

Environmental controls on growth of the massive coral *Porites*

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Abstract

Annual density banding provided growth characteristics for 245 similar-sized, massive colonies of *Porites* from similar locations on 29 reefs from across the length and breadth of the Great Barrier Reef (GBR), Australia. Values obtained were density, extension rate, and calcification rate. Tissue thickness, the depth to which skeletons were occupied by tissue at the time of collection, was also measured. Extension rate, calcification rate, and tissue thickness were significantly greater at the top of colonies than at the sides. Extension rate and calcification rate decreased from north to south along the GBR (latitudinal range of $\sim 9^\circ$) and were significantly and directly related to annual average sea surface temperature (SST; range $\sim 25\text{--}27^\circ\text{C}$). For each 1°C rise in SST, average annual calcification increased by $0.39\text{ g cm}^{-2}\text{ year}^{-1}$ and average annual extension increased by 3.1 mm year^{-1} (c.f. average values of $1.63\text{ g cm}^{-2}\text{ year}^{-1}$ and 12.9 mm year^{-1} , respectively). Density was inversely correlated with extension rate and increased with distance offshore. Data for massive *Porites* colonies from the GBR were extended though 20° of latitude and an average annual SST range of $23\text{--}29^\circ\text{C}$ using published data for the Hawaiian Archipelago (Grigg, R.W., 1981. Coral reef development at high latitudes in Hawaii. Proc. 4th Int. Coral Reef Symp., Manila, Vol. 1, pp. 687–693; Grigg, R.W., 1997. Paleooceanography of coral reefs in the Hawaiian-Emperor Chain — revisited. Coral Reefs 16, S33–S38) and Phuket, Thailand (Scoffin, T.P., Tudhope, A.W., Brown, B.E., Chansang, H., Cheeney, R.F., 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. Coral Reefs 11, 1–11). The response of calcification rate to temperature remained linear. Variation in annual average SST accounted for 84% of the variance. For each 1°C rise in SST, average annual calcification increased by $0.33\text{ g cm}^{-2}\text{ year}^{-1}$ and average annual extension increased by 3.1 mm year^{-1} (c.f. average values of $1.50\text{ g cm}^{-2}\text{ year}^{-1}$ and 11.6 mm year^{-1} , respectively). The sensitivity of calcification rate in *Porites* to SST, combined with observed 20th Century increases in SSTs,

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suggests that calcification rates may have already significantly increased along the GBR in response to global climate change. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Buddemeier and Kinzie (1976) stated that the discovery of annual density banding patterns in massive coral skeletons by Knutson et al. (1972) ‘... rendered almost trivial the previous unsolved problem of measuring long-term growth rates and growth histories retrospectively ...’. These banding patterns allow quantification and dating of average annual growth characteristics for massive coral colonies. Data recovered are skeletal density, linear extension rate and calcification rate. Calcification rate is the product of density and extension rate (see Chalker et al., 1985). Thus, density bands provide records of the performance of massive corals over time and across different environments. Such records allow identification of major environmental controls on coral growth (e.g. Grigg, 1981, 1997; Lough and Barnes, 1992, 1997; Scoffin et al., 1992) and allow projection of possible impacts on coral reef ecosystems of changing climatic conditions as a result of the enhanced greenhouse effect (e.g. Houghton et al., 1996). Records several centuries long (e.g. Hudson, 1981, 1985; Hudson et al., 1994; Lough and Barnes, 1997) allow identification of natural variability and make it possible to recognise unnatural change. Such records have taken on fresh importance with recent concern about possible worldwide degradation of coral reefs (e.g. Ginsburg, 1994; Wilkinson and Buddemeier, 1994; Wilkinson, 1998). Tissue thickness has recently been recognised as an important growth characteristic which affects density banding (Barnes and Lough, 1993; Taylor et al., 1993) and which may respond rapidly to changing environmental conditions (Barnes and Lough, 1992, 1999; True, 1995; Steven, 2000).

Several earlier studies have provided evidence for systematic variations in growth characteristics of the major Indo-Pacific reef-building massive coral *Porites*. Grigg (1981, 1997) used annual density banding to measure extension, density and calcification in colonies of *P. lobata* from 14 reef sites in the Hawaiian Archipelago. Average annual extension and average annual calcification significantly decreased with increasing latitude from 19 to 29°N. Density tended to increase with increasing latitude but the trend was not statistically significant. The decline in calcification rate with increased latitude was attributed to the effects of reduced temperature and, to a lesser extent, reduced light.

Isdale (1981, 1983) used annual density banding to measure average annual extension in over 400 colonies of massive *Porites* from the Great Barrier Reef (GBR). Average annual extension in colonies collected at ~15.5°S was significantly higher than in colonies collected at ~19.0°S. Average annual extension was lowest in colonies at exposed sites within reefs and decreased with distance offshore. Isdale concluded that extension rate decreased with increasing water motion. Risk and Sammarco (1991) measured average skeletal density in *P. lobata* from nine reefs in the central GBR

between ~ 18.5 and $\sim 19.5^\circ\text{S}$. They found that average skeletal density significantly increased with increasing distance across the 75 km wide continental shelf. They suggested this increase in density reflected an inshore to offshore increase in calcification rate and concluded that calcification rate might be inhibited by higher nutrients in inshore waters or enhanced by greater availability of light offshore. Lough and Barnes (1992) also found a significant increase in average skeletal density in massive *Porites* from inshore to offshore on three reefs in the central section of the GBR. However, average annual extension and average annual calcification decreased from inshore to offshore. This finding emphasises the importance of examining all three coral growth variables obtained from skeletal density banding (Dodge and Brass, 1984).

Scoffin et al. (1992) examined extension, density and calcification in massive colonies of *P. lutea* from 11 fringing reefs in the Phuket region, South Thailand. They found an inverse relationship between average skeletal density and extension rate. They also found that average density increased and extension rate decreased along an environmental gradient of increasing ‘hydraulic energy’ (a measure of water motion due to waves and tidal currents). In contrast to the trends described for the GBR and Thailand, Tomascik et al. (1994) demonstrated that average annual extension of massive *P. lutea* in Jakarta Bay, Indonesia increased with increased distance from shore over about 50 km. This result came from a reanalysis of data previously reported by Scoffin (1986). The increase in extension rate was attributed to an increase in water clarity with distance from shore.

In summary, average annual extension, the most frequently measured growth characteristic, decreased with distance from shore on the GBR and in Thailand but increased with distance from shore in Jakarta Bay. Average skeletal density varied inversely with extension rate. Average skeletal density increased with distance from shore on the GBR and in Thailand but showed no clear relationship with latitude along the Hawaiian Archipelago. Average annual calcification decreased with increasing latitude along the Hawaiian Archipelago and decreased with distance offshore on the GBR but showed no relationship with inshore–offshore environmental gradients in Thailand.

In this study we present growth characteristics for 245 similar-sized massive colonies of *Porites* from 29 reef sites located along the length and across the width of the GBR, providing baseline growth data for this important reef-building coral. These data are used to test for systematic variations in *Porites* growth characteristics along the two main environmental gradients on the GBR; latitude and distance across the continental shelf. We combine these with published data to develop a more generalized model of environmental controls, notably temperature, on *Porites* growth in the Indo-Pacific region.

