Environmental controls of coral growth: Data driven multi-scale analyses of rates and patterns of growth in massive Porites corals around the Thai-Malay Peninsula

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CHAPTER TWO

Decline in Growth Rates of *Porites lutea* around Phuket, South Thailand[1]

Of the few studies that have examined in situ coral growth responses to recent climate change, none have done so in equatorial waters subject to relatively high sea temperatures (annual mean >27°C). This study compared the growth rate of *Porites lutea* from eight sites at Phuket, South Thailand between two time periods (December 1984–November 1986 and December 2003–November 2005). There was a significant decrease in coral calcification (23.5%) and linear extension rates (19.4–23.4%) between the two sampling periods at a number of sites, while skeletal bulk density remained unchanged. Over the last 46 years, sea temperatures (SST) in the area have risen at a rate of 0.161°C per decade (current seasonal temperature range 28–30°C) and regression analysis of coral growth data is consistent with a link between rising temperature and reduced linear extension in the order of 46– 56% for every 1°C rise in SST. The apparent sensitivity of linear extension in *P. lutea* to increased SST suggests that corals in this part of the Andaman Sea may already be subjected to temperatures beyond their thermal optimum for skeletal growth.

2.1 Introduction

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[1] Material from this chapter has been published in a peer-reviewed journal:
Tanzil JTI, Brown BE, Tudhope AW, Dunne RP (2009) Decline in growth rates of *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. Coral Reefs 28: 19–528. [The final publication is available at link.springer.com]

As mentioned in the previous chapter, the rate of skeletal growth of corals is a major determinant of their fitness and ecological success, i.e. determining the ability of corals to compete for space and light and repair structural damage caused by anthropogenic disturbance, storms and bioeroders (grazers and borers). Changes in coral growth may thus have profound effects on the resilience of coral reef systems. Effects of anthropogenically driven climate change are predicted to have an important negative impact on coral growth (see Kleypas and Langdon 2006). Based on extrapolation from laboratory experiments, it has been suggested that calcification rates of corals and other calcifying organisms may have already declined by 6–15% over the past 100 years, with predicted decreases of 17–35% by the end of the 21st century relative to pre-industrial levels (Kleypas et al. 1999; Friedrich et al. 2012) due to a decrease in aragonite saturation state caused by ocean acidification.

Despite these predictions, sclerochronology studies that examined coral growth during the 20th century revealed increases in calcification rates over time that were positively correlated with increases in sea surface temperature (SST). Lough and Barnes (1997) observed an increase in calcification rate of 3.5% for every 1°C rise in SST for the massive coral *Porites lutea* between 1906 and 1982 on the Great Barrier Reef, Australia. Similar trends were noted for *Porites* spp. by Bessat and Buigues (2001) for the period 1800–1990 in French Polynesia, and Nie et al. (1997) for the period ~1890–1993 in the South China Sea. Positive relationships between temperature and calcification were also noted in studies that examined coral growth rates over latitudinal scales (Lough and Barnes 2000; Carricart-Ganivet 2004). Such findings have led some scientists to suggest that reduced calcification due to ocean acidification will, at least initially, be countered by an increase in calcification rates due to the rise in SST (Lough and Barnes 2000; McNeil et al. 2004). However, more recent work by Cooper et al. (2008) on the growth of massive *Porites* spp. on the Great Barrier Reef demonstrated a decrease in calcification rate by ~21% between 1988 and 2003, coincident with an increase in SST over the same period.

Many earlier sclerochronology studies sampled reefs subjected to sea temperatures with a mean annual SST <27°C, and it is not yet known how reefs subjected to higher temperatures may be responding to the effects of recent climatic changes. In their earlier overview of the effect of mean annual SST on *Porites* spp. growth in the Indo-Pacific, Lough and Barnes (2000) included growth data from the eastern Andaman Sea, the location of the present study, because it had the highest mean annual SST (>28°C) of a range of locations spanning the Pacific and Indian Ocean. Temperature has been shown to interact with other environmental factors to negatively affect calcification. For example, at temperatures of ~28°C the effects of increased CO_2 partial pressures were much more pronounced in causing a decrease in calcification than at ~25°C (Reynaud et al. 2003). Coles and Jokiel (1978) also noted an interaction between temperature and light, whereby calcification tended to peak at lower light irradiances when exposed to higher temperatures. Given that the global linear warming trend over the last 50 years is nearly twice that for the last 100 years (IPCC 2007), it is possible that reefs in warmer waters have already been exposed to conditions in recent years which might negatively influence calcification rates.

Detailed growth data for *P. lutea* for the period December 1984–November 1986 are available from previous work by Scoffin et al. (1992) for reefs around Phuket, South Thailand, and these present a unique opportunity to examine changes in coral growth over time for reefs which are exposed to relatively high mean temperatures year round (~28–30°C). These reefs have also been subjected to increasing SST over time, in the order of 0.126°C per decade (Brown et al. 1996; Brown 2007). Additionally, comprehensive records of physical environmental variables covering the Phuket region are available from remote sensing data as well as from the Thailand Meteorological Department and from Phuket Marine Biological Centre (PMBC), thus offering the potential to relate any changes in growth to a variety of environmental variables.

