Luminescence and density banding patterns in massive Porites corals around the Thai-Malay Peninsula, Southeast Asia

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ABSTRACT

We characterised the annual luminescent and skeletal density banding patterns in 51 massive *Porites* corals from 15 reefs from six locations around the Thai-Malay Peninsula in Southeast Asia, and explored the seasonal environmental cues/drivers of band formation. Location-specific recurrent annual luminescent banding patterns were found at all study locations with a brighter band occurring towards the end of the year (~Oct/Nov/Dec) (at five locations) and in ~June (one location). Annual density banding patterns could only be discerned at four locations, and were categorised into those that formed a dense band commencing ~Nov/Dec, and those starting ~May/Jun. Overall, compared to luminescence, variations in skeletal density provided a less clear signal for demarcation of annual growth increments. Seasonal variations in luminescence showed clearest relationships with salinity, as a proxy for freshwater/river runoff. No convincing relationship between intra-annual luminescence intensity and density variations was found, which supports the notion that luminescent banding is due to inclusions of fluorophores into the coral skeleton rather than variations in skeletal architecture. The relationships between seasonal density variations and significant wave height and rainfall suggest density banding in this region is likely related to wave energy, or some other correlated environmental parameter/s. The large variability in skeletal banding patterns not only highlights the current relatively poor understanding of their nature and causes, but also the need for replication in their interpretation, especially in settings with complex seasonal hydrodynamic/hydrological patterns such as those found around the Thai-Malay Peninsula.
INTRODUCTION

The discovery of annual banding patterns in massive coral skeletons has not only given valuable insights into skeletal growth processes and rates, but also provided a means to date past environmental conditions under which growth took place (Knutson et al. 1972; Isdale 1984). Banding is reflected as recurrent variations in density (shown using X-radiographs) and/or luminescence intensity (visible under long-wavelength ultraviolet (UV) light) which appear as alternating bands in slices of coral skeleton cut parallel to the colony growth axis (Buddemeier et al. 1974; Isdale 1984). Usually, alternating bands occur in annual couplets (i.e. a pair of high/low density or bright/dull luminescent bands) and can, therefore, be used to identify optimum tracks to measure coral growth, luminescence intensity and elemental/isotopic geochemical tracers (Buddemeier et al. 1974; Lough and Barnes 1990; Scoffin et al. 1992; Lough and Barnes 2000; Tanzil et al. 2009; Lough 2010; Cooper et al. 2012).

There are, however, less straightforward examples of multiple or indistinct bands that complicate the extraction of age and growth information (e.g. Weber 1975; Scoffin et al. 1989). It is also important to acknowledge that annual growth increments defined using bands rely on an assumption that the timing of band formation (e.g. the onset of deposition of bright/dull luminescent or high/low density bands) occurs around the same time of year for each of the year, and, therefore, that ‘years’ so defined represent periods that do not deviate grossly from ~12 months of growth (Buddemeier et al. 1974; Lough and Barnes 1990). As such, understanding the nature, and ultimately the causes of these banding patterns is crucial in ensuring accurate measurements of growth and sclerochronology.
The causes of both luminescent and density banding patterns in corals have been extensively debated (Highsmith 1979; Scoffin et al. 1989; Barnes and Taylor 2001, 2005; Grove et al. 2010). A clear and robust relationship between increased skeletal luminescence and high riverine discharges has repeatedly been shown (Isdale 1984; Smith et al. 1989; Isdale et al. 1998; Lough et al. 2002; Barnes et al. 2003; Hendy et al. 2003; Lough 2007). The principle cause of the luminescence proposed in this case is the incorporation in the coral skeleton of humic/fulvic acids leached from the terrestrial environment into river water (Boto and Isdale 1985; Susic et al. 1991; Zicheng et al. 2002; Grove et al. 2010; Grove et al. 2012; Llewellyn et al. 2012). However, anomalous luminescence peaks in the absence of any major river flow event have been observed (Jones et al. 2009) as well as annually recurring luminescent bands occurring in offshore corals thought to be far removed from terrestrial influences (Scoffin et al. 1989; Klein et al. 1990; Susic et al. 1991; Tudhope et al. 1996; Smithers and Woodroffe 2001). Such observations have led to the proposition that luminescence may also be related to and/or caused by variations in skeletal architecture. Barnes and Taylor (2001) categorised luminescent bands into (1) broad bands as regions associated with annual low-density bands, and (2) narrow lines of strong luminescence associated with seasonal freshwater flood events. In a later paper, however, Barnes and Taylor (2005) conceded that changes in skeletal chemical composition (e.g. trace inclusions from terrestrial runoff) appeared to be the primary cause of both types of luminescent bands – although they maintained that strongly luminescent lines could still be linked to changes in skeletal crystal size and packing. Prouty et al. (2014) noted a lack of luminescent lines in nearshore corals from Guam exposed to seasonal flooding events i.e. conditions where such luminescence
would be expected (Prouty et al. 2014). Ramseyer et al. (1997) found a correlation between luminescence and the skeletal architecture of speleotherms, marine cements, and coral skeletons and subsequently proposed that luminescence was associated with higher porosity and lower calcium carbonate density due to higher inclusions of organic fluorophores. Other studies, conversely, have reported positive relationships between massive *Porites* skeletal density and luminescence (Scoffin et al. 1992; Carricart-Ganivet et al. 2007; Lough 2010, Prouty et al. 2014). As a consequence, the causes of luminescent bands/layers and their relationship with skeletal density remain unclear.

Even greater uncertainty exists in regard to the precise cause/s of annual variations in skeletal density. The appearance of high-density (HD) and low-density (LD) bands, visible in X-radiographs/computer tomography images, are the result of the thickening/thinning of skeletal elements – e.g. thecal walls in *Porites* spp. (Buddemeier and Kinzie 1975, Barnes and Devereux 1988) and exothecal dissepiments and costae in *Orbicella annularis* (Dodge et al. 1992). Factors previously related to density band formation include environmental variables such as sea temperature (e.g. Dodge and Thomson 1974; Weber 1975; Buddemeier et al. 1974; Schneider and Smith 1982; Klein et al. 1993; Highsmith 1979; Lough and Barnes 1990, 1992), cloud cover/light level (Highsmith 1979, Brown et al. 1986, Klein and Loya 1991), salinity/freshwater runoff (Scoffin et al. 1989; Barnes and Taylor 2001), rainfall (Buddemeier and Kinzie 1985; Supriharyono 2004) and wave energy (Scoffin et al. 1992), as well as biological parameters/processes such as tissue thickness (Barnes and Lough 1993) and reproduction (Wellington and Glynn 1983; Mendes 2004). Although there are views that LD bands are produced under “optimum” growth conditions and HD bands accrete during “non
optimum” conditions (Highsmith 1979; Scoffin et al. 1989), neither proximate nor ultimate causes for density banding patterns have been unequivocally demonstrated. Even where a single environmental signal has been found to dominate, relationships can vary among and within locations (see Highsmith 1979; Lough and Barnes 1990). For instance, while formation of HD bands in massive *Porites* corals was associated with seasonal high sea surface temperatures (SSTs) on the Great Barrier Reef (GBR) (Weber 1975; Isdale 1983; Lough and Barnes 1990), the converse was observed on Western Australian reefs (Schneider and Smith 1982), the Red Sea (Klein and Loya 1991) and even within the GBR (Lough and Barnes 1990), where HD bands in some corals formed during the cooler months. Perhaps surprisingly (if SST is the primary control on band formation), marked density banding has also been found in massive corals from equatorial reefs where seasonal fluctuations in mean monthly SSTs occur within very restricted ranges (e.g. mean monthly SSTs ~27–30°C) (Scoffin et al. 1989, 1992; Cahyarini 2008; Suharsono and Cahyarini 2012).