2. Materials

2.1. Coral growth data

Whole colonies of massive *Porites* between 0.2 and 0.5 m in height were collected

from depths of 3–5 m relative to mean low water spring tide levels from 29 reefs on the Great Barrier Reef (GBR, Fig. 1). Colonies were collected from similar environments on each reef — towards the rear of the windward reef flat and on sheltered parts of fringing reefs in the lee of islands. Between six and 15 colonies were collected from each site to give a total of 307 colonies (see Lough et al., 1999).

Colonies were cut vertically into halves with a chain saw fitted with a masonry blade. Fresh water was played onto the blade during cutting. One half of a colony was placed on the moveable bed of a circular saw and at least two 6–7-mm thick slices were removed from vertical planes close the centre of the whole colony. The circular saw blade was lubricated by fresh water. Slices were air-dried and X-radiographed. X-ray positives were used to select two tracks on each slice along which to measure density. These tracks were positioned where the density banding pattern was best displayed and where there was least interruption and distortion of the pattern by macro-architectural

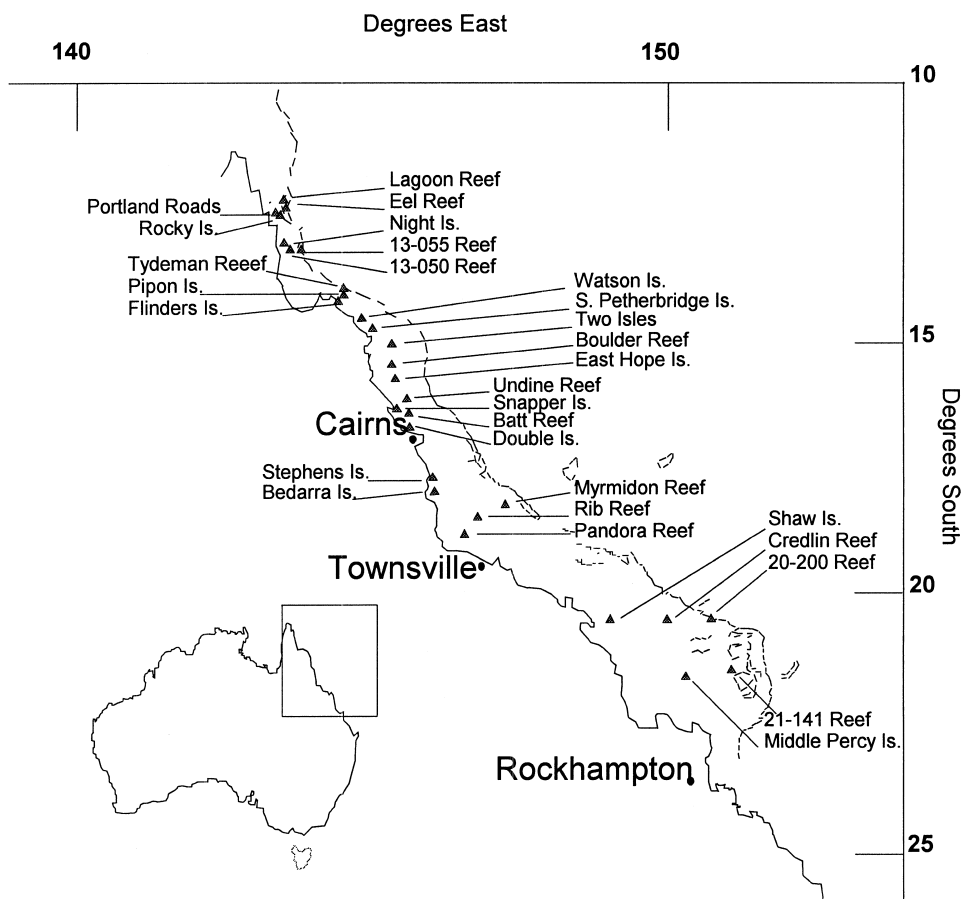


Fig. 1. Map of Great Barrier Reef showing locations of 29 reefs from which corals were collected.

skeletal features, bore holes, cracks and other imperfections. Both tracks started near the origin of the colony. One was close to the vertical growth axis and the other was horizontal or near horizontal (see Lough and Barnes, 1990a). Density was measured along each track with a gamma densitometer (Chalker and Barnes, 1990) having a 4-mm diameter gamma-ray beam (Lough and Barnes, 1990b). A data series of absolute density vs. distance was generated for each track. It was assumed that skeleton of highest density was formed in (austral) mid-summer (see Lough and Barnes, 1990a, 1992). Successive density peaks were then dated backwards from the date of collection of a colony. Of the 307 coral colonies originally collected, 62 were rejected for further analysis because of problems with dating or because the density record was too short (see Barnes et al., 1989; Barnes and Lough, 1990).

The following variables were obtained for the two densitometer tracks for the 245 remaining coral colonies. Each dated year represented the time between successive density peaks.

1. Annual average density (g cm^{-3})
2. Annual extension rate (mm year^{-1})
3. Annual calcification rate determined as the mass of CaCO_3 deposited per unit area per year ($\text{g cm}^{-2} \text{year}^{-1}$ — the product of annual average density and annual extension rate)

The three variables were then averaged for each track for the period 1979–1986, which was common to all 245 colonies.

Skeletal slices were not bleached and coral tissue remained as a dark band around the outside of slices. The thickness of this dark band was the depth to which skeleton was occupied by tissue at the time the colony was collected (tissue thickness, mm; Barnes and Lough, 1992). Effective tissue thickness was also determined by dividing tissue thickness by average annual extension to provide a measure of the time (year) that skeleton was covered by tissue (see Taylor et al., 1993).

The 245 colonies collected comprised *Porites lobata*, *P. lutea*, *P. australiensis* and *P. solida*; the four massive species of *Porites* from the Indo-Pacific and *P. mayeri*, a massive species of *Porites* known only from the GBR (Veron, 1986). The only growth parameter which shows a significant difference with species is average density. This is significantly higher in *P. solida* compared with the other four species (Lough et al., 1999). As colonies of *P. solida* comprised less than 5% of the total analysed (see Table 1), it was considered reasonable to combine growth data from all five species in subsequent analyses.

