

Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef

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Abstract

Temporal and spatial variation in the growth parameters skeletal density, linear extension and calcification rate in massive *Porites* from two nearshore regions of the northern Great Barrier Reef (GBR) were examined over a 16-year study period. Calcification rates in massive *Porites* have declined by approximately 21% in two regions on the GBR ~450 km apart. This is a function primarily of a decrease in linear extension (~16%) with a smaller decline in skeletal density (~6%) and contrasts with previous studies on the environmental controls on growth of massive *Porites* on the GBR. Changes in the growth parameters were linear over time. Averaged across colonies, skeletal density declined over time from 1.32 g cm^{-3} (SE = 0.017) in 1988 to 1.25 g cm^{-3} (0.013) in 2003, equivalent to $0.36\% \text{ yr}^{-1}$ (0.13). Annual extension declined from 1.52 cm yr^{-1} (0.035) to 1.28 cm yr^{-1} (0.026), equivalent to $1.02\% \text{ yr}^{-1}$ (0.39). Calcification rates (the product of skeletal density and annual extension) declined from $1.96 \text{ g cm}^{-2} \text{ yr}^{-1}$ (0.049) to $1.59 \text{ g cm}^{-2} \text{ yr}^{-1}$ (0.041), equivalent to $1.29\% \text{ yr}^{-1}$ (0.30). Mean annual seawater temperatures had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at $\sim 26.7^\circ\text{C}$. There were minor differences in the growth parameters between regions. A decline in coral calcification of this magnitude with increasing seawater temperatures is unprecedented in recent centuries based on analysis of growth records from long cores of massive *Porites*. We discuss the decline in calcification within the context of known environmental controls on coral growth. Although our findings are consistent with studies of the synergistic effect of elevated seawater temperatures and $p\text{CO}_2$ on coral calcification, we conclude that further data on seawater chemistry of the GBR are required to better understand the links between environmental change and effects on coral growth.

Keywords: calcification, climate change, Great Barrier Reef

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Introduction

Massive corals record an environmental history in their calcium carbonate skeletons (Dodge & Vaisnys, 1975). They grow by precipitating calcium carbonate on previously deposited skeleton thereby creating a series of growth bands. The annual nature of the growth bands is well understood (Knutson *et al.*, 1972) as are other

characteristics, including environmental effects on isotopic composition (Gagan *et al.*, 2000; McCulloch *et al.*, 2003), luminescence (Isdale, 1984), and the growth parameters skeletal density, annual extension and calcification rate (Barnes & Lough, 1989). Massive corals of the genus *Porites* are long lived, and distributed widely throughout the Indo-Pacific Ocean, across a range of habitats from turbid inshore to clear offshore waters. Their skeletal records are, therefore, eminently useful as a tool for detecting long-term changes in environmental conditions in tropical ocean surface waters.

Environmental controls on the growth of scleractinian corals include seawater temperature (Jokiel & Coles,

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1978; Highsmith, 1979; Crossland, 1984; Lough & Barnes, 2000), light (Goreau & Goreau, 1959; Bak, 1974; Yentsch *et al.*, 2002), carbonate saturation state (Marubini *et al.*, 2001), water motion (Scoffin *et al.*, 1992; Lesser *et al.*, 1994), and water quality (Marubini & Davies, 1996; Fabricius, 2005). Recent attention has focused on the effects of rising concentrations of atmospheric greenhouse gases due to human activities on corals and coral reefs (Hughes *et al.*, 2003; Lesser, 2004). Rising concentrations of atmospheric greenhouse gases (IPCC, 2001, 2007) have been associated with warming of the tropical oceans, resulting in an increased frequency of mass coral bleaching events since the 1970s (Hoegh-Guldberg, 2005). Concentrations of the principle greenhouse gas CO₂ have risen ~35% in the atmosphere since the late 18th century, presently increasing at about 1% annually. The current concentration of ~379 ppm in 2005 (WMO Greenhouse Gas Bulletin, 2006) is considered to be unprecedented in at least the past 650 000 years (Petit *et al.*, 1999; Siegenthaler *et al.*, 2005). High atmospheric CO₂ leads to increased concentrations of dissolved CO₂ in seawater shifting the seawater carbonate equilibrium towards higher levels of bicarbonate (HCO₃⁻) by CO_{2(aq)} + H₂O + CO₃²⁻ ↔ 2HCO₃⁻. The dissolution of CO₂ reduces pH in ocean surface waters, lowers the availability of carbonate (CO₃²⁻) ions and decreases the calcium carbonate saturation state (Ω), a process called ocean acidification (e.g. Caldeira & Wickett, 2003). Aragonite saturation is predicted to decrease by around 30% by 2050, which is expected to have negative consequences on the growth rates of a range of calcifying biota (Kleypas *et al.*, 1999; Feely *et al.*, 2004; Orr *et al.*, 2005). Although evidence from laboratory experiments has confirmed decreases in calcification rates with reduced aragonite saturation (Gattuso *et al.*, 1998; Langdon *et al.*, 2000; Leclercq *et al.*, 2000; Schneider & Erez, 2006), data from field studies showing long-term declines in coral calcification rates are lacking (Kleypas *et al.*, 1999). The aim of this study was to examine temporal and spatial variation in the growth parameters skeletal density, linear extension and calcification rate in massive *Porites* from two near-shore regions of the Great Barrier Reef (GBR), and to interpret these data in the context of changing environmental conditions.