2.2 Methods

2.2.1 Study site

Sampling took place at eight of the total eleven sites used in Scoffin et al. (1992; Fig. 2.1). Comprehensive details of the individual collection sites are provided in Scoffin et al. (1992). The three sites which were not sampled were Koh Miang (8°39.02N, 98°38.47E), due to restrictions imposed by the Similan Islands Marine Park, and Shark Point (7°47.55N, 98°24.28E) and Ao Man (7°49.55N, 98°24.21E), where sea conditions were adverse at the time of collection. The eight sampling sites also spanned a marked hydraulic energy gradient as described by Scoffin et al. (1992).

2.2.2 Growth data

Between February and April 2007, a single coral lobe of 20–30 cm diameter was collected from the apex of each of eight colonies of *P. lutea*, 1–4 m in diameter at a depth of about 0.5–1 m below the low tide datum at each site following the same methods described in Scoffin et al. (1992). Linear extension rate, bulk density and calcification rate of corals sampled for the period of December 2003–November

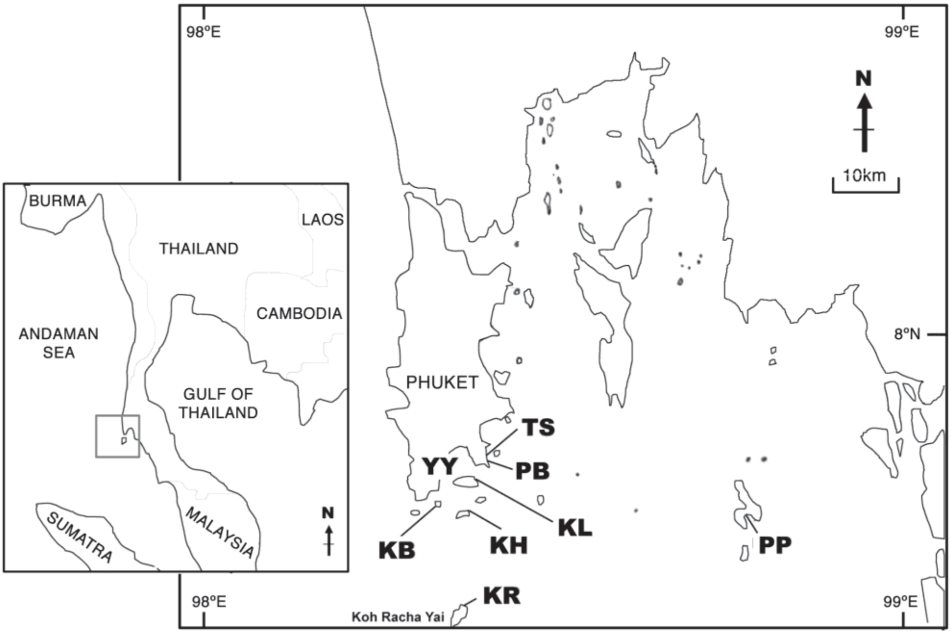

Fig. 2.1. Study area in South Thailand showing reef sampling sites. *KL* Koh Lon; *TS* Tin Smelter; *PB* Porites Bay; *PP* Phi Phi; *YY* Yam Yen; *KB* Koh Bon; *KH* Koh Hae; *KR* Koh Racha Yai

2005 were recovered from luminescent banding patterns in cut sections of coral (see Fig. A2.1 in Appendix 2.5 below). In summary, alizarin staining and regular (sub-annual) sampling over a several year period was used by Scoffin et al. (1992) to determine the timing of deposition of the clear annual fluorescent banding in corals in the study areas; this banding was then used to identify annual growth increments for both studies. While linear extension rates were recovered from all coral slabs collected, only five slabs from each site were used for skeletal bulk density measurements due to limitations on transport of the corals from Thailand to the United Kingdom. Growth and polyp density (corallites cm^{-2} of coral surface) data from the period of December 1984–November 1986 were obtained from Scoffin et al. (1992) and were used for comparison with recent measurements. All parameters were measured following methods used by Scoffin et al. (1992). Observer error was minimised between the two studies by the participation of two of the original authors (BEB and AWT) from the earlier study.

Additional data for linear extension for some sites was also obtained from earlier work for 1990 (Tudhope et al. 1992) and in this study for the years 2001, 2002 and 2003. This data was used in the linear regression analyses for individual sites against mean annual SST (see 2.2.4. Statistical analyses below). Coral tissue thickness has also been recognised as an important growth characteristic that can affect coral growth (Barnes and Lough 1992), and in order to investigate variations in skeletogenesis, tissue thickness of all corals sampled was measured to examine possible relationships between tissue thickness, other growth parameters and hydraulic energy. Tissue thickness was measured using methods described in Barnes and Lough (1992).

2.2.3 Environmental data

Several data sets of regional environmental variables over the period of January 1960–December 2006 were examined. Monthly SST (°C) for the 1°area grid for the location of the study area (07°–08°N; 98°–99 E) was obtained from the HadISST data set (HadISST, Version 1.1, Hadley Centre for Climate Change, UK Meteorological Office) (Rayner et al. 2003). Monthly mean sea level data was obtained from the University of Hawaii Sea Level Centre/National Oceanographic Data Centre Joint Archive for Sea Level for the Ko Taphao Noi station, Phuket (07°49.9 N, 98°25.5 E), ~1.5 km from the inshore sampling sites. Daily rainfall, wind speed and sun hours were obtained from the Phuket Airport weather station (08°06.5 N, 98°91.0 E). Rainfall and wind speed data was available from 1968 to the present, and sun hours from 1981.

