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Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook

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ABSTRACT

Since the early 1980s, episodes of coral reef bleaching and mortality, due primarily to climate-induced ocean warming, have occurred almost annually in one or more of the world's tropical or subtropical seas. Bleaching is episodic, with the most severe events typically accompanying coupled ocean–atmosphere phenomena, such as the El Niño-Southern Oscillation (ENSO), which result in sustained regional elevations of ocean temperature. Using this extended dataset (25+ years), we review the short- and long-term ecological impacts of coral bleaching on reef ecosystems, and quantitatively synthesize recovery data worldwide. Bleaching episodes have resulted in catastrophic loss of coral cover in some locations, and have changed coral community structure in many others, with a potentially critical influence on the maintenance of biodiversity in the marine tropics. Bleaching has also set the stage for other declines in reef health, such as increases in coral diseases, the breakdown of reef framework by bioeroders, and the loss of critical habitat for associated reef fishes and other biota. Secondary ecological effects, such as the concentration of predators on remnant surviving coral populations, have also accelerated the pace of decline in some areas. Although bleaching severity and recovery have been variable across all spatial scales, some reefs have experienced relatively rapid recovery from severe bleaching impacts. There has been a significant overall recovery of coral cover in the Indian Ocean, where many reefs were devastated by a single large bleaching event in 1998. In contrast, coral cover on western Atlantic reefs has generally continued to decline in response to multiple smaller bleaching events and a diverse set of chronic secondary stressors. No clear trends are apparent in the eastern Pacific, the central-southern-western Pacific or the Arabian Gulf, where some reefs are recovering and others are not. The majority of survivors and new recruits on regenerating and recovering coral reefs have originated from broadcast spawning taxa with a potential for asexual growth, relatively long distance dispersal, successful settlement, rapid growth and a capacity for framework construction. Whether or not affected reefs can continue to function as before will depend on: (1) how much coral cover is lost, and which species are locally extirpated; (2) the ability of remnant and recovering coral communities to adapt or acclimatize to higher temperatures and other climatic factors such as reductions in aragonite saturation state; (3) the changing balance between reef accumulation and bioerosion; and (4) our ability to maintain ecosystem resilience by restoring healthy levels of herbivory, macroalgal cover, and coral recruitment. Bleaching disturbances are likely to become a chronic stress in many reef areas in the coming decades, and coral communities, if they cannot recover quickly enough, are likely to be reduced to their most hardy or adaptable constituents. Some degraded reefs may already be approaching this ecological asymptote, although to date there have not been any global extinctions of individual coral species as a result of bleaching events. Since human populations inhabiting tropical coastal areas derive great value from coral reefs, the degradation of these ecosystems as a result of coral bleaching and its associated impacts is of considerable societal, as well as biological concern. Coral reef conservation strategies now recognize climate

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change as a principal threat, and are engaged in efforts to allocate conservation activity according to geographic-, taxonomic-, and habitat-specific priorities to maximize coral reef survival. Efforts to forecast and monitor bleaching, involving both remote sensed observations and coupled ocean–atmosphere climate models, are also underway. In addition to these efforts, attempts to minimize and mitigate bleaching impacts on reefs are immediately required. If significant reductions in greenhouse gas emissions can be achieved within the next two to three decades, maximizing coral survivorship during this time may be critical to ensuring healthy reefs can recover in the long term.

1. Introduction

Climate change is now firmly established as a scientific reality, with a variety of emergent challenges for societies in the coming decades. Global warming and associated increases in sea surface temperatures (SSTs) are now projected to be very likely in the coming decades (IPCC, 2001, 2007; Phinney et al., 2006), and the human "fingerprint" of increased atmospheric CO_2 on the climate signal is also clear (Santer et al., 2007). Combined with the acidifying effect of increasing dissolved carbon dioxide in the ocean (Caldeira and Wickett, 2003; Feely et al., 2004; Kleypas and Langdon, 2006), there is a clear research need to understand the likely impacts of climate change on marine ecosystems, and identify strategies to mitigate harmful effects, where possible. These assessments are already underway (Sarmiento et al., 2004; Grebmeier et al., 2006), but as changes in the climate system begin to mature over the coming years, it will be increasingly important to refine these forecasts by ground-truthing them against observations. This research strategy offers the greatest likelihood of identifying trends in ecosystem response, and maximizes the accuracy of updated forecasts.