Part of the confusion regarding the nature and causes of luminescent and density banding may result from attempts to find a common environmental signal in corals living in very different environmental conditions (see Weber 1975; Highsmith 1979). It could be that formation of banding patterns at different geographical locations is driven by different factors dependent on the specific set of conditions to which the corals are acclimatised. Dating of bands based on solely their position relative to the growing surface of the colony has also been known to cause conflicting reports on timing of density band formation (Barnes and Lough 1993; Taylor et al. 1993; Carricart-Ganivet et al. 2007). Furthermore, description of banding patterns and associations with broader
spatial-scale environmental parameters are sometimes based on single specimens or very small sample sizes (e.g. Klein et al. 1993; Bessat and Buigues 2001; Sazzad et al. 2010). This may produce variable interpretations either because of apparent inherent inter-colony differences in banding patterns (e.g. Lough and Barnes 1990), or artefacts in the methods used for visualising the luminescence (Grove et al. 2010) and skeletal density (Le-Tissier et al. 1994).

Massive corals from the genus Porites are the most widely used for sclerochronological studies in the Indo-Pacific. Their skeletons have been used to reconstruct growth parameters as well as to detect local and global marine environmental changes (e.g. Tudhope et al. 1996; Lough 2007; Cooper et al. 2012). The current study was part of a wider growth rate investigation (Tanzil et al. 2013) and aimed to ascertain the nature of recurrent luminescent and density banding patterns in massive Porites corals from six geographical locations around the Thai-Malay Peninsula in Southeast Asia. We also tested for relationships between banding patterns and several environmental variables in order to explore potential cues or drivers of seasonal band formation. The study involved a large sample size (n=53), different sites in relatively similar environments (15 reefs, 6 locations), as well as multiple years (5yrs; Dec 2004–Nov 2009). Thus the effects of individual colony variations and artefacts in methodology are reduced, and the confidence level increased when attempting to identify common patterns in luminescence/density variations and their potential cues/drivers.

MATERIALS AND METHODS
Study sites

Fifteen reefs from six locations around the Thai-Malay Peninsula (1–8°N, 98–105°E), Southeast Asia (Fig. 1, Table 1) were sampled. The reefs along the east coast of the Peninsula are located in the South China Sea (western Pacific Ocean), whereas reefs along the west coast are in the Andaman Sea (northeastern Indian Ocean). Sites around the Thai-Malay Peninsula all experience year-round high mean monthly SSTs of >27–30°C (Tanzil et al. 2009), which peak during the boreal summer (~June) each year. The region 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 rougher seas during the northeast (NE) monsoon period (~Nov–Mar) whilst similar conditions are experienced on the west coast during the southwest (SW) monsoon (~May–Sep) (Lau and Yang 1997; Wong et al. 2009). The main reason for these effects is the Titiwangsa mountain range which runs through the middle of the Peninsula rising to ~2100m, effectively shielding the east and west coasts from the brunt of the SW and NE monsoons, respectively (Camerlengo and Demmler 1997; Suhaila et al. 2010; Tanggang 2011). Flanking the Thai-Malay Peninsula to the west, the mountain ranges along Sumatra Island, Indonesia also provide additional rain- and wind-sheltering effects for the Peninsula’s west coast, in particular for the southwestern coast, during the SW monsoon (Fig. 1) (Nieuwolt 1968; Wong et al. 2009). High rainfall on the Peninsula (average ~300 mm month⁻¹ in the wet season) and numerous short, swift-flowing rivers east and west of the Titiwangsa mountain range result in considerable runoff and substantial loads of river-transported material being discharged into coastal waters (Fig. 1; see also Fig. 8 for more details). The reefs off the west coast of the
Peninsula within the Malacca Straits (e.g. Pulau Payar and Port Dickson) also receive additional input from rivers along the east coast of Sumatra Island, Indonesia (Fig. 1). As a result, these reefs are subject to low salinities and elevated nutrient concentrations, as well as severe turbidity with sedimentation rates as high as \( \sim 50–100 \) mg cm\(^{-2}\) day\(^{-1}\), (Chua et al. 1998; BOBLME 2011; Lee and Mohamed 2011). By contrast, offshore island reefs on the eastern and northwestern coasts are significantly less turbid, with sedimentation rates averaging \( \sim 0.3 \) mg cm\(^{-2}\) day\(^{-1}\) (Lee and Mohamed 2011). The fact that sites along the east and west coasts of the Thai-Malay Peninsula occur within a relatively narrow geographical range, and share similarities in certain environmental conditions (e.g. SST, photosynthetically active radiation) while others are specific to location (e.g. rainfall, wind) presents a unique opportunity for a natural experiment to examine variations in coral skeletal banding patterns and their relationships with selected environmental parameters.

**Environmental parameters**

Several data sets of monthly-averaged environmental variables over the period Dec 2004–Nov 2009 were examined. Monthly SST (°C) for the 1° area grid encompassing each study location was obtained from the HadISST data set (HadISST, Version 1.1, Hadley Centre for Climate Change, UK Meteorological Office) (Rayner et al. 2003). Sea-surface photosynthetically active radiation (PAR) (µmol m\(^{-2}\) day\(^{-1}\)) for the 0.5° grid area encompassing each study location was obtained from Sea-Viewing Wide Field-of-view (SeaWiFs) monthly level 3 Ocean Color product extracted with the Giovanni online data system, developed and maintained by the NASA GES DISC (Acker and Leptoukh 2007).
Monthly average rainfall (mm month$^{-1}$) was retrieved from the nearest available weather stations to the study locations i.e. Phuket – Phuket Airport (8.108°N, 98.517°E), Pulau Payar – Langkawi Airport (6.333°N, 99.733°E), Port Dickson – Malacca town (2.266°N, 102.250°E), Singapore – Changi Airport, Pulau Tioman – Mersing (2.450°N, 103.833°E), and Pulau Redang – Kuala Terengganu Airport (5.050°N, 103.100°E). Distances of study reefs from these meteorological stations used are given in Table 1. Monthly salinity (ppt) for 0.5º area grids was obtained from Carton-Giese UMD Simple Ocean Data Assimilation (SODA) v2.1.6 (Carton and Giese 2008). Modelled monthly means of significant wave height (SWH) (m) for 1º area grids were acquired from European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-20C global reanalysis (Stickler et al. 2014).

The above environmental variables (i.e. temperature, light, rainfall, salinity and wave height) were selected to represent parameters that might affect coral skeletal luminescence and density band formation. Both salinity and rainfall were used as proxies for the amount of freshwater/river input reaching the reefs since increased riverine humic/fulvic substances and dissolved organic material from terrestrial sources are strongly correlated to coral luminescence in certain locations (Isdale 1984; Susic et al. 1991; Isdale et al. 1998). However, rainfall represented more local terrestrial run-off reaching reefs from coastlines while salinity represented the total freshwater flux not just from coastline/river runoff, but also current-driven movement of freshwater masses. The 0.5º gridded SODA salinity product used here was a reanalysis based on an ocean general circulation model and salinity observations from ships and Argo buoys (Carton and Giese 2008). We chose these data because available data for longer-term in-situ
monthly/seasonal salinity were extremely limited around the study locations. Although there were discrepancies between predicted SODA and in-situ salinities given the coarse spatial resolution and nature of the SODA product, comparison of mean monthly SODA salinity with in-situ measurements taken from one study reef (SG-KU) showed a similar pattern of intra-annual changes in salinity even if SODA estimated higher absolute salinity values and a much smaller salinity range (Fig. S1). Thus local salinities predicted by SODA were likely, at a minimum, to provide a suitable correlative proxy for seasonal variations in the amount of freshwater to which the corals were exposed.