These environmental variables were chosen since they represent conditions that might affect coral calcification. The link between SST and coral calcification is well established (see Lough and Barnes 2000). Water depth (i.e. sea level) has been shown to strongly affect light penetration at Phuket (Dunne and Brown 1996) and hence light availability for light-enhanced calcification. Rainfall was used as an indicator of the amount of terrestrial run-off that reefs might have received, which could affect water turbidity (i.e. light availability), nutrients, and possibly pollutants. Wind speed was used as a proxy for wave action, which would also affect turbidity, particularly on shallow reefs such as those sampled in this study. Sun hours was used as a proxy for the surface solar radiation.

2.2.4 Statistical analyses

Changes in coral growth over time

Separate linear regressions were used to examine trends in linear extension rate, bulk density, calcification and polyp density between the two time periods (December 1984–November 1986 and December 2003–November 2005) at each of the eight sites. Residuals were checked for normality. Spearman ranked correlations were used to test whether the relationship between growth patterns and hydraulic energy remained similar over time. Ranking of hydraulic energy of reef sites followed that used in Scoffin et al. (1992). Pearson’s correlations were used to investi- gate relationships between tissue thickness and other growth parameters, and tissue thickness and hydraulic energy. MINITAB 15 was used for all statistical analyses for changes in growth over time.

Changes in environmental variables over time

The time series of the environmental data sets were examined using Autocorrelation (ACF) and Partial Auto-correlation (PACF) plots and found to contain both a first order correlation and a further seasonal element. The seasonality was removed using Seasonal Decomposition (SPSS 15) followed by an Autoregression using the Prais-Winsten method (SPSS 15) to remove the first order autocorrelation and produce a regression equation for the long-term trend. Residuals were checked using ACF and PACF to ensure that no autocorrelation remained. Trends in the environmental variables were examined for the longest available period of each dataset between the years 1960 and 2006, encompassing the period of growth studies (December 1984–November 2005).

Relationship between coral growth and environmental variables

Linear regression was used to identify relationships between linear extension and environmental variables (i.e. mean annual SST, annual sea level, total annual rainfall, annual wind speed and total annual sun hours) using both the data from 1985 to 1986 and 2004 to 2005, and the additional data from the years 1990, 2001, 2002 and 2003 where available. Differences in linear regressions were examined using analyses of covariance (ANCOVA).

2.3 Results

2.3.1 Changes in coral growth over time

There was a significant reduction in calcification and linear extension at three of the eight sites (Calcification: YY, KB, KH) (Linear Extension: PB, KB, KH) (Table 2.1; Fig. 2.2) between the two time periods. Calcification rates at these sites decreased by an average of 23.5% and linear extension rates by 23.4%. Bulk densities for the periods of December 1984–November 1986 and December 2003–November 2005 were not significantly different (1.19 ± SE 0.02 g cm^{-3} and 1.2 ± SE 0.03 g cm^{-3}, respectively). Correlation analyses suggested that changes in calcification were a function of variations in linear extension ($R=0.782$, $P < 0.001$, $n=39$) and not bulk density ($R=0.189$, $P=0.25$, $n=39$). For polyp density there was a significant increase at two sites (PP, YY), with a mean increase of 42%, although this was highly variable between the two (Table 2.1).

Table 2.1. Data for linear extension, calcification and polyp density from each site at two time periods. Significant trends between the two periods determined by linear regression shown in bold text. ns = non significant. R^2 shown adjusted for degrees of freedom.

Site	1984-1986			2003-2005			Difference	% difference	Linear regression	
	Mean	SE	*n*	Mean	SE	*n*			P	R^2 (%)
Linear extension (cm yr^{-1})										
KL	2.233	0.138	9	1.921	0.102	9	-0.312	-14	ns	
TS	2.19	0.213	11	1.708	0.124	8	-0.483	-22	ns	
PB	**2.369**	**0.181**	**8**	**1.683**	**0.119**	**8**	**-0.685**	**-28.9**	**0.007**	**37.50**
PP	2.189	0.019	7	2.159	0.06	8	-0.029	-1.3	ns	
YY	1.825	0.086	10	1.531	0.115	7	-0.294	-16.1	ns	
KB	**2.055**	**0.116**	**9**	**1.61**	**0.083**	**7**	**-0.466**	**-19.6**	**0.01**	**34.10**
KH	**2.377**	**0.128**	**15**	**1.911**	**0.105**	**8**	**-0.446**	**-21.7**	**0.024**	**18.20**
KR	1.668	0.098	14	1.542	0.125	9	-0.126	-7.6	ns	
Calcification rate (g cm^{-2} yr^{-1})										
KL	2.465	0.132	9	2.356	0.071	5	-0.109	-4.4	ns	
TS	2.212	0.128	11	1.95	0.091	5	-0.262	-11.9	ns	
PB	2.519	0.122	8	2.135	0.189	4	-0.384	-15.3	ns	
PP	2.518	0.054	7	2.57	0.074	4	0.052	2.1	ns	
YY	**2.273**	**0.098**	**10**	**1.683**	**0.156**	**5**	**-0.59**	**-25.9**	**0.005**	**31.9**
KB	**2.515**	**0.097**	**9**	**1.935**	**0.246**	**3**	**-0.58**	**-23.1**	**0.02**	**36.5**
KH	**2.824**	**0.111**	**15**	**2.22**	**0.097**	**6**	**-0.604**	**-21.4**	**0.005**	**31.9**
KR	2.221	0.13	14	2.046	0.179	7	-0.175	-7.9	ns	

