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38 ABSTRACT

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

60 INTRODUCTION

61 The discovery of annual banding patterns in massive coral skeletons has not only given
62 valuable insights into skeletal growth processes and rates, but also provided a means to
63 date past environmental conditions under which growth took place (Knutson et al. 1972;
64 Isdale 1984). Banding is reflected as recurrent variations in density (shown using X-
65 radiographs) and/or luminescence intensity (visible under long-wavelength ultraviolet
66 (UV) light) which appear as alternating bands in slices of coral skeleton cut parallel to the
67 colony growth axis (Buddemeier et al. 1974; Isdale 1984). Usually, alternating bands
68 occur in annual couplets (i.e. a pair of high/low density or bright/dull luminescent bands)
69 and can, therefore, be used to identify optimum tracks to measure coral growth,
70 luminescence intensity and elemental/isotopic geochemical tracers (Buddemeier et al.
71 1974; Lough and Barnes 1990; Scoffin et al. 1992; Lough and Barnes 2000; Tanzil et al.
72 2009; Lough 2010; Cooper et al. 2012).

73 There are, however, less straightforward examples of multiple or indistinct bands
74 that complicate the extraction of age and growth information (e.g. Weber 1975; Scoffin et
75 al. 1989). It is also important to acknowledge that annual growth increments defined
76 using bands rely on an assumption that the timing of band formation (e.g. the onset of
77 deposition of bright/dull luminescent or high/low density bands) occurs around the same
78 time of year for each of the year, and, therefore, that ‘years’ so defined represent periods
79 that do not deviate grossly from ~12 months of growth (Buddemeier et al. 1974; Lough
80 and Barnes 1990). As such, understanding the nature, and ultimately the causes of these
81 banding patterns is crucial in ensuring accurate measurements of growth and
82 sclerochronology.

83 The causes of both luminescent and density banding patterns in corals have been
84 extensively debated (Highsmith 1979; Scoffin et al. 1989; Barnes and Taylor 2001, 2005;
85 Grove et al. 2010). A clear and robust relationship between increased skeletal
86 luminescence and high riverine discharges has repeatedly been shown (Isdale 1984;
87 Smith et al. 1989; Isdale et al. 1998; Lough et al. 2002; Barnes et al. 2003; Hendy et al.
88 2003; Lough 2007). The principle cause of the luminescence proposed in this case is the
89 incorporation in the coral skeleton of humic/fulvic acids leached from the terrestrial
90 environment into river water (Boto and Isdale 1985; Susic et al. 1991; Zicheng et al.
91 2002; Grove et al. 2010; Grove et al. 2012; Llewellyn et al. 2012). However, anomalous
92 luminescence peaks in the absence of any major river flow event have been observed
93 (Jones et al. 2009) as well as annually recurring luminescent bands occurring in offshore
94 corals thought to be far removed from terrestrial influences (Scoffin et al. 1989; Klein et
95 al. 1990; Susic et al. 1991; Tudhope et al. 1996; Smithers and Woodroffe 2001). Such
96 observations have led to the proposition that luminescence may also be related to and/or
97 caused by variations in skeletal architecture. Barnes and Taylor (2001) categorised
98 luminescent bands into (1) broad bands as regions associated with annual low-density
99 bands, and (2) narrow lines of strong luminescence associated with seasonal freshwater
100 flood events. In a later paper, however, Barnes and Taylor (2005) conceded that changes
101 in skeletal chemical composition (e.g. trace inclusions from terrestrial runoff) appeared to
102 be the primary cause of both types of luminescent bands – although they maintained that
103 strongly luminescent lines could still be linked to changes in skeletal crystal size and
104 packing. Prouty et al. (2014) noted a lack of luminescent lines in nearshore corals from
105 Guam exposed to seasonal flooding events i.e. conditions where such luminescence

106 would be expected (Prouty et al. 2014). Ramseyer et al. (1997) found a correlation
107 between luminescence and the skeletal architecture of speleotherms, marine cements, and
108 coral skeletons and subsequently proposed that luminescence was associated with higher
109 porosity and lower calcium carbonate density due to higher inclusions of organic
110 fluorophores. Other studies, conversely, have reported positive relationships between
111 massive *Porites* skeletal density and luminescence (Scoffin et al. 1992; Carricart-Ganivet
112 et al. 2007; Lough 2010, Prouty et al. 2014). As a consequence, the causes of luminescent
113 bands/lines and their relationship with skeletal density remain unclear.

114 Even greater uncertainty exists in regard to the precise cause/s of annual
115 variations in skeletal density. The appearance of high-density (HD) and low-density (LD)
116 bands, visible in X-radiographs/computer tomography images, are the result of the
117 thickening/thinning of skeletal elements – e.g. thecal walls in *Porites* spp. (Buddemeier
118 and Kinzie 1975, Barnes and Devereux 1988) and exothecal dissepiments and costae in
119 *Orbicella annularis* (Dodge et al. 1992). Factors previously related to density band
120 formation include environmental variables such as sea temperature (e.g. Dodge and
121 Thomson 1974; Weber 1975; Buddemeier et al. 1974; Schneider and Smith 1982; Klein
122 et al. 1993; Highsmith 1979; Lough and Barnes 1990, 1992), cloud cover/light level
123 (Highsmith 1979, Brown et al. 1986, Klein and Loya 1991), salinity/freshwater runoff
124 (Scoffin et al. 1989; Barnes and Taylor 2001), rainfall (Buddemeier and Kinzie 1985;
125 Supriharyono 2004) and wave energy (Scoffin et al. 1992), as well as biological
126 parameters/processes such as tissue thickness (Barnes and Lough 1993) and reproduction
127 (Wellington and Glynn 1983; Mendes 2004). Although there are views that LD bands are
128 produced under “optimum” growth conditions and HD bands accrete during “non-

129 optimum” conditions (Highsmith 1979; Scoffin et al. 1989), neither proximate nor
130 ultimate causes for density banding patterns have been unequivocally demonstrated. Even
131 where a single environmental signal has been found to dominate, relationships can vary
132 among and within locations (see Highsmith 1979; Lough and Barnes 1990). For instance,
133 while formation of HD bands in massive *Porites* corals was associated with seasonal high
134 sea surface temperatures (SSTs) on the Great Barrier Reef (GBR) (Weber 1975; Isdale
135 1983; Lough and Barnes 1990), the converse was observed on Western Australian reefs
136 (Schneider and Smith 1982), the Red Sea (Klein and Loya 1991) and even within the
137 GBR (Lough and Barnes 1990), where HD bands in some corals formed during the cooler
138 months. Perhaps surprisingly (if SST is the primary control on band formation), marked
139 density banding has also been found in massive corals from equatorial reefs where
140 seasonal fluctuations in mean monthly SSTs occur within very restricted ranges (e.g.
141 mean monthly SSTs ~27–30°C) (Scoffin et al. 1989, 1992; Cahyarini 2008; Suharsono
142 and Cahyarini 2012).