Significant wave height (SWH) was used as proxy for the amount of surface wave energy shallow reefs might receive, a factor that has previously been related to skeletal density variations (Scoffin et al. 1992). SWH is simulated from ECMWF ERA-20C, a gridded reanalysis product, which assimilates observations of surface pressure and surface marine winds, and accounts for both wind direction and fetch distance (Stickler et al. 2014). As with SODA salinity, we make the assumption that the ECMWF gridded wave product is an adequate indicator of wave energy flux to the study reefs.

Skeletal luminescence and density banding

Fifty-three massive Porites colonies sampled between Oct 2010 and Jan 2012 were analysed for skeletal luminescence and density banding (Table 1). At each of the 15 study sites, colonies ∼1–4m in diameter were sampled at depths ∼2–3m below mid-tide height from within a 100m stretch of fringing reef <1km distance from the nearest rocky outcrop, island or coastline. All cores were taken from the main growth axis of the coral colony using a pneumatic drill fitted with a 5cm diameter, 50cm long diamond bit core
barrel. Although it was not possible to conclusively identify all samples to species level, the majority (~76%) of colonies were positively identified as *Porites lutea* (Tanzil et al. 2013).

In order to ascertain the nature and timing of luminescent and density banding patterns, alizarin staining of tagged colonies was conducted (Table 1). This calcium dye stains the coral skeleton without significantly affecting its growth characteristics or mortality rate (Dodge et al. 1994). The coral can then be left to grow and can be stained repeatedly until the time of sampling, with resulting pink lines indicating specific staining periods in the skeleton. Repeated staining at 5 of the 6 study locations was carried out over a ~2-year period (Table 1). At Port Dickson, where alizarin staining was successfully carried out only once, past samples collected by in 2006 were also used to aid in ascertaining the timing of the bands. Sub-sampling of colonies at different times of the year at all study locations was also conducted in order to further validate the timing of banding patterns.

Slices (~0.7 cm thick) were cut from coral cores, and growth chronology and linear extension rates were resolved from the annual skeletal banding patterns as visualised in Fig. 2. Skeletal density and luminescence intensity measurements for the period ~Dec 2004–Nov 2009 were then obtained along overlapping tracks ~0.2 cm wide along the main growth axis and at a resolution of 72 pixels cm\(^{-1}\) (i.e. at every ~0.014 cm). Skeletal densities 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) (Fig. S2b and S3b). Luminescence intensities were measured from digital images (Canon G10 digital camera) of core slices taken under
long-wavelength (365nm) ultraviolet (UV) light in a customised photography black box. These images were then split into their red, green and blue (RGB) spectral components and the green/blue (G/B) spectral ratio used as a measure of luminescence intensity (Grove et al. 2010). Luminescence intensity measurements were validated against luminometry at the Australian Institute of Marine Science (Barnes et al. 2003) (Fig. S2a and S3a). All image analyses for skeletal density and luminescence intensity extractions were performed using NIH ImageJ (v1.46r) (Rasband 1997–2012).

The study period, Dec 2004–Nov 2009, was used as it provided the best growth axes where luminescence and skeletal density were misaligned due to skewed growth. There were no anomalous events, such as coral bleaching, recorded during these five years, and thus growth rates and banding patterns were considered representative of ‘normal’ growth years. This reduced any complications that could have arisen in the interpretation of density/luminescent bands caused by stress, such as the formation of multiple bands or growth hiatuses (e.g. Cantin and Lough 2014). Sequences of luminescence intensity and density measured for the study period for all cores, with the exception of two cores (RDKR-A and EDT-A), were used to test for any grouping in the timing of the banding patterns as well as any relationships with environmental parameters as outlined below. RDKR-A and EDT-A had peculiar luminescent intensities (Fig. S4) and were excluded as repeat measurements of these cores using the same setup as described above was not possible.

Statistical analyses

Annual luminescent and density banding patterns
Any natural grouping in the timing of annual luminescent and density banding patterns in the cores sampled from the various study locations was identified using agglomerative hierarchical cluster analysis. For each core, sequences of skeletal luminescence and density measurements were partitioned into five 1-year time series (Fig. S5) and then normalised (i.e. zero mean and one unit sample variance). “Shape” information (i.e. seasonality) was thus retained but between year differences in the luminescence/density ranges removed. Because different years and cores had grown at different rates, it was then necessary to align the time series using a dynamic time warping (DTW) algorithm (Giorgino et al. 2009). In this alignment, the sequences were stretched and displaced in order to optimally match each other under the constraint that the start and end points of each 1-year time series match, i.e. effectively translating the data from the spatial domain to a common implied time domain for all corals. DTW was used as it not only accounts for differences in time-series lengths, but can also deal with the possibility of slight misalignment in the luminescent/density time series associated with skewed growth axes and/or artefacts of the sampling methodology. Following alignment, distance measures between individual cores were calculated (as the average Euclidean distances between the five corresponding 1-year sequences of a pair of cores), and similarities between clusters of segments were computed using the Ward-link method (Ward 1963). This linkage method was used since it minimises the variance of the distance within clusters, and performs best compared to other methods when the number of clusters are small (Lerato and Niesler 2012). All analyses were executed using the statistical program R (R Core Team 2012) using R-packages ‘dtw’ (Giorgino 2009) and ‘stats’.
Relationship with environmental parameters

For each core, luminescence intensity and skeletal bulk density measurements for each of the five annual cycles between Dec 2004 and Nov 2009 were assigned to months (60 months for each core) (Fig. S5). The monthly-binned luminescence and density data were then averaged and converted to monthly anomalies (the difference between the monthly-binned data and the average luminescence/density for the period Dec 2004–Dec 2009) for each core. This data were then used to test for any relationship with monthly anomalies in environmental parameters (the difference between a mean monthly value and the overall average) for each of the six study locations. Anomalies were used instead of absolute values as the current study aims to identify potential environmental drivers of annual seasonal cycles of luminescence and density across locations with different baselines (see Table 2).

Relationships between anomalies in skeletal luminescence intensity and density, and anomalies in sea surface temperature (SST), photosynthetically active radiation (PAR), rainfall amount (Rain), salinity (Sal) and significant wave height (SWH) at each of the six study locations were initially investigated using Pearson’s product-moment correlation tests after checking for normality in the datasets.

Subsequently, Generalised Additive Mixed Models (GAMMs) were used to examine region level relationships. Preliminary analysis showed that GAMMs had the best goodness of fit compared to other models explored (e.g. Generalised Least Squares (GLS), Generalised Linear Models (GLM)) as they allowed for linear and non-linear relationships, as well as inclusion of random effects to account for correlation among observations on the same sampling unit (Wood 2006). For each model, the fixed effects
components included a combination of predictors ‘SST, ‘PAR’, ‘Rain’, ‘Sal’ and ‘SWH’, and nested random effects in ‘Location’, ‘Site’ and ‘Core’ (individual colony). A smoothing term (cubic regression spline, df=4) was applied to all the predictor variables. Assumptions of normality, homogeneity of variances as well as possible autocorrelations within the dataset were tested, and variance/autocorrelation terms included into the GAMMs where necessary (refer to Supplemental Information for the final full-model GAMM form used).

