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REPORT

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Coral growth in subtropical eastern Australia

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Abstract Extension rates of corals at two sites in subtropical eastern Australia (Solitary Islands and Lord Howe Island) were measured to determine whether growth was low relative to tropical locations. Growth was measured using alizarin staining of skeletons and X-radiographic analysis, and was compared between colonies, species, and sites. Linear extension of individual *Pocillopora damicornis* colonies averaged 12.4 to 16.1 mm per year at Solitary Islands and Lord Howe Island respectively, which is 50% to 80% of published values for this species at tropical sites. Similarly, average extension of most massive faviid species examined at these sites was between 2.6 mm and 4.6 mm per year, considerably lower than most values reported from lower latitudes (generally 6 mm to 10 mm per year). However, growth rates of *Acropora yongei*, *Turbinaria frondens*, and *Porites heronensis* were close to those of closely-related taxa from the tropics. Causal links between latitude, growth rates of coral colonies, and the potential for reef accretion remain unclear.

Key words Coral growth · Subtropical corals
High latitude reefs

Introduction

While coral reefs are largely restricted to tropical latitudes, there are a number of locations where significant coral-dominated communities extend beyond the tropics into high-latitude sites. These include both the east and west coasts of Australia, Japan, the Hawaiian chain of islands, Florida and the Gulf of Mexico, Bermuda, South America, and southern Africa. In some cases, these communities occur in areas of significant reefal development, while at other sites, reefs do not form. An understanding of the processes which control development of coral reefs is assisted by examination of the factors limiting coral reef formation, i.e. why do benthic communities dominated by corals exist well outside the tropics, and why do such communities fail to accrete sufficiently to form true reefs at many high-latitude sites?

There is a considerable body of evidence that coral reefs are limited to locations where water temperature rarely falls below 18 °C (reviews in Stoddart 1969; Rosen 1988; Veron 1995). While it has been frequently proposed that the reason for this is mortality of corals at lower temperatures (Edmondson 1929; Veron and Done 1979), more recent evidence suggests that a significant number of species of hermatypic corals can survive at temperatures as low as 14°C (reviewed in Veron 1995). Other hypotheses on limits of coral reef development include a reduction in reproductive viability of corals at high latitudes (Veron 1974), reduced capacity of corals to compete with temperate algae or fouling organisms (Johannes et al. 1983; Holmes et al. 1997), and high rates of carbonate solution at high latitudes associated with greater development of epilithic and other algal communities (Barnes and Lazar 1993). However, recent evidence suggests that coral reproduction and recruitment occur successfully at high latitudes (Kenyon 1992; Harriott 1992; Babcock et al. 1994; van Woesik 1995; Wilson and Harrison 1997), and other hypotheses remain largely untested.

Grigg (1982a, b) reported that growth rate of *Porites lobata* and community calcification declined with increasing latitude along the Hawaiian Archipelago. He termed the region where reduced carbonate production at high-latitude sites is just sufficient to offset erosion and subsidence as the "Darwin Point", and argued that this represented a threshold for atoll formation. In other studies of latitudinal changes in growth rates of

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corals, Stimson (1996) reported reduced growth at high-latitude sites for *Pocillopora damicornis* and tabulate *Acropora* species, while Crossland (1981) reported slower growth of both *Acropora formosa* and *Pocillopora damicornis* at the Houtman Abrolhos Islands, subtropical Western Australia, than at tropical sites. However, Smith (1981), Marsh (1992), and Harriott (1998) reported growth rates at high latitude sites for *Porites* and branching *Acropora* corals similar to those reported from the tropics.

Growth rates of corals are reported for two high-latitude sites in eastern Australia; Solitary Islands (30°S) and Lord Howe Island (31°S). Growth rates are compared (1) between colonies of a single species, (2) between sites, (3) between taxa, and (4) with published reports for other locations. Evidence for a decline in coral growth rate with latitude as a factor limiting coral reef formation in eastern Australia is discussed.

Materials and methods

Study sites

The Solitary Islands are a group of five large islands and many small reefs at 30°S on the coast of northern New South Wales, Australia (Fig. 1). These islands mark the southern extent of extensive coral-dominated benthic communities in coastal eastern Australia. Their ecology and benthic communities have been described by Veron et al. (1974) and Harriott et al. (1994). A total of 90 scleractinian coral species have been recorded from the region, and coral cover can reach > 50% in some areas.

Lord Howe Island lies approximately 600 km off the coast of NSW at 31.5°S (Fig. 1) and is fringed by the southernmost coral reefs in the Pacific Ocean. The coral communities of Lord Howe Island have been described and quantified by Veron and Done (1979) and Harriott et al. (1995). Eighty three scleractinian species have been recorded. The seaward side of Lord Howe Island is exposed to oceanic weather conditions and has little reef build-up. The leeward reefs are partly protected from the weather and include a lagoon with reef accretion.