143 Part of the confusion regarding the nature and causes of luminescent and density
144 banding may result from attempts to find a common environmental signal in corals living
145 in very different environmental conditions (see Weber 1975; Highsmith 1979). It could
146 be that formation of banding patterns at different geographical locations is driven by
147 different factors dependent on the specific set of conditions to which the corals are
148 acclimatised. Dating of bands based on solely their position relative to the growing
149 surface of the colony has also been known to cause conflicting reports on timing of
150 density band formation (Barnes and Lough 1993; Taylor et al. 1993; Carricart-Ganivet et
151 al. 2007). Furthermore, description of banding patterns and associations with broader

152 spatial-scale environmental parameters are sometimes based on single specimens or very
153 small sample sizes (e.g. Klein et al. 1993; Bessat and Buigues 2001; Sazzad et al. 2010).
154 This may produce variable interpretations either because of apparent inherent inter-
155 colony differences in banding patterns (e.g. Lough and Barnes 1990), or artefacts in the
156 methods used for visualising the luminescence (Grove et al. 2010) and skeletal density
157 (Le-Tissier et al. 1994).

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

173

174 MATERIALS AND METHODS

175 *Study sites*

176 Fifteen reefs from six locations around the Thai-Malay Peninsula (1–8°N, 98–105°E),
177 Southeast Asia (Fig. 1, Table 1) were sampled. The reefs along the east coast of the
178 Peninsula are located in the South China Sea (western Pacific Ocean), whereas reefs
179 along the west coast are in the Andaman Sea (northeastern Indian Ocean). Sites around
180 the Thai-Malay Peninsula all experience year-round high mean monthly SSTs of >27–
181 30°C (Tanzil et al. 2009), which peak during the boreal summer (~June) each year. The
182 region has a monsoonal climate, although the wet season occurs at different times of the
183 year on the east and west coasts. The east coast typically experiences higher rainfall and
184 rougher seas during the northeast (NE) monsoon period (~Nov–Mar) whilst similar
185 conditions are experienced on the west coast during the southwest (SW) monsoon
186 (~May–Sep) (Lau and Yang 1997; Wong et al. 2009). The main reason for these effects
187 is the Titiwangsa mountain range which runs through the middle of the Peninsula rising
188 to ~2100m, effectively shielding the east and west coasts from the brunt of the SW and
189 NE monsoons, respectively (Camerlengo and Demmler 1997; Suhaila et al. 2010;
190 Tanggang 2011). Flanking the Thai-Malay Peninsula to the west, the mountain ranges
191 along Sumatra Island, Indonesia also provide additional rain- and wind-sheltering
192 effects for the Peninsula’s west coast, in particular for the southwestern coast, during
193 the SW monsoon (Fig. 1) (Nieuwolt 1968; Wong et al. 2009). High rainfall on the
194 Peninsula (average ~300 mm month⁻¹ in the wet season) and numerous short, swift-
195 flowing rivers east and west of the Titiwangsa mountain range result in considerable
196 runoff and substantial loads of river-transported material being discharged into coastal
197 waters (Fig. 1; see also Fig. 8 for more details). The reefs off the west coast of the

198 Peninsula within the Malacca Straits (e.g. Pulau Payar and Port Dickson) also receive
199 additional input from rivers along the east coast of Sumatra Island, Indonesia (Fig. 1).
200 As a result, these reefs are subject to low salinities and elevated nutrient concentrations,
201 as well as severe turbidity with sedimentation rates as high as $\sim 50\text{--}100 \text{ mg cm}^{-2} \text{ day}^{-1}$,
202 (Chua et al. 1998; BOBLME 2011; Lee and Mohamed 2011). By contrast, offshore
203 island reefs on the eastern and northwestern coasts are significantly less turbid, with
204 sedimentation rates averaging $\sim 0.3 \text{ mg cm}^{-2} \text{ day}^{-1}$ (Lee and Mohamed 2011). The fact
205 that sites along the east and west coasts of the Thai-Malay Peninsula occur within a
206 relatively narrow geographical range, and share similarities in certain environmental
207 conditions (e.g. SST, photosynthetically active radiation) while others are specific to
208 location (e.g. rainfall, wind) presents a unique opportunity for a natural experiment to
209 examine variations in coral skeletal banding patterns and their relationships with
210 selected environmental parameters.

211

212 *Environmental parameters*

213 Several data sets of monthly-averaged environmental variables over the period Dec
214 2004–Nov 2009 were examined. Monthly SST ($^{\circ}\text{C}$) for the 1° area grid encompassing
215 each study location was obtained from the HadISST data set (HadISST, Version 1.1,
216 Hadley Centre for Climate Change, UK Meteorological Office) (Rayner et al. 2003). Sea-
217 surface photosynthetically active radiation (PAR) ($\mu\text{mol m}^{-2} \text{ day}^{-1}$) for the 0.5° grid area
218 encompassing each study location was obtained from Sea-Viewing Wide Field-of-view
219 (SeaWiFs) monthly level 3 Ocean Color product extracted with the Giovanni online data
220 system, developed and maintained by the NASA GES DISC (Acker and Leptoukh 2007).

221 Monthly average rainfall (mm month⁻¹) was retrieved from the nearest available weather
222 stations to the study locations i.e. Phuket – Phuket Airport (8.108°N, 98.517°E), Pulau
223 Payar – Langkawi Airport (6.333°N, 99.733°E), Port Dickson – Malacca town (2.266°N,
224 102.250°E), Singapore – Changi Airport, Pulau Tioman – Mersing (2.450°N, 103.833°E),
225 and Pulau Redang – Kuala Terengganu Airport (5.050°N, 103.100°E). Distances of study
226 reefs from these meteorological stations used are given in Table 1. Monthly salinity (ppt)
227 for 0.5° area grids was obtained from Carton-Giese UMD Simple Ocean Data
228 Assimilation (SODA) v2.1.6 (Carton and Giese 2008). Modelled monthly means of
229 significant wave height (SWH) (m) for 1° area grids were acquired from European Centre
230 for Medium-Range Weather Forecasts (ECMWF) ERA-20C global reanalysis (Stickler et
231 al. 2014).

232 The above environmental variables (i.e. temperature, light, rainfall, salinity and
233 wave height) were selected to represent parameters that might affect coral skeletal
234 luminescence and density band formation. Both salinity and rainfall were used as proxies
235 for the amount of freshwater/river input reaching the reefs since increased riverine
236 humic/fulvic substances and dissolved organic material from terrestrial sources are
237 strongly correlated to coral luminescence in certain locations (Isdale 1984; Susic et al.
238 1991; Isdale et al. 1998). However, rainfall represented more local terrestrial run-off
239 reaching reefs from coastlines while salinity represented the total freshwater flux not just
240 from coastline/river runoff, but also current-driven movement of freshwater masses. The
241 0.5° gridded SODA salinity product used here was a reanalysis based on an ocean general
242 circulation model and salinity observations from ships and Argo buoys (Carton and Giese
243 2008). We chose these data because available data for longer-term in-situ

244 monthly/seasonal salinity were extremely limited around the study locations. Although
245 there were discrepancies between predicted SODA and in-situ salinities given the coarse
246 spatial resolution and nature of the SODA product, comparison of mean monthly SODA
247 salinity with in-situ measurements taken from one study reef (SG-KU) showed a similar
248 pattern of intra-annual changes in salinity even if SODA estimated higher absolute
249 salinity values and a much smaller salinity range (Fig. S1). Thus local salinities predicted
250 by SODA were likely, at a minimum, to provide a suitable correlative proxy for seasonal
251 variations in the amount of freshwater to which the corals were exposed.

