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 THREE

Regional Decline in Growth Rates of Massive *Porites* Corals in Southeast Asia[2]

This study reports the first well-replicated analysis of continuous coral growth records from warmer-water reefs (mean annual SST >28.5ºC) around the Thai-Malay Peninsula in Southeast Asia. Based on analyses of 70 colonies sampled from 15 reefs within six locations, region-wide declines in coral calcification rate (~18.6%), linear extension rate (~15.4%) and skeletal bulk density (~3.9%) were observed over a 31-year period from 1980–2010. Decreases in calcification and linear extension rates were observed at five of the six locations and ranged from ~17.2-21.3% and ~11.4-19.6% respectively, while decline in skeletal bulk density was a consequence of significant reductions at only two locations (~6.9% and ~10.7%). A significant link between region-wide growth rates and average annual SST was found, and *Porites* spp. demonstrated a high thermal threshold of ~29.4ºC before calcification rates declined. Responses at individual locations within the region were more variable with links between SST and calcification rates being significant at only four locations. Rates of sea temperature warming at locations in the Andaman Sea (Indian Ocean) (~1.3ºC decade^{-1}) were almost twice those in the South China Sea (Pacific Ocean) (~0.7ºC decade^{-1}), but this was not reflected in the magnitude of calcification declines at corresponding locations. Considering that massive *Porites* spp. are major reef-builders around Southeast Asia, this region-wide growth decline is a cause for concern for future reef accretion rates and resilience. However, this study suggests that the future rates and patterns of change within the region are unlikely to be uniform or dependent solely on the rates of change in the thermal environment.

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3.1 Introduction

Declines in calcification rates have been detected within the last ~20–30 years for several tropical reefs along the Great Barrier Reef, the Mesoamerican Barrier Reef, around Phuket (Thailand), and in the central Red Sea (Cooper et al. 2008; Tanzil et al. 2009; De'ath et al. 2009; Carricart-Ganivet et al. 2012). Although coral calcification rates are influenced by a variety of environmental parameters such as light, nutrients, salinity, pH, and sedimentation (Barnes and Chalker, 1990; Gattuso et al. 1999), several recent studies suggest that these changes in long-term calcification rates have been driven primarily by temperature (Cantin et al. 2010; Cooper et al. 2012; Carricart-Ganivet et al. 2012). The directional shift in calcification rate trajectories implies that, at least on these reefs, environmental and/or biological threshold/s of coral growth may have been exceeded.

A link between coral growth and temperature is considered well-established, with calcification rates repeatedly shown to increase with rising temperature up to a thermal maximum, and then to decline steeply with further increases in temperature (e.g. Clausen and Roth 1975; Jokiel and Coles 1978; Highsmith 1979; Marshall and Clode 2004). Analysis of growth records of massive *Porites* corals along the Great Barrier Reef (GBR) revealed a widespread decline in calcification rates (~14.2%) since ~1990 that is unprecedented within the last four centuries (De'ath et al. 2009). Similar growth reductions for massive *Porites* at four sites in two regions on the Northern GBR were also found by Cooper et al. (2008) (~21%, for 1988–2003), and by Carricart-Ganivet et al. (2012) at one site in the central GBR (~20%, for 1989–2002). These reported declines were inversely related to increased sea surface temperatures (SST), and contrast with the positive relationship between increasing massive *Porites* calcification rates and rising SSTs found earlier on the GBR for the period 1906–1982 (Lough and Barnes 1997). On the basis of these studies, it could be postulated that the thermal-related maximum for massive *Porites* calcification on the GBR was exceeded sometime in the 1980s, resulting in the recently observed declines.

Decreases in calcification rates strongly associated with rising SSTs have also been reported for *Diploastrea heliopora* (~18%, 1976–1997 vs. 1998–2010) in the central Red Sea (Cantin et al. 2010), and for *Porites asteroides* (~30%, for 1998–2009) and *Montastraea faveolata* (~20%, for 1985–2009) at one site on the Mesoamerican Barrier Reef (MBR) (Carricart-Ganivet et al. 2012). The latter study also found that calcification rates of *P. asteroides* (for 1996–2006) and *Montastraea* spp. (for 1977–2003) remained unchanged at an adjacent MBR site (~40km apart) where no trends in annual SSTs were observed over the study periods, thus strengthening the causal link between SST and changes in calcification rates.

In contrast to the declines found on tropical reefs, continued increases in calcification rates have been reported on high latitude cooler-water reefs. Increases in massive *Porites* calcification rates by ~6.2–23.7% (for 1900–2010) were observed along the central and southwestern Australian coast (average annual SSTs ~21–24ºC) (Cooper et al. 2012) which showed a positive relationship with rising SSTs. A similar result for the colonial coral *Cladocora caespitosa* was also found in the eastern Adriatic Sea (Kružić et al. 2012). Notwithstanding possible adaptation to localised thermal regimes and species responses, it is therefore reasonable to suppose that, in addition to the rate of warming, absolute temperature could affect the direction, and possibly extent, of changes in calcification rate on a particular reef.

The directional shift in calcification trajectories observed within the last ~2–3 decades has mainly been reported from reefs subject to sea temperatures with mean annual SSTs <~27ºC. On the northern GBR, the thermal optimum for massive *Porites* growth rates is suggested to be an average annual SST of ~26.7ºC (Cooper et al. 2008) whilst in the Red Sea, summer temperatures beyond 30.25ºC resulted in reduced growth rates in *Diploastrea heliopora* (Cantin et al. 2010).

Although coral growth records have been examined from reefs subject to high all year round SSTs (~average annual SST >28ºC) with seasonal maxima regularly exceeding 30.5ºC (Cahyarini, 2008; Tanzil et al. 2009; Suharsono and Cahyarini 2012), there is still considerable uncertainty regarding the responses of such corals to recent sea warming trends. When comparing growth rates from two time periods (1984–1986 and 2003–2005), Tanzil et al. (2009) demonstrated a recent decline in *Porites lutea* calcification (~23.5%) and linear extension rates (~19.4–23.4%) but for only 3 out of 8 reefs around Phuket, Thailand. Analyses of growth records for different periods between 1953 and 2011 in ten cores sampled from ten reefs across the Indonesian Archipelago (~108º–132ºE) revealed significant changes in linear growth rates in only 3 of the 10 cores, of which two exhibited declines while another showed an increase (Suharsono and Cahyarini 2012). Similar variable patterns were also reported in an earlier study of three cores sampled from three separate reefs in the Seribu Islands, Jakarta Bay (Cahyarini 2008).

The aim of the current study was to test the hypothesis that there has been widespread, thermally-driven decline in coral growth rates around the Thai-Malay Peninsula in Southeast Asia. It examines continuous growth records of massive *Porites* corals from reefs at six geographical locations spanning ~1600km of coastline (Fig. 2.1). Situated on the western border of the 'Coral Triangle' and within the political boundaries of Thailand, Malaysia and Singapore, these reefs are among the most productive and diverse in the world (Gomez 1989). Over 320 species of stony corals have been reported from this region (Harborne et al. 2000). Massive *Porites* species represent one of the most dominant coral genera found throughout this area (Harborne et al. 2000; Dikou and van Woesik 2006; Brown

2007; Toda et al. 2007), and any reduction in their growth rates could potentially contribute to a regional decline in reef accretion rates.

