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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 Introduction

1.1. Importance of Corals and Coral Reefs

Of all Earth's ecosystems, coral reefs support among the highest species diversity and gross productivity (Connell 1978) that generate goods and services (e.g. food, coastal protection, tourism) which directly or indirectly support millions of people worldwide. Coral reefs occupy <0.1% of the world's oceans but is thought that they account for and support >25% of the biodiversity found in these oceans (Spalding and Grenfell 1997; Mulhall 2007). In today's economy, the productivity and biodiversity apparent on coral reefs supports billion-dollar industries. It is estimated that coral reefs provide nearly US$30 billion in net benefits in goods and services to the world economy, ~US$13 billion (~43%) of which is accounted for by coral reefs in Southeast Asia (Cesar 2003). Coral reefs are also hot spots for the pharmaceutical industry. Dozens of antimicrobial and anti-inflammatory properties have been identified in reef species, including the treatment of the human immunodeficiency virus (HIV) AZT found in a Caribbean reef sponge (Mulhall 2007). The calcium carbonate skeletons produced by corals have also been used as bioimplants for bone surgery (Demers et al. 2002). It is needless to say that the coral reefs hold great current, as well as future, value to humans.

On tropical coral reefs, hermatypic scleractinian, or "reef-building", corals form the backbone of the ecosystem. These corals, which live in symbiosis with algae called zooxanthellae (*Symbiodinium* spp.), produce large amounts of calcium carbonate ($CaCO_3$) as they grow (~2–6 kg m^{-2} year^{-1}) (Barnes and Devereux 1984), and are thought to precipitate half of the 1.2×10^{13} mol of calcium delivered to the sea each year (Smith 1978). Their ability to bind calcium and construct massive $CaCO_3$ structures is the basis for reef development, which effectively supports the high productivity and biodiversity associated with coral reefs (Bellwood and Hughes 2001; Chabanet et al. 2005). The production and maintenance of this three-dimensional reef framework also relies on the prerequisite that corals can calcify

faster than the rates of biological, chemical and physical erosion and dissolution to which they are exposed. The rate of skeletal growth of corals is therefore not only essential for their own fitness and ecological success i.e. determining the ability of corals to compete for space and light, and repair structural damage caused by humans, storms, grazers and bioeroders (e.g. Chen et al. 2012; Ferrari et al. 2012; Muko et al. 2012), but can also have profound repercussions on the robustness and resilience of coral reef systems on the whole (Hoegh-Guldberg et al. 2007; Roff and Mumby 2012).

More and more, corals reefs are being subject to stresses that threaten to upset the delicate balance between calcium carbonate production and erosion/dissolution processes. This has not only led to their decline worldwide (Wilkinson 1999), but also inevitably reduce the quality and quantity of ecological goods and services they provide (Moberg and Folke 1999). The stresses that coral reefs face occur at multiple scales. At the local and regional scales, reefs are deteriorating in all areas where human activities are concentrated, due to increased coastal development, seawater pollution (e.g. heavy metals, sedimentation, eutrophication, bacterial and viral diseases), as well as other human pressures (e.g. diving, fishing, tourism). For example, significantly reduced coral accretion rates are experienced on reefs subject to increased sediment loading as a result of increased terrestrial/river runoff (e.g. Tomascik and Sanders 1985; Te 1997; Dikou and van Woesik 2006). In addition to these stresses, corals are also under pressure from effects of climatic changes occurring at a larger, more global scale. Rising ocean temperatures and changing seawater carbonate chemistry (i.e. increase in pCO_2 and reductions in pH and aragonite saturation state) are two major factors predicted to negatively affect coral reefs globally (Gattuso et al. 1998; Kleypas et al. 1999; Marubini and Atkinson 1999; Ohde and van Woesik 1999; Langdon et al. 2000; Leclercq et al. 2002; Langdon et al. 2003; Marubini et al. 2003; Orr et al. 2005). It is therefore important to increase understanding of the effects of changes in these main environmental parameters at multiple scales on the survival of reef corals, especially on their ability to produce calcium carbonate (i.e. calcification). This will not only serve to pre-empt possible undesirable outcomes (e.g. dissolution/destruction of the reef carbonate framework), but also better manage the recovery of coral reefs from both anthropogenic and climatic disturbances.

1.2. Understanding Mechanisms of Coral Growth

Scleractinian coral skeletal growth, or calcification, is fundamentally the process by which corals deposit a calcium carbonate ($CaCO_3$) skeleton in the form of aragonite by combining calcium ions with carbonate ions. The basic unit of a "coral" is the animal itself, or what is referred to as the polyp. Since most scleractinian corals are colonial, the appearance of the coral macrostructure as seen on reefs (i.e. its colony size and shape) is a result of the amalgamation of tube-like

skeletons formed by individual polyps, known as corallites (Fig 1.1). As $CaCO_3$ is secreted by the lower portion of the coral polyp, it produces a cup, or calyx, in which the polyp sits. The walls surrounding the cup are called the theca, and the floor is called the basal plate. Periodically, a polyp will lift off its base and secrete a new basal plate above the old one, creating a series of small chambers one on top of another over time. While the colony is alive, corallites are formed this way thereby elevating the coral. The tube-like corallites are then joined together by horizontal plates and other structures (i.e. the coenosteum) to form the colonial skeletal macrostructure (Veron 2000).
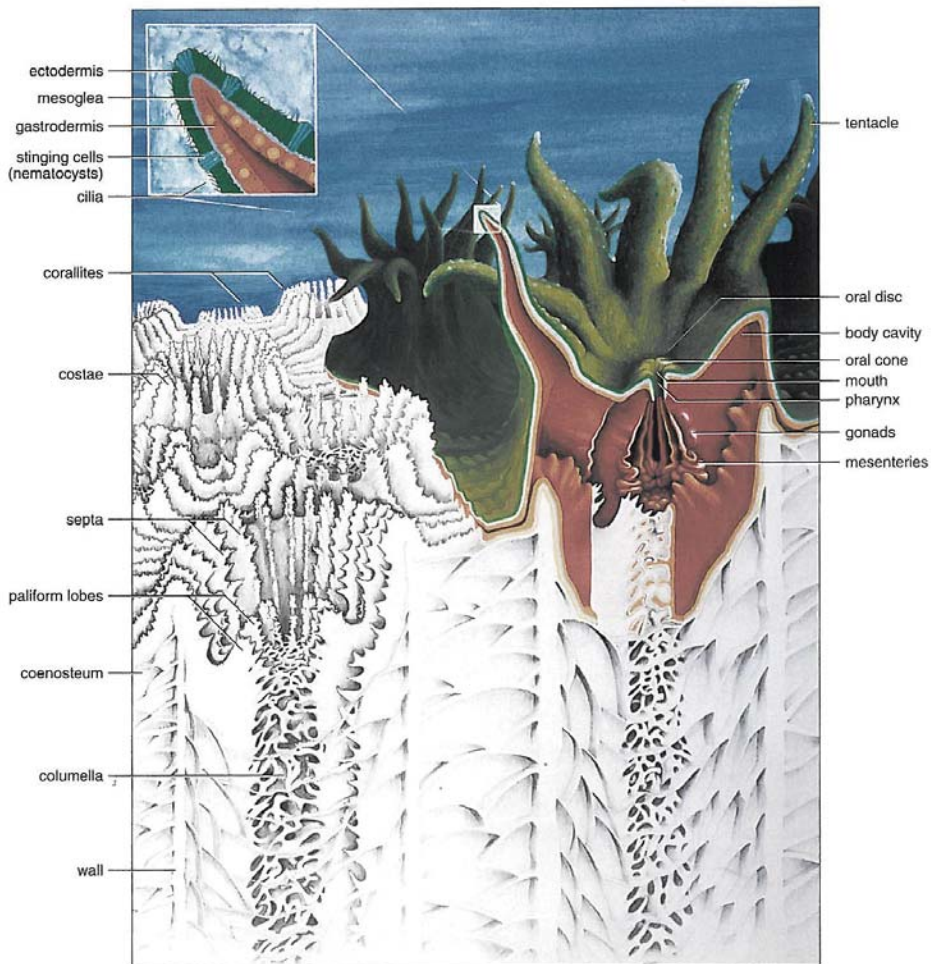

Fig. 1.1. Schematics showing the general structure of the coral polyp and underlying skeleton. Note the tube-like corallites on which the live coral polyp sits (image from Veron 2000).

