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Review Article

Climate change, global warming and coral reefs: Modelling the effects of temperature

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ABSTRACT

Climate change and global warming have severe consequences for the survival of scleractinian (reef-building) corals and their associated ecosystems. This review summarizes recent literature on the influence of temperature on coral growth, coral bleaching, and modelling the effects of high temperature on corals. Satellite-based sea surface temperature (SST) and coral bleaching information available on the internet is an important tool in monitoring and modelling coral responses to temperature. Within the narrow temperature range for coral growth, corals can respond to rate of temperature change as well as to temperature *per se*. We need to continue to develop models of how non-steady-state processes such as global warming and climate change will affect coral reefs.

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1. Introduction

Coral reefs, found predominantly between the tropics of Capricorn and Cancer, provide an environment in which one third of all marine fish species and many thousands of other species are found, and from which 6 million tons of fish are caught annually. This not only provides an income to national and international fishing fleets, but also for local communities, which in addition rely on the local fish stocks to provide nutritional sustenance. The reefs also act as

barriers to wave action and storms by reducing the incident wave energy through wave reflection, dissipation and shoaling, protecting the land and an estimated half a billion people who live within 100 km of reefs.

The growth and subsistence of corals depend on many variables, including temperature, irradiance, calcium carbonate saturation, turbidity, sedimentation, salinity, pH, and nutrients. These variables influence the physiological processes of photosynthesis and calcification as well as coral survival, and as a result coral reefs occur only in select areas of the world's oceans. Meteorological processes can alter these variables, and Fig. 1 summarizes their influences on global and synoptic scales on coral requirements for growth and survival (Walker, 2005; Crabbe et al., 2008a). Coral reefs are cur-

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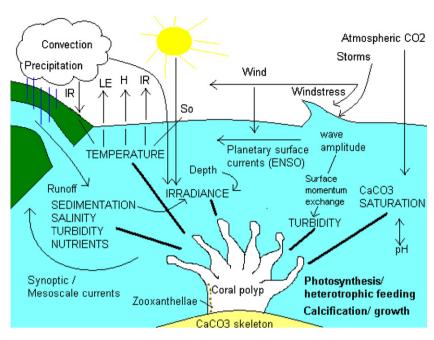


Fig. 1. Schematic diagram summarizing key meteorological processes and coral requirements controlling calcification, photosynthesis, and survival. Adapted from Crabbe et al. (2008a) and Crabbe et al. (2008b).

rently under severe threat from climate change (Lough, 2008), as well as from many other anthropogenic influences, such as pollution and overfishing (Mumby et al., 2007; Crabbe et al., 2008b).

This review will concentrate on the effects of temperature on modern scleractinian (reef-building) corals, and the recent insights that modelling can provide to increase our understanding of coral ecology and survival in a period of climate change.

2. The Influence Of Temperature On Coral Growth

Many studies have examined the impact of air temperature variations on coral growth rates. In a study of the correlation between air temperature and growth rates of coral from a colony of *Porites* lutea in the Great Barrier Reef in the district of Haapiti, Australia (Bessat and Buiges, 2001), measurements were taken from coral cores. For the period from 1958 to 1990, linear regression gave a correlation between air temperature 25 km from where the core was taken and coral skeletal density of r = 0.37; for the same period, the correlation between air temperature and annual calcification rate was lower at r = 0.28. These results indicated that a 1 °C rise in temperature would lead to an increase in the density rate of about 10.5% and an increase in the calcification rate of about 4.5%. Coral calcification rates and extension rates have been highly correlated with sea surface temperatures (SSTs) and to a lesser extent with incoming solar radiation (Nie et al., 1997; Lough and Barnes, 2000). In juvenile corals, temperature causes a transition between isometric and allometric growth scaling in warmer versus cooler years, respectively (Edmunds, 2006; Edmunds, 2008).

