Temporal and spatial variation in the growth of branching corals

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Abstract

Life-history traits (e.g., growth rates) of reef-building corals are fundamental in structuring populations and communities. Importantly, growth rates of corals have been shown to vary with changes in environmental gradients, such as sea surface temperature (SST), light, and aragonite saturation. Accordingly, ongoing changes in environmental conditions due to climate change (e.g., ocean warming and acidification) may be causing long-term changes in coral growth. Corals are particularly sensitive to changing temperature regimes, such that sustained increases in ocean temperatures are generally expected to have negative consequences on coral growth and survivorship. At high-latitude reefs however, projected increases in ocean temperature may actually lead to increases in annual growth rates, by relaxing constraints imposed by cool winter temperatures. This will however, depend upon on the rate and extent of declines in aragonite saturation, which is already much lower at high latitudes. Generally, it is expected that increasing temperature stress will be compounded by ocean acidification, leading to ongoing declines in abundance and survivorship of corals. However, the relative contribution of ocean warming versus ocean acidification on coral growth is poorly understood. The overarching objective of this thesis was to quantify growth rates of branching corals at multiple spatial and temporal scales on Australia's Great Barrier Reef (GBR), to understand how changing environmental conditions may impact on growth of common branching corals.

The first step towards improved understanding of the likely effects of climate change on coral growth was the compilation of extensive data on the growth of corals, testing for spatial, temporal, and taxonomic differences in linear extension versus calcification. Results from the extensive meta-analysis reveal that rates of

linear extension vary greatly among coral species and morphologies, but were highest among arborescent *Acropora* species. Despite large variations in growth rates, they are known to vary spatially and temporally largely in response to environmental gradients, such as light, temperature, water quality, and aragonite saturation. There is also already evidence that the effects of climate change on corals are generally negative, regardless of geographical setting or habitat. However, existing data on growth rates of scleractinain corals is overwhelmingly biased towards massive coral species (e.g., *Porites* spp.), because it is possible to get a complete record of a colonies growth history from a single sample.

To specifically test whether growth rates of branching corals have changed in response to changing environmental conditions such as sea surface temperature and carbonate chemistry, contemporary growth rates were quantified at two locations where coral growth rates had been estimated in the 1980s or 1990s. First, linear extension rates of six scleractinian corals, *Acropora yongei*, *Isopora cuneata*, *Pocillopora damicornis*, *Porites heronensis*, *Seriatopora hystrix*, and *Stylophora pistillata*, were evaluated at a subtropical reef, Lord Howe Island, in 2010/11 and compared to equivalent data collected in 1994/95 by Harriott (1999). At Lord Howe Island there was marked interspecific variation in growth, with *A. yongei* growing almost twice the rate of all other species. Notably, growth rates of *A. yongei* and *P. damicornis* were 30 % less than previously recorded in 1994/95 at Lord Howe Island. However, growth rates of *Porites heronensis* remained unchanged.

At Davies Reef, in the central GBR, contemporary growth rates (linear extension, density, and calcification) for the staghorn coral, *Acropora muricata* was assessed at three different depths (5, 10, and 15 m depths) and over two years (2012-2014). Contemporary growth rates were directly compared to equivalent

measurements made in 1980-82 by Oliver (1987) at the exact same location, assessing how growth rates of *A. muricata* may have changed over three decades. To assist in understanding inter-annual variability in coral growth during this period (1979-2012), annual growth bands were examined for cores taken from massive *Porites* at Davies Reef, in 2012. Similarly, at Davies Reef, linear extension of *A. muricata* in 2012-14 was 5 - 58 % less compared to 1980-82. In contrast, calcification rates of massive *Porites* were highly variable among years and there was no consistent long-term change.

Growth parameters (linear extension, density, and calcification) of *Acropora muricata*, *Isopora palifera*, and *Pocillopora damicornis* were investigated along a 2,345 km latitudinal gradient from Lizard Island (14.67°S) to Davies/Trunk Reef (18.85°S), and Heron Island (23.35°S). The role of environmental factors, such as temperature, aragonite saturation, and light in controlling growth rates of corals at these locations was explored. Growth rates of *A. muricata*, *P. damicornis* and *I. palifera* were similar among the low latitude locations of Lizard Island and Davies/Trunk Reef. But annual linear extension rates of *A. muricata*, *P. damicornis* and *I. palifera* at Heron Island in the southern Great Barrier Reef were 34 %, 33 %, and 20 % less, respectively, when compared to Lizard Island. Spatial variation in growth closely corresponded with differences in the local temperature regime, while differences in carbonate chemistry and light intensity explained little of the apparent differences in growth among these locations.

The relative contribution of temperature versus carbonate saturation state in affecting coral growth cannot easily be partitioned from *in situ* measurements. Therefore, to determine the independent and combined effects of ocean warming and ocean acidification, two common and fast growing *Acropora* corals (*Acropora*

muricata and *Acropora hyacinthus*) were used in a fully factorial experimental study using three temperature treatments (long-term average=26 °C, long-term summer maximum=28.5 °C and a future +2.5 °C temperature stress=31 °C) crossed with three levels of pCO_2 (current=410 µatm, mid century=652 µatm, and end of century=934 µatm). Experimental results exposed temperature-enhanced calcification for *A. muricata* and *A. hyacinthus* but by the end of the experiment, future temperature stress of +2.5 °C led to 10-50 % reduction in calcification across both coral species. End of century pCO_2 reduced survivorship and over long-term led to a 50 % reduction in calcification. Importantly, the few individual that survived the high temperature/ high pCO_2 treatment could be more tolerant genotypes suggesting the potential for some individuals to cope with future climate change scenarios.

In combination, the results from this thesis suggest that climate change is already impacting on growth of branching corals, both at tropical and subtropical locations, which is largely attributable to declines in the growth rates with increasing temperature. It is possible that changes in seawater chemistry are compounding the effects of increasing temperature, and will become increasingly important with time, but either way it appears that climate change is having generally negative effects on the growth, and therefore resilience of branching corals, across a wide range of geographical settings and habitats. We conclude that ongoing changes in environmental conditions, and particularly further increases in temperature (e.g., due to climate change) will lead to general declines in growth rates of corals, which may be further exacerbated by shifts in assemblage structure towards relatively slow-growing, thermo-tolerant species. Importantly, branching corals species are among the most sensitive corals to temperature stress and ocean acidification, but are also amongst the most important corals in contributing to habitat structure and

complexity. Ongoing research and monitoring is essential to understand the cumulative effects of increasing temperature, ocean acidification and other climate-related changes in environmental conditions on key demographic processes of different corals, to develop management strategies to mitigate the effects of climate change, and to facilitate acclimation and adaptation to changing environmental conditions.

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Chapter 1 General Introduction

Growth rates of scleractinian corals are fundamental to the structure and dynamics of coral reef ecosystems (Wells 1957, Goreau 1963, Hart & Kench 2007), and have been the subject of extensive scientific enquiry since the 1800's (e.g., Darwin 1874, Dana 1890). Initial research was motivated by inexorable links between coral growth and reef accretion (Darwin 1874, Dana 1890), and strove for aggregated estimates of bulk calcification. Subsequent research has revealed considerable variability and complexity in growth rates of corals (Mayor 1924, Edmondson 1929, Stephenson & Stephenson 1933) and there have been a plethora of studies on intrinsic (e.g., resource competition) and extrinsic factors (e.g., environmental conditions) that influence growth of individual colonies (reviewed by Pratchett et al. 2015 - Chapter 2). More recently, growth rates have been recognised as one of the most fundamental life-history traits that distinguish functional groups of corals (e.g., Darling et al. 2012) and possible effects of global climate change on coral demographics (De'ath et al. 2009, Cooper et al. 2012) have greatly renewed interest in coral growth.

One of the primary environmental determinants of coral growth is temperature (e.g., Lough & Barnes 2000), such that global climate change and associated ocean warming may pose a considerable threat to the viability and persistence of corals (Hoegh-Guldberg & Bruno 2011), and the diversity of reef organsims that rely on corals (Pratchett et al. 2008, Stella et al. 2011). Effects of climate change on coral growth are highly equivicol (as discussed later), but there is increasing evidence that growth rates of some corals (mostly, massive coral species) have declined significantly over the last 1-2 decades (De'ath et al 2009, Cantin et al. 2010, Tanzil et al. 2013). Growth rates of scleractinian corals are strongly linked to reef health, whereby declining growth rates undermine the capacity for corals to

recover from major disturbances (Manzello 2010) and thereby compromise reef resilience (Anthony et al. 2010). Moreover, if corals are growing more slowly there are likely to be fewer large colonies, which have a disproportionate contribution to reproduction and population replenishment (Wood 1999).

Widespread and sustained declines in the abundance and cover of scleractinian corals (e.g., Caribbean: Gardner et al. 2003, Great Barrier Reef (GBR): Bellwood et al. 2004, De'ath et al. 2012) are generally attributed to increasing rates of coral mortality, linked to acute and/ or chronic disturbances. On the GBR, for example, declines in coral cover over the last 27 years are attributed to severe tropical storms, outbreaks of crown-of-thorns starfish, coral disease, and coral bleaching (De'ath et al. 2012). Notably, this study gives little consideration to chronic disturbances (e.g., sustained shifts in environmental conditions) that may have compounded effects of major acute disturbances (e.g., Hughes et al. 2003, Hughes et al. 2010), as well as having demographic consequences that undermine the viability of local coral populations. If for example, sustained shifts in environmental conditions have lead to a 11 % decline in coral growth, as reported by De'ath et al (2013), this might explain sustained declines in overall cover of scleractinain corals, independent of any major disturbances.

1.1 Effects of climate change on coral growth

Scleractinian corals are considered to be amongst the most sensitive animals to global climate change (Carpenter et al. 2008), largely owing to their propensity to bleach and/ or die when exposed to temperatures that are only 1-2 degrees above normal summer maxima (Liu et al. 2003). Coral bleaching results from the breakdown of the symbiotic relationship between the coral host and algal dinoflagellate, *Symbiodinium*

sp. (commonly referred to as zooxanthellae) following prolonged periods of thermal stress (Smith & Buddemeier 1992, Baker et al. 2008). The zooxanthellae contribute disproportionately to the coral host energetic budgets through photosynthesis (Edmunds & Davies 1986). Whether corals can adapt to the persistent stress from increasing SST remains largely unknown but recent reseach has pointed to the potential for trans-generational acclimation, at least in coral larvae (Putman & Gates 2015). Regardless, there is increasing appreciation that corals are being negatively impacted by changing environmental conditions even if there is no apparent bleaching stress, manifested in sublethal effects of declining growth rates (Bak et al. 2009, Manzello 2010, Cantin et al. 2010, De'ath et al. 2013, Tanzil et al. 2013).

It is predicted that by the end of the century, sea surface temperature (SST) in tropical oceans could increase by 1.8 °C to 6 °C (IPCC 2013). Sustained increases in baseline SST have already pushed corals close to their upper thermal limits, such that periodic temperature anomalies (e.g., during El-Nino Southern Oscillations (ENSO)) have caused extensive coral bleaching (Kleypas et al. 2015), contributing to widespread degradation of coral reef ecosystems (Hough-Guldberg et al. 2007). The strongest bleaching events on the GBR occurred in 1998 and 2002 (Berkelmans & Oliver 1999, Berkelmans et al. 2004) with 42-54 % of reefs bleaching during these periods. Even if bleached corals do not die, the corals experience a temporary cessation of growth. In massive *Porites*, a hiatus in growth was observed following the 1998 and 2002 bleaching events, with growth returning to pre-disturbance rates within four years (Cantin & Lough 2014).

Aside from increasing temperatures, corals are also sensitive (like all calcifying organisms) to changes in seawater chemistry (declines in both pH and aragonite saturation) that are resulting from global climate change (Orr et al. 2005,

Pandolfi et al. 2011). Aragonite saturation (Ω-aragonite) covaries with temperature as a function of solubility and drops below the level necessary to sustain reef growth at tropical limits (Kleypas et al. 1999a). Due to the buring of fossil fuels, atmospheric carbon dioxide has risen from 280 ppm at pre-industrial levels to current concentrations of 400 ppm (IPCC 2013). As 30 % of atmospheric carbon dioxide gets absorbed into the ocean (Sabine et al. 2004), ocean pH has fallen 0.1 units from pre-industrial times leading to a 30 % increase in hydrogen ions (Caldeira & Wickett 2003). Carbon dioxide dissolves in water to form carbonic acid that readily dissociates into hydrogen and bicarbonate ions decreasing the pH and reducing the freely available carbonate ions (CO_3^{2-}) (Kleypas & Yates 2009). This change in ocean chemistry, termed ocean acidification, reduces the freely available carbonate ions making it harder for coral calcification (Orr et al. 2005).

Coral calcification takes place at the base of the coral tissue in an isolated compartment of the calicoblastic ectoderm where aragonite, the modern form of calcium carbonate ($CaCO_3$) is precipitated (Tambutte et al 2011). Corals grow aragonite crystals by elevating the saturation state at the site of calcification (Cohen & McConnaughey 2003, Venn et al. 2011). Corals in ambient external seawater saturation state (Ω_{arag}=3.7) upregulate the internal calcifying fluid saturation state 5-fold higher (Ω_{arag}~19) than the outside seawater (Cohen et al. 2009). But as the seawater saturation state declines, the saturation state of the internal calcifying fluid declines and the rate of $CaCO_3$ precipitation decreases (Cohen et al. 2009). There is increasing evidence that some corals may be able to upregulate this site of calcification to combat ocean acidification at little additional energetic cost (McCulloch et al. 2012). However, most studies show reef-building corals are sensitive to the effects of ocean acidification as the reduced availability of carbonate

ions impacts processes of calcification, which has consequences for growth and survivorship (Gattuso et al. 1999, Langdon & Atkinson 2005, Silverman et al. 2009).

Documented declines in growth rates of corals have been variously attributed to increasing temperatures and/ or ocean acidification (e.g., Cantin et al. 2010, De'ath et al. 2013, Tanzil et al. 2013). Calcification rates of massive *Porites* on the GBR have declined by 11 % since 1990 (De'ath et al. 2013), which was partly linked to declining Ω_{arag} over this period. However, recent research has shown *Porites* to be extremely resilient to ocean acidification (Fabricius et al. 2011) and it may be that temperature stress is the dominant cause for decline. In addition, high temperature stress was suggested as the cause of decline in calcification (18.6 %) of massive *Porites* around the Thai-Malay Peninsula in Southeast Asia as these corals experienced an increased of 0.7 - 1.3 °C per decade from 1980 to 2010 (Tanzil et al. 2013). Similarly, declines in linear extension of *Diplorastea heliopora* in the Red Sea has been attributed to ocean warming (Cantin et al. 2010).

Much of the research on growth of corals has focussed on massive corals (as discussed later), but the few studies that have explored temporal changes in growth rates of branching corals also showed declines in growth (Bak et al. 2009, Manzello 2010). The linear extension of *Acropora palmata* in Curacao was reduced by 7.2-10.7 % from 1971/73 to 2002/04 (Bak et al. 2009). While the local temperature was not outside the thermal optimum for this species and local anthropogenic development was greater in the previous sampling years, change in carbonate chemistry was purported as the main cause for the decline in growth. In Pacific Panama, declines in linear extension were reported for the branching *Pocillopora damicornis* by nearly one third from 1974 to 2006 (Manzello 2010). This reduced growth may be due to thermal stress, ocean acidification or corals contained thermo-

tolerant zooxanthellae, such as Clade D, which are not very productive (Cantin et al. 2009).

Predicted increases in SST combined with declining saturation state of the oceans are likely to lead to changes in the distribution and abundance of reef-building corals (Kleypas et al. 1999a). The relative contribution of these factors are likely to vary geographically, such that at high latitutude, increases in temperature may actually favor coral growth (van Hooidonk et al. 2014) as they are thought to be limited by cooler winter temperatures (Crossland 1984). This positive relationship with increasing calcification was observed in massive *Porites* from the subtropical reef Houtham Abrolhos, where calcification increased by 23.7 % between 1900 and 2010 associated with greater SST anomaly during that period (Cooper et al. 2012). In contrast, the latitudinal limits of reef accretion are likely to be the first affected by ocean acidification. However, we do not know to what extent the local benthic composition can buffer against the effects of ocean acidification (Anthony et al. 2011, 2013) or the potential for coral to up-regulate their internal pH at the site of calcification (Venn et al. 2013) to maintain their growth rates.

While the understanding of temperature controls on growth are well known, the current knowledge of predicting future Ω-aragonite has been restricted to those collected from open ocean waters and it is unclear how it will affect corals in near shore reefs (Kleypas & Landgon 2006). Atmospheric concentrations of pCO_2 are predicted to increase to 550-950 ppm by the end of the century depending on IPCC scenarios (IPCC 2013), resulting in a decrease in seawater pH by 0.3-0.4 units (Caldeira & Wickett 2005). Experimental studies almost invariably show that ocean acidification will lead to declines in calcification of corals (e.g., Gattuso et al. 1998, Marubini et al. 2001, Leclerq et al. 2002, Reynaud et al. 2003, Langdon & Atkinson

2005, Edmunds et al. 2012), especially when comparing end of century levels of pH and aragonite saturation to current ambient conditions. For example, Langdon & Atkinson (2005) showed that growth rates of *Porites compressa* were up to 44 % lower for colonies subject to levels aragonite saturation predicted for the year 2100 ($\Omega_{aragonite}$=2.25) compared to present day ($\Omega_{aragonite}$=3.64). In the first field-based manipulation of carbonate chemistry, Albright et al. (2016) used alakalinity enrichment to demonstrate that net community calcification increases significantly when ocen chemistory is restored to conditons expected to have occurred in pre-industrial times.

Onoging changes in seawater chemistry will be accompanied by marked changes in temperature regimes, though synergistic effects of changes in temperature and aragonite saturation are still unclear. Anthony et al. (2008) showed that declines calcification rates of *A. intermedia* and *P. lobata* with a doubling of pCO_2 were more pronounced at 25-26 °C compared to 28-29 °C. Conversely, Reynaud et al. (2003) observed *Stylophora pistillata* to be insensitive to a doubling of pCO_2 at 25 °C but experienced a 50% reduction in calcification at 28 °C. While many studies have investigated the independent effects of increasing temperature or declining aragonite and generally reveal negative effects on coral calcification, it is the combined affects of changing seawater chemistray and altered temerpature regimes that are of most concern (Raynaud et al. 2003, Chan & Connolly 2013, Harvey et al. 2013), and the limited work in this area is yet to reveal any general patterns in the likely repsonses of corals.

1.2 Importance of studying branching coral growth

Branching corals contribute the most to habitat complexity and are the most important corals for corallivores and coral-dwelling fish (Pratchett et al. 2008), but also have the greatest susceptibility to bleaching (Marshall & Baird 2000). Moreover, recent studies of coral growth have focused on documenting temporal changes in growth rates of massive species (reviewed in Chapter 2), with few studies investigating corresponding changes in growth rates of branching species (but see Bak et al. 2009, Manzello 2010). However, declines in the growth and abundance of branching corals could have profound effects on fish communities, due to reduced habitat complexity (Pratchett et al. 2009). Therefore, the projected changes in the growth, survival and persistence of branching corals on reefs subjected to higher temperature and ocean acidification is of considerable concern (Smith & Buddemeier 1992, Walther et al. 2002).

1.3 Objectives

The overarching objective of this thesis was to test how changing environmental conditions may impact on the growth of common branching corals on Australia's Great Barrier Reef. Given considerable complexities and inherent vagaries in measurements of coral growth, I first compiled extensive meta-data on temporal and spatial patterns of coral growth (Chapter 2), generating general and readily testable hypotheses about likely effects of climate change on coral growth. Subsequent chapters (Chapters 3 & 4) explored decadal changes in the growth rates of specific corals, capitalising on historical measurements of coral growth from Lord Howe Island (Harriott 1999), the southernmost coral reef system in the world, and at Davies Reef (Oliver 1987) in the central GBR. If sustained and ongoing climate change

(specifically, increases in SST and/ or declines in aragonite saturation) is impacting on growth rates of branching corals (e.g., Bak et al. 2009, Manzello 2010), I'd expect that contemporary rates of annual coral growth would be significantly different from comparable measurments of coral growth made in the 1980s. Thereafter, I quantified large-scale spatial variation in growth rates (linear extension, density and calcification) of three dominant branching/columnar coral species (*Acropora muricata*, *Pocillopora damicornis*, *Isopora cuneata*) along the Great Barrier Reef (Chapter 5) relating spatial variation in growth to differences in key environmental parameters. Specifically, I wanted to test if temperature is the main environmental driver in branching coral growth rates as observed in massive species (Lough & Barnes 2000).

Finally, this thesis assessed the response of two Acroporid corals (*Acropora muricata, Acropora hyacinthus*) growth and health in predicted future climate change scenarios (Chapter 6). Without such studies, it is impossible to determine whether temporal changes in growth rates of corals (Chapters 3 & 4) are caused by increasing temperature, ocean acidification or both. Therefore, this experiment determined the independent and synergistic affects that temperature and ocean acidification may have on branching coral growth rates, physiology, and survivorship.

Chapter 2 Spatial, temporal and taxonomic variation in coral growth: Implications for the structure and function of coral reef ecosystems

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2.1 Abstract

Growth is a fundamental biological trait, generally considered to have an important role in structuring populations and communities. Accordingly, many studies have quantified growth rates of scleractinian corals, but using a variety of different methods and measures that may or may not be comparable. The purpose of this review is to compile extensive data on the growth of corals, to relate disparate methods of measuring coral growth, and to explore spatial, temporal and taxonomic variation in growth rates. The most common metric of coral growth is linear extension, measured as unidirectional change in branch length or colony radius. Rates of linear extension vary greatly among corals, being highest among arborescent Acropora species. This is not unexpected given the limited carbonate investment in producing long slender branches compared to solid hemispherical colonies. However, differences in the way that extension rates are actually measured (e.g., linear extension of individual branches versus changes in the planar area of whole colonies) could potentially bias inter-specific comparisons of coral growth. The most comparable measure of growth, which gives unbiased estimates of growth across different growth forms, is average annual calcification or change in weight normalized to a measure of size. Surprisingly, even calcification rates appear to be much higher for branching *Acropora* compared to other coral genera, which contributes to the high extension rates recorded for this genus. Despite inconsistencies and incompatibilities among studies of coral growth, there is clear evidence that coral growth rates vary spatially and temporally, largely in response to light and water quality (e.g., turbidity), temperature, and aragonite saturation state. Ongoing changes in environmental conditions (e.g., due to climate change) are expected to have generally negative consequences for the growth of scleractinian

corals, which may be further exacerbated by shifts in assemblage structure towards relatively slow-growing species.

2.2 Introduction

Scleractinian (hard) corals are fundamental to the geomorphology, biodiversity, and structure of coral reef ecosystems (Goreau 1963, Hoegh-Guldberg 2004, Pratchett et al. 2008). Most notably, scleractinian corals are major contributors to the formation of reef structures (Goreau 1963), as framework builders (Wells 1957) and often contributing disproportionately large amounts to carbonate production (Hart & Kench 2007). Hard corals also contribute to both the productivity (Anthony et al. 2008) and structural complexity of coral reef habitats (Pratchett et al. 2008), providing essential resources (food and shelter) for many reef organisms (Jones et al. 2004, Rotjan & Lewis 2008, Cole et al. 2008, Stella et al. 2011), as well as mediating biological interactions among coral-associated organisms (e.g., competition, Munday 2001, Holbrook & Schmitt 2002; predation, Caley & St John 1996, Coker et al. 2009), thereby promoting co-existence of many species. Consequently, the biodiversity and abundance of reef-associated fauna (such as fishes) is positively correlated with both the abundance and diversity of scleractinian corals (Jones 1988, Munday 2000, Jones et al. 2004, Holbrook et al. 2000, 2002, 2008, Messmer et al. 2011). Sustained declines in the cover of scleractinian corals (Gardner et al. 2003, Bellwood et al. 2004, Bruno & Selig 2007, De'ath et al. 2012, Jackson et al. 2014) are, therefore, a critical concern.

Coral reefs are among the world's most threatened ecosystems (Pandolfi et al. 2003), with 19% of reefs having lost >90% of their live coral cover (Wilkinson 2008). A further 15% of reefs face a similar prospect within the next 10 to 20 years

(Wilkinson 2008). Sustained declines in the abundance (as evaluated through percentage cover) of scleractinian corals are commonly attributed to elevated rates of coral mortality (e.g., Bruno & Selig 2007, De'ath et al. 2012), associated with increasing frequency, severity and variety of disturbances. Perennial causes of coral mortality, such as natural chronic and acute disturbances, are now compounded by a range of anthropogenic disturbances, which can cause extensive and widespread coral mortality (Hughes et al. 2003). Also important are the physiological stresses imposed by these disturbances, as well as environmental changes including both climate change and deterioration in water quality (e.g., De'ath et al. 2009, Carilli et al. 2010, Pandolfi et al. 2011) and their interaction (Crain et al. 2008). On Australia's Great Barrier Reef (GBR), for example, De'ath et al. (2009, 2013) reported that growth rates of massive *Porites* corals declined ~11% from 1990 to 2005. The causes of this decline are not yet clear, but may be linked to recent increases in seawater temperatures and ocean acidification. Significant declines in coral growth rates, especially if accompanied by declines in other demographic rates (e.g., fecundity and recruitment), will contribute greatly to sustained declines in the abundance of corals (Hughes & Tanner 2000), or at the very least, constrain the capacity of corals to recover from periodic disturbances (Hughes et al. 2007, Hoegh-Guldberg et al. 2007).

Studies of growth rates of corals (defined herein as any changes in the physical dimensions of discrete colonies) have a long history, extending to the 1800s (reviewed by Buddemeier & Kinzie 1976) and were initially motivated by questions related to the formation and maintenance of reef structures and carbonate frameworks, and the fundamental knowledge that reef accretion is inexorably linked to coral growth (Darwin 1874, Dana 1890). Studies of coral growth continued through the early 1900s (Mayor 1924, Edmondson 1929, Stephenson & Stephenson

1933), when long-term studies of individual colonies revealed high spatial and temporal variation in growth rates. In light of this, Stephenson & Stephenson (1933) concluded that coral growth must be measured over extended periods (several years), and averaged across multiple colonies, to reliably detect spatial and taxonomic differences. Thereafter, many studies produced data on time-averaged growth rates for different coral species (e.g., Hubbard & Scaturo 1985), and there emerged a strong dichotomy between 'fast-growing' and 'slow-growing' species, which was partly explained by differences in gross morphology (Buddemeier & Kinzie 1976). Increasingly, however, coral species have been categorised into broadly-defined functional groups based on gross colony morphology (such as 'massive', 'bushy', and 'columnar', e.g., Bellwood et al. 2004) or response to disturbances (i.e., winners and losers, Loya et al. 2001), or life history traits, including growth rate (Darling et al. 2012). 'Characteristic' growth rates have been assigned to such functional groups (e.g., bushy and branching corals are 'fast growers' while massive corals are 'slow growers'). However, even within these functional groups there is strong inter- and intra-specific variation in growth rates.

The purpose of this review is to synthesize extensive research on the growth rates of scleractinian corals, and assess the broader utility of species- and location-specific growth-rate measurements to: i) distinguish functional groups of scleractinian corals, and ii) understand the changes in the structure and function of coral assemblages attributed to global climate change. Possible effects of global climate change (De'ath et al. 2009, Cooper et al. 2012) have resulted in renewed interest in coral growth but, as yet, there is no theoretical framework within which the effects of climate change on the growth of different coral taxa in different locations (e.g., across latitudinal gradients) can be explained. Despite quantified long-term

changes in physical conditions on coral reefs (e.g., increasing sea surface temperature (SST)), the reported effects on growth rates of tropical scleractinian corals are equivocal. For example, the growth rates of corals have already declined in some locations and for some taxa (De'ath et al. 2009, Bak et al. 2009, Tanzil et al. 2009, Cantin et al. 2010, Manzello 2010, Tanzil et al. 2013) as SSTs have increased, but in other cases warming is associated with increased growth rates of corals (Cooper et al. 2012). Reconciling these observations requires simultaneous consideration of multiple environmental drivers of coral growth, which vary in their spatial and temporal effects (van Hooidonk et al. 2013), as well as accounting for alternative measures of coral growth (e.g., linear extension versus calcification).

2.3 Contrasting measures of coral growth

A variety of methods have been developed, and are in common use, to quantify 'growth' of reef-building corals (Buddemeier & Kinzie 1976, Holcomb et al. 2013), defined herein as a change in linear dimension, planar area, volume, or mass of the skeleton. For the purposes of this review, we exclude consideration of the effects of environmental conditions on the growth of coral tissue, although we recognize that the growth of tissue and the growth of skeleton are functionally and mechanistically intertwined. The diversity of techniques and approaches to measuring growth rates of corals is partly necessitated by differences in the way that corals grow (e.g., some species deposit carbonate in successive, and strikingly different layers that preserve the entire history of annual growth, while in other species these effects are less evident, Table 2.1), but the specific method(s) selected for measuring coral growth rate also depend on the temporal resolution required (Holcomb et al. 2013), and the specific biological or ecological question(s) motivating the research. Coral biologists

and geomorphologists are generally focussed on rates of carbonate accretion that lead directly to changes in skeletal weight, as well as, or in place of, measures of changes in overall colony dimensions, such as volume, area, or linear dimensions (e.g., Houlbrèque et al. 2004, Browne 2012). Conversely, ecologically-driven research on coral growth, investigating for example competition, predation risk, and susceptibility to disturbance, is generally focused more on the change in overall colony dimensions (most often the ‘area of occupancy’; Gilmour et al. 2013), rather than change in skeletal mass, or calcification.

Table 2.1 Coral taxa reported to have regular growth bands that may or may not be used to retrospectively measure rates of linear extension or calcification throughout the life of the colony.

Corals with distinct growth bands, known to record annual growth	*Acropora palmata* (Gladfelter & Gladfelter 1979) *Agaricia agaricites* (Stearn et al. 1977) *Astrea* (=*Montastraea*) *curta* (Harriott 1999) *Balanophyllia europaea* (Goffredo et al. 2009) *Cladocora caespitosa* (Kružić et al. 2012) *Coelastrea* (=*Goniastrea*) *aspera* (Babcock 1988, 1991) *Colpophyllia natans* (Huston 1985) *Cyphastrea serailea* (Harriott 1999, Roberts & Harriott 2003) *Diploastrea heliopora* (Corrège et al. 2004, Cantin et al. 2010) *Diploria labyrinthiformis* (Dodge & Thomson 1974) *Dipsastrea* (=*Favia*) *pallida* (Highsmith 1979, Harriott 1999) *D. speciosa* (Knutson et al. 1972, Buddemeier et al. 1974) *Gardineroseris planulata* (Guzmán & Cortés 1989) *Goniastrea favulus* (Babcock 1988, 1991) *G. retiformis* (Buddemeier et al. 1974) *G.* (=*Favia*) *stelligera* (Buddemeier et al. 1974) *Hydnophora microconos* (Buddemeier et al. 1974) *Lobactis* (=*Fungia*) *scutaria* (Jokiel & Tyler 1992) *Lophelia pertusa* (Mortensen et al. 1998) *Montastraea cavernosa* (Highsmith et al. 1983) *Orbicella* (=*Montastraea*) *annularis* (Dodge et al. 1974) *O. faveolata* (Saenger et al. 2008) *O. franksi* (Saenger et al. 2008) *Paragoniastrea* (=*Goniastrea*) *australensis* (Harriott 1999) *Pavona clavus* (Wellington & Glynn 1983) *P. duerdeni* (Jokiel & Tyler 1992) *P. gigantea* (Guzmán & Cortés 1989, Wellington & Glynn 1983) *P. varians* (Guzman & Cortes 1989) *Platygyra daedalea* (Simpson 1988) *P. lamellina* (Buddemeier et al. 1974) *P. daedalea* (=*rustica*) (Knutson et al. 1972) *P. sinensis* (Babcock 1988, 1991) *Plesiastrea versipora* (Burgess et al. 2009) *Pleuractis* (=*Fungia*) *granulosa* (Chadwick-Furman et al. 2000) *Porites astreoides* (Stearn et al. 1977, Hubbard & Scaturo 1985) *P. australiensis* (Lough & Barnes 2000) *P. columnaris* (Klein & Loya 1991) *P. compressa* (Grigg 1998, Domart-Coulon et al. 2006) *P. lobata* (Buddemeier et al. 1974) *P. lutea* (Highsmith 1979) *P. mayeri* (Alibert & McCulloch 1997) *P. nodifera* (Al-Rousan et al. 2002) *P. solida* (Barnes & Lough 1989) *Psammocora superficialis* (Guzmán & Cortés 1989) *P. haimiana* (=*togianensis*) (Knutson et al. 1972) *Pseudodiploria* (=*Diploria*) *strigosa* (Guzmán et al. 1991, Logan et al. 1994) *Siderastrea siderea* (Stearn et al. 1977)

Corals with distinct growth bands, known to record annual growth (cont.)	*Solenastrea hyades* (Moore & Krishnaswami 1972) *Stephanocoenia* sp. (Moore & Krishnaswami 1972)
Corals with apparent growth bands, but of uncertain chronology	*Astreopora myriophthalma* (Buddemeier et al. 1974) *Fungia fungites* (Buddemeier et al. 1974) *Herptolitha limax* (Buddemeier et al. 1974) *Isopora* spp. (Anderson & Cantin, unpublished data) *Oulophyllia crispa* (=*aspera*) (Buddemeier et al. 1974) *Pocillopora eydouxi* (Buddemeier et al. 1974) *P. meandrina* (Jokiel & Tyler 1992) *Sandalolitha* (=*Parahalomitra*) *robusta* (Buddemeier et al. 1974)

While changes in the overall size of scleractinian colonies are fundamentally dependent upon the deposition of calcium carbonate (i.e., calcification), the relationship between colony growth and calcification is complex. Calcification (and the associated change in weight of the coral skeleton) does not always relate directly to changes in the overall dimensions of a colony because: i) aragonite (the mineral form of $CaCO_3$ forming the skeletons of scleractinians) is not always laid down in areas of active linear extension (e.g., secondary thickening or infilling in *Acropora*, Gladfelter 1982), ii) differences in gross morphology and the primary axis of growth lead to differing levels of colony expansion for the same quantities of aragonite deposition, iii) the porosity or density of the skeleton varies within and among colonies, and as a function of environmental conditions, thereby obscuring the relationship between skeletal mass and skeletal volume (Buddemeier et al. 1974), and iv) branching corals vary in solidity (i.e., the amount of inter-branch space included within the overall 'displacement' volume of the entire colony, Barry 1965), which has direct ramifications for the total amount of carbonate that must be accreted to extend their maximum dimensions (e.g., mean solid radius, Maragos 1978).

For corals that deposit distinct bands of aragonite that preserve the chronology of growth throughout their lives (e.g., *Porites* spp., De'ath et al. 2009, Cooper et al. 2012; *Diploasterea heliopora*, Cantin et al. 2010, Figure 2.1), retrospective measures of growth have proved important in establishing temporal trends in the growth rates of individual colonies (e.g., De'ath et al. 2009, Carilli et al. 2010). For corals that do not deposit aragonite in regular bands, such that the skeletons do not reveal the life-long chronology of growth, then growth (change in weight, volume, area, or linear dimensions) must be evaluated through direct measurements of individual colonies over time (e.g., Bak et al. 2009). Hence,

intrinsic differences in the ways that different coral species calcify have led to taxonomic biases in the methods used to measure growth rates of corals, and the amount of data available (Buddemeier & Kinzie 1976).

2.3.1 Retrospective measures of coral growth bands

Banding in the skeletons of scleractinian corals, and its relationship to cyclical growth processes, was first recognised in the eighteenth and nineteenth centuries (e.g., Donati 1753, Whitfield 1898). When examining fossil and modern corals, Ma (1933, 1934) noted regular variations in the size and spacing of skeletal elements, which he speculated were linked to seasonal variation in water temperatures (Ma 1937). By studying massive corals collected in Enewetak Atoll following nuclear weapons testing, Knutson et al. (1972) confirmed that "regular alternating dark and light bands" were deposited annually. This discovery of annual low and high density band pairs "rendered almost trivial the previously unsolved problem of measuring long-term growth rates and growth histories" (Buddemeier & Kinzie 1976, page 199), though it is recognised that such banding is limited to a subset of corals (50 of ~750 reef-building scleractinian species, or ~7%) that mainly have a massive or hemispherical colony morphology (see Table 2.1). Although Stimson (1996) showed that the distance between concentric crests on the upper colony surface was representative of annual growth increments for some non-massive species (e.g., *Acropora spicifera*, plate-forming *Montipora* spp., and foliaceous *Merulina* spp.), such proxies of annual growth are not universally apparent in these corals, and are, therefore, of limited use in detecting growth variation.

Annual density banding is now widely recognized as an important tool for measuring growth rates of certain scleractinian corals (see Table 2.1), and has proved useful in relating spatial and temporal variation in growth to environmental variables

(e.g., Lough & Barnes 2000, Cooper et al. 2012). The principal advantages of this approach are i) some coral colonies are several metres in height and, with average growth rates ~1–2 cm yr^{-1}, they can record skeletal accretion over decades-to-centuries (time scales that are unfeasible for direct observation); ii) since derived growth measures are retrospective, they represent growth under natural conditions and are not affected by potential changes in growth rate due to coral collection and handling as occurs in experimental studies; iii) coral skeletons can be preserved after death allowing retrieval of growth measurements for periods in the distant past (e.g., Brachert et al. 2006 observed "ghost structures" of annual bands in *Porites* from the late Miocene), and iv) the density banding chronology provides the basis for reconstructing environmental conditions based on geochemical (e.g., Sr/Ca) and isotopic (e.g., $\delta^{18}O$) tracers incorporated into the $CaCO_3$ skeleton during growth (Lough 2010). Indeed, geochemical analyses to reconstruct changes in climatic conditions are often the primary motive for collecting cores from massive corals (Lough & Cooper 2011), rather than measuring coral growth *per se*. Despite the widespread use of the growth chronologies provided by annual density bands in massive corals, we still do not have a clear understanding of the environmental or endogenous factors that control band formation (Helmle & Dodge 2011).

Early studies on growth of massive corals with density banding were based on collection of whole colonies (Dodge et al. 1974). Given the size of some colonies and the need to preserve them *in situ*, collection of a coral core from the top of a colony is now the preferred approach. One of the first reports of successful coral core collection (Hudson et al. 1976) used a hydraulic coring system adapted from the reef substratum corer of Macintyre (1975). Subsequently, several lightweight, air-powered drilling systems have been developed and are now routinely used (Stearn &

Colassin 1979). For large colonies, the drilling rig is mounted perpendicular to the surface of the colony (Figure 2.1) and successive cores removed in 50–70 cm length sections (Isdale & Daniel 1989). Useful short (25–50 cm length) cores can also be obtained using hand-held drills (Fabricius et al. 2011). Cores are typically 5–10 cm in diameter to increase the chances of obtaining clear banding patterns along a major growth axis (Lough & Barnes 1992, Helmle & Dodge 2011). The resulting hole is filled with a tapered, conical concrete plug (~7 cm in length) that has been pre-soaked in seawater, which is hammered into position so the top is as flush as possible with the colony surface. Plugging the hole prevents bioeroders and sediment invading the core hole, and living coral tissue will, in most cases, recolonize the surface of the plug within one to three years (Matson 2011). Cores are then mounted (e.g., on aluminium trays with Plaster of Paris) and successive slices are removed using a milling machine. Ideally, slices should be 1–3 times as thick as the average diameter of the coral polyp in order to capture the meso-scale skeletal architectural features that form the annual density bands (Barnes & Devereux 1988). For *Porites*, for example, slice thickness is typically 6–7 mm.

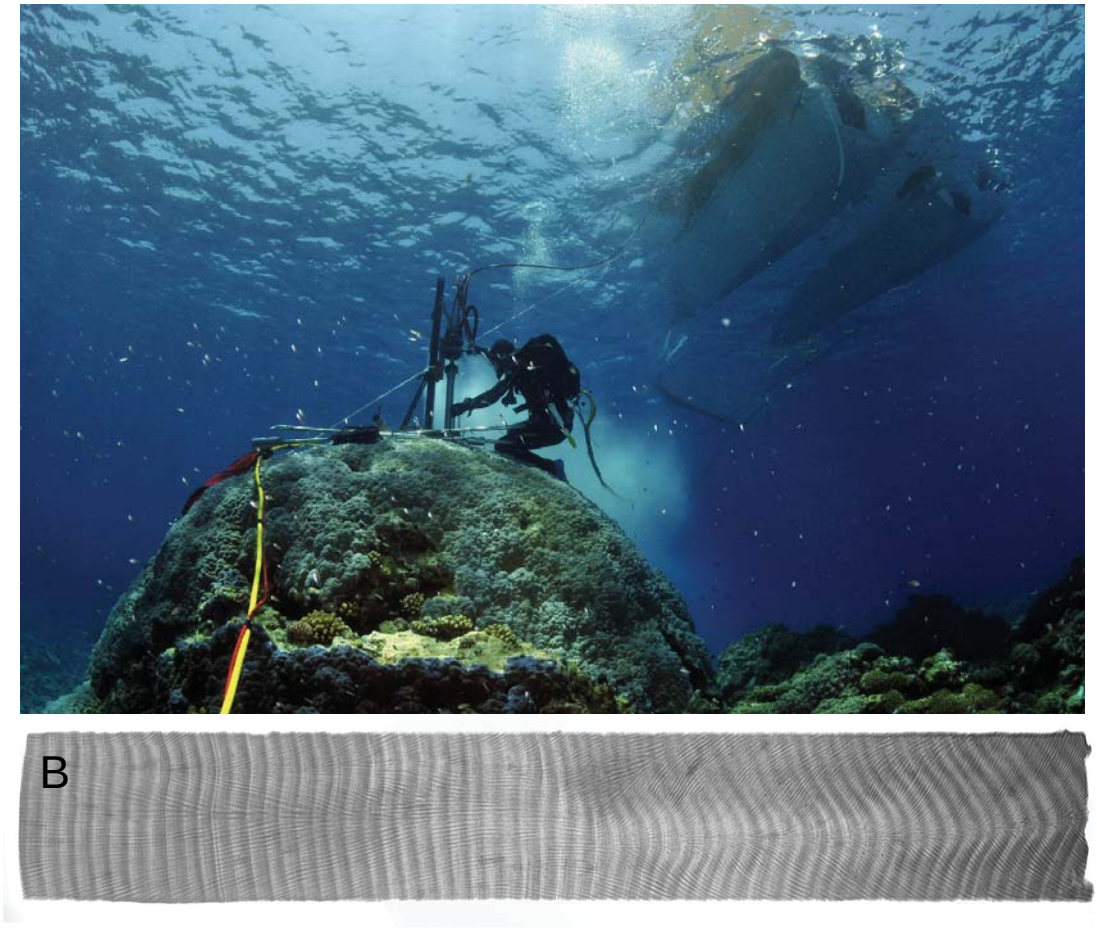

Figure 2.1. A) Drilling rig used to extract long (>2 m in ~70 cm sections) cores from large colonies of massive *Porites* colonies at Rowley Shoals, Western Australia. B) positive X-radiograph of a thin slice (7 mm) of the top ~70 cm section of a representative core from Tantabiddi Reef, Western Australia illustrating the annual high and low density band pairs. The estimated age of this coral is 178 years, but it should be noted that for massive *Porites*, any individual coral polyp has an average life expectancy of just 5 years (Darke & Barnes 1993).

After preparation and slicing of the core, coral skeletal slices are X-rayed to visualise the annual density banding (Helmle & Dodge 2011). Not all colonies of coral species that exhibit banding have clear annual bands; banding can often be distorted by convoluted skeletal growth, macro-architectural features, major injuries, or the presence of boring organisms within the skeleton (Lough & Barnes 1992). As such, it is best to collect at least two cores from each coral colony, as well as coring multiple colonies from a given site. Converting the X-ray negative to a positive print visualises the high density bands as dark and low density bands as light areas of skeleton (Figure 2.1)

Linear extension rate is the simplest, and most often reported, measure of growth that can be measured directly from X-ray negative or positive prints. Using X-radiographs, band width is defined as the linear distance between adjacent bands with equivalent density (e.g., between the tops of adjacent high-density bands, Aller & Dodge 1974). This method has been largely superseded by measures obtained from densitometry (see below). Linear extension has also been measured from luminescent lines (D'Olivo et al. 2013, Tanzil et al. 2013) that are visible when coral slices are viewed and photographed under ultra-violet light. In some locations, such as the nearshore GBR, the occurrence and intensity of luminescent lines reliably record seasonal river flood events (Lough et al. 2002) due to the incorporation of humic acids from soils into the coral skeleton (Boto & Isdale 1985, Grove et al. 2010). High intensity luminescent lines associated with major river flood events can also provide additional dating control of annual density banding patterns in nearshore and mid-shelf reefs (Hendy et al. 2003, Cantin & Lough 2014). Finally, linear extension rates have also been measured from high-resolution geochemical or isotopic sampling of

the coral skeleton (e.g., Stortz & Gischler 2011), although the use of such tracers is rare.