2.2. Environmental data.

Sea surface temperatures (SSTs; °C) were obtained from the GOSTAPlus data set (Version GIST 2.2) produced by the United Kingdom Meteorological Office in collaboration with the Massachusetts Institute of Technology and the Physical Oceanography Distributed Active Archive Center. Monthly data for the GBR region were

Table 1
Number of colonies by species for 245 *Porites* used in analysis

Reef	Latitude (°S)	No. colonies	<i>P. lobata</i>	<i>P. lutea</i>	<i>P. australiensis</i>	<i>P. mayeri</i>	<i>P. solida</i>
Lagoon	12.38	12	5	7	0	0	0
Eel	12.50	13	5	3	2	1	2
Portland Roads	12.60	4	3	1	0	0	0
Rocky Is.	12.60	5	3	1	0	1	0
Night Is.	13.18	12	5	4	2	0	1
13-055	13.30	14	8	3	1	1	1
13-050	13.33	9	5	4	0	0	0
Tydemman	14.00	6	1	3	1	1	0
Pipon Is.	14.12	6	5	1	0	0	0
Flinders Is.	14.15	7	2	2	3	0	0
Watson Is.	14.47	10	8	1	0	1	0
S. Petherbridge Is.	14.73	6	1	1	3	1	0
Two Isles	15.03	9	8	0	1	0	0
Boulder	15.42	6	4	2	0	0	0
E. Hope Is.	15.73	9	9	0	0	0	0
Undine	16.12	5	3	1	1	0	0
Snapper Is.	16.29	8	7	0	0	1	0
Batt	16.38	10	9	1	0	0	0
Double Is.	16.73	7	5	2	0	0	0
Stephens Is.	17.73	10	4	5	0	1	0
Bedarra Is.	18.00	7	6	1	0	0	0
Myrmidon	18.27	9	3	3	0	0	3
Rib	18.48	9	4	3	0	0	2
Pandora	18.80	7	2	3	0	2	0
Shaw Is.	20.45	5	2	0	1	2	0
20-200	20.50	9	7	0	1	0	1
Credlin	20.53	11	6	2	1	2	0
21-141	21.52	14	2	7	2	2	1
Middle Percy Is.	21.65	6	2	3	1	0	0
% of total			54.7	26.1	8.2	6.5	4.5

available for 1903–1994. These data are averages of SST measurements in 1°-latitude-by-longitude squares made by ‘ships of opportunity’, supplemented in recent years by Automatic Weather Stations and buoys (see Bottomley et al., 1990). Annual average SSTs were obtained for the common growth period for the 1°-latitude-by-longitude square associated with each of the 29 reef sites.

Incoming solar radiation (W m^{-2}) data were obtained from the International Satellite Cloud Climatology Project (ISCCP; available from <http://ingrid.ldgo.columbia.edu/>). These estimates are derived from satellite measurements of cloud and atmospheric optical properties. Monthly values of incoming solar radiation were available from July 1983 through June 1991. Average annual incoming solar radiation was obtained for the period 1984–1990 for the 2.5°-latitude-by-longitude square associated with each of the 29 reef sites.

3. Results

3.1. Variation with growth axis

The 245 colonies were generally hemispherical in shape but somewhat wider than they were tall. The average height:width ratio was 0.82 (S.D. = 0.17). Tissue thickness, extension rate and calcification rate were all significantly higher along the vertical growth axis than along the horizontal growth axis (averaging 11, 16 and 15% higher, respectively; Table 2). Effective tissue thickness was slightly, yet significantly, higher along the horizontal growth axis than the vertical growth axis. There was no significant difference in average skeletal density between the vertical and horizontal growth axes. All subsequent analyses are based on average values for the vertical growth axis. Data for this axis dominate published results.

3.2. Relationships between growth variables

Average annual density was significantly and inversely related to average annual extension (Fig. 2a, $r = -0.47$, $p < 0.00$, $n = 245$). Average annual extension was significantly related to average annual calcification (Fig. 2b, $r = 0.88$, $p < 0.00$, $n = 245$). Although used to calculate average annual calcification, average annual density was not significantly related to average annual calcification (Fig. 2c, $r = -0.02$, $p = 0.78$, $n = 245$). Thus, variations in calcification rate were mostly caused by variations in extension rate. Tissue thickness was not significantly correlated with density, extension or calcification. Density was the most conservative growth variable. The standard deviation for average density was typically $< 15\%$ of the average for all 245 colonies (Table 3). Tissue thickness, average annual extension and average annual calcification showed greater variability; standard deviations were about 25% of the averages across all colonies.

Table 2

Comparisons of average (± 1 S.D.) growth characteristics for vertical and horizontal tracks across 245 coral colonies^a

Variable	Vertical growth axis	Horizontal growth axis	Difference	Degrees of freedom	<i>t</i> -value	<i>p</i>
Tissue thickness (mm)	5.3 \pm 1.3	4.6 \pm 1.2	0.7 \pm 1.1	236	9.56	<0.000
Effective tissue thickness (year ⁻¹)	0.44 \pm 0.16	0.46 \pm 0.18	-0.02 \pm 0.11	229	2.20	0.029
Density (g cm ⁻³)	1.28 \pm 0.16	1.29 \pm 0.15	-0.01 \pm 0.1	233	-1.16	0.248
Extension (mm year ⁻¹)	13.0 \pm 3.4	10.9 \pm 3.2	2.1 \pm 2.3	233	13.67	<0.000
Calcification (g cm ⁻² year ⁻¹)	1.63 \pm 0.38	1.38 \pm 0.38	0.25 \pm 0.30	233	12.79	<0.000

^a *t*-values and probabilities for significant differences between the two tracks based on comparisons of dependent samples are also given.

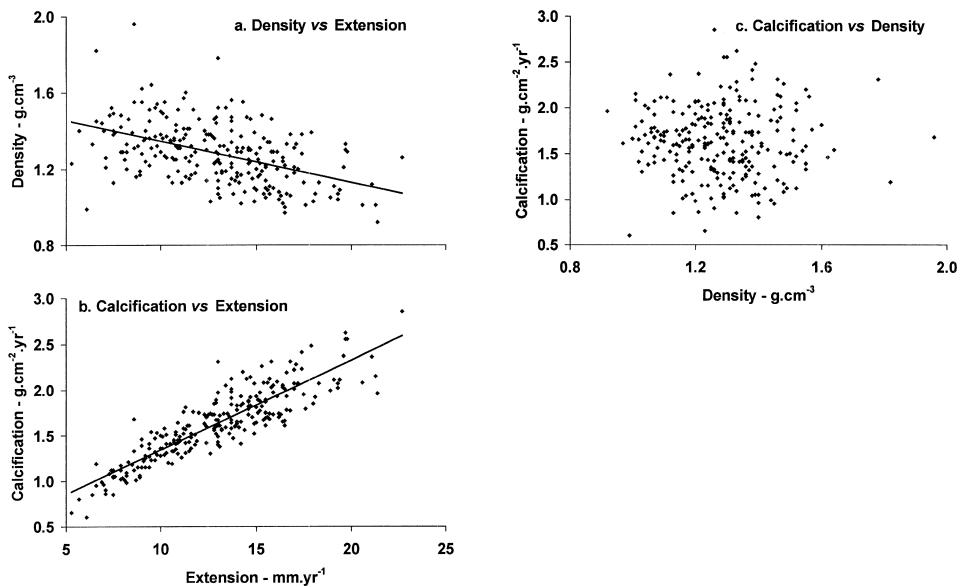


Fig. 2. Scatter diagrams of average growth data for the 245 GBR colonies for the period 1979–1986. (a) Density vs. extension, (b) calcification vs. extension, and (c) calcification vs. density. Regression lines are shown where two growth parameters are significantly linked.