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

259

260 *Skeletal luminescence and density banding*

261 Fifty-three massive *Porites* colonies sampled between Oct 2010 and Jan 2012 were
262 analysed for skeletal luminescence and density banding (Table 1). At each of the 15 study
263 sites, colonies ~1–4m in diameter were sampled at depths ~2–3m below mid-tide height
264 from within a 100m stretch of fringing reef <1km distance from the nearest rocky
265 outcrop, island or coastline. All cores were taken from the main growth axis of the coral
266 colony using a pneumatic drill fitted with a 5cm diameter, 50cm long diamond bit core

267 barrel. Although it was not possible to conclusively identify all samples to species level,
268 the majority (~76%) of colonies were positively identified as *Porites lutea* (Tanzil et al.
269 2013).

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

281 Slices (~0.7 cm thick) were cut from coral cores, and growth chronology and
282 linear extension rates were resolved from the annual skeletal banding patterns as
283 visualised in Fig. 2. Skeletal density and luminescence intensity measurements for the
284 period ~Dec 2004–Nov 2009 were then obtained along overlapping tracks ~0.2 cm wide
285 along the main growth axis and at a resolution of 72 pixels cm⁻¹ (i.e. at every ~0.014 cm).
286 Skeletal densities were analysed using digitised X-ray images (Carricart-Ganivet and
287 Barnes 2007) and verified against gamma densitometry at the Australian Institute of
288 Marine Science (Chalker and Barnes 1990) (Fig. S2b and S3b). Luminescence intensities
289 were measured from digital images (Canon G10 digital camera) of core slices taken under

290 long-wavelength (365nm) ultraviolet (UV) light in a customised photography black box.
291 These images were then split into their red, green and blue (RGB) spectral components
292 and the green/blue (G/B) spectral ratio used as a measure of luminescence intensity
293 (Grove et al. 2010). Luminescence intensity measurements were validated against
294 luminometry at the Australian Institute of Marine Science (Barnes et al. 2003) (Fig. S2a
295 and S3a). All image analyses for skeletal density and luminescence intensity extractions
296 were performed using NIH ImageJ (v1.46r) (Rasband 1997–2012).

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

310

311 *Statistical analyses*

312 Annual luminescent and density banding patterns

313 Any natural grouping in the timing of annual luminescent and density banding patterns in
314 the cores sampled from the various study locations was identified using agglomerative
315 hierarchical cluster analysis. For each core, sequences of skeletal luminescence and
316 density measurements were partitioned into five 1-year time series (Fig. S5) and then
317 normalised (i.e. zero mean and one unit sample variance). “Shape” information (i.e.
318 seasonality) was thus retained but between year differences in the luminescence/density
319 ranges removed. Because different years and cores had grown at different rates, it was
320 then necessary to align the time series using a dynamic time warping (DTW) algorithm
321 (Giorgino et al. 2009). In this alignment, the sequences were stretched and displaced in
322 order to optimally match each other under the constraint that the start and end points of
323 each 1-year time series match, i.e. effectively translating the data from the spatial domain
324 to a common implied time domain for all corals. DTW was used as it not only accounts
325 for differences in time-series lengths, but can also deal with the possibility of slight
326 misalignment in the luminescent/density time series associated with skewed growth axes
327 and/or artefacts of the sampling methodology. Following alignment, distance measures
328 between individual cores were calculated (as the average Euclidean distances between the
329 five corresponding 1-year sequences of a pair of cores), and similarities between clusters
330 of segments were computed using the Ward-link method (Ward 1963). This linkage
331 method was used since it minimises the variance of the distance within clusters, and
332 performs best compared to other methods when the number of clusters are small (Lerato
333 and Niesler 2012). All analyses were executed using the statistical program R (R Core
334 Team 2012) using R-packages ‘dtw’ (Giorgino 2009) and ‘stats’.
335

336 Relationship with environmental parameters

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

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

353 Subsequently, Generalised Additive Mixed Models (GAMMs) were used to
354 examine region level relationships. Preliminary analysis showed that GAMMs had the
355 best goodness of fit compared to other models explored (e.g. Generalised Least Squares
356 (GLS), Generalised Linear Models (GLM)) as they allowed for linear and non-linear
357 relationships, as well as inclusion of random effects to account for correlation among
358 observations on the same sampling unit (Wood 2006). For each model, the fixed effects

359 components included a combination of predictors ‘SST’, ‘PAR’, ‘Rain’, ‘Sal’ and ‘SWH’,
360 and nested random effects in ‘Location’, ‘Site’ and ‘Core’ (individual colony). A
361 smoothing term (cubic regression spline, $df=4$) was applied to all the predictor variables.
362 Assumptions of normality, homogeneity of variances as well as possible autocorrelations
363 within the dataset were tested, and variance/autocorrelation terms included into the
364 GAMMs where necessary (refer to Supplemental Information for the final full-model
365 GAMM form used).

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

378 In addition to information about relative model support, ω_i can also be used to
379 estimate the variable relative importance weights (RIW) by summing the ω_i across all
380 models in the set where a particular predictor variable occurs (Burnham and Anderson
381 2002). As with inferential model weights, RIW can be interpreted as equivalent to the

382 probability that that predictor variable is a component of the best model. A total of 32
383 models were considered (31 models with full-subsets along with an intercept only
384 model). A likelihood-ratio based (pseudo) R^2 (Bartoń 2013) was used to estimate the
385 ‘variance explained’ by fixed effect factors of the top-ranked model, and partial effects
386 plots were used to illustrate the relationships between environmental variables and
387 luminescence intensity and density anomalies.

388

389 Relationship between skeletal luminescence and density

390 Any relationships between monthly luminescence and skeletal density anomalies were
391 tested using Pearson’s product-moment correlation tests at the individual location level.
392 All statistical analyses were performed using the statistical program R (version 2.15.1) (R
393 Core Team 2012), using packages “stats”, “mgcv” (Wood 2006) and MuMIn (Bartoń
394 2012).

395

396 RESULTS

397 *Intra-annual variation in environmental parameters*

398 SSTs at all the study locations averaged $\sim 29^\circ\text{C}$ (Table 2) and were characterised by an
399 annual cycle with a peak \sim May (which marks the warmest period for the region with sea
400 temperatures often reaching $>30^\circ\text{C}$), another smaller peak in October/November, and a
401 minimum in January (Fig. 3a). The annual range of mean monthly SST was, however,
402 relatively small at $\sim 3^\circ\text{C}$ (i.e. $\sim 27\text{--}30^\circ\text{C}$) for locations along the eastern coast of the Thai-
403 Malay Peninsula and $\sim 2^\circ\text{C}$ (i.e. $\sim 28\text{--}30^\circ\text{C}$) for the western coast. SST maxima and
404 minima lagged those of solar radiation (Fig. 3b), which exhibit the characteristic bi-

405 modal peaks (March and September) as the sun passed overhead in its seasonal
406 movement between the two Tropics (Osborne 2000). Monsoonal cloud cover also affects
407 solar radiation such that at Phuket and Pulau Payar (“Pulau” means ‘island’ in Malay and
408 will henceforth be “P.”) the secondary peaks in solar radiation and SST in the latter half
409 of the year (Fig. 3a/b) were largely absent.