3.2 Methods

3.2.1 Study site

Fifteen reefs from six locations situated around the coast of the Thai-Malay Peninsula (1–8ºN, 98–105ºE), Southeast Asia (Fig. 3.1, Table 3.1) were sampled. The reefs along the east coast of the Peninsula are based in the South China Sea (western Pacific Ocean), whereas reefs along the west coast are located in the Andaman Sea (northeastern Indian Ocean). Regionally, the Thai-Malay Peninsula experiences high mean monthly SSTs of >27–30ºC all year round (Tanzil et al. 2009) and has a monsoonal climate, although the wet season occurs at different times of the year on the east and west coasts. The east coast typically experiences higher rainfall and stronger winds during the northeast monsoon (Nov–Feb) whilst similar conditions are found on the west coast during the southwest monsoon (Apr–Oct). As a whole, the Peninsula receives a high seasonal rainfall (average ~300mm per month in the wet season) with considerable runoff and substantial loads of river-transported sediments which are then discharged into coastal waters. Consequently, the inshore reefs are often highly turbid, with sedimentation rates known to reach ~50 mg cm^{-2} day^{-1} and horizontal visibility less than 1m, while offshore reefs on islands situated away from the mainland are significantly less turbid, with sedimentation rates averaging ~0.3 mg cm^{-2} day^{-1} (Lee and Mohamed 2011).

3.2.2 Sea temperature

Monthly sea surface temperatures (SST/°C) for a 1° latitude/longitude area grid at each of the six locations sampled were obtained from the HadISST1 data set (HadISST, Version 1.1, Hadley Centre for Climate Change, UK Meteorological Office) (Rayner et al. 2003). The HadISST1 data were used to examine any temporal changes in SSTs at each location, as well as any relationship between annual growth parameters and SSTs over the study period. Hourly temperatures were also collected from in-situ thermistors (Reefnet Inc. Sensus Ultra and HOBO U22-001) (cross-calibrated) at 12 of the 15 reefs sampled (excluding Port Dickson (PD), Pulau Semakau (SEM) and Pulau Jong (JO)). Record lengths varied between 5- and 20-month periods spanning Nov 2009–Oct 2011 and were used to check the accuracy of HadISST1 data, and verify that temperature regimes sampled on reefs at each location were comparable.

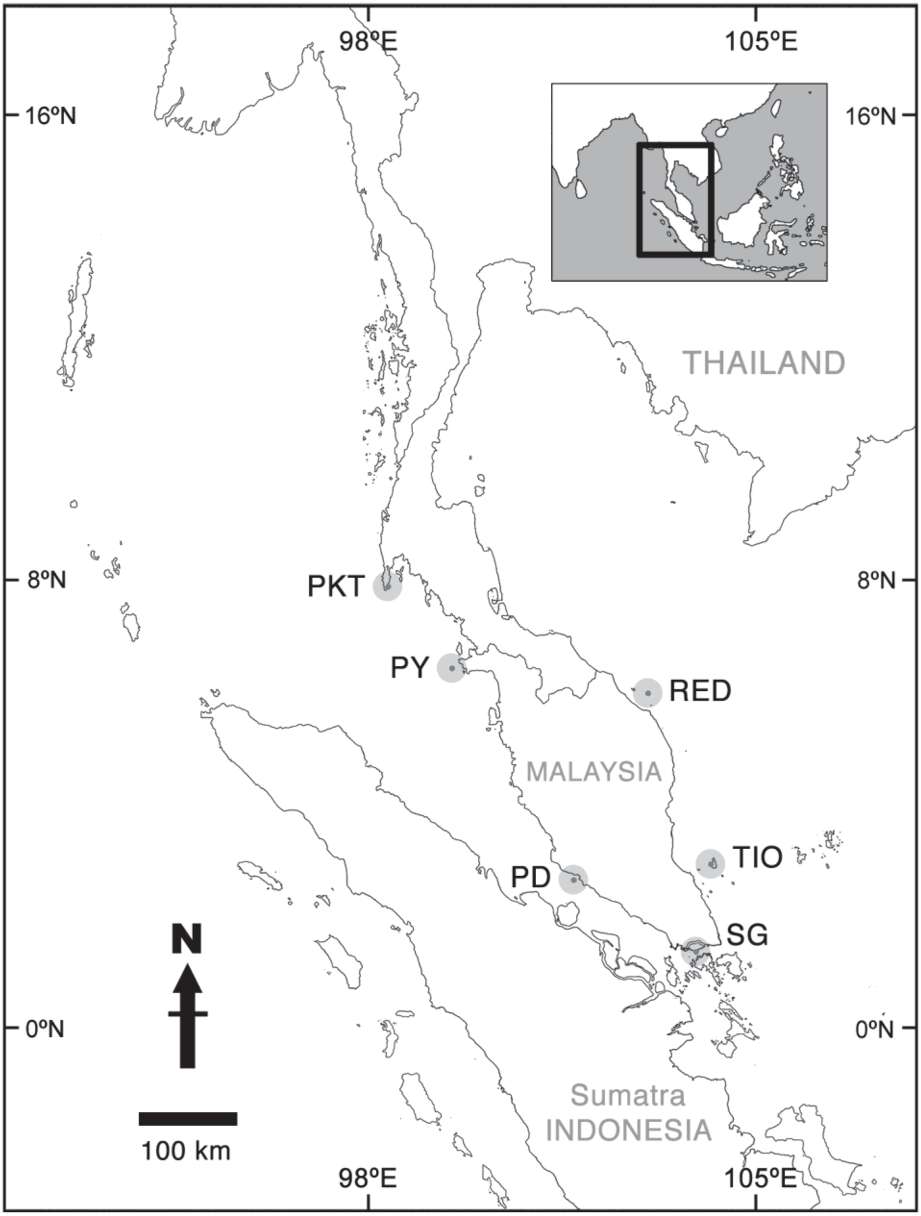


Fig. 3.1. Map showing the six locations sampled around the Thai-Malay Peninsula, Southeast Asia. *PKT* Phuket; *PY* Pulau Payar; *PD* Port Dickson; *SG* Singapore; *TIO* Pulau Tioman; *RED* Pulau Redang

Table 3.1. Coordinates of the 15 reefs sampled within each of the six study locations.

Location	Reef	Latitude (°N)	Longitude (°E)
Phuket (PKT)	Yam Yen (YY)	7.808670	98.399842
	Porites Bay (PB)	7.808795	98.410323
	Koh Hae (KH)	7.745087	98.383352
	Koh Racha Yai (KR)	7.613105	98.372862
P. Payar (PY)	P. Payar house reef	6.063197	100.042028
Port Dickson (PD)	Monkey Bay	2.416383	101.852589
Singapore (SG)	P. Hantu (HT)	1.227286	103.746635
	P. Semakau (SEM)	1.199958	103.756690
	P. Jong (JO)	1.214349	103.786874
	P. Kusu (KU)	1.225487	103.860138
	Raffles Lighthouse (RL)	1.160624	103.740536
P. Tioman (TIO)	Tekek (EDT)	2.817688	104.153781
	P. Tulai (PTU)	2.911470	104.097816
P. Redang (RED)	Redangkalong (RDHR)	5.762533	103.028732
	P. Kerengga Besar (RDKR)	5.754261	103.029364

3.2.3 Measurement of coral growth

Cores from 70 individual massive *Porites* colonies were sampled from the 15 study reefs between Oct 2010 and Jan 2012. All samples were taken from the main growth axis of the coral using a pneumatic drill fitted with a 5 cm diameter, 50cm long diamond bit core barrel at depths ~2–3m below mid-tide height from colonies ~1–4m in diameter (see Fig. A3.1 in Appendix 3.5). Although it was not possible to conclusively identify all sampled colonies to species level, they were of similar morphological characteristics and the majority (~71%) was positively identified as *Porites lutea*. Since similar growth characteristics have been recorded in 3 of the 4 large *Porites* spp. known in the Indo-Pacific (Lough et al. 1999) we are confident that any species effect on growth rate would be negligible in this study. Slices (~7mm thick) were obtained from these cores and examined for annual growth parameters including linear extension (cm year^{-1}) and skeletal density (g cm^{-3}). Linear extension was measured as the breadth of the annual luminescent bands visually estimated from digital photographs of each core taken under ultraviolet light (365nm) (e.g. Fig. A3.2). Measurements were cross-validated with alizarin staining over a two-year period. Skeletal densities for corresponding years were analysed using digitised X-ray images (Carricart-Ganivet and Barnes 2007) and verified against gamma densitometry at the Australian Institute of Marine Science (Chalker and Barnes 1990). Annual calcification rates (g cm^{-2} year^{-1}) were then derived as a function of these two growth parameters. Although growth data is available as far back as the 1930s for some samples, this paper only focuses on analysis of data over the period ~Dec 1979–Nov 2010 in order to maximise sample sizes. In addition, high linear extension rates and high macro-boring activities observed at some sites dictated that reliable growth data for most cores was only available for this time period.