3.3. Variations with latitude and position on shelf

Relationships between *Porites* growth characteristics and environmental gradients were examined using average data for all colonies collected at a reef (Table 4). Two environmental gradients dominate on the Great Barrier Reef (GBR); north to south and inshore to offshore (e.g. Done, 1982; Wilkinson and Cheshire, 1988). The 29 reefs lay along inshore–offshore transects in the northern, central and southern sections of the GBR (Fig. 1). There was a significant correlation between distance offshore and latitude for the 29 reefs ($r = 0.65$, $p < 0.00$, $n = 29$) because the continental shelf widens from about 40 km in the north to about 180 km in the south. Consequently, the distance of a

Table 3

Average (± 1 S.D.) growth characteristics and maximum and minimum values for 245 *Porites* colonies from the Great Barrier Reef

Variable	Average	Minimum	Maximum
Height (m)	0.36 ± 0.94	0.17	0.70
Width (m)	0.45 ± 1.01	0.22	0.92
Height:width ratio	0.82 ± 0.17	0.43	1.53
Tissue thickness (mm)	5.3 ± 1.3	2.4	10.1
Effective tissue thickness (year^{-1})	0.44 ± 0.16	0.15	1.15
Density (g cm^{-3})	1.28 ± 0.16	0.92	1.96
Extension (mm year^{-1})	12.9 ± 3.4	5.3	22.7
Calcification ($\text{g cm}^{-2} \text{ year}^{-1}$)	1.63 ± 0.38	0.60	2.85

Table 4

Average growth characteristics (± 1 S.D.) for the 29 reefs on the GBR based on a common time-period of 1979–1986

Reef	Latitude (°S)	Distance across shelf (%)	Tissue thickness (mm)	Effective tissue thickness (year ⁻¹)	Density (g cm ⁻³)	Extension (mm year ⁻¹)	Calcification (g cm ⁻² year ⁻¹)
Lagoon	12.38	100	5.9 \pm 1.0	0.52 \pm 0.13	1.48 \pm 0.09	11.8 \pm 2.2	1.73 \pm 0.31
Eel	12.50	33	6.2 \pm 0.8	0.44 \pm 0.11	1.32 \pm 0.13	14.9 \pm 3.9	1.95 \pm 0.46
Portland Roads	12.60	0	5.5 \pm 0.3	0.34 \pm 0.09	1.20 \pm 0.12	16.7 \pm 3.3	2.00 \pm 0.46
Rocky Is.	12.60	2	4.2 \pm 1.1	0.27 \pm 0.06	1.32 \pm 0.10	15.5 \pm 1.0	2.05 \pm 0.21
Night Is.	13.18	15	4.6 \pm 0.9	0.40 \pm 0.13	1.36 \pm 0.10	11.9 \pm 2.2	1.60 \pm 0.28
13-055	13.30	48	5.3 \pm 0.7	0.40 \pm 0.07	1.30 \pm 0.09	13.6 \pm 2.6	1.76 \pm 0.37
13-050	13.33	100	5.6 \pm 0.8	0.39 \pm 0.08	1.35 \pm 0.10	14.5 \pm 2.2	1.96 \pm 0.34
Tydemann	14.00	42	5.1 \pm 1.0	0.41 \pm 0.12	1.25 \pm 0.12	12.6 \pm 1.8	1.57 \pm 0.15
Pipon Is.	14.12	11	5.5 \pm 1.0	0.35 \pm 0.06	1.25 \pm 0.11	16.1 \pm 1.7	1.99 \pm 0.11
Flinders Is.	14.15	23	6.7 \pm 1.9	0.58 \pm 0.22	1.19 \pm 0.09	12.3 \pm 3.4	1.48 \pm 0.46
Watson Is.	14.47	32	4.3 \pm 0.7	0.29 \pm 0.07	1.25 \pm 0.15	14.8 \pm 2.3	1.83 \pm 0.24
S. Petherbridge Is.	14.73	15	6.0 \pm 2.4	0.41 \pm 0.23	1.15 \pm 0.10	16.1 \pm 3.7	1.82 \pm 0.30
Two Isles	15.03	26	5.3 \pm 0.7	0.44 \pm 0.10	1.22 \pm 0.10	12.5 \pm 2.5	1.51 \pm 0.23
Boulder	15.42	26	5.5 \pm 1.0	0.42 \pm 0.10	1.21 \pm 0.10	13.6 \pm 3.0	1.63 \pm 0.31
E. Hope Is.	15.73	21	6.0 \pm 1.1	0.38 \pm 0.08	1.18 \pm 0.13	16.0 \pm 1.3	1.88 \pm 0.24
Undine	16.12	45	6.1 \pm 0.8	0.49 \pm 0.09	1.29 \pm 0.08	12.5 \pm 1.5	1.61 \pm 0.25
Snapper Is.	16.29	4	5.3 \pm 1.3	0.33 \pm 0.09	1.10 \pm 0.07	16.5 \pm 2.6	1.81 \pm 0.32
Batt	16.38	41	5.0 \pm 1.2	0.39 \pm 0.14	1.28 \pm 0.13	13.5 \pm 2.5	1.71 \pm 0.22
Double Is.	16.73	2	6.0 \pm 0.9	0.39 \pm 0.07	1.11 \pm 0.11	15.7 \pm 3.1	1.70 \pm 0.23
Stephens Is.	17.73	12	4.5 \pm 0.8	0.36 \pm 0.11	1.16 \pm 0.12	13.1 \pm 2.4	1.50 \pm 0.18
Bedarra Is.	18.00	9	4.4 \pm 1.3	0.33 \pm 0.15	1.14 \pm 0.13	14.8 \pm 3.8	1.65 \pm 0.32
Myrmidon	18.27	100	5.3 \pm 1.5	0.65 \pm 0.21	1.55 \pm 0.21	8.3 \pm 1.2	1.28 \pm 0.22
Rib	18.48	51	7.3 \pm 1.3	0.63 \pm 0.19	1.42 \pm 0.18	12.2 \pm 2.7	1.70 \pm 0.33
Pandora	18.80	15	6.0 \pm 1.0	0.48 \pm 0.15	1.34 \pm 0.21	13.4 \pm 3.6	1.72 \pm 0.28
Shaw Is.	20.45	10	5.2 \pm 0.3	0.61 \pm 0.17	1.28 \pm 0.09	9.2 \pm 3.2	1.16 \pm 0.31
20-200	20.50	99	5.1 \pm 1.4	0.52 \pm 0.17	1.33 \pm 0.15	10.4 \pm 2.9	1.35 \pm 0.27
Credlin	20.53	61	4.2 \pm 1.0	0.50 \pm 0.14	1.28 \pm 0.13	8.8 \pm 2.1	1.11 \pm 0.19
21-141	21.52	68	4.3 \pm 0.8	0.47 \pm 0.13	1.30 \pm 0.12	9.4 \pm 2.2	1.21 \pm 0.24
Middle Percy Is.	21.65	38	5.2 \pm 1.5	0.64 \pm 0.29	1.24 \pm 0.13	9.4 \pm 3.5	1.19 \pm 0.50

reef from the coast was expressed as a percentage of the width of the shelf at that latitude. Percentage distances across the shelf were not significantly correlated with latitude ($r = 0.18$, $p = 0.36$, $n = 29$) showing that these were independent variables.