Materials and methods

Study sites and sampling design

To examine spatial and temporal variation in the coral growth parameters skeletal density, annual extension and calcification rate, we collected 10 colonies of massive *Porites* at each of two coral reefs within each of two

regions (Far Northern and Northern, ~450 km apart; Fig. 1) on the GBR, Australia, in January 2004. In the Far Northern Region, colonies were collected from fringing reefs at Hannah (13°52'S, 143°43'E) and Hay Islands (13°40'S, 143°41'E), and in the Northern Region from High (17°10'S, 146°00'E) and Kent Islands (17°40'S, 146°11'E). The four reefs are located in the coastal zone (i.e. within the 20 m isobath) of the GBR lagoon (Alongi & McKinnon, 2005). Mean annual sea-surface temperature (SST) is ~0.5 °C higher in the Far Northern than in the Northern Region (Rayner *et al.*, 2003). All colonies were ≥30 cm in diameter and were collected from the leeward side of the islands at shallow depths (1–3 m below lowest astronomical tide). In total, 40 colonies were collected during the study but two colonies were excluded due to severe internal bioerosion, leaving a total of 38 colonies for the analysis of growth parameters.

Sclerochronology

The growth parameters skeletal density, annual extension and calcification rate were determined for each colony following procedures described previously (Barnes & Lough, 1989; Chalker & Barnes, 1990; Lough & Barnes, 1990a, b). A slice (~7 mm thick) was cut from the centre of each colony using a large saw with freshwater applied as lubricant, and dried for 12 h at 60 °C. Each slice was then X-rayed using Kodak lanex regular, double-sided emulsion (100 mA, 0.032 s, 45 kV, 150 FFD; Rochester, NY, USA; Supplementary Fig. 1a). The positive X-ray prints were then used to identify two tracks on each colony with clear annual density bands avoiding convolutions in coral growth and bore holes from bioeroders (Lough *et al.*, 1999). Along these tracks, skeletal density was determined with a γ densitometer at 0.25 mm intervals. The X-ray prints were also used to date the annual growth bands based on the assumption that skeleton of greatest density is deposited in summer (Lough & Barnes, 1990a). Once each growth band was dated, it was possible to calculate (i) mean annual skeletal density as the average density between adjacent annual density minima (g cm⁻³); (ii) mean annual extension rate as the linear distance between adjacent annual density minima (cm yr⁻¹); and (iii) mean annual rate of calcification (g cm⁻² yr⁻¹) as the product of skeletal density and annual extension. The three variables were then averaged across the corresponding growth year from the two densitometer tracks (Lough & Barnes, 2000).

SST

SST were obtained for the 1° latitude by longitude box closest to the study locations [centred on 13.5°S, 143.5°E