The first reported continuous measurement of skeletal density along massive coral slices was based on quantitative scanning densitometry of X-radiographs (Buddemeier 1974). This 'photo', 'optical' or 'X-ray' densitometry involves scanning of the X-radiographs (now digital) alongside appropriate $CaCO_3$ standards to obtain absolute skeletal density. Measurements of aluminium bars on the same radiograph as the coral slice, or exposing the film without the coral slice present, allow corrections to be made for non-uniform irradiation of the film, the 'heel effect' (Chalker et al. 1985). More recently, Duprey et al. (2012) presented an accurate digital de-trending approach that circumvents the need for these standards, though this has not, as yet, been generally adopted. X-ray densitometry has been further developed and combined with freely available band identification software (Helmle et al. 2002, CORALXDS www.nova.edu/ocean/coralxds). Skeletal density can also be measured continuously by gamma densitometry, which is based on measurement of the attenuation of a beam of gamma photons through the thickness of the slice (Chalker & Barnes 1990, Draschba et al. 2000). For example, the custom-built gamma densitometer at the Australian Institute of Marine Sciences (AIMS) uses Americium^{241} as the source of gamma photons, providing absolute skeletal density measurements at 0.0254 cm intervals along the skeletal slice, and has primarily been used for extracting growth characteristics of *Porites* spp. from tropical coral reefs off the east and west coasts of Australia (Lough & Barnes 2000, Cooper et al. 2012). Comparable skeletal density measurements have been reported from gamma and X-ray densitometry of the same coral slices (Carricart-Ganivet & Barnes 2007, Tanzil et al. 2013).

Computerised tomography (CT) scanning has also successfully been used to measure variation in skeletal density (Logan & Anderson 1991, Bessat & Buigues 2001). As with X-ray densitometry, this technique requires scanning standards of known density to convert the CT scan density measure (in Hounsfield units) to absolute skeletal density. The main limitation to the use of CT scanning is the cost and availability of CT scanners, which are specialised and expensive compared to readily available medical X-ray units. An advantage of CT scanning is that it generates images along freely chosen sections through the skeleton (Bosscher 1993) and, thus, an optimum measurement track can be selected that avoids areas of distorted or unclear annual banding. CT densitometry can also be undertaken on the whole coral core rather than on slices of the core and has been successfully applied to several massive coral species with different corallite sizes, such as *Siderastrea siderea* (Saenger et al. 2009), *Diploastrea heliopora* (Cantin et al. 2010), *Porites astreoides* (Crook et al. 2013) and massive *Porites* (Carilli et al. 2012). Annual linear extension rates can then be derived from continuous measurements of density versus distance along a core, or along a slice of a core, as the linear distance between equivalent points in adjacent annual bands, e.g., annual density maxima or minima (Figure 2.1B). Note that this measure of linear extension assumes that particular features of the annual density banding patterns are formed at the same time each year, which may not necessarily be true if skeletal density is controlled by exogenous factors.

Using X-radiography, gamma- or CT-densitometry, annual calcification rates (total $CaCO_3$ deposition) can be derived as the product of average annual skeletal density and annual linear extension rate. Overall, these three growth variables (linear extension, skeletal density and overall calcification) are inter-related but the

relationship between them appears to vary with species. For instance, both *Porites* in the Indo-Pacific and *Montastraea* in the Atlantic show an inverse relationship between linear extension rate and average skeletal density (Scoffin et al. 1992, Lough & Barnes 2000, Carricart-Ganivet & Merino 2001) but variation in overall calcification rate is mainly driven by variation in linear extension rate for *Porites* (Scoffin et al. 1992, Lough & Barnes 2000, Elizalde-Rendon et al. 2010) compared with variation in skeletal density for *Orbicella* (Carricart-Ganivet 2004, Dávalos-Dehullu et al. 2008, Carilli et al. 2010). Consequently, all three parameters should be measured to fully describe coral growth characteristics for a particular species and location (Dodge & Brass 1984).

2.4 Direct measures of linear extension

Growth rates must be measured directly for corals that do not exhibit regular density bands in their skeletal structure (e.g, *Acropora pulchra*; Roche et al. 2010). This requires direct measurements of linear dimensions, area, volume, or weight, repeated over time to calculate a time-averaged rate of growth (Shinn 1966, Gladfelter et al. 1978, Barnes & Crossland 1980, Kinzie & Sarmiento 1986). Moreover, the only way to detect temporal changes in the growth of these corals is to compare direct measurements taken years to decades apart (Edmunds 2007, Bak et al. 2009, Anderson & Pratchett 2014). Measuring linear extension (or branch extension; Simpson 1988) by taking repeated measurements from a fixed reference point to the branch tip or colony margin is one means to quantify changes in physical dimensions of coral skeletons. Using this technique, reference points can be natural features (Hughes & Jackson 1985), but are more often established by placing a permanent tag (e.g., plastic bands or cable ties) near the growing tip or colony margin (Shinn 1966,

Yap & Gomez 1981, Simpson 1988, Edmunds 2007, Al-Hammady 2013). This method allows for repeated and continuous measurements of linear extension through time (Bak et al. 2009), though there are concerns that permanent tagging of individual branches (depending on the technique employed) could interfere with the translocation of carbon and energy to the growing branch tips (Oliver et al. 1983), thereby impeding growth. Notably, Oliver (1984) showed that extension rates of tagged branches of *Acropora* depended on the placement of the tag relative to the branch tip, with tags closest to the branch tip causing the greatest reductions in growth.

Given the widespread use of tagging to directly measure linear extension (Table 2.2), several studies have explicitly focussed on resolving potential bias in this method (e.g., Reed 1981, Oliver 1984, Simpson 1988). To test the effect of tagging on growth rates of individual branches, Simpson (1988) directly compared linear extension rates of *Acropora muricata* (=*formosa*) between branches that were tagged versus nearby branches stained with alizarin red (discussed later) and showed that tagged branches grew 15% slower than stained branches in the first month, but thereafter there was no significant difference in growth rates. Similarly, Reed (1981) quantified linear extension for *Oculina varicosa* over a 1 year period and found no difference in growth estimates for branches or colonies that were tagged versus stained with alizarin red. To minimise short-term effects of tagging, it is prudent to tag colonies at least 1 month in advance of initiating growth measurements (*sensu* Bak et al. 2009). Another important consideration is the number of branches per colony that should be tagged and measured to obtain reasonable estimates of linear extension; corals exhibit substantial intra- and intercolony variation in growth (Oliver 1984) and increasing the number of tagged branches per colony, as well as the

number of colonies considered, can provide more precise estimates of growth rates. For *Acropora muricata* (=*formosa*), Simpson (1988) recommended tagging and measuring at least seven branches per colony to account for within-colony variation. However, many studies do not report the number of branches tagged per colony (Table 2.2) and for those that do, the number of branches per colony is often < 7 (Torres et al. 2007).

Table 2.2. Species utilized, number of branches per number of colonies in the study, distance the reference band is placed from the tip and associated reference for studies employing tagging methodology to measure linear extension rate in corals.

Species	No. of branches (colonies)	Distance from tip (cm)	Mortality (% of branches)	Duration	Reference
Acropora cervicornis	13 (1)	10	-	1 year	Shinn 1966
	1 (18)	-	-	88 days	Torres et al. 2007
A. hemprichii	- (15)	-	-	16 months	Ebeid et al. 2009
	- (4)	-	-	-	Al-Hammady 2013
A. muricata (=*formosa*)	-	-	-	250 days	Oliver 1984
	30	3	56.6	344 days	Charuchinda & Hylleberg 1984
	- (24)	-	-	13 months	Jinendradasa & Ekarame 2000
	60 (1)	-	60	2 years	Suresh & Mathew 1993
	30-40 (8)	5	-	13 months	Simpson 1988
A. palmata	49	15	-	2 years	Bak et al. 2009
A. pharaonis	- (15)	-	-	16 months	Ebeid et al. 2009
A. pulchra	2 (5)	-	-	2 years	Yap & Gomez 1985
A. yongei	28 (67)	1-3	9	4 months	Anderson et al. 2012
Isopora (=*Acropora*) *cuneata*	22 (65)	1-3	3	4 months	Anderson et al. 2012
Pocillopora damicornis	23 (67)	1-3	3	4 months	Anderson et al. 2012
Porites heronensis	24 (70)	1-3	3	4 months	Anderson et al. 2012
Seriatopora hystrix	21 (49)	1-3	10	4 months	Anderson et al. 2012
Stylophora pistillata	- (15)	-	-	16 months	Ebeid et al. 2009
	20 (51)	1-3	7	4 months	Anderson et al. 2012

An inherent limitation of studies that measure linear extension based on a limited number of individually tagged branches is that any damage to the specific focal branches will lead to underestimates of growth. Given that injuries accumulate through time (affecting an ever increasing proportion of branches), the effective duration of tagging studies is limited. For example, Charuchinda & Hylleberg (1984) found that only 13 (out of 30) tagged branches of *A. muricata* were undamaged after 344 days, greatly affecting the power of their statistical analyses. Many studies explicitly exclude branches that exhibit no (or sometimes negative) growth, attributing this to extrinsic disturbances (e.g., injuries) or intrinsic effects on growth (such as physiological stresses or changes in pigmentation; Shinn 1966, Neudecker 1981, Bak et al. 2009), or both. At Lord Howe Island, Anderson et al. (2012) found that a disproportionate number of tagged branches of *Seriatopora hystrix* died during the course of a 6-month growth study, largely due to the spread of turf algae that had initially colonized plastic cable ties attached to individual branches (Table 2.1). In some cases the algae had spread to immediately adjacent branches, while other branches were otherwise healthy.

To circumvent potential issues associated with placing permanent tags on coral branches, vital dyes or stains (e.g., alizarin sulphonate, calcein, and oxytetracycline) can be used to mark the underlying coral skeleton at a given time (reviewed by Holcomb et al. 2013), from which all subsequent growth is clearly visible and measurable (Figure 2.2). These stains are incorporated into the skeleton through calcification, and so corals must be exposed to the stain during a period of active growth (e.g., Holcomb et al. 2013). For alizarin sulphonate (commonly referred to as alizarin red), staining is achieved by exposing whole, live colonies to a dilute solution (ca. 10–15 mg L^{-1} alizarin red in sea water; Barnes 1972, Dustan

1975) for at least 3 hours in sunlight (Table 2.3) depending on the species, light intensity, and seawater temperature. At high-latitude reefs, such as Lord Howe Island (31°S) where low temperatures and light intensity potentially limit rates of calcification, staining may be largely ineffective at normal exposure times of 3–4 hours (Harriott 1999). Anderson et al. (2015-Chapter 3), therefore increased exposure times to 8 hours and successfully stained a broad range of different coral species at this location (Figure 2.2).

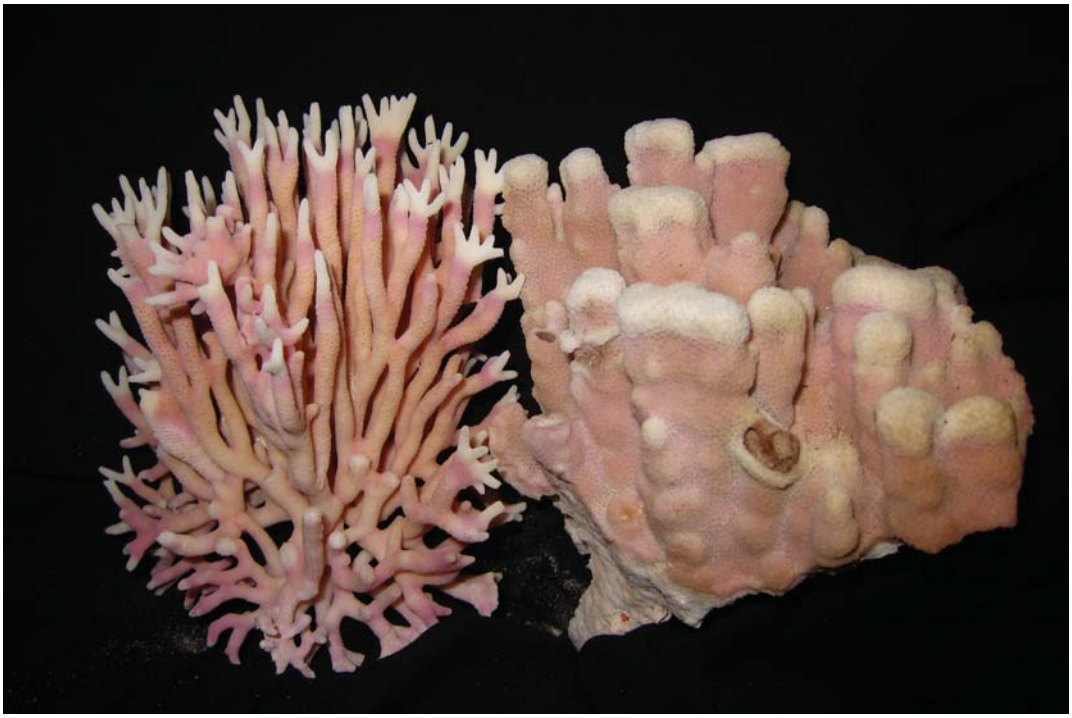

Figure 2.2. Alizarin staining to reveal subsequent rates of radial extension across the entire surface of a A) branching coral (*Seriatopora hystrix*) and B) columnar coral (*Porites heronensis*). Corals were stained in March 2010 (6–8 hours emersion in 10 mg L^{-1} of Alizarin stain mixed in sea water), then reattached to reef substratum in lagoon habitats (4 m depth) at Lord Howe Island. Corals were retrieved in May 2011 and immediately bleached to reveal newly accreted carbonate (in white) above the distinct stain line (pink).

Table 2.3. Spatial and taxonomic variation in exposure time (hours) used for alizarin red *in situ* staining.

Exposure (hours)	Species	Location	Reference
3	*Acropora muricata* (=*formosa*)	Magnetic Is., Davies Reef, GBR	Oliver 1984
4	*A. muricata, Montipora aequituberculata, Turbinaria mesenterina*	Middle Reef, GBR	Browne 2012
4	*Acropora palmata, A. prolifera, A. cervicorns*	US Virgin Is	Gladfelter et al. 1978
4-6	*A. cervicornis*	US Virgin Is	Gladfelter 1984
5	*Pocillopora damicornis*	Panama	Glynn & Stewart 1973
5-6	*Acropora aspera*	India	Suresh & Mathew 1995
6-8	*A. muricata, Pocillopora damicornis, Porites cylindrica* (=*andrewsi*)	Guam	Neudecker 1981
6-8	*Acropora yongei*	Houtman Abrolous	Marsh 1992
7-8	*A. yongei, Pocillopora damicornis, Isopora* (=*Acropora*) *cuneata, Porites heronensis, Seriatopora hystrix, Stylophora pistillata*	Lord Howe Island	Anderson et al. 2015
8	*Acropora muricata, Pocillopora damicornis*	Houtman Abrolous (winter)	Crossland 1981
24	*Porites lutea*	Thailand	Charuchinda & Chansang 1985
24	*Orbicella* (=*Montastraea*) *annularis, Porites astreoides*	US Virgin Is	Gladfelter et al. 1978
36-48	*Orbicella annularis* (28 m)	Jamaica	Dustan 1975
48	*Lophelia pertusa* (deep water coral)	Mexico	Brooke & Young 2009

One limitation of this technique is that alizarin red is toxic to corals (Lamberts 1978), and prolonged exposure or excessive concentrations may ultimately kill corals, or suppress growth. In one study, Dodge et al. (1984) stained *Orbicella* (=*Montastraea*) *annularis* in aquaria using 10 mg L^{-1} of alizarin red for 24 hours (longer than most *in situ* studies) and showed that calcification rates were suppressed for 6 days thereafter. In contrast, Holcomb et al. (2013) investigated the effects of different dyes on the temperate coral *Astrangia poculata* and found that alizarin red did not significantly affect coral growth, but did cause a reduction in polyp extension during staining. Similarly, Marsh (1992) found no adverse effects of alizarin red on *Acropora yongei*, and several studies of massive corals have found no difference between growth rates estimated using X-radiography of density bands compared with growth measured using staining (e.g., *Orbicella annularis*; Mendes & Woodley 2002, Mendes 2004), suggesting that staining does not have lasting or ecologically important effects on growth rates. However, care should be taken to use the minimum exposure time that will result in effective staining for different corals and in different locations.

Major benefits associated with the use of dyes (e.g., alizarin red) to directly measure rates of linear extension are that i) this method is not specific to any type or size of coral (cf. retrospective measures described above) and it can be used on all corals from newly settled polyps to very large colonies with any growth form (Holcomb et al. 2013), ii) patterns of coral growth (e.g., major axes of linear extension, and effects of localised injuries on subsequent growth) can be readily observed across the entire colony or proportion of the colony that was stained, revealing major areas of growth and also accounting for any portions of the colony where growth was compromised due to injuries or damage, and iii) it is possible to

determine the actual amount of calcium carbonate that was added in order to achieve the observed rates of linear extension, providing direct links between these two commonly used metrics of coral growth (discussed later in the section on calcification rates). To measure calcification rates, all white (unstained) carbonate deposited post-staining may be separated from the stained skeletal material and then weighed (Gladfelter 1984, Browne 2012). Alternatively, skeletal extension rates are multiplied by skeletal density to estimate calcification rates (Morgan & Kench 2012). These methods provide highly conservative measures of calcification rate because any calcium carbonate deposited below the stain line cannot be discerned (Manzello 2010), and it can also be difficult to separate the stained and unstained portions of the skeleton. The major drawback of using vital dyes is that corals must be sacrificed to record change in physical dimensions meaning that, unless colonies are sub-sampled through time, the method generates a single time-averaged estimate of coral growth across the period between staining and subsequent collection (Morgan & Kench 2012).

Regardless of measurement technique, a major issue relating to measuring average annual skeletal extension rates of corals is that these data are not directly comparable among corals with different growth forms (Browne 2012). Notably, different measurements are taken depending on the way that the coral colonies grow (Figure 2.3). For complex branching corals (arborescent and caespitose) each branch grows throughout the life of the colony (Wallace 1999) and, therefore, skeletal extension is measured based on the change in the length of individual and often randomly selected branches (‘branch extension’, Oliver et al. 1983, Harriot 1998). In contrast, branch length is finite in other more prostrate branching corals (tabular, digitate, and to a lesser extent, corymbose), such that growth is only apparent when

measuring linear extension of new branches on the periphery of the colony, or when measuring change in horizontal dimensions. When comparing skeletal extension rates between branching and non-branching corals the problem is more acute. It is possible, for example, that the widely reported differences in extension rates between branching versus massive (or hemispherical) colonies, are simply due to the fact that branch extension essentially reflects one-dimensional growth (especially for very slender branches), whereas skeletal extension in hemispherical colonies represents growth in 3 dimensions simultaneously. In most cases, skeletal extension is measured in only one direction (e.g., cores from massive corals are almost invariably taken vertically from the top of the colony, Lough & Cooper 2011) which may over- or under-estimate extension rates compared to studies that average skeletal measurements taken in multiple directions, and at multiple locations across the colony (e.g., Morgan & Kench 2012). In massive *Porites*, for example, linear extension and calcification rates are ~15% higher along the vertical growth axis compared to the horizontal growth axis, likely related to light availability (Lough & Barnes 2000). Moreover, the terms ‘skeletal extension’ and ‘branch extension’ are often used interchangeably (Morgan & Kench 2012), and in some multispecies studies it is not always clear what exactly has been measured for each different coral type, leading to further confusion about the relationship between linear extension and environmental conditions for different species.

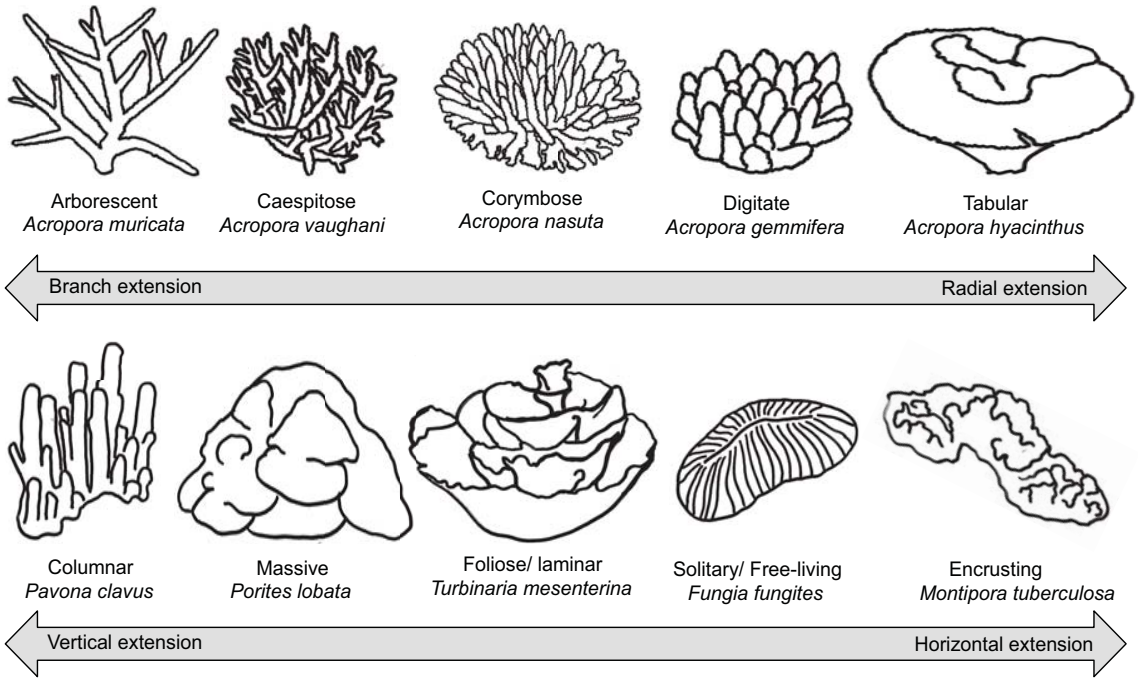

Figure 2.3. Major growth forms of scleractinian corals arranged according to their major growth axis. Change in area of occupation (standardized for colony size by calculating change in arithmetic mean radius) is the most suitable growth metric for corals to the right.

2.4.1 Changes in horizontal planar area or area of occupancy

Growth of colonial organisms, such as corals, is achieved largely through the addition of polyps or modules, the size of which is species specific. In scleractinian corals there is theoretically no intrinsic limit to the number of polyps within a colony and, hence, few intrinsic limits to colony size (i.e., growth is theoretically indeterminate, though some corals may senesce with age, Rinkevich & Loya 1986). However, there are many extrinsic factors that limit colony size, in particular, the decrease in mechanical stability as colony size increases, a feature that is particularly apparent in colonies with tabular or corymbose morphologies (Madin & Connolly 2006, Madin et al. 2014). Furthermore, competition, predation, disease and disturbance are all extrinsic factors that limit colony growth and potentially decrease realised growth rates. In addition, the vulnerability of a colony to agents of partial mortality increases with colony size because the probability of encountering such agents increases with the size of colonies (Jackson 1979, Jackson & Hughes 1985). A large proportion of polyps within a colony can die, yet the colony can still survive. This 'partial mortality' means that, unlike most unitary organisms, coral colonies can decrease as well as increase in size. The incidence of partial mortality is often very high, particularly in some morphologies, such as massive corals (Hughes & Jackson 1985, Babcock 1991, Bythell et al. 1993, Baird & Marshall 2002). Consequently, methods that can detect decreases, as well as increases in colony size, such as arithmetic mean radius (AMR) or changes in weight (as might be determined from a buoyant weight technique, described below), are important in the study of coral demography

Expressing growth as linear extension accurately captures the way that some corals grow; tabular, digitate, encrusting and laminar corals tend to grow in a predictable way (in ideal conditions), adding polyps to the periphery of the colony

(Stephenson & Stephenson 1933). Consequently, rates of radial extension should be largely independent of colony size (Figure 2.4B), whereas many other growth measurements (e.g., changes in the horizontal planar area of colonies, which is equivalent to the "shaded substratum area"; Jackson 1979) effectively decline with increases in colony size. Importantly, proportional increases in the horizontal planar area of corals decline rapidly with colony size (Figure 2.4A), potentially explaining why many early studies report that small colonies "grow" more quickly than larger ones (e.g., Stephenson & Stephenson 1933). As change in projected area summarises the amount of new reef 'space' that a coral colony occupies over a certain growth interval, it is particularly relevant, and widely used, for ecological studies of competition (e.g., Connell 1973, Connell et al. 1997) and population structure (e.g., Bak & Meesters 1999). Changes in planar area can be readily converted to change in AMR, to provide a, size-independent measure of linear growth.

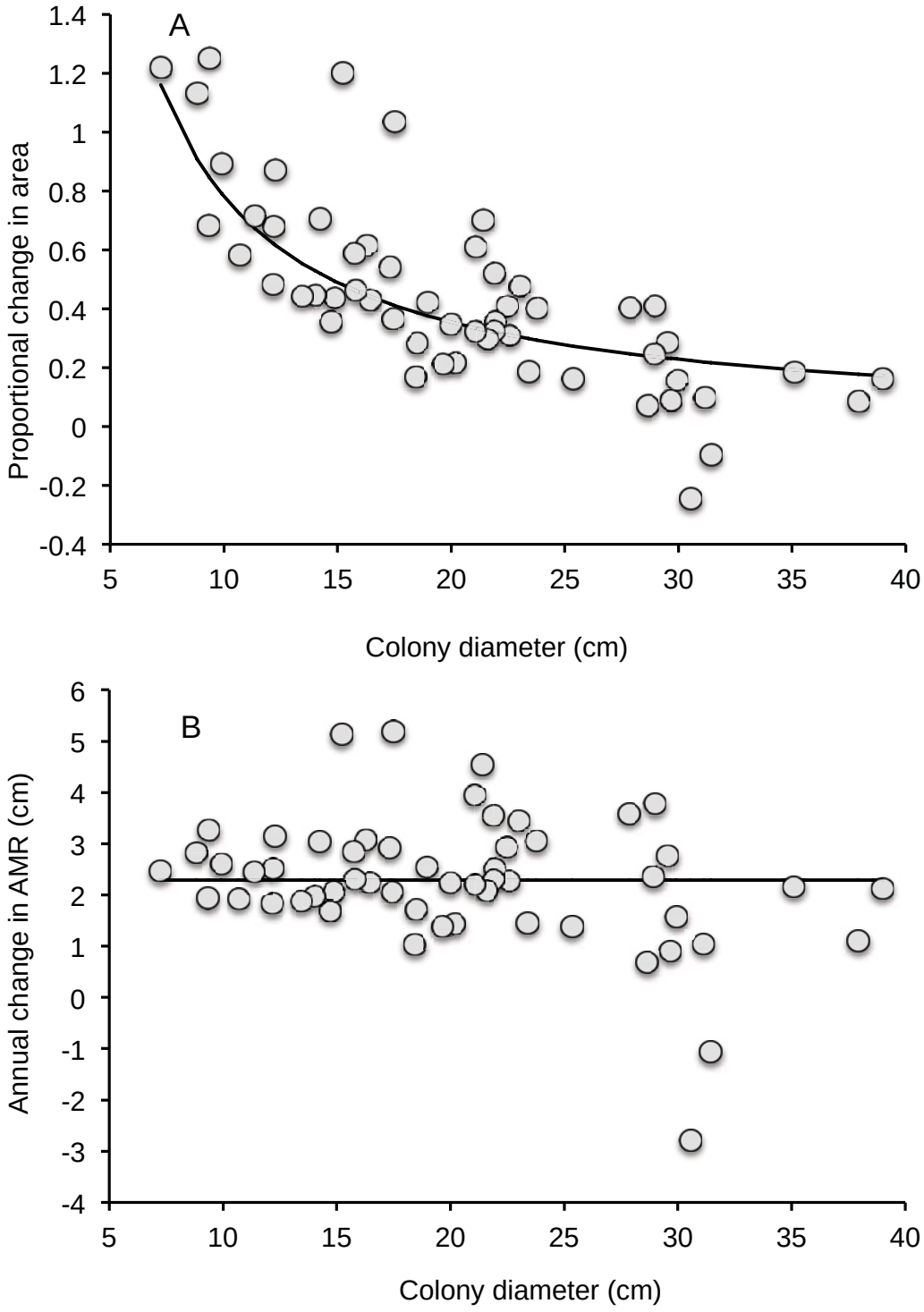

Figure 2.4. A) Proportional change in area and B) annual change in arithmetic mean radius (AMR) versus initial diameter for the digitate coral, *Acropora millepora*, measured over 524 days (April 2009 to October 2010) at the Keppel Islands, inshore Great Barrier Reef. Rather than representing the line-of-best fit, trend lines indicate the theoretical relationship assuming constant radial growth of 2.28 cm yr^{-1}.

Changes in the projected area of scleractinian corals are most commonly determined from planar photographs of individually tagged or identifiable colonies at repeated intervals (e.g., Madin et al. 2014). To do this, it is critical that a 2-dimensional scale bar is included within the photograph, that this scale bar is placed level with the upper surface of the colony, and that the image is recorded with a camera held in a fixed position with the focal plane parallel to the colony surface. The projected area at each time point is estimated by reference to the scale bar. The AMR is then calculated from each image, and it is the change in the estimated radius (not absolute or proportional changes in projected area) that is used to quantify growth. While this process sounds simple there are a number of issues to consider in order to precisely and accurately estimate the projected area and linear extension from photographs, including i) barrel distortion (a lens effect that causes images to be distorted in shape) that can lead to underestimates of projected area (especially for larger colonies) but can be corrected based on the make and model of the camera used, ii) differences in the placement of the scale relative to the surface of the colony; for example, if the scale in one image sits above the surface of the colony and is flush with the surface of the colony in the next image, the second area estimate will be larger, iii) differences in the focal distance for successive photographs of the same colony, which is often corrected by attaching a measuring rod to the camera housing to maintain a fixed focal length , and iv) errors associated with changes in perspective, whereby only photographs taken from directly above and approximately parallel to the surface of the colony will provide accurate estimates of projected area.

The main advantage of estimating rates of linear extension from projected colony area is that colony area is an important determinant of colony fate and fitness, influencing fecundity (Babcock 1991, Hall & Hughes 1996) and probability of

mortality (Madin et al. 2014). There is likely to be a strong positive relationship between skeletal extension rates of corals measured using direct estimates of linear extension and AMR, but direct estimates will not effectively capture negative growth (Anderson K unpublished data, Figure 2.5). Conversely, AMR aggregates positive (vegetative growth) and negative growth (injury and partial mortality), providing an ecologically relevant measure of realized growth.

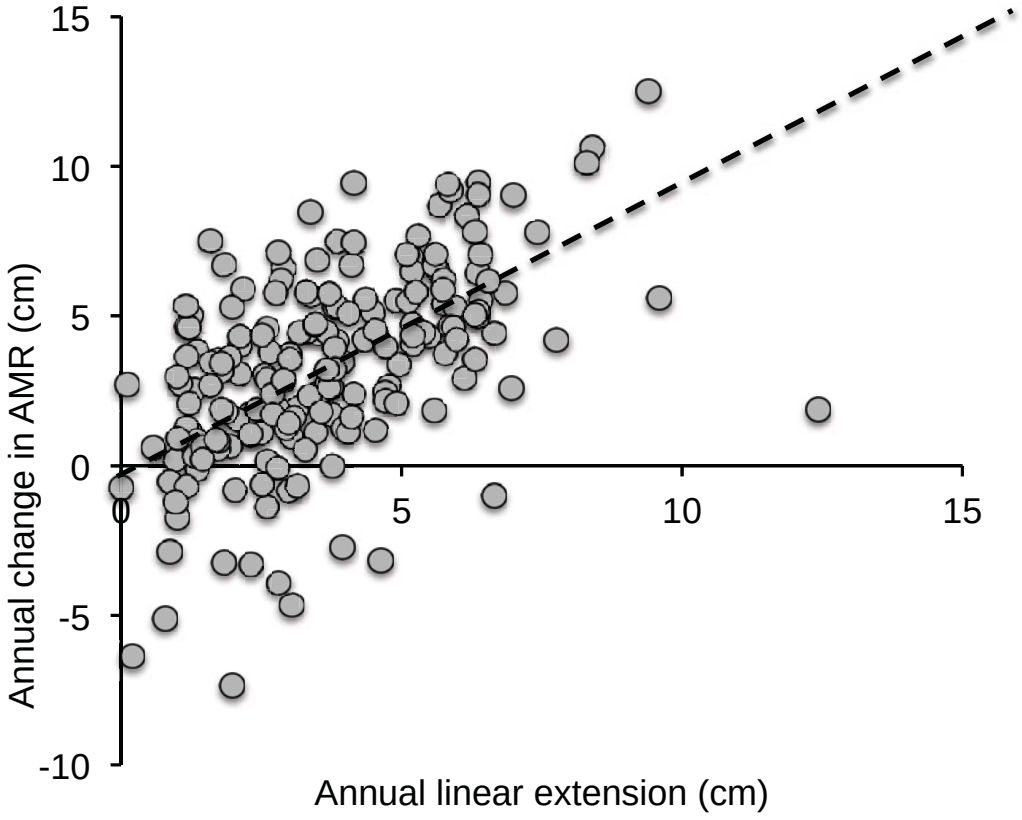

Figure 2.5. Relationship between linear extension and change in arithmetic mean radius (AMR) for *Acropora hyacinthus* on the Great Barrier Reef. Direct estimates of linear extension were derived by placing tags close (within 5 cm) to the circumference of the colony and recording change in the minimum distance from the tag to the circumference after one year. AMR was calculated based on change in projected area determined from photographs of each colony taken one year apart (Unpublished data Anderson K).

Measuring colony area also allows simultaneous exploration of the size structure of coral populations, and temporal changes in size structure have provided important insights into aspects of coral demography, such as population regulation (Bak & Meesters 1999). It is not clear, however, whether estimates of coral growth derived from projected area are comparable among corals with different growth forms. Changes in the area of benthos occupied by coral colonies is considered robust for comparing among corals that have a generally circular projected area and tend to grow primarily in the horizontal plane (e.g., digitate, corymbose and tabular *Acropora*, encrusting corals and massive corals like some *Porites*). However, whether it is possible to derive meaningful estimates of growth from the projected area of colonies with complex shapes (e.g., arboresent *Acropora*), needs to be examined in more detail. Measurement of planar area also disregards vertical growth, which can be the main axis of growth for some corals (e.g., columnar corals) when not constrained by water depth. The relationship between growth rates measured from projected area and other measures of growth (e.g., direct measures of linear extension and calcification) is also unclear and rarely investigated. It is important to establish a common metric of coral growth when comparing corals with different growth forms (e.g., comparing strategies of energy allocation, Leuzinger et al. 2003; defining the functional role of coral species with respect to framework building, Wells 1957). It is clear, however, that many of the aforementioned methods and measures of changes in the physical dimensions of coral colonies (linear dimensions, area, and volume) are not directly comparable across all corals, and the most universal and broadly comparable measure of coral growth probably relates to change in weight or calcification.

2.4.2 Change in weight or calcification

As the growth of scleractinian corals is fundamentally dependent upon the deposition of calcium carbonate, change in weight is one of the most direct and unequivocal measures of coral growth. Moreover, measurements made directly in the currency of calcification (i.e., the mass of $CaCO_3$ accreted per unit time) relate directly to the stoichiometry of the mineral, and can be more easily compared among coral species and among different studies. Moreover, calcification (or the rate at which mass of $CaCO_3$ is added) can be equated to linear extension if gross colony morphology and skeletal porosity are known (see section on 'Calcification rates' below). Early measures of calcification relied on weighing freshly collected corals in air (Gardiner 1901, Finckh 1904), and this technique was still being used in the 1970s (Franzisket 1970). By the 1950s however, T.F. Goreau had pioneered the use of radioactive ^{45}Ca to measure $CaCO_3$ deposited by corals (Goreau 1959), although the difficulties of working with radioactive materials, the requirement for destructive sampling of the coral to complete the analysis, and environmental hazards associated with using radioactive isotopes *in situ* (Goreau & Goreau 1959), have limited adoption of this technique. Even now it is rarely used in coral biology (Marshall & Clode 2004, Al-Horani et al. 2007), though contemporary interest in coral calcification may renew attention to this valuable tool.

Measuring the weight of corals in air has the obvious and significant limitation of subjecting corals to prolonged aerial exposure. To avoid this problem, Bak (1973) weighed corals submerged in seawater and then estimated the dry weight of corals through *in situ* calibration with lead weights. Later, estimates of dry weight were calculated from 'buoyant weight' by Archimedes' Principle (Jokiel et al. 1978), accounting for the density of both seawater and the coral skeleton. Jokiel et al. (1978)

described several configurations of the buoyant weight technique in which resolutions of between 0.1 mg and 2 g could be attained with specimens ranging in weight between 10 g and 5 kg, respectively. Spencer Davies (1989) published further refinements in the buoyant weight technique, making use of electronic top loading balances, and considering the effects of tissue weight on the estimates of skeletal weight. Using this method, Spencer Davies (1989) championed a non-destructive tool with 1% accuracy and a temporal resolution of 24 h with 3–4 cm long branches of *Porites porites*. Buoyant weighing is now regularly used for experimental measurement of growth of small coral fragments ('nubbins'; Birkeland 1976) and larger colonies *in situ* (Bak 1973, Herler & Dirnwöber 2011).

An alternative non-destructive technique to quantify calcification rates is to measure changes in the total alkalinity (A_T in units of µmol kg^{-1}) in the seawater immediately surrounding a coral (Smith 1973, Smith & Kinsey 1978). A_T describes the summed capacity of the ions in seawater to neutralize hydrogen ions (H^+), and is affected by at least 13 ions, including CO_3^{2-} (Chisholm & Gattusso 1991). Since calcification represents the withdrawal of CO_3^{2-} from the dissolved inorganic carbon (DIC) pool of seawater, it affects A_T, with the stoichiometry of the reaction equating 2 molar equivalents of A_T to 1 mol of $CaCO_3$ (Smith & Kinsey 1978, Chisholm & Gattuso 1991). Important advantages of the 'alkalinity anomaly technique' compared to alternative techniques for measuring coral calcification are that it can be used non-destructively in incubations lasting only a few hours (Smith & Kinsey 1978, Chisholm & Gattuso 1991), and does not require the addition of any reagents to seawater during incubations. The technique also enables comparison of day and night calcification rates and is particularly widely used in experimental studies of the effects of various environmental variables on calcification rates (e.g., Tentori &

Allemand 2006). Mostly, however, the alkalinity anomaly technique is used to measure community-level or ecosystem-level rates of calcification (Bates 2002, Hata et al. 2002, Dove et al. 2013). The greatest limitation when using alkalinity anomaly to quantify calcification of individual corals is the limited duration of such studies, whereby calcification is typically measured over much less than 24 hours, and often only during light or dark cycles, not both (Goreau & Goreau 1959).

2.4.3 Variability in coral growth

Despite difficulties in comparing measures of growth across the diverse group of scleractinians, rates of change in linear colony dimensions (linear or radial extension) vary greatly within and among coral taxa (Edmunds 2007, Morgan & Kench 2012). For example, Morgan & Kench (2012) recorded a more than 20-fold variation in extension rates among 12 different coral species in the Maldives, ranging from 2 mm yr^{-1} for the mushroom coral *Fungia fungites* up to 50 mm yr^{-1} for *Acropora nasuta*. It remains unclear to what extent these differences in linear or radial extension can simply be explained by differences in gross morphology, as opposed to inherent differences in energy allocation to growth and/or contrasting effects of calcification rates and skeletal density. As in many studies, Morgan & Kench (2012) concluded that colony morphology was the major determinant of inter-specific differences in skeletal extension rate, showing that branching corals (represented by *Acropora austera* and *A. muricata* (=*formosa*)) had average annual extension rates five times that of massive corals (represented by *Porites lobata*). Similarly, a multispecies comparison of corals in both the Atlantic and Pacific Oceans indicated high among-species variability with growth rates of around ~12 cm yr^{-1} for branching *Acropora* in the Pacific compared with ~0.5 cm yr^{-1} for massive species of *Porites* and *Favia* (Huston 1985). The problem, however, is that extension rates of branching *Acropora*

and massive *Porites* are not directly comparable, and are biased in favour of rapid growth of *Acropora* because extension rates for branching corals are measured along selected branches, which may or may not sum to changes in the mean solid radius of the colony. For massive corals however, extension rates are based on radial extension, which generally occurs across the entire surface of the colony, requiring significant production of calcium carbonate. Importantly, calcification rates may actually be higher for massive corals than for branching corals (Buddemeier & Kinzie 1976). At the very least, skeletons produced by massive corals are likely to persist much longer after the coral has died, directly contributing to the reef framework (Wells 1957).

2.4.4 Linear or radial extension

In preparing this review, a database comprising more than 740 records of coral growth was assembled from the literature, focussing on reported rates of extension and calcification. These data have global coverage, ranging from Lord Howe Island off south-eastern Australia to Kaneohe Bay in Hawaii, from the Red Sea across to the Eastern Pacific and throughout the Atlantic Ocean. Comparison of linear extension rates (mm yr^{-1}), quantified based on density banding patterns, alizarin red staining, direct tagging, photographic analysis, or a combination of these techniques (Table 2.4), reveals a unimodal distribution of growth rates with a geometric mean of approximately 16 mm yr^{-1} (Figure 2.6A). Gross colony morphology clearly influences annual extension rates; massive species accounted for 62% of the lowest quartile of growth records and branching species accounted for 92% of the upper quartile (Figure 2.6). Nevertheless, some massive species do attain high rates of radial extension, while extension rates of branching species are not uniformly high; massive species account for 5% of the upper 25% of growth records and branching

species account for 8% of the lower 25% of growth records (Figure 2.6). These data suggest that additional factors (e.g., environmental conditions and species-specific differences in the way $CaCO_3$ is accreted beneath the coral tissue layers) interact with gross colony morphology to influence annual extension. It is clear for example, that branching *Acropora* have higher rates of linear extension than other branching corals, but branching corals generally grow faster than massive corals regardless of whether comparison is made within (e.g., branching versus massive *Porites*) or among taxonomic groups (Figure 2.6).

Table 2.4. Annual extension rates reported for 148 coral taxa throughout the tropics, based on either direct measurements following tagging or staining, or changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods.