The general structure (e.g. number of septa, presence/absence of columella) and microstructure/micromorphology (e.g. shape of size of septal teeth) of these corallites is thought to be fundamentally "biologically controlled" by genetic characteristics and thus used as criteria in coral taxonomy. Preliminary phylogenetic comparisons between molecular and such skeletal morphology data sets generally yield congruent results and complement one another (Budd et al. 2012), further supporting this notion. However, the rates and patterns of formation of their macrostructure are influenced by both biological as well as environmental controls (Allemand et al. 2011). Given the same or very similar genetic make-up (i.e. within species/sibling species), many scleractinian corals have been shown to exhibit a high degree of morphological plasticity due to variations in the physico-chemical environment (Fig. 1.2). Environmental parameters including temperature (e.g. Jokiel and Coles 1977; Highsmith 1979), light (e.g. Barnes and Chalker 1990), nutrient levels (e.g. Marubini and Davies 1996), hydraulic energy (e.g. Scoffin et al. 1992) and changing seawater carbonate chemistry (e.g. Marubini and Atkinson 1999; Ohde and Hossain 2004) have been known to affect or even drive the patterns and rates of calcification.
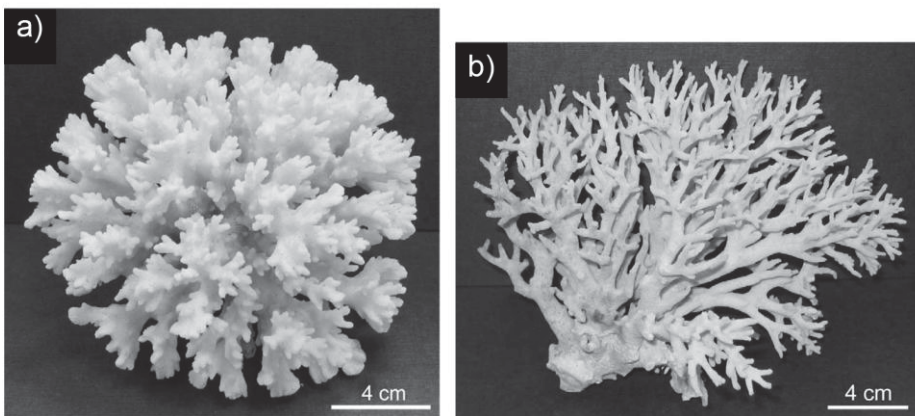

Fig. 1.2. Colony skeleton of the coral species *Pocillopora damicornis* collected from a) a moderately exposed, and b) a very sheltered reef off Singapore (adapted from Todd 2008 with permission).

The actual mechanism of calcification in corals is suggested to involve two possible levels: firstly, the production of an organic matrix (OM), and secondly, the extracellular deposition of calcium carbonate (see Allemand et al. 2011, Ramos-Silva et al. 2013). Although the exact nature and role of OMs produced by the coral is still being investigated, their production is thought to be strongly controlled by cellular activity. Their composition is known to include a combination of proteins, sugars and water, which provide a basic structural

framework for the initial binding of $CaCO_3$ (Isa and Okazaki 1987; Fukuda et al. 2003; Allemand et al. 2011). The quantity, structure and composition of OMs have been taxonomically linked (Cuif et al. 1996; Dauphin et al. 2006, 2008) and, as such, OMs are pegged to play a key role in the basic morphology of coral skeletal elements.
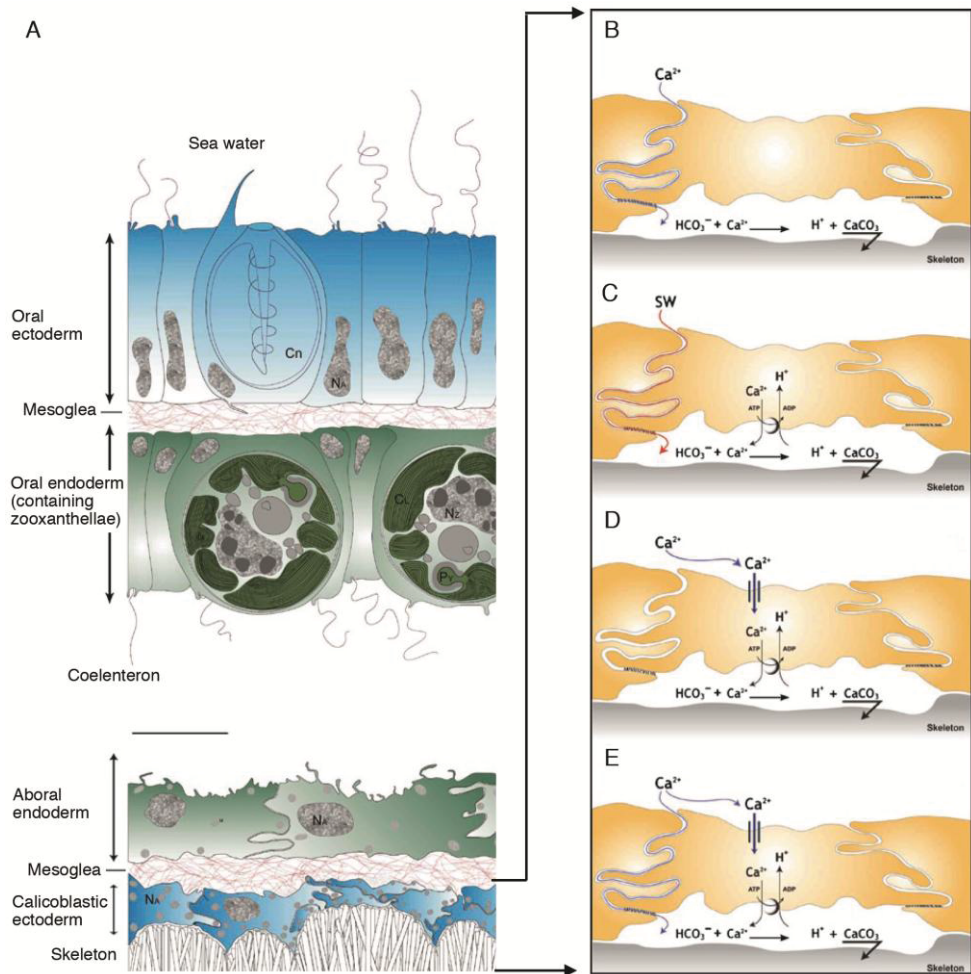
Fig. 1.3. A) Schematic view of a histological section across the coenenchyme (i.e. skeletal tissue between two adjacent polyps). The four hypotheses explaining transfer of ions across the calicodermis to the subcalicoblastic extracellular calcifying medium: B) ions are provided by a passive paracellular pathway between calicoblastic cells, C) bulk seawater provides the essential of ions by a paracellular pathway, D) ions are supplied by an active transcellular pathway through calicoblastic cells, (E) combination of (B) and (D) where calcium ions are provided by both a transcellular and a paracellular pathway (images from Allemand et al. 2011).

Although several hypotheses exist for the process of extracellular deposition of $CaCO_3$, they all agree that it involves some form of pathway/s for the delivery/removal of ions involved in calcification (i.e. H^+, HCO_3^-, Ca^{2+} and CO_3^{2-}) to the calicoblastic region of the coral animal (Allemand et al. 2011) (Fig. 1.3). It is yet unknown how much of this process is "biologically-mediated" by intrinsic controls and how much is environmentally controlled by external dynamics (see Tambutte et al. 2011, Moya et al. 2012). Seawater is rich in calcium ions (Ca^{2+}) relative to carbonate ions (CO_3^{2-}), and therefore the rate of calcification here is largely influenced by the saturation state of carbonate ions (Ω) in the seawater. Intrinsic controls would enable corals to buffer changes in seawater chemistry (e.g. ocean acidification, decrease in Ω), and open the possibility that corals may be able to react and adapt to these changes (Kleypas et al. 2011). However, just how fast and how much corals can do this in the context of the current changing world is still much of a mystery, especially since the nature and extent of environmental changes can have vastly differing effects on the calcification process.