Measurement of extension rates

Extension rates were measured using staining of the skeleton with alizarin (Crossland 1981; Oliver et al. 1983). Plastic bags were placed over colonies and alizarin was released into the bag to produce a concentration of approximately 10 mg/l. The bags were kept in place for 3 to 4 h. Stained corals were marked with a plastic cable tie or wire and plastic label below the staining point for re-location at the time of collection.

Corals at South West and North West Solitary Islands (Fig. 1) were stained on 6–7 December, 1994. The number of colonies stained and subsequent sampling regime are summarised in Table 1. Sample sizes of colonies stained reflect the number of colonies of suitable size which could be found in each area during several dives. Colony sizes were typical for the species, i.e. colony diameter of 20–40 cm for *Pocillopora. damicornis*, *Goniastrea australensis*, *Turbinaria frondens*, and *Acropora valida*, and > 50 cm diameter for the other *Acropora* species.

A small sample of skeleton from a subset of stained colonies was collected on 21 April, 1995 after 20 weeks growth. All colonies which could be found again were sampled on 7 November, 1995, after a total of 49 weeks growth. Mortality of some colonies and a loss of tags between staining and collection was probably linked to severe storms, including swells of > 6 m, which affected the Solitary Islands area in early 1995 (S.D.A. Smith, personal communication). Because of this, the number of colonies collected was smaller than the initial sample in most cases (Table 1).

In addition, not all colonies collected showed a visible pink line indicating successful alizarin staining. None of the 6 colonies of *G. australensis* recovered showed any staining. The average number of branches or colony sections measured to obtain a result for average growth for each colony is presented in Table 1.

Average extension rates per colony during the two time periods (December to April and December to November) were calculated. For *P. damicornis* and *T. frondens*, weekly growth rates for the period April to December were derived by subtracting mean growth for December to April (20 weeks) from mean growth for December to November (49 weeks), and dividing by the number of weeks (29 weeks).

Corals were stained in North Bay at Lord Howe Island (Fig. 1) in both 1993 and 1994. Eight colonies of *P. damicornis* were stained on 22 February, 1993, and sampled on 15 February, 1994, a period of 51 weeks of growth. Other corals (Table 2) were stained on 23 December, 1994 and collected on 1 January, 1996, a period of 53 weeks. All colonies were successfully collected. The rate of successful staining, and number of branches or colony sections measured for each colony to give a result for average extension per colony is presented in Table 2.

At both sites, collected corals were labelled and bleached with dilute hypochlorite solution. Linear extension of branching colonies was measured as growth from the stained point indicating size at the time of staining, to the equivalent point on the edge the colony. Annual extension for each stained colony was calculated for a standard 52 week period as proportional to growth for a 49, 51 or 53 week period.

Massive corals were sliced with a geological saw to a thickness of 4–6 mm. Slices were examined for evidence of a line of alizarin staining and extension was measured from this line to the coral edge along at least three replicate transects. A sub-sample of massive corals was X-rayed, using medical X-ray equipment, and prints from X-rays were checked for pairs of high and low density bands which represent one year's growth (Buddemeier et al. 1974). Growth rate was calculated by measuring the length of an area with clear banding in the direction of vertical growth of the coral representing approximately 10 y growth, and dividing it by the number of band pairs in the area. At least three areas of each coral were measured and the mean result calculated.

Growth rates were examined relative to latitude and annual mean water temperature. Water temperature data were listed for publications where both temperature and growth were reported. Where water temperature data were not presented, these were derived from the tables of Weber and White (1974,1977) and from the Australian Oceanographic Data Centre (www.AODC.gov.au/AODC.html). Water temperature for the Solitary Islands was recorded from submersible water temperature loggers installed at North West and South West Solitary Islands over a 20 month period from 1991 to 1993.

Results

Solitary Islands

Branch extension rates of all *Pocillopora damicornis* colonies averaged 12.4 mm/yr (Table 3), but varied widely between colonies, ranging from 4.7 mm/y – 24.6 mm/y for individual colonies. During the period December to April, extension averaged 0.42 mm/week,