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(Table 2.1…continued from previous page)

Site	1984-1986			2003-2005			Difference	% difference	Linear regression	
	Mean	SE	*n*	Mean	SE	*n*			P	R^2 (%)
Polyp density (polyps cm^{-2})										
KL	0.644	0.026	9	0.74	0.054	9	0.096	14.8	ns	
TS	0.694	0.038	11	0.705	0.047	8	0.011	1.6	ns	
PB	0.678	0.038	8	0.701	0.02	7	0.023	3.5	ns	
PP	**0.513**	**0.043**	**7**	**0.854**	**0.064**	**8**	**0.341**	**66.4**	**0.001**	**55.3**
YY	**0.677**	**0.034**	**10**	**0.793**	**0.038**	**7**	**0.116**	**17.1**	**0.04**	**20.3**
KB	0.753	0.041	9	0.721	0.022	7	-0.031	-4.1	ns	
KH	0.71	0.042	15	0.683	0.022	7	-0.027	-3.8	ns	
KR	0.708	0.029	14	0.763	0.072	9	0.055	7.8	ns	

Spearman ranked correlations showed that relationships between growth parameters and the hydraulic energy of the eight sites were conserved between the two sampling periods with the exception of bulk density where the pattern was only significant for the period December 1984–November 1986 (Scoffin et al. 1992). The lack of correlation between bulk density and hydraulic gradient in the recent data may be due to the reduction in sample size from n=83 to n=39. Tissue depth was positively correlated with linear extension (R=0.251, P<0.05, n=65) and negatively correlated to polyp density (R=-0.358, P<0.01, n=61).

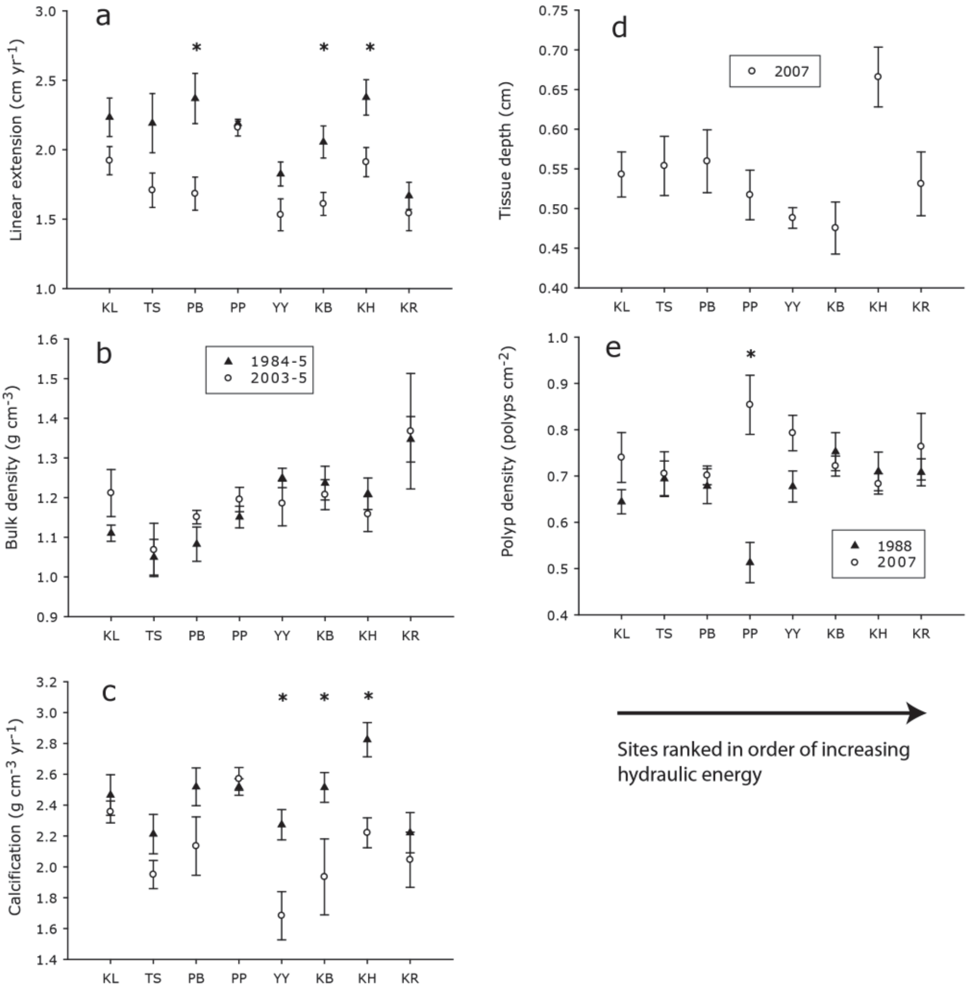

Fig. 2.2. a) Linear extension rate, b) skeletal bulk density, c) calcification rate, for the two time periods 1984–1986 and 2003–2005; d) tissue depth (2007), and e) polyp number per unit area for 1988 and 2007. Sites ranked in order of increasing hydraulic energy (Scoffin et al. 1992). Means ± SE. Asterisks = significant difference between sampling periods from linear regression analysis (Table 1.1)