1.3. Coral Growth in a Changing World

1.3.1. Ocean warming and acidification

Global changes in the Earth's climate are predicted to significantly affect the growth of corals, compromising the existence of coral reefs worldwide (Phinney et al. 2006; IPCC 2007). The two major factors of concern to global coral reef ecosystems are rising ocean temperatures and changing seawater carbonate chemistry (Fig. 1.4) (Gattuso et al. 1998; Kleypas et al. 1999; Marubini and Atkinson 1999; Ohde and van Woesik 1999; Langdon et al. 2000; Leclercq et al. 2002; Langdon et al. 2003; Marubini et al. 2003; Orr et al. 2005; Erez et al. 2011). Over the past century, tropical ocean temperatures have risen by ~1–2˚C and concentration of atmospheric carbon dioxide (henceforth [CO_2]) is estimated to have increased from ~200–280ppm pre-industrialisation to ~380ppm today (Houghton 2003, Sabine et al. 2004). This [CO_2] is only half of the emission that are due to anthropogenic activities; the remainder of which is thought to have been taken up by the oceans (30%) and the terrestrial biospheres (20%) (Sabine et al. 2004). While CO_2 sequestration by the oceans will continue to moderate future climate changes, it reduces the pH of seawater as it dissolves to form carbonic acid. This acidification induces other chemical changes, the most relevant being the decrease in the concentration of marine carbonates and consequently reductions in calcium carbonate saturation levels (Ω). The current seawater pH of 8.08 is already 0.1 units lower than pre-industrial values (Haugan and Drange 1996) and saturation levels of marine carbonates have decreased by 10% compared to that of pre-industrial levels (Orr et al. 2005). By 2100, it has been predicted that CO_2 levels will likely exceed 800ppm (IPCC 2007) causing seawater pH to drop a

further 0.3–0.4 units (Haugan and Drange 1996) and Ω to decrease by ~40% (Kleypas et al. 1999), and average global sea surface temperature to increase by ~0.2℃ per decade (IPCC 2007).

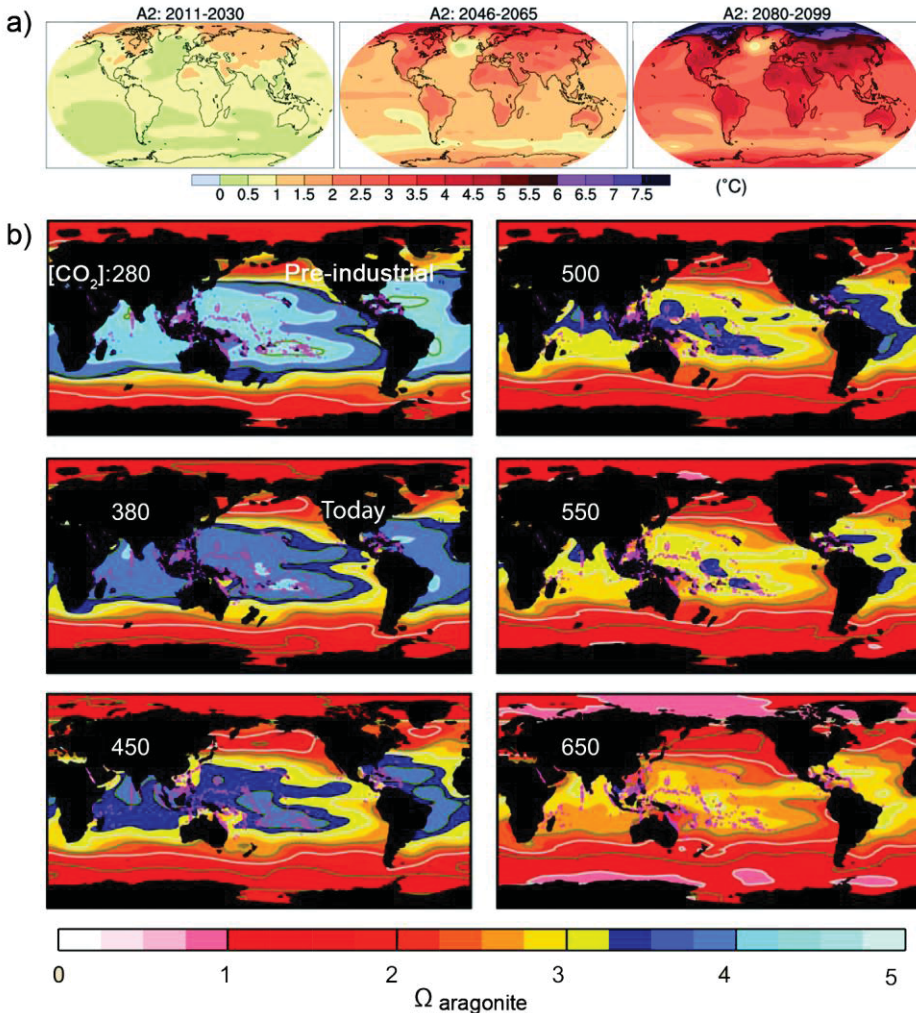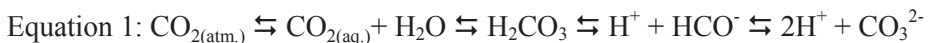Fig. 1.4. Changing ocean conditions: sea warming and acidification; a) Global temperature projections (for A2 scenario) displayed as temperature anomalies relative to the average of the period 1980–1999 (source: IPCC 2007); b) Changes in aragonite saturation state ($\Omega_{aragonite}$) predicted to occur as atmospheric CO_2 concentrations [CO_2] (ppm) increase (images from Hoegh-Guldberg et al. 2007).

Hermatypic scleractinian corals, or "reef-building" corals, have adapted to living in a relatively narrow temperature window (Kleypas et al. 1999), evident as most vigorous coral reef growth can been found within the tropics of Capricorn and Cancer with minimum seawater temperatures of ~18°C (Schumacher 1988; Kleypas et al. 1999). Rising tropical ocean temperatures pose a risk of pushing corals to their upper-thermal limits. The most pertinent example of temperature stress being the breakdown of relationship between the hermatypic coral and its symbiotic algae, zooxanthellae, (Baker et al. 2008) which can provide up to 90% of the coral's daily energy budget (dependent on both coral and zooxanthellae species) (Muscatine et al. 1981; Davies 1984). This phenomenon is typically referred to as coral bleaching and visibly seen as a loss of colouration (Fig. 1.4) when corals lose their zooxanthellae (and zooxanthellae their chlorophyll). Physiologically, this loss of zooxanthellae translates to a loss of major energy resource for the corals' biological processes, including calcification which can all but cease during this stressful period (e.g. Goreau and Macfarlane 1990; Tudhope et al. 1992). Since the 1970s, reports of mass coral bleaching have increased in frequency, with severe bleaching events coinciding with anomalous sea warming events related to the El-Niño Southern Oscillation (ENSO) (Hoegh-Guldberg 1999, Oliver et al. 2009) (Fig. 1.5). While longer-term bleaching records are probably still needed to confidently test the relationship between rising sea temperatures and coral bleaching (Oliver et al. 2009), many scientists have strongly suggested that the occurrence of bleaching events will increase in frequency and intensity with global warming and increased ENSO activity (e.g. Williams and Bunkley-Williams 1990, Hoegh-Guldberg 1999, Donner et al. 2005, Eakin et al. 2009). When corals do survive from bleaching events, their recovery can be slow and calcification can take up to ~2 years before returning to pre-bleaching rates (Suzuki et al. 2003).

Increasing concentration of atmospheric carbon dioxide ($[CO_2]$) is increasing the sequestration of CO_2 by the oceans and the resultant hydrolysis of CO_2 (Equation 1).