3.2.4 Statistical analyses

Linear mixed-effects (LME) models were used for analysis of temporal trends in growth parameters and to examine relationships between growth and sea surface temperature (SST) over the period 1980–2010. Preliminary analysis showed that LME models had the best goodness of fit compared to other linear models explored (e.g. Generalised Least Squares GLS, Generalised Linear Model GLM) because they include random effects and account for correlation among observations on the same sampling unit (Pinheiro and Bates 2000). Based on sampling of the data and exploratory analyses, initial models for each growth parameter included predictors ‘Year’ and ‘SSTave’ (averaged annual SST) as fixed effects, and nested random effects in ‘Location’, ‘Site’ and ‘Core’ (individual colony). Smoothing using natural splines was also included for ‘Year’ and ‘SSTave’ effects where applicable and/or when it improved model fits significantly, with the degree of smoothness selected using cross-validation. Trends at both the regional scale and at the six individual locations sampled were examined. All analyses were performed using the statistical program R (version 2.15.1) (R Core Team, 2012), using packages “nlme” (Pinheiro et al. 2013) and “mgcv” (Wood 2006).

Random effects of the model were identified using Residual Maximum Likelihood (REML) fits. Assumptions of normality, homogeneity of variances as well as possible autocorrelations within the dataset were tested. Model random effects tested included random intercept and/or random slope effects for all nested levels, and a 1st order autoregressive term. Fixed effects of model were selected using Maximum Likelihood (ML) fits. Best model fits were sequentially tested and determined using Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and likelihood ratio tests for the data by region, and for each of the six individual locations. Final models for the various growth parameters were cross validated using generalized additive mixed models (GAMMs) (Wood, 2006) and partial effects plots were used to illustrate the effects of ‘Year’ and ‘SSTave’ on annual linear extension rate, skeletal bulk density and annual calcification rate. All model selection procedures were performed on the data by region as well as for each location, and the best model was selected in each case.

In order to investigate any changes in SSTs over the study period (1980–2010), ordinary least-squares regression analyses (R-package "*nlme*") were performed on monthly gridded HadISST1 data for each of the six locations. Autocorrelations within the SST dataset for each location were tested and, where necessary, the appropriate autoregressive terms were included in the regression model. Differences between monthly averaged (night and day) *in-situ* thermistor temperatures and HadISST1 temperatures, and between reefs within each study location, were investigated using paired t-tests after checking for homoscedascity and normality. *In-situ* thermistor data for one reef at Pulau Redang (RDKR) was homoscedastic but non-normal, and Wilcoxon signed-rank tests were instead used in this case.

3.3 Results

3.3.1 Variation in Sea Temperatures

Over the 1980–2010 study period, regression analyses of seasonally decomposed (12th order autoregressive term) HadISST1 data showed significant rises ($P<0.001$) in SSTs at all six locations studied (Fig. 3.2a). Rates of warming were higher for locations on the western side of the Thai-Malay Peninsula, within the Andaman Sea (Indian Ocean), i.e. Phuket (0.142ºC decade^{-1}), P. Payar (0.126ºC decade^{-1}) and Port Dickson (0.131ºC decade^{-1}), compared to locations along the eastern side of the Peninsula in the South China Sea (SCS) (western Pacific Ocean), i.e. P. Redang (0.071ºC decade^{-1}), P. Tioman (0.076ºC decade^{-1}) and Singapore (0.074ºC decade^{-1}). There was also a difference in the annual temperature regime (mean monthly SSTs averaged for the period 1980–2010) with SCS locations experiencing a larger annual range (~27–30ºC) compared to sites on the Andaman Sea (~28–30ºC) although similar maximum monthly temperatures (~30°C) occur at all locations and at the same time of year (Fig. 3.2b).

Pair-wise comparisons of mean monthly *in-situ* thermistor measurements with the HadISST1 data showed that the latter significantly underestimated temperatures at 9 of the 12 reefs examined (Table 2.2). Only HadISST1 data from P. Tioman (PTU and EDT) and one reef at P. Redang (RDKR) were not significantly different from the *in-situ* record. At three of the locations where contemporaneous thermistor records were obtained from different reefs (Singapore, P. Tioman, and P. Redang) no inter-reef temperature differences were found. At Phuket, however, one of the reefs, Koh Racha Yai (KR) experienced significantly cooler temperatures (monthly averaged *in-situ* temperatures ~0.3–0.6ºC lower) compared to the reefs at Koh Hae, Porites Bay and Yam Yen (Table 2). Koh Racha Yai is the most offshore of the reefs at this location and is subject to periodic pulses of anomalously low-temperature seawater (see Fig. A3.3 in Appendix 3.5).

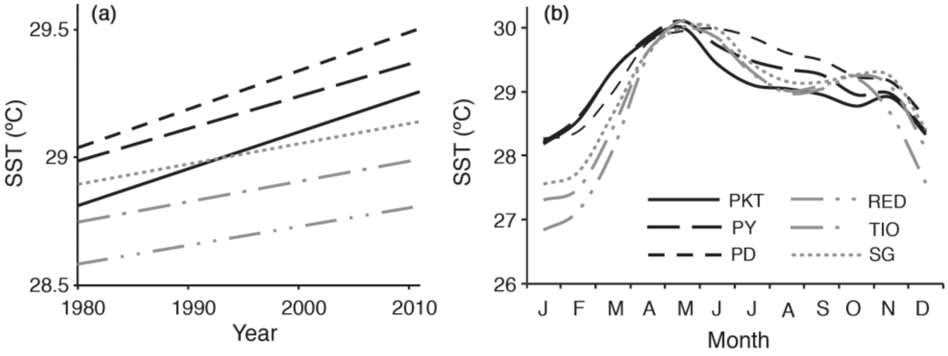


Fig. 3.2. Patterns in sea surface temperature (SST) for all study locations based on HadISST 1° gridded data: (a) trends over time (all slopes $P<0.001$), and (b) seasonal variation in monthly mean temperatures averaged over the period 1980–2010. *PKT* Phuket; *PY* Pulau Payar; *PD* Port Dickson; *SG* Singapore; *TIO* Pulau Tioman; *RED* Pulau Redang

Table 3.2. Pair-wise comparisons of monthly averaged *in-situ* thermistor temperatures with monthly average HadISST1 temperatures and thermistor records between reefs within each location. *P < 005, **P < 0.01, ***P < 0.001