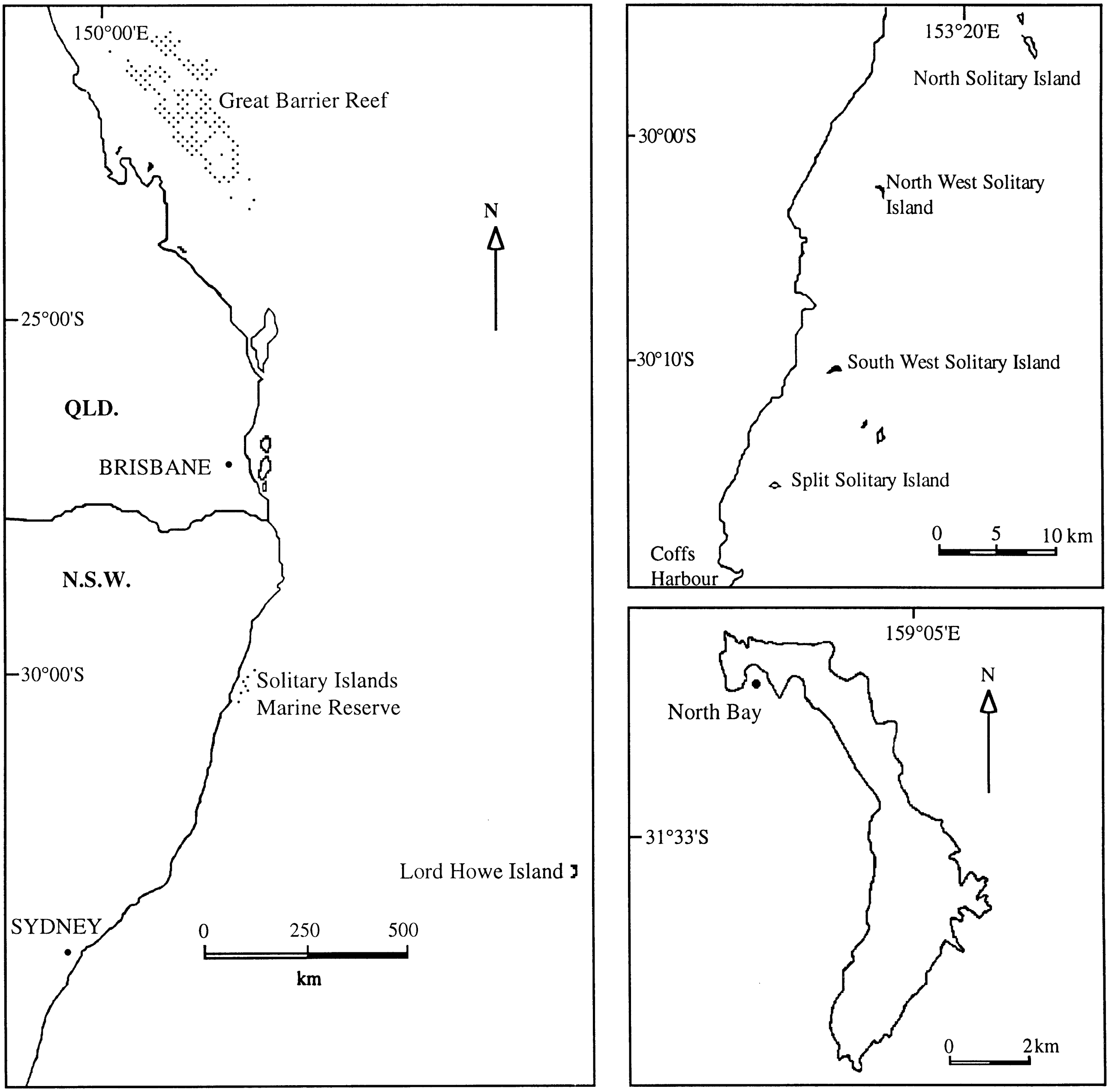

Fig. 1 Map of eastern Australia showing location of study sites, and detail of Solitary Islands and Lord Howe Island showing collection sites

while between April and November, extension averaged just 0.11 mm/week (Table 3).

Annual extension rate of *Turbinaria frondens* was 14.0 mm/y (Table 3). Weekly growth rate from December to April was 0.32 mm/week, while growth rate for the April to November period was 0.23 mm/week. For the branching *Acropora* species, growth rates were 16.7 to 23.6 mm/y, and sample sizes were too small to compare between sample intervals.

No colonies of *G. australensis* collected showed any indication of staining. Three colonies were sectioned and X-rayed, but only one of the three colonies showed a banding pattern consistent with the presence of high- and low-density bands. This colony showed indistinct banding, with a growth rate of 2.9 mm per year averaged over 6 y of growth. Growth form of this species at the Solitary Islands tends to be semi-encrusting, with thin, flattened colonies the most common morphology, compared with the hemispherical form more common for this species at tropical sites.