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

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

427

428 *Annual banding pattern*

429 Luminescent bands

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

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

451 followed by a very broad dull band. The annual pattern at P. Tioman was much less
452 distinct, but generally consisted of two bright and two dull luminescent bands, the first
453 and usually brighter of which started forming ~Dec, and the second estimated ~Jul/Aug.

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

458

459 Skeletal density bands

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

469 Based on the position of alizarin stain/subsampling and alignment with
470 luminescent bands, HD bands in corals sampled from Phuket and P. Payar (west coast
471 locations) were estimated to form between May and Sep with maximum densities
472 ~Jun/Jul (Figs. 4a/b). However, despite this general pattern, complicated narrower
473 multiple dense/less dense lines were also observed within the broad density bands in

474 several specimens. At P. Redang and P. Tioman (east coast locations), density banding
475 was generally clearer and more consistent (Figs. 2 and 4d/e), and consisted of a distinct
476 narrow HD band formed ~Nov–Feb and a much broader LD band formed ~Mar–Oct.

477

478 *Relationship between skeletal luminescence and density*

479 Correlations between seasonal luminescence intensity and density anomalies varied
480 according to location (Table 3), with no significant (at $\alpha=0.05$) relationship at Phuket
481 ($p=0.686$) or Port Dickson ($p=0.063$); a significant but weak negative relationship at P.
482 Payar ($p<0.001$, $r=-0.216$); and significant but weak positive relationships at Singapore
483 ($p<0.001$, $r=0.128$), Tioman ($p<0.001$, $r=0.197$) and P. Redang ($p<0.001$, $r=0.303$).
484 Degrees of freedom given in Table 3.

485

486 *Linkages with environmental parameters*

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

492

493 Luminescence intensity

494 Luminescence and SST were significantly (at $\alpha=0.05$; degrees of freedom given in Table
495 4) positively correlated at Singapore ($p=0.01$, $r=0.250$), but showed significant negative
496 relationships at the other five study locations; Phuket ($p<0.001$, $r=-0.097$), P. Payar

497 ($p<0.001$, $r=-0.265$), Port Dickson ($p<0.001$, $r=-0.374$), P. Tioman ($p<0.001$, $r=-0.156$)
498 and P. Redang ($p<0.001$, $r=-0.508$). PAR was significantly correlated with luminescence
499 at only two study locations – positive at Phuket ($p<0.001$, $r=0.474$) and negative P.
500 Redang ($p<0.001$, $r=-0.375$). The results for rainfall at the location level were similarly
501 variable, with significant inverse correlations at three locations (Phuket – $p<0.001$, $r=-$
502 0.476 ; P. Payar – $p<0.001$, $r=-0.330$; Singapore – $p<0.001$, $r=-0.218$), a significant
503 positive relationship at P. Redang ($p<0.001$, $r=0.188$), and no significant relationships at
504 Port Dickson and P. Tioman. Salinity at all locations was significantly inversely
505 correlated, with r ranging from -0.110 at P. Tioman ($p=0.02$) to -0.504 at Phuket
506 ($p<0.001$) (Table 4). SWH was significantly correlated with luminescence at five
507 locations with positive correlations at P. Tioman ($p<0.001$, $r=0.138$) and P. Redang
508 ($p<0.001$, $r=0.527$), and inversely related at Phuket ($p<0.001$, $r=-0.459$), P. Payar
509 ($p<0.001$, $r=-0.334$) and Singapore ($p<0.001$, $r=-0.217$).

510 The top-ranked model fit for variation in luminescence at the region level based
511 on lowest AIC and highest AIC ω_i included salinity and rainfall effects (Table 5). This
512 produced an AIC ω_i of 0.35 (i.e. 35% chance of this model being the best approximating
513 model describing the data given the set of predictor variables considered), ~ 2 times that
514 of the next competing model based on Δ AIC values of <2 (Table 5) and was therefore
515 chosen as best estimator of seasonal variation in luminescence. Analysis of variable
516 relative importance weights (RIW) revealed that salinity was the strongest predictor
517 variable for seasonal luminescence based on AIC ω_i (RIW=0.99), followed by rainfall
518 amount (RIW=0.61). PAR, SWH and SST all had much smaller RIWs ranging from
519 0.12–0.29 (Fig. 6a). The ‘variance explained’ by only the fixed-effect factors of the top-

520 ranked model (i.e. salinity and rainfall) as estimated by a likelihood-ratio based (pseudo)
521 R^2 was 0.13 (henceforth referred to as ‘marginal R^2 ’), with a residual mean standard error
522 (normalised to the range of observed values) (NRMSE) of 11.2%. Partial effect plots for
523 these terms showed seasonal luminescence was correlated with negative values of salinity
524 but not positive values (Fig. 7a). The relationship between seasonal luminescence and
525 rainfall was less defined, with a possible minimum at rainfall values of ~ 200 mm month⁻¹.
526

527

528 Skeletal density

529 Density and SST were significantly correlated at four of the six study locations, with
530 positive relationships at Phuket ($p < 0.001$, $r = 0.159$) and P. Payar ($p < 0.001$, $r = 0.341$), and
531 negative ones at P. Tioman ($p < 0.001$, $r = -0.355$) and P. Redang ($p < 0.001$, $r = -0.370$).
532 Density and PAR were significantly inversely related at only the south and east coast
533 locations (i.e. Singapore – $p = 0.002$, $r = -0.119$; P. Tioman – $p < 0.001$, $r = -0.225$; P. Redang
534 – $p < 0.001$, $r = -0.353$). Rainfall was positively correlated with density at three study
535 locations; P. Payar ($p < 0.001$, $r = 0.293$), P. Tioman ($p < 0.001$, $r = 0.283$) and P. Redang
536 ($p = 0.013$, $r = 0.113$). Salinity was only significantly correlated with density at the two east
537 locations (P. Tioman – $p < 0.001$, $r = -0.256$; P. Redang – $p < 0.001$, $r = -0.268$). SWH was
538 significantly positively correlated with density at four locations – Phuket ($p = 0.018$,
539 $r = 0.081$), P. Payar ($p < 0.001$, $r = 0.256$), P. Tioman ($p < 0.001$, $r = 0.450$) and P. Redang
540 ($p < 0.001$, $r = 0.391$).