Interestingly, on the Great Barrier Reef (GBR), calcification rates in massive *Porites* colonies declined by approximately 21% in two regions 450 km apart. This was a function primarily of a decrease in linear extension (16%) with a smaller decline in skeletal density (6%) (Cooper et al., 2008) and contrasts with previous studies on the environmental controls on growth of massive *Porites* on the GBR. In a study on reefs of East Africa (McClanahan et al., 2007) it appeared that it was not just the high stability of tropical environments that creates high biological diversity but also large temperature fluctuations that prepares the corals for the unexpected and this may

allow them to persist in what is becoming an increasingly hostile environment.

Growth rates also depend upon minimum seasonal temperatures. Changes in average winter air temperature at the flower garden banks in the Gulf of Mexico were found to correspond to changes in Montastea annularis growth rates (Slowey and Crowley, 1995). Interdecadal changes in the growth rate of the corals corresponded to changes in average minimum winter season air temperatures at New Orleans, Slowey and Crowley (1995) acknowledged that the correspondence between the changes in the two were not one to one because the influence of air temperature on water temperature depends on a number of meteorological and oceanographic factors. The minimum temperatures over the Gulf of Mexico can be caused by the passage of fronts bringing cold dry air from Canada, and probably this process is primarily responsible for stressing corals at the flower gardens and reducing their winter growth rate. There was a major shift towards colder winters during the 1950s and this coincided with the decline of coral growth at the flower gardens.

3. Coral Bleaching

Most of the pigmentation within corals is within the symbiotic algal cells-the zooxanthellae. Coral bleaching is caused by corals losing their zooxanthellae. Thermal bleaching occurs when the coral is exposed to prolonged above-normal (or below-normal) temperatures, resulting in additional energy demands on the coral, depleted reserves, and reduced biomass (Muller-Parker and D'Elia, 1997). The effect of high temperatures can be aggravated by high levels of irradiance (Gleason and Wellington, 1993), although high UV radiation is not a primary factor in causing mass bleaching (Hoegh-Guldberg, 1999). Coral reefs within or near the western Pacific warm pool (WPWP) have had fewer reported bleaching events relative to reefs in other regions. Analysis of SST data indicate that the warmest parts of the WPWP have warmed less than elsewhere in the tropical oceans, which supports the existence of thermostat mechanisms that act to depress warming beyond certain temperature thresholds (Kleypas et al., 2008).

Corals can die as a result of bleaching, though they may partially or fully recover from bleaching events (Lough, 2000). Bleaching causes a decrease in the growth rate of corals, and the time taken for a coral to recover from a bleaching event may be several years or decades. If the frequency of bleaching increases, then the capacity for coral reefs to recover is diminished (Done, 1999). This has been observed during a number of 'natural' events, e.g., 1983-1984 (Glynn, 1990), 1997-1998 (Goreau et al., 2000; Glynn et al., 2001) and 2005 (Wilkinson and Souter, 2008). Experimental studies show that thermal history, in addition to light history, can influence the response of reef-building corals to thermal stress, and therefore, have implications for the modeling of bleaching events (Middlebrook et al., 2008). Significant levels of mortality can occur in a bleaching event before any chance for subsequent recombination of the host-symbiont unit (Jones, 2008). To better understand factors affecting the potential evolution of bleaching resistance in corals in response to increased average sea temperatures, a mathematical model of coevolutionary interactions between partners in a coral-algae mutualistic symbiosis has been developed (Day et al., 2008). This showed that traits in mutualistic symbioses, such as thermal tolerance in corals, are potentially subject to novel kinds of evolutionary constraints and that these constraints are mediated by ecological dynamics. The nature of interspecific control of bleaching resistance and the mode of sexual reproduction interacted to strongly influence the rate of spread of resistance alleles.