Lord Howe Island

Growth of *P. damicornis* at Lord Howe Island varied widely between colonies. Extension per colony

Table 1 Sampling pattern for Solitary Islands corals showing number of colonies stained in the initial sample, the number of colonies which showed staining lines in the April and November samples, and the average number of growth measurements per colony for each species

Species	Initial sample 12/94	Number of stained colonies collected on 4/95	Mean number of measurements/colony 4/95	Number of colonies collected on 11/95	Number of stained colonies 11/95	Mean number of measurements/colony 11/95
Pocillopora damicornis	18	5	3.6	12	10	8.3
Goniastrea australensis	13	0		8	0	
Turbinaria frondens	14	3	3.0	4	3	6.3
Acropora valida	5	4	1.5	2	2	5.0
Acropora robusta	4	0		3	1	3.7
Acropora cytherea	2	1	2.0	2	2	7.0
Acropora solitaryensis	1	0		1	1	10.0

Table 2 Sampling pattern for Lord Howe Island showing number of colonies stained then collected (initial sample), number of colonies which showed staining lines, and average number of growth measurements per colony for each species. At Lord Howe Island, all colonies which were initially sampled were collected later. All colonies except *P. damicornis* in 1993 were stained in 1994

Species	Initial sample	Number which showed staining line	Mean number of measurements/colony
Pocillopora damicornis (1993)	8	5	6.8
Pocillopora damicornis	4	2	6.0
Acropora yongei	12	10	9.9
Porites heronensis	9	6	3.6
Montastrea curta	4	4	5.3
Goniastrea australensis	3	1	3.0
Cyphastrea serailea	3	1	5.0
Favia pallida	2	2	5.5
Seriatopora hystrix	1	1	6.0

averaged 16.1 mm/y (Table 4), and ranged between 11.4 mm/y and 29.1 mm/y for individual colonies. A single colony of *Seriatopora hystrix* had an extension rate of 16.7 mm/y. For *Acropora yongei*, mean extension per colony averaged 49.4 mm/y, ranging from 41.9 mm to 63.9 mm/y for colonies.

Porites heronensis has a variable growth form that ranges from encrusting through to columnar and semi-massive. Vertical extension (i.e. towards the top of the columns) ranged from 9.0 to 11.8 mm/y, with average annual growth of 10.5 mm/y. Growth was generally less rapid towards the sides of the columns, but the rate of lateral growth depended on the morphology of the colony section examined. Mean extension per colony for *Montastrea curta* averaged 2.5 mm/y. Annual rates for other faviid species were similar, i.e. 2.8, 3.3, and 3.4 mm/y (Table 4).

Results were compared for growth rates derived from both staining and analysis of X-rays for the faviid species. For three species, results were similar for the two methods, with values of 2.5 and 2.7 mm/y for *M. curta*, 2.8 and 2.9 mm/y for *G. australensis*, and 3.4 and 2.6 mm/y for *Cyphastrea serailea* from staining and X-rays respectively (Table 4). The results were not compared statistically because staining measures growth rate for a single year, while X-ray analysis averages growth rate over at least a 10 y period. For *Favia pallida*, the growth rate derived from X-rays measured over 17 y of banding was 4.6 mm/y, somewhat higher than the 3.3 mm/y recorded in 1995 from staining for a single colony.

In all cases, the consistency between the growth estimates from staining and X-rays confirmed the annual nature of the banding pattern in this high latitude location. Because results from X-rays were averaged over at least a 10 y period, they are likely to be a more reliable indicator of long-term growth rate than the results of staining.

Relationship between extension and latitude for *P. damicornis*

The relationships between extension, latitude, and temperature were plotted for *P. damicornis* (Fig. 2). Data for extension rates are presented in Table 5. Where more than one value was available for mean extension rate at any location, the mid-point of the range of mean values was used in the analysis. There was a significant negative correlation between latitude and annual mean water temperature for Indo-Pacific reefs ($r = -0.66$, $n = 30$, $P < 0.001$) (Fig. 2a). The Galapagos Islands are colder than expected on the basis of their near-equatorial location because of upwelling, and removal of the data point for the Galapagos Islands improves the correlation ($r = -0.81$, $n = 29$, $P < 0.001$). There was a significant negative correlation between latitude and extension in *P. damicornis* ($r = -0.74$, $n = 14$,

Table 3 Extension data for corals from the Solitary Islands

	Date sampled	Weeks of growth	Mean extension (mm)	SD	Extension/ week (mm)	Annual extension (mm/yr)	SD	Number of colonies
Pocillopora damicornis	6/12/94–21/4/95	20	8.3	2.75	0.42			5
	6/12/94–7/11/95	49	11.7	6.13	0.24	12.4	6.33	10
	21/4/95–7/11/95	29	3.4		0.11			
Turbinaria frondens	6/12/94–21/4/95	20	6.4	0.63	0.32			3
	6/12/94–7/11/95	49	13.1	4.31	0.27	14.0	4.58	3
	21/4/95–7/11/95	29	6.7		0.23			
Acropora valida	6/12/94–21/4/95	20	9.2	5.44	0.46			4
	6/12/94–7/11/95	49	22.3		0.46	23.6		1
	21/4/95–7/11/95	29	13.1		0.45			
Acropora cytherea	6/12/94–21/4/95	20	16.0	4.24	0.80			1
	6/12/94–7/11/95	49	19.7	1.89	0.40	20.9	1.99	2
	21/4/95–7/11/95	29	3.7		0.13			
Acropora solitaryensis	6/12/94–7/11/95	49	15.7		0.32	16.7		1
Acropora robusta	6/12/94–7/11/95	49	21.1	1.81	0.43	22.4	1.93	3