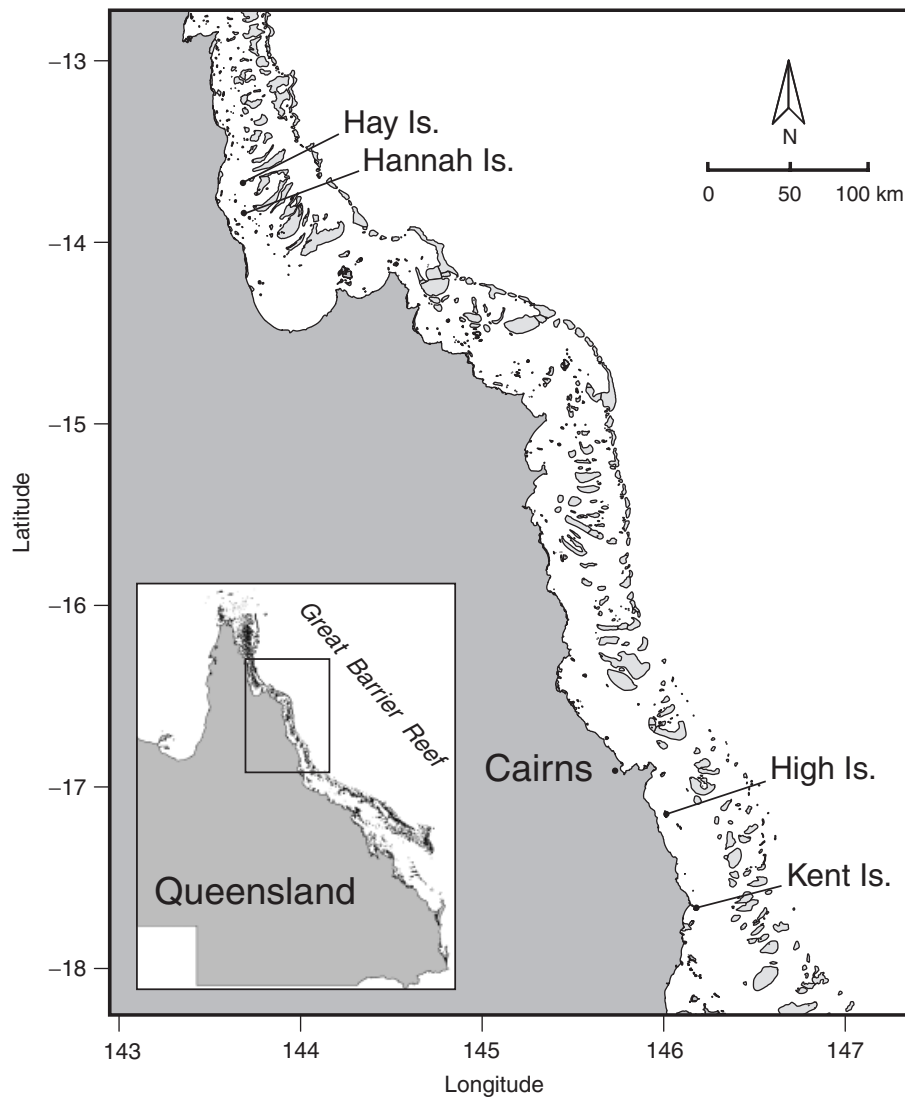


Fig. 1 Map of the Great Barrier Reef, and the reefs for collection of massive *Porites* colonies. Hay and Hannah Islands are in the Far Northern Region, High and Kent Island in the Northern Region of the Great Barrier Reef.

for the Far Northern and 17.5°S, 146.5°E for the Northern GBR, Supplementary material Fig. S1(b)] for 1971–2003 from the global HadISST 1.1 database (<http://www.badc.nerc.ac.uk/data/HadISST/>) (Rayner *et al.*, 2003). Average annual SST corresponding (approximately) to the coral growth years was calculated as arithmetic means of the average monthly values for each box.

Statistical analyses

The statistical analyses investigated how the growth variables (skeletal density, annual extension and calcification rate) varied with year, SST and reef. The age of the annual growth bands in the colonies ranged from

1971 to 2003 [Supplementary material Fig. S1(c)], but there were few bands recorded before 1988, and hence the data selected for analysis focused on the 16-year period from 1988 to 2003. Thus, the data obtained from the 38 colonies were unevenly distributed across years and reefs (Table 1).

The data comprised repeated measures across years on colonies. Such measures are likely to be correlated for individual colonies (Lough & Barnes, 1997), and exploratory data analysis suggested this to be the case (Fig. 2). This correlation was modelled by fitting profiles over time for each of the colonies as part of linear-mixed models analyses (Laird & Ware, 1982; Pinheiro & Bates, 2000). These models comprise fixed and random effects, and a hierarchy of models was explored as follows. For

Table 1 The numbers of colonies observed by (a) year and (b) reef shows the imbalance in the data due to fewer colonies having bands in earlier years

(a)								
Year	1988	1989	1990	1991	1992	1993	1994	1995
<i>n</i>	14	17	19	21	24	28	33	35
Year	1996	1997	1998	1999	2000	2001	2002	2003
<i>n</i>	36	37	38	38	38	38	38	38

