Reply to comment by Kleypas et al. on "Coral reef calcification and climate change: The effect of ocean warming"

Ben I. McNeil,[1] Richard J. Matear,[2] and David J. Barnes[3]

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1. Introduction

[1] In their original paper [*Kleypas et al.*, 1999] and in subsequent papers, Kleypas and others considered how acidification of the surface ocean by rising atmospheric CO_2 might impact coral reef calcification by affecting the aragonite saturation state of seawater (arag). They concluded that coral calcification is already compromised and predicted further declines through the 21st Century. We took this a step further [*McNeil et al.*, 2004] (herein referred to as MMB04) by using a coupled atmosphere-ocean model that takes into account future changes in arag due to rising sea surface temperature (SST), changes in ocean circulation and changes in oceanic biological activity. We also took into account increases in calcification that may be expected due to rising SST by using *in-situ* evidence. In their response to our paper, *Kleypas et al.* [2005] (herein referred to as K05) seek to discredit our finding that coral reef calcification may increase through the 21st Century.

2. Combining the Calcification: SST and Calcification: Ω_{arag} Relationship

[2] Many of their criticisms relate to our choice of the calcification-SST relationship provided by *Lough and Barnes* [2000] (hereinafter referred to as LB2000) and to the relationship itself. This relationship was obtained by correlating the annual average SST with annual average calcification determined from annual density banding patterns in the skeletons of 554 colonies of massive *Porites* from 44 reefs encompassing a SST range of 23 to 29°C. The relationship is linear across the temperature range and accords with other work [*Bessat and Buigues*, 2001; *Carricart-Ganivet*, 2004; *Nie et al.*, 1997].

[3] K05 point out that temperature response curves obtained experimentally show that calcification rates increase with temperature but decline once the temperatures rise above those normally experienced by the experimental corals. We acknowledge this issue in our paper. K05 choose to assume that corals will not adapt or acclimatise. As they point out, it is implicit in our paper that corals will adapt or acclimatise. Interestingly, a similar problem arose with regard to coral bleaching. The position initially adopted was that corals have no defences against factors bringing about bleaching [e.g., *Hoegh-Guldberg*, 1999]. It is now apparent that corals have a variety of mechanisms by which they can accommodate changes in environmental factors that bring about bleaching [*Baker et al.*, 2004; *Brown et al.*, 2002; *Little et al.*, 2004; *Rowan*, 2004].

[4] *McNeil et al.* [2004] (hereinafter referred to as MMB04) assume that the calcification rate of corals is the sum of two linear responses, a temperature response (LB2000) and a Ω_{arag} response [*Langdon et al.*, 2000]. *Kleypas et al.* [2005] (hereinafter referred to as K05) suggest that this assumption is not valid based upon a laboratory study that found the combined effects of elevated temperature and lowering Ω_{arag} were not linear for *Stylophora pistillata* [*Reynaud et al.*, 2003]. Interestingly however, *Reynaud et al.* [2003] also found that calcification did not decrease with lowering Ω_{arag} when holding temperature constant and as such contradicts previous calcification projections from Kleypas and others based solely on Ω_{arag}. As acknowledged in our paper, we suspect that the effects of both Ω_{arag} and SST on calcification rate are more complex and species-dependent than the simple relationships used by *Kleypas et al.* [1999] and MMB04. It is hoped that our study may promote future experiments beyond *Reynaud et al.* [2003] that further investigate the calcification response to elevated CO_2 and SST.

[5] We agree that *Porites* calcification is not equivalent to reef calcification. Unfortunately, there are no equivalent data for whole reefs, or for significant areas within reefs. We took *Porites* calcification to be indicative of overall reef calcification since it is the dominant reef-building coral within the Pacific while *Montastrea*, which shows a similar temperature dependency as *Porites* [*Carricart-Ganivet*, 2004], is the dominant reef-builder in the Atlantic.

3. *Porites* Calcification: Temperature Relationship

[6] K05 suggest that the LB2000 relationship did not take into account light, which co-varies with temperature. Light was taken into account by LB2000: partial correlations showed that solar radiation added only 1.5% to the 83% of variance explained by SST. They also suggest that the relationship is not applicable above ~27°C because a single high SST point was obtained from "a very different environment" (the reefs around Phuket Island, Thailand). In our view, this point is debatable. However, they overlooked a far more telling point. In our paper, we noted a personal communication from J. Lough that data for colonies from the Persian Gulf and New Ireland, Papua New

[1]Centre for Environmental Modelling and Prediction, University of New South Wales, Sydney, New South Wales, Australia.
[2]CSIRO Marine Research, Hobart, Tasmania, Australia.
[3]Australian Institute of Marine Science, Townsville, Queensland, Australia.