541 Region level analyses found the best model fit for seasonal density variations
542 included terms for SWH and Rain based (Table 5). This model produced the lowest AIC

543 as well as the highest AIC.ωi of 0.36. SWH was identified as the strongest predictor
544 variable for seasonal skeletal density (RIW=0.99), followed by Rain (0.91) (Table 5).
545 RIWs for PAR, SST and salinity were much smaller and ranged from 0.13–0.37. The
546 marginal R² for the top-ranked model was low at 0.08, with a NRMSE of 14.6%. Partial
547 effect plots showed that seasonal density exhibited linear positive relationships with both
548 SWH and Rain (Fig 7b).

549

550 DISCUSSION

551 The skeletons of massive *Porites* corals from all six study locations around the
552 Thai-Malay Peninsula were found to contain location-specific recurrent luminescent
553 and/or density banding patterns. Although we interpret these patterns as annual in nature,
554 it is not possible to be certain that they represent exactly one year's growth. Several lines
555 of evidence, however, suggest that the time frame in which these recurrent bands are
556 formed does not deviate markedly from a 12-month period. Firstly, repeated alizarin
557 staining at all locations with the exception of Port Dickson (successfully stained only
558 once) (Table 1), and the subsampling of tagged coral colonies within the period 2009–
559 2011, demonstrated that the bands occurred at the same time of the year, at least within
560 this ~2-year period. Secondly, for Phuket, results from previous growth studies and
561 alizarin staining also align with our luminescent banding chronology i.e. onset of bright
562 band ~Nov/Dec (Charuchinda and Chansang 1985; Chansang et al. 1996; Scoffin et al.
563 1992). Lastly, results from these aforementioned alizarin staining/subsampling and
564 growth studies, together with past sampling efforts and unpublished data (Brown,
565 unpubl.; Lee, unpubl.) also indicate that there are no discernable systematic intra-annual

566 and/or seasonal variations in linear extension rates of massive *Porites* from this region.
567 Overall, there is no evidence to suggest systematic and/or gross misalignment of the
568 anomalies in ‘monthly’ partitioned luminescence/density data used in the current study.
569 We therefore presume that the relationship analysis with anomalies in monthly-averaged
570 environmental parameters, which relies on the assumption that the rate of linear extension
571 throughout the year is constant, is robust. Additionally, the use in the present study of
572 multiple cores (total $n=52$; Phuket $n=12$; P. Payar $n=5$; Port Dickson $n=3$; Singapore
573 $n=15$; P. Tioman $n=9$; P. Redang $n=7$) as well as a span of years (Dec 2004–Dec 2009),
574 will reduce the effects of among-individual variations and increase the confidence level
575 when attempting to identify common patterns.

576 Compared to skeletal density, variations in luminescence intensity provided a
577 clearer signal for demarcation of annual growth increments (Figs. 2 and 4). Annual
578 luminescent banding was apparent at all six study locations, whereas annual density
579 banding patterns could only be discerned at four locations (Phuket, P. Payar, P. Tioman
580 and P. Redang). Even then, at Phuket and P. Payar, complicated narrower multiple
581 dense/less dense lines were seen within the broad density bands in several specimens that
582 made demarcation of the annual chronology challenging. This is consistent with
583 observations from previous growth studies around Southeast Asia, where luminescent
584 banding has been used as the preferred method for extracting sclerochronological
585 information (e.g. Charuchinda and Chansang 1985; Brown et al. 1986; Scoffin et al.
586 1989; Scoffin et al. 1992; Allison et al. 1996; Risk et al. 2003; Tanzil et al. 2009, 2012,
587 2013).

588

589 Luminescent Bands

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

596 Luminescence displayed significant relationships with multiple environmental
597 parameters and $|r|$ ranged widely from 0.10 to 0.53, with a median of 0.32 (Table 4). The
598 strongest correlations (i.e. highest $|r|$) also varied among locations e.g. at Phuket,
599 luminescence showed the strongest relationship with salinity ($r=-0.50$) whilst at P.
600 Redang, SWH was the strongest environmental correlate ($r=-0.53$). This might, at first
601 glance, suggest that the timing of bright/dull luminescent band formation at each
602 individual location was driven by different environmental factors or combinations
603 thereof. However, considering the environmental similarities of the study locations
604 (Table 2), it is reasonable to suppose that any potential environmental cues/causes related
605 to the timing of luminescent and density band formation should be systematically (i.e.
606 only positively or only negatively) correlated at all levels. For example, given similar
607 PAR profiles at all locations (Fig. 3b and Table 2), it makes little ecological sense that
608 PAR would be positively correlated at Phuket ($r=0.47$), inversely related at P. Redang
609 ($r=0.38$) and show no relationship at the remaining four locations. Following this line of
610 reasoning, only salinity fulfilled the criteria by exhibiting a systematic, significant
611 negative relationship with luminescence at all locations ($r=-0.11$ to -0.50) (Table 4).

612 More detailed examination of changes in seasonal luminescence intensity at the
613 region level (encompassing all six locations, 15 reefs, 51 cores) over the five-year period
614 (Dec 2004-Nov 2009) based on a multi-model ‘strength of evidence’ approach, further
615 confirmed salinity as an important predictor variable (Fig. 6a). This region-level analysis,
616 which allowed for non-linear relationships, also identified rainfall amount as a secondary
617 predictor variable and the best model for seasonal luminescence included terms for both
618 salinity and rainfall (marginal $R^2=0.13$; NRMSE=11.2%). The partial effects plots of
619 these variables (Fig. 7a) demonstrate that decreases in salinity below average annual
620 values (i.e. negative anomaly values) accompanied increases in luminescence. Changes in
621 rainfall exerted relatively small effects on variations in luminescence, although higher
622 luminescence can be seen at both higher and lower rainfall.

623 Examining the relationship with salinity further, periods of higher luminescence
624 intensity coincide with periods of lowered salinity at all six study locations (Figs. 3d and
625 4). At Phuket, P. Payar, Port Dickson, P. Tioman and P. Redang this occurred towards the
626 end/beginning of the year and in Aug/Sep at Singapore. The absence of a robust
627 relationship with elevated salinity (i.e. positive anomalies) (Fig. 7a) implies that salinity
628 may need to fall below the annual mean before any change in luminescence occurs.
629 Lough et al. (2002) found that along the length of the GBR, significant luminescence can
630 be induced by drops in salinity of $\sim 1-2\%$, and Barnes and Taylor (2005) have suggested
631 such changes may be associated with changes in skeletal crystal size and packing, or
632 crystal chemistry, or all three. Even though we found significant relationships between
633 luminescence intensity and density for most locations, the effect varied greatly with
634 location (r -values between -0.216 and 0.303) (Table 3). Thus it was concluded that any

635 contribution skeletal architecture may make to seasonal luminescent banding patterns in
636 this region is inconsequential compared to the stronger influence of seasonal inclusions of
637 fluorophores (related to freshwater sources) into the coral skeletons.

