

Coral reef calcification and climate change: The effect of ocean warming

Ben I. McNeil,¹ Richard J. Matear,² and David J. Barnes³

Received 17 September 2004; revised 13 October 2004; accepted 29 October 2004; published 30 November 2004.

[1] Coral reefs are constructed of calcium carbonate (CaCO₃). Deposition of CaCO₃ (calcification) by corals and other reef organisms is controlled by the saturation state of CaCO₃ 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. Our results suggest that present coral reef calcification rates are equivalent to levels in the late 19th century and does not support previous suggestions of large and potentially catastrophic decreases in the future. **INDEX TERMS:** 1615 Global Change: Biogeochemical processes (4805); 1635 Global Change: Oceans (4203); 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4806 Oceanography: Biological and Chemical: Carbon cycling; 4263 Oceanography: General: Ocean prediction. **Citation:** McNeil, B. I., R. J. Matear, and D. J. Barnes (2004), Coral reef calcification and climate change: The effect of ocean warming, *Geophys. Res. Lett.*, *31*, L22309, doi:10.1029/2004GL021541.

1. Introduction

[2] Calcification is the process by which corals produce calcium carbonate (CaCO₃). Coral reef calcification is predicted to decrease 20–60% by 2100, relative to pre-industrial levels [Kleypas *et al.*, 1999; Müller *et al.*, 2004], due to increases in CO₂ levels in the surface ocean as atmospheric CO₂ rises. Such decreases in calcification would cause loss of reefs because construction rates would fall below natural destruction rates. The CaCO₃ 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 CaCO₃. Most authors have used Ω values for aragonite (Ω_{arag}) as it is the form of CaCO₃ deposited by corals and green algae. [Ca²⁺] is quasi-conservative in the ocean, therefore Ω_{arag} is controlled by variations in the carbonate ion (CO₃²⁻). As CO₂ levels rise in seawater via anthropogenic CO₂ uptake,

pH decreases and the seawater carbonate equilibrium is shifted, reducing dissolved CO₃²⁻ and Ω_{arag} [Kleypas *et al.*, 1999]. Although Ω_{arag} remains super-saturated in tropical surface oceans (>1), reduction of Ω_{arag} has been found to reduce calcification by reef organisms [Gattuso *et al.*, 1999; Langdon *et al.*, 2000; Leclercq *et al.*, 2000, 2002; Marubini *et al.*, 2001, 2003]. On the other hand, coral calcification rates have been found to increase with increasing sea surface temperature (SST) [Bessat and Buigues, 2001; Clausen and Roth, 1975; Coles and Coles, 1977; Kajiwara *et al.*, 1995; Lough and Barnes, 2000; Reynaud-Vaganay *et al.*, 1999]. Lough and Barnes [2000] 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. Extension increased 3.1 mm.yr⁻¹ and annual calcification increased 33% for each 1 °C increase in annual SST (Figure 1). A similar relationship between SST and extension rate in massive *Porites* was found in the South China Sea [Nie *et al.*, 1997]. Additional measurements from 27 massive *Porites* from 5 sites in the Persian Gulf and New Ireland (Papua New Guinea) were also found to follow this calcification-temperature 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]. These observed increases in coral reef calcification with ocean warming are most likely due to an enhancement in coral metabolism and/or increases in photosynthetic rates of their symbiotic algae [Buddemeier *et al.*, 2004] and highlight the need to include SST as well as Ω_{arag} in predicting future changes in coral reef calcification due to the enhanced greenhouse effect.

2. Methodology

[3] To quantify future changes in coral reef calcification, we used projections of ocean warming and Ω_{arag} from a coupled atmosphere-ice-ocean carbon cycle model developed by the Commonwealth Scientific Industrial Research Organisation (CSIRO) [Hirst *et al.*, 1996]. This climate model includes oceanic, sea-ice and biospheric sub-models with oceanic eddy parameterization. The oceanic sub-model included a prognostic ocean carbon cycle model that simulated phosphate, Dissolved Inorganic Carbon (DIC) and alkalinity in the ocean and allowed us to determine future CO₂ uptake by the ocean. Climate change feedbacks on Ω_{arag} were determined from two climate model experiments. The ‘control’ experiment did not include atmospheric warming effects of elevated greenhouse gases in the atmosphere while the ‘climate change’ experiment explicitly included these effects [Matear and Hirst, 1999]. For the

¹Centre for Environmental Modelling and Prediction, School of Mathematics, University of New South Wales, Sydney, New South Wales, Australia.

