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

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General Conclusion and Future Work

6.1 General Conclusion

In this thesis, we have aimed to shed light on the environmental controls of coral growth through the analyses of emergent patterns at larger spatio-temporal scales brought about by disturbances, in particular those related to anthropogenic climate change. I started by studying decadal-scale variation in growth rates in relation to several environmental variables at a reef to island spatial scale around Phuket (Thailand; 7–8°N, 97–98°E), and later expanded the study to cover a biogeographic region, sampling sites along >1600km of coastline around the Thai-Malay Peninsula (1–8°N, 97–105°E). In this way, we were able to first identify the most relevant potential environmental driver of coral growth rates, and then tested for significant relationships. We also discussed in detail the implications of our findings from the perspective of coral reef futures in the face of rapid climatic changes.

In Chapter 2, we observed declines in calcification rates (~23.5%) driven by decreases in the *Porites lutea* linear extension rates (~19.4–23.4%) between a ~2 decade period 1985 and 2005 at 3 out of 8 reefs sampled around Phuket. Skeletal densities were found to remain unchanged. This finding, at the time, was rather unexpected, as earlier retrospective growth studies had found increases in growth rates over time (Lough and Barnes 1997; Nie et al. 1997; Bessat and Buigues 2001). When we tested the variations found in linear growth rates against several climatic variables (i.e. rainfall, wind speed, sea level, sun hours, sea surface temperature), our results showed SST to have the strongest and most consistent relationship with decrease in linear growth rates (see Table 2.2) and linear growth rates were predicted to decline by ~44–56% for every 1°C rise in SST for *Porites lutea* around Phuket.

Our follow-up study in Chapter 3 expanded our study area to 15 reefs from 6 locations around the Thai-Malay Peninsula and examined growth records from a longer, more continuous time-span (31 years; 1980–2010). Four of the 15 reefs studied overlapped those sampled in Chapter 2, and served to further validate our previous findings. The main purpose for this was to test the hypothesis that there has been thermally-driven declines in coral growth rates, as well as to ascertain the extent to which coral growth decline/s, if any, has occurred in this region. Our analysis of 31-year continuous growth records (between 1980–2010) extracted from 70 long-lived massive *Porites* corals sampled from around the Thai-Malay Peninsula in Chapter 3 confirmed region-wide declines in coral calcification rate (~18.6%), linear extension rate (~15.4%) and skeletal bulk density (~3.9%). From validation of growth bands used to reconstruct growth rates (as presented in Chapter 5), we are also confident that the decline in growth reported here are indeed of annual rates that are not grossly deviant of ~12-months worth of growth. The region-wide decline in annual growth rates was largely attributed to rising average annual SSTs as found in Chapter 2, with the Thai-Malay Peninsula *Porites* spp. demonstrating a thermal threshold of ~29.4°C before calcification decreased.

Interestingly, the calcification thermal threshold found is much higher than previously reported, and possibly contributes to the average thermal rates of decline in calcification rates for the Thai-Malay Peninsula (average annual SST 27–30°C; ~59% per 1°C rise in SST). This average thermal rate of decline is comparable to those found for cooler-water reefs at the Great Barrier Reef (average annual SST ~25–27°C; ~39–60% per 1°C rise in SST) (Cooper et al. 2008; De'ath et al. 2009) and Mesoamerican Barrier Reef (average annual SST ~27°C; ~86% per 1°C rise in SST) (Carricart-Ganivet et al. 2012). Highsmith (1979) first proposed a model for thermal response of coral growth whereby thermal optimum for growth rate was ~27°C; matrix production declined steeply beyond this and extracellular calcification showed either a slight decrease or a possible short-term increase (Fig. 6.1). This model was later verified by several laboratory experiments on a variety of zooxanthellate corals (e.g. *Stylophora pistillata*, *Pocillopora damicornis*, *Galaxea fascicularis*) (Clausen and Roth 1975; Jokiel and Coles 1978; Reynaud-Vaganay 1999; Marshall and Clode 2004), all of which reported growth rates increasing to a maximum of ~26–27°C and decreasing beyond this narrow temperature range (e.g. Fig. 6.2a). Furthermore, relatively recent field evidence from the Great Barrier Reef (GBR) also supports this stenothermic optimum (Fig. 6.2b).