Table 4 Mean annual extension rate of Lord Howe Island corals

Species	Annual growth (mm/y)	SD	Number of colonies
P. damicornis	16.1	6.37	7
Acropora yongei	49.4	7.01	10
Porites heronensis	10.5	0.98	6
Cyphastrea serailea	3.4		1
C. serailea (from X-ray)	2.6		1
Montastrea curta	2.5	0.32	3
M. curta (from X-ray)	2.7	0.44	3
Favia pallida	3.3	0.01	2
F. pallida (from X-ray)	4.6		1
Goniastrea australensis	2.8		1
G. australensis (from X-ray)	2.9		1
Seriatopora hystrix	16.7		1

$P < 0.01$) (Fig. 2b). There was a positive correlation between annual mean water temperature and extension of *P. damicornis* ($r = 0.64$, $n = 14$, $P < 0.01$) (Fig. 2c), but growth in Hawaii was lower than expected from its annual temperature. Removal of the data point for Hawaii from the analysis improves the correlation ($r = 0.81$, $n = 13$, $P < 0.001$). *P. damicornis* from the Galapagos Islands had growth rates consistent with water temperature rather than latitude.

Discussion

Regional comparisons

Reported extension rates for *Pocillopora damicornis* from all tropical sites except Hawaii are at least double those from the Solitary Islands and Lord Howe Island (Table 5). This result is similar to the analysis of Stimson (1996), who showed a decline in growth rate of *P. damicornis* with increasing latitude. There was no significant difference between annual extension rate of *P. damicornis* at Lord Howe Island and the Solitary Islands (nested ANOVA; $F = 1.09$; $p(F) > 0.31$). Growth at both locations was highly variable between colonies, with the standard deviation about half the mean extension rate at both sites.

At the Solitary Islands, the weekly extension rate of *P. damicornis* during the winter period (April to November) was about one quarter of the rate for the summer period (December to March) (Table 3). Water temperature in the Solitary Islands averaged 19.7°C throughout the winter period in 1993, while summer temperatures in 1992 and 1993 averaged 20°C and 22°C respectively, but were highly variable. The reduction in extension of *P. damicornis* from summer to winter is greater than would be predicted on the basis of the relationship between water temperature and extension rate for a range of sites (Fig. 2c). Possible explanations are that large differences in light availability between summer and winter at this high latitude site might contribute to slowed winter growth, or that there is a threshold temperature at around 20°C below which growth in *P. damicornis* slows greatly.

Extension of massive faviids at high latitude sites was fairly consistent between taxa at 2.5 mm – 4.6 mm per year (Table 6) including sites from sub-tropical Bermuda (32°N). At most tropical sites, extension of massive corals was in the range of 6 mm to 10 mm per year (Table 6). Differences in growth were less clear-cut for comparisons within eastern Australian corals. Faviids from Lord Howe Island (31.5°S) grew 2.5 to 4.6 mm/y, while *Platygyra* and *Goniastrea* from the Great Barrier Reef (18°S) grew 3.8 mm – 6.8 mm/y (Babcock 1988).

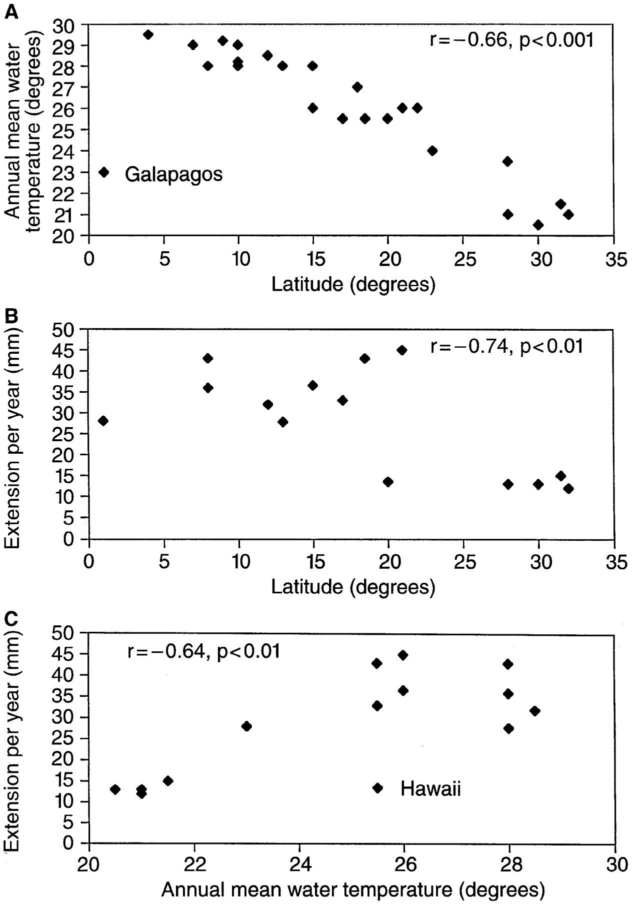

Fig. 2A, B Relationships between latitude, water temperature and extension rate of *Pocillopora damicornis*. **A** Latitude versus mean annual water temperature for Pacific sites. Temperature data from Tables 5 to 8. **B** Latitude versus extension rate. **C** Mean annual water temperature versus extension rate

There was overlap in extension rates of faviid corals between these two widely separated locations, and very large interspecific differences within the Great Barrier Reef corals.

