 2003). However, the all-important rate of change we are currently experiencing may have no precedent over any time scale (for example, Zachos et al., 2008).

3.2. Impacts on reef biota

Although much is known about the chemistry of ocean acidification described above, its biological effects are likely to be complex (Kleypas et al., 2006). The vulnerability of different taxa to acidification depends on the form of carbonate that they secrete. Coralline algae, which are essential for cementing coral rubble into solid reef and which form a critical habitat for the early life history stages of many organisms including corals, secrete high magnesium calcite and are therefore particularly vulnerable to acidification (Kuffner et al., 2007; Jokiel et al., 2008). Coral skeletons are formed of aragonite and most molluscs have shells of calcite.

There is a roughly direct relationship between aragonite saturation and the capacity of corals to calcify when temperatures are near optimum levels (Langdon et al., 2000; Barker and Elderfield, 2002; Feely et al., 2004). This can be studied experimentally (Langdon, 2002) although most effects on reefs will be ecological responses to decreased growth rates and skeletal strength. A decrease in coral growth rate of 14% since 1990 (and unprecedented in the 400 year record examined) has already been observed on corals of the Great Barrier Reef, as a possible response to acidification in combination with elevated temperature stress (Cooper et al., 2008; De'ath et al., 2009). Comparable observations have been made in Thailand (Tanzil et al., 2009) and the Caribbean (Bak et al., 2009).

When CO₂ levels reach approximately 450 ppm, calcification of coralline algae will probably be completely inhibited (Kleypas and Langdon, 2006; Anthony et al., 2008) while calcification of reef-building corals will be reduced by up to 50% (Guinotte et al., 2003; Silvermann et al., 2009) even without consideration of further harmful synergies. Branching corals, especially shallow-water *Acropora* which are primary habitat builders, will become brittle and more easily damaged leading to extensive habitat deterioration. Overall reef building processes will be severely diminished or will cease altogether (Gattuso et al., 1998, 1999; Kleypas et al., 1999; Langdon and Atkinson, 2005) because as much as 90% of carbonates involved in reef building are removed by erosion, even under ideal building conditions. Average decreases in calcification of more than about 10–20% are expected to put most if not all coral reefs into a net negative carbonate budget where reef structures and frameworks are no longer maintained (Hoegh-Guldberg et al., 2007). At 800 ppm, all calcification including that of calcite-secreting molluscs, will cease or be greatly reduced.

Changes in ocean acidification are also likely to have impacts on a range of biological processes in addition to calcification, including impacts on photosynthesis, oxygen exchange and reproduction (see below). Understanding of these changes and their consequences is in its infancy, but most research indicates that relatively

subtle changes in dissolved carbon dioxide and pH can potentially have large-scale impacts (Raven et al., 2005).

4. Critical issues

Three issues of particular importance to the future of coral reefs are highlighted in this article: (1) the role of multiple stressors and synergies, (2) the nature of resilience and (3) the importance of domino effects.

4.1. Multiple stressors

Reef deterioration may occur as a direct response to an individual stressor such as mass bleaching, but it more commonly occurs in response to combinations of different stressors acting simultaneously and often synergistically (Sheppard, 2006; Baker et al., 2008). Rising sea-levels, increasing numbers of high intensity storms, deterioration in water quality and various biotic influences are the principal stressors that will exacerbate the effects of mass bleaching and ocean acidification. It has been shown, for example, that corals bleach at lower temperatures in acidified water (Anthony et al., 2008). Although studies of these complex interactions are at a very early stage it is clear that they substantially hasten the deterioration of reefs.

4.1.1. Sea-level changes

The greatest sea-level changes that have taken place in geological time have been due to slow changes (over millions of years) in the shape of ocean basins, not to the much more rapid (millennia-long) changes of ice volume that have caused the sea-level variations of the Pleistocene. However, in both cases, coral communities have successfully re-located, something which they are clearly able to do (even accommodating an abrupt rise of 36 mm/yr at the termination of the last glaciation (Blanchon et al., 2009)). Anticipated rates of sea-level change this century (≥ 10 mm/yr) (Hansen, 2004; Church and White, 2006; Richardson et al., 2009) are greater than normal rates of reef growth (~ 6 mm/yr) (Vecsei, 2004; Montaggi- oni, 2005). As the rate of sea-level change increases it will likely have a material impact in synergy with other stressors, especially ocean acidification and high-impact weather events, driving shallow reef communities towards an erosional state. This effect of sea-level rise is not likely to be significant for reefs until mid-century but will be preceded by deterioration of living conditions on human-occupied atolls.