²CSIRO Marine Research and Antarctic, Climate and Ecosystem CRC, Hobart, Tasmania, Australia.

³Australian Institute of Marine Science, Townsville, Queensland, Australia.

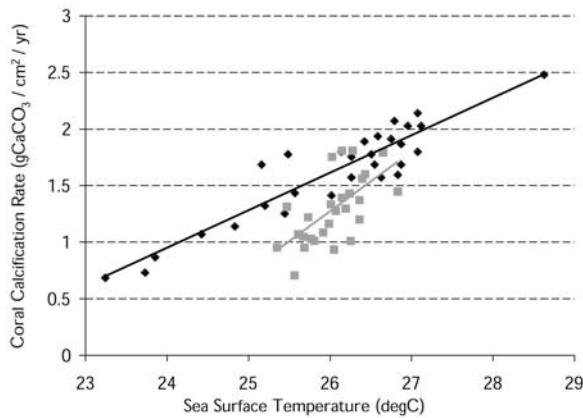


Figure 1. Relationship between annual average SST ($^{\circ}\text{C}$) and coral calcification shown in two separate studies of *Porite* coral colonies where diamonds show the results from Lough and Barnes [2000] and squares from Bessat and Buigues [2001].

climate change experiment, CO_2 levels increased according to atmospheric observations between 1880 to 1995 and followed IS92a projections [Houghton et al., 2001] until the year 2100. The ‘climate change’ experiment included the effects upon Ω_{arag} due to increases in SST and changes in ocean circulation. The climate change feedback on Ω_{arag} was taken as the difference between the ‘climate change’ and ‘control’ experiments.

[4] Changes in coral reef calcification were estimated by combining the output of the climate model with empirical relationships between coral calcification rate and Ω_{arag} and annual SST. The coral reef habitat was defined to be the oceanic area where annual average SST $> 18^{\circ}\text{C}$ [Vaughan, 1919]. Calcification changes in the coral reef habitat due to Ω_{arag} were projected using the observational results of Langdon et al. [Langdon et al., 2000], obtained in a coral reef microcosm, where calcification ($\text{mmol CaCO}_3/\text{m}^2/\text{d}$) = $41.56 \times \Omega_{\text{arag}} - 81.9$. Calcification changes due to SST were projected using the results of Lough and Barnes [Lough and Barnes, 2000] where calcification ($\text{gCaCO}_3/\text{cm}^2/\text{yr}$) = $0.33 \times \text{SST} - 7.07$.

3. Results and Discussion

[5] Our model predicts annual mean SST within the coral reef habitat to increase from $\sim 25^{\circ}\text{C}$ during the 1950s to about 28.2°C in 2100 (Figure 2a). The area of the coral reef habitat expands in association with this ocean warming. In estimating changes in Ω_{arag} and, hence, coral reef calcification since 1880, data for the expanded area of coral reef habitat was not included. The level of warming over the last 50 years from our climate change experiment ($\sim 0.4\text{--}0.5^{\circ}\text{C}$) is comparable to the observed warming within the upper 300 m of the ocean of $\sim 0.3 \pm 0.2^{\circ}\text{C}$ [Levitus et al., 2000] and gives us confidence to exploit the model projections. Furthermore, the current aragonite saturation state within the coral reef habitat was calculated from the global carbon dataset ($\Omega_{\text{arag}} \sim 3.8$) and compares reasonably well with the model result for the same period (Figure 2b). A technique based upon chlorofluorocarbons [McNeil et al., 2003] was used to normalise the carbon observations to 1995, while

standard carbonate dissociation constants [Dickson and Millero, 1987] were used to calculate Ω_{arag} from the in-situ oceanic carbon measurements via the Global Ocean Data Analysis Project [Key et al., 2004].