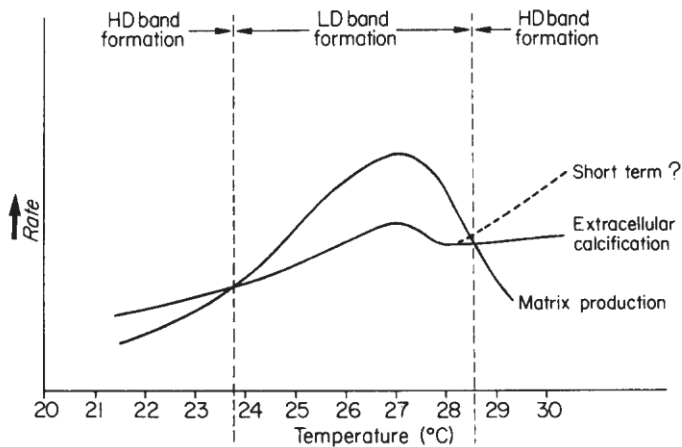


Fig. 6.1. Model of relationship of matrix production and extracellular calcification to temperature (image from Highsmith 1979).

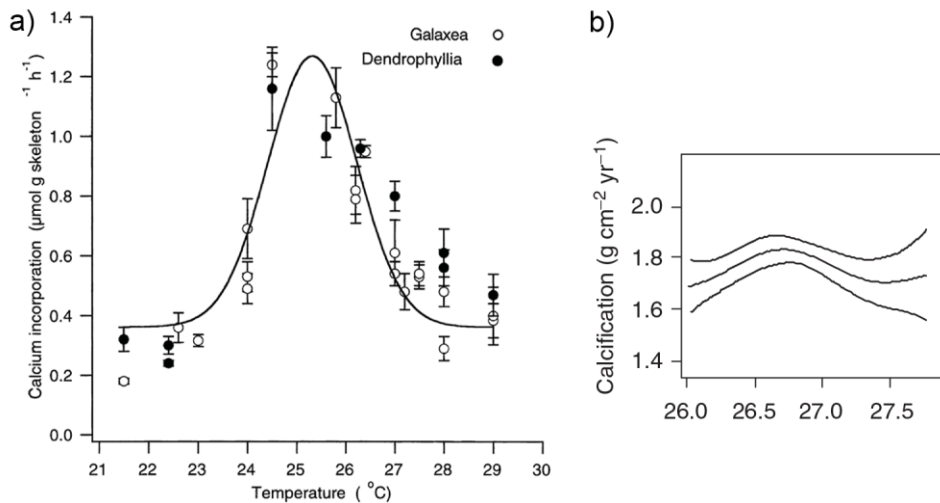


Fig. 6.2. a) Dependency of calcification rate (measured as calcium incorporation per unit mass of skeleton) on temperature in *Galaxea fascicularis* (open circles) and *Dendrophyllia* sp. (closed circles) as measured from a laboratory experiment (image from Marshall and Clode 2004). b) Partial effects plot showing the estimated dependencies (with 95% confidence intervals) of calcification rate ($\text{g cm}^{-2} \text{yr}^{-1}$) on sea surface temperature as found from field-based retrospective growth study at the Northern Great Barrier Reef (image from Cooper et al. 2008).

Our finding of a higher thermal threshold ($>2^{\circ}\text{C}$ than previously found) for massive *Porites* spp. calcification could imply that these corals have adapted to the high thermal regime to which they are exposed, or that some other environmental parameters are at play mitigating the negative effects of sea warming on calcification. Although the results in this thesis suggest rising SST as the main environmental driver of linear growth rates at larger spatio-temporal scales (i.e. biogeographic region), it would be imprudent to expect such a one-dimensional relationship between calcification rate and temperature to exist. Concurrent and/or pre-exposure to other environmental parameters can alter the thermal thresholds for mortality and physiological bleaching in corals (Coles and Jokiel 1978, Fitt et al. 2001, Brown et al. 2002, Middlebrook et al. 2008), a stress response we have clearly demonstrated in Chapter 4 to result in significantly reduced growth rates ($\sim 7\%$ for partially bleached corals and $\sim 28\%$ for severely bleached corals). For example, at reduced light intensities, *Montipora verrucosa* have been known to better withstand higher temperatures without bleaching, while those exposed to lowered salinities had increased mortality when exposed to the same thermal stress (Coles and Jokiel 1978). Such interactions could explain the varying degrees of bleaching between adjacent colonies of *Porites lutea* within the same reef, which were also noted in Chapter 4, as well as the variable between location declines in growth rates reported in Chapter 3. Although temporal trends in growth parameters were relatively clear-cut at the larger regional scale, the responses at individual locations were more variable and declines in calcification and linear extension rates at five of the six locations ranged from $\sim 17.2\text{--}21.3\%$ and $\sim 11.4\text{--}19.6\%$ respectively, while regional decline in skeletal bulk density was a consequence of significant reductions at only two locations, P. Redang ($\sim 6.9\%$) and Port Dickson ($\sim 10.7\%$). The decreases in calcification noted at the five study locations corresponded to thermal rates of declines for every 1°C rise in SST of $\sim 50\%$ at Phuket, $\sim 55\%$ at P. Payar, $\sim 74\%$ at Singapore, 70% at P. Tioman and 96% at P. Redang. These observations suggest that the rate of change in temperature is not the sole driver determining rates of change in calcification at the reef-island scales.