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
Acropora abrotanoides	Yap, Micronesia			125-130	Huston 1985
A. aspera	Java, Southeast Asia	1980-1981	Alizarin	34.95-52.65	Brown et al. 1985
	India, Central Indian Ocean	1988-1989	Alizarin	43.5	Suresh & Mathew 1995
A. austera	Maldives, Central Indian Ocean	2010-2011	Tagging	62.9	Morgan & Kench 2012
A. cerealis	Enewetak Atoll, Micronesia	1972-1976	Tagging	42.9	Stimson 1985
A. cervicornis	Jamaica, Western Caribbean	2000-2008	Digital imagery	102	Crabbe 2009
	Jamaica, Western Caribbean	2006-2009	Digital imagery	111.2	Crabbe 2010
	Eastern Caribbean and Atlantic	1979-1980	Alizarin	100	Gladfelter 1984
	Eastern Caribbean and Atlantic	1977	Alizarin	71	Gladfelter et al. 1978
	Bahamas, Northern Caribbean		Alizarin, Digital imagery	45-145	Glynn 1973
	Florida Keys, Northern Caribbean			40-45	Huston 1985
	Jamaica, Western Caribbean		Direct, Calipers	100-120	Lewis et al. 1968
	Florida Keys, Northern Caribbean	1961-1962	Tagging	109-110	Shinn 1966
	Eastern Caribbean and Atlantic	2001	Tagging	142.35	Torres et al. 2007
	Jamaica, Western Caribbean	1978	Alizarin	35-159	Tunnicliffe 1983
A. cytherea	Maldives, Central Indian Ocean		Direct, radial	58.1	Clark & Edwards 1995
	Solitary Islands, Australia	1994-1995	Alizarin	20.9	Harriott 1999
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	66.7-93.2	Jokiel & Tyler 1992
A. digitifera	Maldives, Central Indian Ocean	2010-2011	Alizarin	37.6	Morgan & Kench 2012
A. divaricata	Maldives, Central Indian Ocean		Direct, radial	41.5	Clark & Edwards 1995
A. elseyi	Waikiki aquarium, Polynesia	1992	Digital imagery	127	Atkinson et al. 1995
	GBR, Australia		Alizarin	38	Oliver 1985
A. eurystoma	Red Sea, Middle Eastern Seas	2001-2002	Alizarin	16.46-52.8	Bongiorni et al. 2003

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
A. florida	GBR, Australia		Alizarin	45	Oliver 1985
A. gemmifera	Maldives, Central Indian Ocean	2010-2011	Alizarin	24	Morgan & Kench 2012
A. granulosa	Egypt, Middle Eastern Seas	1998	Alizarin	5.9-9.24	Kotb 2001
A. hemprichii	Red Sea, Middle Eastern Seas	2011-2012	Tagging	4.75-15.04	Al-Hammady 2013
	Red Sea, Middle Eastern Seas	2001-2002	Tagging	9.6	Ebeid et al. 2009
A. humilis	Maldives, Central Indian Ocean		Direct, radial	19.3	Clark & Edwards 1995
	Enewetak Atoll, Micronesia	1972-1976	Direct, diameter	22.9	Stimson 1985
	Johnston Atoll, Polynesia	1976	X-radiography , growth ridges	9.6-23.7	Jokiel & Tyler 1992
A. hyacinthus	Maldives, Central Indian Ocean		Direct, radial	43.3	Clark & Edwards 1995
	Enewetak Atoll, Micronesia	1975-1978	Direct, diameter	99.3	Stimson 1985
A. intermedia (= *nobilis*)	GBR, Australia		Alizarin	41	Oliver 1985
A. lamarcki	Maldives, Central Indian Ocean	2010-2011	Alizarin	32.4	Morgan & Kench 2012
A. muricata (= *formosa*)	GBR, Australia	2009-2010	Alizarin	63	Browne 2012
	Thailand, Southeast Asia	1984-1986	Alizarin	36-68.4	Chansang et al. 1992
	Thailand, Southeast Asia	1981-1982	Tagging	80	Charuchinda & Hylleberg 1984
	Western Australia, Australia	1979-1980	Alizarin	37-42.9	Crossland 1981
	GBR, Australia	1985	Alizarin	40.15	Dennison & Barnes 1988
	Western Australia, Australia	1979-1980	Alizarin	52-79	Harriott 1998
	Sri Lanka, Central Indian Ocean	1997-1998	Tagging	117.54-120.96	Jinendradasa & Ekarame 2000
	Maldives, Central Indian Ocean	2010-2011	Tagging	58.5	Morgan & Kench 2012
	Guam, Micronesia	1976-1977	Alizarin	33	Neudecker 1981
	GBR, Australia		Tagging	52.8	Oliver 1984
	GBR, Australia		Alizarin	71.3	Oliver 1985

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	GBR, Australia	1981-1982	Alizarin	80-166	Oliver et al. 1983
	Western Australia, Australia	1982-1983	Alizarin, Tagging	137	Simpson 1988
	India, Central Indian Ocean	1988-1989	Tagging	80.5	Suresh & Mathew 1993
A. nasuta	Maldives, Central Indian Ocean	2010-2011	Alizarin	52.8	Morgan & Kench 2012
	Enewetak Atoll, Micronesia	1976-1977	Direct, diameter	39.2	Stimson 1985
A. palmata	Eastern Caribbean and Atlantic	1971-1973	Tagging	88	Bak 1976
	Eastern Caribbean and Atlantic	1977-1978	Tagging	88	Bak 1983
	Eastern Caribbean and Atlantic	2002-2004	Tagging	74-90	Bak et al. 2009
	Jamaica, Western Caribbean	2000-2008	Digital imagery	71	Crabbe 2009
	Jamaica, Western Caribbean	2006-2009	Digital imagery	65	Crabbe 2010
	Jamaica, Western Caribbean	2005-2012	Digital imagery	62.5	Crabbe 2013
	Eastern Caribbean and Atlantic	1977	Alizarin	47.3-99.3	Gladfelter et al. 1978
	Florida Keys, Northern Caribbean			25-40	Huston 1985
	Florida Keys, Northern Caribbean	1992-1996	Digital imagery	69	Lirman 2000
A. pharaonis	Red Sea, Middle Eastern Seas	2001-2002	Tagging	14.7	Ebeid et al. 2009
A. prolifera	Eastern Caribbean and Atlantic	1977	Alizarin	59.2-81.8	Gladfelter et al. 1978
	Florida Keys, Northern Caribbean			37	Huston 1985
A. pulchra	Waikiki aquarium, Polynesia	1992	Digital imagery	206	Atkinson et al. 1995
	Yap, Micronesia			101-172	Huston 1985
	Philippines, Southeast Asia	1980-1981	Tagging	166	Yap & Gomez 1985
A. robusta	Solitary Islands, Australia	1994-1995	Alizarin	22.4	Harriott 1999
	GBR, Australia		Alizarin	55	Oliver 1985
A. solitaryensis	Solitary Islands, Australia	1994-1995	Alizarin	16.7	Harriott 1999
A. spicifera	Western Australia, Australia	1990	Direct, crest to crest	104.2-123.6	Stimson 1996
Acropora spp.	Lord Howe Island, Australia	2010-2011	Alizarin, Tagging	42.42-62.04	Anderson et al. 2012
	Samoa, Polynesia	1917-1920	Digital imagery	30-76	Mayor 1924

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
A. valenciennesi	Sulawesi, Southeast Asia	2001-2002	Tagging	71-333	Crabbe & Smith 2005
A. valida	Solitary Islands, Australia	1994-1995	Alizarin	23.6	Harriott 1999
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	45	Jokiel & Tyler 1992
A. yongei	Lord Howe Island, Australia	1994-1995	Alizarin	49.4	Harriott 1999
	Western Australia, Australia	1991-1992	Alizarin	69.3	Marsh 1992
Agaricia agaricites	Eastern Caribbean and Atlantic	1971-1972	Tagging	24	Bak 1976
	Eastern Caribbean and Atlantic	1981	X-radiography	1.6-1.7	Hubbard & Scaturo 1985
	Jamaica, Western Caribbean	1977-1978	Alizarin, Digital imagery	4.5-6.5	Hughes & Jackson 1985
	Jamaica, Western Caribbean	1985	X-radiography	0.8-1.6	Huston 1985
	Eastern Caribbean and Atlantic	1974-1975	Alizarin, X-radiography	3.5-4.8	Stearn et al. 1977
A. lamarcki	Jamaica, Western Caribbean	1977-1978	Alizarin, Digital imagery	4.5-5.5	Hughes & Jackson 1985
Agaricia spp.	Jamaica, Western Caribbean	2000-2008	Digital imagery	2.47	Crabbe 2009
Astrea (= *Montastraea*) *curta*	Lord Howe Island, Australia	1994-1995	X-radiography, Alizarin	2.5-2.7	Harriott 1999
Astreopora myriophthalma	Enewetak Atoll, Micronesia	1972	X-radiography	7.5-13	Buddemeier et al. 1974
Balanophyllia europaea	Palinuro, Mediterranean	2003-2005	Annual bands, CT Scan	0.96-1.49	Goffredo et al. 2009
Cladocora caespitosa	Adriatic Sea, Mediterranean	2002	X-radiography	3.46	Kružić et al. 2012
Coelastrea (= *Goniastrea*) *aspera*	GBR, Australia	1982-1984	X-radiography	3.9-4.1	Babcock 1988/1991
Colpophyllia natans	Jamaica, Western Caribbean	2000-2008	Digital imagery	6.34	Crabbe 2009

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	Jamaica, Western Caribbean	1985	X-radiography	9.2-10.5	Huston 1985
Cyphastrea ocellina	Hawaiiian Archipelago, Polynesia	1987	Alizarin	4.145	Romano 1990
C. serailia	Lord Howe Island, Australia	1994-1995	X-radiography, Alizarin	2.6-3.4	Harriott 1999
	Australia		X-radiography	7.2-10.4	Roberts & Harriott 2003
Dendrogyra cylindrus	Florida Keys, Northern Caribbean	1994-1995	Direct, vertical	20	Hudson & Goodwin 1997
Diploastrea heliopora	Red Sea, Middle Eastern Seas	2008	CT Scan	1.8	Cantin et al. 2010
	Vanuatu, Melanesia		X-radiography	2-5	Corrège et al. 2004
Diploria labyrinthiformis	Jamaica, Western Caribbean	2000-2008	Digital imagery	4.33	Crabbe 2009
	Northern Caribbean	1973	X-radiography	3.6	Dodge & Thomson 1974
	Florida Keys, Northern Caribbean	1948-1982	X-radiography	3.5	Ghiold & Enos 1982
	Eastern Caribbean and Atlantic	1981	X-radiography	3.3-4.6	Hubbard & Scaturo 1985
	Bermuda, Northern Caribbean	1990	X-radiography	3.25	Logan & Tomascik 1991
	Bermuda, Northern Caribbean	1991	X-radiography	3.71	Logan et al. 1994
Dipsastraea (= *Favia*) *pallida*	Lord Howe Island, Australia	1994-1995	X-radiography, Alizarin	3.3-4.6	Harriott 1999
	Enewetak Atoll, Micronesia	1979	X-radiography	5.7	Highsmith 1979
Dipsastraea (= *Favia*) *speciosa*	Enewetak Atoll, Micronesia	1972	X-radiography	4.5-8.5	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1971	X-radiography	4.6	Knutson et al. 1972
	Japan, Southeast Asia	1966-2007	X-radiography	6.6	Seo et al. 2013
Favia sp.	Maldives, Central Indian Ocean		Direct, radial	7.5	Clark & Edwards 1995
	Sulawesi, Southeast Asia	2001-2002	Tagging	2.86-12.73	Crabbe & Smith 2005
	Sulawesi, Southeast Asia		Digital imagery	8.27	Crabbe et al. 2006

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
Favites sp.	Maldives, Central Indian Ocean		Direct, radial	9.6	Clark & Edwards 1995
Fungia fungites	Enewetak Atoll, Micronesia	1972	X-radiography	10-12	Buddemeier et al. 1974
	Maldives, Central Indian Ocean	2010-2011	Alizarin	2	Morgan & Kench 2012
Gardineroseris planulata	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	10.4	Guzmán & Cortés 1989
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin	6.1	Manzello 2010
Goniastrea (= *Favia*) *stelligera*	Enewetak Atoll, Micronesia	1972	X-radiography	8-12	Buddemeier et al. 1974
Goniastrea edwardsi (= *parvistella*)	Enewetak Atoll, Micronesia	1972	X-radiography	10-12.5	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1950-1971	X-radiography	12.5	Knutson et al. 1972
G. favulus	GBR, Australia	1982-1984	X-radiography	3.8-4.3	Babcock 1988/1991
G. retiformis	Enewetak Atoll, Micronesia	1972	X-radiography	6-9	Buddemeier et al. 1974
G. retiformis	Enewetak Atoll, Micronesia	1979	X-radiography	6.8	Highsmith 1979
cont.	Enewetak Atoll, Micronesia	1971	X-radiography	7.8	Knutson et al. 1972
Heliofungia actiniformis	Indonesia, Southeast Asia	2005-2006	Alizarin	5.7	Knittweis et al. 2009
Herpolitha limax	Enewetak Atoll, Micronesia	1972	X-radiography	10	Buddemeier et al. 1974
Hydnophora microconos	Enewetak Atoll, Micronesia	1972	X-radiography	11.5	Buddemeier et al. 1974
	Maldives, Central Indian Ocean	2010-2011	Alizarin	6.3	Morgan & Kench 2012
Isopora cuneata	Lord Howe Island, Australia	2010-2011	Alizarin, Tagging	17.15-21	Anderson et al. 2012
Leptastrea purpurea	Maldives, Central Indian Ocean	2010-2011	Alizarin	1.8	Morgan & Kench 2012
Lithophyllon (= *Fungia*) *concinna*	GBR, Australia		Alizarin	3.6-11.3	Oliver 1985
Lobactis (=	Hawaiiian Archipelago, Polynesia		Direct	4.6-16.4	Edmondson 1929

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
Fungia) *scutaria*					
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	5.9-10.3	Jokiel & Tyler 1992
Lophelia pertusa	Gulf of Mexico, Northern Caribbean	1979-2013	Digital imagery	19.9	Larcom et al. 2014
Madracis mirabilis	Jamaica, Western Caribbean		Tagging	22	Bruno & Edmunds 1997
Meandrina meandrites	Jamaica, Western Caribbean	2000-2008	Digital imagery	1.22	Crabbe 2009
Merulina ampliata	Singapore, Southeast Asia	1999-2000	Alizarin	10.2-24.6	Dikou 2009
Merulina sp.	Western Australia, Australia	1990	Direct, crest to crest	17.2-29.3	Stimson 1996
Millepora tenera	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	18.5	Jokiel & Tyler 1992
Montastraea cavernosa	Jamaica, Western Caribbean	2000-2008	Digital imagery	6.45	Crabbe 2009
	Belize, Western Caribbean		X-radiography	4.36	Highsmith et al. 1983
Montipora aequituberculata	GBR, Australia	2009-2010	Alizarin	29	Browne 2012
M. capitata	Hawaiiian Archipelago, Polynesia	1996-1997	Alizarin	25.2-42.7	Grottoli 1999
	Hawaiiian Archipelago, Polynesia		Alizarin	26.51	Rodgers et al. 2003
	Hawaiiian Archipelago, Polynesia	1990	Direct, crest to crest	32.5	Stimson 1996
M. digitata	GBR, Australia	1980-1981	Alizarin	30.5	Heyward & Collins 1985
	Philippines, Southeast Asia	2005-2006	Tagging	33.8	Shaish et al. 2010
Montipora sp.	Sulawesi, Southeast Asia	2001-2002	Tagging	1.75-9.74	Crabbe & Smith 2005
	Sulawesi, Southeast Asia		Digital imagery	6.91	Crabbe et al. 2006
	Enewetak Atoll, Micronesia	1972-1978	Direct, diameter	21.7	Stimson 1985
	Western Australia, Australia	1990	Direct, crest to crest	40.3-51.8	Stimson 1996
M. verrilli	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	17.2	Jokiel & Tyler 1992

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
M. verrucosa	Hawaiiian Archipelago, Polynesia		Direct	14	Edmondson 1929
	Hawaiiian Archipelago, Polynesia	1983	Alizarin	16.45-29.2	Cox 1986
Mussismilia braziliensis	Brazil, Eastern Caribbean and Atlantic	1998-2004	Alizarin	8	Kikuchi et al. 2013
Orbicella (= *Montastraea*) *annularis*	Eastern Caribbean and Atlantic	1971-1972	Tagging	8	Bak 1976
	Eastern Caribbean and Atlantic		X-radiography	1.56-10.41	Baker & Weber 1975
	Eastern Caribbean and Atlantic	1990-1991	X-radiography	2-16	Bosscher & Meesters 1992
	Gulf of Mexico, Western Caribbean	1977-1991	X-radiography	8.7	Carricart-Ganivet & Merino 2001
	Carribean, Western Caribbean	1970-1979	X-radiography	8.6-8.9	Carricart-Ganivet 2004
	Mexico, Western Caribbean	1981-1995	X-radiography	8.2-9.1	Carricart-Ganivet et al. 2000
	Jamaica, Western Caribbean	2000-2008	Digital imagery	7.85	Crabbe 2009
	Western Caribbean	2000- 2001	Direct, vertical	4.8-6	Cruz-Piñón et al. 2003
	Eastern Caribbean and Atlantic	1970-1979	X-radiography	9.8	Dodge & Brass 1984
	Jamaica, Western Caribbean		X-radiography	6.2-8.8	Dodge et al. 1974
	Jamaica, Western Caribbean	1971-1972	Alizarin	1.54-6.68	Dustan 1975
	Eastern Caribbean and Atlantic	1987-1989	X-radiography	9.75	Eakin et al. 1994
	Eastern Caribbean and Atlantic	1977	Alizarin	6.6-8.3	Gladfelter et al. 1978
	Panama, Western Caribbean	1985	X-radiography	8	Guzmán et al. 1991
	Belize, Western Caribbean		X-radiography	6.34	Highsmith et al. 1983
	Eastern Caribbean and Atlantic	1981	X-radiography	0.7-11.9	Hubbard & Scaturo 1985
	Gulf of Mexico, Northern Caribbean	1888-1907	X-radiography	6.8-8.9	Hudson & Robbin 1980
	Florida Keys, Northern Caribbean	1928-1978	X-radiography	6.3-11.2	Hudson 1981

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	Florida Keys, Northern Caribbean	1986	X-radiography	8.3	Hudson et al. 1994
	Jamaica, Western Caribbean	1977-1978	Alizarin, Digital imagery	3-4.5	Hughes & Jackson 1985
	Florida Keys, Northern Caribbean			6	Huston 1985
	Jamaica, Western Caribbean	1985	X-radiography	2.8-12.2	Huston 1985
	Florida Keys, Northern Caribbean	1970	X-radiography	17	Knutson et al. 1972
	Jamaica, Western Caribbean	1995-1996	Alizarin, X-radiography	8.55	Mendes & Woodley 2002
	Jamaica, Western Caribbean	1994-1996	Alizarin, X-radiography	8.76	Mendes 2004
	Eastern Caribbean and Atlantic	1981-1982	X-radiography	7.56	Tomascik & Sander 1985
	Eastern Caribbean and Atlantic	1983	X-radiography	8.8-12.4	Tomascik 1990
	Curacao, Eastern Caribbean and Atlantic	1991-1993	X-radiography	5.35-11.58	van Veghel & Bosscher 1995
Orbicella (= *Montastraea*) *faveolata*	Mesoamerican reef, Western Caribbean	2006	Annual bands, CT scan	9.5	Carilli et al. 2010
	Mexico Caribbean, Western Caribbean	2000- 2001	Direct, vertical	6-7.2	Cruz-Piñón et al. 2003
	Florida Keys, Northern Caribbean	1960-2007	X-radiography	8.1	Flannery & Poore 2013
	Florida Keys, Northern Caribbean	1937-1996	X-radiography	7.9	Helmle et al. 2011
	Mexico, Western Caribbean	1835-2002	X-radiography	11.2	Horta-Puga & Carriquiry 2014
	US Virgin Is, Eastern Caribbean and Atlantic	1995-2006	X-radiography	8-12.6	Saenger et al. 2008
Orbicella (= *Montastraea*) *franksi*	Jamaica, Western Caribbean	2000-2008	Digital imagery	5.63	Crabbe 2009
	Bermuda, Northern Caribbean	1998-2001	X-radiography	2.3	Saenger et al. 2008
Oulophyllia crispa (= *aspera*)	Enewetak Atoll, Micronesia	1972	X-radiography	20-22	Buddemeier et al. 1974

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
Paragoniastrea (= *Goniastrea*) *australensis*	Lord Howe Island, Australia	1994-1995	X-radiography, Alizarin	2.8-2.9	Harriott 1999
	Peel Island, Australia		X-radiography	5.6	Roberts & Harriott 2003
Pavona clavus	Costa Rica, Eastern Tropical Pacific	1998-2000	Alizarin	6.1	Gateno et al. 2003
	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	9.6	Guzmán & Cortés 1989
	Costa Rica, Eastern Tropical Pacific	1996-1997	Alizarin, X-radiography	17.8	Jimenéz & Cortés 2003
Pavona clavus cont.	Panama, Eastern Tropical Pacific	2003-2006	Alizarin	9.8	Manzello 2010
	Gulf of Chiriqui/Panama, Eastern Tropical Pacific	1975-1979	X-radiography	9.3-13.2	Wellington & Glynn 1983
	Panama, Eastern Tropical Pacific	1978-1979	Alizarin	14.92-18.42	Wellington 1982
P. duerdeni	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	8.6-11.8	Jokiel & Tyler 1992
P. gigantea	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	8.3	Guzmán & Cortés 1989
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin	9.2	Manzello 2010
	Gulf of Panama, Eastern Tropical Pacific	1975-1979	X-radiography	8.5	Wellington & Glynn 1983
	Panama, Eastern Tropical Pacific	1978-1979	Alizarin	11.67-12.83	Wellington 1982
P. maldivensis	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	11-13.1	Jokiel & Tyler 1992
P. varians	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	3.5	Guzmán & Cortés 1989
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin	3.2	Manzello 2010
Pectinia alcicornis	GBR, Australia	1985	Alizarin	1.2	Oliver 1985
Platygyra	Western Australia, Australia	1963-1983	X-radiography	15-16	Simpson 1988

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
daedalea					
P. daedalea (= *rustica*)	Hawaiiian Archipelago, Polynesia	1971	X-radiography	22	Knutson et al. 1972
P. lamellina	Enewetak Atoll, Micronesia	1972	X-radiography	6.7-8	Buddemeier et al. 1974
P. sinensis	GBR, Australia	1982-1984	X-radiography	6.4-6.8	Babcock 1988/1991
Platygyra spp.	IndoPacific, IndoPacific	1974	X-radiography	4.9-12	Weber & White 1974
Plesiastrea versipora	South Australia, Australia		X-radiography	4.14	Burgess et al. 2009
Pleuractis (= *Fungia*) *granulosa*	Red Sea, Middle Eastern Seas	1992-1995	Direct, growth rings	3.4	Chadwick-Furman et al. 2000
Pocillopora acuta (= *bulbosa*)	GBR, Australia	1932	Direct	25	Manton 1932
	Lord Howe Island, Australia	2010-2011	Alizarin, Tagging	6.6-14.8	Anderson et al. 2012
P. damicornis	Western Australia, Australia	1979-1980	Alizarin	12.2-14.3	Crossland 1981
	Hawaiiian Archipelago, Polynesia	1929	Direct	13.9	Edmondson 1929
	Gulf of Panama, Eastern Tropical Pacific	1971-1972	Alizarin, Digital imagery	32-52	Glynn & Stewart 1973
	Panama, Eastern Tropical Pacific	1974		33.6-39.6	Glynn 1976
	Eastern Tropical Pacific	1971-1974	Alizarin	30.8-38.6	Glynn 1977
	Galapagos, Eastern Pacific		Alizarin	22.4	Glynn et al. 1979
	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	29.8-34.6	Guzmán & Cortés 1989
	Solitary Islands/Lord Howe Island, Australia	1994-1995	Alizarin	12.4-16.1	Harriott 1999
	Costa Rica, Eastern Tropical Pacific	1987-1999	Alizarin	38-66.8	Jimenéz & Cortés 2003
	Egypt, Middle Eastern Seas	1998	Alizarin	6.6-7.39	Kotb 2001

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin	27.8	Manzello 2010
	Hawaiiian Archipelago, Polynesia		Direct, radial	13	Maragos 1972
	Thailand, Southeast Asia	1983	Alizarin	14.29	Martin & Le Tissier 1988
	Guam, Micronesia	1976-1977	Alizarin	29	Neudecker 1981
	GBR, Australia		Alizarin	36.6-43.2	Oliver 1985
	Hawaiiian Archipelago, Polynesia	1987	Alizarin	16.4	Romano 1990
	Western Australia, Australia	1982-1983	Alizarin, Tagging	45	Simpson 1988
	Enewetak Atoll, Micronesia	1972-1976	Direct, diameter	26.4	Stimson 1985
	Western Australia, Australia	1989	Alizarin	9-15	Ward 1995
	Panama, Eastern Tropical Pacific	1978-1979	Alizarin	46.07-54.25	Wellington 1982
P. elegans	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	34.8	Guzmán & Cortés 1989
	Costa Rica, Eastern Tropical Pacific	1996-1997	Alizarin	41.2-52.1	Jimenéz & Cortés 2003
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin	27.4	Manzello 2010
P. eydouxi	Enewetak Atoll, Micronesia	1972	X-radiography	50	Buddemeier et al. 1974
	Costa Rica, Eastern Tropical Pacific	1996-1997	Alizarin	30.8	Jimenéz & Cortés 2003
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	50.4	Jokiel & Tyler 1992
	Samoa, Polynesia	1917-1920	Digital imagery	20-47	Mayor 1924
P. inflata	Costa Rica, Eastern Tropical Pacific	1996-1997	Alizarin	31.5	Jimenéz & Cortés 2003
P. ligulata	Hawaiiian Archipelago, Polynesia		Direct	14.5	Edmondson 1929
P. meandrina	Hawaiiian Archipelago, Polynesia		Direct	14.8	Edmondson 1929
	Costa Rica, Eastern Tropical Pacific	1996-1997	Alizarin	34.2-44.6	Jimenéz & Cortés 2003
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	23	Jokiel & Tyler 1992

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	Maldives, Central Indian Ocean	2010-2011	Alizarin	18.7	Morgan & Kench 2012
	Hawaiiian Archipelago, Polynesia		Alizarin	6	Rodgers et al. 2003
Pocillopora spp.	Samoa, Polynesia	1917-1920	Digital imagery	23-36	Mayor 1924
P. verrucosa	Maldives, Central Indian Ocean		Direct, radial	25.1	Clark & Edwards 1995
	Red Sea, Middle Eastern Seas	2006-2007	Alizarin	17.88	Mass & Genin 2008
	Red Sea, Middle Eastern Seas	2006-2007	Alizarin	37.6	Mass & Genin 2008
	Enewetak Atoll, Micronesia	1972-1976	Direct, diameter	37.2	Stimson 1985
Porites (branching)	Yap, Micronesia			8-10	Huston 1985
P. astreoides	Jamaica, Western Caribbean	1981-1982	Alizarin	3.1-7.3	Chornesky & Peters 1987
	Jamaica, Western Caribbean	2000-2008	Digital imagery	4.07	Crabbe 2009
	Jamaica, Western Caribbean	2006-2009	Digital imagery	4.25	Crabbe 2010
	Western Caribbean		Annual bands, CT Scan	3	Crook et al. 2013
	Mexico/Cuba, Western Caribbean	1997-2004	X-radiography	3.54-3.69	Elizalde-Rendón et al. 2010
	US Virgin Is, Eastern Caribbean and Atlantic	1977	Alizarin	3-8.9	Gladfelter et al. 1978
	Panama, Eastern Tropical Pacific	1985	X-radiography	5.25	Guzmán et al. 1991
	Belize, Western Caribbean		X-radiography	4.75	Highsmith et al. 1983
	US Virgin Is, Eastern Caribbean and Atlantic	1981	X-radiography	1.9-3.1	Hubbard & Scaturo 1985
	Jamaica, Western Caribbean	1977-1978	Alizarin, Digital imagery	7.8-8	Hughes & Jackson 1985
	Jamaica, Western Caribbean	1985	X-radiography	2.2-6.3	Huston 1985
	Florida Keys, Northern Caribbean			3.5-14	Huston 1985
	Bermuda, Northern Caribbean	1989	X-radiography	2	Logan & Tomascik 1991
	Barbados, Eastern Caribbean and Atlantic	1974-1975	Alizarin, X-radiography	5.9-6.5	Stearn et al. 1977

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
P. australiensis	Japan, Southeast Asia	1992-1994	X-radiography	12	Mitsuguchi et al. 2003
P. columnaris	Gulf of Eilat, Middle Eastern Seas	1986-1988	X-radiography	5.68	Klein & Loya 1991
P. compressa	Hawaiiian Archipelago, Polynesia	1983	Alizarin	29.2-32.85	Cox 1986
	Hawaiiian Archipelago, Polynesia	2003-2004	X-radiography	5.9	Domart-Coulon et al. 2006
	Hawaiiian Archipelago, Polynesia		Direct	7.3-10.8	Edmondson 1929
	Hawaiiian Archipelago, Polynesia		X-radiography	7.66-8.13	Grigg 1998
	Hawaiiian Archipelago, Polynesia	1996-1997	Alizarin	23.3-34	Grottoli 1999
	Hawaiiian Archipelago, Polynesia		Alizarin	18.22	Rodgers et al. 2003
P. cylindrica	Philippines, Southeast Asia	1994-1995	Alizarin	30.42	Custodio & Yap 1997
P. cylindrica	Philippines, Southeast Asia	2001-2002	Tagging	12.85	Dizon & Yap 2005
(= *andrewsi*)	Maldives, Central Indian Ocean	2010-2011	Alizarin	7.4	Morgan & Kench 2012
	Guam, Micronesia	1976-1977	Alizarin	25	Neudecker 1981
P. evermanni	Hawaiiian Archipelago, Polynesia		Direct	11.6	Edmondson 1929
P. furcata	Florida Keys, Northern Caribbean			9-22.8	Huston 1985
	US Virgin Is, Eastern Caribbean and Atlantic	1979-1980	Alizarin	53.3	Meyer & Schultz 1985
P. heronensis	Lord Howe Island, Australia	2010-2011	Alizarin, Tagging	9.91-21.29	Anderson et al. 2012
	Lord Howe Island, Australia	1994-1995	Alizarin	10.5	Harriott 1999
P. lichen	Maldives, Central Indian Ocean		Direct, radial	16.3	Clark & Edwards 1995
P. lobaba	GBR, Australia	1993	X-radiography	8-19	Alibert & McCulloch 1997
	GBR, Australia		X-radiography	7.6-18.8	Barnes & Lough 1989
	Enewetak Atoll, Micronesia	1972	X-radiography	7.8-11.5	Buddemeier et al. 1974
	Maldives, Central Indian Ocean		Direct, radial	12.1	Clark & Edwards 1995
	Java, Southeast Asia	1989-1994	X-radiography	11.7-16.3	Edinger et al. 2000
	Hawaiiian Archipelago, Polynesia		Direct	7.1	Edmondson 1929
	Mexico Caribbean, Western Caribbean	1995-2006	X-radiography	4.33	Elizalde-Rendon et al. 2010

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	Japan, Southeast Asia	1980-1993	X-radiography	5.3	Fallon et al. 1999
	Hawaiiian Archipelago, Polynesia		X-radiography	10.1	Grigg 1998
	Hawaiiian Archipelago, Polynesia	1885-2001	X-radiography	3.02-13.49	Grigg 2006
	Hawaiiian Archipelago, Polynesia	1996-1997	Alizarin	5.8-7.8	Grottoli 1999
	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	11.7	Guzmán & Cortés 1989
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	7.1	Jokiel & Tyler 1992
	Gulf of Eilat, Middle Eastern Seas	1986-1988	X-radiography	7.48	Klein & Loya 1991
	Maldives, Central Indian Ocean	2010-2011	Alizarin	14.8	Morgan & Kench 2012
	Philippines, Southeast Asia	1981	X-radiography	13	Pätzold 1984
	Hawaiiian Archipelago, Polynesia		Alizarin	8.07	Rodgers et al. 2003
	American Samoa, Polynesia	2004-2005	Alizarin	1.2-9.8	Smith et al. 2007
	Hawaiiian Archipelago, Polynesia		X-radiography	3-13	Grigg 1982
P. lutea	GBR, Australia	1993	X-radiography	Dec-15	Alibert & McCulloch 1997
	Thailand, Southeast Asia	1990-1991	Alizarin	9.33-24.99	Allison et al. 1996
	Gulf of Aqaba, Middle Eastern Seas	1990-1995	X-radiography	15.2	Al-Rousan et al. 2002
	Moorea, Polynesia	1801-1990	Core analysis, CT scan	10.9	Bessat & Buigues 2001
	Enewetak Atoll, Micronesia	1972	X-radiography	5-13.5	Buddemeier et al. 1974
	Thailand, Southeast Asia	1984-1986	Alizarin	11.1-24.3	Chansang et al. 1992
	Thailand, Southeast Asia	1982-1983	X-radiography	15.4-18.4	Charuchinda & Chansang 1985
	Maldives, Central Indian Ocean		Direct, radial	11.2	Clark & Edwards 1995
	Palmyra Island, Polynesia	1880-2000	X-radiography	20	Cobb et al. 2001
	Sulawesi, Southeast Asia	2001-2002	Tagging	3.98-15.26	Crabbe & Smith 2005
	Sulawesi, Southeast Asia		Digital imagery	9.76	Crabbe et al. 2006
	Hawaiiian Archipelago, Polynesia		Direct	11.6	Edmondson 1929

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	Gulf of Aqaba, Middle Eastern Seas		X-radiography, CT scan	3-8.4	Heiss 1995
	Enewetak Atoll, Micronesia	1979	X-radiography	7.6	Highsmith 1979
	Enewetak Atoll, Micronesia	1985	X-radiography	9-12	Hudson 1985
	Johnston Atoll, Polynesia	1976	X-radiography, growth ridges	7.8	Jokiel & Tyler 1992
	Enewetak Atoll, Micronesia	1971	X-radiography	13.5	Knutson et al. 1972
	Western Australia, Australia	1994	X-radiography	13	Müller et al. 2004
	Republic of Palau, Micronesia	1950-2008	X-radiography	17.73	Osborne et al. 2013
	Red Sea, Middle Eastern Seas	1991-2001	X-radiography	5.66	Rosenfeld et al. 2003
	Thailand, Southeast Asia	1984-1986	Alizarin, X-radiography	13.7-23.2	Scoffin et al. 1992
	Japan, Southeast Asia	2002-2008	X-radiography	3.41	Sowa et al. 2013
	Japan, Southeast Asia	1997-1998	X-radiography	7	Suzuki et al. 2000
	Thailand, Southeast Asia	2003-2005	Alizarin, X-radiography	15.31-21.59	Tanzil et al. 2009
	China, Southeast Asia	1980-2006	X-radiography	11.3	Zhao et al. 2014
P. mayeri	GBR, Australia	1993	X-radiography	13	Alibert & McCulloch 1997
P. nigrescens	Maldives, Central Indian Ocean		Direct, radial	17.8	Clark & Edwards 1995
P. nodifera	Red Sea, Middle Eastern Seas	1990-1995	X-radiography	11.2	Al-Rousan et al. 2002
P. porites	Florida Keys, Northern Caribbean			8.3-20	Huston 1985
	Jamaica, Western Caribbean	1987	Alizarin	13.3	Spencer Davies 1989
P. rus	Philippines, Southeast Asia	1994-1995	Alizarin	24.33	Custodio & Yap 1997
P. solida	GBR, Australia	1938-1982	X-radiography	7.2	Lough & Barnes 1990
Porites spp.	Gulf of Aqaba, Middle Eastern Seas	2011-2012	X-radiography	10.09	Al-Rousan & Felis 2013
	GBR, Australia		X-radiography	8.02-14.01	Barnes & Lough 1993
	GBR, Australia	1980-2003	X-radiography	13-15.1	Cantin & Lough 2014
	GBR, Australia	2003	X-radiography	12.8-15.2	Cooper et al. 2008
	GBR, Australia	2005	X-radiography	12.4-14.3	De'ath et al. 2009

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
	GBR, Australia	1981-2002	X-radiography, luminescent	7.1-16.6	D'Olivo et al. 2013
	Red Sea, Middle Eastern Seas	1971-1991	X-radiography	4.18-14.39	Heiss 1996
	GBR, Australia	1979-1986	X-radiography	12.9	Lough & Barnes 2000
	Indonesia, Southeast Asia	1979-1984	X-radiography	10	Maier et al. 2004
	Samoa, Polynesia	1917-1920	Digital imagery	17-44	Mayor 1924
	Japan, Southeast Asia		X-radiography	6.35	Sowa et al. 2014
	Thai-Malay Peninsula, Southeast Asia	1980-2010	X-radiography, luminescent	18.81	Tanzil et al. 2013
	Thailand, Southeast Asia	1989-1990	Alizarin, fluorescent bands	22.33	Tudhope et al. 1992
Psammocora haimiana (= *togianensis*)	Enewetak Atoll, Micronesia	1972	X-radiography	29-30	Buddemeier et al. 1974
	Enewetak Atoll, Micronesia	1971	X-radiography	29	Knutson et al. 1972
P. stellata	Hawaiiian Archipelago, Polynesia		Direct	5.7	Edmondson 1929
	Costa Rica, Eastern Tropical Pacific	1996-1997	Alizarin	9.5-18.7	Jimenéz & Cortés 2003
P. superficialis	Costa Rica, Eastern Tropical Pacific	1985-1987	X-radiography, Alizarin	6.2	Guzmán & Cortés 1989
	Peel Island/Wellington Point, Australia		X-radiography	2-2.5	Roberts & Harriott 2003
Pseudodiploria (= *Diploria*) *clivosa*	Florida Keys, Northern Caribbean			4-8.8	Huston 1985
	Eastern Caribbean and Atlantic	1987-1989	X-radiography	4.45	Eakin et al. 1994
	Panama, Eastern Tropical Pacific	1985	X-radiography	5.6	Guzmán et al. 1991
	Florida Keys, Northern Caribbean			3.5-10	Huston 1985
	Bermuda, Northern Caribbean	1991	X-radiography	3.33	Logan et al. 1994
Sandalolitha (= *Parahalomitra*) *robusta*	Enewetak Atoll, Micronesia	1972	X-radiography	12	Buddemeier et al. 1974
Seriatopora	Lord Howe Island, Australia	2010-2011	Alizarin, Tagging	19.49-19.53	Anderson et al. 2012

Coral Species	Location, Region	Sampling date	Methodology	Annual extension (mm yr^{-1})	Reference
hystrix	Lord Howe Island, Australia	1994-1995	Alizarin	16.7	Harriott 1999
	Enewetak Atoll, Micronesia	1972-1976	Direct, diameter	22.1	Stimson 1985
Siderastrea radians	Florida Keys, Northern Caribbean			1.5-5	Huston 1985
S. siderea	Belize, Western Caribbean	1995-2008	X-radiography	4.02	Castillo et al. 2011
	Jamaica, Western Caribbean	2000-2008	Digital imagery	7.47	Crabbe 2009
	Panama, Eastern Tropical Pacific	1991-1992	X-radiography	4.7	Guzmán & Thudhope 1998
	Panama, Eastern Tropical Pacific	1985	X-radiography	4.8	Guzmán et al. 1991
	Eastern Caribbean and Atlantic	1981	X-radiography	1.5-3.1	Hubbard & Scaturo 1985
	Florida Keys, Northern Caribbean			1.5-2.3	Huston 1985
	Florida Keys, Northern Caribbean	2010-2012	Alizarin, Buoyant weight	2.6	Kuffner et al. 2013
	Barbados, Eastern Caribbean and Atlantic	1974-1975	Alizarin, X-radiography	4.1-5.4	Stearn et al. 1977
Solenastrea hyades	North Carolina, Northern Caribbean		X-radiography	15	Moore & Krishnaswami 1972
Stephanocoenia sp.	Eastern Caribbean and Atlantic	1981	X-radiography	1.8	Hubbard & Scaturo 1985
	Jamaica, Western Caribbean		X-radiography	5	Moore & Krishnaswami 1972
Stylophora pistillata	Lord Howe Island, Australia	2010-2011	Alizarin, Tagging	11.62-20.6	Anderson et al. 2012
	Red Sea, Middle Eastern Seas	2001-2002	Alizarin	15.05-17.72	Bongiorni et al. 2003
	Red Sea, Middle Eastern Seas	2001-2002	Tagging	19.4	Ebeid et al. 2009
	Egypt, Middle Eastern Seas	1998	Alizarin	6.51-9.24	Kotb 2001
	Red Sea, Middle Eastern Seas	1989-1990	Alizarin	24.61	Liberman et al. 1995
Turbinaria frondens	Solitary Islands, Australia	1994-1995	Alizarin	14	Harriott 1999
T. mesenterina	GBR, Australia	2009-2010	Alizarin	11	Browne 2012

Among the branching morphologies, variation in branching pattern also influences growth rates, with annual extension being highest for the open branching (arborescent) and tabular *Acropora* (mean extension ± standard error 90 ± 6.3 mm and 73 ± 12.2 mm respectively, Figure 2.6). Species with more complex branching patterns, that have higher rates of secondary branching (caespitose, Figure 2.3), display greater inter-specific and inter-generic variation in growth rates. For the caespitose *Acropora*, growth rates varied in the range 38–127 mm yr^{-1} for a single species (*Acropora elseyi*) observed at Lizard Island (northern GBR, Oliver 1985) compared with the Waikiki aquarium in Oahu, Hawaii (Atkinson et al. 1995) suggesting that environmental conditions do influence extension rates. Columnar morphologies (i.e., species that form thick pillars with greater skeleton deposition per unit tissue) also grow slower, on average, than the arborescent forms. However, as for the caespitose morphologies, there is some evidence of a taxonomic contribution to inter-generic variation in growth, with columnar *Montastraea* and *Pavona* growing more slowly than other genera with similar morphology (Figure 2.6). The distinct difference in growth rates between corymbose and tabular *Acropora* is somewhat unexpected based on branching patterns alone. These branching morphologies are quite similar (Figure 2.3), wherein corymbose colonies have small branches that project upwards from densely calcified basal branches. However, tabular morphologies have shorter branchlets and, typically, a smaller base of attachment compared with the longer (and sometimes anastomosing) branchlets of the corymbose morphs (Wallace 1999). Evidently, species' investment in a broader base of attachment to the substratum, as evident in corymbose and digitate branching morphologies, as well as in massive and encrusting morphologies, is associated with lower annual extension rates of the colony (Figure 2.6).

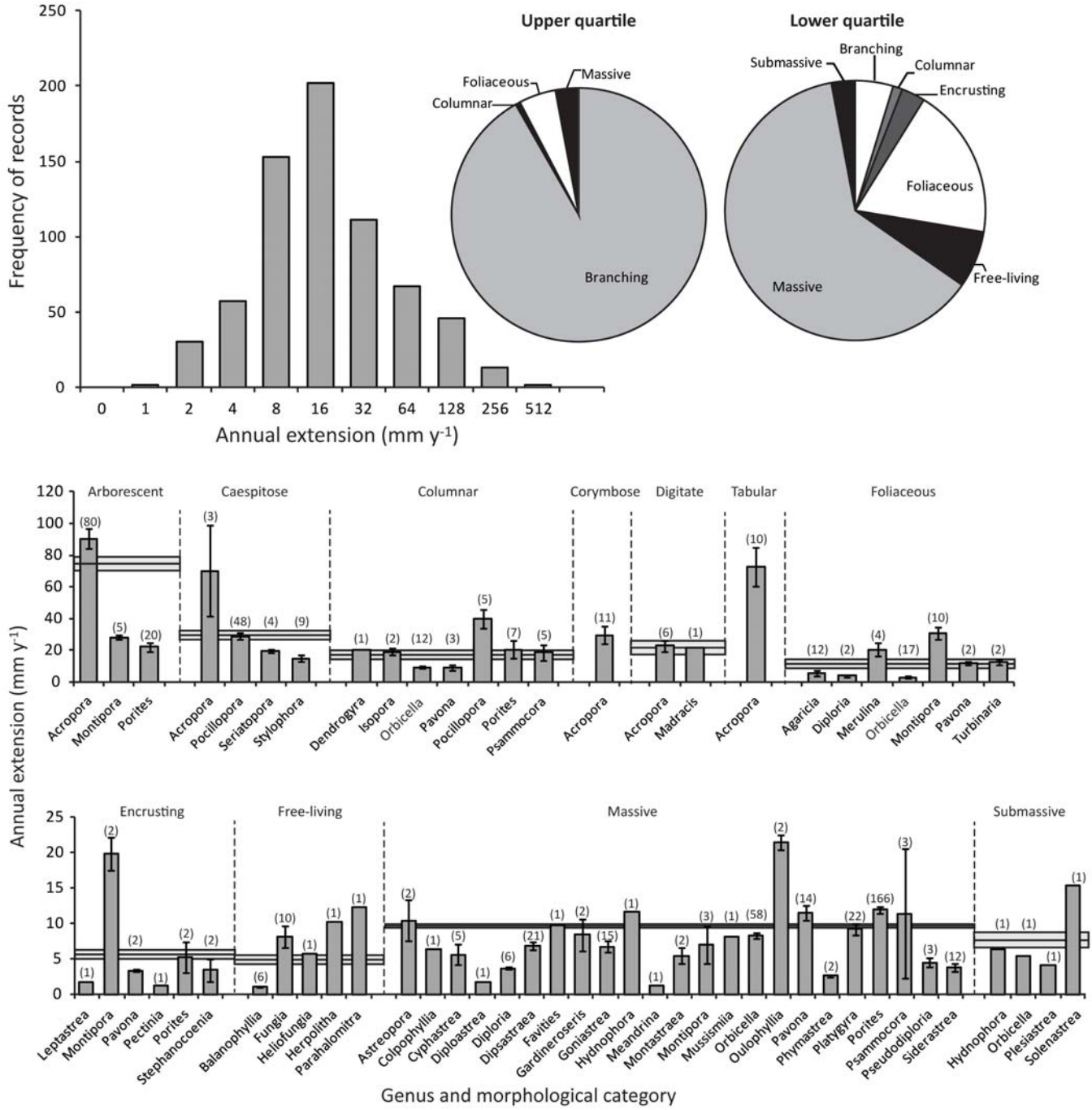

Figure 2.6. Variation in annual extension rates (mm) of corals with different gross morphology. Top panel shows the distribution of reported extension rates across all coral taxa (note the geometric scale, showing the lower limit of each extension rate class), with pie charts showing the representation of corals with different growth forms in the upper (faster growing taxa) and lower quartile (slower growing taxa). Lower panel shows mean (± SE) extension rates recorded for reef-building corals by genus and growth form. Numbers in brackets indicate the number of records for each genus. Grey horizontal bars indicate mean (± SE) extension rates for distinct growth forms (averaged across relevant taxa). No distinction is made between branch extension, radial extension, or AMR. Source data presented in Table 2.4.

2.4.5 Calcification rates

Pronounced differences in skeletal extension rates of scleractinian corals, as described above, are generally attributed to differences in: i) growth form and associated patterns of calcification (Jackson 1991), ii) the extent to which skeletons are porous or perforate (Hughes 1987), and iii) physical conditions (e.g., light and water motion). In contrast, calcification rates are considered to be broadly similar (or at least much less variable compared to linear extension) across different coral species and growth forms (Maragos 1972, Buddemeier & Kinzie 1976). However, small differences in mass-specific calcification rates can translate into large differences in extension (Buddemeier & Kinzie 1976), and marked inter-specific differences in calcification have been recorded in some studies. Goreau & Goreau (1959) recorded a three-fold difference in the calcification rates of branching versus massive corals, on the basis of measurements of calcium uptake by small, standardized fragments of 13 coral species in Jamaica. Considerable inter-specific variation in calcification rates has also been recorded with long-term measures (over 13 months; February 2010 to March 2011) of skeletal extension (Morgan & Kench 2012). Morgan & Kench (2012) reported calcification rates ranging from 0.22 g cm^{-2} yr^{-1} for *Leptastrea purpurea* (an encrusting coral) up to 2.96 g cm^{-2} yr^{-1} for *Acropora nasuta* (a corymbose coral). This 13-fold difference in calcification rate among sympatric species is at least equivalent to the inter-specific variation in reported rates of linear extension.

Comparisons of calcification rates (g cm^{-2} yr^{-1}) measured over more than one year and quantified based on either X-radiography for massive corals with preserved density banding, or directly estimated from the physical dimensions and density of skeletal material accreted within a known period, e.g., after staining (Table 2.5),

reveal a unimodal distribution of calcification rates with a geometric mean of 1.45 ± 0.99 g cm^{-2} yr^{-1} (mean ± standard deviation). Data in Morgan & Kench (2012), who reported both annual extension and calcification rates for 32 colonies across 12 species, indicates that there is an asymptotic relationship between species-specific estimates of average annual calcification with average annual extension (Figure 2.7). This shows that enhanced extension rates of *Acropora* corals are at least partially attributable to higher overall calcification rates, and not just their morphology or unique (perforate) structure of their skeletons. Nevertheless, the effect of gross morphology on calcification rates is complex and confounded by taxonomic differences. Among species of *Acropora*, arborescent growth forms (e.g., *A. palmata* and *A. muricata*) exhibit the highest rates of calcification (2.93 ± 1.12 g cm^{-2} yr^{-1}, mean ± SD), but are within the range of variation recorded for other more compact (corymbose and digitate) species of *Acropora* (Figure 2.8). For *Porites*, however, average annual calcification rates are much higher for massive species (e.g., *P. lobata* and *P. astreoides*) than branching species (e.g., *P. cylindrica*).

Table 2.5. Calcification rates (g cm^{-2} yr^{-1}) reported for scleractinain coral species throughout the tropics, based on either direct measurements follow tagging or staining, or changes in overall colony dimensions, retrospective measurements of density banding couplets using X-radiography, or a combination of methods.