2.3.2 Changes in environmental parameters over time

There was a significant increase in SST ($P<0.0001$) at a rate of 0.161°C per decade for the period examined (i.e. 1960–2006) (Fig. 2.3). This increase is of a similar order to the previously reported trend at this location between 1946 and 1995 (0.126°C per decade; Brown et al. 1996). There was also a significant rise in sea level over the time period 1960–2006 ($P<0.001$) at a rate of 30.7 mm per decade and a significant ($F_{[1:551]}=67.5$, $P<0.001$) increase in the number of occurrences of positive sea level anomalies during this period. Sun hours (1981–2005), rainfall (1968–2006) and wind speeds (1968–2006) all had no significant long-term trends.

2.3.3 Relationship between coral growth and environmental variables at specific sites

Since the linear regressions had demonstrated significant differences in linear extension for three sites, separate linear regressions were computed for annual extension data from each reef site against annual metrics of SST, sea level, total rainfall, wind speed and sun hours.

For linear extension, adding the additional data (1990, 2001, 2002, 2003) to that for the two growth periods, gave significant linear regressions between mean annual SST and linear extension for five of the eight sites (KL, TS, PB, KH, and KB) (Table 2.2). The intercepts of these regression lines were significantly different (ANCOVA, $P<0.01$) but not the slopes ($P=0.54$), indicating that at each site the scale of temperature dependence of linear extension was the same (Fig. 2.4). Using a pooled slope there was a 19.4% decrease in linear extension over the mean SST range from 1984 to 2005. This compares to a value of 23.4% from the earlier regressions for three sites. At a further site, YY, a significant regression was found for a function $y = a + be^{-x}$ ($P=0.043$) which is also shown in Fig. 2.4 for comparison.

In 2003, *P. lutea* colonies around Phuket bleached, but the event was not severe and recovery was rapid (N. Phongsuwan pers. comm.). Removal of data for 2003 from the linear regressions (Table 2.2) had no overall effect on results other than for KL where the regression with SST was no longer significant ($P=0.067$), probably due to the reduction in N. This result suggests that any bleaching in 2003 did not affect the relationship between mean annual SST and linear extension. For mean annual rainfall there was no relationship with linear extension at any site, whilst at one site, PP, sea level and wind speed were both significantly negatively related. At two sites, KL and PB, mean sun hours and linear extension were significantly positively related (Table 2.2).