We also acknowledge that our analyses did not encompass other known key environmental controllers of growth. The most pertinent parameters being increased human disturbance-related environmental parameters (i.e. eutrophication, nutrients, turbidity, sedimentation) and decreases in pH and aragonite saturation state (Ω_{arag}) over time. One of the major constraints the current study faced was undoubtedly obtaining reliable real-time environmental data. Temporal data for nutrients, sedimentation and pH although available for one site (Porites Bay (PB); see Fig. 2.1) were both extremely sparse (discrete sampling, low resolution) and reliability questionable, and were therefore not used. What pH data were available showed no trend in sea surface pH from 1990 to 2006 (range 7.8–8.9; mean $8.24 \pm \text{SD } 0.18$) (S. Khokiattiwong pers. comm.) and no other evidence to suggest a marked decrease in pH or Ω_{arag} over the last two decades that would result in the significant decrease in coral calcification rates seen in the current study. Although

there have been some data collected from open oceans, no reliable long-term record of acidification of coastal waters exists where most tropical reefs are found. Coastal systems are considered more complex and dynamic than open seas, with influences not just from oceanic sources but land-based inputs and tidal circulation (Nicholls et al. 2007). Large rivers affecting fluctuations in salinity, nutrients and input of organic and inorganic carbon can play a more direct role in dictating changes in seawater carbonate chemistry compared effects from increased atmospheric $p\text{CO}_2$ alone (Gattuso et al. 1998). Based on discussion in Chapter 5, it is highly likely that these corals sampled from around the Thai-Malay Peninsula are affected by substantial river runoff.

In order to circumvent the lack of key long-term environmental data, we employed a ‘space-for-time’ substitution approach and analysed and compared growth rate changes from sites that varied in environmental conditions. In both Chapters 2 and 3, we sampled sites across an inshore to offshore gradient with the consideration that increased human disturbances (e.g. dredging, tourism, development) exist closer to shore compared to further offshore (see Fig. 1.7 in Introduction). Although such ‘space-for-time’ substitution analysis relies on the assumption that reaction to changes in the focal variable over time will be the same over space (Pickett 1989), such an approach remains extremely useful when crucial temporal data is not available/usable as in our case. When comparing growth rates trends across this spatial gradient, we found that the growth decreases did not systematically differ significantly between inshore–offshore sites (Figure 2.4). This result is not consistent with any change one may expect in the inshore to offshore gradients such as in turbidity, nutrients, pollution and salinity over time. Nevertheless, this thesis also concentrated on investigating key environmental controls of growth in only a group of coral species i.e. massive *Porites* spp. which have since shown to be robust when subject to of high sedimentation conditions (e.g. Brown et al. 1990) and, in more recent studies, to lowered pH and Ω_{arag} (e.g. Fabricius et al. 2011; Edmunds et al. 2012) as discussed later in Section 6.2.1.

In this thesis, we have shown that the larger spatial-temporal scale (biogeographic) decline in growth rates in the warmer water reefs around the Thai-Malay Peninsula seem to be driven mainly by sea temperature. The resilience of coral reef ecosystems as a whole has been found to be considerably sensitive to the growth rates of corals (e.g. Hoegh-Guldberg et al. 2007; Roff and Mumby 2012), as rapid individual growth of corals not only increases the population recovery rate, but also provides a competitive advantage over algae (Roff and Mumby 2012). This region-wide decline in coral growth rates we report is therefore a cause for concern for future reef accretion rates and ecosystem resilience considering massive *Porites* spp. is a major reef builder throughout the Indo-Pacific (see Madin et al. 2012; Roff and Mumby 2012). However, this thesis has also provided some evidence that there has been marked variability in growth declines in the last ~30 years at the reef-island scales, which suggests that future rates and patterns of

change within the region are also unlikely to be uniform. Based on current trajectories, it is predicted that while reefs in some locations may be more vulnerable to declines, others will possibly not register significant changes in growth rates in the foreseeable future – these reefs may provide refugia for corals and coral-associated organisms in the face of rapid climatic changes and, if identified, could be made a priority for conservation.