[6] Previous estimates of future changes to Ω_{arag} have assumed the oceanic CO_2 system to be in steady-state with rising atmospheric CO_2 [Kleypas et al., 1999]. In reality, factors other than the atmospheric concentration of CO_2 influence uptake of atmospheric CO_2 by the oceans. For example, simulations [Matear and Hirst, 1999; Sarmiento et al., 1998] show that sea surface warming and a slowdown in the thermohaline circulation will reduce oceanic storage of anthropogenic CO_2 by as much as 20% by 2100, with warming having the greatest effect. Our simulations suggest these climate change feedbacks cause Ω_{arag} in the coral reef habitat to be $\sim 25\%$ higher in 2100 than estimates based upon steady state models (Figure 2b).

[7] 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.

[8] Lough and Barnes [2000] show an increase in coral reef calcification on the Great Barrier Reef of about 4%

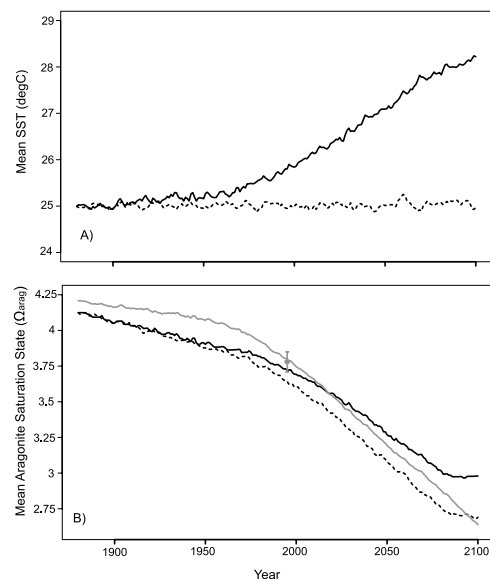


Figure 2. Simulated changes within the coral reef habitat (see methods for description). a) Mean sea surface temperature and b) Mean aragonite saturation state (Ω_{arag}). Dotted line denotes the control experiment while the solid black line denotes the climate change experiment. The observed mean aragonite saturation state for the year 1995 ($\sim 3.8 \pm 0.15$) is also shown. The solid grey line is the aragonite saturation state assuming thermodynamic equilibration with atmospheric CO_2 concentrations (IS92a) with constant alkalinity ($2270 \mu\text{mol}/\text{kg}$) and is used to show the potential bias making such an assumption without considering climate change impacts.

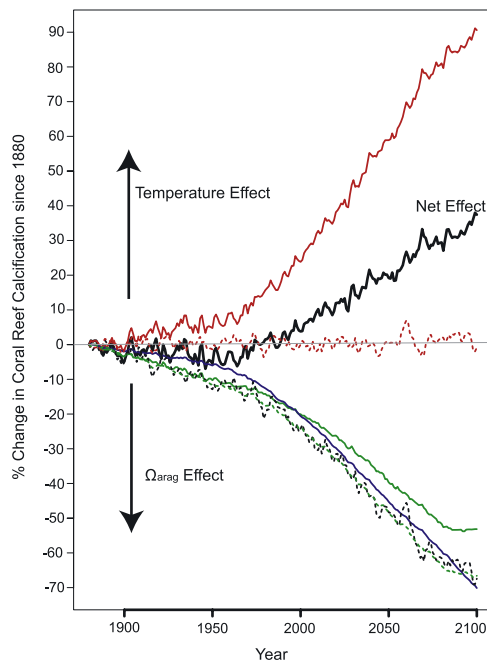


Figure 3. Annual mean percentage change in coral reef calcification relative to pre-industrial levels (1880) for control experiment (dashed lines) and climate change experiment (solid lines). The green lines show the projected changes from variations in aragonite saturation state while the red lines show the projected changes associated with ocean warming. The combined climate change response is shown by the solid black line. For comparison, the solid blue line is equivalent to previous projections [Kleypas *et al.*, 1999; Müller *et al.*, 2004] that calculate Ω_{arag} from thermodynamic equilibration of atmospheric CO_2 .

between 1900 and 1979 which is slightly different to our model results that suggest only minor changes (~ 0 – 1%) for that period. It is important to emphasise however that our results represent an average over the entire coral reef community and therefore cannot be solely compared with results from the Great Barrier Reef. Regional changes to coral reef calcification will vary considerably depending on local CO_2 conditions and ocean warming. It will be important to undertake more specific regional analysis of models so as to better understand future changes to regions such as the Great Barrier Reef. 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 (zooxanthellae) [Hoegh-Guldberg, 1999].