Equation 1: $CO_{2(atm.)} \leftrightarrows CO_{2(aq.)} + H_2O \leftrightarrows H_2CO_3 \leftrightarrows H^+ + HCO^- \leftrightarrows 2H^+ + CO_3^{2-}$

The shift in the seawater carbonate system causes both pH and carbonate ion concentration to decrease. Seawater pH is decreased due to the hydrolysis of CO_2, which simultaneously increases the hydrogen ion concentration $[H^+]$, aqueous $[CO_2]$ and dissolved inorganic carbon concentrations [DIC] while decreasing carbonate ion concentrations $[CO_3^{2-}]$. Calcium carbonate saturation state (Ω), a measure of the ion activity product of calcium (Ca^{2+}) and carbonate (CO_3^{2-}) relative to the apparent solubility product for a particular calcium carbonate mineral phase (i.e. calcite, High Mg-calcite, or aragonite) (Kleypas et al. 1999), is used to describe changes in seawater carbonate chemistry. Ω is largely determined by $[CO_3^{2-}]$ as $[Ca^{2+}]$ is nearly conservative in seawater; Ω values <1 and >1 respectively indicate under-saturated and super-saturated conditions. Coral
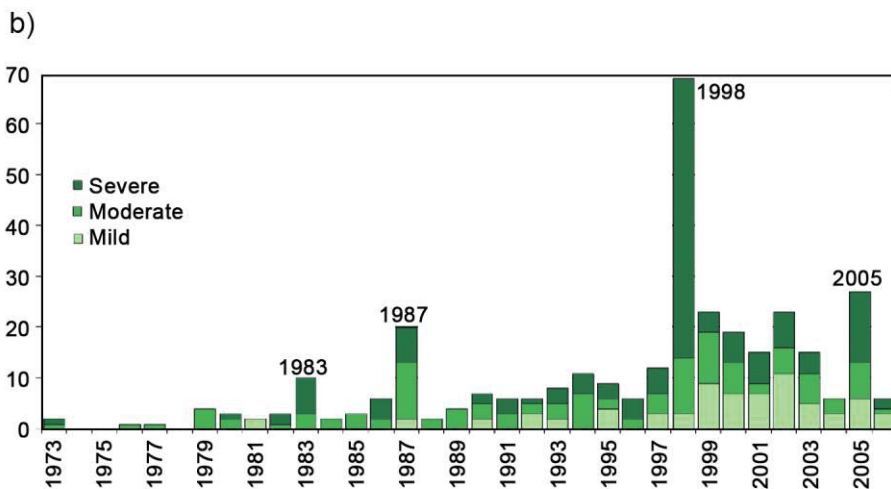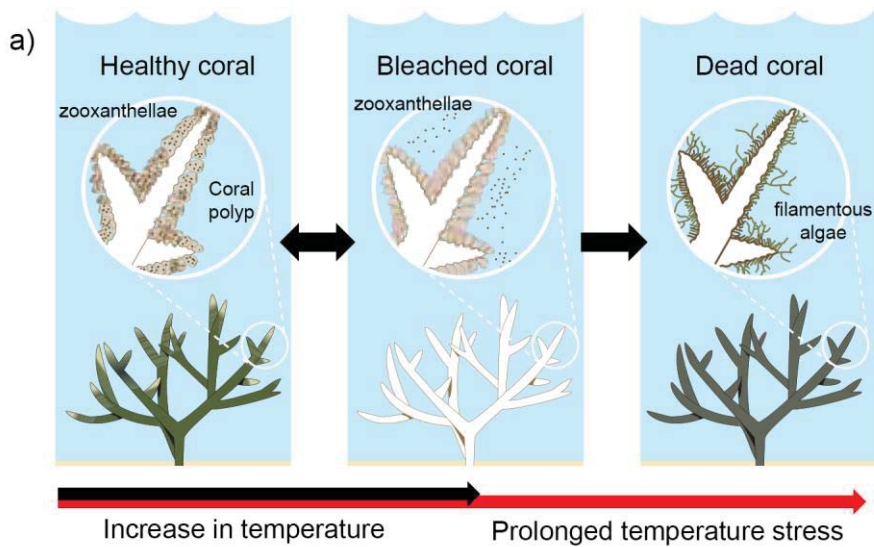
Fig. 1.5. a) Schematic of coral bleaching when corals lose their zooxanthellae and colouration (turning visibly white) when subject to high temperature stress (typically ~1–2ºC the summer maximum). Recovery when temperatures return to normal is possible, but prolonged thermal stress can cause irreversible damage and whole colony mortality (adapted from Marshall and Schuttenberg 2006). b) Graph showing the number of countries reporting bleaching in ReefBase (www.reefbase.org) over time. The years 1983,1987, 1998 and 2005 are major bleaching years that coincide with the El-Niño Southern Oscillation (ENSO) events (adapted from Oliver et al. 2009).

calcification requires that seawater be supersaturated with carbonate mineral aragonite (Ω_{arag}) (Orr et al. 2005) and the predicted decrease in Ω_{arag} will make it more difficult for corals to form biogenic calcium carbonate ($CaCO_3$).

Experimental evidence show that a decrease in Ω_{arag} results in reduced coral calcification rates (Gattuso *et al.* 1998, Kleypas *et al.* 1999, Kleypas and Langdon 2006). However, how much changing Ω_{arag} affects calcification is still unclear with results appearing to be both species and location specific. Average calcification rates have been shown to decrease by as little as ~5–10% per unit decrease in Ω_{arag} to as much as 25–40% per unit decrease in Ω_{arag} in laboratory experiments (Kleypas and Langdon 2006; Langdon and Atkinson 2005) (Fig. 1.6). Based on extrapolation, it is thought that decreases in Ω_{arag} have caused average reef calcification to decline by 6–15% over the past century, with predicted decreases of 17–35% by the end of the 21st century relative to pre-industrial levels (Kleypas et al. 1999; Friedrich et al. 2012). Results from field studies in the northern Red Sea by Silverman et al. (2007, 2009) also suggest that large coral colonies, and perhaps entire coral reefs, will start to dissolve if atmospheric CO_2 doubles.

1.3.2. Other environmental disturbances

Although rising SST and ocean acidification are predicted to be the key drivers affecting the future of corals and reef systems worldwide, the effects of other global climatic as well as more local/regional environmental changes should not be overlooked. Globally, increase in mean sea level and changes in cloud cover and rainfall patterns are additional factors predicted to affect corals and their growth processes. Both sea level and rainfall/cloud cover can alter the amount of light that reaches the reef (required for photosynthesis of the symbiotic zooxanthellae in corals), while rainfall patterns can affect the amount of hydraulic energy and physical damage received by reefs (e.g. via storm events). Mean sea level is suggested to have increased by 10–20cm in the 20th century while average rainfall has risen at a rate of ~0.2–1% per decade, along with it increases in cloud cover by ~2% and heavy precipitation events such as thunderstorms by ~2–4%. By 2100, global mean sea level to is expected to rise up to 88cm, with further increases in average global rainfall, cloud cover and higher intensity storm events (Phinney et al. 2006; IPCC 2007).