(b)				
Reef	Hannah	Hay	High	Kent
<i>n</i>	9	9	10	10

each response, a saturated fixed model was selected initially, and was adequately complex to include all effects of interest. It contained smooth trends over years (natural splines, $df = 4$), smooth effects in SST (natural splines, $df = 4$), reef effects and all first-order interactions between these terms. The random components of the model were then selected based on the Akaike Information Criterion (AIC) with the model fitted by restricted maximum likelihood estimation (Pinheiro & Bates, 2000). This involves calculation of AIC for all models of interest and then choosing the one with the minimum AIC. The random effects considered included combinations of (1) smooth profiles across years (natural splines, $df = 3$), (2) linear profiles over years and (3) random intercepts for each coral. The random effects selected were: (1) for skeletal density, linear trends in years with additive effects of colonies, and (2) for annual extension and calcification rate, only effects of colonies. Once the random structure was selected, the fixed components of the model were assessed for each response. A preliminary analysis showed interactions to be negligible, and only main effects were considered thereafter. For each response, the degree of smoothness for terms involving years and SST were estimated by cross validation (Wood, 2006). The estimates are documented in Table 2. All analyses were done using the statistical program R (R Development Core Team, 2006).

Results

There was significant variation in all three growth parameters among the 38 *Porites* colonies over the period 1988–2003 (Fig. 2). When averaged across colonies, skeletal density declined over time from 1.32 g cm^{-3} ($SE = 0.017$) in 1988 to 1.25 g cm^{-3} (0.013) in 2003, an average annual decline of $0.00475 \text{ g cm}^{-3}$ (0.0017) or $0.36\% \text{ yr}^{-1}$ (0.13) (Fig. 3a). Annual extension declined from 1.52 cm yr^{-1} (0.035) to 1.28 cm yr^{-1} (0.026)

[i.e. $0.0133 \text{ cm yr}^{-1}$ (0.0039) or $1.02\% \text{ yr}^{-1}$ (0.39)]. Consequently, calcification rate declined from $1.96 \text{ g cm}^{-2} \text{ yr}^{-1}$ (0.049) to $1.59 \text{ g cm}^{-2} \text{ yr}^{-1}$ (0.041), equivalent to an annual decline of $0.0243 \text{ g cm}^{-2} \text{ yr}^{-1}$ (0.0051) or $1.29\% \text{ yr}^{-1}$ (0.30). SST had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at $\sim 26.7^\circ\text{C}$ (Fig. 3b). At higher and lower temperatures both parameters declined by $\sim 15\%$ per $^\circ\text{C}$. Differences in coral growth parameters across the four reefs were small when adjusted for temporal trends and regional differences in SST, with marginally lower extension and calcification rates on the two northern reefs compared with the far northern reefs (Fig. 3c).

Discussion

This study has shown that calcification rates in massive *Porites* in two nearshore regions $\sim 450 \text{ km}$ apart on the GBR have declined by 21% over a 16-year study period between 1988–2003. A range of environmental factors known to influence coral growth may have contributed to this decline. Seawater temperature is an important environmental factor controlling coral growth (Highsmith, 1979; Crossland, 1984; Lough & Barnes, 2000). Several laboratory studies have found nonlinear responses in calcification to temperature, with a peak around $25\text{--}26^\circ\text{C}$ and decreasing beyond this range (Jokiel & Coles, 1978; Marshall & Clode, 2004). Our finding of a modal response in coral calcification to SST, with maxima at 26.7°C , suggests a thermal optimum in calcification may occur around this SST also in the field. A previous study has shown that along a latitudinal gradient, long-term average growth rates in *Porites* were related linearly to long-term mean annual SST, with each 1°C increase in SST corresponding to an increase of $0.39 \text{ g cm}^{-2} \text{ yr}^{-1}$ in calcification and 3.1 mm yr^{-1} in annual extension (Lough & Barnes, 2000). The results of that study are not strictly comparable with our results