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Guinea followed the LB2000 temperature: calcification relationship. Average annual SSTs for New Ireland (29.5°C) exceed those for Phuket Island (28.7°C).

[7] K05 suggest that the *Porites* temperature: calcification curve is a response to temperature-related changes in Ω_{arag}. We explored the possible contributions that variations in Ω_{arag} would make to the LB2000 relationship by using the recently published global ocean carbon data set [*Key et al.*, 2004] with standard CO_2 dissociation constants. We calculate Ω_{arag} to vary between 3.88 to 4.02 within the temperature range 23–29°C; considerably less than the estimate by K05. 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 LB2000. We also directly determined in situ Ω_{arag} in the western Pacific using measurements of dissolved inorganic carbon (DIC), alkalinity (ALK) and salinity. For latitudes relevant to LB2000, the range of in situ Ω_{arag} is between 3.9 and 4.1 which would vary calcification by ≈24% - again, compared with the observed 340% variation [*calculations and graphs can be obtained from B.I.McN*].

[8] K05 suggest that a "spatially derived relationship should not be applied to temporal predictions" because "changes from one latitude to another likely involve genetic differences between locally adapted (over thousands of years) corals and are thus unrelated to phenotypic changes that would occur within a single individual". Figure 7 in LB2000 does not support this view where this issue was examined; it shows the temporally derived data from *Lough and Barnes* [1997] to fit well with the spatially derived relationship. Further, *Bessat and Buigues* [2001] show a temporal response of *Porites* calcification to changing SST similar to the relationship that we used. The contrast of spatially and temporally-derived SST: calcification data does not bear close examination. Each of the points making up the spatially derived relationship of LB2000 is annual calcification averaged over several years of growth common to a number of different coral colonies. Thus, each point is the resultant of calcification over time, i.e., the resultant of a temporal relationship. It is unlikely that a linear relationship with average annual SST would account for 83% of the variation in average annual calcification if corals at the diverse locations have locally adapted SST: calcification curves with slopes significantly different from that of the overall relationship.

4. Definition of Coral Reef Habitat

[9] MMB04 defined the reef habitat as the oceanic area where SST exceeds 18°C in the control climate simulation. It is true that a more appropriate definition would have included water depth. Unfortunately however, coarse resolution climate models do not sufficiently resolve the shallow water environment from the open ocean. Having a reef habitat with an average baseline SST less than the present day value for the reef environment does not in itself bias our projections since we only use the climate change simulation to project the change in SST from our baseline value. Our definition of reef habitat therefore gives a broad indication of the likely future changes in calcification rate. We believe our projections are more realistic than *Kleypas et al.* [1999], because we explicitly include climate change induced changes in SST, DIC, ALK, salinity and Ω_{arag}, rather than prescribing a uniform warming of 2°C. Our study does not include the "poleward" expansion of the reef habitat with global warming as suggested by K05. It is limited to changes within the present reef habitat.

5. Other Temperature Effects

[10] We noted in our paper that our predictions did not take account of "adverse future effects of coral bleaching". K05 suggest that this is unrealistic. We feel we acted properly by defining the problem addressed by our paper–projected changes in coral reef calcification rate with global warming – and by acknowledging coral bleaching may significantly alter our predictions. There is a sharp contrast between the paucity of recent experimental work relating coral calcification to climate change and the considerable recent work linking other aspects of coral metabolism, especially coral bleaching, to climate change.

6. Conclusion

[11] There can be no doubt that the response of corals, coral reefs and other significant reef organisms to climate variability will be complex. MMB04 took into account factors not previously included in equivalent analyses and obtained a result different from those previously reported. We are aware of uncertainties in our findings. Even so, we feel they provide a useful addition to our understanding of the issue. In our view, they would be useful even if they served only to highlight those uncertainties. To us, the fundamental research question that remains to be answered is, "Can organisms and ecosystems accommodate, acclimatise to or adapt to rising temperatures faster than ocean temperatures may rise?"

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D. J. Barnes, Australian Institute of Marine Science, PMB 3, Mail Centre, Townsville, QLD 4810, Australia.
R. J. Matear, CSIRO Marine Research, GPO Box 1538, Hobart, Tas 7001, Australia.
B. I. McNeil, Centre for Environmental Modelling and Prediction, University of New South Wales, Sydney, NSW 2052, Australia. (b.mcneil@unsw.edu.au)