In order to refine the best environmental predictors of seasonal variations in luminescence intensity and density at the region level, a multi-model “strength-of-evidence” approach was used (Burnham and Anderson 2002). This involves not only using Akaike Information Criterion (AIC) to determine the best model for the given data, but also inferential model weights i.e. Akaike weights (AIC.\(\omega_i\)). These inferential model weights (\(\omega_i\)) are the relative likelihoods of models given the data ranging from 0 to 1 and, when normalised across a set of candidate models, can be interpreted as probabilities i.e. the chance that a given model is the best approximating model describing the data given the candidate set of models (Burnham and Anderson 2002). The (relative) evidence for models can also be judged by the ratio of their \(\omega_i\). Given a model pair, this ratio represents the odds that one model is better than the other from an information theory perspective (Burnham and Anderson 2002, 2004).

In addition to information about relative model support, \(\omega_i\) can also be used to estimate the variable relative importance weights (RIW) by summing the \(\omega_i\) across all models in the set where a particular predictor variable occurs (Burnham and Anderson 2002). As with inferential model weights, RIW can be interpreted as equivalent to the
probability that that predictor variable is a component of the best model. A total of 32
models were considered (31 models with full-subsets along with an intercept only
model). A likelihood-ratio based (pseudo) $R^2$ (Bartoń 2013) was used to estimate the
‘variance explained’ by fixed effect factors of the top-ranked model, and partial effects
plots were used to illustrate the relationships between environmental variables and
luminescence intensity and density anomalies.

Relationship between skeletal luminescence and density

Any relationships between monthly luminescence and skeletal density anomalies were
tested using Pearson’s product-moment correlation tests at the individual location level.
All statistical analyses were performed using the statistical program R (version 2.15.1) (R
Core Team 2012), using packages “stats”, “mgcv” (Wood 2006) and MuMIn (Bartoń
2012).

RESULTS

Intra-annual variation in environmental parameters

SSTs at all the study locations averaged ~29°C (Table 2) and were characterised by an
annual cycle with a peak ~May (which marks the warmest period for the region with sea
temperatures often reaching >30°C), another smaller peak in October/November, and a
minimum in January (Fig. 3a). The annual range of mean monthly SST was, however,
relatively small at ~3°C (i.e. ~27–30°C) for locations along the eastern coast of the Thai-
Malay Peninsula and ~2°C (i.e. ~28–30°C) for the western coast. SST maxima and
minima lagged those of solar radiation (Fig. 3b), which exhibit the characteristic bi-
modal peaks (March and September) as the sun passed overhead in its seasonal movement between the two Tropics (Osborne 2000). Monsoonal cloud cover also affects solar radiation such that at Phuket and Pulau Payar (“Pulau” means ‘island’ in Malay and will henceforth be “P.”) the secondary peaks in solar radiation and SST in the latter half of the year (Fig. 3a/b) were largely absent.

Average rainfall for the study locations varied between ~170 and ~235 mm month\(^{-1}\) (Table 2), with maximum rainfall observed ~Jul–Oct for locations along the west coast (i.e. Phuket, P. Payar, Port Dickson) and ~Nov–Jan for locations along the east coast (i.e. P. Redang, P. Tioman, Singapore) (Fig. 3c). The split in peak rainfall periods seen at these east and west locations corresponds with the NE and SW monsoon periods, respectively, as described earlier. Seasonal variations in rainfall and salinity were similar only at P. Redang and P. Tioman, where lowest salinities coincided with periods of highest rainfall and vice versa (Fig. 3c/d). At Phuket, P. Payar and Port Dickson, salinity minima occurred in ~Nov/Dec, while at Singapore lowest values were observed in ~Aug/Sep (Fig. 3d).

Maximum mean monthly significant wave height (SWH) occurred between Nov–Mar, corresponding with the NE monsoon period, at the three east and south coast locations (P. Redang, P. Tioman and Singapore) (Fig. 3e). At Phuket and P. Payar, mean SWH peaked ~Jun–Aug, with positive anomalies generally overlapping with the SW and NE monsoon periods. Mean monthly SWH at Port Dickson and Singapore were much lower compared to the other locations (Table 2, Fig. 3e). At Port Dickson, no seasonal variation in SWH was observed.
Annual banding pattern

Luminescent bands

We found location-specific repeating luminescent banding patterns (Figs. 2 and 4) – i.e. luminescent banding patterns were cyclically reproducible among the different coral colonies sampled from the same location, but not between locations. Cluster analysis (CA) of DTW aligned, normalised annual luminescence variations found two distinct groups (Fig. 5a) – 1) cores from Phuket, P. Payar, Port Dickson, P. Redang and P. Tioman, and 2) cores from Singapore. There was also a tendency for cores from the same location to cluster together (Fig. 5a).

The luminescent bands for cores from the first group were generally characterised by the brighter-band occurring towards the end of the year i.e. ~Oct/Nov/Dec. For Phuket corals, the annual pattern consisted of one broad bright band (commencing ~Nov/Dec) and one broad dull luminescent band of approximately equal thickness. A similar pattern and timing of band formation was found for corals sampled at P. Payar (~250 km south of Phuket) with the exception of a narrow, fainter secondary luminescent line visible within the broad dull luminescent band (Fig. 2) estimated to form ~Jul/Aug. At Port Dickson, the annual pattern also consisted of a broad bright and dull luminescent band couplet. However, sub-sampling of corals (Table 1) and comparison with material from past sampling efforts suggest that bright-band accretion commenced slightly earlier (~Oct) at this location compared to its west coast counterparts. The ratio of thicknesses of the bright vs. dull band couplets in Port Dickson cores also varied more from year to year (Figs. 2 and 4c). At P. Redang, on the east coast, the annually repeating luminescent band couplet consisted of a bright narrow luminescent band commencing in ~Nov/Dec,
followed by a very broad dull band. The annual pattern at P. Tioman was much less
distinct, but generally consisted of two bright and two dull luminescent bands, the first
and usually brighter of which started forming ~Dec, and the second estimated ~Jul/Aug.

For the Singapore cores, the annual pattern consisted of a distinct broad bright
band formed in ~Jun–Nov and a broad dull band formed in ~Dec–May. However, within
the broad dull luminescent band, a secondary annual luminescent line of usually much
lower relative intensity was also visible (Fig. 2).

Skeletal density bands

Clear alternating low and high density bands, annual in nature, were observed at Phuket,
P. Payar, P. Tioman and P. Redang, while no distinct annual density banding could be
discerned in corals from Singapore and Port Dickson (Figs. 2 and 4). Cluster analysis of
DTW aligned, normalised skeletal density variations again split the data into two main
groups (Fig. 5b). Although the assignment of core location to each group was less
consistent compared to luminescence intensity, cores from Phuket and P. Payar largely
occurred in one group, whilst those from Redang and Tioman in the other. Cores from
Singapore and Port Dickson appeared in both groups, as a result of the lack of discernable
density banding patterns at these locations (Fig. 2 and 4).

Based on the position of alizarin stain/subsampling and alignment with
luminescent bands, HD bands in corals sampled from Phuket and P. Payar (west coast
locations) were estimated to form between May and Sep with maximum densities
~Jun/Jul (Figs. 4a/b). However, despite this general pattern, complicated narrower
multiple dense/less dense lines were also observed within the broad density bands in
several specimens. At P. Redang and P. Tioman (east coast locations), density banding was generally clearer and more consistent (Figs. 2 and 4d/e), and consisted of a distinct narrow HD band formed ~Nov–Feb and a much broader LD band formed ~Mar–Oct.

Relationship between skeletal luminescence and density

Correlations between seasonal luminescence intensity and density anomalies varied according to location (Table 3), with no significant (at α=0.05) relationship at Phuket (p=0.686) or Port Dickson (p=0.063); a significant but weak negative relationship at P. Payar (p<0.001, r=-0.216); and significant but weak positive relationships at Singapore (p<0.001, r=0.128), Tioman (p<0.001, r=0.197) and P. Redang (p<0.001, r=0.303).