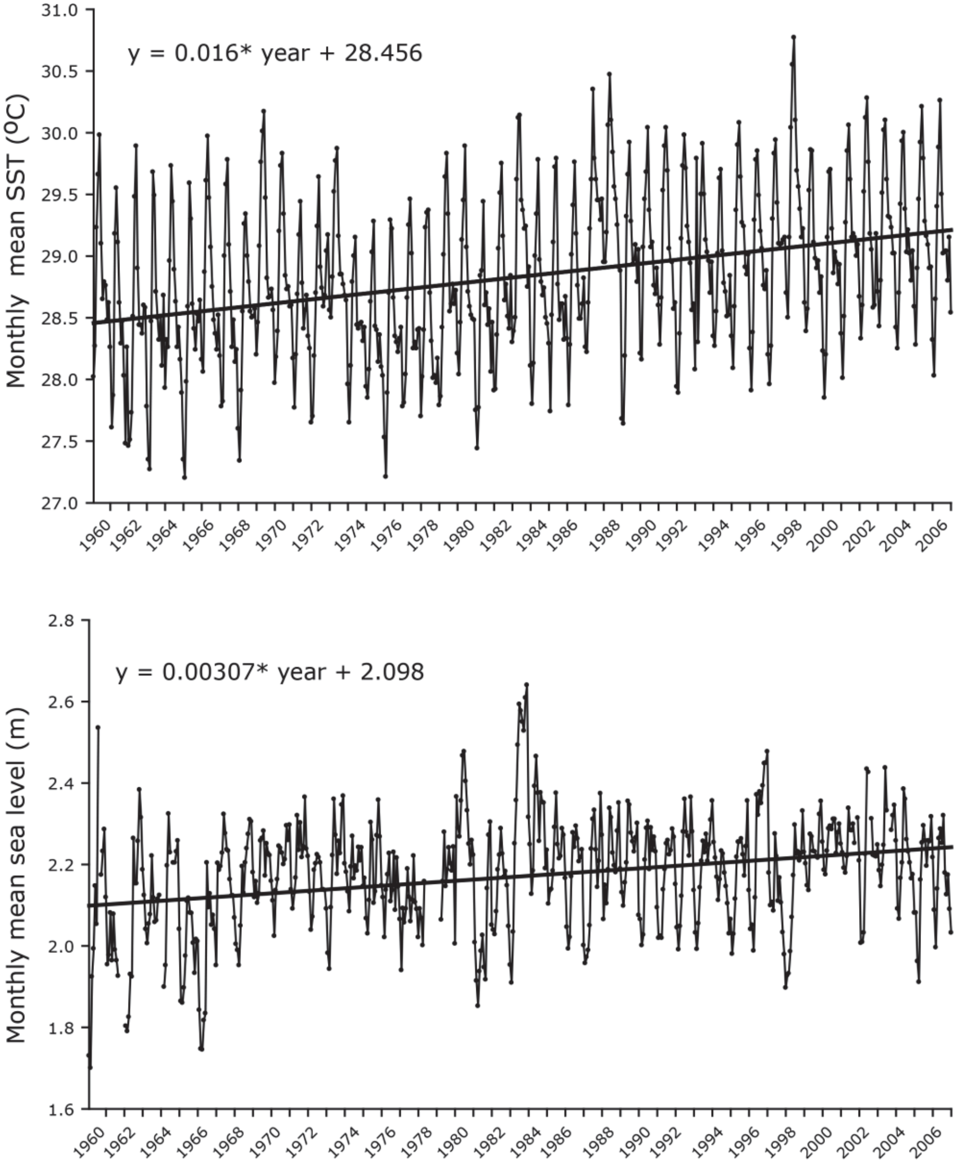

Fig. 2.3. Time series for a) sea surface temperature (SST) and b) sea level for the Phuket region from 1960 to 2006. Regression lines and equations are shown ($P<0.001$)

Table 2.2. Linear regressions for the relationship between linear extension and environmental variables. All residuals were normally distributed and all R^2 shown are adjusted for degrees of freedom. ns = non significant; –ve or +ve is the direction of the slope of the line in each case

			Environmental variables (mean annual values)				
Site	Years analysed	*n*	SST	Sea level	Rainfall	Wind speed	Sun hours
KL	1985, 1986, 2002, 2003, 2004,2005	42	$P < 0.02$, $R^2 = 10.7\%$ **-ve**	ns	ns	ns	$P = 0.041$, $R^2 = 7.8\%$ **+ve**
TS	1985, 1986, 2002, 2003, 2004, 2005	45	$P < 0.017$, $R^2 = 10.6\%$ **-ve**	ns	ns	ns	ns
PB	1985, 1986, 1990, 2002, 2003, 2004, 2005	50	$P < 0.0001$, $R^2 = 27.8\%$ **-ve**	ns	ns	ns	$P = 0.006$, $R^2 = 13.1\%$ **+ve**
PP	2001, 2002, 2003, 2004, 2005	30	ns	$P < 0.0001$ $R^2 = 25.9\%$ **-ve**	ns	$P < 0.0001$ $R^2 = 51.9\%$ **-ve**	ns
YY	1985, 1986, 2003, 2004, 2005	35	ns - $P = 0.0508$ Non linear ($y = a + be^{-x}$) $P = 0.043$, $R^2 = 15.9\%$ **-ve**	ns	ns	ns	ns
KH	1985, 1986, 2002, 2003, 2004, 2005	55	$P < 0.001$, $R^2 = 15.9\%$ **-ve**	ns	ns	ns	ns
KB	1985, 1986, 2004, 2005	28	$P < 0.001$, $R^2 = 30.7\%$ **-ve**	ns	ns	ns	ns
KR	1985, 1986, 2001, 2002, 2003, 2004, 2005	61	ns	ns	ns	ns	ns

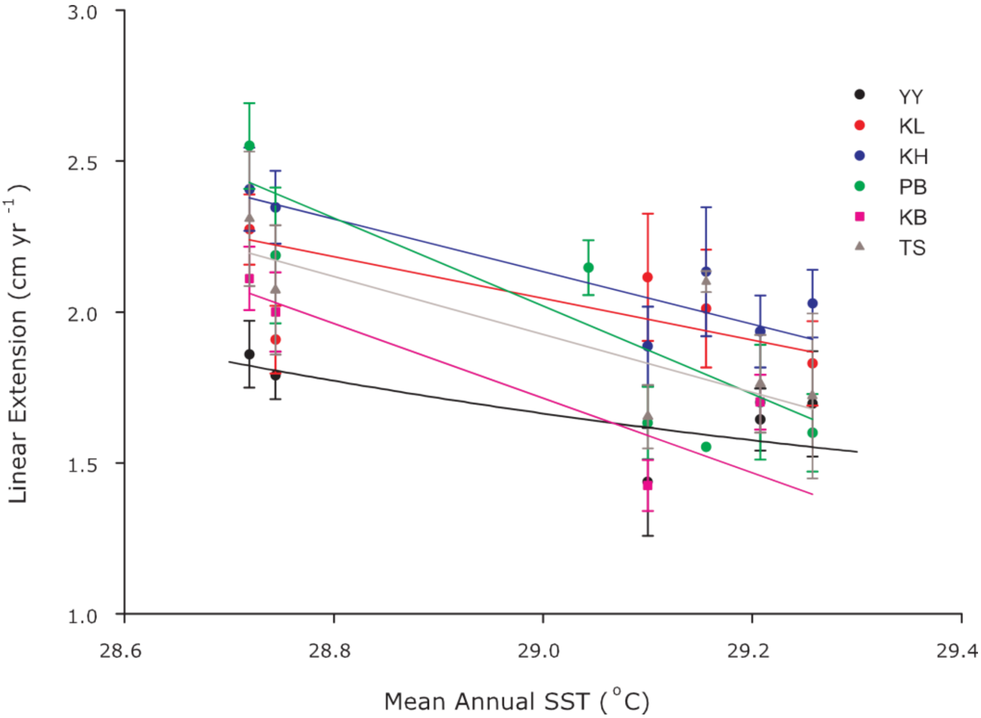

Fig. 2.4. Regressions of linear extension rates (mean ± SE) of corals sampled from six of the sites plotted against mean annual SST. See Table 2 for regression parameters

