CORAL REEF CALCIFICATION AND CLIMATE CHANGE: THE EFFECT OF OCEAN WARMING

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ABSTRACT
Coral reefs are constructed of calcium carbonate ($CaCO_3$). Deposition of $CaCO_3$ (calcification) by corals and other reef organisms is controlled by the saturation state of $CaCO_3$ in seawater (Ω) and sea surface temperature (SST). Previous studies have neglected the effects of ocean warming in predicting future coral reef calcification rates. In this study we take into account both these effects by combining empirical relationships between coral calcification rate and Ω and SST with output from a climate model to predict changes in coral reef calcification rates. Our analysis suggests that annual average coral reef calcification rate will increase with future ocean warming and eventually exceed pre-industrial rates by about 35% by 2100. There is evidence however to suggest that different corals display different sensitivities to changes in Ω_{arag} and SST [*Reynaud et al.,* 2003]. Considering that both these environmental parameters are likely to change considerably in the future, additional experiments on a variety of differing coral species will be crucial to obtain a better understanding of future coral reef stability.

INTRODUCTION
Calcification is the process by which corals produce calcium carbonate ($CaCO_3$). Coral reef calcification is predicted to decrease 20-60% by 2100, relative to pre-industrial levels [*Kleypas et al.,* 1999], due to increases in CO_2 levels in the surface ocean as atmospheric CO_2 rises. Such decreases in calcification would cause loss of reefs because construction rates would fall below natural destruction rates. The $CaCO_3$ saturation state of seawater (Ω) is defined by: $\Omega = \frac{[Ca^{2+}][CO_3^{2-}]}{\lambda}$, where λ is the solubility coefficient of different forms of $CaCO_3$. Most authors have used Ω values for aragonite (Ω_{arag}) as it is the form of $CaCO_3$ deposited by corals and green algae. As CO_2 levels rise in seawater via anthropogenic CO_2 uptake, pH decreases and the seawater carbonate equilibrium is shifted, reducing dissolved CO_3^{2-} and Ω_{arag} [*Kleypas et al.,* 1999]. Reduction of Ω_{arag} has been found to reduce calcification of some coral species in laboratory experiments. On the other hand, coral calcification rates have been found to increase with increasing sea surface temperature (SST) [*Bessat and Buigues*, 2001; *Lough and Barnes*, 1997; 2000]. *Lough and Barnes* [2000] (herein referred to as LB2000) showed a significant positive correlation between annual average SST and calcification ($R^2 \sim 0.8$) amongst 554 massive *Porites* colonies from 44 reefs in Australia, Hawaii and Thailand through a temperature range of 23°C to 29°C (Fig. 1). Additional measurements from 27 massive *Porites* from 5 sites in the Persian Gulf and New Ireland (Papua New Guinea) are also consistent with this relationship [*J.Lough*, unpublished data, 2004]. Furthermore, recent work has shown that calcification in *Montastrea*, the chief reef-building coral in the Atlantic, is nearly twice as sensitive to temperature as massive *Porites* [*Carricart-Ganivet*, 2004].

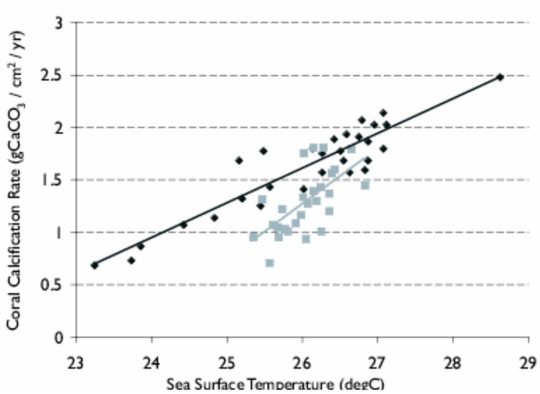
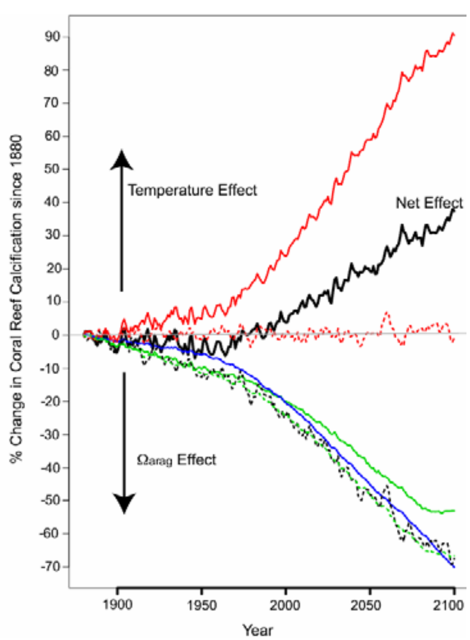