638 In addition to salinity, the present study used rainfall as a proxy for terrestrial
639 freshwater runoff reaching reefs from coastlines and found that higher luminescence was
640 associated with both higher and lower rainfall. This is consistent with earlier studies
641 where bright luminescent bands were noted to have formed during both low rainfall
642 periods (e.g. Phuket, Thailand and Seribu Islands, Indonesia) (Scoffin et al. 1992, 1998)
643 and high rainfall periods (e.g. Papua New Guinea and Great Barrier Reef, Australia)
644 (Scoffin et al. 1989; Lough 2011). This unclear relationship, however, may be more an
645 indication of the suitability (or lack thereof) of using localised rainfall as a proxy for the
646 dominant source of freshwater/river input to reefs rather than a dichotomy in the response
647 of luminescence to rainfall. In cases where high correlations between rainfall, river
648 discharge and luminescence are observed e.g. on the inshore GBR (Isdale et al. 1998;
649 Lough 2007), effects from a single major river and/or landmass usually dominate.
650 However, in more complex hydrological systems – such as those found around the Thai-
651 Malay Peninsula – the interplay of wind-driven circulation, bathymetry, topography and
652 numerous river systems (Wyrтки 1961; Rixen et al. 2011; Rizal et al. 2012; Jha and Singh
653 2013) may complicate the relationship between rainfall and freshwater runoff reaching
654 the reefs. This is demonstrated by the disjoint in salinity and rainfall patterns found at
655 Phuket, P. Payar, Port Dickson and Singapore (Fig. 3c, d). Measurements of $\delta^{18}\text{O}$ (as a
656 proxy for SST and salinity values) from massive *Porites* skeletons sampled around
657 Phuket and Port Blair (Andaman Islands) also provide further evidence of this disjoint i.e.

658 lowest salinities in ~Nov–Mar occurring during the lowest rainfall period over this area
659 (Allison et al. 1996; Rixen et al. 2011).

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

681 clear band estimated to form ~Nov–Feb (Fig. 4d).

682

683 Density Bands

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

698 There is considerable evidence that wave energy and average coral density are
699 related. Brown (1984) found that skeletons of *Acropora aspera* corals in more exposed
700 environments were denser. Scoffin et al. (1992) also identified water movement as the
701 predominant influence on skeletal bulk density which increased along a gradient of
702 increasing hydraulic energy around Phuket reefs. A similar finding was reported by
703 Tanzil et al. (2009). Within limits, increased water movement is believed to be beneficial

704 to corals by flushing waste, removing sediment, reducing salinity and temperature
705 extremes as well as enhancing the diffusion of nutrients, bicarbonate, and gases by
706 reducing the thickness of the diffusion boundary layer around the coral (see review Todd
707 2008). Patterson et al. (1991) found primary production and respiration rates in *Orbicella*
708 *annularis* increased with increasing water motion over an incubation period of ~24 hrs.
709 Similarly, Comeau et al. (2014) found net calcification in corals (based on an assemblage
710 which included massive *Porites*) increased strongly as a function of increasing flow.
711 Conversely, high wave energy can test the mechanical strength of the coral colony
712 structure. Having higher skeletal density would reduce the likelihood of breakage and
713 increase colony survivorship in such environs (Madin et al. 2012). It is, therefore, feasible
714 that the intra-annual variation seen in the Thai-Malay Peninsula massive *Porites* involves
715 a response to seasonal changes in wave energy on the reef. However, it should also be
716 reiterated that the aim of the current study was to explore potential cues or drivers of
717 (validated) seasonal skeletal banding patterns, and consequentially generate relevant
718 hypotheses. Further investigations are required to confirm the relationships suggested
719 here, especially considering the low marginal R^2 of 0.08 (NRMSE=14.6%) of the best
720 regional seasonal density model.

721 It is, however, clear that intra-annual density variations in massive *Porites* corals
722 from the low-latitude Thai-Malay Peninsula reefs are not driven by temperature as
723 evident from the different timing in density banding onset (Figs. 2 and 4) despite the very
724 similar SST profile at all the study locations (Fig. 3a). This is not surprising since mean
725 monthly SSTs around the Thai-Malay Peninsula range only ~2–3°C, from ~27/28°C to
726 ~30°C, and temperature may therefore play only a minor role in driving seasonal

727 calcification changes. In contrast, at many higher-latitude reefs where SST ranges are
728 much higher (e.g. northern GBR ~19–28°C; northern Red Sea ~20–27°C), the formation
729 of massive *Porites* density bands have been strongly linked to seasonal SSTs (Lough and
730 Barnes 1990; Barnes and Lough 1993; Klein and Loya 1991; Al-Rousan 2012). There is,
731 however, a curious dichotomy in such temperature-associated apparent timing of density
732 band formation. For example, at the GBR (13–22°S), HD bands form in the austral
733 summer months when SSTs peak (Lough and Barnes 1990, Barnes and Lough 1993). By
734 contrast, at the Gulf of Eilat/Aqaba, northern Red Sea (~28–29.5°N), the apparent timing
735 of HD bands coincides with boreal winter, when SSTs are lowest (Klein and Loya 1991;
736 Al-Rousan 2012). It is possible there are differences in coral responses to seasonal
737 temperature fluctuation based on distinct geographical regions, or consider that thermal
738 seasonality may not be the primary control of density band formation (e.g. Lough et al.
739 2015). There may also be dating errors that contribute to the conflicting reports. For
740 example, depending on tissue thickness and coral linear extension rate, dating of density
741 bands based solely on their position relative to the growing surface of the colony can
742 result in dating errors of up to eight months (Barnes and Lough 1993; Taylor et al. 1993;
743 Carricart-Ganivet et al. 2007). Nevertheless, such variability in responses highlights our
744 relatively poor understanding of skeletal banding patterns and their drivers. Interestingly,
745 the apparent timings of HD band formation at both the northern GBR and Gulf of
746 Eilat/Aqaba seem to coincide with periods of greater seasonal weather activity i.e.
747 Australian monsoon and tropical cyclone season from Nov–Apr at the GBR (Ramsay et
748 al. 2007), and storms in the Gulf of Eilat/Aqaba during winter months generating fairly
749 choppy conditions (Mancy 1993).

750 It is unlikely that seasonal density bands in massive *Porites* are driven by annual
751 cycles of sexual reproduction, as suggested for some other coral species (Wellington and
752 Glynn 1983; Mendes 2004). Massive *Porites* species are gonochoric broadcast spawners
753 observed to participate during multi-specific spawning events (Guest 2004, Stoddart et al.
754 2012, Chelliah et al. 2015), the majority of which occur within Feb–May across various
755 sites around the Thai-Malay Peninsula including at Phuket, Singapore and P. Tioman
756 (Guest 2004, Kongjandtre et al. 2010, Chelliah et al. 2015). On GBR, mass coral
757 spawning occurs ~Oct–Dec (Baird et al. 2009) when HD band are starting to form. In
758 contrast, spawning occurs ~April–July in the northern/central Red Sea (Bouwmeester et
759 al. 2015) coinciding with apparent LD band formation.