2.4 Discussion

In this study, the annual nature of fluorescent banding in the coral skeletons was used to identify annual growth increments, and hence to identify areas from which to measure the growth parameters (linear extension, bulk density and calcification rate). It is important to acknowledge that annual growth increments defined in this way rely on an assumption that the timing of band formation (in this case the onset of deposition of bright fluorescent bands) occurs at the same time of year for each of the years of interest, and, therefore, that ‘years’ so defined represent 12 months of growth (and not, for example, 11 or 13 months). There are several lines of evidence that suggest this was the case. Firstly, over the period 1986–1991 *Porites* coral heads at the study site were regularly stained with alizarin, and subsampled, and the results indicated that over this period the timing of onset of fluorescent band deposition was the end of November to the beginning of December in each case, and was highly reproducible between corals and sites (Scoffin et al. 1992). Furthermore, analysis of the environmental records, including SST, sun hours, wind and rainfall indicate that the two sampling intervals for this study (1984–

1986 and 2003–2005) were not unusual in terms of the timing of environmental seasonality, i.e. the onset of the NE and SW monsoon and associated changes in cloudiness, rainfall, and the seasonal cycle of SST were close to the long term averages. Thus, it is unlikely that the coral band-defined ‘years’ are in error by more than about 1 month over the two-year sampling periods. This relatively small uncertainty (<5%) cannot explain the measured reduction in linear extension for the recent period compared to the earlier period. Additional supporting evidence comes from coral cores. Examination of a core from a *P. lutea* colony from PB (Scoffin et al. 1992) indicates that the growth increment for December 1984–November 1986 was not anomalous compared to adjacent years. Finally, growth data for the additional years (1990, 2001, 2002, 2003), which are shown in Fig. 2.4, confirms that growth for the period December 2003– November 2005 was also not anomalous.

The current study found a decrease in rates of calcification (23.5%) and linear extension (between 19.4% and 23.4%) of *P. lutea* at a number of the sampled sites in the eastern Andaman Sea between the periods December 1984–November 1986 and December 2003–November 2005. Among the climatic variables examined in this study, variations in SST over the last two decades related most closely to the variations in linear extension rates. An increase of 0.42°C in SST was found between the two specific growth periods examined (from 28.73 ± SD 0.55°C in December 1984–November 1986 to 29.15°C ± SD 0.54°C in December 2003–November 2005), of a similar order to the decadal increase of 0.1606°C for the 40 year period analysed from 1960–2006. These variations in SST and the decreases in extension and calcification rates suggest a decrease in extension rate of approximately 46–56% for every 1°C rise in SST.

Cooper et al. (2008) also observed a decrease in calcification (~21%), linear extension (~16%) and bulk density (~6%) of colonies of the massive coral *Porites* on the northern Great Barrier Reef over a 16-year period (1988–2003) that also coincided with an increase in SST (0.24°C per decade) over the 16 years examined. In addition, Cooper et al. (2008) defined an optimum temperature of 26.7°C for extension and calcification of massive *Porites* on the Great Barrier Reef, with extension and calcification rates decreasing by 15% per 1°C either side of this temperature. This result is consistent with other experimental studies, where the optimum temperature for calcification was ~27°C (Clausen and Roth 1975; Highsmith 1979; Marshall and Clode 2004; Al-Horani 2005). Taking Cooper et al.’s (2008) values, the decrease in linear extension in massive *Porites* was ~41% for every 1°C rise in SST. The reefs around Phuket sampled in the current study experience an average monthly mean SST of >28°C with maximum summer SSTs reaching >30°C (Fig. 3), higher than those found on the northern Great Barrier Reef by Cooper et al. (2008) (average SST <27°C). Notwithstanding this difference, the decrease in coral growth rates for these reefs around Phuket and those in the cooler northern Great Barrier Reef (average SST <27°C) are comparable, although there is some evidence that the higher overall SST at Phuket is associated with a slightly larger decrease in linear extension. On the basis of these two studies alone, it is difficult to be certain whether the warmer sea temperature regime at Phuket is a factor associated with a more precipitous decline or whether the corals in each location are thermally acclimatised to their respective local regimes. However, it should be noted that while Cooper et al. (2008) recorded a decline in linear extension, calcification and skeletal density over time, the current study found a decrease in only calcification and linear extension rates while bulk density remained unchanged.

The principle of light-enhanced coral calcification, mediated by zooxanthellae activity, is well established (Goreau and Goreau 1959; Barnes and Chalker 1990; Gattuso et al. 1999). It is interesting to note that photosynthesis in cultured zooxanthellae is impaired at temperatures above 30ºC (Iglesias-Prieto et al. 1992) and it follows that any negative effect on zooxanthellae activity could ultimately influence skeletal growth in *Porites*. Earlier work, involving a comparison of monthly rates of linear extension and calcification with environmental variables in *Acropora cervicornis* by Gladfelter (1984), suggested that temperatures outside the optimal range might cause a decrease in linear extension while calcification was more influenced by light availability. Since seasonal maximum temperatures now regularly exceeding 30°C in the eastern Andaman Sea, it is possible that linear extension in corals is constrained by the steadily rising sea temperatures in the region.