4.1.2. Storm impacts

Predicted increases in the frequency and severity of high-energy storms partly due to increases in ocean surface temperature (Emanuel, 2005; Webster et al., 2005) may already be affecting reefs in some geographic regions including the Great Barrier Reef (Nott and Hayne, 2001). The damage from such storms will be exacerbated by weakening of the reef structure resulting from increasing acidification. Increases in rainfall from changed weather events can also be damaging to reefs as demonstrated by very destructive rainfall on the Great Barrier Reef in 2009 (Great Barrier Reef Marine Park Authority, in press). In some geographic regions, changes in the seasonal pattern of rainfall poses a risk to annual reproductive cycles of corals as surface-born coral larvae are intolerant of low salinity.

4.1.3. Fisheries impacts

Over-fishing affects almost all reefs to varying degrees, while destructive fishing, notably blast fishing, is more geographically confined, but its effects can be intense. The close connection between healthy fish communities and wider reef health has long

been known (Hughes, 1994; Roberts, 1995), although more recent studies have greatly enhanced our understanding of this relationship. The removal of top predators, especially sharks, reduces overall species diversity and alters the trophic structure, leading to loss of biomass and the demise of other critical trophic groups including many larger herbivores (Friedlander and DeMartini, 2002; Dulvy et al., 2004; Knowlton and Jackson, 2008). This, and the widespread direct removal of herbivorous fish, allows macro-algae to overgrow corals and to prevent resettlement of new corals in damaged reefs (Aronson and Precht, 2006; Hughes et al., 2007). Destructive fishing destroys the very structure of the reef as well as living communities and often leaves loose rubble which can take many years to recover (Burke et al., 2002; Fox et al., 2005). Overall, where fishing impacts can be minimised, the diverse and productive ecosystems which result appear to be more resilient and recover more rapidly from bleaching or other perturbations (Hughes et al., 2007).

4.1.4. Water quality

Coral reefs and coral communities are highly sensitive to water quality, largely a matter of sediment loads (which affects light penetration), nutrients and environmental contaminants. Terrestrial runoff from urban development, agriculture and deforestation are the principal causes of diminished water quality (Fabricius, 2005). Runoff impacts have become such a worldwide phenomenon, that only reefs well removed from highly populated land masses have escaped degradation of some sort. This is now the subject of considerable research and mitigation expenditure on the Great Barrier Reef (Furnas, 2003; Hutchings et al., 2005) as it offers one of the few management options that will enhance reef resilience prior to critical threshold levels being reached due to climate change.

4.1.5. Biotic responses

Widespread observations have been made of the impacts of pathogen and parasite outbreaks on keystone marine species in coral reef environments causing coral diseases, but also impacting echinoderms, turtles and seagrasses (Harvell et al., 2004; Ward and Lafferty, 2004). Predator outbreaks such as the crown of thorns starfish, also have significant impacts on many reefs. There is evidence that many of these impacts are increasing in frequency and expanding their geographic scope. Such impacts may be symptoms of a wider malaise, with increasing prevalence linked to the poor health of the patient/host as a result of other human impacts. Importantly there is also growing evidence of synergies between these impacts and other stressors, particularly with coral bleaching (Miller et al., 2006; Bruno et al., 2007; Harvell et al., 2007).

It is also important to consider the biotic response to existing mass bleaching and coral mortality. Even where corals recover from mass bleaching there is likely to be reduction in growth and fecundity. Coral communities destroyed by bleaching can be quickly reduced to beds of debris which have little of the biodiversity of healthy reefs. These can recover if the frequency of bleaching events and resilience allow, but will go into a state of ecological collapse if conditions for recovery are inadequate. When this happens, the substrate may become covered with blue-green cyanobacterial slime (Veron, 2008a), a covering which appears to be ecologically stable. In such cases, only some macro-algae, notably *Halimeda*, can form any sort of three-dimensional re-growth supporting only a tiny fraction of the former reef diversity.

4.2. Resilience

Resilience – the capacity of a reef to recover from major disturbance – is primarily determined by the frequency, intensity and

nature of stressors, the extent and nature of the damage, and the 'health' of the reef and its environment.