Coral reef ecosystems are particularly sensitive to climate-induced changes in the physical environment. Since the 1980s, coral reef "bleaching", caused by unusually high sea temperatures, has had devastating and widespread effects worldwide. As a result, a significant body of research has accumulated on the causes and consequences of bleaching. Research spans the fields of cellular physiology, organismal biology, ecology and ecosystem biology, and includes timescales ranging from milliseconds to decades. This justifies a critical re-assessment of the accumulated knowledge base, focusing on the long-term ecological impacts of warming, and recovery trajectories following disturbance. Moreover, the more recent discovery that coral reefs are not only threatened by increasing temperatures, but also by ocean acidification (Gattuso et al., 1998; Kleypas et al., 1999), galvanizes the need for a comprehensive update on bleaching that highlights uncertainties in how climate change effects might interact. The objective of this review is therefore to synthesize knowledge on the long-term ecological effects of coral bleaching, including a quantitative synthesis of biogeographic differences in recovery response, collate information on timescales and trends in recovery processes, refine our forecasts where necessary, and identify potential strategies that might maximize coral reef survival in the coming years.

1.1. Coral reef bleaching: Definition

Reef-building corals, as well as numerous species of reef-dwelling cnidarians, mollusks, polychaetes, protists and other taxa, are hosts to dinoflagellate symbionts in the genus *Symbiodinium*. These symbionts, commonly referred to as "zooxanthellae", are generally obligate for their hosts, contributing to their host's energetic budgets through the provision of photosynthates, as well as accelerating calcification in many skeleton-forming taxa (Muscatine and Porter, 1977). This dependence on photosynthetic, oxygen-producing autotrophs, while having clear benefits, also imparts distinct costs. Environmental extremes, such as high temperature or irradiance, damage the symbionts' photosynthetic machinery, resulting in the overproduction of oxygen radicals. This leads to eventual cellular damage in the symbionts and/or their hosts, and can lead to the expulsion of symbionts and the eventual breakdown of the symbiosis (Lesser, 2006). The loss of zooxanthellae (and/or a reduction in their pigment concentrations) as a result of this process is referred to as "bleaching". In extreme cases, bleaching leads to the visible paling of the host organism, as the yellow-brown pigmentation of the symbionts is lost (Fig. 1). In scleractinian (stony) corals some 50% or more of the total symbiont community must be lost before paling is typically visible to the naked eye (Fitt et al., 2000), and in many taxa, including corals, bleaching turns the host organism white, as the calcareous skeleton becomes visible through the coral's transparent tissues.

Many coral species contain a variety of non-photosynthetic pigments of host origin that are not diminished in concentration or lost during bleaching events. These pigments can result in bleached corals that appear pink, chartreuse, purple, yellow or other colors, rather than the more typical white. Bleaching events, when they occur, are usually not confined to the principal reef-builders themselves, the scleractinian corals, but also involve numerous other metazoan and protist hosts on reefs. Consequently, the term "coral reef bleaching" is a better descriptor of these reef-wide events (rather than the more restrictive term "coral bleaching").

1.2. Coral reef bleaching events

The number of coral reef bleaching reports, driven principally by episodic increases in sea temperature, has increased dramatically since the early 1980s (Glynn, 1993; Hoegh-Guldberg, 1999; Hughes et al., 2003; Hoegh-Guldberg et al., 2007). Many of these events, and recovery from them, have now been studied over decadal scales. The frequency and scale of coral bleaching events during the past few decades have been unprecedented, with hundreds of reef areas exhibiting bleaching at some point, and, on occasion, whole ocean basins affected. Consequently, much has been written about coral reef bleaching during the past three decades, and several compilations are available in the published literature (Williams and Bunkley-Williams, 1990; Glynn, 1996; Brown, 1997a; Wilkinson, 2000, 2004; Coles and Brown, 2003; Wilkinson and Souter, 2008), as well as online in various databases maintained by agencies such as the WorldFish Center, NOAA, and GBRMPA.

The occurrence of mass bleaching events correlates well with observed increases in global sea temperatures, and particularly thermal anomalies. This relationship was clearly observed in the Caribbean basin during the 1980s and 1990s, when annual coral bleaching increased logarithmically with SST anomalies (McWilliams et al., 2005). A 0.1 °C rise in regional SST resulted in a 35% increase in the number of areas that reported bleaching, and mass bleaching events occurred at regional SST anomalies of 0.2 °C and above (Fig. 2). Bleaching within affected regions is not uniform, exhibiting patchy affects over micro (mm to cm) to meso (km) scales. Such variability results from fluctuations in environmental conditions, spatial heterogeneity of reef surfaces, genetic