Coral Species	Location, Region	Date Sampled	Method	Calc	Reference
Acropora austera	Maldives, Central Indian Ocean	2010-2011	Direct, water displancement	1.82	Morgan & Kench 2012
A. digitifera	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	2.29	Morgan & Kench 2012
A. gemmifera	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	1.42	Morgan & Kench 2012
A. lamarcki	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	1.83	Morgan & Kench 2012
A. muricata	GBR, Australia	2009-2010	Alizarin, water displacement	6.30	Browne 2012
(=*formosa*)	Maldives, Central Indian Ocean	2010-2011	Direct, water displancement	1.71	Morgan & Kench 2012
A. nasuta	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	2.96	Morgan & Kench 2012
A. palmata	Eastern Caribbean and Atlantic	1977	Staining, weight	0.82-1.89	Gladfelter et al. 1978
Balanophyllia europaea	Mediterranean, Mediterranean	2003-2005	CT, annual bands	0.10	Goffredo et al. 2009
Dipsastraea (=*Favia*) *pallida*	Enewetak Atoll, Micronesia	1979	X-radiography, mercury displacement	0.82	Highsmith 1979
Fungia fungites	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	0.41	Morgan & Kench 2012
Gardineroseris planulata	Panama, Eastern Tropical Pacific	2003-2006	Alizarin, buoyant weight	0.98	Manzello 2010
Goniastrea retiformis	Enewetak Atoll, Micronesia	1979	X-radiography, mercury displacement	1.16	Highsmith 1979
Hydnophora microconos	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	0.43	Morgan & Kench 2012
Leptastrea purpurea	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	0.31	Morgan & Kench 2012
Montipora aequituberculata	GBR, Australia	2009-2010	Alizarin, water displacement	1.5	Browne 2012
Orbicella (=*Montastraea*)	Mexico and Eastern Tropical Pacific	1977-1991	X-radiography, freezing method	1.39	Carricart-Ganivet & Merino 2001

Coral Species	Location, Region	Date Sampled	Method	Calc	Reference
annularis					
	Mexico and Eastern Tropical Pacific	1970-1990	X-radiography, freezing method	1.4-1.43	Carricart-Ganivet 2004
	Mexico and Eastern Tropical Pacific	1977-1995	X-radiography, freezing method	1.39-1.53	Carricart-Ganivet et al. 2000
	Eastern Caribbean and Atlantic		X-radiography	0.32-1.76	Baker & Weber 1975
	Eastern Caribbean and Atlantic	1970-1979	X-radiography, gamma densitometry	1.23	Dodge & Brass 1984
O. faveolata	Florida Keys, USA, Northern Caribbean	1937-1996	X-radiography, densitomentry	0.91	Helmle et al. 2011
	Mexico, Western Caribbean	1985-2009	X-radiography, gamma densitometry	0.97-1.51	Carricart-Ganivet et al. 2012
O. franksi	Mexico, Western Caribbean	1977-2005	X-radiography, gamma densitometry	0.84	Carricart-Ganivet et al. 2012
Pavona clavus	Guiri-Guiri, Pacific Costa Rica, Eastern Tropical Pacific	1998-2000	Alizarin, x-radiography	2.00	Gateno et al. 2003
	Gulf of Chiriqui, Eastern Tropical Pacific	1975-1979	X-radiography	0.11	Wellington & Glynn 1983
	Gulf of Panama, Eastern Tropical Pacific	1975-1979	X-radiography	0.17	Wellington & Glynn 1983
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin, buoyant weight	1.64	Manzello 2010
P. gigantea	Gulf of Panama, Eastern Tropical Pacific	1975-1979	X-radiography	0.12	Wellington & Glynn 1983
	Panama, Eastern Tropical Pacific	2003-2006	Alizarin, buoyant weight	1.35	Manzello 2010
P. varians	Panama, Eastern Tropical Pacific	2003-2006	Alizarin, buoyant weight	0.63	Manzello 2010
Pocillopora meandrina	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	1.33	Morgan & Kench 2012
Porites astreoides	Mexico and Eastern Tropical	1998-2009	X-radiography, gamma	0.79-	Carricart-Ganivet et al. 2012

Coral Species	Location, Region	Date Sampled	Method	Calc	Reference
	Pacific		densitometry	0.81	
	Mexico and Eastern Tropical Pacific	1998-2006	X-radiography, digitized image	0.52-0.71	Elizalde-Rendon et al. 2010
	Mexico and Eastern Tropical Pacific		Annual bands, CT Scan	0.48	Crook et al. 2013
P. cylindrica	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	0.44	Morgan & Kench 2012
P. lobata	American Samoa, Polynesia	2004-2005	Buoyant weight	0.19-1.39	Smith et al. 2007
	Java, Southeast Asia	1989-1994	X-radiography, buoyant weight	1.39-2.19	Edinger et al. 2000
	Maldives, Central Indian Ocean	2010-2011	Alizarin, water displacement	1.38	Morgan & Kench 2012
P. lutea	Aqaba, Middle Eastern Seas		X-radiography, CT scan	0.49-0.94	Heiss 1995
	Enewetak Atoll, Micronesia	1979	X-radiography, mercury displacement	1.07	Highsmith 1979
	Thailand, Southeast Asia	1990-1991	Alizarin, volumn displacement	0.6-1.4	Allison et al. 1996
	Thailand, Southeast Asia	2003-2005	Staining, X-radiography, buoyant weight	2.21-2.82	Tanzil et al. 2009
	Thailand, Southeast Asia	1984-1986	staining and core analysis	2.07-2.78	Scoffin et al. 1992
	Moorea, Polynesia	1801-1990	CT scan	1.25	Bessat & Buigues 2001
	Japan, Southeast Asia	2002-2008	X-radiography	0.54	Sowa et al. 2013
P. mayeri	GBR, Australia	1993	X-radiography	1.6-1.7	Alibert & McCulloch 1997
P. nodifera	Red Sea	1990-1995	X-radiography, gamma densitometry	0.92	Al-Rousan et al. 2002
Porites spp.	GBR, Australia	1980-2003	X-radiography, gamma densitometry	1.58-1.91	Cantin & Lough 2014
	GBR, Australia	1990-2005	X-radiography, gamma	1.51-	De'ath et al. 2009

Coral Species	Location, Region	Date Sampled	Method	Calc	Reference
			densitometry	1.76	
	Northern GBR, Australia	2003	X-radiography, gamma densitometry	1.59-1.96	Cooper et al. 2008
	Phuket Thailand, Southeast Asia	1989-1990	annual fluorescent bands	2.27	Tudhope et al. 1992
	GBR, Australia	1979-1986	X-radiography, gamma densitometry	1.63	Lough & Barnes 2000
	Rib Reef, Australia, Australia	1989-2002	X-radiography, gamma densitometry	1.51	Carricart-Ganivet et al. 2012
	GBR, Australia	1981-2002	X-radiography, water displacment	1.15-1.94	D'Olivo et al. 2013
	Thai-Malay Peninsula, Southeast Asia	1980-2010	X-radiography, gamma densitometry	2.08	Tanzil et al. 2013
Siderastrea siderea	Florida Keys	2010-2012	Alizarin, buoyant weight	0.99	Kuffner et al. 2013
Turbinaria mesenterina	GBR, Australia	2009-2010	Alizarin, water displacement	3.70	Browne 2012

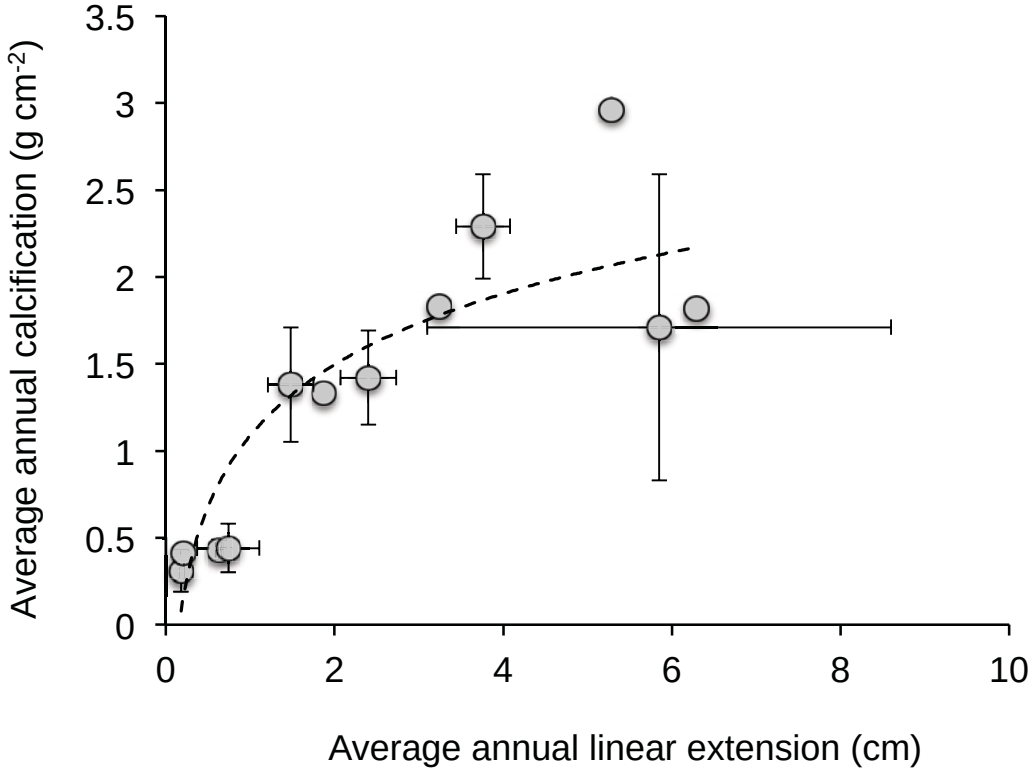

Figure 2.7. Relationship between average annual extension rate (cm) and average annual calcification rate (g cm^{-2}) for 12 coral species; *Leptastrea purperea*, *Fungia fungites*, *Hydonophora microconos*, *Porites cylindrica*, *P. lobata*, *Pocillopora meandrina*, *Acropora gemmifera*, *A. lamarcki*, *A. digitifera*, *A. nasuta*, *A. formosa* and *A. austera* (in order of mean extension). Redrawn from data in Morgan & Kench (2012)

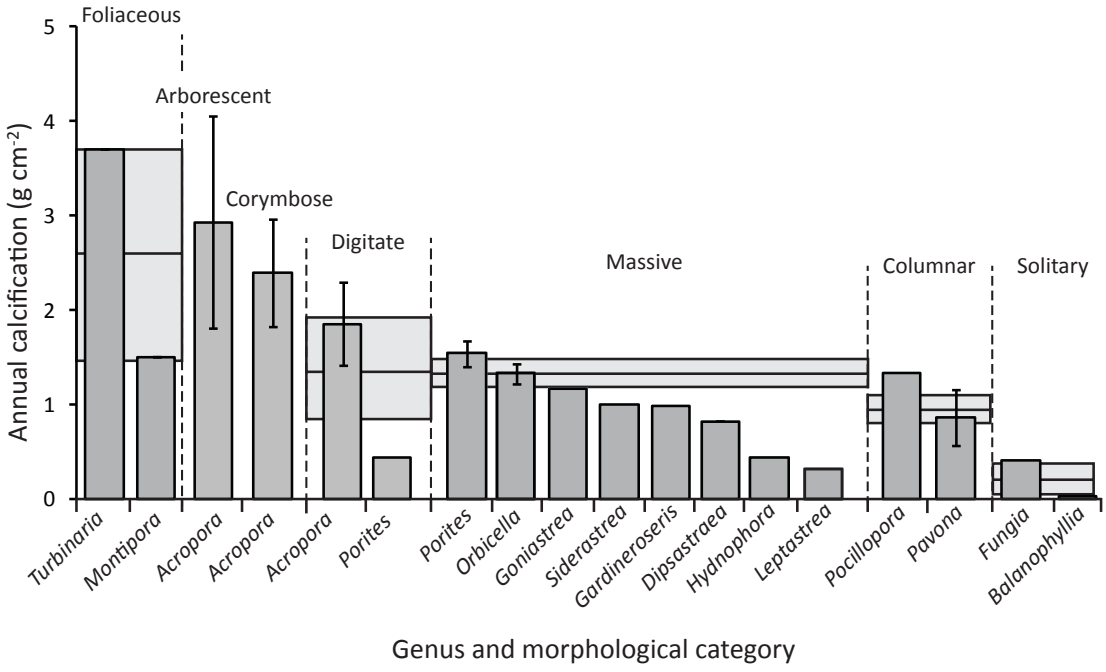

Figure 2.8. Average annual calcification rates (g cm^{-2}) based on either X-radiography for massive corals with preserved density banding, or directly estimated from the physical dimensions and density of skeletal material accreted within a known period, for branching and other corals. Grey horizontal bars indicate mean (± SE) calcification rates for distinct growth forms (averaged across relevant taxa). Source data presented in Table 2.5.

2.4.6 Spatial variation in coral growth

Spatial variation in coral growth is apparent at many different scales (reviewed by Buddemeier & Kinzie 1976), generally reflective of the broad range of environmental parameters that influence coral growth (see below), and the spatial scales over which these parameters vary. However, there is also considerable variability in growth rates among conspecific and sympatric corals (Goreau & Goreau 1959, Huston 1985, Babcock 1991, Clark & Edwards 1995), which is attributed to inherent differences in the growth and disturbance history of individual colonies. Competition, for example, both with other corals (Tanner 1997) and macroalgae (Tanner 1995) can substantially reduce fitness and growth rates of corals. Tanner (1997) showed that increases in the proportional area of *Acropora hyacinthus* subjected to experimentally induced contact with congeners were less than half (28–48% yr^{-1}) that of colonies located >15 cm away from potential competitors (95% yr^{-1}). Moreover, coral colonies within the same habitat and location are often subject to very different levels of predation and other chronic injuries (Pisapia et al. 2014), which can ultimately have an impact on growth (Cox 1986, Henry & Hart 2005).

Spatial gradients in the growth rates of corals are particularly apparent in relation to water depth, due to increased prevalence of faster growing species in shallow waters (Bak 1976), as well as fairly consistent declines in the linear extension and calcification rates of individual coral species with increasing depth (Huston 1985), reflecting the strong effect of light in promoting coral calcification (Allemand et al. 2011). Maximum growth rates for most coral species tend to occur in water <10 m depth (e.g., 10 m for *Orbicella* (=*Montastraea*) *annularis*, Barnes & Taylor 1973; <5 m for *Acropora cervicornis*, Gladfleter et al. 1978; 1–5m for *Porites astreoides*, Huston 1985), though Huston (1985) showed that the average annual growth rate of *Montastraea cavernosa* was significantly higher at 20 m than at 10 m

or 30 m, while *Agaricia agaricites* showed no change in growth rate with depth (from 0–30 m).

There are at least three mechanisms by which light intensity may enhance calcification. These mechanisms can operate through: i) a direct energetic pathway, asincreasing light generally increases photosynthesis and photosynthetically fixed carbon can be used as a respiratory substrate to support the energy costs of calcification; ii) an organic carbon pathway that provides the pre-cursors of the organic matrix necessary to build the skeleton; or iii) the removal of protons from the site of calcification to maintain pH conditions and stoichiometry favoring deposition of $CaCO_3$ (Allemand et al. 2011). In addition to these effects, the bulk density of coral skeletons can vary with depth, being generally higher in deeper water (Baker & Weber 1975), and also in response to turbulence to reduce the risks of breakage (Brown et al. 1985); together these effects modulate a trade-off between linear extension rates and skeletal density. In some species, the effects of depth-related declines in photosynthetic rate on calcification may be alleviated by photoadaptation (Dubinsky & Falkowski 2011) as increasing exploitation of a diverse array of heterotrophic modes of feeding in order to supplement carbon requirements. One notable consequence of depth-dependent changes in calcification rates of corals is the occurrence of pronounced changes in colony morphology (Barnes 1973, Rosenfeld et al. 2003, Anthony et al. 2005, Pandolfi & Budd 2008, Einbinder et al. 2009). Within a species, colonies typically become thinner, flatter and morphologically less complex with increasing depth, presumably to make maximal use of limited light availability (Anthony et al. 2005), or because calcification rates decrease due to declining light availability and, thus, declining photosynthesis rates. However, despite the intuitiveness of this hypothesis in many cases, the possibility that deep and shallow morphologies might be genetically distinct (i.e., sibling species (e.g., Barnes

1973 versus Knowlton et al. 1992) cautions against assuming that depth-dependent changes in calcification are the sole cause of such changes in phenotype.

Another important gradient over which coral growth is reported to vary is distance offshore, from nearshore reefs dominated by terrestrial influences to outer-edge reefs dominated by oceanic influences (Lough et al. 1999, Scoffin et al. 1992, Lough & Cooper 2011), which affects wave energy, light, turbidity, nutrient levels and salinity regimes together with pollution and other anthropogenic disturbances. Two conflicting patterns of changing growth characteristics along inshore to offshore gradients have been reported: i) greater linear extension rates in clearer, less turbid waters (e.g., *Orbicella* (=*Montastraea*) *annularis* in Jamaica, Aller & Dodge 1974, Dodge et al. 1974; *O. annularis* at Key Largo, Hudson 1981; *Porites* sp. in Indonesia, Tomascik et al. 1993; *Porites* sp. at Mayotte Island, Preiss et al. 1995); versus ii) greater rates of linear extension in more turbid, inshore waters (e.g., *Orbicella annularis* in the southern Gulf of Mexico, Carricart-Ganivet & Merino 2001; *Porites* sp. on the GBR, Lough et al. 1999; *Porites* sp. in Thailand, Scoffin et al. 1992). These contrasting patterns in growth characteristics along inshore to offshore gradients are likely due to the complexity associated with simultaneous spatial variation in a range of different environmental drivers (e.g., light, turbidity, wave action, and nutrients), which are likely to vary in importance among location and among coral species (Lough & Cooper 2011).

At larger spatial scales, there are apparent differences in the growth rates of corals with latitude, variously ascribed to large-scale gradients in light, temperature and also seawater chemistry (Grigg 1981, Logan & Tomascik 1991, Kleypas et al. 1999a). Anderson et al. (2015) reported that linear extension rates of *Acropora* and *Pocillopora* corals at Lord Howe Island (31.5°S), which is the world's southernmost coral reef, were one-third to a half of extension rates reported for tropical congeners. Examining massive *Porites lobata* across

~10° of latitude (from 19–29°N) in the Hawaiian Archipelago, Grigg (1981) found a significant inverse relationship between both linear extension and calcification rates and latitude. Grigg (1981) showed that extension rates in *P. lobata* decline 1.08 mm yr^{-1} per degree of latitude, and attributed these changes to changes in both light and temperature, which together accounted for ~54% of the variance in calcification rates. Similarly, Lough & Barnes (2000) found that both linear extension and calcification rates of massive *Porites* decreased with increasing latitude across 245 similar-sized colonies from 29 reefs on the GBR, which was attributed largely to changes in temperature along this gradient (12°S to 21°S). Although irradiance co-varies with SST across latitude, Lough & Barnes (2000) found that latitudinal variation in growth rates of massive *Porites* was most strongly correlated with SST.

2.4.7 Temporal variation in coral growth

Temporal variation in coral growth is apparent at scales ranging from diel patterns associated with switches from autotrophy to heterotrophy in light versus dark (e.g., Barnes & Crossland 1980), to strong seasonal patterns represented by the annual density bands apparent in many coral species (Table 2.1), and increasingly apparent long-term trends linked to global climate change (e.g., Bak et al. 2009). Buddemeier & Kinzie (1976) explicitly reviewed diurnal, weekly, monthly and annual variability in coral growth. Up until the mid-1970s, short- to intermediate-term variability in coral growth was well known, and discussion focussed on the merits of extrapolating short-term (hourly) measurements of calcification rates to provide meaningful longer-term estimates of radial extension. Interestingly, similar arguments still apply today, but the more important concern is the extent to which results from laboratory studies conducted under carefully controlled environmental conditions (and often over very short time frames) relate to field conditions where there are fluctuations in a wide range of environmental parameters. This distinction is particularly important when predicting

responses of corals to projected climate change, based on short-term experimental exposure to elevated temperatures and reduced pH (Pandolfi et al. 2011). The most significant change in research on coral growth since Buddemeier & Kinzie (1976) is the emerging focus on global climate change and long-term trends (interdecadal) in growth rates. Today, there is significant interest in documenting long-term trends in the growth of individual corals (Cooper et al. 2008, 2012, Edmunds 2007, De'ath et al. 2009, Cantin et al. 2010, Tanzil et al. 2013) or testing for interdecadal changes in the annual growth rates of coral species (not necessarily the same colonies) from the same location (Bak et al. 2009, Tanzil et al. 2009, Manzello 2010, Anderson et al. 2015), to establish effects of sustained changes in temperature, seawater chemistry, or both on coral growth.

Information on long-term trends (i.e., over decades - centuries) in growth rates of corals comes mostly from cores taken from long-lived massive corals (mostly *Porites*), which enables detailed analysis of long-term trends in growth of individual corals. In some studies, temporal trends in coral growth are determined from a single core or coral colony (Bessat & Buigues 2001, Saenger et al. 2009, Stortz & Gischler 2011), but it is unclear to what extent these patterns reflect general responses to changing environmental conditions, as opposed to patterns of growth specific to the individual colony. Hereafter, all data presented on long-term trends in coral growth, based on retrospective analysis of density banding in coral cores, come from studies that considered multiple colonies and often multiple cores per colony. Within such studies there are two distinct signals that point to the effects of climate-induced changes in temperature and seawater chemistry on coral growth; i) sustained changes in annual extension or calcification (Cooper et al. 2008), considered indicative of long-term changes in local environmental conditions (Lough & Cantin 2014), versus ii) interruptions in growth associated with distinct stress events (e.g., bleaching; Cantin et al. 2010, Cantin & Lough 2014).

Cooper et al. (2008) presented the first evidence that calcification rates of massive *Porites* may be declining, based on cores from 10 colonies located in nearshore environments in the northern GBR (14–18°S). They reported a decrease of ~20% in calcification rates from 1988 to 2003, and while they did not directly attribute observed declines in coral growth to either ocean warming or ocean acidification, they did note that these corals were regularly exposed to temperatures well beyond their thermal optima. Further south, sampling of massive *Porites* at three reefs (Pandora, Rib and Myrmidon) at increasing distances from the mainland revealed a significant decrease in calcification rates between 1961–1965 and 2001–2005 at both Pandora and Myrmidon, but not Rib (Lough 2008). Thereafter, De'ath et al. (2009, 2013) reported widespread and significant declines in calcification of corals with massive gross morphologies from 1990 to 2005, based on 328 *Porites* growth records from 69 reefs in the GBR. The magnitude of this decline was initially overestimated (~14%) due to errors in estimating the widths of outermost bands, but even after correcting for this, declines in coral growth during this period (11%) were still substantial, significant, and unprecedented in at least the past 400 years (De'ath et al. 2013). Again, the authors did not specifically attribute the decline to ocean warming or acidification but ruled out several local factors (e.g., declining water quality) that might otherwise account for recent declines in coral growth. Although critical of the findings of De'ath et al. (2009), D'Olivo et al. (2013) when examining recent growth rates in the central GBR, concluded that inshore growth rates have significantly declined (which they attributed to declining water quality) and that midshelf and offshore growth rates "appear to be undergoing a transition from increasing to decreasing rates of calcification, possibly reflecting the effects of CO_2 driven climate change" (p. 999).

While retrospective measures of coral growth in long cores of massive *Porites* tend to reveal contemporary declines (mostly since 1990) in annual extension and calcification, there are exceptions to this trend. For example, based on 27 *Porites* cores from six Western

Australian reefs at latitudes between 17–28°S, Cooper et al. (2012) reported no significant change in regional average calcification rates between 1900 and 2010. Rates of SST warming varied, however, between reef sites, being only ~0.02°C per decade in the northernmost Rowley Shoals and ~0.10°C per decade in the southernmost Houtman Abrolhos Islands. The rates of change in calcification also varied regionally and appeared to match the rates of SST warming. Only small changes in calcification occurred at sites of small SST warming whereas significant increases in calcification occurred at the two most southerly sites where warming was greatest. Massive *Porites* corals at Rowley Shoals and the Houtman Abrolhos Islands have unusually high calcification rates, especially given the relatively low temperatures at these locations. This suggests that the effects of ocean warming on coral growth may vary with latitude, and that corals on high latitude reefs may initially respond to increasing temperatures with increasing coral growth, as was previously suggested by Buddemeier & Kinzie (1976). Whether such increases in calcification can be sustained over longer time-frames (cf. GBR where calcification initially increased then declined, Lough & Barnes 2000) is debateable, especially given the 2011 thermal stress event that affected Western Australian coral reefs and resulted in significant coral bleaching (Wernberg et al. 2013, Feng et al. 2013).

Aside from sustained declines in coral growth rates, corals may respond to acute temperature stress events with a temporary decline in coral growth (Carilli et al. 2009, D'Olivo et al. 2013), especially after bleaching. Carilli et al. (2009), for example, examined cores taken from 92 colonies of *Orbicella* (=*Montastraea*) *faveolata* across the Mesoamerican Reef in 2006. The majority of colonies exhibited high-density stress bands associated with the 1998 bleaching event (Carilli et al. 2009). Moreover, most of the cores showed a decrease in linear extension that persisted for 2–8 years after the bleaching. This stress event, evident in the coral growth records, appeared to be unprecedented in the

previous 75–150 years at least (Carilli et al. 2010). Seemingly healthy colonies of *Diploastrea heliopora* colonies in the Red Sea also exhibited a distinct skeletal signature that could be linked to extreme temperatures in 1998 (Cantin et al. 2010). Annual average extension in the period 1998–2008 was 30% lower than in the period 1925–1997, and Cantin et al. (2010) concluded that further increases in local temperatures may lead to complete cessation of calcification within 30–60 years, assuming that thermal acclimation capacity of corals is limited (as indicated by Rodolfo-Metalpa et al. 2014).

Growth records from massive *Porites* in the central GBR also showed anomalies associated with the 1998 bleaching event. D'Olivo et al. (2013) reported a 40% reduction in linear extension rates of massive *Porites* after bleaching, which lasted for three years. Cantin & Lough (2014) also found distinct signatures of recent disturbances in cores of corals from the central GBR, including partial mortality and abrupt declines in linear extension and calcification rates, detected as abnormally narrow high-density bands, associated with both the 1998 and 2002 bleaching events. The occurrence and magnitude of these depressions in coral growth varied among sites and years, but all corals recovered and were growing at normal rates within four years. The extent to which growth of massive *Porites* colonies is disrupted (in duration and severity) following severe thermal stress is ascribed to individual differences in their thermal history (Castillo et al. 2011, 2012, Carilli et al. 2012). Carilli et al. (2012) showed that corals from sites with low temperature variability showed a 45% decline in linear extension and calcification rates and extensive partial mortality, whereas coral from sites with high inter-annual SST variability showed no partial mortality and only ~20% decrease in calcification and linear extension rates after bleaching.

For corals where the entire growth history is not preserved in the skeleton (e.g., most *Acropora* species) the only way to detect temporal changes in growth rates is to measure growth rates directly at specific intervals (e.g., Edmunds 2007, Bak et al. 2009). Not

surprisingly, there are few data on long-term changes in growth rates of branching corals. However, the data available suggest that branching corals are equally, if not more, susceptible to sustained changes in environmental conditions (Manzello 2010). For instance, Bak et al. (2009) reported a 7.2–10.7% reduction in linear growth of *A. palmata* from 1971–1973 to 2002–2004 in the Caribbean, which aside from acute disturbances (e.g., disease epidemics) might be partly due to ongoing declines in aragonite saturation of seawater, as was documented at nearby locations (Gledhill et al. 2008). At nearby, but offshore locations, the average annual SST had also increased 0.8°C from 1971–1973 to 2002–2004, but this was not considered to have influenced the temporal decline in coral growth (Bak et al. 2009). Similarly, Manzello (2010) attributed declines in skeletal extension of *Pocillopora damicornis* (0.9% yr^{-1}) from 1974 to 2006 in Pacific Panama to ocean acidification rather than increasing temperatures. Between 2004 and 2006, annual extension rates of six coral species (*P. damicornis*, *P. elegans*, *Pavona clavus*, *P. gigantea*, *P. varians*, and *Gardineroseris planulata*) were up to 53% lower than in the 1970s and 1980s in the same locations (Manzello 2010). In the Indo-Pacific, interdecadal declines in the average annual extension rates have been documented for *Acropora yongei* and *Pocillopora damicornis* (values in 2010/11 were 30% of that recorded in 1994/95), but growth rates of two other species (*Seriatopora hystrix* and *Porites heronensis*) had increased (albeit very slightly) over the same period (Anderson et al. 2015). Environmental drivers of these observed changes in the growth rates of reef-building corals are unclear, but it is notable that average annual SST has increased 0.15°C from 1994/5 to 2010/1 at Lord Howe Island. Also, declines in aragonite saturation are expected to impact high latitude locations first (Orr et al. 2005), and may already be limiting calcification of faster-growing corals at Lord Howe Island, as these are known to be adversely affected by changes in aragonite saturation (Fabricius et al. 2011).

2.5 Functional importance of coral growth

Investigating coral growth provides insight into how corals respond to changing environmental conditions, and how they allocate energy to alternative metabolic processes (Leuzinger et al. 2012, Madin et al. 2012). The size of colonies is an important determinant of the fate and fitness of individual colonies (e.g., Hughes & Jackson 1980, Hughes 1984, Hall & Hughes 1996), such that fundamental changes or differences in growth rates *should* influence population and community ecology. Declines in extension rates of newly settled corals (e.g., Albright et al. 2008) will almost certainly lead to increased rates of early post-settlement mortality (Babcock & Mundy 1996, Penin et al. 2010) by extending the time that individuals are exposed to size-specific agents of mortality, such as incidental predation by grazing fishes and physiological stress. However, the extent to which inter-specific variation in coral growth influences, for instance, the relative or absolute abundance of coral species is unclear (Margos 1972, Hughes 1984) and may warrant specific examination.

The specific role of coral growth in the function and performance of scleractinian corals may be difficult to discern simply by comparing demographic rates among the few well-studied species (Babcock 1991). Similarly in other systems (e.g., terrestrial plant systems), investigations into how species diversity and composition relate to ecosystem function have failed to produce general principles (Lawton 1999, Simberloff 2004, McGill et al. 2006), often attributed to the complexity and diversity of species-specific functional roles. To address this limitation, community ecologists are increasingly focussed on trait based approaches for comparing functional diversity among locations, habitats, and assemblages (e.g., McGill 2006). It is anticipated that functional diversity (rather than species richness) will provide much greater insights into ecosystem processes (Hooper et al. 2005, Cadotte et al. 2011), such as differences in resilience to environmental disturbances among habitats, locations and assemblages (Folke et al. 2004). Accordingly, there is a concerted push to

compile data on a wide range of species traits for scleractinian corals (Baird et al. 2009, Díaz & Madin 2011, Edmunds et al. 2011), largely with a view to understanding the selective effects of different disturbances (e.g., bleaching and disease) on the structure and function of coral assemblages. Functional analyses of scleractinian corals do, however, lag well behind that of many other groups of organisms (e.g., terrestrial plants).

2.5.1 Growth and functional classifications of reef corals

Coral species have been variously assigned to guilds (Fagerstrom 1991), functional groups (Murdoch 2007), and adaptive strategies (Darling et al. 2012) based on a range of different traits. However, growth rate is often the predominant trait used to distinguish, and categorise, scleractinian corals. Most recently, Darling et al. (2012) compared 11 traits across 143 species to distinguish various life-history strategies, which were broadly aligned with the three adaptive strategies (competitors, ruderals and stress-tolerators) proposed by Grime (1977). Aside from growth form (which in itself is linked to variation in growth rate, see Figure 2.6 and Figure 2.) the most influential trait distinguishing these groups was average annual growth rates, or more specifically annual extension rates (mm yr^{-1}). Darling et al. (2012) noted that both coral growth and skeletal density depend on environmental conditions, but did not explicitly test for potential biases related to spatial (geographic) variation in temperature, light, or any other environmental factors.

If growth-related traits are to be included in analyses of coral function(s), it is important to gain a better understanding of the functional relationships between coral growth and various environmental drivers. Such understanding has been achieved in plant ecology by measuring growth-related traits under controlled conditions (Grime & Hunt 1975) resulting in the quantification of comparative traits such as maximum potential growth rate, R_{max} (Evans 1972). For scleractinian corals, this requires: i) extensive laboratory-based trials to establish comparative growth rates under carefully controlled and standardised environmental

conditions, and ii) the establishment and analysis of a comprehensive trait database (see for example the LEDA Traitbase for Northwest European flora; Kleyer et al. 2008), which includes specific information about the location, timing and relevant environmental conditions for each estimate of coral growth. Environmental factors known to influence coral growth rates include temperature (Glynn & Stewart 1973, Weber & White 1974, Lough & Barnes 2000, Tanzil et al. 2009), depth/light (e.g., Oliver et al. 1983, Wellington 1982, Houlbrèque et al. 2003, Hoogenboom et al. 2010), prey availability (Wellington 1982), competition (Neudecker 1977), water flow (Nakamura & Yamasaki 2005, Schutter et al. 2010), and sedimentation (Rogers 1990, Crabbe & Smith 2005). If growth rate is considered to be an important functional and adaptive trait of scleractinian corals, then it is essential to establish the degree of intra- and inter-specific variation in coral growth rates across natural ranges for each of these environmental variables.

2.5.2 Growth versus abundance of scleractinian corals

The extent to which inter-specific differences in the growth rates of corals actually influence their patterns of abundance is rarely tested, and anecdotal observations are highly conflicting (e.g., Goreau & Goreau 1959 versus Maragos 1972). There are also no substantive data sets with which to relate spatially and temporally explicit measures of coral growth to variability in the relative abundance of different corals. This may be unnecessary if there are strong and consistent taxonomic differences in coral growth regardless of location (e.g., Figure 2.6). Inter-specific differences in the growth rates of corals can clearly play a role in structuring coral assemblages under certain conditions (e.g., Connell et al. 2004, Bode et al. 2012). It has been shown for example, that in some tidal pools fast-growing corals outcompete slower-growing corals (Connell et al. 2004) and thereby dominate the coral assemblage. However, there are also many factors that may moderate the outcomes of competitive interactions and prevent fast growing corals from monopolizing available space (Connell et al. 2004). The

question is whether stochastic and extrinsic processes (e.g., disturbance) generally obscure the role of specific traits in structuring populations and communities, or whether it is the diversity and complexity of traits that make it difficult to resolve the individual contribution of coral growth. The prevailing view among coral ecologists is that species composition is largely structured by disturbance, at least within contemporary reef environments (Karlson & Hurd 1993, Pandolfi 2002). Perhaps a more valid test of the importance of coral growth is, therefore, the extent to which growth affects the rate of recovery across different corals in the aftermath of major disturbances.

Rates of recovery for coral assemblages devastated by major disturbances depend on the relative contribuitions of recruitment versus growth of remanant corals (Connell et al. 1997, Halford et al. 2004, Linares et al. 2011). In the Indo-Pacific it is invariably fast-growing *Acropora* and *Pocillopora* species that contribute most to rapid increases in coral cover. Following localised bleaching in the central GBR in 2001/2 coral cover increased by up to 10% yr^{-1}, due to rapid increases in the cover of tabular *Acropora hyacinthus*, which was almost entirely attributable to growth of existing colonies (Linares et al. 2011). By 2010, the proportional cover of *Acropora* (relative to combined cover of all other reef-building corals) was much higher than it was immediately prior to the disturbance. The corollary of these results is that if all corals are severely depleted in cover, then recovery will be conditional upon recruitment and subsequent growth of new colonies, which will greatly extend the time (4–5 years) until regeneration of coral cover becomes apparent (e.g., Gilmour et al. 2013). However, even in these cases, fast-growing corals (e.g., *Acropora* and *Pocillopora*) will tend to make a disproportionate contribution to initial increases in total coral cover (e.g., Gilmour et al. 2013). Gilmour et al. (2013) showed that cover of *Acropora* spp. increased from <5% to >20% within a decade after catastrophic bleaching at Scott Reef, Western Australia, while there was negligible change in the cover of Poritidae during this period, though slow growing

corals would presumably recover given sufficient time. Interestingly, in the Caribbean, examples of reef recovery following catastrophic disturbances are becoming increasingly rare (Idjadi et al. 2006).

2.6 Environmental constraints on coral growth

Although scleractinian corals occur throughout the world's oceans (Dodds et al. 2009), tropical coral reefs only form under specific environmental conditions, which occur primarily in shallow, warm tropical waters (Kleypas et al. 1999a, Lough & Barnes 2000). Among the range of factors that vary with latitude, temperature plays a fundamental role in controlling rates of metabolic processes for all organisms due to increases in metabolism and enzymatic activity (e.g., Angilletta 2009). In general, rates of physiological processes, like respiration and calcification, display a non-linear threshold relationship with temperature (e.g., Pörtner 2002). Insolation is also an important driver of coral calcification because light availability influences photosynthesis by symbiotic algae which, in turn, promotes calcification by both i) providing energy for calcification (Barnes & Chalker 1990), and ii) removing H^+ ions that are produced during calcium carbonate precipitation (Allemand et al. 2011). Consequently, factors that reduce light penetration into seawater (e.g., turbidity associated with terrestrial run-off and sediment re-suspension) can influence calcification rates. As corals are mixotrophic organisms that obtain part of their nutritional requirements through feeding on plankton and suspended particulate matter, and absorbing dissolved nutrients (Ferrier-Pagès et al. 2011), the availability of these sources of nutrition can also influence coral calcification. Finally, net accretion of calcium carbonate is critically dependent upon the availability of carbonate ions in seawater (Tambutté et al. 2011), which is in turn influenced by seawater temperature and pH, which control the relative concentrations of different inorganic carbon

molecules (i.e., dissolved CO_2, bicarbonate HCO_3^- and carbonate CO_3^{2-}). Each of these environmental factors, and their specific effects on coral growth, are discussed below.

2.6.1 Temperature

Temperature is an important factor affecting calcification, and thereby growth rates, in scleractinian corals (e.g., Weber & White 1974, Jokiel & Coles 1977, Edmunds 2005, Tanzil et al. 2013), including deep-water azooxanthellate species (Naumann et al. 2014). The typical relationship with temperature for any measure of performance, including growth, is a parabolic curve where moderate increases in temperature may have beneficial effects on performance, while exposure to increasing temperatures above the thermal optima will generally result in rapid declines in performance (Deutsch et al. 2008). Optimal temperatures for calcification and growth (generally around 25–28°C) are often close to the long-term maximum summer temperature experienced at a given location (Weber & White 1974, Jokiel & Coles 1977, Tanzil et al. 2013). The majority of studies on the effect of temperature on coral calcification and growth simply compare locations (mainly different latitudes) with varying temperature regimes. Within the range of naturally occurring temperatures, and when these remain below thermal optima, calcification rates show fairly constant rates of increase with increasing temperature. For instance, for massive *Platygyra* sp. sampled from 21 locations across in the Indo-Pacific, rates of linear extension increased from 4.9 mm yr^{-1} at 23.9°C to 12.0 mm yr^{-1} at 29.3°C, with an estimated increase in growth of 0.9 mm yr^{-1} per 1°C increase in temperature (Weber & White 1974). Similarly, for *Orbicella* (=*Montastraea*) *annularis* in the Caribbean, extension rates increased 0.94 mm yr^{-1} per 1°C increase in temperature across a SST range of 25–29°C (Weber & White 1977). More recent studies of massive corals have revealed similar trends. For Indo-Pacific *Porites* (based on multiple samples at 49 reef sites from Hawaii to the southern GBR), average linear extension and calcification rates significantly increased with increasing average SST, while average skeletal

density decreased, giving a temperature sensitivity of 2.98 mm yr^{-1} per °C for extension rate and 0.33 g cm^{-2} yr^{-1} per °C for calcification rate across a SST range of 23.1–29.5°C (Lough 2008). In the Gulf of Mexico, the calcification rate of *Orbicella annularis* showed a temperature sensitivity of 0.57 g cm^{-2} yr^{-1} per °C, although concomitant increases in skeletal density meant that linear extension of this species actually declined with increasing SST (Carricart-Ganivet 2004).

Sustained declines in calcification or linear extension of massive *Porites* have been reported from very warm waters (>28.5°C) around the Thai-Malay peninsula (Tanzil et al. 2013). Based on 70 cores from six locations, Tanzil et al. (2013) reported a region wide decline of ~19% in calcification and ~15% decline in linear extension rates between 1980 and 2010. Similarly, in the South China Sea (8°N) there have been sustained declines in calcification rates of massive *Porites* from 1920 to 1980 with a slight increase from 1980 to 2000 (Shi et al. 2012). Calcification rates also decreased in the Arabian Gulf between 1987–1990 and 1999–2002 (Poulsen et al. 2006) and at Misima Island, Papua New Guinea between 1984–1988 and 1989–1993 (Barnes & Lough 1999).

The observed linear relationship between average Indo-Pacific *Porites* calcification rates and average SST (for SST below the thermal optimum, Lough & Barnes 2000) has been extrapolated to assess whether corals are calcifying as expected in different reef environments. For example, Lough & Cantin (2014) suggest that calcification rates observed at two southern reefs off the coast of Western Australia, as reported by Cooper et al. (2012), are significantly higher than expected assuming constant temperature-performance relationships across all locations. Although caution must be used when extrapolating relationships observed under specific conditions to other environments, this suggests that other factors, such as improved water clarity or local acclimation to lower temperatures, might offset the effects of spatial temperature gradients. Indeed, such factors were proposed

to explain the high calcification rates of southerly coral reefs in previous studies (e.g., Smith 1981), and the observation that optimal temperatures for coral growth are close to local summer maximum temperatures suggests that there is considerable thermal acclimation. Nevertheless, a significant constraint in projecting effects of increasing temperature on scleractinian corals is limited data with which to establish temperature-performance relationships across the full range of current and projected temperatures for different coral species and populations (Hoeke et al. 2011). It is unclear, for example, whether latitudinal differences in growth rates simply reflect direct physiological effects of temperature (i.e., assuming that coral species, regardless of locations, have similar temperature-performance relationship), or whether corals are locally adapted, such that different populations have different temperature-performance curves and different thermal optima.

2.6.2 Light

Along with temperature, light is among the most important physical factors affecting the growth rates of zooxanthellate corals (Baker & Weber 1975). Pioneering work by Goreau (1959) demonstrated that light, acting through the endosymbiotic algae of hermatypic corals, considerably increases the rate of calcification, and suggested that the decrease in light intensity with depth below the ocean surface limits the absolute rate at which these corals calcify (Goreau 1961, 1963). Similarly, Muscatine (1973) considered light to be the primary environmental factor that controls the depth distribution of corals and the rates of overall reef accretion. At large spatial scales, such as along latitudinal gradients, it is difficult to tease apart the relative importance of changes in temperature versus changes in insolation as drivers of changes in coral growth rates. However, when observed along depth gradients, the relationship between light intensity and coral growth is non-linear, with the highest growth rates observed at moderate light levels typically experienced at water depths of >5 m (Baker & Weber 1975). In very shallow water, light intensities are well above the level required to

saturate photosynthesis and tend to inhibit calcification (Barnes & Taylor 1973), likely due to photoinhibition (e.g., Hoogenboom et al. 2009).

Within the coral growth database compiled for this review, water depth was recorded with resolution of at least 3 m for >450 growth records for 108 different species worldwide. Across species with massive colony morphologies and other non-branching morphologies (including free-living, foliose, encrusting and columnar forms) there is an overall negative correlation between depth and annual extension rates (Kendall's rank correlation, t = -0.27, p < 0.001, n = 210 and t = -0.36, p < 0.001, n = 102 for massive and other morphologies respectively). However, there is a wedge-shaped distribution of growth rates for these morphologies, with very high variation in annual extension rates observed in shallow, high light, environments (Figure 2.7). This variation might reflect among-species variation in the underlying relationships between photosynthesis and light (i.e., depth), and between calcification and depth. Alternatively, these data indicate that several other factors influence coral growth in shallow waters but that light availability likely limits the growth of massive and other non-branching morphologies in deeper waters. In contrast, there was no clear relationship between depth and annual extension for the branching morphologies (t = 0.01, p = 0.85, n = 148). The absence of a clear trend for these species could be related to the reduced depth range (30 m compared with 60 m for massive and other non-branching morphologies, Figure 2.7). Alternatively, variation in growth for these species is likely to be linked to differences in colony morphology (e.g., capacity for self shading in erect and branching corals), corallite-level morphological features, difference in tissue optical properties, or species-specific concentrations of screening pigments (Kaniewska et al. 2008, 2011).