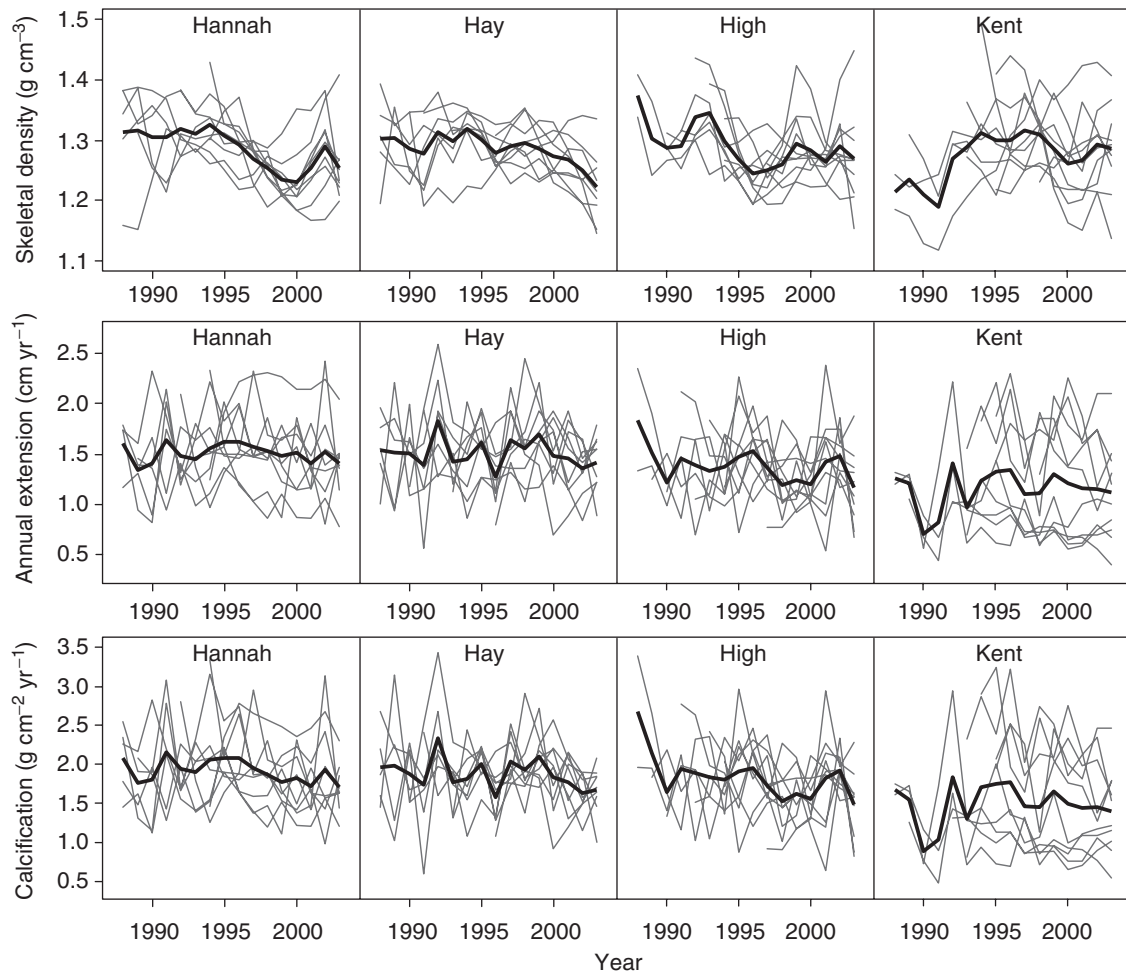


Fig. 2 Temporal profiles for skeletal density, annual extension and calcification rate over years. The grey lines indicate individual corals and the black lines indicate the mean profiles. The variation of annual extension and calcification are large (coefficient of variation, CV = 30.5% and 30.3%, respectively) compared with skeletal density (CV = 9.1%).

since we estimated effects of SST after adjusting for reef (hence latitudinal) effects and temporal trends. However, our finding of a nonlinear relationship of coral growth and temperature adds further evidence to recent arguments (Kleypas *et al.*, 2005) rebutting a prediction of ~35% increase in coral calcification beyond preindustrial levels due to warming oceans (McNeil *et al.*, 2004).

Thermal stress is also an important environmental control on coral growth, occurring with increasing frequency and intensity within recent decades. Increases in SST above the upper thermal limit of corals can have negative physiological consequences on coral energetic reserves (Anthony *et al.*, 2007) and tissue biomass (Fitt *et al.*, 2000). Further, Suzuki *et al.* (2003) found that calcification of massive *Porites* from the GBR declined following the 1998 bleaching event. Mean monthly SST maxima for the Northern and Far North-

Table 2 Cross-validated estimates of smoothness (degrees of freedom) of trends in years and sea-surface temperature for skeletal density, annual extension and calcification.