760 To summarise, we found location-specific recurrent annual luminescent and
761 density banding patterns in massive *Porites* from around the Thai-Malay Peninsula and
762 identified potential environmental cues/drivers of these banding patterns. Seasonal
763 variations in luminescence showed the clearest relationships with salinity, as a proxy for
764 freshwater/river runoff. The lack of a convincing relationship between luminescence
765 intensity and intra-annual variations in density, support the notion that the timing of the
766 deposition of bright/dull luminescent bands is due to inclusions of fluorophores into the
767 coral skeleton rather than, as previously suggested by Barnes and Taylor (2001, 2005),
768 variations in skeletal architecture. Seasonal variations in skeletal density variations
769 reported here are likely related to wave energy, or some other linked environmental
770 parameter/s. It is, however, important to remember that correlations do not confer
771 causation, and further validation is required to ascertain cause and effect of the
772 environmental parameters identified in the present study on variations in both density and

773 luminescence intensity. The great variability in the appearance and timing of
774 luminescence and density banding patterns as well as occurrence of quasi-annual
775 lines/bands demonstrated in the current study also stresses the importance of properly
776 validating the timing of band formation (e.g. through alizarin staining, repeated
777 subsampling, geochemical dating) as well as the need for replication when interpreting
778 them.

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1199 FIGURE LEGENDS

1200

1201 Figure 1. Map of study locations around the Thai-Malay Peninsula. PKT – Phuket, PY –
1202 P. Payar, PD – Port Dickson, SG – Singapore, TIO – P. Tioman, RED – P. Redang. (The
1203 abbreviation “P.” in each case stands for Pulau = island).

1204

1205 Figure 2. Images of representative coral slices showing annual variation in luminescence
1206 intensity (photographed under ultraviolet light (365nm), left side of image) and density
1207 (X-ray positive print, right side of image) for each study location over period ~Dec 2004
1208 to ~Dec 2009. The timing of the bands formation was ascertained through alizarin
1209 staining, and repeated subsampling of tagged colonies at multiple time points over a 2-
1210 year period (Table 1). Core tops and luminescent/density band patterns were aligned and
1211 cross-checked in the multiple samples from the same site, and also across sites. The
1212 approximate timing of Dec 2004 and 2009 is shown. The black lines delineate one year’s
1213 growth.

1214

1215 Figure 3. Monthly averaged anomalies for a) SST, b) photosynthetically active radiation
1216 (PAR), c) rainfall, d) salinity, and e) significant wave height (SWH) over the period Dec
1217 2004–Nov 2009 for the six study locations. Confidence intervals omitted for clarity.

1218

1219 Figure 4. Monthly averaged luminescence intensity and skeletal density anomalies over
1220 the period Dec 2004–Nov 2009 for locations along the western (a-c) and eastern (d-f)
1221 coasts of the Thai-Malay Peninsula. Error bars indicate \pm one standard error. Note the

1222 difference in scale for luminescence for graphs c and f. See Table 2 for absolute mean
1223 values of luminescence and density at each location.

1224

1225 Figure 5. Dendograms of agglomerative hierarchical clustering of dynamic time warping
1226 (DTW) sequence aligned, normalised variation in a) luminescence intensity, and b)
1227 skeletal density for cores from Phuket (PKT), P. Payar (PY), Port Dickson (PD),
1228 Singapore (SG), P. Tioman (TIO), and P. Redang (RED) over the period Dec 2005–Nov
1229 2009.

1230

1231 Figure 6. Histograms of the relative importance weights (RIW) (calculated from AIC,
1232 AICc and BIC weights) of the five environmental predictor variables (SST – sea surface
1233 temperature anomaly; PAR – photosynthetically active radiation anomaly; Rain – rainfall
1234 anomaly; Salinity – salinity anomaly; SWH – significant wave height anomaly) for a)
1235 luminescence intensity anomalies, and b) skeletal density anomalies, based on the 32
1236 GAMM models examined.

1237

1238 Figure 7. Partial effects plot showing relationships between a) luminescence intensity
1239 anomaly and anomalies in salinity/ppt (Sal), and rainfall/mm month⁻¹ (Rain), and b)
1240 skeletal density anomaly/g cm⁻³ and anomalies in significant wave height/m (SWH) and
1241 rainfall/mm month⁻¹ (Rain). Dashed line denote 95% confidence interval of the model;
1242 tick marks on the inside of the x-axis of each partial plot denotes the locations of the
1243 covariate values that applies to the plot.

1244

1245 Figure 8. Average monthly discharge ($\text{m}^3 \text{s}^{-1}$) of selected major rivers around the Thai-
1246 Malay Peninsula (river discharge data from Siripong 1990, the RivDis1.1 (Vörösmarty et
1247 al. 1998) and the Department of Irrigation and Drainage Malaysia). PKT – Phuket, PY –
1248 P. Payar, PD – Port Dickson, SG – Singapore, TIO – P. Tioman, RED – P. Redang

1 Table 1. Details of study sites, and the dates and number of colonies stained with alizarin red-S. (The abbreviation “P.” in each case
 2 stands for Pulau = island).

Peninsula coast, Sea	Location, Country	Reef name	Latitude (°N)	Longitude (°E)	Water clarity (m)	Type of fringing reef	Distance from mainland Peninsula (km)	Distance from Met. station (km)	Alizarin staining dates (dd/mm/yyyy)	Colonies sampled
West, Andaman Sea	Phuket, Thailand (PKT)	Yam Yen (YY)	7.80867	98.39984	<3	Inshore	~35	~35	25/01/2010, 06/10/2011	1
		Porites Bay (PB)	7.80880	98.41032	<5	Inshore	~35	~35	–	2
		Koh Hae (KH)	7.74509	98.38335	>8	Nearshore island	~40	~40	–	4
		Koh Racha Yai (KR)	7.61311	98.37286	>20	Offshore island	~55	~55	25/01/2010, 04/10/2011	5
	P. Payar,	P. Payar house	6.06320	100.04203	>8	Offshore	~25	~45	27/03/2010,	5

	Malaysia (PY)	reef (PYHR)				island			21/06/2011	
	Port Dickson, Malaysia (PD)	Monkey Bay (MB)	2.41638	101.85259	<2	Inshore	<1	~45	5/6/14	3
South, South China Sea	Singapore, Singapore (SG)	P. Hantu (HT)	1.22729	103.74664	<3	Nearshore island	~20	~30	02/07/2009, 09/11/2009, 15/11/2010, 14/06/2011	3
		P. Semakau (SEM)	1.19996	103.75669	<3	Nearshore island	~20	~30	–	2
		P. Jong (JO)	1.21435	103.78687	<4	Nearshore rock island	~20	~25	–	3
		P. Kusu (KU)	1.22549	103.86014	<3	Nearshore island	~20	~20	–	4
		Raffles Lighthouse	1.16062	103.74054	<5	Offshore island	~25	~35	02/07/2009, 09/11/2009,	3

