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

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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.


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: Ω = [Ca2+]2[CO32-]/Ksp, where Ksp is the solubility coefficient of different forms of CaCO3. Most authors have used Ω values for aragonite (Ωarag) as it is the form of CaCO3 deposited by corals and green algae. [Ca2+] is quasi-conservative in the ocean, therefore Ωarag 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 Ωarag [Kleypas et al., 1999]. Although Ωarag remains super-saturated in tropical surface oceans (>1), reduction of Ωarag 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 (R2 ~ 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 Ωarag 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 Ωarag 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 Ωarag 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
climate change experiment, CO₂ 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 Ωₐrag due to increases in SST and changes in ocean circulation. The climate change feedback on Ωₐrag was taken as the difference between the ‘climate change’ and ‘control’ experiments.

Changes in coral reef calcification were estimated by combining the output of the climate model with empirical relationships between coral calcification rate and Ωₐrag and annual SST. The coral reef habitat was defined to be the oceanic area where annual average SST > 18°C [Vaughan, 1919]. Calcification changes in the coral reef habitat due to Ωₐrag were projected using the observational results of Langdon et al. [Langdon et al., 2000], obtained in a coral reef microcosm, where calcification (mmol CaCO₃/m²/d) = 41.56 × Ωₐrag – 81.9. Calcification changes due to SST were projected using the results of Lough and Barnes [Lough and Barnes, 2000] where calcification (gCaCO₃/cm²/yr) = 0.33 × SST – 7.07.

3. Results and Discussion

Our model predicts annual mean SST within the coral reef habitat to increase from ~25°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 Ωₐrag 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 (~0.4–0.5°C) is comparable to the observed warming within the upper 300 m of the ocean of ~0.3 ± 0.2°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 (Ωₐrag ~ 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 Ωₐrag from the in-situ oceanic carbon measurements via the Global Ocean Data Analysis Project [Key et al., 2004].

Previous estimates of future changes to Ωₐrag have assumed the oceanic CO₂ system to be in steady-state with rising atmospheric CO₂ [Kleypas et al., 1999]. In reality, factors other than the atmospheric concentration of CO₂ influence uptake of atmospheric CO₂ 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 CO₂ by as much as 20% by 2100, with warming having the greatest effect. Our simulations suggest these climate change feedbacks cause Ωₐrag in the coral reef habitat to be ~25% higher in 2100 than estimates based upon steady state models (Figure 2b).

Our results show that changes in coral reef calcification associated with ocean warming outweigh those associated with decreases in Ωₐrag (Figure 3). In our model, coral reef calcification decreases by up to 7% from pre-industrial levels up until 1964 as the CO₂ effects outweighs the temperature effect. After 1964 however, ocean warming far outweighs the CO₂ 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.

Lough and Barnes [2000] show an increase in coral reef calcification on the Great Barrier Reef of about 4%...
We used sensitivity to estimate changes in rates of coral reef community 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; Kaijwara 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

Observational studies show clearly that increasing SST and decreasing \( \Omega_{\text{arag}} \) 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 \( \Omega_{\text{arag}} \) 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 \( \Omega_{\text{arag}} \). Our projections may be deemed more realistic than previous projections because they incorporate additional environmental parameters that will change in the future (SST and \( \Omega_{\text{arag}} \)). There is evidence however to suggest that different corals display different sensitivities to changes in \( \Omega_{\text{arag}} \) 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.

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

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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: $\Omega_{arag}$ 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 ($\Omega_{arag}$). While the response of calcification to $\Omega_{arag}$ 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 $\Omega_{arag}$ on calcification, and the results [Reynaud et al., 2003] do not support the assumption that the calcification responses to temperature and $\Omega_{arag}$ 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 $\Omega_{arag}$, 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 $\Omega_{arag}$ 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°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 $>27$°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
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 Guiñther, 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/algae 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 [Véron, 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 Ωavg 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 proposed 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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Reply to comment by Kleypas et al. on “Coral reef calcification and climate change: The effect of ocean warming”

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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 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 integrates 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: $\Omega_{\text{arag}}$ 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 $\Omega_{\text{arag}}$ 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 $\Omega_{\text{arag}}$ 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 $\Omega_{\text{arag}}$ when holding temperature constant and as such contradicts previous calcification projections from Kleypas and others based solely on $\Omega_{\text{arag}}$. As acknowledged in our paper, we suspect that the effects of both $\Omega_{\text{arag}}$ 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
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 $\Omega_{arag}$. We explored the possible contributions that variations in $\Omega_{arag}$ 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 $\Omega_{arag}$ 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 $\Omega_{arag}$ quoted by Langdon et al. [2000] as an upper limit [cf. Reynaud et al., 2003], we estimate that temperature-related changes in $\Omega_{arag}$ 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 $\Omega_{arag}$ 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 $\Omega_{arag}$ 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 result 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.

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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