Model terms	Skeletal density	Annual extension	Calcification
Years	3.00	1.20	1.39
Sea-surface temperature	1.00	3.58	3.11

Estimates were based on linear mixed effects models.

ern Region are 28.87 and 29.13 °C, respectively, for the period 1900–2003 (HadISST dataset). The cumulative number of degree heating months, an index of thermal stress and an extension of the degree heating week indicator (Liu *et al.*, 2003), was 1.33 in the Northern Region in both 1998 and 2002, and 1.06 and 0.88 in the Far Northern Region. Indeed, nearshore reefs in our

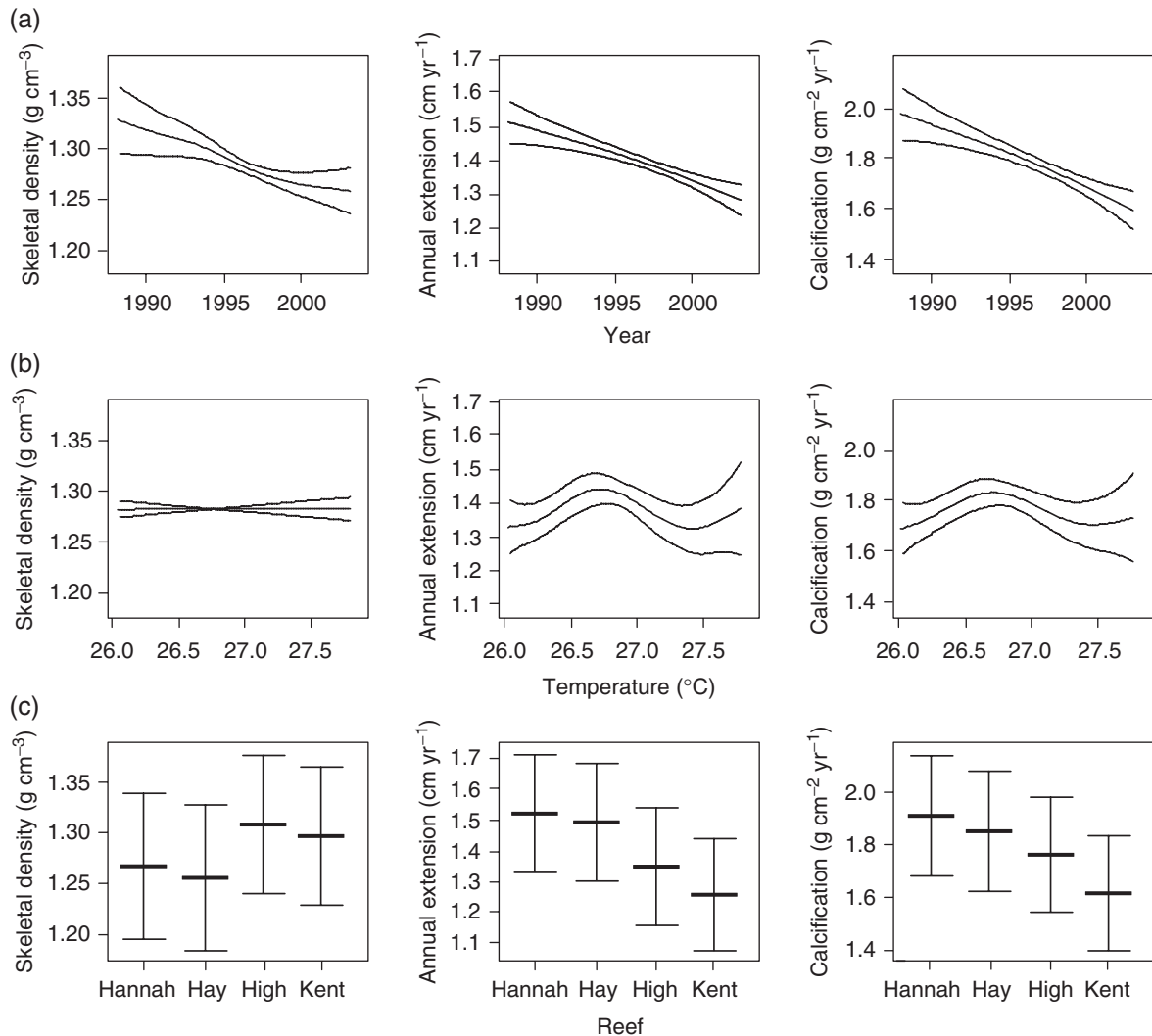


Fig. 3 Partial effects plots showing the estimated dependencies (with 95% confidence intervals) of skeletal density, annual extension and calcification on (a) year, (b) sea surface temperature and (c) reef. Hannah and Hay Island are in the Far Northern Region, High and Kent in the Northern Region of the Great Barrier Reef. Each partial effects plot is adjusted for the effects of the other two explanatory variables.