4. Modelling The Effects Of High Temperature On Corals

The frequency that corals will be bleached in the future has been estimated by using projections of future sea surface temperatures from four different general circulation models (GCMs) forced by the IPCC IS92a emission scenario (Hoegh-Guldberg, 1999). The SST projections were combined with thermal thresholds for corals, derived by using the Integrated Global Ocean Services System (IGOSS) dataset provided by the Joint World and Scientific Meteorological Organization (WMO) and United Nations Educational, Scientific and Cultural Organization (UNESCO), Joint Intergovernmental Oceanographic Commission's (JCOMM) Technical Commission for Oceanography and Marine Meteorology, and from literature and Internet reports of bleaching events. All SST projections indicated that the frequency of bleaching events is set to rise rapidly, with the highest rates in the Caribbean, Southeast Asia, and Great Barrier Reef, and the lowest rates in the central Pacific. The frequency of bleaching events was predicted to become annual in most oceans by 2040, and the Caribbean and Southeast Asia are projected to reach this point by 2020, triggered by seasonal changes in seawater temperature rather than by El Niño events.

The geographical patterns and the timing of probable repeat occurrences of coral mortality in the Indian Ocean have been estimated (Sheppard, 2003). Forecast sea surface temperatures at 33 sites in the Indian Ocean were blended onto historical sea surface temperatures. The forecast temperatures were estimated by using the IS92a scheme, which follows a median path. These studies indicate a 50% probability of SSTs being warm enough by 2030 for the occurrence of coral bleaching events at Comoros and Chagos in the Indian Ocean, and by 2070 in the Saudi Arabian Gulf.

In order to predict imminent rises in SSTs, the U.S. National Oceanic and Atmospheric Administration's Coral Reef Watch (NOAA CRW) develops and operationally produces satellite-based coral bleaching nowcasts and alerts available on the Internet (Liu et al., 2006). These products are based on nighttime-only Advanced Very High Resolution Radiometer (AVHRR) sea surface temperatures from operational NOAA polar-orbiting satellites, and, for example,

Gowth rate vs. rate of temperature change

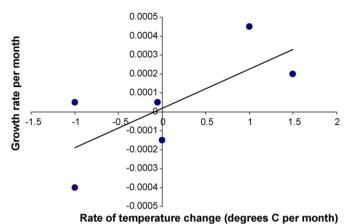


Fig. 2. Influence of the rate of change of temperature on the growth rate of an *Acropora palmata* coral colony from Curaçao (Bak, 1976). R^2 = 0.53. For details see the text.

provided alerts for the 2005 Caribbean mass-bleaching event, indicating that average ocean temperatures during July–October 2005 for the Caribbean exceeded temperatures seen at any time during the past 154 years (NOAA, 2008). Similar systems are in use for the Great Barrier Reef (Maynard et al., 2008).

Modelling of growth rates (by weight; Bak, 1976) of the branching coral *Acropora palmata* with temperature on a Curaçao coral reef, using a smoothing spline to produce a nonparametric fit to the data, suggested that the 30-day averaged maximum daily temperature could explain about 3% of the variability in the time-dependent growth rate (Crabbe et al., 2008a). Interestingly, the temperature correlation was negative, suggesting that during the measurement period, temperatures rose to higher than optimum temperatures for growth, thus inhibiting coral growth, but were not sufficiently high to cause bleaching of this species. Thus what would normally be a positive correlation became a slight but significant negative correlation.

For *Acropora palmata* colonies on fringing reefs off the north coast of Jamaica, over the period 2002–2007, the rate of growth of *Acropora palmata* was largely proportional to *rate of change of SST*, with R^2 = 0.935 (Crabbe, 2007). If we now model the growth rate data of *Acropora palmata* from Curaçao (Bak, 1976) with rate of change of temperature (Fig. 2), then R^2 = 0.53, rather than the small negative correlation if only temperature, rather than rate of change of temperature, is taken into account. These modelling studies suggest that within the narrow temperature range for coral growth, corals respond to rate of temperature change as well as to temperature *per se*.

5. Conclusion

Climate processes and extremes can influence the physiological processes responsible for the growth of coral reef colonies. Coral growth takes place within narrow limits of temperature, irradiance, salinity, pH, and turbidity, all variables that are influenced by climate and weather. In a number of empirical models for coral growth, small changes in temperature and rates of temperature change can significantly influence coral colony growth rates. We need to continue to develop models of how non-steady-state processes such as global warming and climate change will effect coral reefs, and on whether corals or their symbiont algae will evolve to keep pace with the climate and environmental changes.

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