Tissue thickness showed no systematic variation with percent distance across the shelf or latitude (Fig. 3a). Effective tissue thickness showed a significant increase with percent distance across the shelf (Fig. 3b; $r = 0.47$, $p = 0.01$, $n = 29$) and increase in latitude ($r = 0.53$, $p < 0.00$, $n = 29$). Average skeletal density did not vary with latitude ($r = 0.01$, $p = 0.98$, $n = 29$) but increased significantly with percent distance across the shelf (Fig. 3c; $r = 0.71$, $p < 0.00$, $n = 29$). Average annual extension decreased significantly with both increase in latitude ($r = -0.65$, $p < 0.00$, $n = 29$) and increase in percent distance across the shelf (Fig. 3d; $r = -0.56$, $p < 0.00$, $n = 29$). Average annual calcification decreased significantly with increasing latitude ($r = -0.79$, $p < 0.00$, $n = 29$) but was not significantly related with percent distance across the shelf ($r = -0.32$, $p = 0.09$, $n = 29$; Fig. 3e).

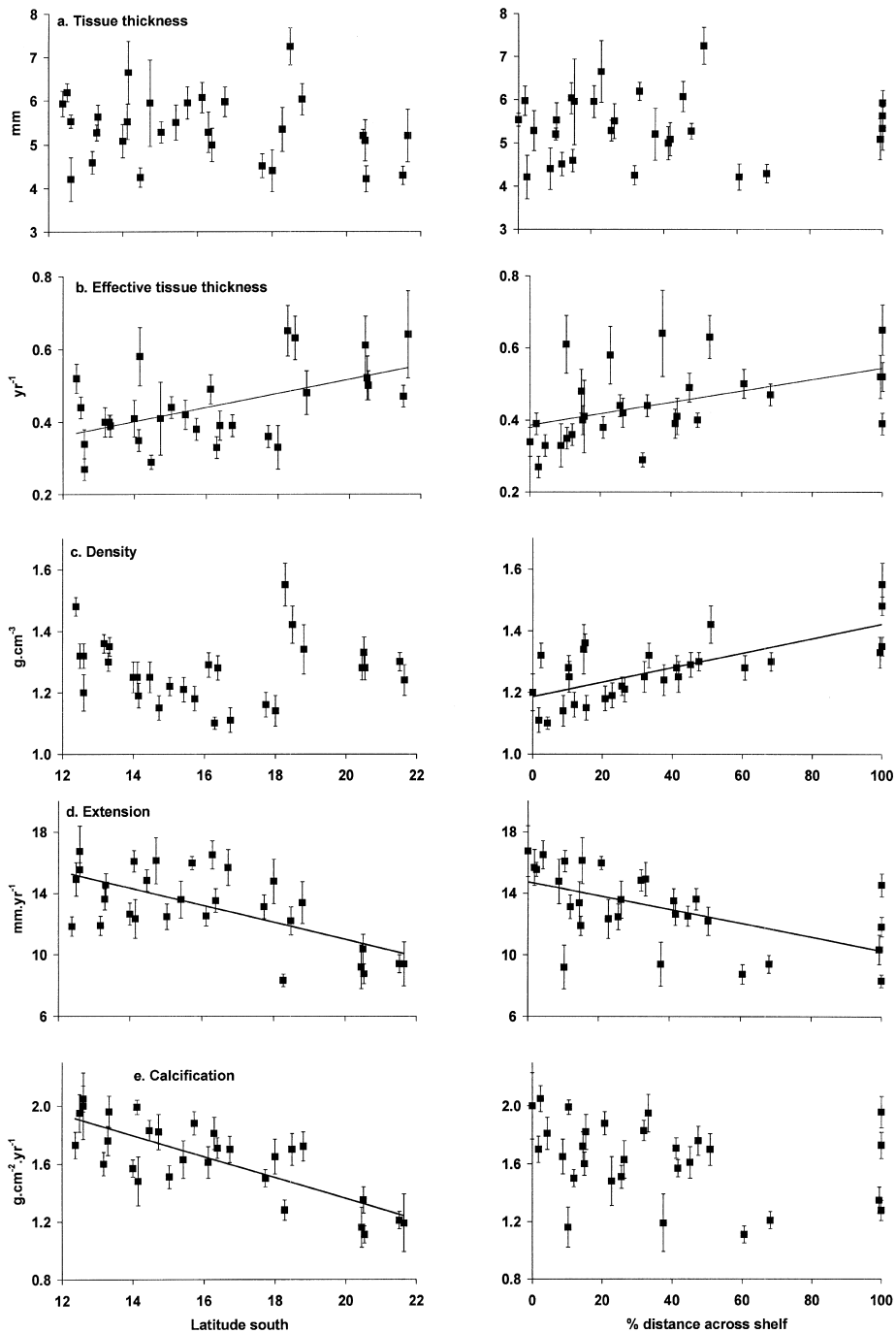


Fig. 3. Values (\pm S.E.) averaged across colonies from each of the 29 GBR reefs for (a) tissue thickness, (b) effective tissue thickness, (c) density, (d) extension, and (e) calcification plotted against latitude south (left) and % distance across shelf (right). Regression lines are shown where there is a statistically significant link.

3.4. Linkages with environmental variables

Average annual extension and average annual calcification for the 29 reefs decreased significantly with increased latitude. Both average annual sea surface temperature (SST) and average annual incoming solar radiation significantly decreased with increase in latitude ($r = -0.98$, $p < 0.00$, $r = -0.65$, $p < 0.00$, respectively). The relationship between solar radiation and latitude was not as strong as that between SST and latitude because incoming solar radiation is reduced in the northern GBR due to greater average cloud cover (see, for example, Fig. 7 in Lough, 1998).

Average annual calcification was significantly correlated with average annual SST ($r = 0.84$, $p < 0.00$) and average annual incoming solar radiation ($r = 0.59$, $p < 0.00$). Partial correlations showed that average annual calcification was significantly correlated with annual average SST (partial $r = 0.74$, $p < 0.00$, allowing for the relationship with solar radiation) but not with average annual incoming solar radiation (partial $r = 0.10$, $p = 0.62$, allowing for the relationship with SST). Similarly, average annual extension was significantly correlated with average annual SST ($r = 0.72$, $p < 0.00$) and with average annual incoming solar radiation ($r = 0.58$, $p < 0.00$). Partial correlations showed that extension was significantly correlated with average annual SST (partial $r = 0.55$, $p < 0.00$, allowing for the relationship with solar radiation) but not with average annual solar radiation ($r = 0.22$, $p = 0.26$, allowing for the relationship with SST). Thus the decrease of average annual extension and average annual calcification in *Porites* colonies with increased latitude on the GBR was primarily due to a decrease in average annual SST.

The linear regression between average annual extension and average annual SST [extension = $3.11(\text{SST}) - 69.02$] explained 52% of the variance ($F_{[1,27]} = 29.33$, $p < 0.00$). Average annual extension in massive *Porites* on the GBR increased by 3.1 mm year^{-1} for each 1°C rise in annual average SST. The multiple regression of extension against average annual SST and % distance across the shelf explained 69% of the variance ($F_{[2,26]} = 28.56$, $p < 0.00$).