[9] Reefs form because red algae cement together a framework built of coral skeletons and then sediments, mostly created by erosion, green algae and foraminifera, become cemented into cavities in this structure. 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. Although calcification in *Montastrea*, the most significant reef-builder on Atlantic reefs, is much more sensitive to temperature, it seemed appropriate to base our estimates upon *Porites*, the more conservative and most thoroughly documented genus. We used *Porites* temperature sensitivity to estimate changes in rates of coral reef commu-

nity calcification with temperature. There are other data for the temperature sensitivity of calcification in corals and other reef organisms [Clausen and Roth, 1975; Coles and Coles, 1977; Kajiwara *et al.*, 1995; Reynaud *et al.*, 2003] which may suggest the existence of an upper temperature limit for coral reef calcification [Buddemeier *et al.*, 2004]. 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* and *Montastrea* quoted here were obtained from measurements on coral colonies that grew at locations representing a range of temperatures (23°C to 29°C) and showed no declines at high and low temperatures. Despite this observation, the potential existence of a thermal upper limit for other coral species is important in the context of climate change and should be further explored.

4. Conclusion

[10] Observational studies show clearly that increasing SST and decreasing Ω_{arag} have opposing effects for coral reef calcification. We combine output from a climate model with empirical measurements of coral reef calcification with respect to both Ω_{arag} and sea surface temperature (SST) to project coral reef calcification rates under climate change. Our results suggest that climate change will increase the net rate of coral reef calcification significantly by the year 2100 as the effect of ocean warming far outweighs those due to decreases in Ω_{arag} . Our projections may be deemed more realistic than previous projections because they incorporate additional environmental parameters that will change in the future (SST and Ω_{arag}). 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.

[11] **Acknowledgment.** B.I.M was supported through a grant from the Australian Research Council while R.J.M was supported through the Australian Greenhouse Office Climate Change Program.

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B. I. McNeil, Centre for Environmental Modelling and Prediction, School of Mathematics, University of New South Wales, Sydney, NSW 2052, Australia. (b.mcneil@unsw.edu.au)

R. J. Matear, CSIRO Marine Research and Antarctic, Climate and Ecosystem CRC, Hobart, Tas 7001, Australia.

D. J. Barnes, Australian Institute of Marine Science, Townsville, Qld 4810, Australia.

Comment on “Coral reef calcification and climate change: The effect of ocean warming”

J. A. Kleypas,¹ R. W. Buddemeier,² C. M. Eakin,³ J.-P. Gattuso,⁴ J. Guinotte,⁵ O. Hoegh-Guldberg,⁶ R. Iglesias-Prieto,⁷ P. L. Jokiel,⁸ C. Langdon,⁹ W. Skirving,¹⁰ and A. E. Strong¹⁰

Received 28 December 2004; accepted 8 March 2005; published 20 April 2005.

Citation: Kleypas, J. A., et al. (2005), Comment on “Coral reef calcification and climate change: The effect of ocean warming,” *Geophys. Res. Lett.*, 32, L08601, doi:10.1029/2004GL022329.

1. Introduction

[1] *McNeil et al.* [2004] present an analysis indicating that rising sea surface temperature will have a uniformly positive effect on coral calcification over the coming century. The authors claim that this will outweigh the negative effects of declining carbonate ion concentration and result in a substantial increase in net coral reef calcification by the year 2100. We agree that temperature will play an important role in future coral reef calcification; this point is not new, and we find the authors’ statement that “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” to be seriously flawed. Many of their critical assumptions are not supported by existing information on the limits of coral growth and calcification, present day coral reef distributions, and temperature responses. We review their assumptions in the context of this existing knowledge.