Weber and White (1974) examined mean annual extension rate for *Platygyra* from a wide range of Indo-Pacific locations and derived a linear relationship between temperature and growth for the temperature range 23.9°C to 29.3°C. Extrapolating this relationship to the annual mean temperature at Lord Howe Island (21.5°C) gives an extension rate of just over 3 mm per year. This estimate is very similar to the results of growth recorded for closely related faviid corals from Lord Howe Island (Tables 4, 6) of 2.6 mm – 4.6 mm per year.

Several reports have indicated reduced growth of massive *Porites* at higher latitudes (Grigg 1982a, b; Lough and Barnes 1997), but Smith (1981) reported (without presenting data) that growth rate of massive *Porites* at a high-latitude site (Houtman Abrolhos) was similar to that of corals from the tropics. For branching or columnar *Porites*, extension rate of *Porites heronensis* at Lord Howe Island was as high as extension of other branching or columnar *Porites* species from both Atlantic and Pacific tropical sites (Table 7). Only extension rates for branching species from Guam and Samoa were higher than those reported from Lord Howe Island.

A review of extension rates of *Acropora* species indicates that growth rates for *Acropora* at Lord Howe Island and the Solitary Islands are at the lower end of the range for tropical sites, with extension for most sites at least double that for the Solitary Islands (Table 8). The pattern is not absolute, as a number of species from Lizard Island on the Great Barrier Reef (15°S) had linear extension rates of 38–45 mm/y (Oliver 1985), lower than the rate for Lord Howe Island. Marsh

Table 5 Growth variation with region for *Pocillopora damicornis* (for references see Table 9)

Latitude	Mean water temperature °C	Location	Linear extension (mm/y)	Reference (see Table 9)
1°N	23	Galapagos	28	1
8°N	28	Panama	27.6–5767	2,3
8°N	28	Costa Rica	31–39	4,5,6
12°N	28.5	Guam	29–36.7	7,8
13°S	28	Samoa	27.8	9
15°S	26.0	Lizard Island	36.6	10
17°S	25.5	Low Isles[a]	31.5–35.9	11
18.5°S	25.5	Palm Island	43.2	10
20°N	25.5	Hawaii	13–13.9	12,13
21°S	26	Dampier Archipelago	45	14
28°S	21	Houtman Abrolhos	12.2–14.3	15
30°S	20.5	Solitary Islands	12.4	16
31.5°S	21.5	Lord Howe Island	16.1	16
32°S	21	Rottnest Island	9–15[b]	17

[a] Note, Low Isles, GBR is called Gibraltar in Buddemeier and Kinzie (1974) and Huston (1985)
[b] Estimated as 2 X six month measurement (January–June)

Table 6 Growth variation in massive faviid coral species (for references see Table 9)

Latitude	Mean water temperature °C	Location	Species	Linear growth (mm/y)	Reference
4°S	29.5	New Guinea	*Platygyra* sp	10.3	18
7°S	29	Palau	*Platygyra* sp	9.1	18
10°N	29	Enewetak	*Platygyra lamellina*	6.7–8.0	19
			Goniastrea retiformis	5–9.5	20
			Favia pallida	5 to 7	20
			Favia speciosa	5.6–8.5	19
			Favia stelligera	8 to 12	19
10°N	28	Panama	*Diploria strigosa*	4.6–5.9	21
			Montastrea annularis	5.0	22
			Montastrea cavernosa	3.2	22
12.5°N		Aruba	*Diploria strigosa*	4.3–4.6	23
13°N	27.5	Barbados	*M. annularis*	5–25	22,24
15°N	28	Mariana Islands	*Platygyra* sp.	9.4	18
17°N		Honduras	*M. annularis*	4 to 11	22
18°N	28	Jamaica	*M. annularis*	4.7–11.3	22,25
			M. cavernosa	2.0–6.8	22, 25
			Colophyllia natans	5.7–9.3	25
18°N		Virgin Islands	*M. annularis*	9.7–10.4	26
			D. labyrinthiformis	3.4	27
18°N		Belize	*M. annularis*	7.1	22
			M. cavernosa	3.2	22
18°S	27	Fiji	*Platygyra* sp	10.3	18
18°S	25.5	GBR	*Platygyra sinensis*	6.4–6.8	28
			Goniastrea aspera	3.9–4.1	28
			Goniastrea favulus	3.8–4.3	28
21°S	26	Dampier Archipelago	*Platygyra* sp	15–16	14
22°S	26	New Caledonia	*Platygyra* sp	7	18
23°S	24	Heron Island	*Platygyra* sp	4.9	18
25°S	26.5	Florida	*M. annularis*	4.6–11.3	22,29
			M. cavernosa	3.2	22
			D. labyrinthiformis	3.5	29
26°N	28.5	Bahamas	*Diploria strigosa*	3.5–10.0	31
			D. labyrinthiformis	4.9–7.5	31
28°N		E. Flower Banks	*M. annularis*	7.1–10.6	32
			Diploria strigosa	5	33
30°S	20.5	Solitary Islands	*Goniastrea australensis*	2.9	16
31.5°S	21.5	Lord Howe Island	*Montastrea curta*	2.6	16
			Favia pallida	4.6	16
			Goniastrea australensis	2.9	16
			Cyphastrea serailea	2.6	16
32°N	22.3	Bermuda	*D. labyrinthiformis*	3.0–4.7	34,35
			Diploria strigosa	3.3	35