Location	Reef	Paired t-test		t	df	P	Mean difference	SE
Phuket	PB	vs.	HadISST1	6.921	7	***	0.293	0.111
	YY	vs.	HadiSST1	2.185	15	*	0.491	0.123
	KH	vs.	HadISST1	4.284	9	**	0.404	0.128
	KR	vs.	HadISST1	4.025	19	***	0.335	0.075
	PB	vs.	YY	1.296	5	0.2514	–	–
	PB	vs.	KH	1.950	7	0.0922	–	–
	PB	vs.	KR	4.674	7	**	0.645	0.111
	YY	vs.	KH	0.652	4	0.543	–	–
	YY	vs.	KR	3.646	15	**	0.304	0.083
	KH	vs.	KR	3.303	9	**	0.275	0.083
P. Payar	PY	vs.	HadISST1	28.502	4	***	0.084	0.037
Singapore	HT	vs.	HadISST1	3.362	15	**	0.617	0.154
	KU	vs.	HadISST1	2.528	19	*	0.653	0.163
	RL	vs.	HadISST1	2.409	15	*	0.604	0.135
	HT	vs.	RL	1.696	15	0.111	–	–
	HT	vs.	KU	1.936	15	0.072	–	–
	RL	vs.	KU	1.559	15	0.140	–	–
P. Tioman	PTU	vs.	HadISST1	1.245	15	0.232	–	–
	EDT	vs.	HadISST1	1.294	15	0.215	–	–
	PTU	vs.	EDT	0.317	15	0.756	–	–
P. Redang	RDHR	vs.	HadISST1	5.177	5	**	0.620	0.086
		Wilcoxon s-r test		**W**	**n**	**P**		
	RDKR	vs.	HadISST1	15	5	0.0625	–	–
	RDKR	vs.	RDHR	15	5	0.0625	–	–

3.3.2 Regional trends in growth rates

Within the Thai-Malay Peninsula region there was a significant decline in all measured growth parameters in massive *Porites* corals over the period 1980–2010 (Fig. 3.3). The calcification rate decreased by 18.61% ($n=70$, $P<0.001$) and was driven primarily by the decline in linear extension rate (15.44%, $n=70$, $P<0.001$). On average, calcification and linear extension rates declined annually by 0.0144 ± SE 0.0026g cm^{-2} year^{-1} and 0.0104 ± SE 0.0020 cm year^{-1} respectively. Skeletal bulk density showed a lower rate of decline at 0.0015 ± SE 0.0006 g cm^{-3} year^{-1} and an overall reduction of 3.94% ($n=70$, $P<0.05$) over the 31-year study period.

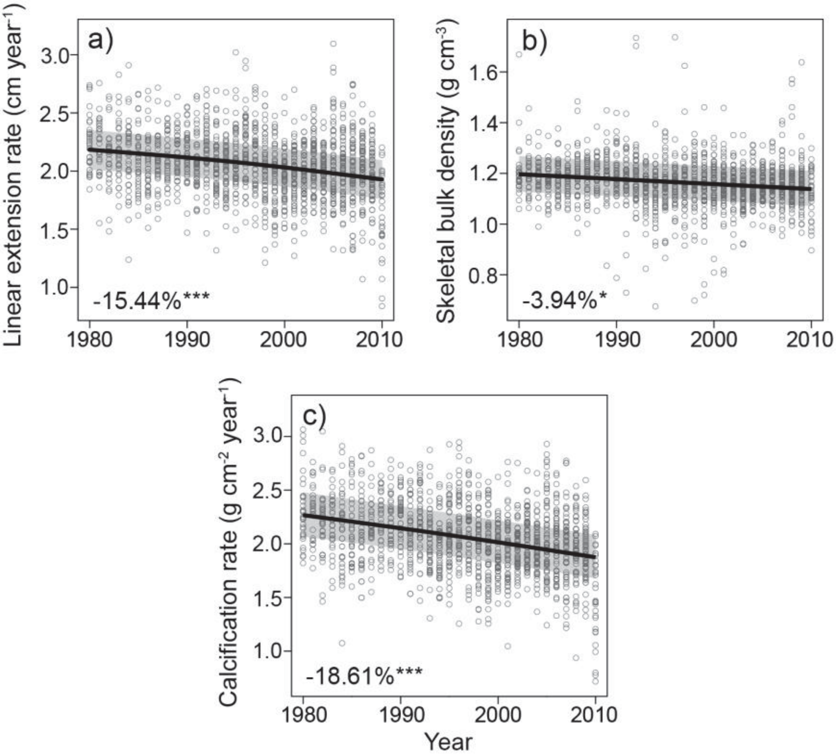


Fig. 3.3. Changes in annual growth parameters (a) linear extension rate, b) skeletal bulk density, and c) calcification rate) over the period 1980–2010 for the Thai-Malay Peninsula region. The solid line represents the best fit linear mixed effects (LME) model; *P<0 05, ***P<0.001; gray area denotes 95% confidence interval

3.3.3 Location trends in growth rates

There was variability in the trend and pattern of growth rates over time between locations (Figs. 3.4 and 3.5) with significant declines in both calcification and linear extension rates at five of the six locations. Calcification rates decreased by 20.52% at Phuket ($P<0.05$), 21.57% at P. Payar ($P<0.001$), 17.18% at Singapore ($P<0.001$), 18.17% at P. Tioman ($P<0.05$) and 21.30% at P. Redang ($P<0.001$). Linear extension rates were reduced by 19.59% ($P<0.05$) at Phuket, 15.77% ($P<0.01$) at P. Payar, 11.43% (0.007 ± SE 0.003cm year^{-1}, n=22, $P<0.05$) at Singapore, 16.78% ($P<0.01$) P. Tioman, and 15.21% ($P<0.001$) at P. Redang (Table 3.3). There were no significant changes in calcification and linear extension rates at Port Dickson, but there was a significant reduction in skeletal bulk density of corals sampled at this location by 10.68% ($P<0.01$). A significant decrease in skeletal bulk density also occurred at P. Redang (6.87%; $P<0.05$). No significant changes in skeletal bulk densities were found at Phuket ($P=0.849$), P. Payar ($P=0.0541$), P. Tioman ($P=0.498$) and Singapore ($P=0.090$).

3.3.4 Relationship between growth rates and sea temperature

At a regional level, temporal changes in all growth parameters covaried strongly with average annual SST (Fig. 3.6). There was a significant non-linear relationship for both calcification ($P<0.001$) and linear extension rate ($P<0.01$) against average annual SST. Both growth parameters declined rapidly above average annual SSTs of ~29.4ºC. Skeletal density, however displayed a significant positive linear relationship with SST ($P<0.05$). At individual locations, the relationship between calcification rates and SSTs was variable. Significant relationships were found at only 4 of the 6 study locations, P. Payar ($P<0.001$), Singapore ($P<0.05$), P. Tioman ($P<0.001$) and P. Redang ($P<0.001$) (Fig. 3.7). At P. Payar, Singapore and P. Redang, there was a modal effect such that calcification peaked at ~29.4ºC, ~29.2ºC and ~28.7ºC respectively, while at P. Tioman calcification declined only at SSTs above ~28.8ºC. There was no relationship between calcification rate and SST at Port Dickson ($P=0.53$) and Phuket ($P=0.22$). At Phuket, the earlier comparison of *in-situ* temperatures had revealed a significant difference in temperature regimes between Ko Racha (KR) (Fig. A3.2) and other reefs within this location. As a result, further analyses were conducted treating KR as a separate location which yielded a borderline, but still not significant, relationship at Phuket (with KR excluded) ($P=0.056$) and no significant relationship at KR ($P=0.40$).