Linkages with environmental parameters

Mean monthly anomalies in skeletal luminescence intensity and density were compared with monthly anomalies in sea surface temperature (SST), photosynthetically active radiation (PAR), rainfall (Rain), salinity (Sal), and significant wave height (SWH). Relationships between luminescence and density with environmental parameters described henceforth will refer to the relationships of their anomalies.

Luminescence intensity

Luminescence and SST were significantly (at α=0.05; degrees of freedom given in Table 4) positively correlated at Singapore (p=0.01, r=0.250), but showed significant negative relationships at the other five study locations; Phuket (p<0.001, r=-0.097), P. Payar
(p<0.001, r=-0.265), Port Dickson (p<0.001, r=-0.374), P. Tioman (p<0.001, r=-0.156) and P. Redang (p<0.001, r=-0.508). PAR was significantly correlated with luminescence at only two study locations – positive at Phuket (p<0.001, r=0.474) and negative P. Redang (p<0.001, r=-0.375). The results for rainfall at the location level were similarly variable, with significant inverse correlations at three locations (Phuket – p<0.001, r=-0.476; P. Payar – p<0.001, r=-0.330; Singapore – p<0.001, r=-0.218), a significant positive relationship at P. Redang (p<0.001, r=0.188), and no significant relationships at Port Dickson and P. Tioman. Salinity at all locations was significantly inversely correlated, with r ranging from -0.110 at P. Tioman (p=0.02) to -0.504 at Phuket (p<0.001) (Table 4). SWH was significantly correlated with luminescence at five locations with positive correlations at P. Tioman (p<0.001, r=0.138) and P. Redang (p<0.001, r=0.527), and inversely related at Phuket (p<0.001, r=-0.459), P. Payar (p<0.001, r=-0.334) and Singapore (p<0.001, r=-0.217).

The top-ranked model fit for variation in luminescence at the region level based on lowest AIC and highest AIC.ωi included salinity and rainfall effects (Table 5). This produced an AIC.ωi of 0.35 (i.e. 35% chance of this model being the best approximating model describing the data given the set of predictor variables considered), ~2 times that of the next competing model based on ∆AIC values of <2 (Table 5) and was therefore chosen as best estimator of seasonal variation in luminescence. Analysis of variable relative importance weights (RIW) revealed that salinity was the strongest predictor variable for seasonal luminescence based on AIC.ωi (RIW=0.99), followed by rainfall amount (RIW=0.61). PAR, SWH and SST all had much smaller RIWs ranging from 0.12–0.29 (Fig. 6a). The ‘variance explained’ by only the fixed-effect factors of the top-
ranked model (i.e. salinity and rainfall) as estimated by a likelihood-ratio based (pseudo) R² was 0.13 (henceforth referred to as ‘marginal R²’), with a residual mean standard error (normalised to the range of observed values) (NRMSE) of 11.2%. Partial effect plots for these terms showed seasonal luminescence was correlated with negative values of salinity but not positive values (Fig. 7a). The relationship between seasonal luminescence and rainfall was less defined, with a possible minimum at rainfall values of ~200 mm month⁻¹. Skeletal density Density and SST were significantly correlated at four of the six study locations, with positive relationships at Phuket (p<0.001, r=0.159) and P. Payar (p<0.001, r=0.341), and negative ones at P. Tioman (p<0.001, r=-0.355) and P. Redang (p<0.001, r=-0.370). Density and PAR were significantly inversely related at only the south and east coast locations (i.e. Singapore – p=0.002, r=-0.119; P. Tioman – p<0.001, r=-0.225; P. Redang – p<0.001, r=-0.353). Rainfall was positively correlated with density at three study locations; P. Payar (p<0.001, r=0.293), P. Tioman (p<0.001, r=0.283) and P. Redang (p=0.013, r=0.113). Salinity was only significantly correlated with density at the two east locations (P. Tioman – p<0.001, r=-0.256; P. Redang – p<0.001, r=-0.268). SWH was significantly positively correlated with density at four locations – Phuket (p=0.018, r=0.081), P. Payar (p<0.001, r=0.256), P. Tioman (p<0.001, r=0.450) and P. Redang (p<0.001, r=0.391). Region level analyses found the best model fit for seasonal density variations included terms for SWH and Rain based (Table 5). This model produced the lowest AIC.
as well as the highest AIC.oi of 0.36. SWH was identified as the strongest predictor variable for seasonal skeletal density (RIW=0.99), followed by Rain (0.91) (Table 5). RIWs for PAR, SST and salinity were much smaller and ranged from 0.13–0.37. The marginal R² for the top-ranked model was low at 0.08, with a NRMSE of 14.6%. Partial effect plots showed that seasonal density exhibited linear positive relationships with both SWH and Rain (Fig 7b).

DISCUSSION

The skeletons of massive Porites corals from all six study locations around the Thai-Malay Peninsula were found to contain location-specific recurrent luminescent and/or density banding patterns. Although we interpret these patterns as annual in nature, it is not possible to be certain that they represent exactly one year’s growth. Several lines of evidence, however, suggest that the time frame in which these recurrent bands are formed does not deviate markedly from a 12-month period. Firstly, repeated alizarin staining at all locations with the exception of Port Dickson (successfully stained only once) (Table 1), and the subsampling of tagged coral colonies within the period 2009–2011, demonstrated that the bands occurred at the same time of the year, at least within this ~2-year period. Secondly, for Phuket, results from previous growth studies and alizarin staining also align with our luminescent banding chronology i.e. onset of bright band ~Nov/Dec (Charuchinda and Chansang 1985; Chansang et al. 1996; Scoffin et al. 1992). Lastly, results from these aforementioned alizarin staining/subsampling and growth studies, together with past sampling efforts and unpublished data (Brown, unpubl.; Lee, unpubl.) also indicate that there are no discernable systematic intra-annual
and/or seasonal variations in linear extension rates of massive *Porites* from this region.

Overall, there is no evidence to suggest systematic and/or gross misalignment of the anomalies in ‘monthly’ partitioned luminescence/density data used in the current study. We therefore presume that the relationship analysis with anomalies in monthly-averaged environmental parameters, which relies on the assumption that the rate of linear extension throughout the year is constant, is robust. Additionally, the use in the present study of multiple cores (total \(n=52\); Phuket \(n=12\); P. Payar \(n=5\); Port Dickson \(n=3\); Singapore \(n=15\); P. Tioman \(n=9\); P. Redang \(n=7\)) as well as a span of years (Dec 2004–Dec 2009), will reduce the effects of among-individual variations and increase the confidence level when attempting to identify common patterns.

Compared to skeletal density, variations in luminescence intensity provided a clearer signal for demarcation of annual growth increments (Figs. 2 and 4). Annual luminescent banding was apparent at all six study locations, whereas annual density banding patterns could only be discerned at four locations (Phuket, P. Payar, P. Tioman and P. Redang). Even then, at Phuket and P. Payar, complicated narrower multiple dense/less dense lines were seen within the broad density bands in several specimens that made demarcation of the annual chronology challenging. This is consistent with observations from previous growth studies around Southeast Asia, where luminescent banding has been used as the preferred method for extracting sclerochronological information (e.g. Charuchinda and Chansang 1985; Brown et al. 1986; Scoffin et al. 1989; Scoffin et al. 1992; Allison et al. 1996; Risk et al. 2003; Tanzil et al. 2009, 2012, 2013).
Luminescent Bands

The timing of the annual luminescent bands was consistent for the majority of the study locations (Phuket, P. Payar, Port Dickson, P. Tioman and P. Redang) with the onset of the brighter band occurring towards the end of the year (Oct/Nov/Dec) whereas in cores from Singapore this was observed in June (Figs. 2 and 4). The magnitude of intra-annual variation in luminescence was most marked at Port Dickson and Singapore, followed by Phuket and P. Payar. At P. Tioman and P. Redang variation was relatively small (Fig. 4).