Increased storm events have been known to cause physical destruction of the reef structure and organisms by increased wave action and subsequent movement of coral rubble, increased sedimentation and turbidity (through re-suspension and runoff) which can hinder reef recovery (Brown 1997, Gardner et al 2005). During such events fragile coral growth forms (i.e. branching and foliose) suffer greatly from breakage and more massive forms from dislodgement, which can cause them to fall down steep slopes and possibly cause further damage (Wodley et al. 1981,

Harmelin-Vivien and Laboute 1986, Heron et al. 2005). Increase in rainfall amounts have also been linked with increases in terrestrial runoff and river inputs into the coastal system (e.g. Fabricius 2004, Justic et al. 2005), both of which increase sedimentation resulting in higher turbidity. Dunne and Brown (1996) demonstrated that light in turbid water is strongly attenuated close to the water surface across the inshore-offshore gradient at Phuket, where an increase in water depth from 1m to 2m in more turbid waters decreased photosynthetically active radiation (PAR) values by ~23%, compared to ~13% in clearer waters. The symbiotic algae, zooxanthellae (*Symbiodinium* spp.), hosted by hermatypic corals are autotrophs that live and photosynthesise in the coral's gastrodermal tissue layer. These symbionts provide the coral host with sunlight-derived assimilates which can, as mentioned previously, contribute up to ~90% of the coral's daily energy budget (dependent on both coral and zooxanthellae species) (Muscatine et al. 1981; Davies 1984). Although the exact mechanisms are still unclear, a tight coupling between these symbionts and host is thought to promote calcification through the concept of "light-enhanced calcification" (Goreau and Goreau 1959; Barnes and Chalker 1990; Gattuso et al. 1999). At reduced light intensities, coral calcification can be reduced by a factor of 2–3 compared to at higher light intensities (Barnes and Chalker 1990). The combined effects of these variables would ultimately result reduced light availability to the coral necessary for "light-enhanced calcification" (Goreau and Goreau 1959; Barnes and Chalker 1990; Gattuso et al. 1999). The predicted increase in sea level is also predicted affect the amount of light that current shallow reefs receive (via increased attenuation) (Hoegh-Guldberg 1999). Currently, sea level rise is occurring slower than coral growth rates and therefore may have limited or even positive impact on coral reefs, particularly for shallower/intertidal reefs (Brown 1997, Hubbard 1997). However, the accumulation of other environmental disturbance which can slow growth rates may expose corals to the effects of rising sea levels, possibly "drowning" them when they are unable to keep up with sea level rise.

It should, however, be noted that while the effects of increased rainfall/storm events and sea level described above are mostly negative and precautionary, these environmental disturbances also offer ecological benefits. Increased water movement and cloud cover (associated with rainfall/storm events) can help alleviate thermal stress on corals (as described in 1.3.1), cooling waters through shading the sea surface from solar radiation, transfer of latent heat (evaporative cooling) as well as local upwelling bringing in deeper cooler water to the surface (Heron et al. 2005).
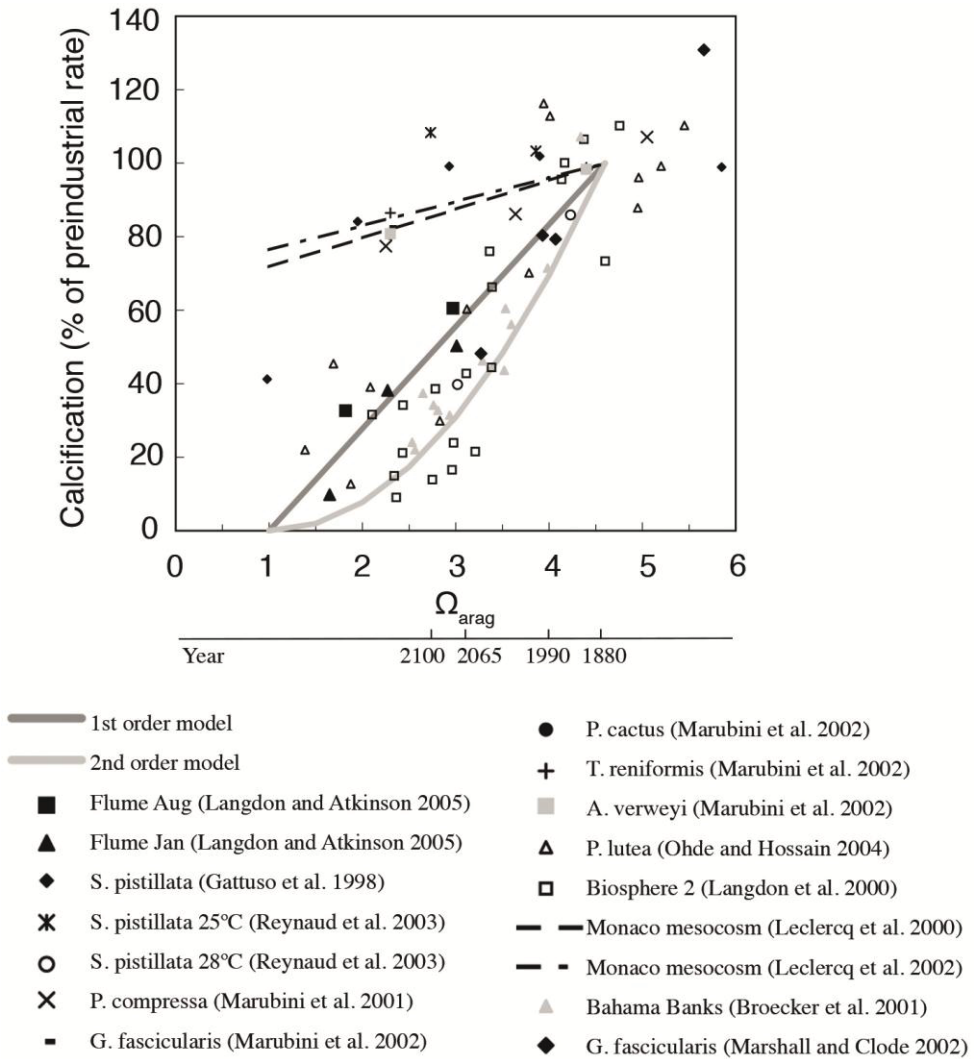
Fig. 1.6. Data from 15 different studies on various groups of coral species illustrating the effect of aragonite saturation state (Ω_a) on calcification rate expressed as a percentage of the preindustrial rate ($\Omega_a = 4.6$). Although all studies generally agree that reduced Ω_a causes reduced calcification rate, note the varying degrees to which Ω_a affects calcification rate trajectories (dashed line vs. solid line) (image from Langdon and Atkinson 2005).

In addition to these global-scale climatic changes, coral reefs are also under pressure from more local/regional scale environmental changes. Of particular concern is increased coastal land use and terrestrial/river runoff which has resulted in eutrophication becoming increasingly prevalent on coral reefs (Fabricius 2004). Eutrophication corresponds to an increase in nutrient concentrations, in sediment load and in development of algae (see Fabricus 2004), all of which, again, reduces the amount of light received by the coral as well as imposing other stresses on coral growth (Fig. 1.7). Corals subject to high sedimentation typically show a decline in skeletal growth related to physical smothering (e.g. Tomascik and Sanders 1985; Te 1997; Dikou and van Woesik 2006). Extraneous inputs of nutrients are also known to result in reduced growth rates (e.g. Kinsey and Davies 1979; Marubini and Davies 1996; Ferrier-Pagès 2000, 2001; Loya et al. 2004). In the Red Sea, Loya et al. (2004) observed a 3–4 fold decrease in calcification of *Stylophora pistillata* receiving increased nutrients from fish farms. Several laboratory experiments have also monitored lower calcification rates by up to 50% under different enrichments in ammonium and nitrate (Marubini and Davies 1996; Ferrier-Pagès 2000, 2001).