		(RL)							15/11/2010	
East, South	P. Redang,	Redangkalong	2.81769	104.15378	>20	Offshore	~30	~3	29/10/2009,	4
China Sea	Malaysia	house reef				island			25/05/2010,	
	(RED)	(RDHR)							12/04/2011	
		Kerengga Besar	2.91147	104.09782	>20	Offshore	~30	~3	28/10/2009,	4
		(RDKR)				rock outcrop			26/05/2010,	
									14/04/2011	
	P. Tioman,	EDT house reef	5.76253	103.02873	>10	Offshore	~50	~50	10/03/2010,	5
	Malaysia	(EDT)				island			05/07/2011	
	(TIO)									
		P. Tulai (PTU)	5.75426	103.02936	>15	Offshore	~50	~55	10/03/2010,	5
						island			04/07/2011	

1

2

1 Table 2. Average values \pm 1 SD for average linear extension rates (LE), skeletal density, luminescence intensity and various
 2 environmental parameters for the period Dec 2004–Nov 2009

Location	LE rates (cm year ⁻¹)	Skeletal density (g cm ⁻³)	Lumin. Intensity	SST (°C)	PAR ($\mu\text{mol m}^{-2}$ day ⁻¹)	Rainfall (mm month ⁻¹)	Salinity (psu)	SWH (m)
Phuket	2.00 \pm 0.14	1.11 \pm 0.16	0.55 \pm 0.10	29.12 \pm 0.55	45.13 \pm 4.33	198.39 \pm 181.17	31.93 \pm 0.40	0.86 \pm 0.22
P. Payar	1.91 \pm 0.18	1.11 \pm 0.10	0.71 \pm 0.08	29.23 \pm 0.56	45.02 \pm 4.36	200.13 \pm 137.84	31.58 \pm 0.34	0.55 \pm 0.14
Port Dickson	2.16 \pm 0.14	0.92 \pm 0.11	0.93 \pm 0.19	29.37 \pm 0.61	44.95 \pm 3.47	169.95 \pm 100.67	31.87 \pm 0.33	0.10 \pm 0.01
Singapore	1.85 \pm 0.14	0.97 \pm 0.15	0.74 \pm 0.18	28.01 \pm 0.87	38.78 \pm 4.26	196.13 \pm 129.72	31.99 \pm 0.32	0.15 \pm 0.06
P. Tioman	1.89 \pm 0.10	1.23 \pm 0.13	0.49 \pm 0.05	28.84 \pm 0.93	43.54 \pm 5.99	209.83 \pm 156.86	32.21 \pm 0.32	0.45 \pm 0.22
P. Redang	2.03 \pm 0.12	1.15 \pm 0.09	0.44 \pm 0.04	28.69 \pm 1.11	43.83 \pm 7.39	235.32 \pm 269.49	32.41 \pm 0.45	0.65 \pm 0.35

3

4

- 1 Table 3. Result of Pearson's correlation tests between anomalies in skeletal luminescence intensity and density. df = number of sample
2 pairs minus two.

Lumin vs. Density			
Location	p	<i>r</i>	df
Phuket	0.686	0.015	697
P. Payar	<0.001	-0.216	286
Port Dickson	0.063	0.140	176
Singapore	<0.001	0.128	813
P. Tioman	<0.001	0.249	478
P. Redang	<0.001	0.305	418

3

1 Table 4. Results of Pearson's correlation tests between monthly averaged anomalies in
 2 luminescence intensity and skeletal density, and SST (°C), photosynthetic active radiation
 3 (PAR) ($\mu\text{mol m}^{-2} \text{ day}^{-1}$), rainfall (mm month^{-1}), salinity (ppt) and significant wave height
 4 (SWH) (m) over the period Dec 2004–Nov 2009. Blue text = significant positive
 5 correlation (i.e. $p < 0.05$); Red text = significant negative correlations; Black text = no
 6 significant correlations. df = number of sample pairs minus two.

	Peninsula coast	Location		SST	PAR	Rain	Salinity	SWH
Luminescence	West	Phuket	p	0.010	<0.001	<0.001	<0.001	<0.001
			r	-0.097	0.474	-0.458	-0.504	-0.459
			df	697	593	697	573	697
	West	P. Payar	p	<0.001	0.058	<0.001	<0.001	<0.001
r			-0.256	0.123	-0.322	-0.350	-0.334	
df			286	237	286	277	286	
	West	Port Dickson	p	<0.001	0.889	0.800	<0.001	0.097
r			-0.473	0.011	-0.019	-0.401	0.126	
df			176	148	176	145	176	
	South	Singapore	p	<0.001	0.955	<0.001	<0.001	<0.001
r			0.250	0.002	-0.218	-0.243	-0.217	
df			813	701	813	670	813	
	East	P. Tioman	p	<0.001	0.144	0.274	0.021	<0.001
r			-0.156	-0.068	0.047	-0.110	0.138	
df			538	466	538	439	538	
	East	P. Redang	p	<0.001	<0.001	<0.001	<0.001	<0.001
r			-0.485	-0.375	0.194	-0.287	0.527	
df			418	418	418	341	418	

Density	West	Phuket	p	<0.001	0.630	0.182	0.167	0.018
			r	0.159	-0.02	0.051	0.058	0.081
			df	697	593	697	573	697
	West	P. Payar	p	<0.001	0.552	<0.001	0.609	<0.001
			r	0.341	-0.039	0.293	0.034	0.256
			df	286	237	286	277	286
	West	Port Dickson	p	0.096	0.068	0.584	0.238	0.596
			r	0.127	-0.149	0.042	-0.098	0.04
			df	176	148	176	145	176
South	Singapore	p	0.276	0.002	0.043	0.845	0.223	
		r	0.038	-0.119	0.071	0.008	0.043	
		df	813	701	813	670	813	
East	P. Tioman	p	<0.001	<0.001	<0.001	<0.001	<0.001	
		r	-0.355	-0.255	0.283	-0.256	0.45	
		df	538	466	538	439	538	
East	P. Redang	p	<0.001	<0.001	0.013	<0.001	<0.001	
		r	-0.37	-0.353	0.113	-0.268	0.391	
		df	418	418	418	341	418	

1

2

1 Table 5. Best 5 GAMM models based on AIC and their respective Δ (difference from
 2 lowest model AIC value), inferential models weights (ω_i), evidence ratios (ER) for
 3 luminescence intensity anomalies (LUMINESCENCE) and skeletal density anomalies
 4 (DENSITY). SST – sea surface temperature anomaly; PAR – photosynthetically active
 5 radiation anomaly; Rain – rainfall anomaly; Sal – salinity anomaly; SWH– significant
 6 wave height.

	AIC	Δ AIC	AIC. ω_i	ER	Model
Luminescence	-5755.475	0	0.350	–	Sal + Rain
	-5754.113	1.362	0.177	1.976	Sal
	-5753.317	2.158	0.119	2.942	Sal + PAR
	-5752.753	2.722	0.090	3.900	Sal + Rain + PAR
	-5752.241	3.234	0.069	5.038	Sal + Rain + SWH
Density	-5859.724	0	0.363	–	SWH + Rain
	-5858.761	0.963	0.224	1.619	SWH + Rain + Sal
	-5857.875	1.849	0.144	2.521	SWH + Rain + SST
	-5856.074	3.65	0.058	6.203	SWH + Rain + Sal + SST
	-5855.896	3.828	0.054	6.780	SWH + Rain + Sal + PAR

7