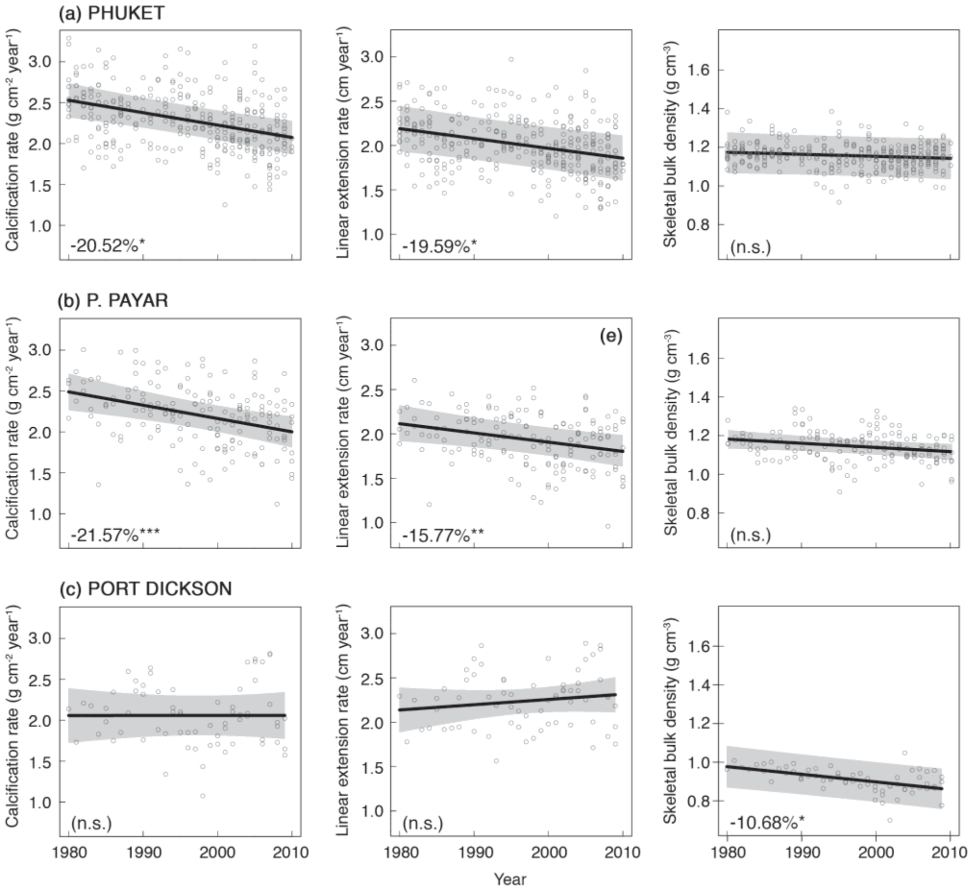


Figure 3.4. Changes in annual growth parameters (calcification rate, linear extension rate and skeletal bulk density) over the period 1980–2010 at locations along the western coast of the Thai-Malay Peninsula – (a) Phuket, (b) P. Payar, and (c) Port Dickson. The solid line represents the best fit linear mixed effects (LME) model; *P<0.05, **P<0.01, ***P<0.001, n.s. = not significant; gray area denotes 95% confidence interval

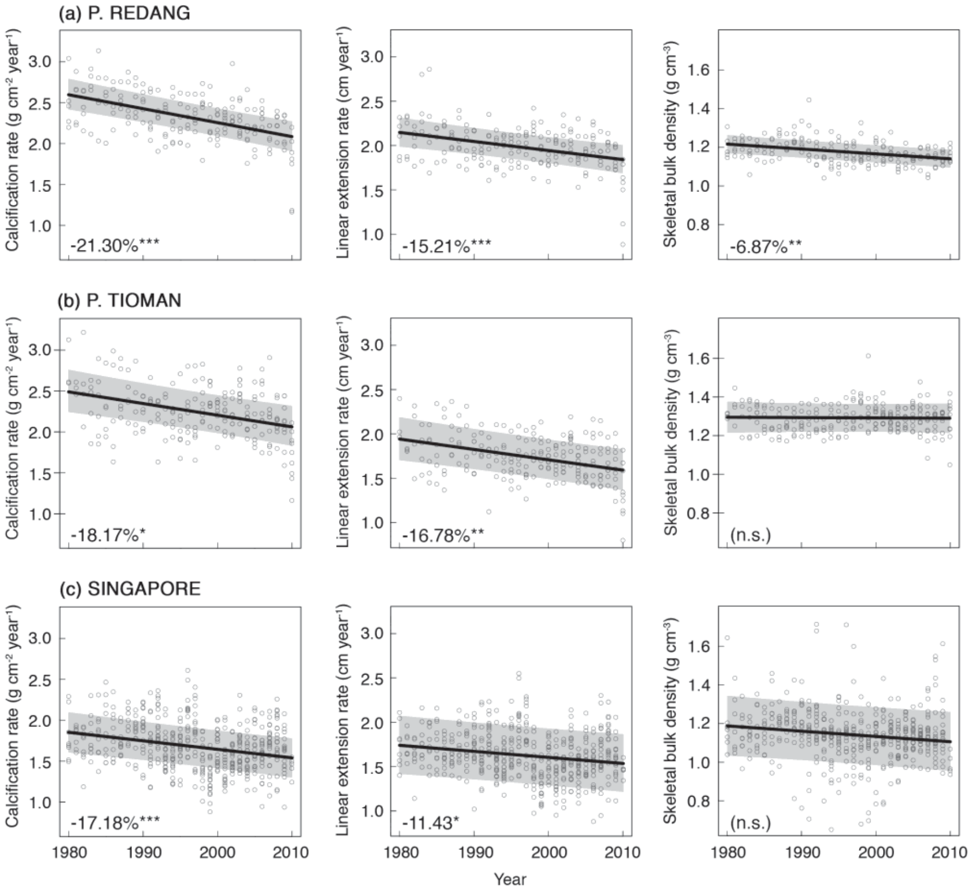


Figure 3.5. Changes in annual growth parameters (calcification rate, linear extension rate and skeletal bulk density) over the period 1980–2010 at locations along the western coast of the Thai-Malay Peninsula – (a) P. Redang, (b) P. Tioman, and (c) Singapore. The solid line represents the best fit linear mixed effects (LME) model; *P<0.05, **P<0.01, ***P<0.001, n.s. = not significant; gray area denotes 95% confidence interval

Table 3.3. Results of linear mixed effects (LME) models testing the relationship between calcification rate (g cm^{-2} $year^{-1}$), linear extension rate (cm $year^{-1}$) and skeletal bulk density (g cm^{-3}) over the period 1980–2010. *P<005, **P<0.01, ***P<0.001, N.A. = not applicable

Growth parameter	Study area	n	Slope	SE	P	% change over study period
Calcification rate	REGIONAL	70	-0.0144	0.0026	***	-18.61
	Phuket	21	-0.0178	0.0084	*	-20.52
	P. Payar	7	-0.0164	0.0044	***	-21.57
	Port Dickson	3	-0.0019	0.0060	0.752	N.A.
	Singapore	22	-0.0106	0.0032	***	-17.18
	P. Tioman	10	-0.0148	0.0059	*	-18.17
	P. Redang	7	-0.0171	0.0026	***	-21.30
Linear extension rate	REGIONAL	70	-0.0104	0.0020	***	-15.44
	Phuket	21	-0.0153	0.0062	*	-19.59
	P. Payar	7	-0.0105	0.0035	**	-15.77
	Port Dickson	3	0.0043	0.0060	0.480	N.A.
	Singapore	22	-0.0068	0.0027	*	-11.43
	P. Tioman	10	-0.0106	0.0037	**	-16.78
	P. Redang	7	-0.0102	0.0023	***	-15.21
Skeletal bulk density	REGIONAL	70	-0.0015	0.0006	*	-3.94
	Phuket	21	-0.0003	0.0013	0.849	N.A.
	P. Payar	7	-0.0015	0.0008	0.054	-3.94
	Port Dickson	3	-0.0034	0.0013	*	-10.68
	Singapore	22	-0.0022	0.0013	0.090	-5.96
	P. Tioman	10	-0.0010	0.0018	0.498	N.A.
	P. Redang	7	-0.0027	0.0010	**	-6.87