Luminescence displayed significant relationships with multiple environmental parameters and $|r|$ ranged widely from 0.10 to 0.53, with a median of 0.32 (Table 4). The strongest correlations (i.e. highest $|r|$) also varied among locations e.g. at Phuket, luminescence showed the strongest relationship with salinity ($r$=-0.50) whilst at P. Redang, SWH was the strongest environmental correlate ($r$=-0.53). This might, at first glance, suggest that the timing of bright/dull luminescent band formation at each individual location was driven by different environmental factors or combinations thereof. However, considering the environmental similarities of the study locations (Table 2), it is reasonable to suppose that any potential environmental cues/causes related to the timing of luminescent and density band formation should be systematically (i.e. only positively or only negatively) correlated at all levels. For example, given similar PAR profiles at all locations (Fig. 3b and Table 2), it makes little ecological sense that PAR would be positively correlated at Phuket ($r$=0.47), inversely related at P. Redang ($r$=0.38) and show no relationship at the remaining four locations. Following this line of reasoning, only salinity fulfilled the criteria by exhibiting a systematic, significant negative relationship with luminescence at all locations ($r$=-0.11 to -0.50) (Table 4).
More detailed examination of changes in seasonal luminescence intensity at the region level (encompassing all six locations, 15 reefs, 51 cores) over the five-year period (Dec 2004-Nov 2009) based on a multi-model ‘strength of evidence’ approach, further confirmed salinity as an important predictor variable (Fig. 6a). This region-level analysis, which allowed for non-linear relationships, also identified rainfall amount as a secondary predictor variable and the best model for seasonal luminescence included terms for both salinity and rainfall (marginal $R^2=0.13$; NRMSE=11.2%). The partial effects plots of these variables (Fig. 7a) demonstrate that decreases in salinity below average annual values (i.e. negative anomaly values) accompanied increases in luminescence. Changes in rainfall exerted relatively small effects on variations in luminescence, although higher luminescence can be seen at both higher and lower rainfall.

Examining the relationship with salinity further, periods of higher luminescence intensity coincide with periods of lowered salinity at all six study locations (Figs. 3d and 4). At Phuket, P. Payar, Port Dickson, P. Tioman and P. Redang this occurred towards the end/beginning of the year and in Aug/Sep at Singapore. The absence of a robust relationship with elevated salinity (i.e. positive anomalies) (Fig. 7a) implies that salinity may need to fall below the annual mean before any change in luminescence occurs.

Lough et al. (2002) found that along the length of the GBR, significant luminescence can be induced by drops in salinity of ~1–2‰, and Barnes and Taylor (2005) have suggested such changes may be associated with changes in skeletal crystal size and packing, or crystal chemistry, or all three. Even though we found significant relationships between luminescence intensity and density for most locations, the effect varied greatly with location ($r$-values between -0.216 and 0.303) (Table 3). Thus it was concluded that any
contribution skeletal architecture may make to seasonal luminescent banding patterns in
this region is inconsequential compared to the stronger influence of seasonal inclusions of
fluorophores (related to freshwater sources) into the coral skeletons.

In addition to salinity, the present study used rainfall as a proxy for terrestrial
freshwater runoff reaching reefs from coastlines and found that higher luminescence was
associated with both higher and lower rainfall. This is consistent with earlier studies
where bright luminescent bands were noted to have formed during both low rainfall
periods (e.g. Phuket, Thailand and Seribu Islands, Indonesia) (Scoffin et al. 1992, 1998)
and high rainfall periods (e.g. Papua New Guinea and Great Barrier Reef, Australia)
(Scoffin et al. 1989; Lough 2011). This unclear relationship, however, may be more an
indication of the suitability (or lack thereof) of using localised rainfall as a proxy for the
dominant source of freshwater/river input to reefs rather than a dichotomy in the response
of luminescence to rainfall. In cases where high correlations between rainfall, river
discharge and luminescence are observed e.g. on the inshore GBR (Isdale et al. 1998;
Lough 2007), effects from a single major river and/or landmass usually dominate.
However, in more complex hydrological systems – such as those found around the Thai-
Malay Peninsula – the interplay of wind-driven circulation, bathymetry, topography and
numerous river systems (Wyrtki 1961; Rixen et al. 2011; Rizal et al. 2012; Jha and Singh
2013) may complicate the relationship between rainfall and freshwater runoff reaching
the reefs. This is demonstrated by the disjoint in salinity and rainfall patterns found at
Phuket, P. Payar, Port Dickson and Singapore (Fig. 3c, d). Measurements of δ¹⁸O (as a
proxy for SST and salinity values) from massive *Porites* skeletons sampled around
Phuket and Port Blair (Andaman Islands) also provide further evidence of this disjoint i.e.
lowest salinities in ~Nov–Mar occurring during the lowest rainfall period over this area
(Allison et al. 1996; Rixen et al. 2011).

Alternating monsoon currents (MC) in the South China and Andaman Seas drive
the decoupling of the monsoon-related hydrological cycle and salinity observed in this
region (Rizal et al. 2012). For example, wind-driven circulation flushes more saline,
clearer waters from the South China Sea during the NE monsoon (Nov–Mar) through the
sites around Singapore when rainfall and river discharge (Figs. 3c, 8 and S6) tends to be
highest, reducing the effect of seawater dilution. The opposite is seen during the SW
monsoon (May–Sep) when a combination of tidal- and wind-driven currents allows more
turbid, lower salinity waters from the Java Sea and Malacca Straits to drift/reside longer
in Singapore waters thus producing a counterintuitive salinity minimum during the less
rainy monsoon period at this location (Fig. 3c, d) (Robinson et al. 1953; Chen et al. 2005;
Rizal et al. 2012). Similarly, seasonal differences in current strength through the Malacca
Straits flushes lower salinity, more turbid waters towards the northern mouth of the
Straits during the NE monsoon period (Selvarajah 1961; Rizal et al. 2012), affecting
locations such as P. Payar and Phuket. These phenomena could explain the generally
higher luminescence intensities observed during the drier, lower rainfall season in Porites
specimens from Singapore, Port Dickson, Phuket and P. Payar, and also the occurrence of
an additional luminescence maximum at P. Tioman (~Jul/Aug), which does not coincide
with high rainfall periods, or annual river discharge patterns (Figs. 4e and 8). Only at P.
Redang does high rainfall and river flow coincide with low salinity (Figs. 3c, d and 8),
which could suggest a more straightforward hydrological cycle at this location. Variation
in skeletal luminescence at this location was also much more clear-cut with just a single
clear band estimated to form ~Nov–Feb (Fig. 4d).

Density Bands

Intra-annual variations in skeletal bulk density at the six study locations were categorised into 1) HD band deposition commencing ~Nov/Dec at P. Tioman and P. Redang (east coast locations), 2) HD band formation starting ~May/Jun at Phuket and P. Payar (west coast locations), and 3) no discernable bands at Singapore and Port Dickson (south and southwestern locations) (Fig. 5b). As with luminescence, skeletal density displayed significant relationships with multiple environmental parameters with mostly weak correlation coefficients ($|r|=0.07–0.45$; median $|r|=0.27$) (Table 4). SWH, Rain and PAR had significant unidirectional relationships with density at least half of the study locations. However, only the positive relationship with SWH was systematic at all study locations where discernable density banding patterns were observed i.e. Phuket, P. Payar, P. Tioman and P. Redang ($r=0.08–0.45$). Region level analysis also identified SWH as the most important predictor of seasonal density, followed closely by Rain (Fig. 7b), and both environmental parameters showed positive linear relationships with seasonal density variations.