Fig. 1: Relationship between annual average SST (°C) and coral calcification for *Porites* coral colonies where diamonds show the results from *Lough and Barnes* [2000] and squares from *Bessat and Buiges* [2001].

The LB2000 relationship between calcification and SST could be influenced by either light and/or Ω_{arag} variations. Light was taken into account by LB2000 and partial correlations showed that solar radiation added only 1.5% to the 83% of variance explained by SST. We determine Ω_{arag} to vary between 3.88 to 4.02 within the temperature range (23-29°C). Using the rather high dependency of calcification upon Ω_{arag} quoted by *Langdon et al.* [2000] as an upper limit (cf. [*Reynaud et al., 2003*]), we estimate that temperature-related changes in Ω_{arag} could only increase calcification by ≈15% in comparison to the observed 340% increase in *Porites* calcification rate from the LB2000 relationship. Based on these determinations, light and Ω_{arag} do not have a significant impact on the LB2000 relationship. The observed increase in coral reef calcification with ocean warming could be due to an enhancement in coral metabolism and/or increases in photosynthetic rates of their symbiotic algae. This highlights the need to include SST as well as Ω_{arag} in predicting future changes in coral reef calcification.

FINDINGS

Changes in coral reef calcification were estimated by combining the output of the CSIRO climate model with empirical relationships between coral calcification rate and Ω_{arag} and annual SST. Calcification changes in the coral reef habitat (SST >18°C) due to Ω_{arag} were projected using the observational results of Langdon et al., [2000], while calcification changes due to SST were projected using the results of Lough and Barnes [2000]. Our results show that changes in coral reef calcification associated with ocean warming outweigh those associated with decreases in Ω_{arag} (Figure 3). In our model, coral reef calcification decreases by up to 7% from pre-industrial levels up until 1964 as the CO_2 effects outweighs the temperature effect. After 1964 however, ocean warming far outweighs the CO_2 effect and stimulates recovery of coral reef calcification. Rates recover to their pre-industrial values by about 1995 and are 35% higher than pre-industrial levels by 2100. It is also important to recognize that coral reef calcification and the changes suggested here are separate to the adverse future effects of coral bleaching which is associated with the corals symbiotic micro-algae (zooxanthallae).



Here, we use in-situ data for the temperature sensitivity of calcification in massive *Porites*, the most significant reef-building coral in the Indo-Pacific. There are other data for the temperature sensitivity of calcification in corals which may suggest the existence of an upper temperature limit for coral reef calcification [*Reynaud et al.,* 2003]. However, these data were obtained by subjecting organisms collected from one location to a range of temperatures, the extremes of which the organisms never experience. It is then not surprising that such experiments indicate declines in calcification towards the extremes. Data for *Porites* quoted here showed no declines at high and low temperatures. Despite this, the potential existence of a thermal upper limit for other coral species is important and should be further explored.

Fig. 2: Annual mean percentage change in coral reef calcification relative to pre-industrial levels (1880) for control experiment (dashed lines) and climate change experiment (solid lines). The green lines show the projected changes from variations in aragonite saturation state while the red lines show the projected changes associated with ocean warming. The combined climate change response is shown by the solid black line.

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