The linear regression between average annual calcification and average annual SST [calcification = $0.39(\text{SST}) - 8.60$] on the GBR explained 70% of the variance ($F_{[1,27]} = 62.90$, $p < 0.00$). Thus, a 1°C rise in average annual SST increased average annual calcification by $0.39 \text{ g cm}^{-2} \text{ year}^{-1}$.

3.5. Environmental controls on *Porites* growth characteristics of the Indo-Pacific

The above relationships between variations in *Porites* growth characteristics at 29 reef sites on the GBR cover a latitudinal range from ~ 12 – 22°S and an average annual SST range from ~ 25 – 27°C . These average characteristics were combined with previously published measurements of density, extension and calcification for Hawaii (Grigg, 1981, 1997) and Thailand (Scoffin et al., 1992). The combined data describe average *Porites* growth characteristics for 44 reef sites with a latitudinal range from 8 to 29° . The range of average annual SST was from 23.1 – 28.7°C and the range of average annual incoming solar radiation was from 221 – 254 W m^{-2} .

For the 44 reef sites, average annual extension was significantly and inversely

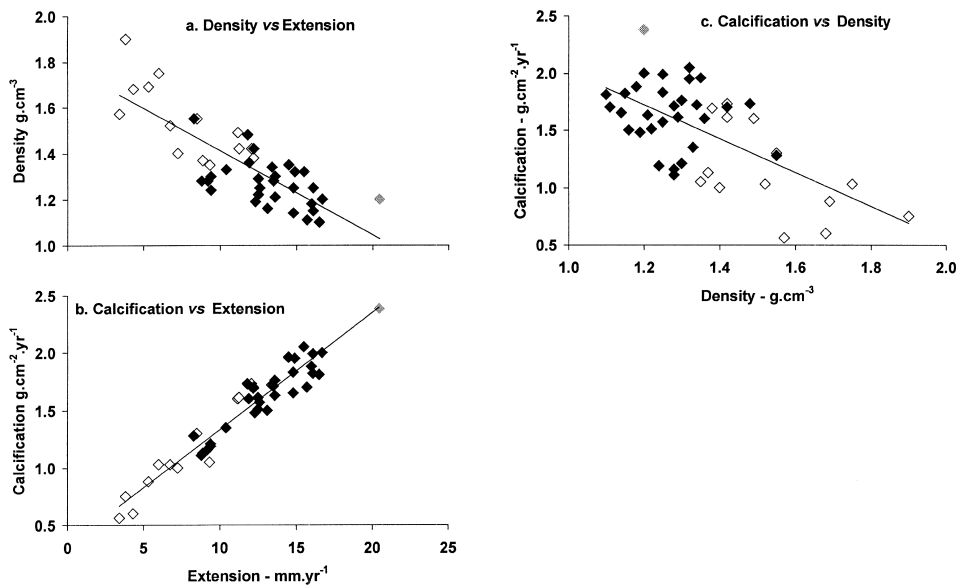


Fig. 4. Scatter diagrams of growth data averaged across colonies from each of the 44 Indo-Pacific reefs (see text). (a) Density vs. extension, (b) calcification vs. extension, and (c) calcification vs. density. Solid diamonds represent 29 GBR reefs, clear diamonds represent 14 reefs from the Hawaiian Archipelago and the grey diamond represents a reef at Phuket, Thailand. Regression lines are shown where there is a statistically significant link.

correlated with average skeletal density (Fig. 4a; $r = -0.80$, $p < 0.00$, $n = 44$) and significantly correlated with average annual calcification (Fig. 4b; $r = 0.96$, $p < 0.00$, $n = 44$). Average skeletal density was significantly inversely correlated with average annual calcification (Fig. 4c; $r = -0.64$, $p < 0.00$, $n = 44$). These two variables were not significantly linked in the data set for colonies from the GBR (Fig. 2a).

Over all 44 coral reef sites, average skeletal density was significantly related to both average annual SST (Fig. 5a; $r = -0.69$, $p < 0.00$) and average annual solar radiation (Fig. 5d; $r = -0.70$, $p < 0.00$). Average annual SST and average annual incoming solar radiation for the 44 sites were significantly correlated ($r = 0.69$, $p < 0.00$). Partial correlations of density vs. average annual SST and density vs. average annual solar radiation were both significant ($r = -0.41$, $p = 0.01$; $r = -0.42$, $p = 0.01$, respectively). The multiple regression equation [density = $-0.064(\text{SST}) - 0.008(\text{SR}) + 4.901$] explained 57.1% of the variance in density ($F_{[2,41]} = 27.32$, $p < 0.00$).

Average annual extension of *Porites* from the 44 reef sites was significantly correlated with both average annual SST and average annual incoming solar radiation ($r = 0.91$, $p < 0.00$; $r = 0.71$, $p < 0.00$, respectively). Partial correlations were significant for extension vs. annual SST ($r = 0.83$, $p < 0.00$) but not for extension vs. annual solar radiation ($r = 0.27$, $p = 0.08$). The regression equation [extension = $3.11(\text{SST}) - 68.96$] explained 83.5% of the variance in extension rate ($F_{[1,42]} = 212.56$, $p < 0.00$). Thus,