Northern study area experienced severe (>60% bleached coral cover) bleaching in 1998 and moderate (1–30%) bleaching in 2002 (Berkelmans *et al.*, 2004). Our Far Northern Region was not surveyed in 1998 but experienced major bleaching (i.e. 30–60%) in 2002. Thus, an increasing frequency in thermal stress may in part explain the observed decline in calcification of *Porites* colonies in the northern GBR.

A range of other environmental factors are also known to affect coral growth in particular light and turbidity (Barnes & Chalker, 1990). While the growth parameters in shallow-water massive *Porites* ($n = 245$) along a 9° latitudinal gradient on the GBR were unrelated to surface irradiance (Lough & Barnes, 2000),

linear extension in four species of massive corals decreased along a light gradient from 1 to 30 m water depth (Huston, 1985). Similarly, skeletal density and calcification rate in the coral *Montastraea annularis* increased with decreasing turbidity and sedimentation, while linear extension decreased (Carricart-Ganivet & Merino, 2001) although this may have been a growth response to increasing SST (Carricart-Ganivet, 2004). Wave energy is also an important environmental factor influencing coral growth. Colonies growing in wave-exposed conditions have greater skeletal density and lower linear extension compared with those protected from wave action (Scoffin *et al.*, 1992). In our study, all colonies were sampled on the leeward side of continen-

tal islands. As light, turbidity and waves vary spatially in relation to sediment resuspension by wind on the GBR (Larcombe *et al.*, 1995; Orpin *et al.*, 2004), these factors may have contributed to the marginal differences in coral growth between the four reefs. Dissolved inorganic nutrients and sedimentation can also have negative effects on coral growth (e.g. Ferrier-Pages *et al.*, 2000 and review by Fabricius, 2005). In the Northern Region, land use in catchments has intensified over the last 150 years (predominantly for cattle grazing, and sugarcane and banana cropping, Furnas, 2003). In contrast, the Far Northern Region is sparsely populated, has no cropping and only localized low-density cattle grazing, and hence the amount of pollutants in terrestrial runoff is low compared with the Northern Region (Brodie *et al.*, 2007). Levels of nutrients and turbidity in reef waters are indeed substantially lower in the Far Northern than in the Northern Region (Fabricius & De'ath, 2004). However, the coral growth parameters of this study showed only minor differences between regions after controlling for temperature effects. The observed temporal decline in coral growth in both regions is, therefore, not consistent with changing water quality.

Large-scale interdecadal changes in seawater chemistry may also potentially explain the decline in coral calcification. Currently, the surface waters on coral reefs are supersaturated with the calcium carbonate minerals aragonite and calcite. Given that calcification rates of marine biota are proportional to the saturation state of calcium carbonate, the predicted decline in the saturation of aragonite under various climate change scenarios is cause for considerable concern (Smith & Buddemeier, 1992; Feely *et al.*, 2004). For example, Kleypas *et al.* (1999) estimated that aragonite saturation state (Ω_{arag}) had decreased from preindustrial levels of 4.6 ± 0.2 to current levels of 4.0 ± 0.2 . A further study by Kleypas & Langdon (2002) estimated that the doubling of atmospheric $p\text{CO}_2$ by 2065 would result in a decrease in the concentrations of seawater CO_3^{2-} of $\sim 35\%$. Similarly, Orr *et al.* (2005) predicted that the upper ocean layers at high latitudes would become undersaturated with aragonite by 2050 and further suggested that current carbonate concentrations in tropical surface waters had already declined by $29 \mu\text{mol kg}^{-1}$ ($\sim 10\%$) compared with preindustrial levels.

Recognizing that carbonate chemistry is a key determinant of calcification rates in corals, a number of experiments have reported the effects of manipulating aragonite saturation, pH and $p\text{CO}_2$ on coral growth (Gattuso *et al.*, 1998; Marubini & Atkinson, 1999; Langdon *et al.*, 2000; Leclercq *et al.*, 2000; Marubini *et al.*, 2001). For example, Langdon *et al.* (2000) found a

12-fold increase in coral calcification corresponding to a 55% increase in CO_3^{2-} concentration, while Leclercq *et al.* (2000) also reported linear declines with $\sim 30\%$ decrease in calcification when aragonite saturation decreased from Ω_{arag} 5.4 to 1.3 as a function of increasing $p\text{CO}_2$. Similarly, Schneider & Erez (2006) found that a $\sim 30\%$ decrease in CO_3^{2-} concentration resulted in a $\sim 50\%$ decline in calcification in *Acropora eurystoma*. These and other studies show that lowering aragonite saturation, as a function of increasing concentrations of atmospheric CO_2 , can lead to declines in coral growth.