The way in which nutrients interact with calcification is still poorly known and the combined effects are still debated. Generally, nutrients highly enhance the growth and photosynthetic activity of the coral algal component, which might lead to a disruption of their symbiosis, and especially the coupling between photosynthesis and calcification (e.g. by reducing the amount of dissolved inorganic carbon available for calcification) (Gattuso et al. 1999). Interestingly, there are also studies which report the opposite, and have linked high coral growth rates seen in areas receiving increased terrestrial runoff to increased nutrient input to the reef system (Meyer and Schulz 1985; Scoffin et al. 1992; Edinger et al. 2000, Koop et al. 2001; Bongiorni et al. 2003). 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 are usually attributed to increased linear extension rates without corresponding increases in skeletal bulk densities (Takabayashi 1996; Koop et al. 2001, Dunn et al. 2012). Dunn (2012) noted that although colonies of *Acropora muricata* exposed to increased phosphate concentrations grew more rapidly, their skeletal densities were almost halved by the end of a ~4-month experimental period. However, increased calcification rates at the expense of reduced skeletal bulk densities may prove to be unsustainable in the long-term (Madin et al. 2012). Reduced skeletal densities can cause corals to be more vulnerable to breakage from physical disturbances (e.g. from increases in storm activity/intensity) as well as colonisation by natural bioeroders, further impacting their already lowered skeletal integrity (Nanniga 2006; Edinger et al. 2000, Muko et al. 2012).
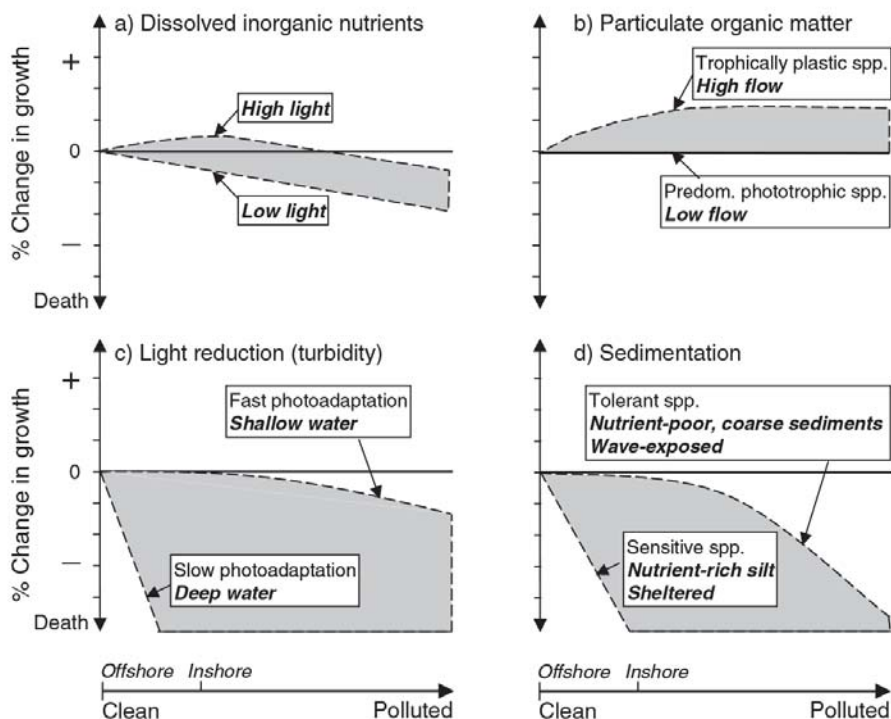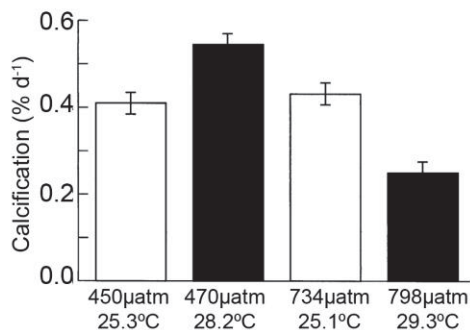
Fig. 1.7. Schematic representation of the direct effects of eutrophication (as result of terrestrial runoff) on coral growth and survival along environmental gradients. Plotted are changes in coral growth in response to (a) uptake of dissolved inorganic nutrients, (b) feeding on suspended particulate organic matter, (c) light reduction from turbidity, hence reduction in gross photosynthesis, and (d) disturbance by sedimentation. The x-axis represents a hypothetical water quality gradient from offshore–inshore water quality to polluted conditions, which also indicates the relative positions of offshore and inshore conditions unaltered by human activities. The y-axis scale represents relative units of changes in growth, with severe long-term reduction in growth effectively representing colony death. Grey shading is used to approximate typical response envelopes due to species-specific differences (normal font) and local environmental conditions (bold italic font) (image from Fabricius 2004).
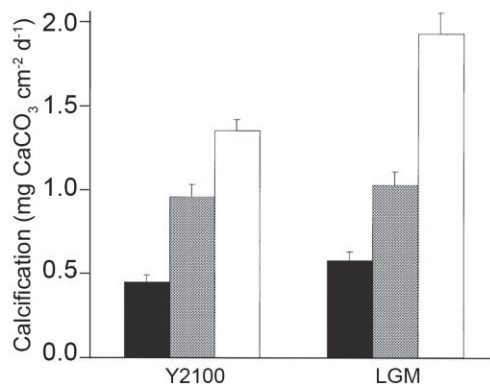
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1.3.3. Interacting effects of environmental variables

All in all, it is reasonable to say that coral reef ecosystems are under the threats of local direct anthropogenic stresses, and of the more extended stresses of global change, which include, in addition to a raise in temperature and ocean acidification, an elevation of the sea level and changes in rainfall, cloud cover, and storm activity. Individually, these environmental variables have been shown to significantly affect coral growth. When combined, however, their impacts are even less understood and can interact in any number of permutations to either exacerbate and/or mask one another's effects on calcification. For example, Coles and Jokiel (1978) noted an interaction between temperature and light, where calcification tended to peak at lower light irradiances when exposed to higher temperatures. Marubini and Atkinson (1999) and Langdon and Atkinson (2005) studied the interacting effects of calcification and nutrient enrichment and both reported that calcification decreased with nutrient enrichment in low Ω_{arag}, but increased in high Ω_{arag} treatments (Fig. 1.8). Such results may indicate that as Ω_{arag} decreases, nutrient enrichment from terrestrial runoff and river inputs (caused by increased rainfall) may augment further decreases in coral calcification. Another pertinent interaction reported is between CO_2 partial pressures (and hence lower Ω_{arag}) and temperature: Reynaud et al. (2003) reported that at higher temperatures (~28ºC) the effects of increases in CO_2 partial pressures were much more pronounced in causing a decrease in calcification than at lower temperatures (~25ºC). This suggests that rising SST and ocean acidification may have more pronounced effects on reefs in warmer waters than in cooler waters. The implication of such interacting effects of environmental variables is that observations made in manipulative laboratory experiments, though increasing our understanding of physiological processes involved in calcification may not ultimately reflect the real responses of corals exposed to actual conditions in the field.

A) Light & temperature

Calcification (% d⁻¹)

0.6
0.4
0.2
0.0

450µatm 470µatm 734µatm 798µatm
25.3°C   28.2°C   25.1°C   29.3°C

B) Ω_{arag} & light

Calcification (mg CaCO₃ cm⁻² d⁻¹)

2.0
1.5
1.0
0.5
0.0

Y2100   LGM

C) Ω_{arag} and nutrient

mmol CaCO₃ m⁻² h⁻¹

15
10
5
0

● Ambient nutrient
◆ 10x ambient nutrient
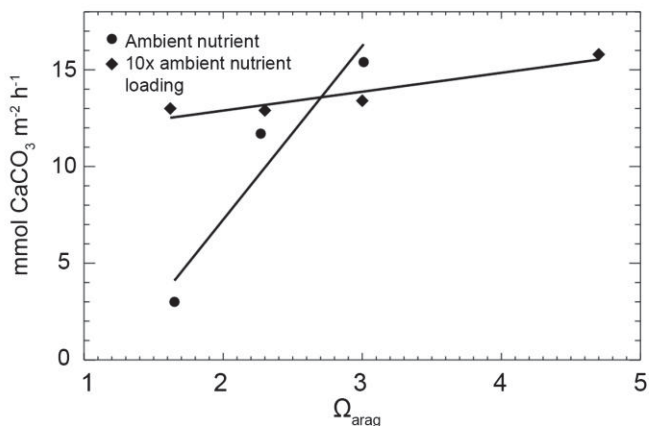 loading

1   2   3   4   5
Ω_{arag}

Fig. 1.8. Graphs showing a) calcification rates of *Stylophora pistillata* at low and high pCO2 and temperatures (image from Reynaud et al. 2003), b) calcification rates of *Porites compressa* under three different light regimes (black bar = lowest light; hatched bar = medium light; white bar = highest light) and two different aragonite saturation states (Y2100 = predicted Ω_{arag} for the year 2100; LGM = predicted Ω_{arag} of the last glacial maximum) (image from Marubini et al. 2001), and c) interacting effects of altered Ω_{arag} and nutrient enrichment on calcification rate of *Porites compressa* and *Montipora capitata* assemblages (image from Kleypas and Langdon 2006).