6.2 Future Work

6.2.1 Growth changes in other coral species

This thesis explored the growth changes and processes involved in massive *Porites* spp. corals, with a focus on the species *Porites lutea*. Although the decline in growth rates reported in the current thesis for massive *Porites* corals is undoubtedly worrying considering it is one of the most dominant reef-builders in the Indo-Pacific, little is known how other species in tropical warm-water reefs have thus far responded to the recent climatic and environmental changes. To date, only retrospective growth records from massive *Porites* spp. (*P. lutea*, *P. lobata*, *P. australiensis*, *P. solida*, *P. asteroides*) (Nie et al. 1997; Lough et al. 1999; Cooper et al. 2008; De'ath et al. 2009; Tanzil et al. 2009; Carricart-Ganivet et al. 2012; Tanzil et al. 2013), *Montastrea* spp. (*M. annularis*, *M. faveolata*, *M. franksi*) (Helmle et al. 2011; Carricart-Ganivet et al. 2012), *Diploastrea heliophora* (Cantin et al. 2010) and *Siderastrea sideria* (Castillo et al. 2011) have been relatively well-studied. There is considerable evidence for variability in the coral calcification response to climatic and environmental changes across not only geographical ranges but between species (Fig. 6.3; see also Fig. 1.6 in Introduction).

It may be possible certain species with “hardy” genotypes have adapted to become highly efficient calcifiers or able to direct more of their energy budget to calcification (Pandolfi et al. 2011). For example, in terms of the effects of ocean acidification on massive *Porites*, Edmunds et al. (2012) found that calcification in massive *Porites* spp. was largely unaffected by changes in pCO₂ after a 1-month mesocosm incubation period. Fabricius et al. (2011) also observed no significant difference in the calcification rates of massive *Porites* spp. exposed to volcanic CO₂ seeps compared to unexposed sites in Papua New Guinea. Over a temporal scale, Pelejaro et al. (2005) found no link between growth rates in a *Porites* colony from the western Coral Sea and pH and Ω_{arag} (reconstructed from boron isotopic compositions in the coral core examined) in the last 300 years. These laboratory and field results suggest the robustness of massive *Porites* corals to ocean acidification-related changes in seawater carbonate chemistry. Nevertheless, the variability in the effects of CO₂-induced ocean on rates of biogenic calcium carbonate production on a variety of zooxanthellate corals has been well documented (see Kleypas and Langdon 2006; Pandolfi et al. 2011), and effects on

perhaps other species currently not examined in this thesis should not be discounted. It will therefore be increasingly crucial to study the growth changes and patterns in other key dominant species (e.g. *Acropora* spp., *Montipora* spp.) on coral reefs today in order to reduce uncertainty when projecting coral reef futures worldwide.

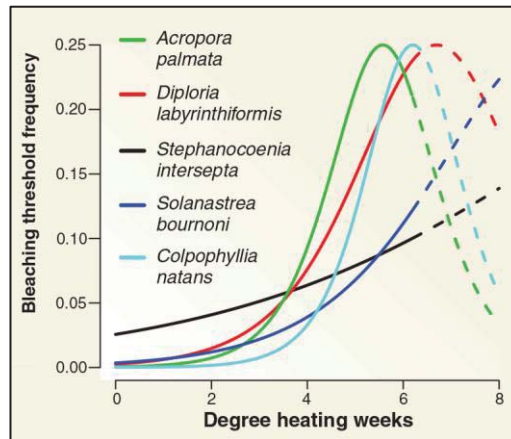


Fig. 6.3. Estimated probability distribution of bleaching thresholds for five species of Caribbean corals, based on logistic regression models fitted to bleaching data from the Florida Keys and Dry Tortugas, under environmental conditions corresponding to the average observed for each species (sourced from Pandolfi et al. 2011). See Figure 1.5 in Introduction for similar inter-species variability in responses to Ω_{arag} .