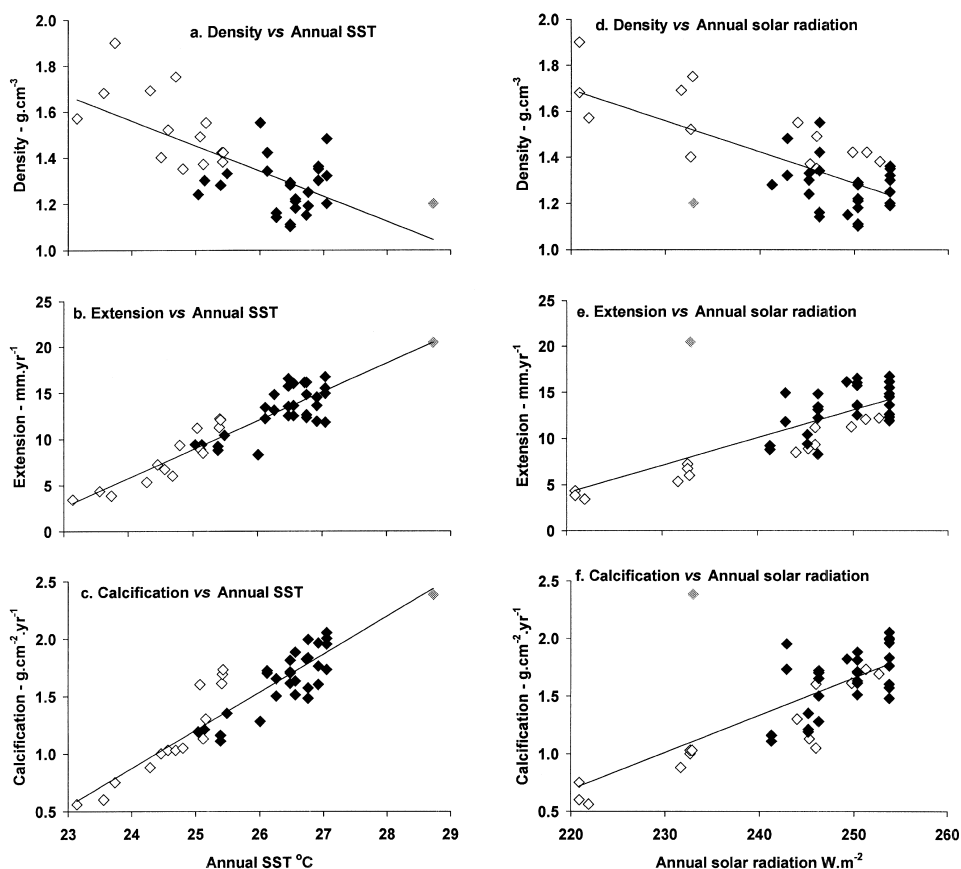


Fig. 5. Scatter diagrams of growth data averaged across colonies from each of the 44 Indo-Pacific reefs (see text) vs. annual average SST: (a) Density, (b) extension and (c) calcification. Growth data vs. annual average incoming solar radiation: (d) density, (e) extension, and (f) calcification. Solid diamonds represent 29 GBR reefs, clear diamonds represent 14 reefs from the Hawaiian Archipelago and the grey diamond represents a reef at Phuket, Thailand. Regression lines are shown where there is a statistically significant link.

extension rate of *Porites* from the Indo-Pacific appears to be primarily related to average annual SST. The relationship implies a change in average annual extension of 3.1 mm year⁻¹ for each 1°C change in annual average SST.

Average annual calcification of *Porites* from the 44 reef sites was significantly correlated with average annual SST and average annual incoming solar radiation ($r = 0.91$, $p < 0.00$; $r = 0.72$, $p < 0.00$, respectively). Partial correlations were significant for calcification rate vs. average annual SST ($r = 0.83$, $p < 0.00$) and for calcification rate vs. average annual incoming solar radiation ($r = 0.31$, $p = 0.05$). The primary control appeared to be average annual SST because including solar radiation added only 1.5% to the explained variance. The regression equation [calcification =

$0.33(\text{SST}) - 7.07]$ explained 83.6% of the variance in average annual calcification ($F = 213.59$, $p < 0.00$). This equation provides for a change in calcification rate of $0.33 \text{ g cm}^{-2} \text{ year}^{-1}$ for each 1°C change in average annual SST.

Relationships between SST and extension rate and calcification rate were examined separately for average annual maximum SST and average annual minimum SST. The relationships demonstrated that average annual minimum SST rather than average annual maximum SST was the main contributor to the relationships between extension rate and calcification rate with SST (see Fig. 6 for calcification vs. maximum and minimum SST). Extrapolation of the regression line for minimum SST vs. calcification (see Fig. 6b) indicated that average annual calcification ceases at $\sim 17.5^\circ\text{C}$ — very close to the often quoted lower limit (18°C) for coral reef formation first reported by Vaughan (1919).

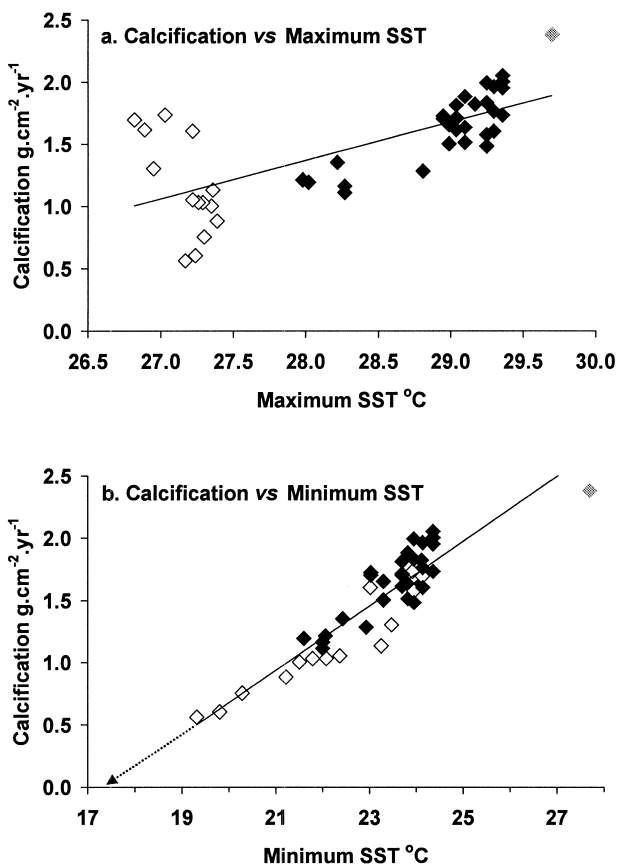


Fig. 6. Scatter diagram of calcification averaged across colonies from each of the 44 Indo-Pacific reefs vs. (a) average maximum SST and (b) average minimum SST. The regression line for calcification vs. minimum SST has been extrapolated (dashed line) to zero calcification. Solid diamonds represent 29 GBR reefs, clear diamonds represent 14 reefs from the Hawaiian Archipelago and the grey diamond represents a reef at Phuket, Thailand. Regression lines are shown where there is a statistically significant link.

4. Discussion

The length of time that tissue resided over skeletal elements was slightly higher at the side of colonies than at the top. The decrease in calcification rate between the top and side of colonies would, therefore, appear to be mostly due to the decrease in extension rate. Variation in light between the top and sides of colonies is the only factor that could produce such a systematic trend across many colonies from many locations. Thus, light may be a major factor influencing extension rate in *Porites*. Such an influence may not arise from the well-recognized linkage between light intensity and calcification rate. Calcification in these shallow-water colonies is unlikely to have been light-limited since photosynthesis would have been saturated through most of the day (e.g. Barnes and Chalker, 1990). The link between extension and light may simply be the result of the colonies distributing their resources so that they grow more towards the light (Kawaguti, 1937a,b; see also Yonge, 1963).

As noted previously (Scoffin et al., 1992; Lough and Barnes, 1997) annual average extension was significantly inversely correlated with average skeletal density. This accords with the notion that variations in skeletal density result from variations in the thickening applied to the initial deposits responsible for extension (Barnes and Lough, 1993) because a higher extension rate allows less time for thickening (assuming no significant change in tissue thickness). As previously noted (Barnes and Lough, 1993) variations in average annual calcification were almost entirely associated with variations in extension rate.

On the Great Barrier Reef (GBR), the major physical influences which vary across shelf relate to a gradient from sheltered, more turbid, terrestrially-influenced coastal waters to more exposed, less turbid, oceanic waters at the edge of the continental shelf (Done, 1982; Wilkinson and Cheshire, 1988). At more exposed, shelf-edge, reefs *Porites* extend less and, as a consequence, the deposited skeleton has higher density. However, as also noted by Scoffin et al. (1992) for Thai corals, extension was highest and density lowest in sheltered regions of lowest ‘hydraulic energy’ and also greatest turbidity. High turbidity, nutrient levels and terrestrial inputs on the GBR are largely confined to a relatively narrow (10–15 km) band near the coast (Liston, 1990; Wolanski, 1994; Furnas and Mitchell, 1997). The cross-shelf gradient in extension rate and skeletal density observed on the GBR might, therefore, be a growth response to greater availability of nutrients for coral growth in nearshore reefs compared with offshore reefs.