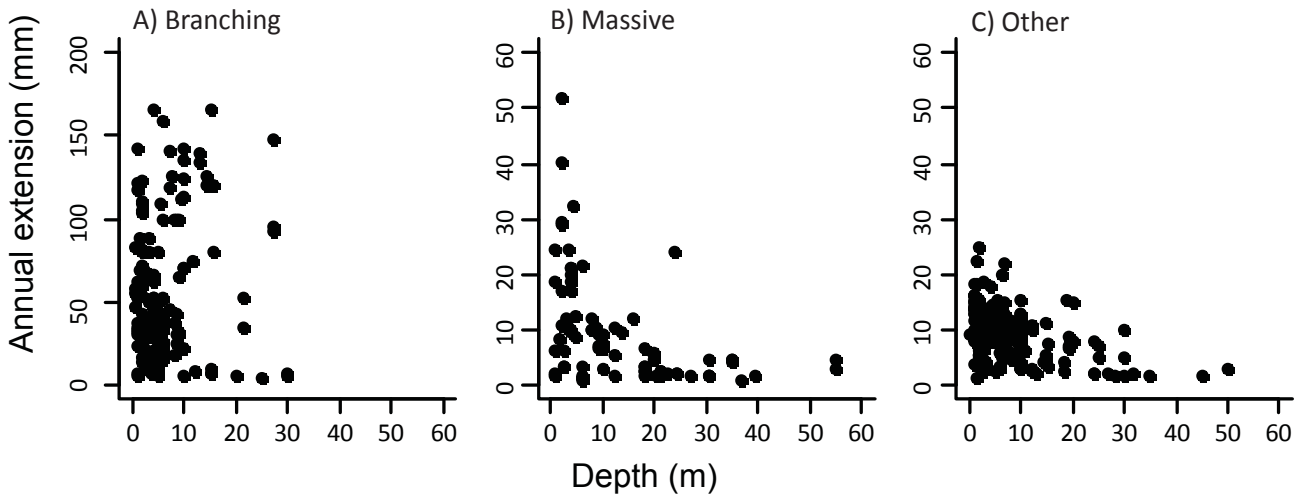

Figure 2.7. Relationship between depth and average annual extension rates (mm) for branching, massive and other non-branching colony morphologies. Points are individual growth records for different species in different studies. Note differences in scale on y-axis.

2.6.3 Water quality

Increasing anthropogenic transformation of coastal environments, such as land clearing, coastal development and dredging, are directly contributing to increased sedimentation and pollution in near-shore environments (Hughes et al. 2003, Hassan et al. 2005). These activities increase the suspended particulate matter, nutrients and turbidity present in seawater, which can directly reduce coral growth by smothering coral tissues as well as indirectly reducing growth by decreasing light availability for photosynthesis (reviewed by Fabricius 2005) or increasing susceptibility to disease (Pollock et al. 2014). Not surprisingly, therefore, several studies have documented comparatively low rates of linear extension or calcification in nearshore environments with particularly high levels of suspended sediments (Dodge et al. 1974, Tomascik & Sander 1985, Tomascik 1990, Hudson et al. 1994, Carricart-Ganivet & Merino 2001, Jiménez & Cortés 2003, Crabbe & Smith 2005, Guzmán et al. 2008, Ebeid et al. 2009, Sowa et al. 2014). However, Browne (2012) found growth rates of *Acropora*, *Montipora* and *Turbinaria* on an inshore reef, Middle Reef, comparable to those at other sites on the Great Barrier Reef. The majority of these studies have focused on massive corals where retrospective measurements of coral growth rates are related to changes in annual variation in rainfall and flood events (McCulloch et al. 2003, D'Olivo et al. 2013).

On inshore reefs of the GBR, declines in calcification rates (of ~0.6% per decade in the period 1930–2008) of massive *Porites* were observed (D'Olivo et al. 2013). Early declines in calcification and growth in these nearshore habitats were directly attributed to high sediment and nutrient loads from river discharges (D'Olivo et al. 2013). However, such effects are compounded by thermal stress. On the central GBR declines in linear extension rates of *Porites* due to the 1998 mass bleaching were only observed among corals from inshore reefs (not mid or outer shelf reefs) that are regularly affected by river discharge during flood events (Cantin & Lough 2014). Although such studies on massive *Porites* have

been used as a proxy for overall reef health (Dodge et al. 1974, Tomascik & Sander 1985), some have documented similar growth rates on polluted and unpolluted reefs (although bioerosion had led to net erosion of polluted reefs, Edinger et al. 2000). Also noteworthy is the observation that skeletal density and calcification rates of *Orbicella annularis* may decrease with increasing turbidity while extension rates increase, indicating that some corals living under adverse conditions maintain skeletal extension via a reduction in skeletal density (Carricart-Ganivet & Merino 2001). Also some corals (notably *Fungia horrida*) have been shown to ingest sediment and may derive additional nutition from organic-rich sediments (Rosenfeld et al. 1999).

Increased sedimentation due to declining water quality is generally expected to lead to reductions in coral growth as most corals expend substantial energy in actively clearing sediments. Active sediment rejection behaviour (e.g., ciliary transport of particles, mucus production, tissue expansion, tentacle manipulation of particles, extrusion of mesenteries, and pulsing of tissues) has been observed in a wide range of Indo-Pacific (Stafford-Smith & Ormond 1992) and Caribbean (Hubbard & Pocock 1972, Bak 1976) species. While corals with enhanced capacity for sediment rejection will be more tolerant of high turbidity, this exacts an energetic cost that is likely to reduce growth rates.

2.6.4 Prey acquisition

While light has traditionally been thought to be an important limiting factor for coral growth, corals obtain carbon and nutrients from a variety of sources (reviewed by Goreau et al. 1971, Muscatine 1973, Houlbrèque & Ferrier-Pagès 2009). Among-colony variation in rates of heterotrophic feeding can influence growth; overall skeletal growth of *Stylophora pistillata* was 30% higher in colonies that were experimentally fed with natural zooplankton (Ferrier-Pagès et al. 2003), and growth of *Goniastrea retiformis* was 10% higher in colonies that were provided with suspended particulate matter as a food source (Anthony & Fabricius 2000).

Moreover, the provision of a heterotrophic food source can allow corals to maintain active calcification when kept in almost complete darkness for several months (Hoogenboom et al. 2010). Aside from providing a direct supply of nutrients to the coral host, heterotrophic feeding by scleractinian corals can also stimulate photosynthesis (Ferrier-Pagès et al. 2003, Houlbrèque et al. 2003, 2004) by relieving nutrient limitation of symbionts, leading to elevated symbiont densities, elevated concentrations of photosynthetic pigments, or both (e.g., Dubinsky et al. 1990).

The extent to which corals rely on autotrophic versus heterotrophic carbon sources is thought to vary among coral species, although there are few data that directly quantify these differences. Among the Scleractinia, which includes asymbiotic, facultatively symbiotic and obligately symbiotic corals, species range between those that are exclusively reliant on heterotrophic feeding (e.g., *Tubastraea* and *Madrepora*) to those that can obtain 100% of their daily energy requirements from photsynthesis (e.g., *Montipora capitata*, Grottoli et al. 2006). Early work divided corals along an autotrophy-heterotrophy continuum based on polyp size and the surface area to volume ratio of particular colony morphologies (Porter 1976). However, more recent work indicates that even species with very small polyps (e.g., *Montipora* and *Pocillopora*) can consume significant amounts of particulate matter under certain conditions (Anthony 2000, Grottoli et al. 2006). Although all corals are capable of heterotrophic feeding, there is pronounced interspecific variation in feeding rates (Ferrier-Pagès et al. 2011). This is likely related to differences in the way that coral species capture food. Some species directly capture particles using their tentacles (e.g., *Stylophora*), others extrude filaments for external digestion of prey (e.g., *Galaxea*, Wijgerde et al. 2011) and others appear to use mucus nets (Lewis & Price 1975), or ciliary movement to transfer particles to the mouth of the polyp (e.g., *Mycetophyllia reesi*, a species that lacks tentacles, Goldberg 2002). Further research is required to assess the mechanisms that underlie variation

in feeding rates (such as polyp size, colony morphology, tentacle size and nematocyst density), and how this variation influences among-species variation in calcification and growth.

The use of multiple feeding modes provides corals with additional capacity to adjust their physiology to suit local environmental conditions. For instance, some species increase their heterotrophic feeding rates in deeper water where light is limited (Grottoli 1999, Palardy et al. 2005, 2008), or along turbidity gradients which are associated with reduced light levels together with increased availability of suspended particulate matter (Anthony 2000). This capacity to switch to a more-heterotrophic feeding mode may enhance coral survival during bleaching events. In one study, Grottoli et al. (2006) observed that plankton feeding was slightly upregulated in two species of *Porites* in Hawaii after bleaching, but substantially increased in *Montipora capitata* to a level where heterotrophic feeding was sufficient to meet the coral's basic metabolic costs. As corals can use heterotrophic carbon to fuel calcification, this capacity for upregulation of heterotrophic feeding during periods when photosynthetic carbon supply is reduced (e.g., during bleaching events or periods of high turbidity), potentially mitigates some of the negative impacts of climate change on coral growth. However, sufficiently high heterotrophic feeding rates have only been documented for one coral species, *Montipora capitata*, to date (Grottoli et al. 2006). Moreover, increased reliance on plankton feeding depends critically on an abundant plankton supply at a time when the phenology and distribution of plankton appear to be changing rapidly (Richardson 2008).

2.6.5 Seawater chemistry

Since the Industrial Revolution, atmospheric CO_2, the main greenhouse gas, has increased by ~40% from a pre-industrial value of 280 ppm to 391 ppm in 2011 and is rising at a rate of ~0.5% per year (Forster et al. 2007, Hartmann et al. 2013). Depending on global actions to mitigate greenhouse gas emissions, the atmospheric concentrations of CO_2 could be between

400 and 900 ppm by 2100 (Moss et al. 2010). As ~30% of anthropogenic carbon dioxide is absorbed into the oceans (Stocker et al. 2013), increasing atmospheric CO_2 has profound impacts on the carbonate chemistry of the oceans (Gattuso et al. 1999). The relative concentration of calcium and carbonate ions in seawater is typically expressed as an aragonite saturation state, or Ω_{arag} and the chemistry of calcium carbonate crystal deposition dictates that calcification can occur only when $\Omega_{arag} > 1$ (e.g., Gattuso et al. 1999, Tambutté et al. 2011). Several different forms of inorganic carbon are present in seawater in a dynamic equilibrium that depends on pH (e.g., Gattuso et al. 1998). As atmospheric CO_2 dissolves into seawater, carbonic acid is produced which then breaks down into hydrogen and bicarbonate ions, decreasing the pH and reducing availability of carbonate ions (Kleypas et al. 1999b, Kleypas & Langdon 2013). Therefore, declines in aragonite saturation state linked to increasing partial pressure of carbon dioxide (CO_2) in seawater, as seawater absorbs CO_2 from the atmosphere, are likely to affect coral calcification (Gattuso et al. 1998). Indeed, a doubling of CO_2 from pre-industrial levels will reduce the concentration of carbonate ions in surface waters by 30 % (Langdon et al. 2000), reducing aragonite saturation (Ω-aragonite) from historical levels of >4.0 typically found in coral reef waters to <2.8 (Kleypas et al. 1999b).

There is still a great deal of work to be done to increase our understanding of the effects of ocean acidification on marine calcifiers. Overall, the literature reveals a generally negative effect of near-future ocean acidification on growth, but there are highly variable responses among different taxa (Kroeker et al. 2013, Comeau et al. 2013, 2014). Experimental studies suggest that there is a consistent negative effect of ocean acidification on calcification of reef corals (e.g., Pandolfi et al. 2011, Chan & Connolly 2013, Comeau et al. 2013, 2014). In addition, field studies of the composition of coral communities close to volcanic seeps, where there is a natural elevation of pCO_2 and a decrease in pH, have shown

that coral diversity declines close to volcanic seeps although coral cover varied little and massive *Porites* growth rates were unaffected by proximity to seeps (Fabricius et al. 2011). In the Mediterranean, scleractinian corals were absent from low pH (7.4–7.5) areas close to natural CO_2 vents, with coincident reductions in sea urchin and coralline algal abundance (Hall-Spencer et al. 2008). Similarly, Caribbean corals show reductions in calcification along natural gradients in pH and Ω_{arag} (Crook et al. 2013). However, predictions that a fixed Ω-aragonite threshold exists for coral calcification (Hoegh-Guldberg et al. 2007) are contradicted by thriving reefs in locations where Ω-aragonite is naturally low (Manzello et al. 2008, Comeau et al. 2013). Moreover, predictions of the effects of ocean acidification on reef accretion often do not take into account the ability for corals to regulate the pH of their calcifying medium (McCulloch et al. 2012). Detailed studies of the ability of corals to regulate the medium between the skeleton and the lower tissue layer where calcification takes place reveal that the decrease in pH in this medium is gradual relative to the changes in pH in the external seawater, and that corals can partially mitigate the effects of ocean acidification by regulating this medium (Venn et al. 2013). McCulloch et al. (2012) further suggest that the energetic cost of pH regulation will be minimal.

2.7 Projected changes in coral growth

Coral reefs are reported to be among the most sensitive ecosystems to the ongoing effects of global climate change (Walther et al. 2002), because scleractinian corals (which are the main habitat-forming organisms on tropical reefs) bleach, and often die, following even moderate and temporary increases in ocean temperatures. In 1998, for example, 90 % of corals bleached and died across vast tracts of reef in the Indian ocean, and the temperatures that caused this widespread coral mortality are expected to become a regular (even annual) occurrence in coming decades (Donner 2005). This does not necessarily mean that there will

be annual episodes of significant and widespread coral bleaching (Hughes et al. 2003, van Hooidonk et al. 2013), as there is already evidence of corals acclimatising, through physiological changes, and/or adapting, through genetic change, to changing thermal regimes (Pandolfi et al. 2011, Guest et al. 2012). For example, coral assemblages subject to severe bleaching appear less susceptible to bleaching during subsequent thermal anomalies of equivalent magnitude (Pratchett et al. 2013). Nonetheless, corals living in warmer waters, above their thermal optima, may grow more slowly (Anthony et al. 2011). Indeed, one of the expected trade-offs for corals that associate with thermally tolerant genotypes of zooxanthellae (e.g., *Symbiodinium* type-D, Berkelmans & van Oppen 2006) is reduced growth (Little et al. 2004, Jones & Berkelmans 2010). Jones & Berkelmans (2010) showed that colonies of *Acropora millepora* experimentally infected with type-D *Symbiodinium* grew 29–38 % (depending on environmental conditions) slower than conspecifics infected with type-C2 *Symbiodinium*. Moreover, increasing temperatures above the thermal optima for corals (discussed above), as well as bleaching itself, will suppress growth (e.g., Cantin & Lough 2014).

The specific effects of increasing ocean temperatures on coral growth are expected to vary both spatially and taxonomically. At high latitudes (on subtropical reefs) increases in ocean temperatures may intially lead to increased rates of coral growth (e.g., Cooper et al. 2012), especially if growth is constrained during the coolest months by a minimum temperature threshold for net calcification. There is limited data on seasonal variation in growth rates of corals at high latitudes, but it is often assumed that reef-building (hermatypic) corals cease growing when exposed to temperatures <17–18 °C (Lough & Barnes 2000), which has been used to account for the constrained latitudinal extent of most reef-building corals (Stehli & Wells 1971). If so, then sustained warming may reduce or eliminate the period that corals are not growing, leading to overall increases in annual growth (Figure

2.10B). Alternatively, where growth of corals is constrained largely by maximum summer-time temperatures (e.g., at low latitudes), then sustained increases in ocean temperatures will be expected to have generally negative effects on coral growth, if not survivorship (Figure 2.10B). This thesis is partly supported by documented changes in inter-decadal growth rates of long-lived corals, such as *Porites* (Figure 2.10A), whereby ocean warming has already resulted in declines in the calcification rates of corals in low latitudes and naturally warmer locations (e.g., Red Sea, Cantin et al. 2010; Thai-Malay peninsula, Tanzil et al. 2013). Moreover, equatorial species diversity of corals decreased during the previous interglacial (130,000-115,000 years ago), when sea surface temperatures exceeded present values by at least 0.7°C (Kiessling et al. 2012).

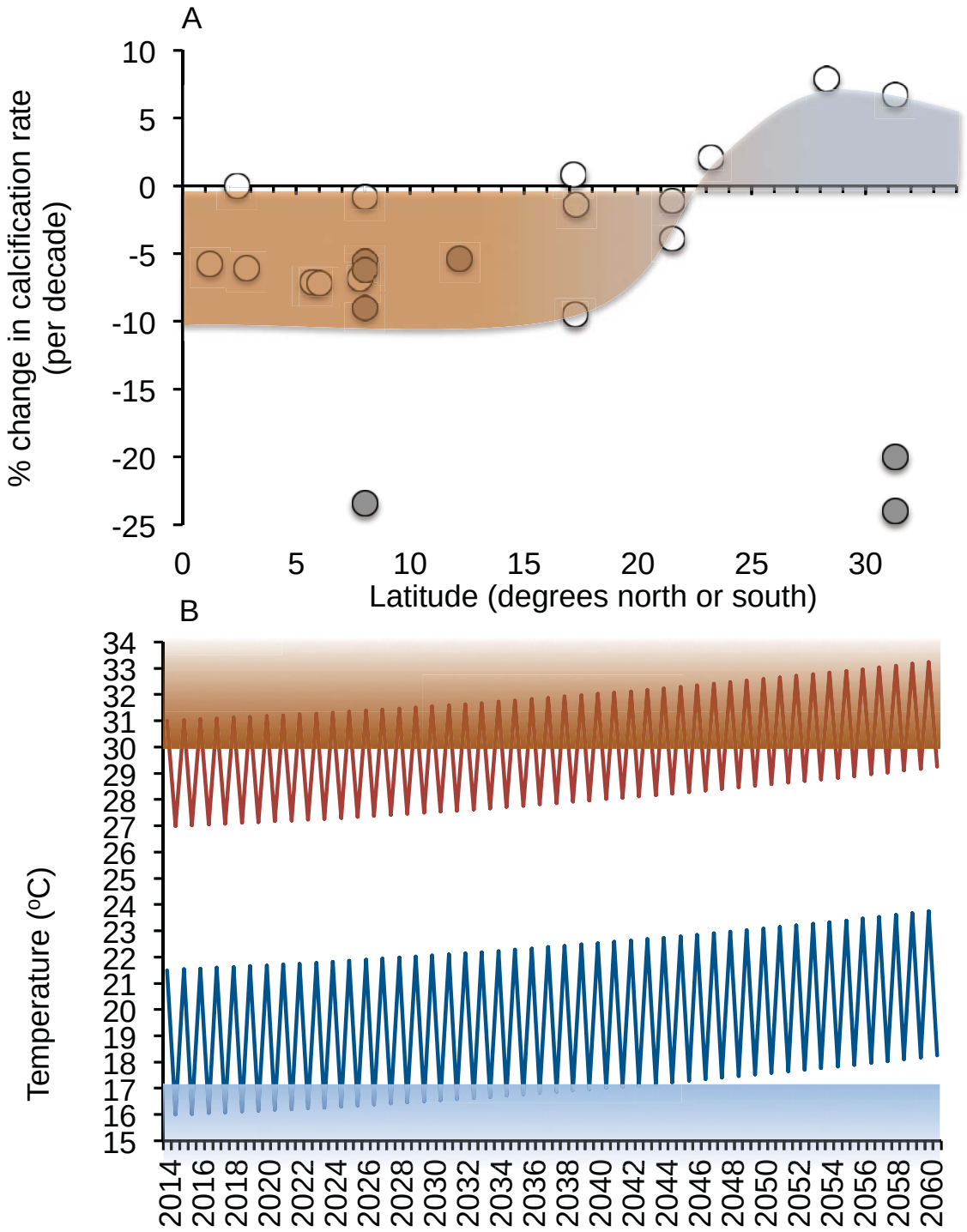

Figure 2.8. A) Latitudinal variation in documented changes in coral growth (% change in calcification or extension) based on retrospective measures (open circles) and temporally discrete direct measurements (shaded circles). B) Illustration of latitudinal differences in effects of increasing temperature on coral growth assuming fixed maximum and minimum temperature thresholds for coral growth. Ocean warming at high latitude reefs (indicated in blue) may result higher rates of coral growth as corals spend less time exposed to temperatures below the minimum temperature threshold for net growth. At low latitudes (orange) meanwhile, corals will be increasingly exposed to temperatures above the maximum thermal threshold and are likely to grow slower with ongoing warming.

Cooper et al. (2012) documented increased growth of massive *Porites* at Coral Bay (23.2°S) and the Houtman Abrolhos Islands (28.3°S), which are the southernmost locations where cores have been taken from massive corals. This initial increase in growth rates may not, however, be sustainable given recent observations of mass bleaching in response to thermal stress at these high latitude coral reefs (e.g. Moore et al. 2012). While there are no massive *Porites* growing at Lord Howe Island (31^{o}S), Anderson et al. (2015) directly measured linear extension of columnar *P. heronensis* and found that average annual growth in 2010–2011 was 9.7% higher (11.52 mm) than equivalent measurements taken in 1994–95 (10.50 mm). While there was significant inter-colony variation in annual extension rates for *P. heronensis* in 2010–11, the temporal change in the growth rate (6.5 % per decade) is very similar to that reported by Cooper et al. (2012) at Houtman Abrolhos Islands. If, however, we compare direct measures of linear extension and calcification across latitudes for corals that do not have records of growth preserved in the skeletons (e.g., *Acropora*) then this trend is no longer apparent (Figure 2.10). For example, the greatest magnitude of proportional change in coral growth (-20.0 % per decade) has been recorded for branching corals (*A. yongei* and *Pocillopora damicornis* at the high latitude reef, Lord Howe Island (Anderson et al. 2015). One possible explanation for these results is that low and declining levels of aragonite saturation are already limiting calcification at high latitudes, and that these effects are stronger than any beneficial effects of increasing temperature (van Hooidonk et al. 2014).

Experimental tests of the effects of declining aragonite saturation on coral calcification were reviewed by Chan & Connolly (2013) who found that calcification rates decline by 10–25% per unit decrease in aragonite saturation from 4 to 2. Projected differences in rates of decline are largely dependent on the method used to measure calcification, while rates were consistent across fast and slow growing coral species (Chan & Connolly 2013). Resulting changes in the calcification and growth of reef-building corals will

manifest at different times in different locations (van Hooidonk et al. 2014), owing to inherent geographic variation in background levels of aragonite saturation (Andersson et al. 2008, Pelejero et al. 2010). Notably however, the reefs that are likely to be least affected by ocean warming will be the first and worst affected by declining aragonite saturation, due to already low staturation states at high latitudes.

Declines in the calcification rates of individual corals due to declining growth rates might be further compounded by shifts in assemblage structure towards comparatively slow-growing species (Riegl & Purkis 2009, Comeau et al. 2014). Most disturbances (e.g., climate-induced coral bleaching, outbreaks of crown-of-thorns starfish, and severe tropical storms) have disproportionate effects on erect branching corals, such as *Acropora* and *Pocillopora* (Loya et al. 2001, McClanahan et al. 2004, Pratchett et al. 2014) suggesting that increasing incidence of acute disturbances may lead to increasing dominance of massive corals, such as *Porites* (e.g., Alvarez-Filip et al. 2011). However, resilience depends not only on species' resistance to disturbance, but also their capacity to recover in the aftermath of major disturbances (Hughes et al. 2003, Baker et al. 2008, Pandolfi et al. 2011). This is especially important after severe disturbances that cause high rates of mortality across a broad range of different coral species; the long-term persistence of different species will depend more on their capacity for recovery (Hughes et al. 2003, Baker et al. 2008), rather than on minor differences in rates of mortality.

Virtually all studies that have forecast changes in the structure of coral assemblages due to climate change, whether based on qualitative frameworks or quantitative projections, have focussed on interspecific differences in susceptibility to disturbance (e.g., Marshall & Baird 2000, Loya et al. 2001) and the proportion of colonies that bleach or die in a given population. Persistent shifts in the relative abundance of different corals may, however, be further affected by differential effects of environmental change on key demographic process,

such as growth (De'ath et al. 2009, Carricart-Ganivet et al. 2012). If for example, the recovery capacity of *Acropora* is compromised, then even moderate increases in the frequency of acute disturbances (e.g., climate-induced coral bleaching) could lead to even more rapid shifts in dominance towards more robust and resistant taxa. Such shifts in assemblage structure would have significant effects on topographic structure and habitat complexity, with potentially important effects on fishes and mobile invertebrates that associate with live coral habitats (Pratchett et al. 2008, Stella et al. 2011). Even moderate changes in the calcification rates of corals, especially if these are combined with directional shifts in the composition of coral assemablages, could also have important effects on reef accretion.

2.7.1 Consequences for habitat structure

Just as not all corals contribute equally to framework building (Wells 1957), corals are not equivalent when it comes to creating habitat for reef-associated organisms (e.g., reef fishes). Branching corals (e.g., branching *Porites* and arborescent *Acropora*) provide the greatest range of different microhabitats, and therefore, support the greatest diversity of different fishes and mobile invertebrates (Coker et al. 2014). Moreover, *Acropora* and *Pocillopora* corals (which are the predominant branching corals throughout much of the Indo-Pacific) are the preferred prey for corallivorous fishes and invertebrates (Cole et al. 2008, Rotjan & Lewis 2008). Selective depletion of these faster growing corals may, therefore, lead to corresponding shifts in the composition of local fish assemblages (if not overall declines in the abundance of fishes) as has been shown in Moorea, French Polynesia (Berumen & Pratchett 2006). Coral assemblages on the north coast of Moorea have been subject to multiple disturbances (including bleaching, tropical cyclones and outbreaks of crown-of-thorns starfish) over the last 30 years, which have had a disproportionate effect on *Acropora* corals (Adjeroud et al. 2002, Berumen & Pratchett 2006, Pratchett et al. 2013). As *Acropora*

became increasingly scarce, coral-feeding butterflyfishes that specialise on *Acropora* (e.g., *Chaetodon trifascialis* and *C. reticulatus*) have become increasingly rare. In contrast, generalist coral-feeding butterflyfishes, and especially those that specialise on *Pocillopora* (e.g., *Chaetodon pelewensis*) have been resilient to shifts in composition of coral assemblages (Berumen & Pratchett 2006). Similarly, Bellwood et al. (2006) showed that some fishes (habitat generalists) increase in abundance following localised coral depletion, which may compensate for the loss of specialist fishes with strong dependence on corals. However, extensive coral loss almost invariably leads to net declines in the abundance and diversity of coral reef fishes (reviewed by Wilson et al. 2006, Pratchett et al. 2008) and these declines are particularly pronounced when coral loss is associated with pronounced declines in topographic structure and habitat complexity (e.g., Sano et al. 1987, Graham et al. 2006).

Branching corals that are important in providing habitat for coral reef fishes and invertebrates (*Acropora* and *Pocillopora*) are disproportionately susceptible to mechanical damage and dislodgement (Madin & Connolly 2006). Projected increases in the severity of tropical cyclones with climate change (Emanuel 2005, Christensen et al. 2013, but see also Klotzbach 2006), are likely to cause fundamental shifts in the relative abundance of corals with different shapes (Madin et al. 2008). Notably, the tabular coral, *Acropora hyacinthus*, which is a dominant coral on exposed reef crests in the Indo-West-Pacific (Linares et al. 2011) is particularly susceptible to hydrodynamic forces and expected to decline in abundance with increased frequency of severe tropical storms (Madin et al. 2008). If declines in calcification also lead to weaker skeletons (Hoegh-Guldberg et al. 2007), then corals will have even greater sensitivity to physical damage caused by tropical cyclones (Madin et al. 2008). This will lead to fewer, but also smaller and flatter corals on reefs in the future, which will directly impact habitat availability for reef-associated organisms.

2.7.2 Consequences for reef accretion

Reef accretion results in the construction of a three-dimensional biogenic structure on the sea floor. It is constrained at its upper bound by sea level itself, and the distance from the accreting reef surface to sea level is often referred to as 'accommodation space', or the remaining potential for vertical reef growth. Reef accretion is a function of the biogenic accummulation of carbonate and sediment on the one hand, and the sum of its physico-chemical and biological destruction, dissolution or transport away from the accreting reef on the other (Perry et al. 2008). Thus, reef accretion is dependent upon a number of processes that facilitate either production of calcium carbonate or its removal from the reef. Although corals, and in some cases coralline algae, are the primary framework builders in modern reef accretion, this has not always been the case, with many reef building episodes throughout the >500 million year history of metazoans characterized by non-coral reef builders. For example, many Cretaceous reefs were built primarily from the remains of large bivalves (rudists), which formed extensive 3-dimensional structures above the surrounding sea floor (Wood 1998). Today however, scleractinian corals dominate reefs, so it is important to understand the degree to which carbonate production is dependent upon both the cumulative growth of corals on the reef, and the relative contribution to that carbonate production among different coral taxa.

Of particular concern for degraded coral reefs around the world are the expected changes in coral assemblage composition and structure due to climate change, as well as the ongoing changes brought about by more local stressors (Pandolfi et al. 2011). Will this change in taxonomic structure affect the ability of coral reefs to accrete? For example, is the rate and magnitude of reef accretion any different between reefs characterized by a fast-growing assemblage dominated by branching corals (e.g., *Acropora* spp.) versus a slower-growing assemblage dominated by massive corals (e.g., Faviidae)? Few studies have

documented differences in reef-scale calcification among reefs with different benthic composition. In one such study, reef flats dominated by coralline algae tended to have lower calcification rates than areas dominated by massive *Porites* colonies (Atkinson & Grigg 1984). Similarly, Gattuso et al. (1996) measured higher calcification on a hard coral dominated reef compared with a reef with low coral cover. However, such studies do not elucidate the relative importance of changes in coral cover and species composition compared with other environmental factors that also vary among reefs. Given the importance of reef accretion rate to the longevity of coral reefs, the impending changes to taxonomic composition on coral reefs due to climate change and other stressors, and the presumed integral relationship between coral growth and reef accretion, it is important to consider how reef coral assemblage structure is related to reef accretionary rates.

Much of what we know about rates of reef accretion comes from the Holocene fossil record of the past 10,000 years (Montaggioni 2005). Using a paleo-reconstruction of water depth, Hubbard (2009) assessed the relationship between depth and accretion rates on Caribbean Holocene reefs dominated either by fast-growing branching corals (i.e., *Acropora cervicornis*) or by slower-growing massive corals (e.g., *Orbicella annularis*). Even though maximum reef accretion rate decreased with depth in his analyses, Hubbard (2009) found no correlation between water depth and accretion rate for either assemblage, due to large variance in accretion across all depth ranges. Importantly, the difference between the regression lines for branching and massive corals is not statistically significant (Figure 2.9). In another study of the Holocene fossil reefs of Belize, accretion rates increased with *increasing* paleo water depth, and reef accretion in reef settings characterized by massive corals occurred *faster* than those characterized by branching acroporid corals (Gischler 2008). Thus, the common view that reefs characterized by shallow branching corals *always* show the highest accretion rates (e.g. Schlager 1981) is not supported in the Caribbean Sea.

However, more recent studies from the Indo-Pacific (Tahiti) do show a higher rate of reef accretion associated with *Acropora* dominated reefs (Camoin et al. 2012, Blanchon et al. 2014). We clearly need a much greater understanding of the regional variability associated with the relationship between coral growth rate, dominance, and reef accretion rates.

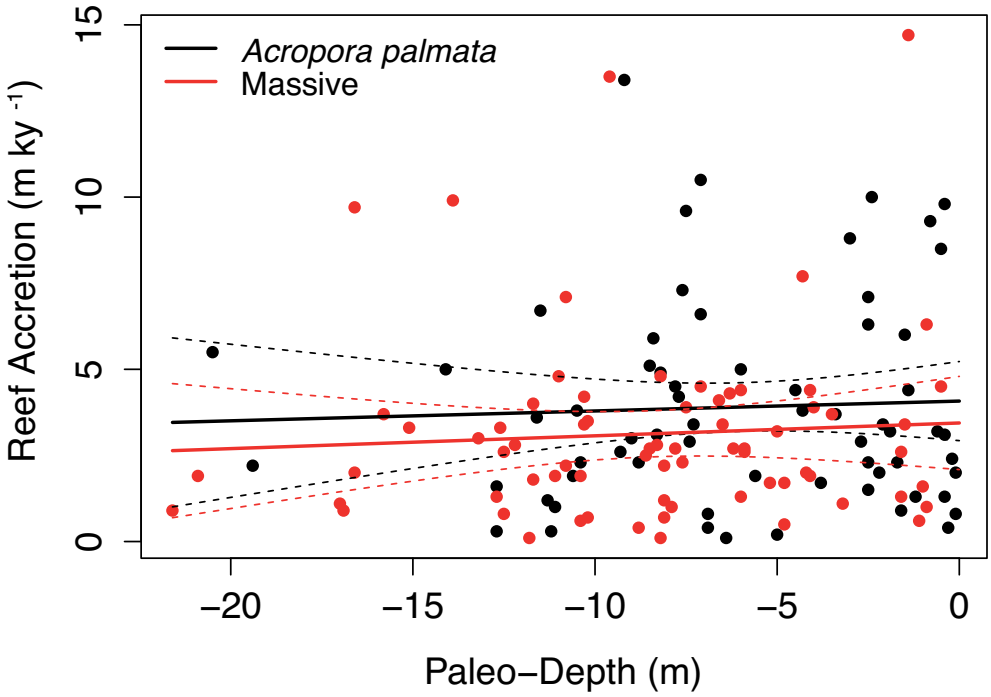

Figure 2.9. Accretion rates (m ky^{-1}) for paleo coral assemblages dominated by branching corals, specifically *Acropora palmata*, or massive corals. Notably there is no apparent difference in rates of reef accretion with changes in depth or between the dominant corals. Redrawn based on data in Hubbard (2008).

The relationship between biodiversity of reef corals and spatial distribution of reef growth in the fossil record may also inform projected changes in reef growth following widespread degradation of coral reefs. In a study of Oligocene through Neogene sections from the Panama Paleontology Project in the Caribbean (Johnson et al. 2008), there were no clear patterns between coral diversity and reef development through this time interval (~28.5–1.0 million years ago). Even though the taxonomic composition of coral assemblages has varied through time in this dataset, no clear pattern emerged between intervals with a regional distribution of extensive coral reef development and coral community composition. One potential implication of this result is that processes involved in carbonate production may be less important to overall reef growth in space and time when considered against the negative processes of bioerosion, dissolution, mechanical breakdown and off-reef transport, as well as environmental limitations associated with light, accommodation space, and wave energy.

Concern over the effects of ongoing and future climate change on coral reefs has led to studies of the net carbonate production rates of living reefs (as a proxy for reef accretion), with particular attention paid to increased rates of coral bioerosion and decreased rates of coral calcification. For example, Perry et al. (2013) found a Caribbean-wide trend of decreasing net carbonate production from which they calculated reef accretion rates that were far lower than during the Holocene in the same areas. Future work needs to take into account the differences in sea level dynamics between Holocene and modern settings. For example, the rise in sea level since the Last Glacial Maximum (LGM) has resulted in some of the highest reef accretion rates ever recorded (Macintyre & Glynn 1976), and care must be taken when comparing estimates of modern accretion rates, within a period when sea level has only fluctuated by one or two metres over the past several thousand years, with estimates of ancient values during periods of rapid sea level rise. Available space on the substratum, and

other environmental factors including temperature, wave energy and light intensity, are all determinants of reef growth and destruction.

2.7.3 Conclusions and future directions

The role of coral growth (calcification and associated increases in the physical dimensions of individual colonies) in structuring coral populations and assemblages, or even reef ecosystems, is difficult to isolate from multiple other factors. The abundance of corals (typically measured as areal coverage) depends on processes that contribute to both increases (e.g., reproduction, recruitment and vegetative growth) and decreases (e.g., injury and mortality) in population size. Moreover, there is likely to be as much variation (spatial, temporal and taxonomic) in exposure and susceptibility to disturbances, or repair responses (Meesters et al. 1996, Garzón-Ferreira et al. 2005, Pisapia et al. 2014, Madin et al. 2014), as there is variability in growth rates. There may also be direct trade-offs between growth and mortality (e.g., faster growing, erect, branching corals are disproportionately susceptible to hydrodynamic forces caused by severe storms, Madin & Connolly 2006). Systematic declines in coral growth would, however, be expected to compound the effects of increasing frequency of major disturbances, leading to fewer and smaller corals (e.g., McClanahan et al. 2008), which will have important ramifications for the structure and function of reef ecosystems (Wilson et al. 2006, Pratchett et al. 2008).

A key area for future research is to explicitly investigate the influence of vegetative growth in structuring populations and assemblages of scleractinian corals. One way to do this is to document demographic rates (e.g., growth, injury and mortality) across a large number of individually tagged colonies in a given population or assemblage (e.g., Babcock 1991, Edmunds & Elahi 2007, Madin et al. 2014). Given the work involved, this has only ever been done for a few specific coral species, but also, previous such studies have recorded long-term changes in colony size (typically maximum diameter or area, e.g., Hughes & Tanner 2000,

Edmunds & Elahi 2007), providing estimates of realized growth that are confounded by injury and partial mortality. Alternatively, experimental approaches that quantify maximum potential growth rates of species can be combined with field estimates of realised growth under different environmental conditions to establish the extent to which abundance is limited by instrinsic maximum growth rate or environmental constraints on growth; integral projection models offer great potential for this kind of work (Edmunds et al. 2014).

Calcification rates provide the most direct and readily comparable measure of growth across different reef-building corals (e.g., branching versus massive corals), especially when measured or averaged over longer periods to dampen out marked diel and seasonal differences. Calcification rates can also be measured at the reef scale for coral assemblages under natural field conditions (e.g., Gattuso et al. 1996), providing a means to relate species-specific calcification of individual colonies to larger scale reef accretion rates. Moreover, calcification rates can often be measured (or at least approximated) alongside routine estimates of linear extension (e.g., based on bandwidth for cores from corals with annual density banding, Aller & Dodge 1974). However, most of the existing data on coral growth is for average annual skeletal extension rates (Table 2.4), based on measurements of branch, radial (realised and actual), vertical or horizontal extension. In many studies, skeletal extension is measured in only one direction (e.g., cores from massive corals are almost invariably taken vertically from the top), which may over- or under-estimate (depending on the primary growth axis) extension rates relative to studies that average skeletal measurements taken in multiple directions and at multiple locations across the colony (e.g., Morgan & Kench 2012). For example, Lough and Barnes (2000) showed that linear extension in massive *Porites* was 15% higher along the vertical axis of the colony compared to the horizontal axis. To maximise the utility of skeletal extension estimates for comparing across taxa and among studies, it is important to record both horizontal and vertical extension, or at

the very least, it should be very clear exactly what was measured. Similarly, for complex branching corals, it would be useful to have information on both average annual branch extension as well as changes in the AMR across a wide range of species and different sized colonies to test if (or how) these two metrics actually relate to each other. Even if there is no apparent relationship, then at least AMR can be used in multispecies comparisons. Consistent and comparable data on growth rates of reef-building corals should then be compiled into a single global database (e.g., coraltraits.org).

An important and ongoing area of research is to test for long-term trends in coral growth, which may be attributable to environmental changes. Sustained declines in the linear extension and calcification of some corals are already apparent (Edmunds 2005, De'ath et al. 2009, Tanzil et al. 2009, Bak et al. 2009, Manzello 2010, Cantin et al. 2010, Tanzil et al. 2013), despite relatively moderate environmental changes that have been recorded to date. However, effects of climate change will vary spatially (e.g., with latitude) and also taxonomically (Cooper et al. 2012, Anderson et al. 2015). Therefore, much more research is required to discern these differences effectively as well as to account for climate change impacts beyond ocean warming (e.g., ocean acidification), linking long-term measurements of coral growth to measurements of temperature and seawater chemistry within the very habitats and locations where corals are sampled. Much more research is also required to quantify long-term changes in growth rates across a broader range of different coral species, especially those corals that are not amenable to retrospective measures of coral growth (e.g., *Acropora*, *Pocillopora*), but nonetheless are important habitat-forming species. Existing observational and experimental data tend to suggest that climate change and ocean acidification will have mostly negative effects on coral growth. Even at high-latitude reefs where there may be initial beneficial effects of increasing temperatures (Figure 2.10), low and declining levels of aragonite saturation are expected to constrain coral growth (Chan &

Connolly 2013). These relatively short-term studies do not, however, provide insights into the capacity of corals to adapt or acclimatize to changing environmental conditions. Just as there are indications that corals may be becoming less susceptible to bleaching (Guest et al. 2012, Pratchett et al. 2013), growth rates of corals may re-adjust or even increase after a period of acclimatization to altered environmental conditions.

Chapter 3 Species-specific declines in the linear extension of branching corals at a subtropical reef, Lord Howe Island

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Anderson KD, Heron SF, Pratchett MS (2015) Species-specific declines in the linear extension of branching corals at a subtropical reef, Lord Howe Island. *Coral Reefs* 34:479-490.

3.1 Abstract

Reef-building corals are sensitive to changing temperature regimes, such that sustained increases in ocean temperatures are generally expected to have negative effects on coral growth and survivorship. At high latitude reefs however, projected increases in ocean temperature may actually increase coral growth (relaxing constraints imposed by cool winter temperatures), though this will depend upon on the rate and extent of declines in aragonite saturation, which is already much lower at high latitudes. This study quantified linear extension rates of six scleractinian corals, *Acropora yongei*, *Isopora cuneata*, *Pocillopora damicornis*, *Porites heronensis*, *Seriatopora hystrix*, and *Stylophora pistillata*, at Lord Howe Island in 2010/2011. Contemporary growth rates were compared to equivalent data collected in 1994/1995. There was marked interspecific variation in growth rates, with *A. yongei* growing almost twice the rate of all other species. Temporal changes in annual growth also varied among species. Growth rates of both *A. yongei* and *P. damicornis* had significantly decrease by 30 % compared to recorded rates in 1994/95. However, growth rates of *P. heronensis* had not changed. Declines in the growth rates of these branching species may be attributable to declines in aragonite saturation and/or increases in summertime temperatures above limits for optimal growth, but either way it appears that climate change is having negative effects on corals, even at subtropical locations.

3.2 Introduction

Coral reefs are among the most vulnerable ecosystems to the sustained and ongoing effects of global climate change (Walther et al. 2002) owing to the stenothermic nature of reef-building corals (Hoegh-Guldberg 1999). Corals bleach and may die when weekly sea surface temperatures (SST) exceed the usual summertime maximum sea-surface temperature (SST) by 1 ℃ or more (Liu et al. 2003). Global SST have increased an average of 0.7 ℃ since pre-industrialization and are further projected to increase by 0.6-2.0 ˚C by 2100 (IPCC 2013). In tropical oceans, SST are projected to increase by at least 1.8 ℃, and up to 6 ℃ by 2100 (IPCC 2007). These extreme increases in SST may cause comprehensive loss of corals (Hoegh-Guldberg et al. 2007), though corals tend to be strongly adapted to the local environmental temperature regimes (Hughes et al. 2003), and may therefore have capacity to acclimate to changing thermal regimes. The occurrence of broad-scale and multi-specific coral bleaching is linked to long-term accumulation of heat stress, which is measured as Degree Heating Weeks (DHW); DHW values of 4 ℃-weeks have been linked to significant coral bleaching, while DHW greater than 8 ℃-weeks results in widespread bleaching and significant mortality (Liu et al. 2013, Eakin et al. 2010). Bleaching susceptibility varies greatly among coral taxa (Marshall & Baird 2000, Loya et al. 2001), leading to strong selective mortality and marked directional shifts in the structure of coral assemblages (e.g., Pratchett et al. 2011). Importantly, future coral communities may be dominated by thermally tolerant coral species or corals that can rapidly colonize reef habitats in the aftermath of severe bleaching events (Hughes et al. 2003).

Aside from increasing temperatures, calcifying organisms, such as corals, will be significantly affected by declines in aragonite saturation that are linked to increasing partial pressures of carbon dioxide both in the atmosphere and ocean (Kleypas & Yates 2009). Since the Industrial Revolution, atmospheric carbon dioxide (CO_2) has increased from 280 ppm to

390 ppm and is rising at a rate of ~0.5% per year (Forster et al. 2007). By 2100, it is predicted that atmospheric concentrations of CO_2 will be at least double preindustrial levels (560 ppm, IPCC 2007). About 30% of the anthropogenic carbon dioxide has been absorbed into the ocean since the Industrial Revolution (IPCC 2013), having profound impacts on the ocean chemistry (Gattuso et al. 1999). Atmospheric CO_2 dissolves into water to produce carbonic acid (Hough-Guldberg et al. 2007). Carbonic acid then dissociates into hydrogen and bicarbonate ions, decreasing the pH and reducing availability of carbonate ions (Kleypas & Yates 2009). A doubling of CO_2 from preindustrial levels will reduce the concentration of carbonate ions by 30% (Langdon et al. 2000), reducing tropical ocean surface aragonite saturation (Ω-aragonite) to <2.8 (Kleypas et al. 1999b).

Corals can generally withstand slow or gradual changes in environmental conditions (e.g., recovering from mild bleaching events), but these changes may significantly affect growth and calcification (Hough-Guldberg 1999). Sustained declines in the growth rates of massive corals have been reported in tropical regions of Australia (Cooper et al. 2008; De'ath et al. 2009), Thailand (Tanzil et al. 2013), and in the Red Sea (Cantin et al. 2010), and are almost invariably linked to climate-induced changes in local environmental conditions. For massive corals, long-term changes in linear extension can be determined retrospectively by taking cores from large and long-lived colonies, and quantifying the dimensions of annual density banding couplets (Buddemeier et al. 1974, Lough 2008). For branching corals, however, annual growth patterns are not readily preserved in the skeleton (Roche et al. 2010), so the only way to detect temporal changes in growth rates is to directly measure growth rates at specific intervals (Bak et al. 2009). Not surprisingly, there is little data on changes in growth rates of branching corals. However, branching corals are key contributors to the biological and physical structure of reef habitats (Pratchett et al. 2008, Coker et al. 2014) and

any declines in growth rates, structural integrity, and ultimately abundance of branching corals will have major ramifications for biodiversity and productivity of coral reefs.