(1992) reported high extension rates (69 mm/y) for *A. youngei* from Rottnest Island near Perth, Western Australia at latitude 32°S, while extension rate of *A. formosa* at Houtman Abrolhos was within the range reported for more tropical sites (Harriott 1998). Gladfelter (1984) reported that temperature does not affect extension of *Acropora cervicornis* within its optimal temperature range of 20°–29°C, and growth varied little from Jamaica (18°N) to Florida (25°N).

For *Turbinaria frondens*, the only growth data from a comparable species are for *T. mesenterina* from Magnetic Island on the Great Barrier Reef. Extension rates of corals > 10 cm in diameter averaged 16 to 19 mm per year (Willis 1987), compared with 14 mm per year for corals from the Solitary Islands. Extension of *T. frondens* varied relatively little between summer and winter samples at the Solitary Islands (Table 3). *Turbinaria* is a dominant taxon in most subtropical locations in eastern Australia (Harriott et al. 1994, 1995; Harriott et al. 1999), and its ability to grow at a reasonable rate through the southern winter may reflect its suitability for these high latitude sites (Table 9).

Coral growth and reef accretion

Buddemeier and Kinzie (1974) reviewed data on coral growth rates and concluded that there was no causal connection between coral growth and reef growth. Veron (1995) concluded that the distribution of corals and the distribution of reefs were both limited by temperature through interactive ecological processes.

Table 7 Growth variation with region for branching and columnar *Porites* (for references see Table 9)

Latitude	Mean water temperature °C	Location	Species	Linear growth (mm/y)	Reference
9°N	29.2	Yap	*Porites* (branching)	8 to 10	36
12°N	28.5	Guam	*Porites cylindrica*	25	8
13°S	28	Samoa	*Porites* (branching)	7 to 48	9
18°N	28	Jamaica	*Porites astreoides*	2.5–4.5	25
			Porites porites	6 to 21	25
20°N	25.5	Hawaii	*Porites* (branching)	8 to 10	13
			Porites compressa	3–17.7	13
25°N	26.5	Florida	*Porites astreoides*	4.0–4.3	37
26°N	28.5	Bahamas	*Porites astreoides*	4.6–7.2	34
28°N	23.5	Red Sea	*Porites columnaris*	5.7	38
31.5°S	21.5	Lord Howe Island	*Porites heronensis*	10.5	16
32°N	22.3	Bermuda	*Porites astreoides*	2	34

Table 8 Growth variation for branching *Acropora* corals (for references see Table 9)

Latitude	Mean water temperaature °C	Location	Species	Linear growth (mm/y)	Reference
9°N	29.2	Yap	*A. pulchra*	101–172	36
10°N	28	Philippines	*A. pulchra*	118–120	39
10°N	28.2	Thailand	*A. formosa*	approx. 80	40
13°S	28	Samoa	*A. formosa*	185	9
13°N	27.5	Barbados	*A. cervicornis*	145	41
15°S	26	Lizard Island	*A. formosa*	71.3	10
			A. robusta	55	10
			A. noblis	41	10
			A. elseyi	38	10
			A. florida	45	10
18°N		Virgin Islands	*A. cervicornis*	100–120	42
18°N	28	Jamaica	*A. cervicornis*	100–120	43,44
18°S	25.5	Palm Island GBR	*A. formosa*	80–120	45
21°S	26	Dampier Archipelago	*A. formosa*	100–137	14
24°N		Dry Tortugas	*A. cervicornis*	40	31
25°N	26.5	Florida	*A. cervicornis*	70–130	46
27°N	28.5	Bahamas	*A. cervicornis*	45	41
28°S	21	Houtman Abrolhos	*A. formosa*	37–76	15,47
30°S	20.5	Solitary Islands	*A. valida*	23.6	16
			A. cytherea	20.9	16
			A. robusta	22.4	16
31.5°S	21.5	Lord Howe Island	*A. yongei*	49.4	16
32°S	21	Rottnest Island	*A. yongei*	69.3	48