6.2.2 Interacting effects of temperature and nutrients on coral growth patterns

In Chapter 3, we found a lack of decline in calcification and linear extension rates at one of the six study locations, Port Dickson (PD) (see Fig. 3.4). Normal growth rates have previously been observed on eutrophic reefs (Edinger et al. 2000), with nutrient enrichment known to positively affect coral calcification rates (e.g. Meyer and Schultz 1985, Koop et al. 2001, Bongiorni et al. 2003, Dunn et al. 2011). Meyer and Schultz (1985) observed that nutrient enrichment from fish organic matter sources caused significant increases in coral calcification while Koop et al. (2001) found similar results on reefs with added phosphorous. However, calcification increases as a consequence of nutrient enrichment usually result in higher linear growth rates, but not to bulk density (Koop et al. 2001, Dunn et al. 2011). Dunn (2012) noted that although colonies of *Acropora muricata* exposed to increased phosphate concentrations (0.2–0.5mg/l) grew more rapidly, they produced less dense, more porous skeletons. At the highest phosphate treatment,

skeletal density was almost halved by the end of the 120-day experimental period. Nutrient concentrations have general increased around the coastal waters of Port Dickson in recent years, with organic phosphorus concentrations notably increasing by ~50% from ~0.08mg/l in 1990 to ~0.12mg/l a decade later (Praveena et al. 2011). This, along with the observed pattern of growth change at Port Dickson (i.e. unchanged calcification and linear extension rates and significantly reduced skeletal bulk density), suggest that possible declines related to increased seawater temperatures may have been compensated by the coral's responses to nutrient enrichment. Additionally, there has also been evidence that nutrient enrichment can mitigate the adverse effects of elevated pCO₂ on coral calcification, by allowing corals to utilise more dissolved inorganic carbon and thus increasing gross carbon fixation (Holcomb 2010).

It is possible that the positive effects of nutrients may, however, be limited to a certain threshold, after which coral calcification may experience the negative compounding of both temperature and nutrients on calcification rates. Increased calcification rates at the expense of reduced skeletal bulk densities may also prove unsustainable for the coral organism in the long-term (Madin et al. 2012). Reduced skeletal densities can cause the coral to be more vulnerable to breakage from physical disturbances as well as colonisation by natural bioeroders, further impacting its already lowered skeletal integrity (Edinger et al. 2000, Muko et al. 2012). Several studies have found that levels of bioerosion in both live corals and coral rubble were significantly higher on reefs subject to eutrophication than on unpolluted offshore reefs (Rose and Risk 1985; Sammarco and Risk 1990; Chen et al. 2012). Already, the average skeletal bulk densities at Port Dickson are the lowest ever recorded in any massive *Porites* growth studies, averaging only ~0.9 g cm⁻³ over the study period (Table A3.1).

Whether the nutrient threshold for coral growth will manifest itself as a more obvious overall reduction in calcification rates, or a less apparent reduction in skeletal densities beyond which can be sustainable for balancing physical, chemical and biological erosion, is yet unknown. Therefore, two lines of enquiry for future studies can be followed: 1) understanding the threshold at which calcification rates will be negatively impacted by extraneous nutrient inputs (and responsible nutrient species e.g. nitrate, nitrite or phosphorus), and 2) investigating the critical skeletal density required for balancing erosion effects i.e. at what point is low skeletal density too low?

6.2.3 The effect of water flow on coral density

In Chapter 5, we found variations in skeletal density (i.e. HD and LD band formation) of the Thai-Malay Peninsula *Porites* corals were most consistently related to an index used as proxy for sea surface roughness (SSR) instead of SST

(as previously modeled; see Fig. 6.1). As there have been experimental data suggesting that water flow does significantly affect coral growth (e.g. Sebens et al. 1997; Kaandorp 1999), our data-driven result seems plausible. However, the SSR proxy used in the current study only explained a maximum of ~13.4% in the variation found in skeletal density (Table 5.4) and further investigation is needed in order to ascertain whether this reflects the suitability of the SSR proxy used or an indication that other equally/more important factors are involved. Furthermore, previous experimental studies relating temporal coral growth to water flow has yet to examine its effects specifically on skeletal density, most focusing on overall calcification rates (see Todd 2008). Further manipulative experiments could therefore be conducted to aid in validating the potential link between water flow and temporal variations in skeletal density reported in Chapter 5. An alternative study could make use of smaller-scale field settings by perhaps high-resolution monitoring of in-situ water flow via the use of Acoustic Doppler Velocimeters (ADVs) or other equivalent flow instruments.