2. Combining the Calcification: Temperature and Calcification: Ω_{arag} Relationships

[2] The authors assume that calcification in corals and other reef-building organisms is the sum of two linear responses to temperature and aragonite saturation state (Ω_{arag}). While the response of calcification to Ω_{arag} does

appear to be generally linear with increasing CO_2 [e.g., *Langdon et al.*, 2000; *Leclercq et al.*, 2000], coral response to increasing temperature is not linear. Calcification rates typically increase with temperature, eventually reaching a plateau at or below the normal peak summer temperature, and then decline rapidly beyond that [*Jokiel and Coles*, 1977; *Marshall and Clode*, 2004]. This optimum temperature varies according the ambient temperature of the coral’s environment (summarized by *Marshall and Clode* [2004]). That is, while coral calcification may initially increase with rising temperature, that increase is unlikely to continue throughout a 2–3°C rise.

[3] Many investigators recognize that temperature and CO_2 may interactively affect calcification. However, only one experimental study has been published on the combined effects of temperature and Ω_{arag} on calcification, and the results [*Reynaud et al.*, 2003] do not support the assumption that the calcification responses to temperature and Ω_{arag} are additive. Also, the authors’ assumption that *Porites* calcification is the same as net coral reef calcification is not supported by previous work.

3. The *Porites* Calcification: Temperature Relationship

[4] *McNeil et al.* [2004] largely base their predictions on an excellent dataset of painstakingly measured calcification rates from massive *Porites* cores [*Lough and Barnes*, 2000]. However, this is a calcification:temperature correlation and not a true calcification:temperature curve, as it was derived from corals spanning a range of latitudes with gradients not only in temperature, but also in light and Ω_{arag} , both of which co-vary with temperature [*Kleypas et al.*, 1999a, 1999b; *Gattuso and Buddemeier*, 2000]. For example, carbonate chemistry measurements from their locations are essentially lacking, but a quick estimate of Ω_{arag} across the temperature range they used (23–29°C) is about 3.9–4.7.

[5] In addition, this dataset covers the area where mean annual SST $\sim 27^\circ\text{C}$, with one point between 28–29°C that was obtained from a very different environment. Most of the world’s reefs occur in waters with present-day mean annual SSTs $> 27^\circ\text{C}$ [*Kleypas et al.*, 1999b]. Linear extrapolation of this relationship to higher temperatures is thus not appropriate.

[6] Finally, this spatially derived relationship should not be applied to temporal predictions. Changes from one latitude to another likely involve genetic differences between locally adapted (over thousands of years) corals and

¹National Center for Atmospheric Research, Boulder, Colorado, USA.

²Kansas Geological Survey, University of Kansas, Lawrence, Kansas, USA.

³NOAA/National Climatic Data Center, Boulder, Colorado, USA.

⁴Laboratoire d’Océanographie, CNRS-Univ. Paris VI, Villefranche-sur-mer Cedex, France.

⁵Marine Conservation Biology Institute, Redmond, Washington, DC, USA.

⁶Centre for Marine Studies, Univ. Queensland, St Lucia, Australia.

⁷Universidad Nacional Autónoma de México, Cancún, México.

⁸Hawaii Institute of Marine Biology, Kaneohe, Hawaii, USA.

⁹Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Florida, USA.

¹⁰Satellite Oceanography Division, Office of Research and Applications, National Environmental Satellite, Data, and Information Service, NOAA Science Center, Camp Springs, Maryland, USA.

are thus unrelated to the phenotypic changes that would occur within a single individual.

4. Other Temperature Affects

[7] The authors admit that their analysis ignores the likelihood of coral bleaching. This omission is unrealistic given the history of mass bleaching over the last few decades. Their model produces an average 3°C warming within their defined coral reef habitat, which based on current observations, would likely cause significant coral bleaching [Hoegh-Guldberg, 1999] that, even in corals that survive, causes calcification to slow down or stop. They also fail to consider a body of literature on the negative effects of elevated temperatures (regardless of bleaching) on coral metabolism [Coles and Jokiel, 1977, 1978; Leder et al., 1991; Fitt et al., 2001], reproduction [Szmant and Gassman, 1990], resistance to disease [Harvell et al., 2002], and larval settlement [Jokiel and Guinther, 1978]. All of these factors affect calcification, and including them would overturn the central thesis of McNeil et al. [2004] that ocean warming will lead to increased coral reef calcification by the end of this century.