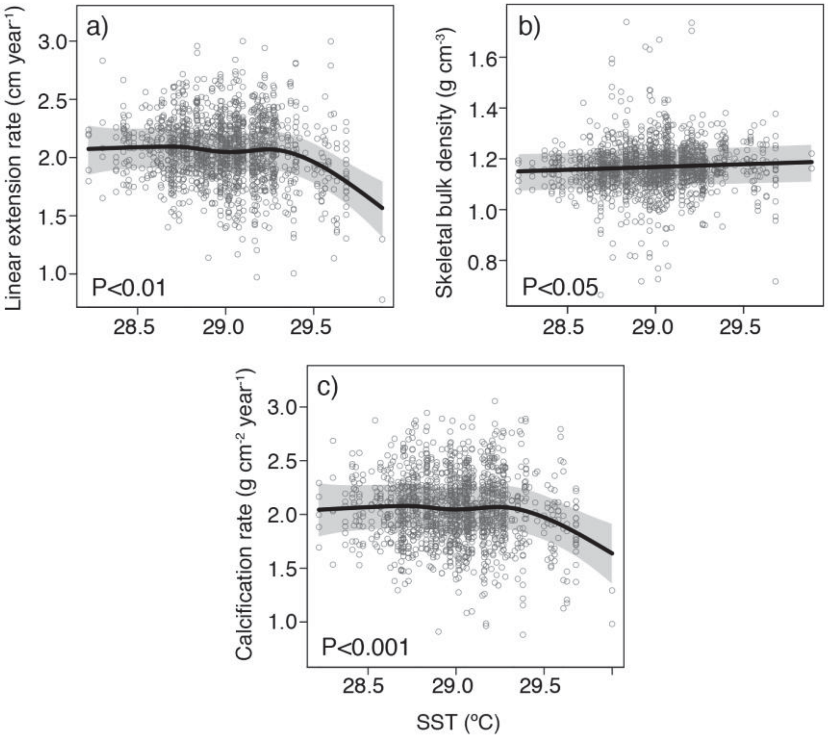


Figure 3.6. Region-level relationships between annual growth parameters (a) linear extension rate, b) skeletal bulk density, and c) calcification rate) with average annual sea surface temperature (SST). *P<005, **P<0.01, ***P<0.001; gray area denotes 95% confidence interval

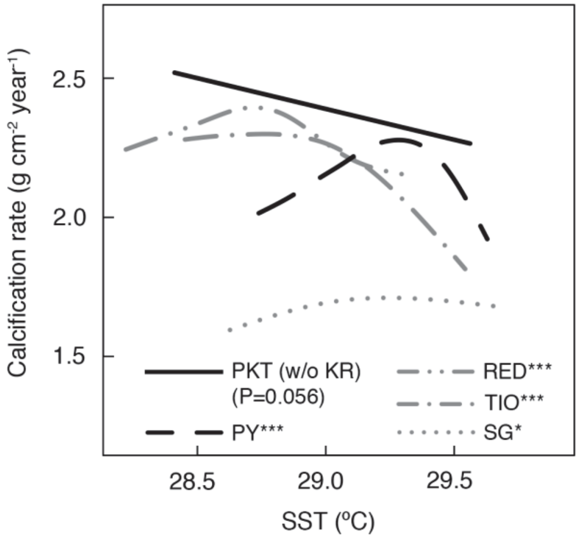


Figure 3.7. Partial-effects plot showing only the significant and borderline relationships between calcification rate and averaged annual sea surface temperature (SST) at the various study locations. PKT (w/o KR) – Phuket (with data from Koh Racha Yai excluded), *PY* P. Payar; *RED* P. Redang; *TIO* P. Tioman; *SG* Singapore; *P<005, ***P<0.001; Confidence intervals were omitted for clarity

3.4 Discussion

This study, involving six sampling locations around the Thai-Malay Peninsula, shows that there has been a region-wide decline in calcification rate (~18.6%), linear extension rate (~15.4%) and skeletal bulk density (~3.9%) of massive *Porites* spp. over a 31-year period from 1980–2010. The decrease in calcification rate was driven mainly by reduced linear extension rate rather than changes in skeletal density, in common with other studies on the Great Barrier Reef (Barnes and Lough 1993; Lough and Barnes 2000; Cooper et al. 2008; De'ath et al. 2009) and earlier work at Phuket (Tanzil et al. 2009). Indeed, at the local level reduced linear extension was the sole factor responsible for decreased calcification at four of the six study locations (Phuket, P. Payar, Singapore, P. Tioman) where no significant changes in skeletal density were recorded. Decreased calcification was also found at P. Redang as a product of both reduced linear extension (15.2%) and a smaller fall in skeletal density (6.9%). At Phuket, the decrease in calcification (~20.5%) and linear extension rates (~19.6%) are comparable with values in Tanzil et al. (2009) of 23.5% and 19.4–23.4% respectively, notwithstanding differences between methodologies, i.e. the use in Tanzil et al. (2009) of discontinuous growth records between two periods (Dec 1984–Nov 1986 and Dec 2003–Nov 2005) compared to continuous growth records in the present study.

The region-wide decrease in calcification rate covaried significantly with average annual SST. Similar declines in *Porites* calcification rates over the last ~20–30 years have been linked to rising SST on the Great Barrier Reef (~14.2–21%, for periods between 1988–2005) (Cooper et al. 2008; De'ath et al. 2009; Carricart-Ganivet et al. 2012) and at one site on the Mesoamerican Barrier Reef (MBR) (~30%, between 1998–2009) (Carricart-Ganivet et al. 2012). Rising SST has also been implicated in falling calcification rates of *Diploastrea helipora* in the Red Sea (~18%, between 1998–2008) (Cantin et al. 2010) and *Montastraea spp*. on the MBR (~20%, between 1985–2009) (Carricart-Ganivet et al. (2012). Compared to the GBR (average annual SST ~25–27ºC) and MBR (average annual SST ~28ºC), the Thai-Malay Peninsula reefs experience warmer sea temperatures throughout the year (average annual SSTs >28.5°C, maximum summer SSTs >30°C) (Fig. 2b) and as such, one might expect a more severe impact of sea warming on coral growth rates compared to other locations if *Porites* is at or close to its upper temperature threshold. However, the average annual rate of decline in *Porites* calcification (~0.6% per year) is actually lower than for the GBR (~1.29–1.44% per year) (Cooper et al. 2008; De'ath et al. 2009; Carricart-Ganivet et al. 2012) and the MBR (~2.5% per year) (Carricart-Ganivet et al. 2012).

Recent studies have also demonstrated a relationship between the rate of seawater warming and the magnitude of change in calcification rate (Helmle et al. 2011; Carricart-Ganivet et al. 2012; Cooper et al. 2012) with Cooper et al. (2012) recording correspondingly smaller changes in *Porites* calcification rates over the period 1900–2010 on western Australian reefs with lower rates of warming (~0.02ºC decade^{-1}) compared to those with higher rates (~0.1ºC decade^{-1}). If account is taken of the differing rates of warming on the Thai-Malay Peninsula (~0.1ºC decade^{-1}), GBR (~0.24–0.29ºC decade^{-1}) and MBR (~0.24ºC decade^{-1}), the rates of decline in calcification for these locales would be ~59%, ~39–60% and ~86% respectively for every 1ºC rise in SST. Despite therefore being subject to a warmer sea temperature regime, the Thai-Malay reefs have not, at a regional level, been subject to faster rates of decline than cooler water reefs on the GBR and MBR.

Part of the reason for these apparently anomalous findings might be attributed to the higher thermal threshold (~29.4ºC) found in Thai-Malay Peninsula *Porites* spp. before calcification starts to decline. This is considerably higher than the thermal peak of ~26.7ºC reported by Cooper et al. (2008) for the northern GBR. The latter figure is very similar to that obtained in experimental studies on a range of zooxanthellate corals where calcification rates rose to a thermal maximum of ~26–27ºC before declining (Clausen and Roth 1975; Jokiel and Coles 1978; Reynaud-Vaganay et al. 1999; Marshall and Clode 2004). In contrast, in the current study, the temperature/rate dependency appears not to show any rise at lower temperatures (Fig. 3.6) for either calcification or linear extension. Although this may simply be a factor of the very restricted temperature span of only 2ºC (28–30ºC), the 'flat' portion of the relationship is nonetheless much broader than might be expected if this was simply the tail end of a 'peak'. It should also be noted that the HadISST1 data significantly underestimated the *in situ* sea temperature at the majority of the reefs sampled. Consequently, the true value of the thermal threshold for massive *Porites* calcification around the Thai-Malay Peninsula is likely to be even higher than described here.