Effective temperature minima for corals were those inducing significant mortality while the minima for reefs were those below which reef construction could not be sustained. He reported studies of tolerances of some corals for sustained low temperatures and so argued that reef development is not limited by the low temperature tolerance of corals. In a study of growth rates of *Porites lobata* over a 10° latitudinal range in Hawaii, Grigg (1982a, b) reported that annual extension rate declined from 13 mm/y at 19.5°N to 3 mm/y at 28.5° N. Coral cover and calcification rate also declined with increasing latitude. Grigg (1982a, b) concluded that accretion of calcium carbonate would not balance bioerosion and subsidence at the most poleward sites. He termed the point where calcification just balances subsidence and bioerosion as the "Darwin Point".

In eastern Australia, subsidence of substrata is not a factor in high latitude coral communities. The coral communities at the Solitary Islands and Lord Howe Island have relatively high coral species diversity and cover (Harriott et al. 1994; Harriott et al. 1995) relative to the Hawaiian communities studied by Grigg (1982a, b). The change in extension rate with latitude in Eastern Australia is species-specific; extension rates for some taxa were at the lower end of the range reported for tropical sites, while for other taxa extension rate was less than for similar tropical taxa.

With respect to latitudinal changes in total calcification, there are few studies. Harriott (1997) reported that

Table 9 Reference list for tables 5 to 8. Number in parenthesis is the reference number of review papers from which the data were taken

1 Glynn et al. 1979 (6)
2 Glynn 1976 (25)
3 Wellington 1982 (25)
4 Glynn 1977 (6)
5 Glynn and Stewart 1973 (25)
6 Guzman and Cortes 1989
7 Neudecker 1977 (25)
8 Neudecker 1981
9 Mayor 1924
10 Oliver 1985
11 Stephenson and Stephenson 1933
12 Maragos 1972 (6)
13 Edmondson 1929 (35)
14 Simpson 1988
15 Crossland 1981
16 Present study
17 Ward 1995
18 Weber and White 1974
19 Buddemeier et al. 1974 (35)
20 Highsmith 1979
21 Guzman et al. 1991 (35)
22 Weber and White 1977
23 Eakin et al. 1993 (35)
24 Tomascik 1990
25 Huston 1985
26 Baker and Weber 1975
27 Hubbard and Scaturo 1985
28 Babcock 1988
29 Hudson et al.1994
30 Ghiold and Enos 1982
31 Vaughan 1915 (30)
32 Hudson and Robbin 1981
33 Rezak et al. 1985 (35)
34 Logan and Tomascik 1991
35 Logan et al. 1994
36 Tamura and Hada 1932 (25)
37 Kissling 1977 (30)
38 Klein and Loya, 1991
39 Yap and Gomez 1985
40 Charuchinda and Hylleberg 1984
41 Glynn 1973
42 Gladfelter 1984
43 Lewis et al. 1968
44 Tunnicliffe 1980
45 Oliver et al. 1983
46 Shinn 1966
47 Harriott 1998
48 Marsh 1992

subtropical *A. formosa* corals had higher skeletal density than tropical samples of the same species in Western Australia. Because subtropical *A. formosa* had lower extension rates (Harriott 1998), but higher skeletal density than reported for tropical sites, it is possible that total calcification (the product of density and extension) varied little with latitude, but no direct comparisons are possible because both extension and skeletal density data are not available for the same tropical site. On the basis of presently available data, it is difficult to conclude that reduction in coral growth rate with latitude alone is a significant factor limiting coral reef development in Eastern Australia.

In subtropical Australia, the substrate is frequently rocky, with scattered corals attached directly to the rock surface (Harriott et al. 1994; Harriott et al. 1995; Harriott et al. 1999). The rarity at most sites of *in situ* dead coral is an indication that corals may be removed from the substrate by the severe wind and swell conditions which are common on this coast, preventing accumulation of limestone. A similar relationship between wave exposure and reef accretion was reported for Hawaii (Grigg 1998). The fact that there is a build-up of reef structure only on the leeward shore of Lord Howe Island similarly supports the importance of ocean conditions in reef accretion. Many corals in these subtropical Australian reefs also appear to have significant internal bioerosion and weak attachments to the rock surfaces (unpublished data). Loss of skeletal material *in situ*, as a result of high rates of bioerosion relative to calcification, in addition to the removal of coral skeletons from reefs in severe weather conditions, may contribute to the failure of these high latitude coral communities to build reefs.

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