[8] Also implicit in their analysis is that corals and coral reef communities will adapt/acclimatize to rising temperature. This assumption is overstated, as the mechanisms involved [Rowan, 2004] are likely to apply to a few survivors rather than whole intact communities. Further, it appears likely that the price of high-temperature survival will be a symbiotic coral/algal partnership that is less productive than those adapted to more optimal conditions [Ware et al., 1996; Baker et al., 2004]. Adaptation of coral communities has been documented only on the century-to-millennium time scales of natural climate change [Veron, 1995].

[9] Finally, the authors do not consider that temperature change is unlikely to be smooth and gradual. The IPCC projects that increases in temperature variability will be at least as important as increases in the mean, which for corals could mean more frequent exposure to bleaching-level thermal stress.

5. Definition of Coral Reef Habitat and Comparison With Previous Results

[10] McNeil et al. [2004] define coral reef habitat as the region where SST > 18°C. In reality, reef habitat is confined to a much smaller region (mainly, the additional constraint of water depth < 30 m). Their definition of habitat produces an average baseline temperature of 26°C, which is cooler than the present-day average temperature of reefs (average 27.6°C) [Kleypas et al., 1999b], and likely skews their results, particularly if their model predicts greater warming in the open ocean than in reef areas. Also, their definition of habitat does not take into account that poleward expansion of reef distribution due to warming is limited by other variables [Guinotte et al., 2003].

[11] McNeil et al. [2004] imply that the Kleypas et al. [1999a] estimate of future Ω_{arag} did not take into account temperature and alkalinity feedbacks on the carbonate system. In fact, the Kleypas et al. study included a

comparable temperature rise to that used by McNeil et al., as well as modeled feedbacks on alkalinity.

6. Summary

[12] McNeil et al. [2004] attempt to address an important question about the interactions of temperature and carbonate chemistry on calcification, but their projected values of reef calcification are based on assumptions that ignore critical observational and experimental literature. Certainly, more research is needed to better understand how changing temperatures and carbonate chemistry will affect not only coral reef calcification, but coral survival. As discussed above, the McNeil et al. [2004] analysis is based on assumptions that exclude potentially important factors and therefore needs to be viewed with caution.

[13] **Acknowledgment.** The views, opinions, and findings contained in this report are those of the authors and should not be construed as an official National Oceanic and Atmospheric Administration or U.S. Government position, policy, or decision.

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- J.-P. Gattuso, Laboratoire d’Océanographie, CNRS-Universite Paris VI, BP 28, F-06234 Villefranche-sur-mer Cedex, France.
- J. Guinotte, Marine Conservation Biology Institute, 15805 NE 47th Court, Redmond, WA 98052, USA.
- O. Hoegh-Guldberg, Centre for Marine Studies, University of Queensland, St Lucia, QLD 4072, Australia.
- R. Iglesias-Prieto, Universidad Nacional Autónoma de México, Apartado Postal 1152, Cancún QR 77500, México.
- P. L. Jokiel, Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744, USA.
- J. A. Kleypas, National Center for Atmospheric Research, P.O. Box 3000, Boulder, CO 80307–3000, USA. (kleypas@ucar.edu)
- C. Langdon, RSMAS, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA.
- W. Skirving and A. E. Strong, NOAA/NESDIS/ORR/SO – E/RA3, NOAA Science Center, 5200 Auth Road, Camp Springs, MD 20746–4304, USA.
-
- R. W. Buddemeier, Kansas Geological Survey, University of Kansas, 1930 Constant Avenue, Lawrence, KS 66047, USA.

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. Barnes³

Received 2 February 2005; revised 1 March 2005; accepted 8 March 2005; published 20 April 2005.

Citation: McNeil, B. I., R. J. Matear, and D. J. Barnes (2005), Reply to comment by Kleypas et al. on “Coral reef calcification and climate change: The effect of ocean warming,” *Geophys. Res. Lett.*, 32, L08602, doi:10.1029/2005GL022604.

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 CO₂ 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 CO₂ 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

¹Centre for Environmental Modelling and Prediction, University of New South Wales, Sydney, New South Wales, Australia.

²CSIRO Marine Research, Hobart, Tasmania, Australia.

³Australian Institute of Marine Science, Townsville, Queensland, Australia.

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 CO₂ 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 $\approx 15\%$ 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 $\approx 24\%$ - 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)