For skeletal bulk density, a significant region-wide linear positive relationship with SST (Fig. 3.6b) was also found and is most likely the result of deposition of short-lived high-density 'stress' bands during episodes of anomalous warming events (Smithers and Woodroffe 2001; Cantin et al. 2010). The rate of increase, however, was minimal being only ~3% for every 1ºC rise in SST and was observed only at Port Dickson and P. Redang.

Although temporal trends in growth parameters were relatively clear-cut at a regional level, the responses at individual locations were more variable in a similar manner to the GBR (Cooper et al. 2008; De'ath et al. 2009) and western Australia (Cooper et al. 2012). The regional decline in skeletal bulk density was a consequence of significant reductions at only two locations, P. Redang (~6.9%) and Port Dickson (~10.7%) while decreases in calcification and linear extension rates were found at five of the six locations within relatively tight ranges (~17.2–21.6% and ~11.4–19.6% respectively).

For the relationship between calcification rate and SST, the marked decline at the regional scale was also not mirrored at the local level, where responses were highly variable. For example, at Port Dickson, despite a rate of warming of ~0.13ºC decade^{-1}, there was no significant decline in calcification rate. Also, although the other five locations experienced a relatively similar and limited thermal environment, the rates of decline in calcification did not correspond to the respective magnitude of sea warming observed. Finally, there appeared to be no relationship between the decrease in calcification rate at selected sites around Phuket and rising SSTs. These inconsistencies question the widespread influence of rising sea temperatures as the main determinant of growth rate.

Port Dickson (PD) represents the only location of the six sampled that did not show a decline in calcification rate over time (Fig. 3.4c). Although the number of cores sampled here (n=3) was low compared to other locations (n=7–22), nonetheless all three cores produced relatively consistent variations in temporal growth patterns, and offered some degree of confidence in the results. Neither calcification nor linear extension rates showed significant changes over time, though skeletal bulk density was markedly reduced by ~10.7%, representing the largest fall for any location sampled. The skeletal bulk density at PD is also the lowest for the region, averaging only ~0.925 g cm^{-3} over the study period (Table S3.1). Situated in the southern part of the Malacca Straits and receiving major riverine inputs, the reefs around PD grow in an environment which is more estuarine than marine, with relatively low salinity (~27–32psu) and pH (~6.2–8.4 units), and rich primary productivity (Robinson et al. 1953; Chua et al. 1998; BOBLME 2011; Praveena et al. 2011). In recent decades, the water quality at PD has been affected by increased sewage, industrial, and agricultural waste loadings into the Malacca Straits (Chua et al. 1998; BOBLME 2011, Praveena and Aris 2013). Nutrient enrichment is a factor known to increase coral calcification rates (Meyer and Schultz 1985; Bongiorni et al. 2003; Koop et al. 2001; Dunn et al. 2012) and has previously been linked to high growth rates found on eutrophic reefs that prevail at the expense of lowered skeletal bulk densities (Edinger et al, 2000; Koop et al. 2001). It is possible, therefore, that increased nutrient concentrations at PD have a marked impact on growth of massive *Porites* at this location, and are masking any temperature-related effects on calcification.

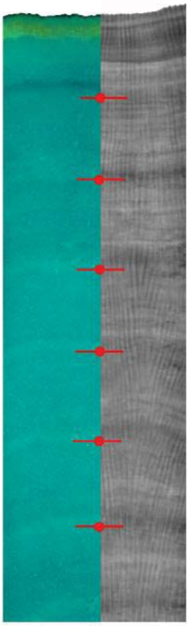
Rates of sea temperature warming at sites on the Andaman Sea coast (Indian Ocean) were almost twice those in the South China Sea (SCS) (Pacific Ocean) (Fig. 3.2a). This difference is consistent with the 2–3 times faster rates of warming reported in the Indian Ocean compared to the Pacific Ocean over the last 60 years (Williams and Funk 2011). However, this east/west split in SST increase was not reflected in the patterns of reduced calcification at sampled locations. The temperature related rates for every 1° rise in SST were ~50% at Phuket and ~55% at P. Payar, both on the Andaman Sea coast, while rates of decline in the South China Sea were ~74% at Singapore, 70% at P. Tioman and 96% at P. Redang. Based on the rate of warming alone these patterns are the converse of what might be expected, however the corals of the Andaman Sea exist within a much more restricted temperature environment than those of the South China Sea (Fig. 3.2b) and exhibit physiologies that are particularly resilient to environmental stresses (Brown 2007; LaJeunesse et al. 2010) which may play a role in the diminished temperature response observed. It would also be imprudent to expect a one-dimensional relationship between calcification rate and temperature to exist. For example, Cooper et al. (2012) found a significant decrease in massive *Porites* calcification rates (~11.6%, for 1900–2010) on a western Australian reef, which coincided with a relatively low decadal rate of increase in SST (0.02ºC per decade), while adjacent reefs with similar rates of warming sampled showed no declines.

There was also a lack of any pattern in temperature thresholds above which calcification declined between locations, with values ranging from the lowest (~28.4ºC) at P. Redang, to the highest (~29.4ºC) at P. Payar (Fig. 3.7). These results may also be a consequence of the seasonal temperature regimes prevailing at each location as described above. Although these observations originate in thermal settings where seasonal ranges are small, nonetheless they suggest that the rate of change in temperature is not the sole driver determining rates of change in calcification.

Finally, although the decline in the calcification rate around Phuket (~20.5%) coincided with a significant sea warming period (~0.14ºC per decade), there was no significant relationship between calcification rates and average annual SSTs (P=0.22). This contrasts with earlier findings by Tanzil et al. (2009), where variations in SST between 1985 and 2005 were closely related to variations in linear extension rates for 6 of 8 sites. In the current study, when KR was excluded on the basis of its unique and dissimilar sea temperature regime compared to adjacent reefs, a borderline but non-significant relationship was found between calcification rates and SST (P=0.056). At KR, where the calcification rate decreased by ~33.6%, the absence of a relationship was stronger (P=0.8) consistent with results from Tanzil et al. (2009) who found no significant relationship between linear extension rate and SST. Reefs at KR are subject to large amplitude internal waves (LAIWs) (Osborne and Burch 1980; Wall et al. 2012) which are a feature of the Andaman Sea. These cause pulsed upwelling events that deliver packets of cold and low pH water to shallower shelf areas and cause intermittent drops as large as 10ºC in sea temperature and 0.6 pH (Schmidt et al. 2012; Wall et al. 2012). Pulses of cold water from LAIWs could explain the generally lower temperatures observed at KR and this, together with a variable temperature regime, may contribute to the lack of a relationship between calcification rate and SST.