A 300-year coral core showed that pH varied naturally by 0.3 pH units over ~ 50 -year cycles in the semienclosed lagoon of Flinders Reef (located in oceanic waters 150 km off the GBR in the Coral Sea), which was interpreted in the context of interdecadal climate variability influencing lagoonal flushing by trade winds (Pelejero *et al.*, 2005). Contrary to results from laboratory experiments, the variation in aragonite saturation and pH within the lagoon of Flinders Reef had no apparent effect on calcification in this coral (Pelejero *et al.*, 2005). However, the reconstruction is based on a single coral core in a semienclosed environment, thus limiting generalizations about effects of variations in seawater pH on calcification and on processes in more open regions like the GBR. Indeed, the variation among the temporal profiles of our individual colonies suggests that the observed changes in calcification may not have been detected without the substantial number of colony replicates used in this study.

It is not possible to determine whether the observed decline in calcification was due to changes in seawater chemistry because data on aragonite saturation for the GBR are lacking. However, the atmospheric concentration of CO_2 at Mauna Loa, Hawaii, was 351.44 ppm in 1988 increasing to 375.61 ppm in 2003 (Keeling & Whorf, 2005) representing an increase of 6.4% ($0.40\% \text{ yr}^{-1}$) over the study period. Assuming a Ω_{arag} of 4.0 in 2003 (Kleypas *et al.*, 1999), the increase in atmospheric CO_2 corresponds to an approximate Ω_{arag} of 4.26 in 1988, equivalent to a 6.1% decline in saturation. Experimental evidence suggests the relationship between coral calcification and aragonite saturation is linear (Marubini & Thake, 1999; Langdon *et al.*, 2000; Leclercq *et al.*, 2000; Schneider & Erez, 2006) although some have reported nonlinear responses (Gattuso *et al.*, 1998; Ohde & van Woesik, 1999). Nevertheless, the 21% decline in coral calcification presented here is 3.5-fold greater than is predicted from laboratory studies. The discrepancy between our results and the laboratory and mesocosm studies suggests the existence of some other factors or synergistic mechanisms contributing to the observed decline in coral growth.

Growth records from long cores of massive *Porites* showed that mean calcification was $\sim 4\%$ higher in the 50-year period from 1930 to 1979 compared with the previous 50 years (i.e. 1880–1929, Lough & Barnes, 1997). It was suggested that calcification in some corals might, at least initially, increase with rising SST (Lough & Barnes, 2000; Carricart-Ganivet, 2004) and air temperature (Bessat & Buigues, 2001). Up to 1982, there was no evidence of a size or age-dependent decline in calcification rates in long cores spanning several centuries of growth (Lough & Barnes, 1997). We found a decrease in calcification for the subsequent period between 1988 until 2003, despite a concurrent average SST increase of $0.024 \pm 0.017 \text{ }^\circ\text{C yr}^{-1}$ on the GBR. This suggests that calcification rates in massive corals have decreased in response to changing environmental conditions since the studies by Lough & Barnes (1997, 2000) were completed.

The synergistic effects of elevated seawater temperatures and changing seawater chemistry on coral physiology have only recently gained attention. Calcification in *Stylophora pistillata* declined by 50% in experimental treatments of elevated seawater temperatures and $p\text{CO}_2$ (Reynaud *et al.*, 2003). The long-term effects of the increasing frequency of mass bleaching events, coupled with changing seawater chemistry, on the growth rates of corals on the GBR are poorly understood, but the results of Reynaud *et al.* (2003) provide some insight to the patterns of decline reported here. A recent study suggested that coral calcification should have started declining due to a lowering of aragonite saturation (Kleypas *et al.*, 1999). Here, it has not been possible to assess the observed decline in calcification rates in massive *Porites* in the context of changes in aragonite saturation state as these data are not available for the GBR. However, the existence of a 21% decline in coral calcification in the two study regions is of concern. Given the economic and ecological value of the GBR and other coral reefs around the world, the monitoring of pH and aragonite saturation, coupled with controlled experiments on synergistic effects of increasing SST and a range of water quality variables including aragonite saturation, are required to better understand the links between environmental change and their effects on coral growth.

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Supplementary material

The following material is available for this article online:

Fig. S1. (a) X-ray of a coral slice showing a 33-year growth record for a massive *Porites* from Kent Island in the Northern Region of the Great Barrier Reef, (b) mean annual sea surface temperature for the Northern Region over the same period and (c) calcification rate of the colony. Dashed lines are 95% confidence intervals.

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