1.4. Coral Growth as a Multi-Scale Problem

In previous sections of this chapter, we have shown that coral calcification is a product of interconnected biologically- and environmentally-induced processes. In a coral polyp, hierarchical modular biological components exist in the form of cells and tissues whereby inter-linked physiological processes take place influencing, and also influenced by, their surrounding environment; the culmination of which is the accretion of calcium carbonate ($CaCO_3$) and "emergence" of the coral skeletal macrostructure (colonial growth-form) (Gattuso et al. 1999; Allemand et al. 2011) (Fig. 1.9). Changes in coral calcification can therefore be seen as being brought about by a combination of multi-scale internal (in the absence of disturbance) as well as external dynamics.

Detailed information on processes at small spatio-temporal scales (e.g. processes occurring at cellular and tissue levels) and sophisticated mathematical and computational approaches are undoubtedly extremely useful for understanding underlying mechanisms (e.g. Filatov et al. 2010; Kaandorp et al. 2011, Tamunolis et al. 2011, Kim et al. 2012, Rotman et al. 2012, Chindapol et al. 2013). However, when it comes to making quantitative predictions about real systems on larger scales, working with smaller scales/simple models may prove challenging. For example, as mentioned in Section 1.2.1, extrapolation from laboratory experiments and models suggests that reef coral calcification rates has already declined by 6–15% over the 20th century, with predicted decreases of up to 60% by the end of the 21st century relative to pre-industrial levels (Kleypas et al. 1999; Silverman et al. 2007, 2009; Friedrich et al. 2012) due to decrease in marine carbonate saturation state. However, evidence from retrospective growth records from massive corals from the Great Barrier Reef, French Polynesia and South China Sea during the 20th century contradict such predictions and instead revealed increased growth rates (linear extension rates and derived calcification rates) over the same time frame (Heiss et al. 1993; Lough and Barnes 1997; Nie et al. 1997; Bessat and Buigues 2001). Such example clearly demonstrates the disjoint that can occur between results obtained from model simulations and smaller-scale manipulative experiments vs. what is occurring/observed in the real system.
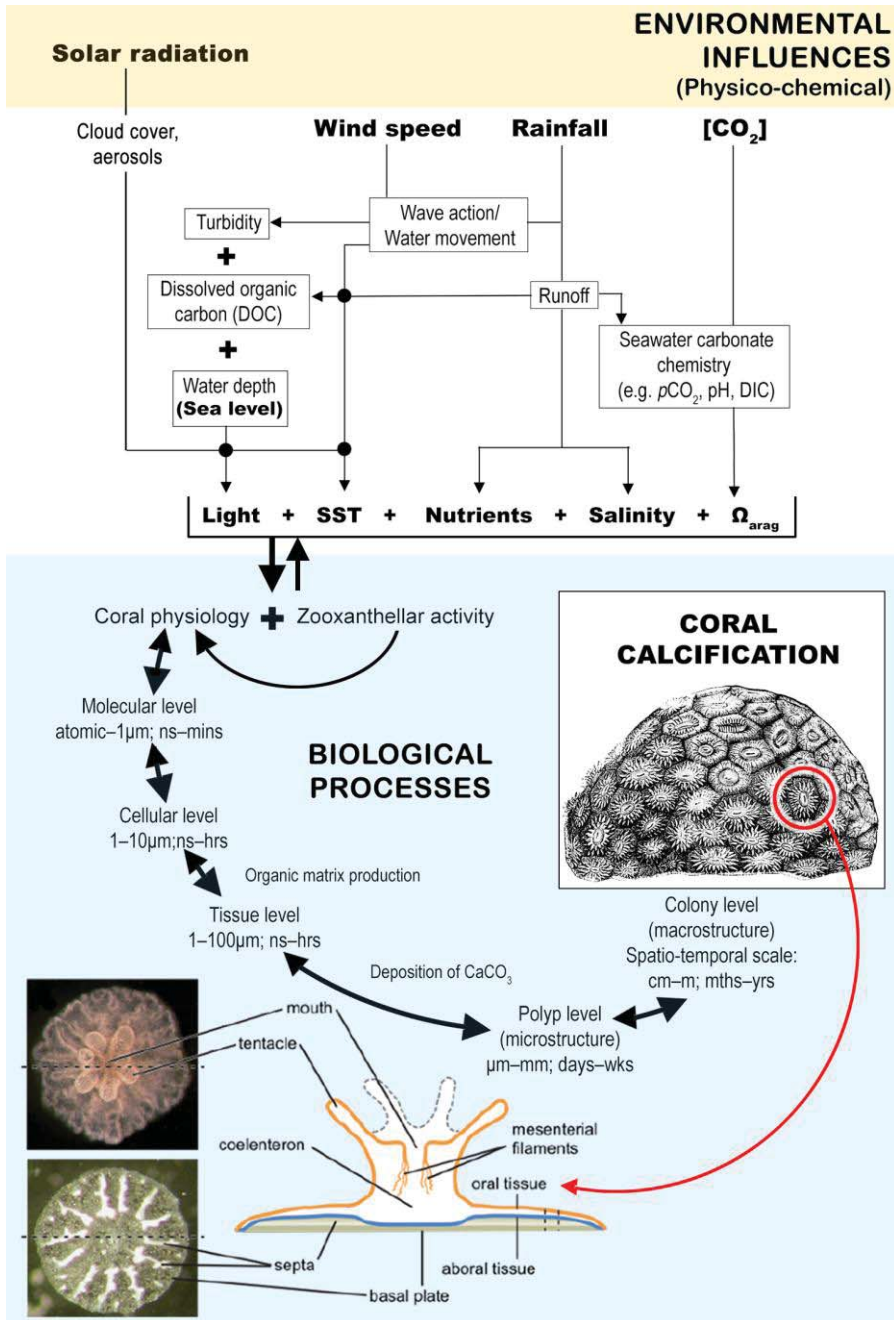
Fig. 1.9. Schematic diagram of the interplay of various environmental and biological variables involved in coral calcification.
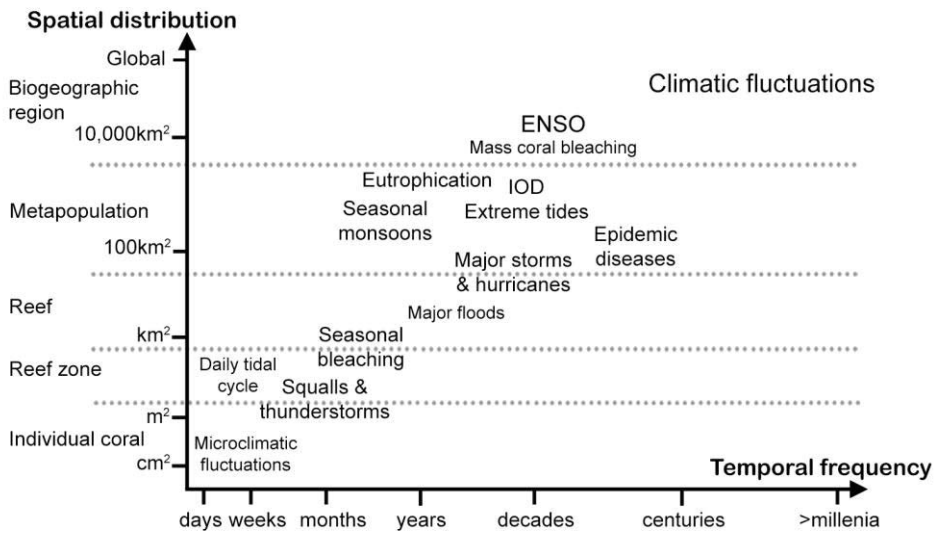
Fig. 1.10. Multi-scale representation of spatial distribution of corals and their habitats, and spatial and temporal distribution of disturbances faced by corals (adapted and modified from Nyström and Folke 2001; Chabanet et al. 2005).