There is considerable evidence that wave energy and average coral density are related. Brown (1984) found that skeletons of *Acropora aspera* corals in more exposed environments were denser. Scoffin et al. (1992) also identified water movement as the predominant influence on skeletal bulk density which increased along a gradient of increasing hydraulic energy around Phuket reefs. A similar finding was reported by Tanzil et al. (2009). Within limits, increased water movement is believed to be beneficial
to corals by flushing waste, removing sediment, reducing salinity and temperature extremes as well as enhancing the diffusion of nutrients, bicarbonate, and gases by reducing the thickness of the diffusion boundary layer around the coral (see review Todd 2008). Patterson et al. (1991) found primary production and respiration rates in *Orbicella annularis* increased with increasing water motion over an incubation period of ~24 hrs. Similarly, Comeau et al. (2014) found net calcification in corals (based on an assemblage which included massive *Porites*) increased strongly as a function of increasing flow. Conversely, high wave energy can test the mechanical strength of the coral colony structure. Having higher skeletal density would reduce the likelihood of breakage and increase colony survivorship in such environs (Madin et al. 2012). It is, therefore, feasible that the intra-annual variation seen in the Thai-Malay Peninsula massive *Porites* involves a response to seasonal changes in wave energy on the reef. However, it should also be reiterated that the aim of the current study was to explore potential cues or drivers of (validated) seasonal skeletal banding patterns, and consequentially generate relevant hypotheses. Further investigations are required to confirm the relationships suggested here, especially considering the low marginal $R^2$ of 0.08 (NRMSE=14.6%) of the best regional seasonal density model.

It is, however, clear that intra-annual density variations in massive *Porites* corals from the low-latitude Thai-Malay Peninsula reefs are not driven by temperature as evident from the different timing in density banding onset (Figs. 2 and 4) despite the very similar SST profile at all the study locations (Fig. 3a). This is not surprising since mean monthly SSTs around the Thai-Malay Peninsula range only ~2–3°C, from ~27/28°C to ~30°C, and temperature may therefore play only a minor role in driving seasonal...
calcification changes. In contrast, at many higher-latitude reefs where SST ranges are much higher (e.g. northern GBR ~19–28°C; northern Red Sea ~20–27°C), the formation of massive Porites density bands have been strongly linked to seasonal SSTs (Lough and Barnes 1990; Barnes and Lough 1993; Klein and Loya 1991; Al-Rousan 2012). There is, however, a curious dichotomy in such temperature-associated apparent timing of density band formation. For example, at the GBR (13–22°S), HD bands form in the austral summer months when SSTs peak (Lough and Barnes 1990, Barnes and Lough 1993). By contrast, at the Gulf of Eilat/Aqaba, northern Red Sea (~28–29.5°N), the apparent timing of HD bands coincides with boreal winter, when SSTs are lowest (Klein and Loya 1991; Al-Rousan 2012). It is possible there are differences in coral responses to seasonal temperature fluctuation based on distinct geographical regions, or consider that thermal seasonality may not be the primary control of density band formation (e.g. Lough et al. 2015). There may also be dating errors that contribute to the conflicting reports. For example, depending on tissue thickness and coral linear extension rate, dating of density bands based solely on their position relative to the growing surface of the colony can result in dating errors of up to eight months (Barnes and Lough 1993; Taylor et al. 1993; Carricart-Ganivet et al. 2007). Nevertheless, such variability in responses highlights our relatively poor understanding of skeletal banding patterns and their drivers. Interestingly, the apparent timings of HD band formation at both the northern GBR and Gulf of Eilat/Aqaba seem to coincide with periods of greater seasonal weather activity i.e. Australian monsoon and tropical cyclone season from Nov–Apr at the GBR (Ramsay et al. 2007), and storms in the Gulf of Eilat/Aqaba during winter months generating fairly choppy conditions (Mancy 1993).
It is unlikely that seasonal density bands in massive *Porites* are driven by annual cycles of sexual reproduction, as suggested for some other coral species (Wellington and Glynn 1983; Mendes 2004). Massive *Porites* species are gonochoric broadcast spawners observed to participate during multi-specific spawning events (Guest 2004, Stoddart et al. 2012, Chelliah et al. 2015), the majority of which occur within Feb–May across various sites around the Thai-Malay Peninsula including at Phuket, Singapore and P. Tioman (Guest 2004, Kongjandtre et al. 2010, Chelliah et al. 2015). On GBR, mass coral spawning occurs ~Oct–Dec (Baird et al. 2009) when HD band are starting to form. In contrast, spawning occurs ~April–July in the northern/central Red Sea (Bouwmeester et al. 2015) coinciding with apparent LD band formation.

To summarise, we found location-specific recurrent annual luminescent and density banding patterns in massive *Porites* from around the Thai-Malay Peninsula and identified potential environmental cues/drivers of these banding patterns. Seasonal variations in luminescence showed the clearest relationships with salinity, as a proxy for freshwater/river runoff. The lack of a convincing relationship between luminescence intensity and intra-annual variations in density, support the notion that the timing of the deposition of bright/dull luminescent bands is due to inclusions of fluorophores into the coral skeleton rather than, as previously suggested by Barnes and Taylor (2001, 2005), variations in skeletal architecture. Seasonal variations in skeletal density variations reported here are likely related to wave energy, or some other linked environmental parameter/s. It is, however, important to remember that correlations do not confer causation, and further validation is required to ascertain cause and effect of the environmental parameters identified in the present study on variations in both density and
luminescence intensity. The great variability in the appearance and timing of luminescence and density banding patterns as well as occurrence of quasi-annual lines/bands demonstrated in the current study also stresses the importance of properly validating the timing of band formation (e.g. through alizarin staining, repeated subsampling, geochemical dating) as well as the need for replication when interpreting them.
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FIGURE LEGENDS

Figure 1. Map of study locations around the Thai-Malay Peninsula. PKT – Phuket, PY – P. Payar, PD – Port Dickson, SG – Singapore, TIO – P. Tioman, RED – P. Redang. (The abbreviation “P.” in each case stands for Pulau = island).

Figure 2. Images of representative coral slices showing annual variation in luminescence intensity (photographed under ultraviolet light (365nm), left side of image) and density (X-ray positive print, right side of image) for each study location over period ~Dec 2004 to ~Dec 2009. The timing of the bands formation was ascertained through alizarin staining, and repeated subsampling of tagged colonies at multiple time points over a 2-year period (Table 1). Core tops and luminescent/density band patterns were aligned and cross-checked in the multiple samples from the same site, and also across sites. The approximate timing of Dec 2004 and 2009 is shown. The black lines delineate one year’s growth.

Figure 3. Monthly averaged anomalies for a) SST, b) photosynthetically active radiation (PAR), c) rainfall, d) salinity, and e) significant wave height (SWH) over the period Dec 2004–Nov 2009 for the six study locations. Confidence intervals omitted for clarity.

Figure 4. Monthly averaged luminescence intensity and skeletal density anomalies over the period Dec 2004–Nov 2009 for locations along the western (a-c) and eastern (d-f) coasts of the Thai-Malay Peninsula. Error bars indicate ± one standard error. Note the
difference in scale for luminescence for graphs c and f. See Table 2 for absolute mean values of luminescence and density at each location.