Effects of climate change on reef-building corals could vary geographically (Hoegh-Guldberg et al. 2007) such that there is now a concerted effort to identify areas that could serve as refuges from devastating effects of future climate impacts (Guinotte et al. 2003). Previous discussions have centred on high latitude coral reefs where increases in temperature may actually have a beneficial effect on coral growth (Cooper et al. 2012) and coral diversity (Guinotte et al. 2003). Conversely, subtropical reefs are marginal habitats for reef growth given the declines in Ω-aragonite at high latitudes (Kleypas et al. 1999a), and this is likely to worsen with ocean acidification. Increases in global temperatures at subtropical locations are expected to result in increased growth rates (e.g., Cooper et al. 2012), largely due to sustained growth during winter months when growth rates are presently slower (Crossland 1984). However, deleterious effects of ocean acidification may offset any beneficial effects of increasing temperature at these locations (van Hooidonk et al. 2014). The relative effects of increasing temperature versus declines in already low levels of aragonite saturation, may vary among coral species due to inherent differences in their susceptibility to temperature (Marshall & Baird 2000) and aragonite saturation (Fabricius et al. 2011, Edmunds et al. 2012).

The aim of this study was to quantify current growth rates of scleractinian corals (particularly, branching corals) at a high latitude coral reef, Lord Howe Island, located 700 km south of the Great Barrier Reef. Well-developed coral reefs on the northwestern side of Lord Howe Island represent the southernmost extent of coral reef growth (Spalding et al. 2001), and may therefore provide an important refuge for reef-building corals exposed to increasing effects of global climate change. By measuring growth rates for a range of different corals species at Lord Howe Island (*Acropora yongei*, *Porites heronensis*,

Pocillopora damicornis, *Isopora cuneata*, *Stylophora pistillata* and *Seriatopora hystrix*), this study will address the paucity of information on spatial and temporal variation in growth rates of branching corals. Importantly, annual growth rates for many of the same coral species were quantified in 1994/95 (Harriott 1999), enabling direct comparisons of growth rates to test whether growth rates have increased or decreased over the last 1.5 decades. This study provides the first ever assessment of climate change leading to increases or decreases in growth of branching corals at high latitudes.

3.3 Methods

3.3.1 Study site

This study was conducted at Lord Howe Island, located 600 km off the coast of New South Wales, Australia during December 2010-December 2011 (Figure 3.1a). At 31.5˚S, Lord Howe Island represents Australia's southernmost reef system where there is positive (albeit very slow) carbonate accretion (Harriott et al. 1995). The coral communities at Lord Howe Island are relatively depauperate, comprising approximately 83 species (Harriott et al. 1995), but coral cover can be very high (37 %) (e.g., Hoey et al. 2011). Sampling for the current study was conducted within the extensive lagoon system on the western side of the island in depths of 2-4 m (Figure 3.1b).

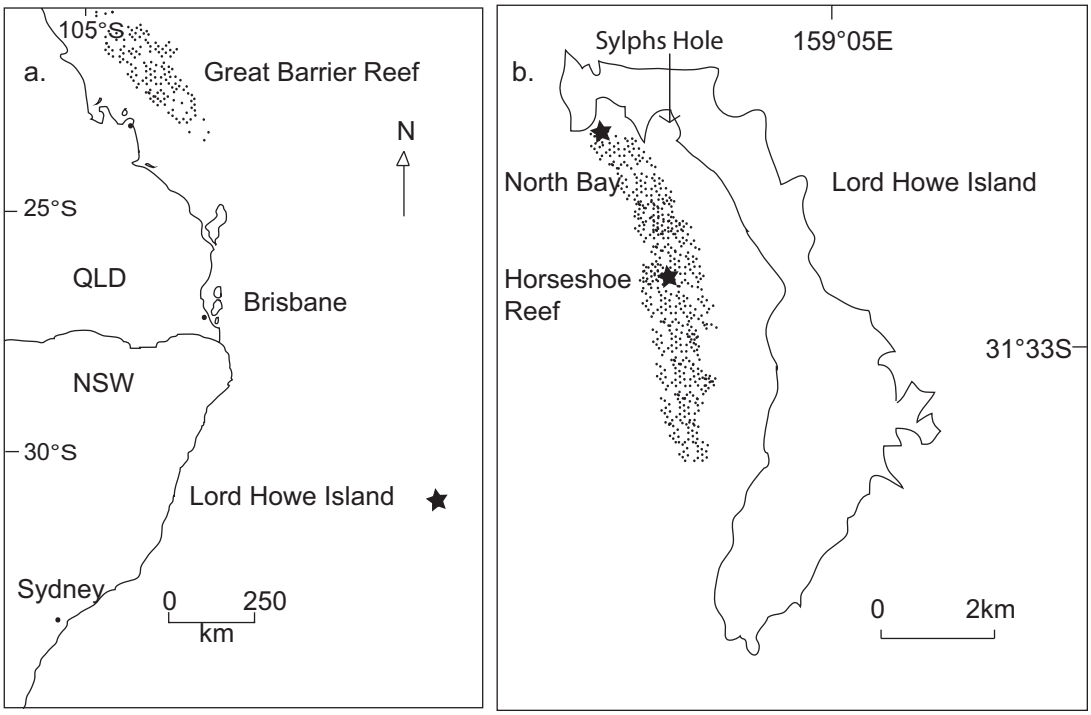

Figure 3.1. a.) Map of the east coast of Australia. b.) Map of Lord Howe Island showing the two sampling sites, Horseshoe Reef and North Bay.

3.3.2 Environmental Data

Sea surface temperature (SST) data for the study period were collected by Australian Institute of Marine Science temperature loggers deployed at 2.4 m on the reef flat of the lagoonal system in North Bay, Lord Howe Island (AIMS 2014). The ReefNet Sensus Ultra sensor was deployed March 2009 to May 2013 recording the SST instantaneously at 30 min intervals (AIMS 2014). The daily average, maximum, and minimum SST were extracted for the December 2010-December 2011 study period from the AIMS data centre.

To provide context for changes between observations described here and the 1994/95 study (Harriott 1999), weekly satellite SST data at 1/24° (~4 km) spatial resolution were extracted for the northern lagoon for the period 1985-2012. Weekly data were derived from the Pathfinder v5.2 night-only, 4 km-daily SST dataset, with gaps filled following Heron et al. (2010). Trends in SST were calculated for the summer (December-March) and winter (April-November) seasons and annually. In addition, accumulated thermal stress was investigated using the Degree Heating Weeks (DHW) metric (Liu et al. 2003), calculated from the weekly SST data.

Ocean chemistry parameters in the vicinity of Lord Howe Island were determined from research cruise data compiled in the Surface Ocean CO_2 Atlas (SOCAT; Sabine et al. 2012). Measurements in the vicinity of Lord Howe Island were taken in May 1995; August, October and November 2005; April 2008; and August 2009, fortuitously covering a comparable time period to the growth rate measurements. To consider the influence of ocean chemistry upon growth rate differences between the 1994/95 observations and those undertaken in this study, while avoiding issues of seasonal variation (see Gledhill et al. 2008), only the 1995 and 2008 data were considered. Measurements in 1995 were in the open ocean to the southwest of Lord Howe Island, ~ 100 km W/SW, near 157.998°E, 31.714°S; for 2008, data near to this location, at 157.999°E, 31.893°S, were analysed. Measured values of SST and sea surface

salinity (SSS) were used to estimate the total alkalinity, A_T, following Lee et al. (2006), which for the subtropics region was determined as:

$$A_T = 2305 + 58.66(\text{SSS} - 35) + 2.32(SSS - 35)^2 - 1.41(SST - 20) + 0.04(SST - 20)^2.$$

The aragonite saturation state at the sea surface was estimated by applying the CO2SYS analysis tool (Lewis & Wallace 1998) using the above parameters combined with the partial pressure (or fugacity) of CO_2 in water ($fC0_2$), from the research cruise data.

3.3.3 Coral Growth

Growth rates of six coral species (*Acropora yongei*, *Porites heronensis*, *Pocillopora damicornis*, *Isopora cuneata*, *Stylophora pistillata* and *Seriatopora hystrix*) were measured over three time frames: summer (December 2010 to March 2011), winter (April 2011 to November 2011) and annual (December 2010-December 2011, Table 3.1). These corals were chosen as they are highly abundant at Lord Howe Island with contrasting morphologies. At the start of each time period, replicate colonies of each species were sealed within large volume plastic bags (ca. 70 L) containing Alizarin Red stain (12 mg L^{-1}) mixed in sea water (Lamberts 1978; Harriott 1999). Alizarin Red is directly incorporated into the skeletons of actively growing corals, but previous studies have had poor success in staining corals on high latitude reefs (Harriott 1999) presumably due to low temperatures and reduced light irradiance (Kleypas et al. 1999a). Accordingly, corals were sealed within bags for 7-8 h, exceeding immersion times (3-4 h) typically used in tropical locations (e.g., 3 h on Davies Reef, Oliver et al. 1983). Following staining, coral colonies were repositioned and reattached to the reef using plastic cable ties, ensuring minimal disruption to live tissue and growth axis. To ensure adequate staining time, branches were collected from a subsample of coral colonies (n=5 colonies) and placed in a dilute (10-15%) hypochlorite solution to remove the tissue and test that underlying skeletons were effectively stained. These colonies were not included in the study.

Table 3.1. Summary of the coral sample size (N) and number of branches measured (n) for each sampling time period at Lord Howe Island. As well, the percentage of colonies stained but not recovered throughout the study.

Species	Summer N (n)	Winter N (n)	Annual N (n)	% Not recovered	Total N (n)
Acropora yongei	4 (45)	4 (45)	1 (9)	40%	9 (99)
Isopora cuneata	4 (44)	2 (17)	1 (8)	42%	7 (69)
Pocillopora damicornis	3 (36)	4 (48)	1 (12)	38%	8 (96)
Porites heronensis	4 (48)	3 (27)	-	42%	7 (75)
Seriatopora hystrix	4 (48)	4 (48)	2 (24)	33%	10 (120)
Stylophora pistillata	4 (48)	6 (71)	-	44%	10 (119)

Corals stained in December 2010 were left on the reef for 4 or 12 months before being collected. A second batch was stained after 4 months (at the end of March 2011) and remained on the reef for 8 months (until December 2011). Entire colonies were then placed in a 10-15% hypochlorite solution mixed with freshwater for 12-18 h, and then dried in the sun. The linear extension was measured as the minimum distance (mm) from the point of staining to tip of appropriate branch, blade, or column using plastic callipers. Twelve replicate measurements were taken for each colony; on branching corals this involved randomly selecting 9-12 different branches. For the column and blade morphologies, 8-12 measurements per colony were taken at random points along the staining line of the columns or blades (Figure 3.2). In 1994/95, Harriott (1999) quantified annual linear extension of *A. yongei*, *Porites heronensis*, *Seriatopora hystrix* and *Pocillopora damicornis* in North Bay, Lord Howe Island, using the same methods presented in this study. Both studies conducted staining *in situ* but Harriott (1999) placed bags over individual colonies (rather than detaching them and completely sealing them within Alizarin Red solution), and corals were exposed to the stain for only 3-4 h, leading to low rates of effective staining in some corals (e.g., only one colony of *S. hystrix* was effectively stained).

Figure 3.2. Stained colony of *Porites heronensis* showing new growth (white) above the stain line (pink) on the columns.

To compare the subtropical linear extension rate of the corals species observed at Lord Howe Island to that detected on tropical reefs, a meta-analysis was conducted collecting published data from a range of tropical locations in both the Atlantic and Pacific Oceans. Where there were limited data on species-specific growth rates, data were compiled on mean growth rates for the respective genus across tropical locations.

3.3.4 Statistical analysis

To determine significant variation in the seasons for each coral species, a linear mixed-effect model (lme) was used to analyse the variance in monthly coral growth between species and seasons. First the data were evaluated for normality. The species and seasons were combined to treat the unique combination of each as categories. The lme analysed the monthly coral growth with the fixed factor of each combined species-season, and random effects of colony and branch.

Annual linear extension (mm yr^{-1}) for each species was determined by standardizing for variation in sample size (N) and time period studied (T= number of sampling months for summer (4), winter (8), annual (12)) to obtain a standardized monthly growth (μ):

$$\frac{\Sigma(N \times T \times \mu)}{\Sigma(N \times T)}$$

which was converted to annual extension. To test for temporal changes in growth rates of corals from 1994/95 to 2010/11, independent t-tests were conducted to directly compare linear extension of *A. yongei, Pocillopora damicornis, Seriatopora hystrix, and Porites heronensis*. For *A. yongei*, *Pocillopora damicornis*, and *Porites heronensis,* samples sizes were unequal to those of Harriott (1999) in 1994/95 so the Welch's t-test for unequal sample size and variance was performed. For *S. hystrix,* Harriott (1999) only recorded growth for a single colony and therefore a one-sample student's t-test was used. All analyses were completed using *R 3.1.0* (R Core Team 2014).

3.4 Results

3.4.1 Seasonal variation in growth

A total of 85 colonies from six species were stained during this study, of which 60% (51/85) of the colonies were recovered and used to quantify the linear extension (Table 3.1). Based on the linear mixed-effects model (taking into account the random effects of between and within colony variance) there was a marked variation in monthly growth rates between seasons and species (Figure 3.3). All corals grew faster during summer than in winter (Figure 3.3), but only *A. yongei* (lme, t=-4.722, df=34, p=<0.001) and *Porites heronensis* (lme, t=-3.904, df=34, p=<0.001) showed significant seasonal variation in growth rates (Table 3.2). The linear extension for *A. yongei* during the winter season (2.14 ± 0.19 mm $month^{-1}$; mean ± SE) was 40% less compared to summer (3.58 ± 0.21 mm $month^{-1}$) and for *P. heronensis* the linear extension during winter (0.48 ± 0.04 mm $month^{-1}$) was one quarter of the summer rate (1.80 ± 0.08 mm $month^{-1}$, Figure 3.3). Among species, the summer growth rate of *A. yongei* was significantly higher than all other species (Table 3.2). Interspecific variation in growth rates was much lower during winter, with growth rates of *A. yongei* much closer to that recorded for other corals (Figure 3.3). *Acropora yongei* still had the highest rate of annual linear extension (33.51 ± 1.81 mm yr^{-1}) among the species (Figure 3.4).

The lowest linear extension recorded was for *Porites heronensis* during the winter months (0.48 ± 0.04 mm $month^{-1}$, Figure 3.3) and grew significantly slower (Table 3.2). However summer-time extension rates recorded for *P. heronensis* (1.80 ± 0.08 mm $month^{-1}$) were comparable to summer rates in all other species, except *A. yongei* and *Pocillopora damicornis* (lme, t=-5.939, df=34, p=0.000, and lme, t=-3.609, df=34, p=0.001, respectively). During summer months, the slowest growing coral was *P. damicornis* (1.18 ± 0.08 mm $month^{-1}$), which also had the lowest annual linear extension rate (Figur 3.4). Mean annual linear extension rates for *Pocillopora damicornis* were 10.7 ± 0.5 mm yr^{-1}, compared to 12.1

± 1.0 mm yr^{-1} for *Porites heronensis*, 16.2 ± 0.5 mm yr^{-1} for *Stylophora pistillata*, 19.0 ± 1.1 mm yr^{-1} for *I. cuneata*, 19.6 ± 0.7 mm yr^{-1} for *Seriatopora hystrix*, and 33.5 ± 1.8 mm yr^{-1} for *A. yongei* (Figure 3.4)

3.4.2 Changes in coral growth since 1994/95

Inter-decadal changes in the mean annual linear extension were apparent for some, but not all coral species (Table 3.3). Mean annual linear extension rates for *Porites heronensis* (Table 3.5a) and *Seriatopora hystrix* (Figure 3.5b) recorded in 2010/11 were not significantly different compared to annual growth rates (10.5 ± 0.98 mm yr^{-1} and 16.7 mm yr^{-1}, respectively) recorded in 1994/95 (t=-0.484, df=6.179, p=0.32 and t=1.235, df=9, p=0.12, respectively). However, 2010/11 growth rates for both *A. yongei* and *Pocillopora damicornis* were significantly lower than had been recorded in 1994/95 (t=2.480, df=10.16, p=0.016 and t=1.794, df=11.63, p=0.049, respectively). For *A. yongei*, growth rates recorded in 2010/11 were 32% lower than recorded in 1994/95 (49.4 ± 7.0 mm yr^{-1}, Figure 3.5c)

3.4.3 Coral genus growth rates

The annual growth rate of *A. yongei* was less than half of the tropical *Acropora* growth rate (genus average 80.4 ± 7.2 mm yr^{-1}, Figure 3.5c). Similarly, *Pocillopora damicornis* subtropical growth was almost a third of that determined from tropical locations (35.6 ± 2.4 mm yr^{-1}; Fig. 5d). To contrast, the growth of columnar *Porites heronensis* is similar to that displayed by the *Porites* genus (11.4 ± 0.09 mm yr^{-1}, Figure 3.5a). It should be noted that most data from tropical locations for *Porites* spp. are massive growth form (Table 3.4). There are minimal or no comparable growth estimates for *Stylophora* spp. and *Seriatopora* spp. from tropical locations. This is because most growth studies used buoyant weight techniques (e.g., Ferrier-Pages et al. 2000) that cannot be directly compared to linear extension data.

Table 3.2. The full results for linear mixed effects model for *A. yongei, I cuneata, S. hystrix, S. pistillata, P. heronensis* and *P. damicornis* comparing each coral species and each season.

The species, intercept, value, standard error (Std. Error), degrees of freedom (DF), t value and p value are given. Bold p values indicated a significant value ($p<0.05$).

Species	Value	Std. Error	DF	t value	p value
A. yongei summer Intercept	3.592	0.21	479	16.751	
A. yongei winter	-1.432	0.30	34	-4.722	**<0.001**
I. cuneata summer	-1.709	0.30	34	-5.623	**<0.001**
I cuneata winter	-2.353	0.38	34	-6.165	**<0.001**
S. hystrix summer	-1.826	0.30	34	-6.043	**<0.001**
S. hystrix winter	-2.077	0.30	34	-6.873	**<0.001**
S pistillata summer	-1.930	0.30	34	-6.387	**<0.001**
S. pistillata winter	-2.341	0.28	34	-8.475	**<0.001**
P. heronensis summer	-1.795	0.30	34	-5.939	**<0.001**
P. heronensis winter	-3.114	0.34	34	-9.188	**<0.001**
P. damicornis summer	-2.411	0.33	34	-7.391	**<0.001**
P. damiconis winter	-2.882	0.30	34	-9.536	**<0.001**
A. yongei winter Intercept	2.159	0.21	479	10.062	
I. cuneata summer	-0.276	-3.29	34	-0.909	0.370
I. cuneata winter	0.920	0.38	34	-2.411	**0.022**
S. hystrix summer	0.394	0.30	34	-1.302	0.202
S. hystrix winter	0.644	0.30	34	-2.132	**0.040**
S pistillata summer	0.498	0.30	34	-1.646	0.109
S. pistillata winter	0.908	0.28	34	-3.287	**0.002**
P. heronensis summer	0.362	0.30	34	-1.199	0.239
P. heronensis winter	1.682	0.34	34	-4.960	**<0.001**
P. damicornis summer	0.979	0.33	34	-2.999	**0.005**
P. damiconis winter	1.449	0.30	34	-4.794	**<0.001**
I. cuneata summer Intercept	1.883	0.22	479	8.744	
I cuneata winter	0.644	0.38	34	-1.685	0.101
S. hystrix summer	0.117	0.30	34	-0.387	0.701
S. hystrix winter	0.368	0.30	34	-1.216	0.233
S pistillata summer	0.222	0.30	34	-0.731	0.470
S. pistillata winter	0.632	0.28	34	-2.282	**0.029**
P. heronensis summer	0.086	0.30	34	-0.284	0.778
P. heronensis winter	-1.406	0.34	34	-4.140	**<0.001**
P. damicornis summer	0.702	0.33	34	-2.149	**0.039**
P. damicornis winter	1.173	0.30	34	-3.873	**0.001**
I cuneata winter Intercept	1.239	0.32	479	3.924	
S. hystrix summer	0.527	0.38	34	1.383	0.176
S. hystrix winter	0.276	0.38	34	0.724	0.474
S pistillata summer	0.422	0.38	34	1.109	0.275
S. pistillata winter	0.012	0.36	34	0.033	0.974
I. cuneata winter Intercept cont.					
P. heronensis summer	0.558	0.38	34	1.465	0.152

Species	Value	Std. Error	DF	t value	p value
P. heronensis winter	0.762	0.41	34	-1.855	0.072
P. damicornis summer	0.058	0.40	34	-0.146	0.885
P. damiconis winter	0.529	0.38	34	-1.389	0.174
S. hystrix summer Intercept	1.766	0.21	479	8.292	
S. hystrix winter	0.251	0.30	34	-0.833	0.411
S. pistillata summer	0.515	0.30	34	-0.346	0.732
S. pistillata winter	0.515	0.28	34	-1.871	0.070
P. heronensis summer	0.031	0.30	34	0.104	0.918
P. heronensis winter	1.288	0.34	34	-3.811	**0.001**
P. damicornis summer	0.585	0.33	34	-1.799	0.081
P. damicornis winter	1.056	0.30	34	-3.506	**0.001**
S. hystrix winter Intercept	1.515	0.21	479	7.114	
S. pistillata summer	0.147	0.30	34	0.487	0.629
S. pistillata winter	0.264	0.28	34	-0.959	0.344
P. heronensis summer	0.282	0.30	34	0.937	0.356
P. heronensis winter	1.038	0.34	34	-3.069	**0.004**
P. damicornis summer	0.334	0.33	34	-1.028	0.311
P. damicornis winter	0.805	0.30	34	-2.673	**0.012**
S. pistillata summer Intercept	1.661	0.21	479	7.802	
S. pistillata winter	0.411	0.28	34	-1.493	0.145
P. heronensis summer	0.135	0.30	34	0.450	0.656
P. heronensis winter	1.184	0.34	34	-3.503	**0.001**
P. damicornis summer	0.481	0.33	34	-1.478	0.149
P. damicornis winter	0.952	0.30	34	-3.160	**0.003**
S. pistillata winter Intercept	1.251	0.17	479	7.184	
P. heronensis summer	0.546	0.28	34	1.985	0.055
P. heronensis winter	-0.774	0.32	34	-2.456	**0.019**
P. damicornis summer	-0.070	0.30	34	-0.234	0.817
P. damicornis winter	0.541	0.28	34	-1.967	0.057
P. heronensis summer Intercept	1.797	0.21	479	8.438	
P. heronensis winter	1.320	0.34	34	-3.904	**<0.001**
P. damicornis summer	0.616	0.33	34	-1.895	0.067
P. damicornis winter	1.087	0.30	34	-3.609	**0.001**
P. heronensis winter Intercept	0.477	0.26	479	1.818	
P. damicornis summer	0.703	0.36	34	1.955	0.059
P. damicornis winter	0.233	0.34	34	0.689	0.496
P. damicornis summer Intercept	1.181	0.25	479	4.801	
P. damicornis winter	0.471	0.33	34	1.447	0.157

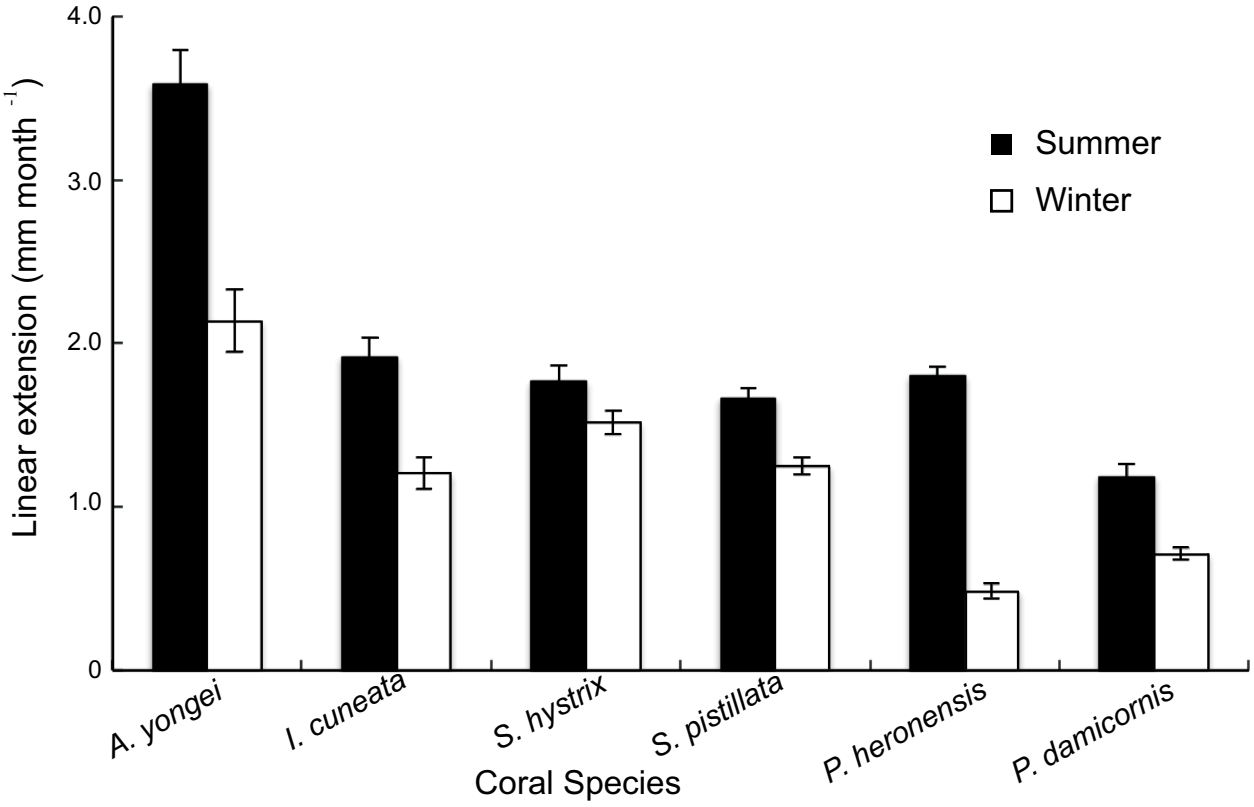

Figure 3.3. Seasonal linear extension rates (mm month^{-1} ± SE) of corals *Acropora yongei*, *Isopora cuneata*, *Seriatopora hystrix*, *Stylophora pistillata*, *Porites heronensis*, and *Pocillopora damicornis* at Lord Howe Island for the summer (Dec 10-Mar 11) and winter (Apr 11-Nov 11).

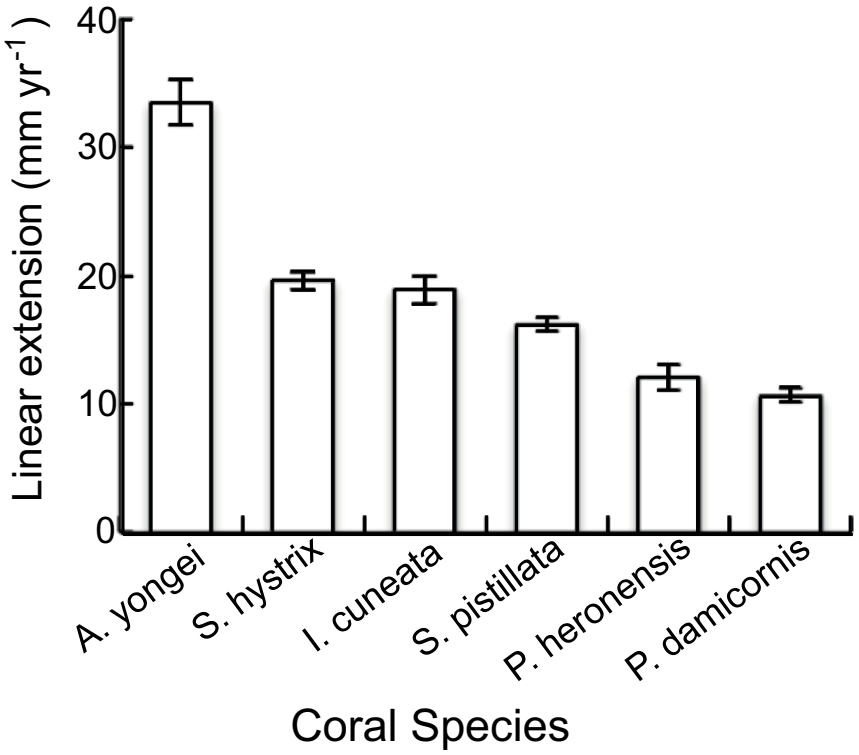

Figure 3.4. The annual linear extension rates (mm year^{-1} ± SE) of *Acropora yongei, Seriatopora hystrix, Isopora cuneata Stylophora pistillata, Porites heronensis* and *Pocillopora damicornis* at Lord Howe Island for Dec 2010-Dec 2011.

Table 3.3. Values utilized for the Welch's t-test (*Acropora yongei, Pocillopora damicornis, Porites heronensis*) and student's t-test (*Seriatopora hystrix*) for Alizarin Red stained corals in both the present study and Harriott (1999).

Species	Mean (mm/yr)	Std. Dev	N	Harriott (1999) (mm/yr)	Harriott N	t-value	Df	P
A. yongei	33.51	18.03	9	49.4	10	2.480	10.16	0.016
P. damicornis	10.67	5.19	8	16.1	7	1.794	11.63	0.049
P. heronensis	12.09	8.64	7	10.5	6	-0.484	6.179	0.32
S. hystrix	19.64	7.53	10	16.7	1	1.235	9	0.12

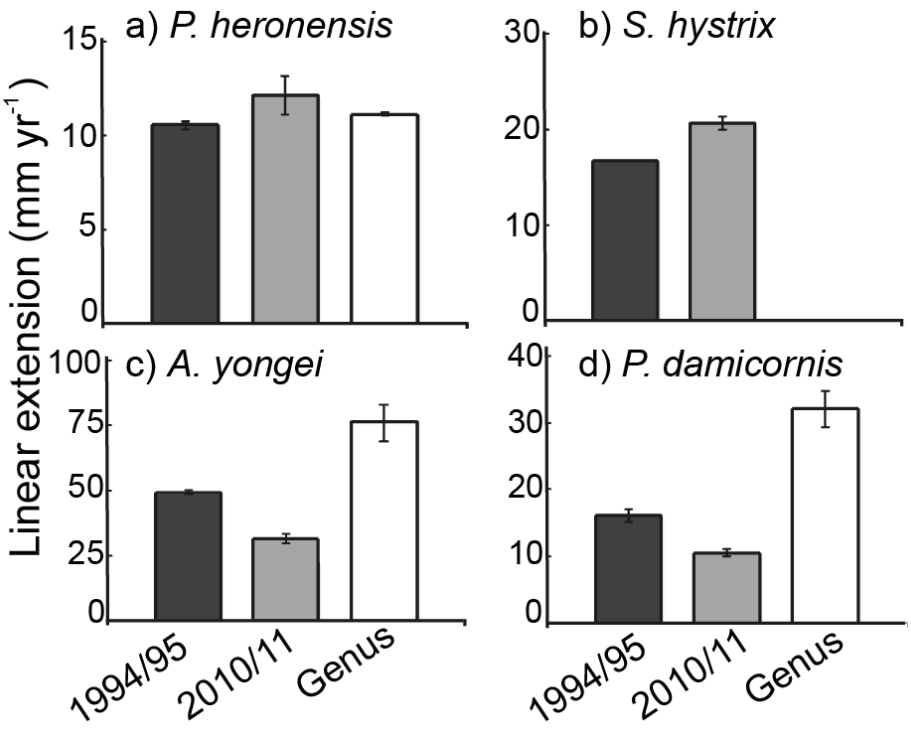

Figure 3.5. Comparison of annual linear extension rates (mm year^{-1} ± SE) for a) *Porites heronensis*, b) *Seriatopora hystrix*, c) *Acropora yongei*, and d) *Pocillopora damicornis* from 1994/5 published in Harriott (1999), the present study conducted in 2010/11 and the averaged genus linear extension from metadata analysis. For the list of linear extension rates utilised see Table 3.4.

Table 3.4. Metadata for *Acropora, Pocillopora* and *Porites* to determine genus annual linear extension rate (mm yr^{-1}). If a range was given, the average value was utilized. GBR=Great Barrier Reef.

Coral Species	Location	Latitude	Annual extension (mm yr^{-1})	Reference
Acropora austera	Maldives	18	63.0	Morgan & Kench 2012
Acropora cervicornis	Florida	24	109.5	Shinn 1966
A. cervicornis	Jamaica	18	141.0	Tunnicliffe 1983
A. cervicornis	Jamaica	18	102.0	Crabbe 2009
A. cervicornis	Jamaica	18	110.0	Lewis et al. 1968
A. cervicornis	US Virgin Is	17	100.0	Gladfelter 1984
A. cervicornis	US Virgin Is	17	71.0	Gladfelter et al. 1978
A. cervicornis	Barbados	13	145.0	Glynn 1973
Acropora digitifera	Maldives	18	38.0	Morgan & Kench 2012
Acropora elseyi	Lizard Island, GBR	-15	38.0	Oliver 1985
Acropora florida	Lizard Island, GBR	-15	45.0	Oliver 1985
Acropora muricata	Maldives	18	59.0	Morgan & Kench 2012
A. muricata	Guam	12	33.0	Neudecker 1981
A. muricata	Phuket, Thailand	8	80.0	Charuchinda & Hylleberg 1984
A. muricata	Sri Lanka	7	118.5	Jinendradasa & Ekarame 2000
A. muricata	Middle Reef, GBR	-13	63.0	Browne 2012
A. muricata	Lizard Island, GBR	-15	71.0	Oliver 1985
A. muricata	Davies Reef, GBR	-19	80.0	Oliver et al. 1983
A. muricata	Dampier Archipelago	-21	118.5	Simpson 1988
Acropora gemmifera	Maldives	18	24.0	Morgan & Kench 2012
Acropora lamarcki	Maldives	18	32.0	Morgan & Kench 2012
Acropora nasuta	Maldives	18	5.0	Morgan & Kench 2012
Acropora nobilis	Lizard Island, GBR	-15	41.0	Oliver 1985
Acropora palmata	Jamaica	18	71.0	Crabbe 2009
A. palmata	US Virgin Is	17	64.5	Gladfelter et al. 1978
A. palmata	Curacao	12	88.0	Bak 1983
A. palmata	Curacao	12	82.0	Bak et al. 2009
A. palmata	Curacao	12	90.0	Bak 1976
Acropora prolifera	US Virgin Is	17	59.0	Gladfelter et al. 1978
Acropora pulchra	Philippines	10	119.0	Yap & Gomez 1985
A. pulchra	Yap	9	136.5	Tamura & Hada 1932

Coral Species	Location	Latitude	Annual extension (mm yr^{-1})	Reference
Acropora robusta	Lizard Island, GBR	-15	55.0	Oliver 1985
Acropora valenciennesi	Sulawesi, Indonesia	6	202.0	Crabbe and Smith 2005
Acropora genus			**80.4 ± 7.2**	
Pocillopora damicornis	Hawaii	20	13.5	Edmondson 1929
P. damicornis	Hawaii	20	13.5	Maragos 1972
P. damicornis	Guam	12	30.0	Neudecker 1981
P. damicornis	Costa Rica	11	52.5	Jimenez & Cortes 2003
P. damicornis	Panama	9	42.0	Glynn & Steward 1973
P. damicornis	Costa Rica	8	35.0	Guzman & Cortes 1989
P. damicornis	Panama	8	54.0	Wellington 1982
P. damicornis	Panama		37.0	Glynn 1976
P. damicornis	Panama	8	28.0	Manzello 2010
P. damicornis	Galapagos	1	22.0	Glynn et al. 1979
P. damicornis	Lizard Island, GBR	-15	37.0	Oliver 1985
P. damicornis	Low Island, GBR	-17	33.5	Stephenson & Stephenson 1933
P. damicornis	Palm Island, GBR	-19	43.0	Oliver 1985
P. damicornis	Dampier Archipelago	-21	45.0	Simpson 1988
Pocillopora elegans	Costa Rica	11	46.5	Jimenez & Cortes 2003
P. elegans	Costa Rica	8	35.0	Guzman & Cortes 1989
P. elegans	Panama	8	27.0	Manzello 2010
Pocillopora eydouxi	Enewotak Atoll	11	50.0	Buddemeier et al. 1974
P.eydouxi	Costa Rica	11	31.0	Jimenez & Cortes 2003
Pocillopora inflata	Costa Rica	11	32.0	Jimenez & Cortes 2003
Pocillopora meandrina	Costa Rica	11	39.5	Jimenez & Cortes 2003
Pocillopora genus			**35.6 ± 2.4**	
Porites sp.	Hawaii	20	9.0	Edmondson 1929
Porites sp.	Sulawesi, Indonesia	-6	10.0	Maier et al. 2004
Porites sp.	GBR	-12 to -23	14	De 'ath et al. 2009
Porites sp.	Northern GBR	-13 to -17	14.0	Cooper et al. 2008
Porites sp.	Central GBR	-18	11.5	Barnes & Lough 1993
Porites sp.	GBR	-12 to -22	13	Lough & Barnes 2000
Porites (branching)	Yap	9	9.0	Tamura &Hada 1932
Porites astreoides	Bermuda	32	2.0	Logan & Tomascik 1991
P. astreoides	Florida	24	4.0	Kissling 1977

Coral Species	Location	Latitude	Annual extension (mm yr^{-1})	Reference
P. astreoides	Mexico	20	30.0	Crook et al. 2013
P. astreoides	Jamaica	18	8.0	Hughes & Jackson 1985
P. astreoides	Jamaica	18	4.0	Crabbe 2009
P. astreoides	Jamaica	18	5.0	Huston 1985
P. astreoides	US Virgin Is	18	3.5	Gladfelter et al. 1978
P. astreoides	US Virgin Is	18	3.0	Hubbard & Scaturo 1985
P. astreoides	Barbados	13	6.5	Strean et al. 1977
P. astreoides	Panama	9	5.0	Guzman et al. 1991
Porites compressa	Hawaii	20	10.5	Edmondson 1929
Porites cylindrica	Maldives	18	7.0	Morgan & Kench 2012
P. cylindrica	Guam	12	25.0	Neudecker 1981
Porites lobata	Hawaiiian Archipelago	20	13.0	Griggs 1982
P. lobata	Red Sea	29	7.0	Klein & Loya 1991
P. lobata	Maldives	18	15.0	Morgan & Kench 2012
P. lobata	Enewotak Atoll	11	9.0	Buddemeier et al. 1974
P. lobata	Philippines	10	13.0	Patzold 1984
P. lobata	Costa Rica	8	15.0	Guzman & Cortes 1989
P. lobata	Java	-7	14.0	Edinger et al. 2000
P. lobata	American Samoa	-14	10.0	Smith et al. 2007
P. lobata	Rib Reef	-18	13.5	Barnes & Lough 1989
P. lobata	Wheeler Reef	-19	19.0	Alibert & McCulloch 1997
P. lobata	Davies Reef	-19	8.0	Alibert & McCulloch 1997
Porites lutea	Red Sea	30	15.0	Al-Rousan et al. 2002
P. lutea	Enewotak Atoll	11	14.0	Buddemeier et al. 1974
P. lutea	Enewotak Atoll	11	8.0	Highsmith 1979
P. lutea	Eniwetok Atoll	11	14.0	Knutson et al. 1972
P. lutea	Thailand	8	12.5	Alibert & McCulloch 1997
P. lutea	Thailand	8	18.5	Scoffin et al. 1992
P. lutea	Thailand	8	17.0	Tanzil et al. 2009
P. lutea	Sulawesi	6	9.5	Crabbe & Smith 2005
P. lutea	French Polynesia	-18	10.0	Bessat & Buigues 2001
P. lutea	Davies Reef , GBR	-19	15.0	Alibert & McCulloch 1997
P. lutea	Ningaloo Reef, WA	-22	14.0	Muller et al. 2004
Porites mayeri	Davies Reef, GBR	-19	13.0	Alibert & McCulloch 1997
Porites porites	Jamaica	18	13.0	Davies 1989
Porites genus			**11.4 ± 0.9**	

3.4.4 Environmental data

From the *in situ* temperature loggers at Lord Howe Island, the average SST during summer months was 24.5^{o}C and daily mean values ranged from 21.4 ^{o}C to 27.8 ^{o}C (December 2010 to March 2011). In comparison, there was an average of 20.4^{o}C in April to November 2011 (Figure 3.6a), for which daily mean values ranged from 15.6 ^{o}C to 25.1 ^{o}C. The average *in situ* SST at Lord Howe Island for the entire 2010/11 study period was 21.8°C.

Satellite SST weekly mean values were consistent with the *in situ* logger data (Figure 3.6b) but with a suppressed range in each season, as was expected due to the reduced temporal resolution of the (weekly) satellite data; viz., summer temperatures ranged 22.28–25.04 ℃ with an average of 24.07 ℃, while for winter the range and average were 18.46–24.45 ℃ and 20.64 ℃, respectively. Linear trends in the satellite SST for 1985-2012 were 0.110 (summer), 0.133 (winter), and 0.147 (annual) ℃ decade^{-1}. When considering only the period 1995-2010, encompassing the growth rate observations, temperature trends were 0.271 (summer), 0.052 (winter), and 0.175 (annual) ℃ decade^{-1}. Accumulated thermal stress (DHW) exceeded 8 ℃-weeks in three years: 1998 and 2010 (coincident with observed bleaching; Harrison et al. 2011) and 2009.

Cruise data from May 1995 recorded SST of 21.61 ℃ and SSS of 35.42 psu, from which the total alkalinity, A_T, was estimated as 2328 μmol kg^{-1}. Combined with the measured partial pressure of CO_2 (309.01 μatm) the aragonite saturation state was estimated as 3.64. The corresponding values from the April 2008 data were 22.97 ℃, 34.71 psu, 2284 μmol kg^{-1}, 334.71 μatm, and 3.49, respectively. This represents an average reduction in the aragonite saturation state of 0.32 % yr^{-1} during the 13-yr period.

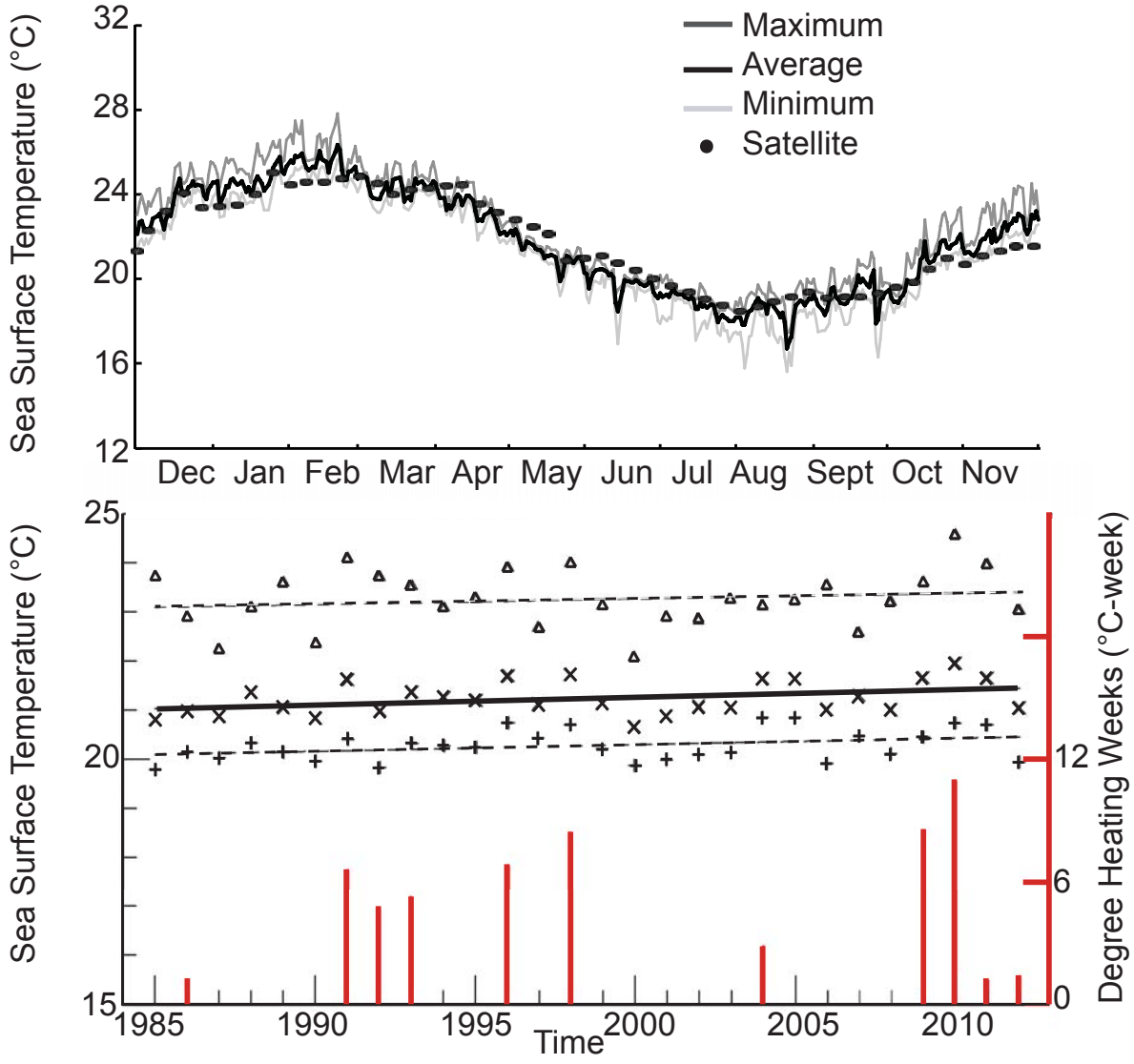

Figure 3.6. (a) The variation in sea surface temperature (°C) during the 2010-2011 study period at Lord Howe Island. The daily maximum (dark grey), average (black) and minimum (light grey) *in situ* temperatures recorded at North Bay within the lagoon system are displayed (AIMS 2014) along with the weekly satellite temperatures (circles). (b) History of sea surface temperature and thermal stress for the period 1985-2012. Annual (×), summer (Dec-Mar, Δ) and winter (Apr-Nov, +) mean temperature and linear trends are displayed, along with the annual maximum Degree Heating Weeks (red).