Since their first occurrences in the late 1970s, most mass bleaching events in the Indo-Pacific have been linked to El Niño cycles which occur at intervals of 4–7 years. The intensity of events has varied, but at these frequencies most reefs have made at least partial recovery (Bruno and Selig, 2007; Wakeford et al., 2008). In future, mass bleaching events will become more frequent as they de-couple from El Niño cycles, and more severe as ocean temperatures rise. They are currently on track to become annual events, with lethal temperature thresholds being reached most summers (Veron, 2008a). As the frequency and intensity of bleaching events rise, the extent and number of reefs involved will also rise, involving ever-increasing numbers of species over increasing depth-ranges. As this damage becomes more extensive, the capacity of corals to regrow from fragments or from immigration of larvae will inevitably decline.

A degraded environment, whether natural or human-induced, has a strong influence on reef resilience. Thus, over-fishing and water quality degradation (through increased sedimentation and nutrient pollution, as commonly occurs throughout the Caribbean, south-east Asia and the Indian Ocean perimeter) reduce the resilience of reefs to bleaching (Wilkinson, 2008). These chronically stressed reefs are now at high risk of reverting to semi-permanent algal or cyanobacterial communities (Veron, 2008a). In contrast, reefs remote from additional human stresses can make rapid recoveries (Aronson and Precht, 2006; Grimsditch and Salm, 2006; Hughes et al., 2007), returning to their former diversity in as little as a decade.

There is substantial geographic variation in temperature thresholds for bleaching. During the time of early mass bleaching events, the occurrence of unbleached corals in areas of naturally high temperatures (notably the southern Red Sea and Persian/Arabian Gulf) suggested a substantial degree of natural tolerance. However, most of these areas have more recently been damaged to some extent (Wilkinson, 2008). In short, the temperature at which bleaching occurs varies geographically, but the incidence of bleaching is almost universal.

Genetic diversity among corals and zooxanthellae can potentially enable adaptation, and thereby enhance resilience. Where there has been sufficient time and suitable conditions, many reefs that have been impacted by bleaching have recovered or are in the process of recovery (Sheppard et al., 2002; Sheppard and Obura, 2005; Grimsditch and Salm, 2006; Lasagna et al., 2008). This can involve an increase in the temperature tolerance of individual colonies by a shift to relatively heat-tolerant clades of zooxanthellae in surviving colonies (Brown et al., 2002; Thornhill et al., 2006; Maynard et al., 2008). Such modification of symbioses is important (Baker, 2001; Obura, 2009), but it is very unlikely to offer any long-term solution to mass bleaching because of a mismatch in time scales. The time scale of current impacts is in years to decades whereas that of evolutionary adaptation for highly dispersed long-lived animals like corals is in millennia at least. It is important to note that these changes also necessarily involve a narrowing of the genetic diversity within a population and hence a likely reduction in resilience to other stress factors.

4.3. Domino effects

Coral reefs occupy a truly unique position on Earth, for they are geological structures made by combinations of living organisms that have evolved the capacity to harness the abundant resources of air, seawater and sunlight. Reefs grow on solid substrates, but only at the interface of sea and atmosphere and only where light and temperature permit. To do this, reef-building organisms have evolved complex ecologies with tight interdependencies between

key species, all dominated by many types of symbiotic relationships between plants and animals.

Reefs are particularly vulnerable to environmental changes, especially disruptions to the pathways of the carbon cycle on which they are totally dependent. Unlike any other major ecosystem, such disruptions can be of both marine and terrestrial origin. It is therefore hardly surprising that reefs have been especially impacted by all the great mass extinction events of the past (Sepkoski, 1995; Stanley, 2001).

The outlook for reefs in the face of today's rapid global warming is exceptionally serious. The mounting evidence warning of the imminent demise of reefs is perhaps the strongest signal yet that the planet is on the brink of an environmentally-led mass extinction, for this appears to have been what happened in the remote past (Veron, 2008b). Whether or not this is so, reefs are likely to be the first major planetary-scale ecosystem to collapse in the face of climate changes now in progress (Sheppard et al., 2009). This raises the question: will this collapse be restricted to reefs or does it have wider implications? It is already clear that, although mass bleaching is a reef phenomenon, the effects of ocean acidification (Mcleod et al., 2008; UNESCO, 2009) will directly impact all carbonate-dependent taxa: not only corals, but calcareous algae, most molluscs, many crustaceans, echinoderms and planktonic taxa, and other groups that rely on carbonates for skeletal growth (Pörtner et al., 2004; Guinotte and Fabry, 2008). This includes fish (Munday et al., 2008) which are particularly vulnerable during early stages in their life-cycle (Kikkawa et al., 2004; Ishimatsu et al., 2004) and also the pelagic ecosystem of the Southern Ocean (Moy et al., 2009) which is dependent on krill. Research on these issues is still in its infancy, but the enormity of the threat is nevertheless real.