Figure 5. Dendograms of agglomerative hierarchical clustering of dynamic time warping (DTW) sequence aligned, normalised variation in a) luminescence intensity, and b) skeletal density for cores from Phuket (PKT), P. Payar (PY), Port Dickson (PD), Singapore (SG), P. Tioman (TIO), and P. Redang (RED) over the period Dec 2005–Nov 2009.

Figure 6. Histograms of the relative importance weights (RIW) (calculated from AIC, AICc and BIC weights) of the five environmental predictor variables (SST – sea surface temperature anomaly; PAR – photosynthetically active radiation anomaly; Rain – rainfall anomaly; Salinity – salinity anomaly; SWH – significant wave height anomaly) for a) luminescence intensity anomalies, and b) skeletal density anomalies, based on the 32 GAMM models examined.

Figure 7. Partial effects plot showing relationships between a) luminescence intensity anomaly and anomalies in salinity/ppt (Sal), and rainfall/mm month$^{-1}$ (Rain), and b) skeletal density anomaly/g cm$^{-3}$ and anomalies in significant wave height/m (SWH) and rainfall/mm month$^{-1}$ (Rain). Dashed line denote 95% confidence interval of the model; tick marks on the inside of the x-axis of each partial plot denotes the locations of the covariate values that applies to the plot.
Figure 8. Average monthly discharge (m$^3$ s$^{-1}$) of selected major rivers around the Thai-Malay Peninsula (river discharge data from Siripong 1990, the RivDis1.1 (Vörösmarty et al. 1998) and the Department of Irrigation and Drainage Malaysia). PKT – Phuket, PY – P. Payar, PD – Port Dickson, SG – Singapore, TIO – P. Tioman, RED – P. Redang
Table 1. Details of study sites, and the dates and number of colonies stained with alizarin red-S. (The abbreviation “P.” in each case stands for Pulau = island).

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<th>Peninsula coast, Sea, Country</th>
<th>Location, Country</th>
<th>Reef name</th>
<th>Latitude (^\circ)N</th>
<th>Longitude (^\circ)E</th>
<th>Water clarity (m)</th>
<th>Type of fringing reef</th>
<th>Distance from mainland Peninsula (\text{km})</th>
<th>Distance from Met. station (\text{km})</th>
<th>Alizarin staining dates (\text{dd/mm/yyyy})</th>
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<td>Yam Yen (YY)</td>
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<td>98.39984</td>
<td>&lt;3</td>
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<td>~35</td>
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<td>100.04203</td>
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<td>104.15378</td>
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<td>10/03/2010, 05/07/2011</td>
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<td>10/03/2010, 04/07/2011</td>
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Table 2. Average values ± 1 SD for average linear extension rates (LE), skeletal density, luminescence intensity and various environmental parameters for the period Dec 2004–Nov 2009

<table>
<thead>
<tr>
<th>Location</th>
<th>LE rates (cm year(^{-1}))</th>
<th>Skeletal density (g cm(^{-3}))</th>
<th>Lumin. Intensity</th>
<th>SST (ºC)</th>
<th>PAR (µmol m(^{-2}) day(^{-1}))</th>
<th>Rainfall (mm month(^{-1}))</th>
<th>Salinity (psu)</th>
<th>SWH (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phuket</td>
<td>2.00 ± 0.14</td>
<td>1.11 ± 0.16</td>
<td>0.55 ± 0.10</td>
<td>29.12 ± 0.55</td>
<td>45.13 ± 4.33</td>
<td>198.39 ± 181.17</td>
<td>31.93 ± 0.40</td>
<td>0.86 ± 0.22</td>
</tr>
<tr>
<td>P. Payar</td>
<td>1.91 ± 0.18</td>
<td>1.11 ± 0.10</td>
<td>0.71 ± 0.08</td>
<td>29.23 ± 0.56</td>
<td>45.02 ± 4.36</td>
<td>200.13 ± 137.84</td>
<td>31.58 ± 0.34</td>
<td>0.55 ± 0.14</td>
</tr>
<tr>
<td>Port Dickson</td>
<td>2.16 ± 0.14</td>
<td>0.92 ± 0.11</td>
<td>0.93 ± 0.19</td>
<td>29.37 ± 0.61</td>
<td>44.95 ± 3.47</td>
<td>169.95 ± 100.67</td>
<td>31.87 ± 0.33</td>
<td>0.10 ± 0.01</td>
</tr>
<tr>
<td>Singapore</td>
<td>1.85 ± 0.14</td>
<td>0.97 ± 0.15</td>
<td>0.74 ± 0.18</td>
<td>28.01 ± 0.87</td>
<td>38.78 ± 4.26</td>
<td>196.13 ± 129.72</td>
<td>31.99 ± 0.32</td>
<td>0.15 ± 0.06</td>
</tr>
<tr>
<td>P. Tioman</td>
<td>1.89 ± 0.10</td>
<td>1.23 ± 0.13</td>
<td>0.49 ± 0.05</td>
<td>28.84 ± 0.93</td>
<td>43.54 ± 5.99</td>
<td>209.83 ± 156.86</td>
<td>32.21 ± 0.32</td>
<td>0.45 ± 0.22</td>
</tr>
<tr>
<td>P. Redang</td>
<td>2.03 ± 0.12</td>
<td>1.15 ± 0.09</td>
<td>0.44 ± 0.04</td>
<td>28.69 ± 1.11</td>
<td>43.83 ± 7.39</td>
<td>235.32 ± 269.49</td>
<td>32.41 ± 0.45</td>
<td>0.65 ± 0.35</td>
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</table>
Table 3. Result of Pearson’s correlation tests between anomalies in skeletal luminescence intensity and density. df = number of sample pairs minus two.

<table>
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<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phuket</td>
<td>0.686</td>
<td>0.015</td>
<td>697</td>
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<tr>
<td>P. Payar</td>
<td>&lt;0.001</td>
<td>-0.216</td>
<td>286</td>
</tr>
<tr>
<td>Port Dickson</td>
<td>0.063</td>
<td>0.140</td>
<td>176</td>
</tr>
<tr>
<td>Singapore</td>
<td>&lt;0.001</td>
<td>0.128</td>
<td>813</td>
</tr>
<tr>
<td>P. Tioman</td>
<td>&lt;0.001</td>
<td>0.249</td>
<td>478</td>
</tr>
<tr>
<td>P. Redang</td>
<td>&lt;0.001</td>
<td>0.305</td>
<td>418</td>
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Table 4. Results of Pearson’s correlation tests between monthly averaged anomalies in luminescence intensity and skeletal density, and SST (°C), photosynthetic active radiation (PAR) (μmol m\(^{-2}\) day\(^{-1}\)), rainfall (mm month\(^{-1}\)), salinity (ppt) and significant wave height (SWH) (m) over the period Dec 2004–Nov 2009. Blue text = significant positive correlation (i.e. \(p<0.05\)); Red text = significant negative correlations; Black text = no significant correlations. \(df\) = number of sample pairs minus two.

<table>
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<tr>
<th>Peninsula coast</th>
<th>Location</th>
<th>SST</th>
<th>PAR</th>
<th>Rain</th>
<th>Salinity</th>
<th>SWH</th>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
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<td>573</td>
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Table 5. Best 5 GAMM models based on AIC and their respective $\Delta$ (difference from lowest model AIC value), inferential models weights ($\omega_i$), evidence ratios (ER) for luminescence intensity anomalies (LUMINESCENCE) and skeletal density anomalies (DENSITY). SST – sea surface temperature anomaly; PAR – photosynthetically active radiation anomaly; Rain – rainfall anomaly; Sal – salinity anomaly; SWH – significant wave height.

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<th>ER</th>
<th>Model</th>
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<td>-5754.113</td>
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