Taking a multi-scale approach and addressing the problem of coral calcification at different spatio-temporal levels may therefore elucidate patterns at relatively larger scales, which can be used as feedback to increase understanding of underlying smaller-scale processes. This will ultimately also raise confidence in model predictions. Additionally, corals exist in an "open system". This means that the immediate environment around the coral macrostructure, which can be regarded as the interface for the interaction between internal and external dynamics, is in turn affected by disturbances from other interconnected, multi-scale systems in which they are embedded (e.g. reefs, islands, region, global) (Fig. 1.10). As a result of this complexity, integrating knowledge of processes occurring at different spatio-temporal scales is required to interpret patterns in real systems (Murdoch and Aronson 1999).

1.5. Overview of this Thesis

The main aim of this thesis is to identify possible environmental controls of coral calcification through the analyses of emergent patterns across a larger spatio-temporal scale brought about by disturbances, in particular those related to anthropogenic climate change. Information provided in this thesis will hopefully increase understanding of environmentally-controlled calcification and improve predictions of future trends and responses of coral reefs to disturbances in similar environments. Results obtained may also help identify reefs which, under deteriorating environmental conditions, demonstrate higher resilience (as measured by growth rates) compared to others. Such reefs may consequently hold higher conservation value, and perhaps act as refugia for corals and coral-associated species.

1.5.1. General methods

Skeletal growth rates and patterns in this thesis are obtained through detailed field observation and reconstruction of past trends using sclerochronology. As in dendrochronology (study of growth rings in trees), properly validated sclerochronological methods (study of annual growth bands in corals) (Fig. 1.11) can provide great insight to the long-term temporal dynamics of relationship/s between coral growth and the environment (e.g. Lough and Barnes 1997; Bessat and Buigues 2001; Tanzil et al. 2009). By accounting for relevant experimental variables (abiotic and biotic), employing data-driven analyses and combining such temporal information with multi-scale location comparisons (i.e. reefs within locations that vary in climatic and/or environmental conditions) can provide valuable insights into the systematic variation in coral growth characteristics in relation to the environment (Pickett 1989; Fukami and Wardle 2005).

In order to reduce influences from biological factors, the current research focuses on just one particular group of massive corals from the genus *Porites* (Fig. 1.11), considered as the "industry standard" for sclerochronological studies. Variations in growth rates and patterns of these corals are investigated and, subsequently, any links with environmental drivers at both spatial (inshore to offshore and across latitudinal scales) as well as temporal scales identified. The study area for this research encompasses the warmer-water equatorial reefs (i.e. average annual SSTs >28ºC) around the Thai-Malay Peninsula in Southeast Asia, where both sea warming and ocean acidification are expected to have more pronounced combined effects. Additionally, inshore–offshore gradients of environmental variables exist around the Peninsula (Chua and Ross 2002; Brown 2007), providing a natural experimental setting to explore interacting effects between these larger scale climatic changes (e.g. SST & ocean acidification) and other local environmental or coastal influences on coral growth processes.
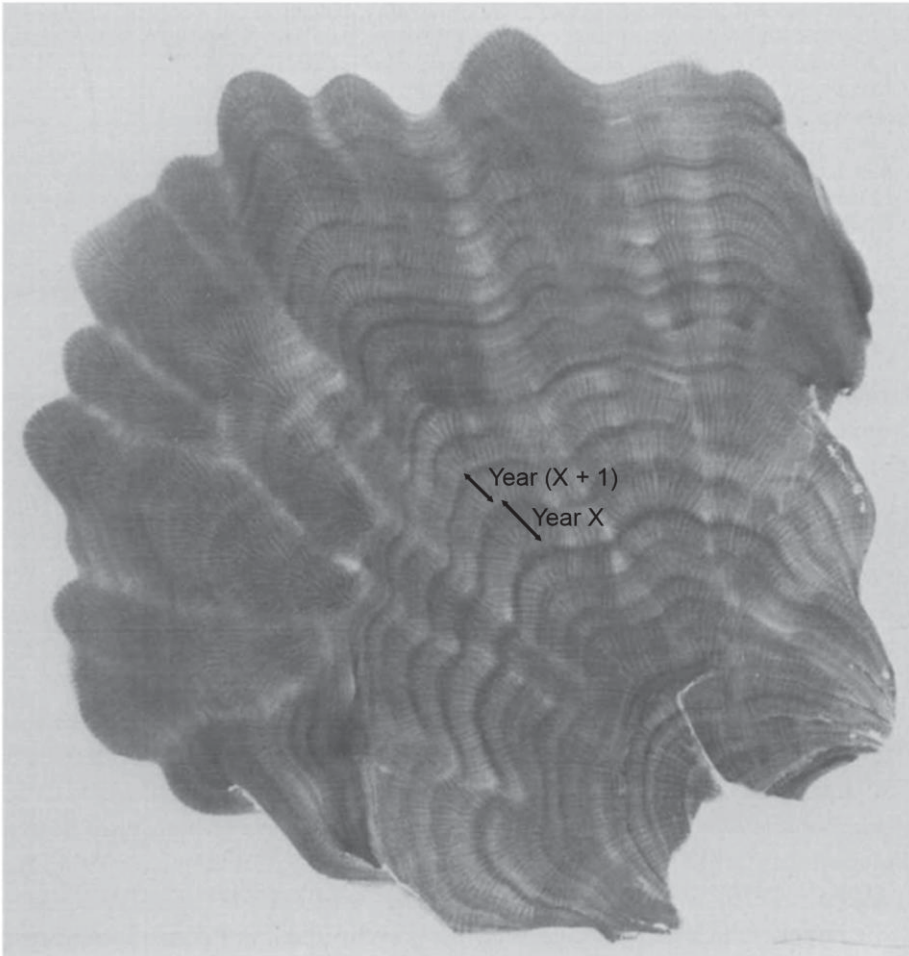
Fig. 1.11. An example of banding in the skeleton of a massive *Porites* coral: X-radiograph image showing density banding in corals which can be used for sclerochronological purposes (e.g. dating, extraction of growth information). Each couplet of high- and low-density bands is equivalent to one year's worth of growth in this specimen (adapted from Highsmith 1979).

1.5.2. Chapters overview

In the following Chapter 2, we introduce a preliminary study to ascertain whether any changes in coral calcification rates have occurred over decadal timescale (two decades; 1985–2005), and examined patterns in the relationship between variations in growth rates and several climatic variables (i.e. SST, rainfall, wind speed, solar radiation as estimated from sun hours, and sea level). In this chapter, we also examined reefs along an inshore to offshore gradient with the assumption that offshore sites are less impacted by human activities. By sampling in such a manner, we aimed to shed light on how local-scale disturbances may have interacted with more larger-scale, global disturbances in their effects on coral growth processes. The site for this study was the reefs around Phuket, south Thailand (meta-population scale, within 7–8ºN and 98–99ºE)

In Chapter 3, we re-applied similar schlerochronological methodology as seen in Chapter 2 but on an even larger spatio-temporal, regional scale. Over 30 years worth of growth information was obtained from corals sampled around the bio-geographic region of the Thai-Malay Peninsula covering >1600km of coastline within 0–8ºN and 98–105ºE). In this Chapter 3, we also validated the relationship between growth and any environmental parameter/s discerned from Chapter 2.

In Chapter 4, we present results of the effects of anomalous, acute thermal disturbance to coral calcification in a real reef system. This chapter follows the mass coral bleaching event experienced in 2010 around Phuket, south Thailand and analysed growth rates and patterns of severely bleached as well as less visibly bleached *Porites lutea* corals.

In Chapter 5, we explore the patterns of density and luminescent banding patterns in coral skeletons which are used as proxies of annual growth increments as well as other sclerochronological purposes. As temporal records of annual growth rates are obtained from such coral banding patterns, it is important to understand their nature and causes in order to establish that these bands truly represent of annual growth increments. Here, we used the reefs along the east vs. the west coasts of the Thai-Malay Peninsula that share similarities in certain environmental conditions (e.g. SST) while others are specific to location (e.g. rainfall, wind) as a natural experiment to examine variations in banding patterns and their relationship/s with selected environmental parameters.

Finally, in Chapter 6, we summarise and conclude the work presented in this thesis, and I describe possible lines of future research.