3.5 Discussion

3.5.1 Temporal declines in coral growth

This study revealed substantial (<32 %) and significant declines in the rates of linear extension for *A. yongei* and *Pocillopora damicornis* from 1994/95 to 2010/11 (Table 3.3). This is a marked contrast to the work by Cooper et al. (2012) who revealed increasing calcification rates of *Porites* at high latitude reefs in Western Australia. Cooper et al. (2012) showed that beneficial effects of increasing temperature at high latitudes were directly proportional to the extent of warming. However, if the rate of warming is too high then it is almost certain that maximum temperatures will exceed the local thermal optimum, potentially leading to net negative effects on coral growth (Foster et al. 2014). Declines in coral growth recorded during this study may be attributable to sustained increases in temperature, which has increased 0.262 ℃ from 1994/95 to 2010/11. Alternatively, suppressed growth of corals in 2010/11 may be directly attributable to acute thermal stress and associated coral bleaching (Harrison et al. 2011) in the 2009/10. During the 2009/10 summer, *in situ* temperature measurements exceeded 28°C (~2–3 °C above normal summer maximum, Harrison et al. 2011); the satellite accumulated thermal stress (DHW) in the lagoon exceeded 10.8 ℃-weeks (Figure 3.6b). Extensive bleaching (across >90% of corals) was recorded at some specific locations (Sylph's Hole and Comet's Hole) in 2010 (Harrison et al. 2011), though elsewhere at Lord Howe Island coral bleaching was largely limited to pocilloporid and *Montipora* corals. Aside from bleaching, elevated temperatures may temporally suppress growth of corals (e.g., Cantin & Lough 2014), and it may be that low growth rates recorded for *A. yongei* and *Pocillopora damicornis* corals in 2010/11 are directly attributable to the thermal anomaly (if not actual bleaching) in the previous year. No significant temporal change in growth was recorded for *Porites heronensis* or *Stylophora pistillata* possibly suggesting they are more resilient to increasing temperatures (but see McClanahan et al. 2009), though only

one colony of *S. pistillata* was sampled in 1994/95, limiting confidence in earlier estimates of coral growth for this species.

Temporal declines in the growth of branching species have been reported in the tropics (e.g., Bak et al. 2009, Manzello 2010) and are invariably linked to negative effects of sustained and ongoing climate change. Bak et al. (2009) found a 7.2-10.7 % reduction in linear growth of *A. palmata* between 1971-1973 and 2002-2004 in the Caribbean (which equates to declines of 0.23-0.35 % yr^{-1}). They attributed the decline to reduced carbonate saturation in the Caribbean (Gledhill et al. 2008), which can lead to a decrease in coral calcification causing a reduction in linear extension of corals (Kleypas et al. 1999b). Similarly, Manzello (2010) recorded a one-third reduction in extension rates of *Pocillopora* in Pacific Panama from 1974 to 2006 (or an annual decline of 0.9 % yr^{-1}). Manzello (2010) attributes this decline to recent effects of ocean acidification and/ or increases in the proportion of heat-tolerant zooxanthellae within host corals (in direct response to past thermal stress events), which may suppress growth. Rates of decline in coral growth recorded previously for branching corals (e.g., 0.23-0.35% yr^{-1} to 0.9% yr^{-1}, Bak et al. 2009 and Manzello 2010, respectively) broadly correspond to the rates of decline recorded at Lord Howe for *A. yongei* (2.0 % yr^{-1}) and *Pocillopora damicornis* (2.13 % yr^{-1}), but it is unclear whether these declines are attributable to increasing temperature (be it sustained increases or acute thermal stress events) or declines in aragonite saturation.

3.5.2 Carbonate chemistry

The Southern Pacific Ocean is already under-saturated with respect calcium carbonate (Kleypas et al. 1999a). Decadal declines in the saturation state of the Pacific have been observed (0.34% yr^{-1}, Feely et al. 2012, and 0.32% yr^{-1} demonstrated here) and are projected to accelerate (Orr et al. 2005), which may be limiting the available aragonite for coral accretion at Lord Howe Island. Importantly, we found no change in growth of *Porites*

heronensis compared to that in 1994/95 (Harriott 1999). This supports work based on volcanic carbon seeps by Fabricius et al. (2011) where they found *Porites* may be insensitive to changes in pH (a decrease from 8.1 to 7.8), whereas branching species were adversely affected. Therefore, if ocean acidification is limiting the growth of *A. yongei* and *Pocillopora damicornis*, this study may represent the first documented evidence that climate-related changes in seawater chemistry are already affecting scleractinian corals at high latitude reefs. In support of this hypothesis, there is evidence that *Pocillopora* and *Acropora* corals are much more susceptible to changes in seawater chemistry than *Porites* corals (e.g., Fabricius et al. 2011, Edmunds et al. 2012), which would explain interspecific differences in responses of the corals at Lord Howe Island.

Benefits to productivity from increasing temperatures in subtropical locations may be offset by deleterious effects of declining aragonite saturation (van Hooidonk et al. 2014). Unlike temperature, which is inherently variable on multiple time-scales, interannual changes in ocean acidification will be gradual but persistent, leading to sustained increases in the physiological costs for corals already growing in areas with low levels of aragonite saturation (Hoegh-Guldberg & Bruno 2010). Yet, it is unclear how the corals at Lord Howe will persist as there is potential for extensive buffering of seawater chemistry within reef systems (Anthony et al. 2011) due to the extensive growth of macroalgae and seagrass (Hoey et al. 2011), combined with strong inter-specific variation in sensitivity of corals to ocean acidification (Fabricius et al. 2011, Edmunds et al. 2012). It is likely therefore, that high latitude reefs will provide some measure of refuge for corals against extreme warm events that will increasingly occur on tropical coral reefs. However, if ocean acidification is already limiting the growth of some branching species at Lord Howe, the algal buffering capacity may not be sufficient to prevent the switch from a coral-dominated reef to an algae-

dominated reef system in the future (Koch et al. 2013). Such effects will only become apparent through careful ongoing monitoring of coral growth at these locations.

Aside from climate-related changes in thermal regimes and seawater chemistry, temporal declines in linear extension of the key habitat-forming corals at Lord Howe Island could be attributed to changes in water quality, salinity, the incidence of disease, increased competition, and/or coral predation, all of which influence coral growth (e.g., Oliver et al. 1983, Hudson et al. 1994, Kleypas et al. 1999a, Langdon et al. 2000, Lough & Barnes 2000, Crabbe & Smith 2005, Guinotte & Fabry 2008). While there is no published data on long-term changes in water quality or salinity at Lord Howe Island, land-based sources of pollutants are carefully regulated under the Lord Howe Island Act of 1981, in which the entire island in 1982 was listed as a UNESCO World Heritage Site of global significance. Importantly, 70% of the island is subject to significant constraints on development and construction (UNESCO 2014), such that any changes in water quality are expected to be minimal and very localised (e.g., Harriott et al. 1995), largely concentrated in Sylph's Hole. Coral cover reported in each of the two study periods (1994-95 and 2010-11) was very similar (Harriott et al. 1995, Hoey et al. 2011), further suggesting changes in coral growth are not due to fundamental changes in biotic interactions (e.g., competition among corals). There was also no evidence of coral disease (or any other obvious constraints on coral growth) reported during the latest survey.

3.5.3 Seasonal coral growth trends

The growth of corals at latitudinal extremes tends to be limited by low temperature and light during winter months (Crossland 1984, Kleypas et al. 1999a). At Lord Howe Island, the average SST during summer months was 24.5^{o}C and ranged from 21.4 ^{o}C to 27.9 ^{o}C (December to March), versus an average of 20.4^{o}C (ranging from 15.6 ^{o}C to 25.1 ^{o}C) in April to November (AIMS 2014, Figure 3.6). The growth rates for all species considered in this

study (*A. yongei, Seriatopora hystrix, I. cuneata, Stylophora pistillata, Porites heronensis* and *Pocillopora damicornis*) were lower during winter, compared to summer months. Moreover, the annual growth of *A. yongei* and *Pocillopora damicornis* at Lord Howe Island was well below the annual growth recorded for the respective genera of corals in tropical locations (Figure 3.5). This data suggest that winter temperatures do constrain coral growth at Lord Howe Island, albeit only very slightly for some coral species. Contrary to previous studies (e.g., Fallon et al. 1999) there was no cessation of growth during winter months. Temperature trends in winter over the 28-yr satellite time-series were 20% greater than in summer, suggesting the potential for increasing winter productivity. Sustained increases in ocean temperatures (Lough 2012) may therefore have a beneficial effect on coral growth at this high latitude location (e.g., Cooper et al. 2012) enabling higher or sustained growth during winter months. The questions is whether increased summer temperatures will start to have a negative effect on coral growth (Foster et al. 2014), thereby offsetting any potential benefit of warmer, more-productive winters. It is also unclear to what extent winter growth is limited by low temperature versus low light availability (Grigg 1982), as mean daily solar radiation in the winter in the subtropics can be 35% that of the summer maximum (Crossland 1981).

This study has revealed significant temporal (inter-decadal and seasonal) variation in the linear extension of corals at Lord Howe Island. Importantly, Lord Howe Island is situated at the latitudinal limit of reef accretion (Spalding et al. 2001) and increasing temperatures are expected to have beneficial effects on reef growth at such high latitudes (*sensu* Cooper et al. 2012). However, this study revealed a <32 % decline in growth rates of *A. yongei* and *Pocillopora damicornis* in 2010/11 compared to 1994/95, which may attributable to either excessive increases in sea surface temperature (inter-decadal or seasonal) or climate related changes in seawater chemistry, specifically declines in already-low levels of aragonite

saturation. While further work is required to establish the relative contributions of increasing temperature versus declining aragonite saturation to temporal changes in growth of the dominant reef-building corals at Lord Howe Island, either way it appears that climate change is having negative effects on corals even at subtropical locations. While some subtropical locations may provide refuges for biodiversity during extreme climate change (Greenstein & Pandolfi 2008), our data suggest that high latitude reef coral assemblages are likely to be affected due to climate change.

Chapter 4 Long-term changes in coral growth rates at Davies Reef, central Great Barrier Reef, Australia

4.1 Abstract

Demographic processes such as growth can have an important influence on the population and community structure of reef-building corals. Moreover, ongoing changes in environmental conditions (e.g., ocean warming and acidification) may be causing long-term changes in coral growth. This study quantified contemporary growth rates (linear extension and calcification) for the staghorn coral, *Acropora muricata,* at Davies Reef, central Great Barrier Reef Australia. Growth rates were measured in each of three different depths (5, 10, and 15 m depth) and over two years (2012-2014) at 6-month intervals to assess both seasonal and interannual variability. Results of this study were directly compared to equivalent measurements made in 1980-82 at the exact same location, assessing how growth rates of *A. muricata* may have changed over three decades. To assist in understanding inter-annual variability in coral growth this study examined annual growth bands for cores taken from massive *Porites* providing continuous growth and environmental records of flooding history for Davies Reef over the entire period (1979-2012). Linear extension rates of *A. muricata* were significantly lower in 2012-14 compared to 1980-82, especially at depth (10 and 15 m depth). In contrast, calcification rates of massive *Porites* were highly variable among years, but there was no consistent long-term change or decline. Given that branching corals, such as *A. muricata*, contribute most to habitat complexity and reef structure, declines in growth rates of these corals will likely have major ramifications for the structure of coral reef ecosystems.

4.2 Introduction

Coral reefs are highly dynamic ecosystems affected by multiple disturbances, such as the sustained and ongoing effects of global climate change (Walther et al. 2002, Carpenter et al. 2008). Increasing frequency, severity and diversity of disturbances are leading to declines in coral cover across many reef systems (Carpenter et al. 2008, De'ath et al. 2012), which is of considerable concern because corals are important in providing structural complexity, food and shelter. Consequently, widespread and significant coral loss has corresponding impacts on the abundance and diversity of reef-associated organisms (Pratchett et al. 2008, Coker et al. 2014), leading to declines in reef productivity and compromising ecosystem function (Jones et al. 2004, Anthony et al. 2008, Descombes et al. 2015).

The sustained and ongoing effects of global climate change, including both increasing surface temperature (SST) and changes in seawater chemistry, are expected to have major effects on coral populations and communities (Hoegh-Guldberg et al. 2007, Kleypas et al 1999b, Lough 2012). Most notably, subtle changes in local temperature regimes can cause extensive coral bleaching (Jokiel & Coles 1977, 1990), which can result in extensive coral mortality (Hoegh-Guldberg 1999, Baker et al. 2008). However, ocean warming may also have a range of sublethal effects, often leading to declines in coral growth (reviewed in Chapter 2 - Pratchett et al. 2015). There is already evidence corals are being pushed beyond their upper thermal optima leading to suppressed growth in the warmest periods of the year (Foster et al. 2014).

Along with increasing SST, ocean acidification is of considerable concern for the growth and survival of corals (Hoegh-Guldberg et al. 2007, Guinotte & Fabry 2008). The hydrolysis of CO_2 in seawater increases the hydrogen ion concentration, reducing oceanic pH along with concurrent reductions of the freely available carbonate ion [CO_3^-] reef building corals use to form calcium carbonate skeletons (Feely et al. 2004, Orr et al. 2005, IPCC

2013). Changes in seawater chemistry will have severe consequences for calcifying organisms (Gattuso et al. 1999, Orr et al. 2005); for corals, reduction in calcification rates and linear growth (Langdon et al. 2000, Jokiel et al. 2008, Venn et al. 2013) are evident. Notably, some coral taxa, specifically branching species, seem to be more affected by high CO_2 conditions (Fabricius et al. 2011, Edmunds et al. 2012).

Changes in coral growth (calcification and linear extension) of multiple species have been observed globally due to changing environmental conditions (Bak et al. 2009, De'ath et al. 2013, Cantin et al. 2010, Chapter 3 - Anderson et al. 2015). For massive corals, changes in linear extension rates and calcification can be determined retrospectively by taking cores from long-lived colonies and quantifying growth parameters (linear extension, skeletal density and calcification) from the annual density banding couplets visible under X-ray (Buddemeier et al. 1974, Lough 2008). Sustained declines in the growth of massive corals have been revealed in several locations, including tropical Australia (Cooper et al. 2008, De'ath et al. 2013), the Red Sea (Cantin et al. 2010) and Thailand (Tanzil et al. 2013), which are mainly attributed to thermal stress. In contrast, at high latitude reefs, growth rates (calcification) of massive *Porites* have increased with increasing temperature anomaly (Cooper et al. 2012), but columnar *Porites heronensis* linear extension has remained similar to 1994/95 (Chapter 3 - Anderson et al. 2015). For branching corals, annual growth patterns are not readily preserved in the skeleton due to secondary infilling (Roche et al. 2010) so the only way to detect temporal changes in coral growth is to compare to equivalent measurements taken at different time periods (Bak et al. 2009, Chapter 3 - Anderson et al. 2015). Branching coral growth rates have shown declines in both tropical (Bak et al. 2009, Manzello 2010) and subtropical regions (Chapter 3 - Anderson et al. 2015). The decline in growth rates of branching *Acropora palmata* (0.23-0.35 % yr^{-1}) (Bak et al. 2009), *Pocillopora* (0.9 % yr^{-1}) (Manzello 2010), and, *Acropora yongei* and *Pocillopora damicornis*

(2.0 % yr^{-1}) (Chapter 3 - Anderson et al. 2015), were attributed to a declining saturation state and/or thermal stress.

The aim of this study was to quantify contemporary rates of coral growth (specifically, linear extension and calcification) for both a branching coral, *Acropora muricata,* and massive *Porites* at Davies Reef. Importantly, linear extension rates of *A. muricata* were quantified from May 1980 - Jan 1982 by Oliver (1987) enabling direct comparison of growth rates in corals over three decades. In each period (1980-82 and 2012-14), growth rates of *A. muricata* were quantified at 5, 10 and 15 m, testing whether long-term changes in coral growth were consistent among these habitats. Coral cores were analysed of massive *Porites*, quantifying calcification rates from 1979-2012, to help assess if growth rates are changing due to natural variability in environmental conditions or gradual changes associated with climate change,. Massive *Porites* cores provided continuous records of growth and flood events at Davies Reef to provide insight into natural variability in coral growth during the 30-year period.

4.3 Methods

4.3.1 Coral Growth

This study was conducted at Davies Reef (S 18°49.801, E 147°39.097) a central reef on the Great Barrier Reef, Australia. Davies Reef is located ~100 km east-northeast of Townsville, Queensland. *A. muricata* corals were sampled on the western, leeward side of the reef front (Figure 4.1)

Acropora muricata (nee *A. formosa*) was abundant in the deep lagoonal outcroppings on the reef crest, as well as, in shallow depths near the crest. Corals were first stained with Alizarin dye at Davies Reef on October 21, 2012. The same staining technique was employed in the present study, following Oliver (1987) allowing for direct comparison of coral linear

extension between 1980-82 and 2012-2014. However, Oliver (1987) stained corals at smaller intervals whereas we investigated biannual growth. At 5, 10 and 15 metre depth, a total of 60 branches were stained each sampling period. Each branch was enclosed in a 1 litre plastic bag and secured with a rubber band. A syringe was inserted under the elastic, injecting 12 mg L^{-1} of Alizarin dye into each bag. As the corals use the alizarin stained seawater for calcification, the red dye gets incorporated into the skeleton as a distinct known timepoint. After four hours, the bags were removed and the colonies tagged at the base for relocation.

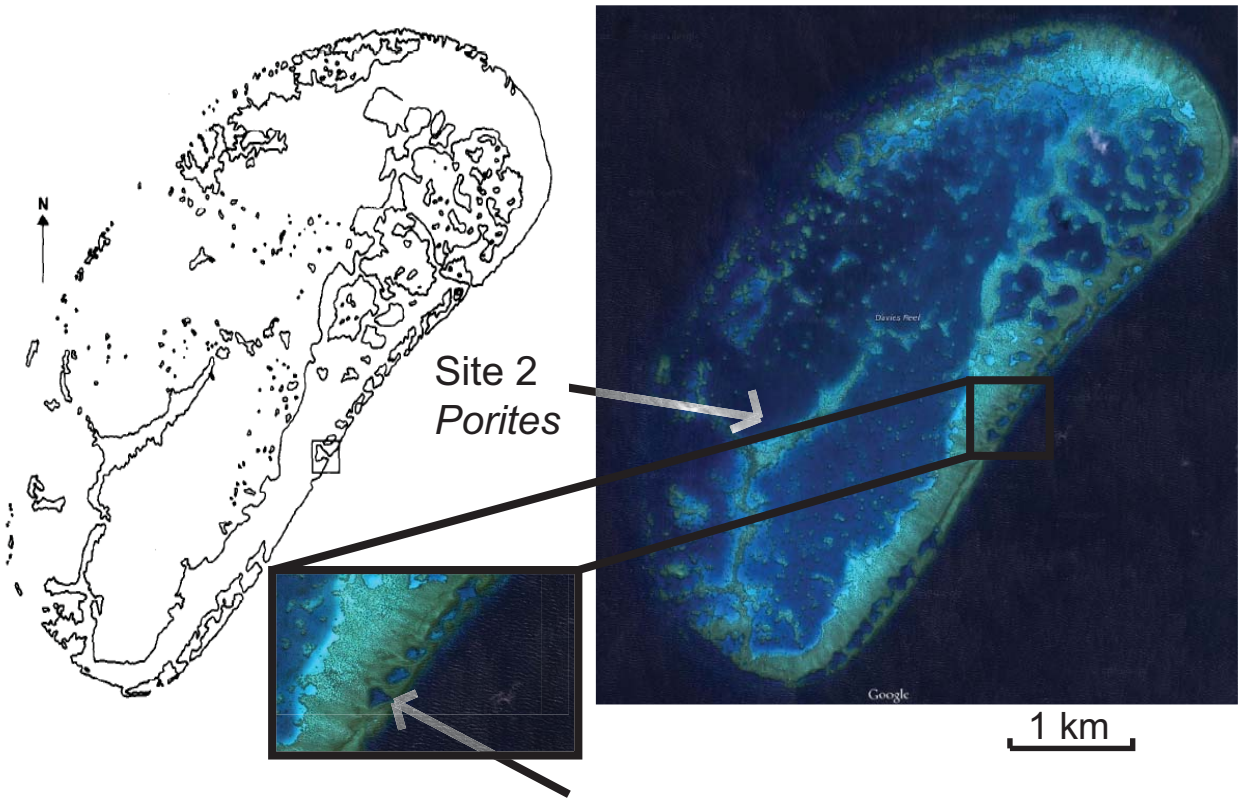

Figure 4.1. Site Map for Davies Reef with the original map from Oliver 1987 (left) and adapted Google Earth map (2015) on the right.

At the end of the 2012/13-summer growth period (Oct 2012 - April 2013), coral fragments (maximum 10 cm) of each stained branch tip were removed using bone cutters. In addition, another 60 branches taken from 20 colonies were stained using the same methodology as previously described. The corals stained in April 2013 were collected in late October 2013 quantifying the 2013-winter linear extension (May 2013 - Oct 2013). This pattern of staining and collection continued for another year determining the 2013/14-summer (Nov 2013 - April 2014) and 2014-winter (May 2014 - Oct 2014) growth rates, encompassing a 2-year assessment of coral growth, taking into account both seasonal variation and annual variation.

After collection, coral fragments were placed into 10 % diluted sodium hypochlorite to remove the tissue exposing the stained skeleton. The linear extension of the branch was measured on the axial branch (mm) from the point of stain line to the branch tip using plastic callipers. To determine bulk skeletal density, branches were cut along the stain line with an Allegro Supercut sliding geological saw with a 2 mm saw blade ensuring no stain was visible on the skeleton and the cut portion represented only new growth. The dry weight (g) of the cut branch tips was measured. Branches were dipped in paraffin wax and the total enclosed volume was determined using water displacement technique (Oliver et al. 1983, Browne et al. 2012). Skeletal bulk density was then determined by the dry weight divided by enclosed volume. Calcification rates of the branch were calculated by multiplying the linear extension by the density (Lough & Barnes 2000, Browne et al. 2012).

Massive *Porites* coral cores were used to evaluate inter-annual variability in coral growth throughout the time period of interest (1979-2012) by quantifying the growth parameters from the annual high and low density-banding couplets. Coral cores were collected from a total of 7 *Porites* colonies on May 7-13, 2013. Colonies were collected from 5-7 m depth in the back reef lagoon of Davies Reef (Figure 4.1, Site 2, -18.8304°S,

147.6321°E). Coral slices were prepared following Lough & Barnes (2000). Cores were air dried, then mounted on aluminium trays and three 6.5 mm thick slices removed. Slices were then X-rayed and converted to positive prints. Gamma densitometry was used to measure skeletal density at 0.254 mm sampling intervals along the maximum vertical growth axis on the slice from each core that showed clear annual density bands (Barnes & Lough 1989). Since the high-density bands are formed in summer, and low-density band in winter for GBR *Porites* colonies, sequential low-density peaks are used to produce an annual growth chronology from the living tissue layer based on the date of collection of each core.

Once the coral cores are dated growth parameters can be determined by measuring the distance between adjusted low-density minima such as, annual linear extension (cm yr^{-1}), annual average skeletal density (g cm^{-3}), and annual calcification rate (g cm^{-2} yr^{-1}). In addition, the occurrence and intensity of luminescent lines were visually assessed along the coral core slices (measured by fluorescence spectrometry), following Lough (2011). The annual range of luminescence between the previous winter minimum and summer maximum was determined as a proxy for measuring freshwater flood events that had impacted the mid shelf reef at Davies Reef. Some cores dated back further than the period of interest (1979-2012) and the whole range was utilized for luminescence signatures to understand the historic impact of freshwater flood events on this mid-shelf reef.

4.3.2 Environmental Parameters

Light and sea surface temperature

Variation in light intensity and SST with depth were measure with a HOBO pendant ® temp/light data logger, which was deployed from October 30, 2013 until May 08, 2013. Overtime, biofilm covered the light sensor obstructing the readings; therefore variation in light intensity (lux) with depth was quantified for the first month of deployment of each sensor (Oct 30-Nov 30, 2013). Daily *in situ* seawater temperatures at 4 m depth during the

course of the study (Nov 2012-Oct 2014) was determined from the AIMS, Davies Reef automatic weather station (http://data.aims.gov.au/metadataviewer/uuid/5fc91100-4ade-11dc-8f56-00008a07204e). Temperature sensors (Omega Interchangeable Thermistors) instantaneously record sea temperatures every 30 minutes and the remote station provides real-time data via HF radio signals (AIMS 2015).

To provide context since the early 1980s (Barnes 1983, 1988, Barnes & Devereux 1984), a temperature time-series was extracted for 1980-2014 from the Extended Reconstructed Sea Surface Temperature (ERSST) dataset (2° and monthly resolution). Satellite SST data of higher-resolution, both spatially (1/24°, ~4 km) and temporally (weekly), were also derived for the period 1985-2012 from the Pathfinder v5.2 night-only, 4 km-daily SST dataset, with gaps filled following Heron et al. (2010). However, as these data did not overlap the full time period of interest, 4 km-monthly composites were calculated and used to bias adjust the spatially and temporally lower resolution ERSST data to ensure relevance to the study site. Trends in bias-adjusted ERSST were calculated for the summer (November-April) and winter (May-October) seasons and annually. In addition, accumulated thermal stress was calculated from bias-adjusted ERSST using the Degree Heating Months (DHM) metric (Donner et al. 2005). Values were converted to Degree Heating Weeks (DHW, Liu et al. 2003) for ease of comparison with established ecologically-relevant thresholds for significant bleaching and mortality of 4 and 8 ℃-weeks (Liu et al 2003). DHW values of 4 °C-weeks have been linked to significant coral bleaching, while DHW 8 °C-weeks results in widespread bleaching and significant mortality on the reef (Eakin et al. 2010, Liu et al. 2013).

Analysis of the Pacific Decadal Oscillation, a robust reoccurring pattern of ocean-atmosphere climate variability over the Pacific basin, (PDO, Mantua et al. 1997) was also undertaken using PDO index values from http://jisao.washington.edu/pdo/PDO.latest. This

monthly index is derived using optimally interpolated SST values in the North Pacific Ocean. During a positive phase, the west Pacific becomes cooler and part of the eastern ocean warms; during a negative phase, the opposite occurs (Mantua et al. 1997). Noteable, the PDO was negative (warming of the eastern Pacific) during the 1998-bleaching event (Kleypas et al. 2015).

4.3.3 Statistical Analysis

Acropora muricata

Variation in linear extension rates and calcification rates (standardized to one-month intervals) for *A. muricata*, was analysed using two-way analysis of variance (ANOVA) to test for differences among depths and time periods, using the package *nlme* (Pinheiro et al. 2012). For all models, the fixed effects were depth and season. We examined model assumptions, including normality of errors and homogeneity of variances, graphically. To correct for heteroscedasticity and non-normality, we applied square-root transformations to the calcification data set. For all models, if the interaction was non-significant, it was removed ($p>0.05$) and an additive model used. Tukey post hoc test was utilised to investigate specific differences among fixed effects. The software program R (R Development Core Team 2015) was used for all analyses.

Annual extension and calcification rates were determined at each depth by adding the summer and winter values standardizing for variation in sample size. Annual linear extension rates and standard deviation for 1980-82 were determined by taking the mean extension rate given for each 11 sampling periods (Appendix A Table A1, Davies 1987). The mean extension (cm 30 $days^{-1}$) was converted to cm yr^{-1} for the temporal comparison. A Welch's t-test for unequal sample size, unequal variance was then performed for each depth.

Massive Porites

Annual rates of linear extension, density, and calcification for massive *Porites* were determined from 1979 to 2012 mean rates of all cores at Davies Reef. To determine the variability in each coral compared to the average at Davies Reef, 95% confidence intervals (CI) were determined for each coral core and the site average. The site average 95% CI were constructed on years prior to known major disturbances, i.e. the 1998 bleaching event, to represent historical baselines from 1979-1997. To, assess the response variables (linear extension, density and calcification) a generalised linear model (glm) was fitted to determine variability in sampling years and coral cores. The models were normally distributed and fitted with a Gaussian distribution. Linear regression was used to assess if there was a significant variation in the mean linear extension and calcification rates through time. The software program R (R Development Core Team 2015) was used for all analyses.

4.4 Results

4.4.1 Acropora muricata coral growth

Contemporary rates of linear extension (sampled from 2012 to 2014) for *A. muricata* at Davies reef averaged 0.48 ± 0.02 cm month^{-1} (mean ±SE) across all depths and sites. *A. muricata* average linear extension significantly varied between depth but not season (Figure 4.2a., Table 4.1a). Average linear extension was significantly greater at 5 m (0.65 cm month^{-1} ± 0.04) when compared to 10 m (0.49 cm month^{-1} ± 0.03) (Tukey post hoc, t value=-2.280, p=0.012) and 15 m depths (0.52 ± 0.04) (Tukey post hoc, t value=-2.543, p=0.031), but similar linear extension rates were found between 10 m and 15 m (Tukey post hoc, t value=0.529, p=0.857).

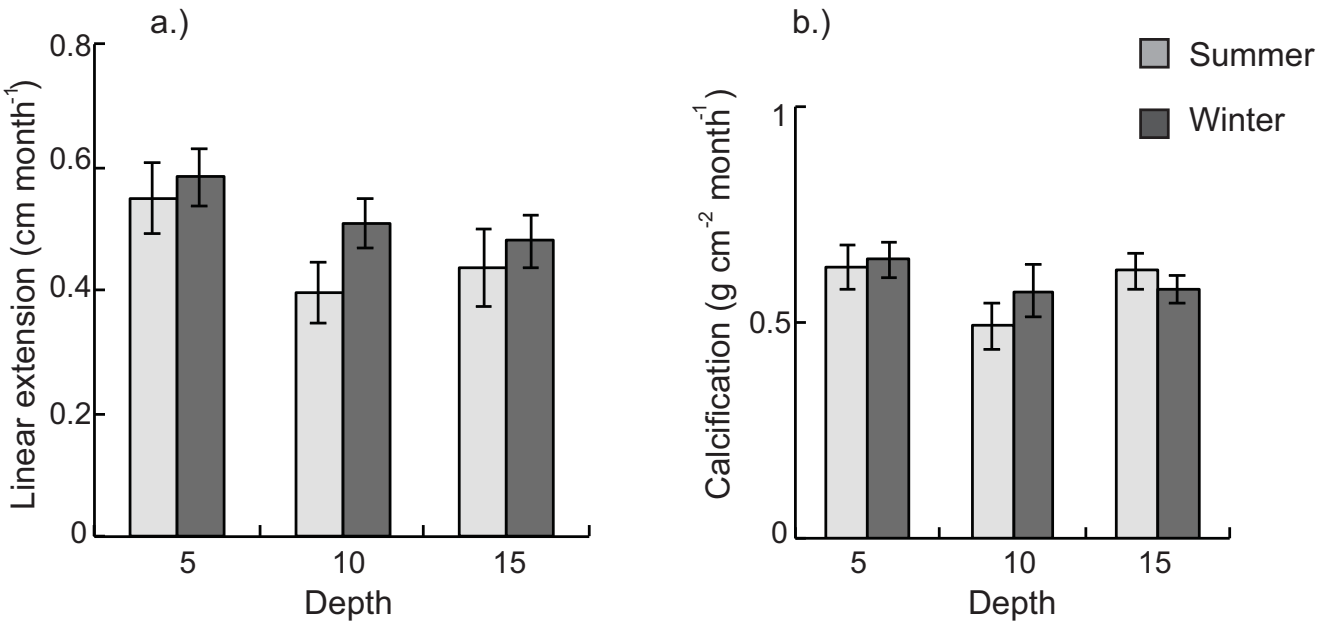

Figure 4.2. a.) Average linear extension rate (cm months^{-1}) and (b.) calcification rate (g cm^{-2} months^{-1}) in the summer (Nov-Apr) and winter (May-Oct) periods at 5, 10 and 15 m depths at Davies Reef, Australia, from 2012-2014.

Table 4.1.) Results of the two-way ANOVA for a.) linear extension b.) calcification and c.) density with depth and season. Sample size is reduced for density due to limited ability to section minimal growth with the geological saw.

a.) Linear Extension	DF	Mean Sq	F value	p value
Depth	2	1774	5.901	0.003
Season	1	1010	3.335	0.069
Residuals	210	300		
b.) Calcification	Df	Mean Sq	F value	p value
Depth	2	0.5581	3.237	0.042
Season	1	0.0768	0.446	0.505
Residuals	182	0.1724		
c.) Density	Df	Mean Sq	F value	p value
Depth	2	0.032	1.528	0.220
Season	1	0.031	1.495	0.223
Residuals	175	0.021		

Calcification rates from 2012 to 2014 averaged 0.59 g cm^{-2} $month^{-1}$ ± 0.02 across depths. There was a significant effect of depth on calcification, but not seasonal variability (Table 4.1b). Average branch calcification rates were greatest at 5 m (0.64 g cm^{-2} $month^{-1}$ ± 0.03), significantly greater than at 10 m (0.53 g cm^{-2} $month^{-1}$ ± 0.04) (Tukey post hoc, t value=-2.434, p=0.042). However, calcification rates were similar when comparing 5 m and 15 m (Tukey post hoc, t value=-0.770, p=0.722) and 10 m and 15 m (Tukey post hoc, t value=1.660, p=0.223). The average branch density for the study was 0.91 ± 0.01 g cm^{-3} which did not significantly vary with depth or season (Table 4.1c)

4.4.2 Temporal comparison between 1980-82 versus 2012-14

The average annual linear extension across all depths from 2012 to 2014 was 6.6 ± 0.2 cm yr^{-1}. At 5, 10 and 15 m depth the average annual linear extensions were 7.8 ± 0.2 cm yr^{-1}, 5.7 ± 0.2 cm yr^{-1}, and 6.3 ± 0.2 cm yr^{-1}, respectively. The corresponding mean annual calcification rates for the period 2012-2014 was 7.10 ± 0.32 g cm yr^{-1}, 5.69 ± 0.40 g cm yr^{-1} and 6.78 ± 0.34 g cm yr^{-1} at 5, 10 and 15 m depth. The average linear extension from 2012 to 2014 was lower than 1980-82 by 5 % at 5 m, 54 % at 10 m and 58 % at 15 m (Table 4.2, Figure 4.3). In the present study, growth rates were greatest at 5 m and decreased by 27 % and 19% at 10 and 15 m, respectively, whereas Oliver (1987) reported increasing linear extension rate with increasing depth.

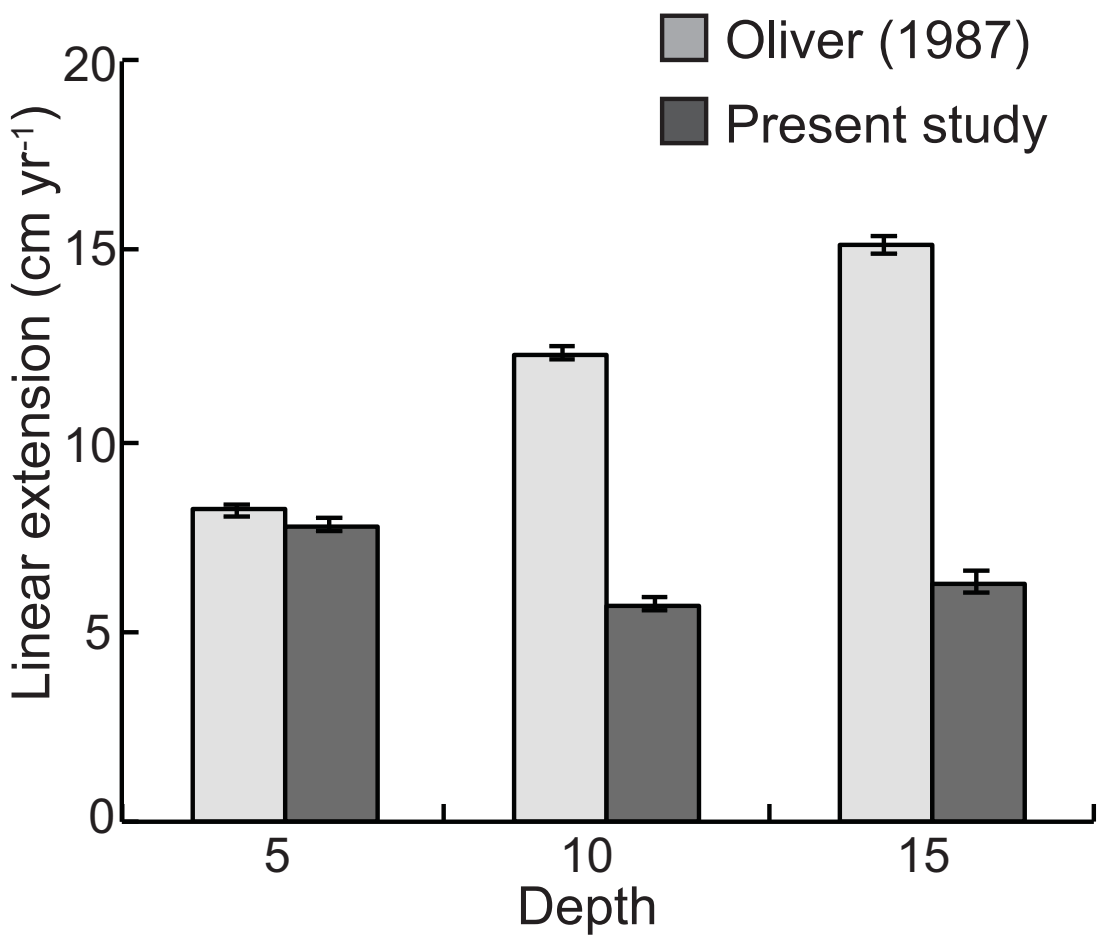

Figure 4.3. Linear extension (mm yr^{-1} ± SE) at 5, 10 and 15 m depths at Davies Reef for the 2012-2014 present study and 1980-82 study (Oliver 1987).

Table 4.2 Values utilised for the Welch's t test at 5, 10 and 15 m depths for stained *A. muricata* branches in both the present study from 2012-2014 and Oliver (1987) from 1980-82.

	Present Study			Oliver (1987)					
Depth (m)	Mean	SD	*N*	Mean	SD	*N*	*t* value	*df*	*p*
5	7.8	1.59	74	8.2	3.59	449	1.759	223.0	0.040
10	5.7	1.58	61	12.3	3.76	468	24.71	169.2	0.000
15	6.3	1.99	79	15.1	5.88	440	24.58	358.7	0.000

4.4.3 Massive Porites coral growth

The average linear extension of *Porites* at Davies Reef from 1979-2012 was 1.59 ± 0.03 cm yr^{-1} (Table 4.3). The linear extension was highly variable and significantly varied among years and corals (glm, $p<0.05$, Table 4.4a) but there was no clear relationship ($R^2=0.161$, $p=0.385$). The average density was 1.35 ± 0.01 g cm^{-3} (95% CI: 0.04) and significantly varied by coral (glm, $p<0.05$, Table 4.4b) but not by year (glm, $p>0.05$, Table 4.6). The average calcification was 2.12 ± 0.08 g cm^{-2} (Table 4.3) and significantly varied by year and coral (Figure 4.4) (glm, $p<0.05$, Table 4.4c) but did not significantly vary through time ($R^2=0.157$, $p=0.430$). To provide context for the *Acropora* comparison between 1980-82 and 2012-2014, average calcification of *Porites* in 2012 was 11.5 % lower (1.90 ± 0.24 g cm^{-2} yr^{-1}) compared to 1980-82 (2.15 ± 0.14 g cm^{-2} yr^{-1}). Luminescent signatures were observed within the skeletal growth patterns *Porites* about once per decade (1.2 per decade), with the most prominent signature observed in 1991 (Figure 4.5).

Table 4.3 Growth parameters, linear extension (LE, cm yr^{-1}), density (g cm^{-3} yr^{-1}), and calcification (g cm^{-2} yr^{-1}) with 95% confidence intervals (CI) for the 7 corals from Davies Reef and the site average (Site Avg)

Coral ID	N	LE Mean±SE	LE 95% CI	Density Mean±SE	Density 95% CI	Calcification Mean±SE	Calcification 95% CI
DAV61A	34	1.51±0.04	0.08	1.25±0.01	0.02	1.88±0.05	0.10
DAV63B	16	2.03±0.10	0.20	1.34±0.02	0.05	2.72±0.16	0.31
DAV64A	34	1.19±0.05	0.10	1.47±0.01	0.03	1.76±0.08	0.16
DAV65B	33	1.72±0.05	0.10	1.32±0.01	0.02	2.28±0.07	0.14
DAV67A	34	1.83±0.07	0.14	1.24±0.01	0.02	2.27±0.09	0.17
DAV69A	34	1.72±0.08	0.16	1.55±0.01	0.03	2.70±0.13	0.26
DAV70A	32	1.38±0.05	0.11	1.27±0.02	0.03	1.76±0.08	0.15
Site Avg		1.59±0.03	0.12	1.35±0.01	0.01	2.12±0.04	0.17

Table 4.4 Full results for the generalized linear model (glm) with gaussian distribution for *Porites* (a) linear extension, (b) density and (c) calcification.

a) Linear extension

	Estimate	Std. Error	t value	p
(Intercept)	1.044	0.14	7.560	-
YEAR1979	0.240	0.21	1.135	0.258
YEAR1980	0.455	0.20	2.302	0.023
YEAR1981	0.337	0.19	1.799	0.074
YEAR1982	0.511	0.19	2.725	0.007
YEAR1983	0.490	0.19	2.613	0.010
YEAR1984	0.540	0.19	2.882	0.004
YEAR1985	0.530	0.19	2.828	0.005
YEAR1986	0.593	0.19	3.164	0.002
YEAR1987	0.481	0.19	2.566	0.011
YEAR1988	0.481	0.19	2.566	0.011
YEAR1989	0.413	0.19	2.205	0.029
YEAR1990	0.426	0.19	2.274	0.024
YEAR1991	0.375	0.19	2.004	0.047
YEAR1992	0.625	0.19	3.335	0.001
YEAR1993	0.299	0.19	1.595	0.112
YEAR1994	0.255	0.19	1.360	0.176
YEAR1995	0.443	0.19	2.364	0.019
YEAR1996	0.555	0.19	2.962	0.003
YEAR1997	0.470	0.18	2.616	0.010
YEAR1998	0.434	0.18	2.415	0.017
YEAR2000	0.844	0.18	4.697	<0.001
YEAR2001	0.742	0.18	4.132	<0.001
YEAR2002	0.448	0.18	2.495	0.014
YEAR2003	0.684	0.18	3.810	<0.001
YEAR2004	0.542	0.18	3.020	0.003
YEAR2005	0.548	0.18	3.051	0.003
YEAR2006	0.492	0.18	2.738	0.007
YEAR2007	0.212	0.18	1.183	0.238
YEAR2008	0.528	0.18	2.941	0.004
YEAR2009	0.517	0.18	2.879	0.004
YEAR2010	0.289	0.18	1.607	0.110
YEAR2011	0.633	0.18	3.525	0.001
YEAR2012	0.250	0.18	1.394	0.165
CORALDAV63B	0.508	0.10	4.845	<0.001
CORALDAV64A	-0.316	0.08	-3.878	<0.001
CORALDAV65B	0.209	0.08	2.542	0.012
CORALDAV67A	0.324	0.08	3.970	<0.001
CORALDAV69A	0.216	0.08	2.645	0.009
CORALDAV70A	-0.134	0.08	-1.614	0.108

Table 4.4. continued. Full results for the generalized linear model (glm) with gaussian distribution for *Porites* (a) linear extension, (b) density and (c) calcification.

b) Density

	Estimate	Std. Error	t value	p
(Intercept)	1.252	0.026	47.300	-
YEAR1979	0.037	0.041	0.903	0.368
YEAR1980	0.072	0.038	1.892	0.060
YEAR1981	0.034	0.036	0.958	0.340
YEAR1982	0.051	0.036	1.426	0.156
YEAR1983	0.018	0.036	0.512	0.609
YEAR1984	0.007	0.036	0.206	0.837
YEAR1985	0.025	0.036	0.707	0.480
YEAR1986	0.036	0.036	0.999	0.319
YEAR1987	0.043	0.036	1.185	0.238
YEAR1988	0.032	0.036	0.902	0.368
YEAR1989	0.017	0.036	0.461	0.645
YEAR1990	0.000	0.036	0.002	0.998
YEAR1991	-0.002	0.036	-0.063	0.950
YEAR1992	0.006	0.036	0.169	0.866
YEAR1993	0.012	0.036	0.322	0.748
YEAR1994	-0.051	0.036	-1.427	0.155
YEAR1995	-0.045	0.036	-1.260	0.209
YEAR1996	-0.008	0.036	-0.216	0.829
YEAR1997	-0.001	0.034	-0.037	0.970
YEAR1998	0.040	0.034	1.170	0.244
YEAR2000	-0.018	0.034	-0.523	0.602
YEAR2001	0.004	0.034	0.116	0.908
YEAR2002	-0.002	0.034	-0.054	0.957
YEAR2003	-0.006	0.034	-0.170	0.865
YEAR2004	0.002	0.034	0.066	0.947
YEAR2005	-0.067	0.034	-1.946	0.053
YEAR2006	-0.052	0.034	-1.523	0.130
YEAR2007	-0.058	0.034	-1.672	0.096
YEAR2008	-0.054	0.034	-1.581	0.116
YEAR2009	-0.058	0.034	-1.689	0.093
YEAR2010	-0.057	0.034	-1.656	0.100
YEAR2011	-0.041	0.034	-1.183	0.239
YEAR2012	-0.006	0.034	-0.174	0.862
CORALDAV63B	0.109	0.020	5.420	<0.001
CORALDAV64A	0.224	0.016	14.342	<0.001
CORALDAV65B	0.073	0.016	4.629	<0.001
CORALDAV67A	-0.009	0.016	-0.567	0.572
CORALDAV69A	0.299	0.016	19.118	<0.001
CORALDAV70A	0.027	0.016	1.722	0.087

Table 4.4. continued. Full results for the generalized linear model (glm) with gaussian distribution for *Porites* (a) linear extension, (b) density and (c) calcification.

c) Calcification

	Estimate	Std. Error	t value	p
(Intercept)	1.243	0.200	6.232	-
YEAR1979	0.423	0.306	1.385	0.168
YEAR1980	0.724	0.285	2.537	0.012
YEAR1981	0.499	0.271	1.842	0.067
YEAR1982	0.780	0.271	2.882	0.004
YEAR1983	0.693	0.271	2.56	0.011
YEAR1984	0.731	0.271	2.701	0.008
YEAR1985	0.755	0.271	2.789	0.006
YEAR1986	0.851	0.271	3.145	0.002
YEAR1987	0.726	0.271	2.682	0.008
YEAR1988	0.646	0.271	2.388	0.018
YEAR1989	0.588	0.271	2.172	0.031
YEAR1990	0.590	0.271	2.18	0.031
YEAR1991	0.519	0.271	1.918	0.057
YEAR1992	0.878	0.271	3.243	0.001
YEAR1993	0.431	0.271	1.594	0.113
YEAR1994	0.287	0.271	1.06	0.291
YEAR1995	0.552	0.271	2.038	0.043
YEAR1996	0.765	0.271	2.828	0.005
YEAR1997	0.674	0.259	2.599	0.010
YEAR1998	0.670	0.259	2.583	0.011
YEAR2000	1.174	0.259	4.524	<0.001
YEAR2001	1.080	0.259	4.164	<0.001
YEAR2002	0.680	0.259	2.621	0.010
YEAR2003	0.954	0.259	3.678	<0.001
YEAR2004	0.754	0.259	2.908	0.004
YEAR2005	0.635	0.259	2.449	0.015
YEAR2006	0.596	0.259	2.296	0.023
YEAR2007	0.203	0.259	0.784	0.434
YEAR2008	0.648	0.259	2.497	0.013
YEAR2009	0.605	0.259	2.332	0.021
YEAR2010	0.295	0.259	1.138	0.257
YEAR2011	0.810	0.259	3.121	0.002
YEAR2012	0.347	0.259	1.339	0.182
CORALDAV63B	0.845	0.152	5.573	<0.001
CORALDAV64A	-0.120	0.118	-1.018	0.310
CORALDAV65B	0.392	0.119	3.297	0.001
CORALDAV67A	0.388	0.118	3.292	0.001
CORALDAV69A	0.792	0.118	6.725	<0.001
CORALDAV70A	-0.119	0.120	-0.993	0.322

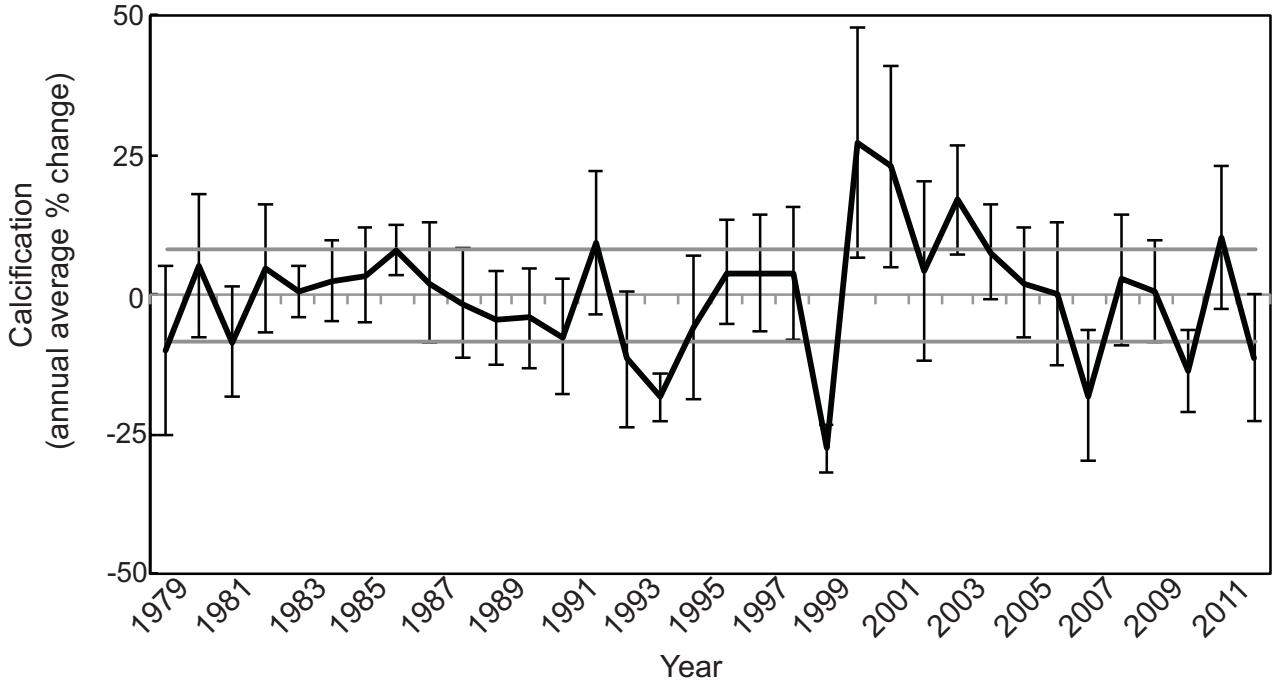

Figure 4.4. Average annual standardized *Porites* calcification anomaly for Davies Reef from 1979-2012 as a percentage difference to baseline calcification (1979-1997) prior to 1998 mass bleaching event (± SE). Grey lines represent ±95% confidence intervals around the baseline mean calcification (2.12 g cm^{-2} yr^{-1} ± 0.50; 95% CI=7.9%).