Results presented here show that average annual extension in *Porites* from the Indo-Pacific changes by 3.1 mm year^{-1} per 1°C change in average annual sea surface temperature (SST; range $22\text{--}29^\circ\text{C}$). Nie et al. (1997) report a similar relationship between annual extension of *Porites* and annual SST for samples of *P. lutea* from the northern part of the South China Sea (range $26\text{--}28^\circ\text{C}$). The sensitivity of extension in *Porites* to temperature is about three times greater than reported by Weber et al. (1975) for Indo-Pacific *Platygyra* spp. (0.9 mm year^{-1} per $^\circ\text{C}$ for an SST range of $23.9\text{--}29.3^\circ\text{C}$) and for Caribbean *Montastrea annularis* ($0.94 \text{ mm year}^{-1}$ per $^\circ\text{C}$ for an SST range of $25\text{--}29^\circ\text{C}$).

Lough and Barnes (1997) reported a significant relationship between annual variations in calcification rate averaged across ten *Porites* colonies and annual variations of SST on

the GBR. This relationship (based on 80 years of data) accounted for 31% of the variance ($F_{[1,78]} = 35.34$, $p < 0.00$) and gave an increase in calcification rate of $0.17 \text{ g cm}^{-2} \text{ year}^{-1}$ for each 1°C increase in SST. It appears, at first sight, as if calcification rates in *Porites* might be about half as sensitive to inter-annual variations in SSTs as to variations in average annual SST over latitude. However, the published data closely matched the linear fit between average annual SST and calcification for the 44 Indo-Pacific sites (Fig. 7). Thus, variation in calcification rate of *Porites* with average annual SST appears to be similar whether examined over space or time.

These results allow assessment of possible impacts of global climate change on coral reef ecosystems. For example, based on our previously published average GBR calcification data for the period 1746–1982 (Lough and Barnes, 1997; data not affected by the slope of the temperature response curve), average annual calcification for successive 50-year periods ($\text{g cm}^{-2} \text{ year}^{-1}$; $\pm \text{S.D.}$) was: 1780–1829 = 1.48 ± 0.10 , 1830–1879 = 1.48 ± 0.11 , 1880–1929 = 1.47 ± 0.05 and 1930–1979 = 1.53 ± 0.07 . The increase in calcification rate between the last two 50-year periods of $0.06 \text{ g cm}^{-2} \text{ year}^{-1}$ was significant ($t = 4.85$, $p < 0.00$) and matches the observed increase in average annual SSTs on the GBR of $\sim 0.25^\circ\text{C}$ (see Lough, 1999). This increase of $\sim 4\%$ in calcification rate conflicts with the estimated decrease in coral calcification rate of 6–14% over the same time period suggested by Kleypas et al. (1999) as a response to changes in ocean chemistry.

Percentage changes in average annual calcification of *Porites* over the 20th Century were estimated from the observed SST difference along the GBR between the first (1903–1922) and last (1979–1998) 20-year periods of observation combined with the relationship between calcification and average annual SST (Fig. 5c). The SST-associated increase in calcification is estimated to be $< 5\%$ in the northern GBR, $\sim 12\%$ in the central GBR, $\sim 20\%$ in the southern GBR and to increase dramatically (up to $\sim 50\%$) to the south of the GBR (Fig. 8).

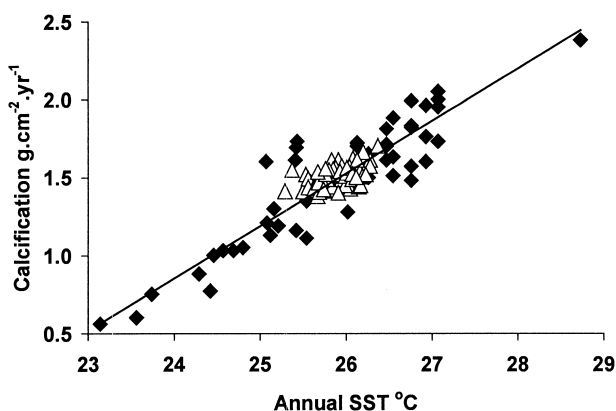


Fig. 7. Scatter diagram of annual average SST vs. average calcification rate for colonies from each of the 44 Indo-Pacific reefs (solid diamonds) and the associated regression line. Also shown are data from Lough and Barnes (1997) for annual calcification vs. average annual SST for ten GBR corals over the period 1903–1982 (open triangles).

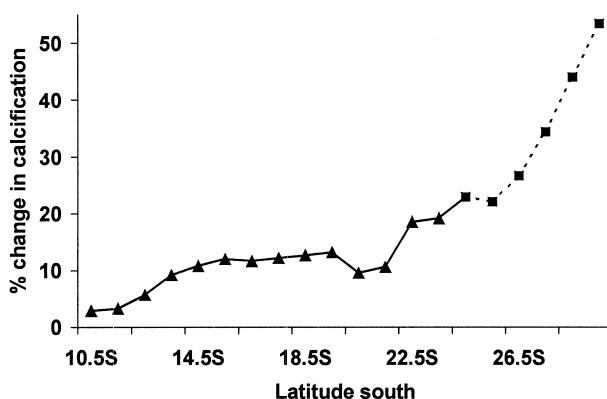


Fig. 8. Percentage increase in calcification of massive *Porites* along the GBR estimated from observed SST differences between 1903–22 and 1979–98. Estimates based upon the relationship shown in Fig. 5c. Triangles and solid line represent regions within the GBR; squares and dashed line represent regions to the south of the GBR. Brisbane is at latitude 27.5°S. The Solitary Islands, which have extensive coral communities but no reefs, are around 30.0°S.

5. Conclusions

- Differences in light availability probably cause the significant differences in rates of extension and calcification between the tops and sides of shallow-water, massive *Porites*.
- Extension rate in massive *Porites* is inversely related to average skeletal density.
- Extension rate in massive *Porites* is directly linked with calcification rate.
- Average skeletal density increases and average extension rate decreases with increasing distance offshore on the Great Barrier Reef.
- Rates of extension and calcification in massive *Porites* are strongly linked with average annual sea surface temperature (SST). Average annual extension increases by $\sim 3 \text{ mm year}^{-1}$ and average annual calcification increases by $\sim 0.3 \text{ g cm}^{-2} \text{ year}^{-1}$ for each 1°C increase in SST.
- The sensitivity of calcification rates of *Porites* to SST suggests that calcification rates will, at least initially, increase as a result of global warming due to the enhanced greenhouse effect. There is some evidence that the calcification rate of massive *Porites* on the GBR has already increased over the present century in association with a SST increase of $\sim 0.25^\circ\text{C}$.

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