As far as the immediate future is concerned, the failure of reefs will have knock-on effects to other reef-associated ecosystems (Fabry et al., 2008). These impacts have been reviewed for the Great Barrier Reef (Pandolfi et al., 2003; Fabricius et al., 2007; Johnson and Marshall, 2007; Lough, 2007) and associated island biota (Turner and Batianoff, 2007), seagrass beds (Waycott et al., 2007; Björk et al., 2008), mangroves (Mcleod and Salm, 2006), marine reptiles (Hamann et al., 2007), marine mammals (Lawler et al., 2007), seabirds (Congdon et al., 2007), pelagic ecosystems (Kingsford and Welch, 2007) and estuarine habitats (Sheaves et al., 2007).

5. Remedial options

The speed at which climate change is impacting reef ecosystems leaves little opportunity for evolutionary processes to come to the aid of corals and other reef inhabitants as they would have done over geological intervals of time. Survival will be highly dependent upon any natural resistance already existing in the gene pools today. Some management interventions will, for a time, increase reef resilience, the most important of which are (a) reducing the harvest of herbivorous fish to sustainable levels (Hughes et al., 2007), (b) maintaining an effective trophic pyramid by protecting sharks and other top predators, (c) managing all aspects of water quality and (d) minimising any other direct anthropogenic impacts and stressors. Such actions can be supported through the use of large networks of marine protected areas and other direct management interventions such as improved control of watershed-based activities whose effects on water quality are often severe. Most of these management activities are already in place for the Great Barrier Reef Marine Park (Great Barrier Reef Marine Park Authority, 2009) and must be a priority for all reef regions. A wider array of other actions have also been recommended (Mcleod et al., 2008). Nevertheless, these actions cannot offer long-term protection from the consequences of increasing atmospheric CO₂ levels as they pass critical thresholds.

Efforts at emissions reductions have thus far been limited in magnitude and weak in implementation, and it is critical that this situation is reversed to enable rapid and dramatic cuts (Vaughan et al., 2009; Royal Society, 2009). However, cumulative carbon emissions to date have already committed atmospheric CO₂ to remaining above 330 ppm for at least the next millennium³ (Lenton, 2006). Thus, to return to a safe level for corals will demand maintaining, enhancing and probably creating carbon dioxide sinks in addition to strong cuts to CO₂ emissions (Lenton and Vaughan, 2009). If such a strategy is pursued, it will be critical to consider all possible benefits and limitations and employ great caution, before allowing planetary scale carbon dioxide removal schemes to proceed (Royal Society, 2009). Some large scale carbon dioxide removal options such as ocean fertilization still require proof of their effectiveness and may risk serious side effects (Harvey, 2008; Lenton and Vaughan, 2009; Royal Society, 2009). Alternative climate geoengineering options, which involve a reduction in the amount of solar radiation absorbed by the Earth, will have no effect on ocean acidification (Blackstock et al., 2009).

As custodians of geological history, reefs offer both immense geological evidence and stark recent testimony to the potentially catastrophic effects of destabilising global climate. Although, being carbonate platforms, they are particularly sensitive to disruptions of the carbon cycle, their demise is symptomatic of damage to the entire biosphere as this cycle plays a dominant part in all ecosystems. When taken together, the abruptly accelerating deterioration of terrestrial and marine ecosystems and the increasingly disturbing global extinction rates may eventually become indistinguishable from the records of mass extinctions captured in the remains of long-fossilised coral reefs. The difference is that this time humanity will have been the cause and also one of the species to suffer.

The extreme gravity of the current predicament is now widely acknowledged by reef and climate scientists. It is also acknowledged that only drastic action starting now will prevent wholesale destruction of reefs and other similarly affected ecosystems. Should humanity not be successful in preventing these threats from becoming reality (Rojelj et al., 2009), no amount of management or expenditure will save future generations from the consequences of our failed guardianship.

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³ Over 350 PgC have been emitted from fossil fuel burning and 165 PgC from land use change to date, equivalent to nearly 250 ppm. The airborne fraction of added CO₂ remains around 20% on the millennial timescale, i.e. 50 ppm of the already added CO₂ will be with us for over a 1000 years. Adding this to the preindustrial level of 280 ppm gives 330 ppm.

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