6.2.4 Coral geochemistry

Scleractinian corals can live for centuries, depositing layers of calcium carbonate skeleton continuously throughout this time. The calcium and carbonate building blocks of the coral skeleton are extracted from seawater, and so contains isotopes of oxygen, carbon, as well as trace metals (e.g. Sr, Mg, U, Th, Ba, B etc) (Grottoli 2001; Lough 2010). The rate of co-precipitation of these elements with the skeleton is controlled by both the composition of surrounding seawater, as well as by other physical and biological factors. By analysing these trace elements, information including sea-surface temperatures (SSTs), river runoff, rainfall, upwelling, salinity, pH and anthropogenic influences (Lewis et al. 2007; Pelejero and Calvo 2007; Lough 2010) can be retrieved from the coral skeleton, reconstructing the environment in which the corals grew where/when instrumental records may not be available (Allemand et al. 2004). For example, it may be possible, if properly validated and calibrated, to circumvent the lack of long-term instrumental ocean acidification data by reconstructing pH with ^{11}B as a geochemical proxy (e.g. Pelejero et al. 2005). Palaeo-environmental record of how corals assimilate trace elements into their coral skeleton can also further our understanding of the coral calcification process (e.g. Grottoli 2001).

Of particular interest to the current thesis is the use of geochemistry to reconstruct past river runoff using coral skeletal barium (Ba) to calcium (Ca) concentration ratios (i.e. Ba/Ca), and relating it to the luminescent banding pattern described in Chapter 5. Terrestrial/river runoff are relatively depleted in calcium (Ca), and enriched in barium (Ba) as well as other rare-earth elements compared with coastal seawaters. The incursion of such runoff into the coastal environment would therefore results in a significant increase in the Ba/Ca ratios in the coastal

seawater and have been used to reconstruct terrestrial/riverine sediment and organic material input into reef systems (e.g. Grove 2012).

In Chapter 5, we alluded that seasonal river runoff is the most probable environmental driver of the luminescent banding patterns seen in massive *Porites* corals around the Thai-Malay Peninsula. As no in-situ longer-term instrumental records were available, we used ocean data assimilated modeled salinity (Carton Giese SODA) and remotely sensed [Chl-a] (SeaWiFs) as proxies of river runoff. Both these parameters are sampled at relatively low spatial resolution (0.25–0.5° grids) compared to reef-scale processes and are known for their own quirks and errors when applied in coastal waters (e.g. Tan et al. 2006). Using Ba/Ca ratio a geochemical potential proxy for the amount of river runoff received by the coral's immediate surrounding, it would then be possible to further verify the link between river runoff and luminescence intensity in the Thai-Malay Peninsula *Porites* corals. River runoff information extracted from coral skeletal Ba/Ca changes will in itself be also extremely useful for tracking the changes in terrestrial input reaching coastal reefs in relation to, for example, land-use changes over time. Nevertheless, use of any geochemical proxy in such a way would need careful and extensive validation against in-situ measurements of comparable resolution. In addition to external environmental influences, coral skeletal chemical composition, and its subsequent interpretation, can also be affected by growth rates (e.g. Goodkin and Hughen 2005). It is therefore crucial that any analysis should be done along the maximum growth axis of the colony and take into account possible effects from variations in growth rates (e.g. replicating suitable number of colonies instead of analysing only single specimens).

6.2.5 Complex systems modeling

Though not exactly understood, coral calcification or biomineralisation involves multiple interconnected biologically- and environmentally-induced mechanisms occurring at multiple scales. Hierarchical modular biological components exist in the coral in the form of cells, tissues and polyps whereby inter-linked processes take place influencing, and also influenced by, their surrounding environment; the culmination of which is the accretion of calcium carbonate (Fig. 1.1). At present, numerous studies have increased our understanding of coral biomineralisation mechanisms at the cellular as well as molecular levels (e.g. Allemand et al. 2011, Tambutté et al. 2011, Ramos-Silva et al. 2013). Combined with information from larger-scale observations, such as those presented in the current thesis, complex systems modeling of coral biomineralisation linking various levels of calcification processes could be attempted (i.e. gene regulation and organic matrix formation, physiology, colony-level calcification and more ecological scale observations).