Considering that massive *Porites* spp. is a major reef builder on reefs around the Thai-Malay Peninsula, the regional average decline in coral growth rate shown here is no doubt a cause for concern for future reef accretion rates and reef resilience (see Madin et al. 2012; Roff and Mumby 2012). Given the observed rate of sea warming and associated calcification decline, a linear projection suggests that massive *Porites* corals around the Thai-Malay Peninsula may cease calcifying within the next ~150 years. However, the present study also shows that there has been marked variability in growth declines in the last ~30 years. It suggests that future rates and patterns of change within the region are also unlikely to be uniform. Based on current trajectories, it is predicted that while reefs in some locations may be more vulnerable to declines, others will possibly not register significant changes in growth rates in the foreseeable future. The fact that such variability exists within a relatively similar and limited thermal environment implies involvement of environmental drivers of long-term coral growth changes other than sea temperature alone. This is not surprising considering that coastal reefs, such as those around the Thai-Malay Peninsula and throughout Southeast Asia, receive large inputs from numerous river systems and tend to experience high spatio-temporal variations between many physical, chemical and biological properties (Nicholls et al. 2007), more so than the open seas. It is therefore likely that future calcification responses of reefs around the Thai-Malay Peninsula will continue to vary greatly between locations, and depend not only on the trajectory of oceanic-scale climatic changes (e.g. rises in SST and pCO_2), but also on other land-based/localised sources of environmental change. Such variability, undoubtedly, implies that it is crucial for efforts examining spatio-temporal changes in coral growth rates within similarly dynamic environments to be well-replicated.

3.5 Appendix



P. Redang
(RDKR-P1)

Fig. A3.1. Image of representative coral slice (RDKR-P1) showing annual variation in luminescence intensity (taken under ultraviolet light (365nm) - left side of image) and density (X-ray – right side). Red markers indicate the onset of the bright luminescent band (~Nov/Dec) and annual growth increments were measured as distance between red markers.

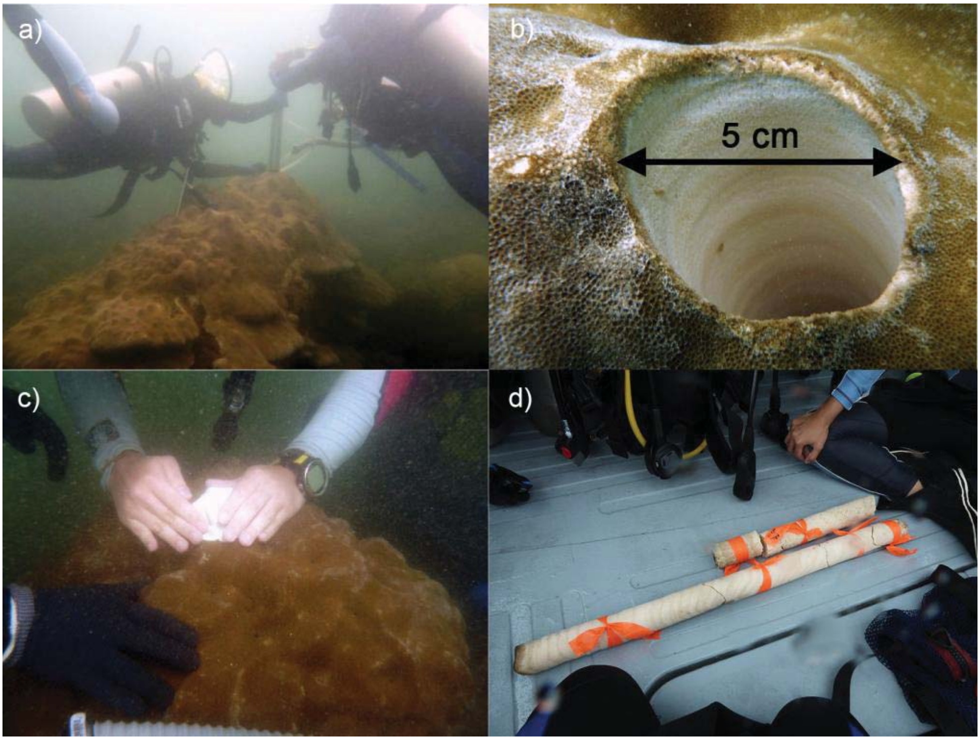


Fig. A3.2. The coral sampling process – a) coring of massive *Porites* using pneumatic drill set-up, b) hole left after retrival of 5cm diameter core; c) coring hole is patched up with marine epoxy, and d) example of cores retrieved.

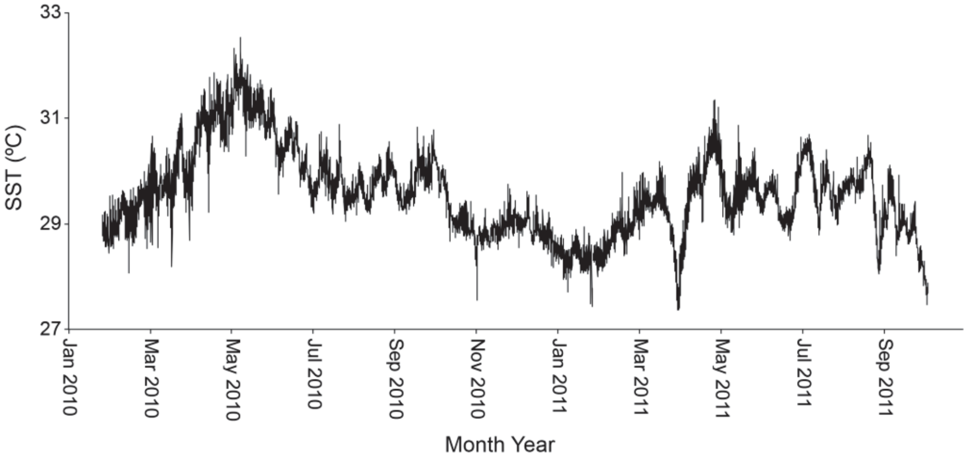


Fig. A3.3. Instantaneous hourly measurements of sea temperature (~2–3m at mid-tide) at Koh Racha Yai (KR), Phuket.

Table A3.1. Mean calcification rate, linear extension rate and skeletal density (± 1 SD) averaged over the study period (1980–2010) for the Thai-Malay Peninsula (REGIONAL), individual study locations (shaded gray) and individual reefs within each location.

Study area	n	Calcification rate ($g\ cm^{-2}\ year^{-1}$)	Linear extension ($cm\ year^{-1}$)	Skeletal density ($g\ cm^{-3}$)
REGIONAL	70	2.083 ± 0.379	1.881 ± 0.403	1.149 ± 0.198
Phuket	21	2.288 ± 0.290	2.075 ± 0.383	1.122 ± 0.137
YY	5	2.288 ± 0.298	2.242 ± 0.304	1.020 ± 0.052
PB	6	2.273 ± 0.364	2.169 ± 0.447	1.063 ± 0.130
KH	4	2.550 ± 0.180	2.316 ± 0.146	1.107 ± 0.0637
KR	6	2.127 ± 0.164	1.681 ± 0.175	1.275 ± 0.103
P. Payar	7	2.229 ± 0.201	1.960 ± 0.208	1.139 ± 0.053
Port Dickson	3	2.053 ± 0.250	2.218 ± 0.125	0.925 ± 0.104
Singapore	22	1.707 ± 0.329	1.662 ± 0.451	1.127 ± 0.284
HT	4	2.159 ± 0.079	2.340 ± 0.132	0.925 ± 0.027
SEM	4	1.753 ± 0.161	1.682 ± 0.312	1.055 ± 0.107
JO	2	1.491 ± 0.122	1.465 ± 0.174	1.019 ± 0.035
KU	9	1.510 ± 0.285	1.358 ± 0.317	1.311 ± 0.371
RL	3	1.780 ± 0.339	1.776 ± 0.392	1.012 ± 0.041
P. Tioman	10	2.238 ± 0.232	1.720 ± 0.298	1.307 ± 0.127
EDT	5	2.087 ± 0.145	1.574 ± 0.248	1.344 ± 0.144
PTU	5	2.428 ± 0.170	1.902 ± 0.274	1.270 ± 0.109
P. Redang	7	2.319 ± 0.218	1.968 ± 0.220	1.185 ± 0.060
RDHR	3	2.381 ± 0.242	2.051 ± 0.283	1.176 ± 0.076
RDKR	4	2.272 ± 0.222	1.906 ± 0.176	1.191 ± 0.056