Although increases in SST showed the strongest and most consistent relationship with decrease in linear extension rates, the effects of other changing environmental variables should not be discounted. Increased nutrients (e.g. Marubini and Davies 1996), decreased light (Barnes and Chalker 1990) and changes in seawater chemistry (i.e. increase in CO_2 partial pressure (pCO_2) along with decreases in pH and aragonite saturation state (Ω_{arag})) (e.g. Reynaud et al. 2003) have also been shown to reduce calcification. While human disturbances (e.g. dredging, tourism, development) around Phuket have increased in recent years, there is no evidence that either nutrients or sediments have influenced the observed decrease in calcification. The decrease in coral growth did not differ between sites (ANCOVA slopes P=0.54), a result which is not consistent with any change in the inshore to offshore gradient over time. Sea level over the last 50 years has been rising faster in the Andaman Sea than anywhere else in the world (Church et al. 2004). The 30.7 mm decadal increase during the growth study period (1984–2005) rep- resents a rise of 6 cm, which could negatively influence both light penetration and ultimately coral growth in the turbid and highly coloured water types that characterize the region (Dunne and Brown 1996).

Water quality records from around Phuket showed no trend in sea surface pH from 1990 to 2006 (range 7.8–8.9; mean 8.24 ± SD 0.18) (S. Khokiattiwong pers.

comm.). Previous work by Pelejero et al. (2005) based on a *P. lutea* core suggested that natural fluctuations in pH and Ω_{arag} in the last ~300 years within the lagoon of Flinders Reef (Australia) had no apparent effect on calcification. There is no other evidence to suggest a marked decrease in pH or Ω_{arag} over the last two decades that would result in the significant decrease in coral calcification rates seen in the current study. Nevertheless, effects of increased temperatures and decreased Ω_{arag} have been observed to augment reductions in calcification. Reynaud et al. (2003) reported that at higher $p\mathrm{CO}_2$ (i.e. implying lower pH and Ω_{arag}), an increase in temperature reduced calcification in *Stylophora pistillata* by as much as ~60% demonstrating that the effects of Ω_{arag} cannot be disregarded.

Since *P. lutea* along with other *Porites* species are the dominant reef-building corals in the eastern Andaman Sea (Phongsuwan and Chansang 1992; Brown 2007), the decrease in growth rates recorded in this study might imply a decline in the 'health' of these reefs. However, ecological studies have demonstrated that the reefs in this region are in good condition in terms of hard coral cover and species diversity despite rising sea temperatures (Brown and Phongsuwan 2004; Brown 2007). Although the observed reduction in coral growth rate reported at these sites provides cause for some concern, it is important to view this in context. Massive *Porites* corals in this area currently have high linear extension and calcification rates when compared to other locations in the Indo-Pacific (Lough and Barnes 2000). A modest reduction in coral growth, therefore, does not in itself imply that the corals and/or reefs are in imminent danger of major structural and compositional change (e.g. over the next 1–2 decades). However, the longer-term future of these corals and reef systems will potentially depend on the trajectory of rising SST and $p\mathrm{CO}_2$. The impact of these factors on coral growth (singly and combined), when the changes are applied relatively gradually but essentially unidirectional over decadal and longer time frames, remains poorly understood and warrants further study through manipulative field and laboratory studies, as well as through detailed field observation and reconstruction of past trends through sclerochronology.

2.5 Appendix

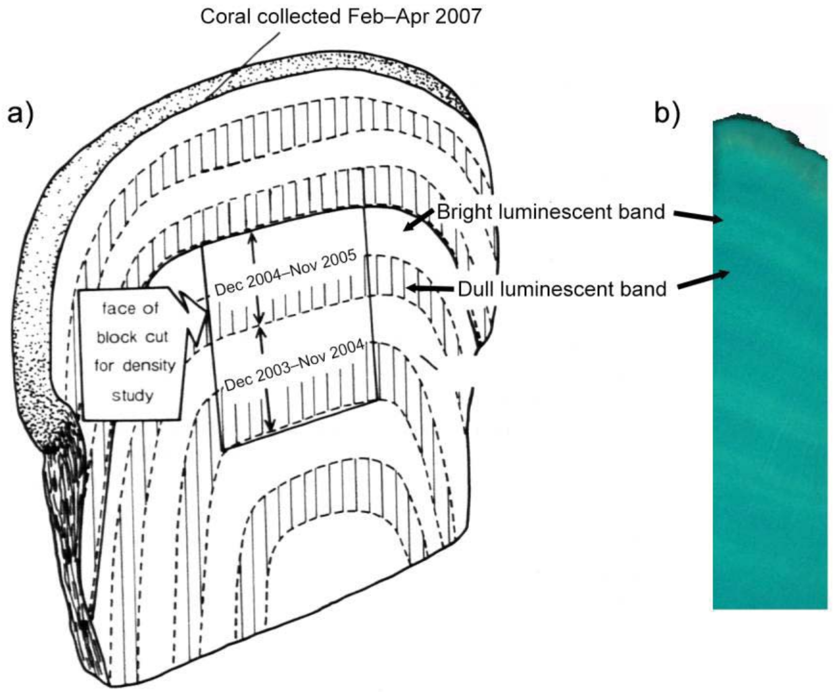

Fig. A2.1. a) Schematic illustration indicating the position of the block cut out for density measurement, and b) the bright/dull luminescent bands as seen in slabbed *P. lutea*.