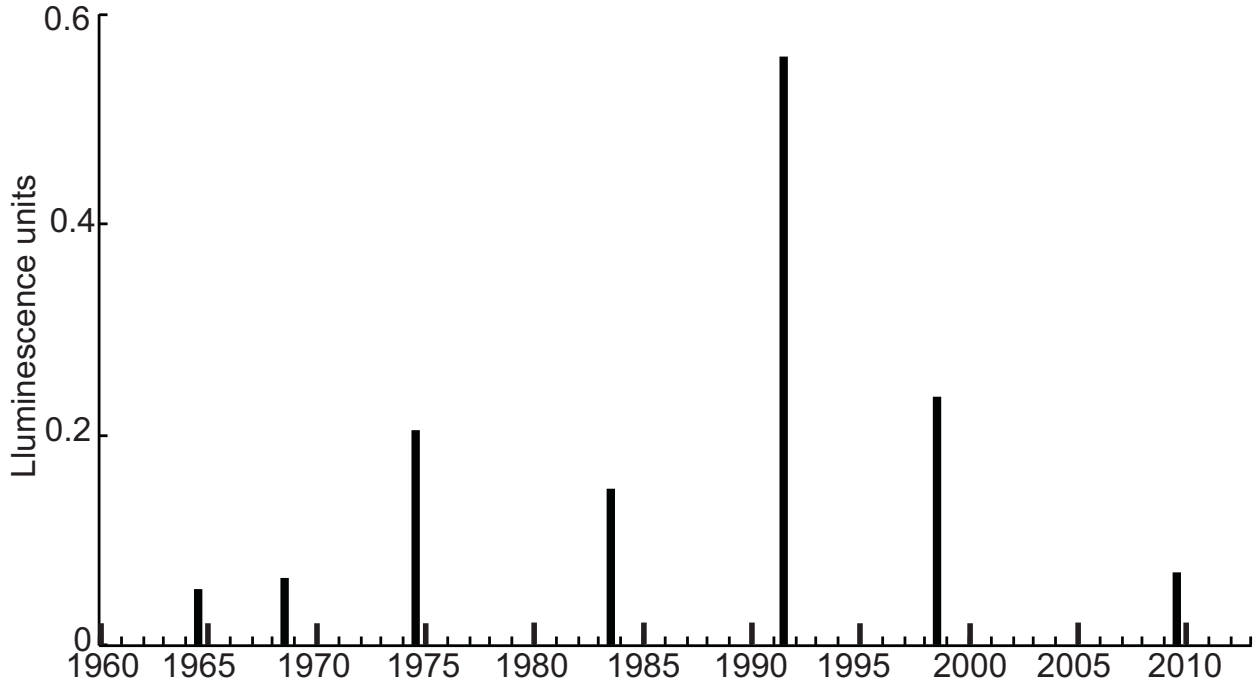

Figure 4.5. Average annual anomalies of luminescence range from the visually assessed luminescence signatures, 1960-2012, from coral slices on a mid shelf reef, Davies Reef.

4.4.4 Environmental Parameters

Light and temperature

Determined from the in situ loggers, at the deep (15 m) site average daily light intensity (1019 lux) were 21% of the values at the 5 m site (4778 lux). At the 10 m site (2809 lux), light was 58% of the values at the 5 m site. The temperature recordings of the *in situ* loggers deployed during the 2013-14 summer (Nov 1, 2013- April 30, 2014) showed average daily temperature decreased with depth (Table 4.5) The difference in average daily temperature between the deep and shallow site ranged from 0.02 – 0.58 °C. Despite the large range between depths, average daily temperature between depths differed by a maximum of 0.1 °C (Table 4.5) Temperatures were more stable at the deep site and became more variable at shallower depths (Table 4.5).

Sea surface temperature during the entire study period ranged from 22.4 – 30.5 °C (Figure 4.6a) with an average annual temperature of 25.9 ± 0.3°C (AIMS 2015). The maximum and minimum monthly SST during the study period was 28.4°C in February 2013 and 22.4 °C in August 2014, respectively. The average seasonal difference varied by 3.1 °C, with a winter (May – Oct) average during the study of 24.4 ± 0.4°C and summer (Nov – Apr) average of 27.5 ± 0.3°C.

Table 4.5. Temperature statistics at Davies Reef for the 2013-14 summer at 5, 10 and 15 m depths.

Depth	Mean (°C) ± SE	Max (°C)	Min (°C)	95% CI	Mean daily variance (°C) ± SE
5	27.79 ± 0.04	29.65	26.39	0.083	0.66 ± 0.02
10	27.72 ± 0.04	29.25	26.00	0.084	0.62 ± 0.02
15	27.62 ± 0.04	29.05	26.00	0.086	0.50 ± 0.01

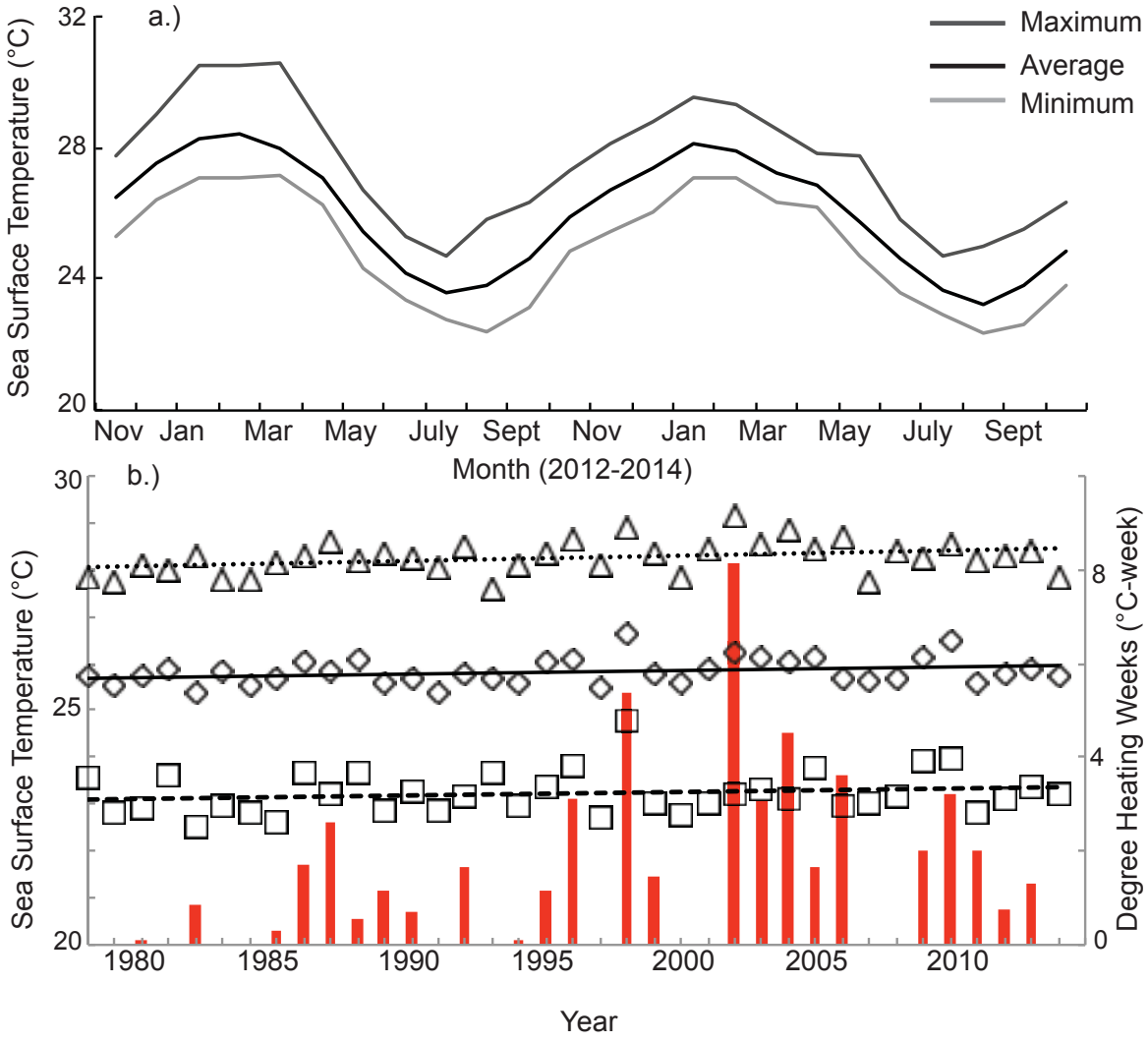

Figure 4.6. a.) Maximum, average and minimum sea surface temperature (°C) from Nov 2012-Oct 2014 at Davies Reef, Australia and b.) Sea surface temperature maximum (Δ), average (X) and minimum (+) determined and associated Degree Heating Weeks (°C-weeks) from 1980-2014 at Davies Reef.

The relevance of the spatially-broad ERSST data at the study site was examined by comparison with high-resolution satellite PFv5.2 SST data for the period 1985-2012. This revealed a strong linearity between these independent datasets (r^2 = 0.92), with ERSST warmer than the satellite data across the range of observed values. Importantly, the linearity indicated that ERSST values were consistent in representing conditions on the reef. ERSST values were bias adjusted by the linear relationship to reflect the temperature on the reef (i.e., ERSST ' = 1.11*ERSST -3.52 ℃).

ERSST values during Nov 2012-Oct 2014 reflected similar characteristics to the *in situ* data, though with reduced range (23.2-28.4 ℃) as expected for monthly resolution data. Summer and winter seasonal averages (27.4 ± 0.2 ℃ and 24.2 ± 0.2 ℃, respectively), as well as the difference between these (3.2℃), were comparable with the *in situ* data. ERSST ' values encompassing the full time period (1979-2014) were used to determine linear trends using annually-averaged (0.064 ℃/decade) as well as seasonally-averaged summer (0.065 ℃/decade) and winter (0.061 ℃/decade) temperature values (Figure 4.6b). Annual maximum accumulated thermal stress peaked in 2002 at 8.1 ℃-weeks (Figure 4.6b).

PDO index values were generally positive in the early part of the period of interest, flipping around 1998 to become generally negative, consistent with the described PDO reversal (Figure 4.7) (Strong & Magnusdottir 2009).

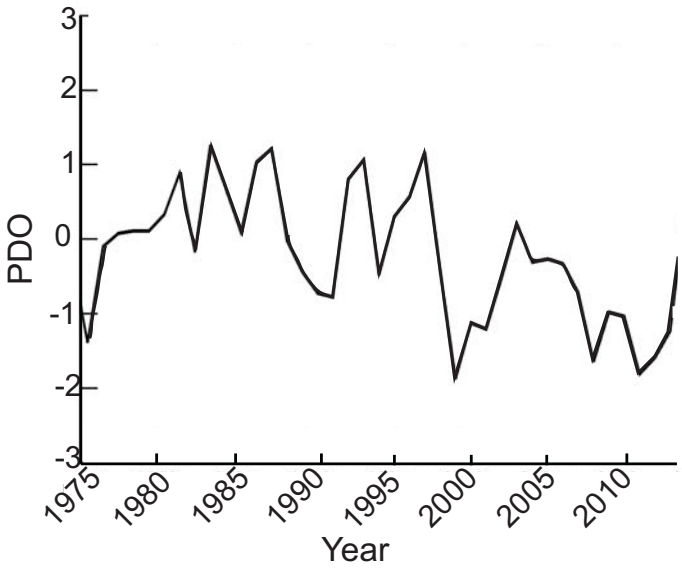

Figure 4.7. The Pacific Decadal Oscillation (PDO) from 1975 to present.

4.5 Discussion

4.5.1 Significant temporal variation

The annual linear extension rate of *A. muricata* was significantly lower in 2012-14, compared to 1980-82. If there were sustained declines in coral growth throughout this period, this equates to a decline in coral growth of 0.17 - 1.93 % yr^{-1} (Figure 4.3), which is equivalent to the rate reported for other branching corals in other tropical (Bak et al. 2009, Manzello 2010) and subtropical locations (Chapter 3 - Anderson et al. 2015). Significant declines in growth rates of the staghorn *Acropora palmata* (0.23-0.35 % yr^{-1}) in the Caribbean and branching *Pocillopora* (0.9 % yr^{-1}) in the Eastern Tropical Pacific were documented (Bak et al. 2009, Manzello 2010). At a subtropical reef at Lord Howe Island, Australia, linear extension of *A. yongei* and *P. damicornis* declined by ~2.0 % yr^{-1} over 1.5 decades (Chapter 3 - Anderson et al. 2015).

However, at the shallower depth of 5 m where we would expect the most change, the variation between Oliver (1987) and the present study was the least. An explanation may be due to thermal stress to the region during Oliver (1987) sampling from May 1980 - Dec 1981; bleaching events were reported for the central Great Barrier Reef region in 1980 and extensive bleaching in 1982 (Oliver 1985). Oliver et al. (1983) noted that growth rates of *A. muricata* were depressed during mid-summer and mid-winter at Davies Reef from 1980-81. Bleaching events often affect the shallowest sites to a greater extent which may explain the trends in growth observed for 1980-82. The *Porites* cores corroborate the stress with an average 12 % decline is calcification from 1980 to 1981.

Documented declines in growth rates of reef-building corals are variously attributed to changes in temperature regimes and/ or ocean acidification (Bak et al. 2009, Manzello 2010, De'ath et al. 2013, Tanzil et al. 2013, Chapter 3 - Anderson et al. 2015). Bak et al (2009) attributed declines in growth of *A. palmata* measured over 30-years in the Caribbean

to a reduction of aragonite saturation in the Caribbean (Gledhill et al. 2008) which can reduce the available carbonate for calcification leading to reduced growth (Kleypas et al. 1999). Similarly, Manzello (2010) attributed the reduction in linear extension of *Pocillopora* in Pacific Panama from 1974-2006 to ocean acidification and/or increases in thermo tolerant *Symbiodinium*. Interesting, the declines in linear extension at the 10 and 15 m depths (1.8 - 1.93 % yr^{-1}, respectively) are similar to those reported for branching *A. yongei* (2.0 % yr^{-1}) at a high latitude reef, Lord Howe Island, in Australia (Chapter 3 - Anderson et al. 2015). Again, the decline was attribute to declines in available aragonite and/or thermal stress related to climate change.

In contrast to the reduced growth found in branching *A. muricata* at Davies Reef, calcification of massive *Porites* was highly variable through time but displayed no long-term change (Figure 4.4). When comparing calcification rates of *Porites* between the *A. muricata* sampling periods of 1980-82 versus 2012, average calcification rates were 11.5 % lower in the later years. However, growth rates of *Porites* displayed significant interannual variation with a pronounced reduction in calcification following the 1998-bleaching event. The corals had recovered after 2 years (by 2000) and even exhibited enhanced calcification (relative to the pre-1998 baseline). De'ath et al. (2013) reported a decline in *Porites* calcification by 11.4 % from 1990 to 2005 in 328 corals along the Great Barrier Reef. The period of decline in calcification recorded by De'ath et al. (2013) spanned the two worst bleaching events (1998 and 2002) in the history of the GBR (Berkelmans et al. 2004) that resulted in reduced calcification. It is likely that these corals had not completely recovered from the negative impact on calcification by 2005. This new set of *Porites* calcification records at Davies Reef indicate a negative anomaly in 1998, similar to De'ath et al (2013), followed by a decade of calcification rates that are comparable or greater than the historical baseline pre-1998. Moreover, differences between studies may arise from the variability in the locations of the

corals sampled as De'ath et al. (2013) encompassed the whole breadth of the GBR (cross shelf and >2000 km of reef separation) and our study was restricted to one mid-shelf reef. Our results are similar to Cantin & Lough (2014), where mass-bleaching events in 1998 and 2002 caused a hiatus in growth of *Porites*, but returned to pre-disturbance rates after 4 years.

The growth rate recovery potential of the less thermo-tolerant branching species following a bleaching event is largely unknown. Based on a study at Scott Reef in Western Australia, the 1998-bleaching caused coral cover of *Acropora* to decrease from 50 % to 10 % (Gilmour et al. 2013). Coral cover stayed ~10 % from 1998 to 2002 until recruitment of coral larvae to the reef increased (Gilmour et al. 2013). As an increase in coral cover was not evident until the reoccurrence of larval recruitment, this may suggest the remaining 10 % of *Acropora* to survive the bleaching were hindered in growth for a minimum of 4 years following the 1998 bleaching.

Thermal stress has also been shown to disproportionately affect branching species (Marshall & Baird 2000, Loya et al. 2001). In this study, the average annual SST at Davies Reef has shown a warming trend at a rate of 0.064 ℃ decade^{-1} from 1980-present. This rate is slightly less than that observed for tropical oceans (0.08 °C decade^{-1}) (Lough 2012) which are projected to increase by 0.6 to 2.0 °C by 2100 (IPCC 2013). It has been predicted that frequency of thermal anomalies capable to cause coral bleaching could occur annually or bi-annually at a majority of the world's coral reefs by 2030-2050 without a significant increase in thermal tolerance (Donner et al. 2005). Based on satellite data, Davies Reef had experienced DHW > 4 ℃-weeks (indicative of coral bleaching, Liu et al. 2003) three times over the last three decades with a greater frequency of recorded DHW occurring in the last 15 years (seven DHW >3 experienced since 1996) (Figure 4.6). This may be in conjunction with the reversal of the Pacific Decadal Oscillation that is negative in the later years resulting in

warming of the west Pacific, which can increase the frequency of temperature stress through time, hindering growth and the potential for recovery.

Gradual changes in ocean conditions, such as declining aragonite saturation may have a disproportionate impact on branching corals, compared to massive corals species (Fabricius et al. 2011, Edmunds et al. 2012). For example, *Porites* corals have been shown to grow even in areas with low pH and aragonite saturation (Fabricius et al. 2011), such as at volcanic carbon dioxide seeps, whereas branching corals are generally absent from such environments. The global oceans have observed a steady decline of 0.1 pH units since the Industrial Revolution due to increases in anthropogenic carbon dioxide concentrations in the atmosphere (IPCC 2013). Albright et al. (2016) naturally altered the carbonate chemistry in an isolated reef system at One Tree Island on the GBR, elevating the aragonite saturation to values expected in pre-industrial times. They observed a significant (7%) decline in community calcification when comparing between present day and pre-industrial levels of aragonite saturation state (Albright et al. 2016). This innovative field-based study shows sustained and ongoing changes in ocean acidification is having a negative impact on net community calcification rates of reef assemabalges. This supports numerous experimental studies that show declines in calcification of corals (11-40 %) when exposed to reduced aragonite saturation state (Gattuso et al. 1998, Marubini et al. 2001, Leclerq et al. 2002, Reynaud et al. 2003, Langdon & Atkinson 2005, Edmunds et al. 2012). Moreover, Albright et al. (2013) quantified seasonal variation in the aragonite saturation at Davies Reef and plotted net calcification rate versus Ω_{arag} to determine a "threshold" at which the community transitions from net calcification to net dissolution, but noted that only 25-27 % of the variation in net community calcification is explained by Ω_{arag}. However, they found present diel variation in carbonate saturation on Davies reef flat was to be 29.6 % and 14.1 % below the community calcification threshold in summer and winter, respectively (Albright et al.

2013). A higher state of dissolution during summer months may contribute to the lack of seasonal variability in growth of *A. muricata* in this study.

Luminescent signatures in *Porites* coral cores correlate to freshwater rainfall accumulation (Isdale 1984, Lough et al. 2002, Lough et al. 2015). The known records of major floods during the course of the analyses were 1974, 1991, 2010 (Lough et al. 2015) and only these major floods had a far-reaching impact and potential to transport water quality issues to Davies Reef. Notable declines in calcification are evident following the 1991 flood events that were observed in the luminescence signatures (Figure 4.5). An analysis of the relative risk of degraded water quality on the GBR based on data encompassing 2001-2012 (Waterhouse et al. 2014) indicated that Davies Reef was at low to very low risk of water quality impacts from terrestrial sources. This was confirmed by luminescence signatures that showed only major flood events reached Davies Reef and were recorded in the skeletons on average ~1 per decade (Figure 4.5). Moreover, the rate of recovery from bleaching was double the rate observed from *Porites* on inshore reefs (Cantin & Lough 2014) suggesting the local environmental conditions at this midshelf reef are more favourable for growth compared to inshore reefs. Therefore, this mid-shelf reef is more likely at risk to global climate threats, and the decline in growth of *A. muricata* detected is less likely to be a result of coastal development and water quality issues.

Environmental controls on coral growth

While SST and aragonite saturation produce large-scale gradients in reef growth (Kleypas et al. 1999a), local environmental conditions such as depth (and associated declines in light intensity) can affect coral growth rates (reviewed in Chapter 2 - Pratchett et al. 2015). The linear extension in *A. muricata* at Davies Reef was highly variable among branches, sample times and depths. The average annual linear extension for the 2-years was greatest at 5 m (7.77 cm ± 0.18), and decreased at 10 m (5.72 cm ± 0.20) and 15 m (6.31 mm ± 0.22)

(mean ± SE). These results are similar to linear extension of *A. muricata* at 7 to 11 m depth quantified from 1994-95 at a high latitude site in Western Australia (5.0 - 7.6 cm 11.5 months^{-1}) (Harriott 1998). However, Crossland (1981) reported growth rates on the same species and location of almost half (3.7 - 4.3 cm yr^{-1}) at a depth of 2 m where seasonal macroalgae blooms occurred. Macroalgae blooms had occurred at Davies Reef during the 2012/13 summer leading to mortality and likely the reduced growth of some branches during that sampling time period (although visually affected branches were not used in analysis). In addition, the present growth rates are comparable to that determined in 2009-2010 at Middle Reef, Australia (6.3 cm yr^{-1}), an inshore reef located 95 km inland from Davies Reef (Brown et al. 2012). However, *A. muricata* in the Indo-Pacific had reported growth rates in excess of 10.0 cm yr^{-1} (Table 4.6) postulating that the growth rates at Davies Reef (presently comparable to high latitude and inner shore reefs) during the course of this study were being suppressed.

Table 4.6. Reported linear extension for *Acropora muricata* (*A. formosa*) from the Indo-Pacific.

Location	**Date Sampled**	**Latitude**	**Annual extension (cm yr^{-1})**	**Reference**
Maldives	2010-2011	4°18N	3.9-7.8	Morgan & Kench 2012
Sri Lanka	1997-1998	6.54°N	11.8-12.1	Jinendradasa &Ekarame 2000
Thailand	1981-82	8°N	8	Charuchinda & Hylleberg 1984
Thailand	1984-1986	8°N	3.6-6.8	Changsang et al. 1992
India	1988-1989	10°33.5N	8.1	Suresh &Mathew 1993
Guam	1976-1977	12°N	3.3	Neudecker 1981
Middle Reef, Australia	2009-2010	12.5°S	6.3	Browne 2012
Lizard Island, Australia	1985	15°S	7.1	Oliver 1985
Hopkinson Reef, Australia	1985	18°34S	4	Dennison &Barnes 1988
Davies Reef Australia	1981-92	18.5°S	8.0-16.6	Oliver et al. 1983
Davies Reef Australia	2012-14	18.5°S	5.7-7.7	Present Study
Nelly Bay, Australia	1981-82	19°10S	5.3	Oliver 1984
Dampier Archipelago, Australia	1982	21°S	10.0-13.7	Simpson 1988
Houtman Arbolhous, Australia	1979-1980	29°S	3.7-4.3	Crossland 1981
Houtman Arbolhous, Australia	1994-95	29°S	5.2-7.9	Harriott 1998

An inverse correlation of growth with depth has often been observed, most studied in massive species such as *Orbicella* sp. and *Porites* sp. (Baker & Weber 1975, Highsmith et al. 1983, Hubbard & Scaturo 1985, Huston 1985). There is a lack of literature on branching corals depth variation. In the present study, linear extension declined with depth; growth rates were greatest at 5 m and decreased by 27 % and 19 % at 10 and 15 m, respectively. In contrast, Oliver (1987) observed increasing linear extension with increasing depth but in the final month of his sampling the growth rates were similar among depths. He also suggests intensive sampling may have contributed to a damaged growth repair response increasing the linear extension at depth (Oliver 1987). Kotb (2001) observed an inverse relationship of growth and depth in *Stylophora pistillata* (0.92, 0.75, and 0.65 cm yr^{-1} at depth of 5, 15, and 30 m, respectively). However, for *Acropora granulosa* linear extension peaked at 15 m (0.92 mm yr^{-1}) in comparison to 5 and 30 m (0.63 and 0.59 cm yr^{-1}, respectively) in the Red Sea (Kotb 2001). A decline in growth is expected given the change in environmental conditions with depth, mainly light availability and sea surface temperature, which have been shown to affect coral growth (Goreau 1959, Marshall & Clode 2004, Hoogenboom et al. 2010, Allemand et al. 2011). In the present study, light intensity and temperature declined with depth supporting this hypothesis.

Calcification rates of corals increase with temperature to a maximum growth rate at an optimal temperature and then decrease (Clausen & Roth 1975, Jokiel & Coles 1977, Marshall & Clode 2004). However, corals are locally adapted to their environment (Clausen & Roth 1975) and the optimal temperature is likely to vary with species and location. In the present study, seasonal variation in linear extension was not observed across depths. Tropical SST has significantly risen over the past decades (Lough 2012). The maximum temperature recorded was 29.7°C at 5 m depth from the temperature loggers placed *in situ* during the 2013/14 summer (30.5°C was the maximum recorded in Feb 2013 by AIMS, 2015). The

average monthly SST during the study was 25.9°C ± 0.3 (AIMS 2015), and it is possible that summer SST are now being pushed beyond the optima, potentially leading to slower growth during summer months. These results are similar to that of Foster et al. (2014), who found little seasonal differences or reduced growth in summer (~40 % across locations and species) in Western Australia attributed to high temperature stress during 2011-2013 summers.

To conclude, this study revealed significant variation in linear extension between 1980-82 and 2012-2014 in the growth rates of *A. muricata* on a central, midshelf reef on the Great Barrier Reef across depths. In contrast, although growth rates of *Porites* were highly variable through time showing marked reductions due to infrequent flood events and the 1998-mass bleaching event, there was not a significant change through time. It is likely that the combination of increasing temperature stress along with reductions in aragonite saturation state is limiting the potential for recovery of branching *A. muricata*, hindering growth rates. Whereas the less sensitive, more thermo tolerant *Porites* is able to recover from bleaching events and persist through time. While more works needs to be done to continue monitoring growth rates of branching corals at this site, providing a more concrete estimate of changes through time, but it appears climate related increases in SST and declining saturation state may be hindering growth rates of branching corals on the Great Barrier Reef.

Chapter 5 Variation in growth rates of branching corals along the Great Barrier Reef

5.1 Abstract

Coral growth is an important component of reef health and resilience. However, few studies have investigated variation in growth rates over multiple temporal and spatial scales, especially for branching corals, which are important contributors to the structure and complexity of reef habitats. This study assessed growth (specifically, linear extension, density, and calcification) of three dominant coral species (*Acropora muricata*, *Pocillopora damicornis* and *Isopora palifera*) at three distinct locations (Lizard Island, Davies/Trunk Reef, and Heron Island) separated by 100s of kilometres along Australia's Great Barrier Reef. Annual growth rates of all species were highest at Lizard Island and exhibited a negative trend with increasing latitude among locations. Observed differences in growth corresponded with spatial variation in annual temperature, suggestive of a positive relationship between temperature and growth. This does not however, necessarily suggest that ocean warming will have positive effects on coral growth of these corals. Continued monitoring of coral growth rates, in combination with environmental conditions (e.g., temperature and reef carbonate chemistry) is essential to establish impacts of climate change on the coral reef ecosystems.

5.2 Introduction

Coral reefs are important ecosystems, providing invaluable goods and services to tropical nations (Moberg & Roonback 2003) as well as supporting a great diversity of reef-associated organisms (Pratchett et al. 2008, Pellissier et al. 2014, Rogers et al. 2014). The condition and productivity of coral reef ecosystems are strongly correlated with live coral cover, as well as the structural complexity and habitat diversity of coral-rich habitats (e.g., Graham et al. 2015). Consequently, widespread declines in coral cover and structural complexity, as reported in a number of locations (Jones et al. 2004, Graham et al. 2015) directly undermine the ecological and economic value of reef ecosystems. Sustained and ongoing declines in abundance of corals are largely attributed to increasing diversity, frequency and severity of acute disturbances (e.g., De'ath et al. 2012). However, sustained declines in key demographic rates (e.g., growth) for corals, as documented by De'ath et al. (2009) and Cantin et al. (2010), may also contribute to declining abundance of reef corals.

Seawater temperature is a major environmental factor controlling rates of coral growth and calcification (Clausen & Roth 1975). For massive *Porites*, for example, calcification rates have been shown to increase by 0.3 g cm^{-1} $year^{-1}$ for every 1 °C increase in annual average SST across a wide range of reefs (Lough & Barnes 2000). However, sustained increases in sea surface temperature (SST) due to climate change are of concern for corals (Walther et al. 2002), because even small changes in local environmental conditions can have significant deleterious impacts. Most notably, corals may bleach when the local temperatures exceed typical summer maxima by 1 °C (Jokiel & Coles 1990). However, even before corals bleach, increases in local temperatures may lead to sustained declines in growth or performance. The optimum temperature for coral calcification, for example, is typically 1-3 °C below the local summer maxima (e.g., Clausen & Roth 1975, Bessat & Buigues 2001, Marshall & Clode 2004, Cooper et al. 2008, Cantin et al. 2010), such that ocean warming will

constrain coral growth by reducing the time that environmental conditions are conducive to maximum rates of calcification (Pratchett et al. 2015 – Chapter 2). Sustained increases in SST above the long-term maximum has been purported as a key factor contributing to the observed decline in massive corals globally (Australia: De'ath et al. 2013, Thailand: Tanzil et al. 2013, Red Sea: Cantin et al. 2010, Florida: Helme et al. 2011).

The other climate related threat to calcifying organisms, such as reef corals, is ocean acidification (Kleypas & Yates 2009). Increases in atmospheric carbon dioxide (CO_2) from 280 ppm in the pre-industrial period to present day concentrations of 401 ppm (NOAA http://www.esrl.noaa.gov/gmd/ccgg/trends/global.html, Forster et al. 2007) have resulted in an decrease in the surface ocean pH from a global average of 8.21 to 8.10, as well as corresponding shifts in aragonite saturation (Hough-Guldberg et al. 2007). As the aragonite saturation declines, the carbonate saturation state of the internal calcifying fluid declines and the rate of calcification decreases (Cohen et al. 2009). Moreover, calcification is energetically costly because the corals require removal of H^+ ions from the calcifying fluid for expenditure of the ATP (energy) for calcification (Furla et al. 2000, Cohen & McConnaughey 2003). Declining saturation state has been purported as a cause for observations of reduced linear extension rates of corals in the Eastern Tropical Pacific (Manzello 2010) and Caribbean (Bak et al. 2009).

Aragonite saturation, temperature and light intensity are the key environmental processes controlling coral growth and calcification across latitudinal gradients (Kleypas et al. 1999a, Lough & Barnes 2000, Couce et al. 2012, Muir et al. 2015). For massive species, it has been observed that linear extension and calcification rates of massive *Porites* decrease significantly with increasing latitude, corresponding with positive relationships between temperature and growth (e.g., Grigg 1982, Lough & Barnes 2000). A vast majority of the work on coral growth is conducted with massive corals because of the permanent record of

annual growth retained within their skeleton in the form of consistent inter-annual fluctuations in skeletal density (Knutson et al. 1972, Buddemeier et al. 1974), and yet we don't know whether the same is true of branching corals that are arguably the most ecologically important corals (e.g., Coker et al. 2014).

In comparison to massive species, the variation in the nature of growth and sensitivity to disturbances of branching species may lead to a more complex spatial relationship. Branching corals grow by rapid primary linear skeletal accretion followed by secondary infilling (Roche et al. 2010) obscuring any record of past growth. To measure changes in the growth rates of such corals, it is necessary to directly measure growth at specific time intervals. To measure linear extension for example, a reference point (such as a stain line or tag) must be fixed on multiple coral branches, at multiple spatial scales and subsequently measured over time to gain a specific understanding of growth rates (Chapter 2- Pratchett et al. 2015). The lack of historic records of coral growth for branching species has limited our ability to detect changes in growth and calcification across long-term timescales. Even so, branching species may be much more sensitive to thermal stress compared to massive species (Marshall & Baird 2000, but see Guest et al. 2012) and at low latitudes temperatures may already exceed the optimum for growth (e.g., Jokiel & Coles 1977), such that further increases in temperatures may constrain survivorship and/ or growth (Pratchett et al. 2015 – Chapter 2).

The purpose of this study was to quantify growth rates (specifically, linear extension, density and calcification) of three ostensibly branching corals (*Acropora muricata*, *Pocillopora damicornis* and *Isopora palifera*) at three distinct locations along the length of the Great Barrier Reef, Australia. Until recently, much of the work on changes in growth rates of corals along marked environmental gradients, and documented effects of climate change on coral growth, focused on massive corals (Chapter 2 - Pratchett et al. 2015).

Branching coral species are however, important contributors to reef complexity, and therefore, reef biodiversity (Coker et al. 2014). Declines in the growth rates of branching corals, which are among the fastest growing corals, may also have significant impacts on reef growth (reviewed in Chapter 2 - Pratchett et al. 2015). Investigating variability in growth of branching corals over large spatial scales, where there are substantial differences in environmental conditions, may provide insight into how these corals will respond to changing environmental conditions. This study is also the first to quantify the nature of skeletal banding in *I. palifera*, as this branching reef-building species produces vertical columns with skeletal accretion patterns similar to massive corals (e.g., *Porites* spp).

5.3 Methods

5.3.1 Coral species

Coral growth (specifically, linear extension, density, calcification) was quantified for three coral species (*Acropora muricata* (cf. *A. formosa*), *Pocillopoa damicornis*, and *Isopora palifera*) that were common and abundant at widely separated locations along the length of the GBR. *Acropora muricata* is a staghorn coral that often dominates in shallow water lagoons, forming large mono-specific thickets. It is also widespread and found throughout the Indo-Pacific (Veron 1986). *Pocillopora damicornis* is an abundant, ubiquitous species found throughout the Indo-Pacific (Veron 1986). The recent amendment of the *Pocillopora* complex taxonomy (Schmidt-Roach et al. 2014) was used to aid identification of *P. damicornis. Isopora palifera* is abundant in high wave energy areas such as reef slopes, crests and flats, forming submassive clumps that contain columns and ridges (Veron 1986). The longest possible columns were chosen to retrospectively determine coral growth in *I. palifera* and the possible nature of annual banding.

5.3.2 Study sites

This study was conducted at three distinct locations, spread along 1,187 km of Australia's Great Barrier Reef. The northernmost location was Lizard Island (14.7°S), followed by Davies Reef (18.8°S) and Trunk Reef (18.4°S), and finally Heron Island (23.4°S) in the south. At each of the three locations, coral growth was documented at 2 sites for *A. muricata* and *P. damicornis*, but only 1 site for *I. palifera* (Figure 5.1a-o). Study sites were specifically selected to provide comparable habitat and depth (5 m) at each reef, while also selecting areas with high abundance of each of the specific study species. In the central sector, *Pocillopora damicornis* was poorly represented at the first reef we visited (Davies Reef) and therefore, additional sampling was undertaken at another nearby reef, Trunk Reef (Figure 5.1i).

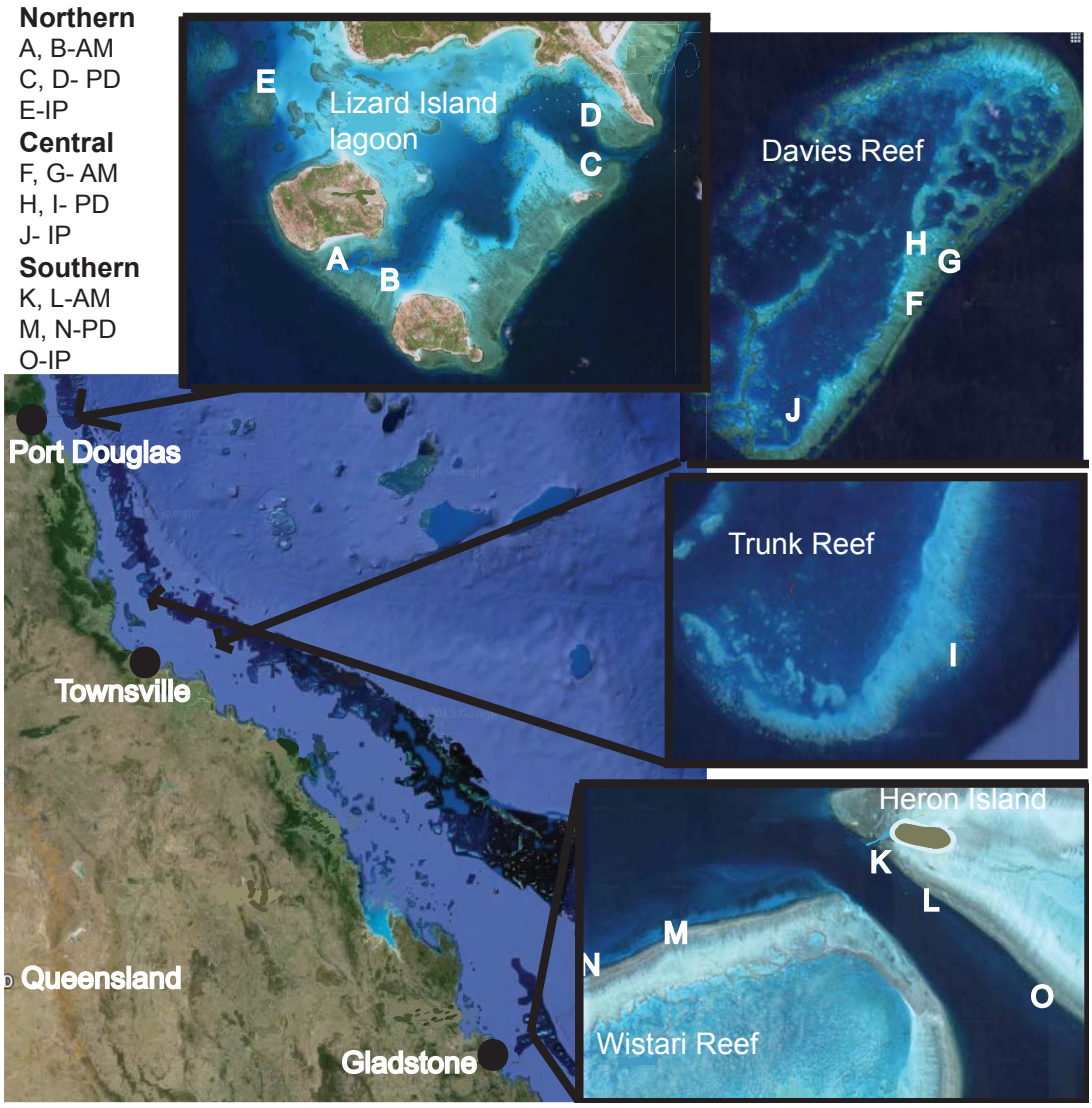

Figure 5.1. Map of study sites along the Great Barrier Reef. Sites A,B (*A. muricata)*, C,D (*P. damicornis*), E (*I. palifera*) were in the northern sector at Lizard Island. Sites F, G (*A. muricata*), H, I, (*P. damicornis*), J (*I. palifera*) were in the central sector at Davies and Trunk Reef. Sites K, L, (*A. muricata*), M, N (*P. damicornis*), O (*I. palifera*) were in the southern sector at Heron Island. AM=*Acropoca muricata*. PD=*Pocillopora damicornis*. IP=*Isopora palifera.* Figure was adapted from Google Earth.

5.3.3 Coral growth

To quantify annual (or bi-annual) growth rates for each coral species, replicate colonies and/or branches were stained *in situ* using Alizarin Red. As calcification takes place, the dye gets incorporated into the skeleton producing a permanent reference against which to measure all subsequent skeletal growth. The concentration of Alizarin used was 12 mg L^{-1} and corals were exposed to the dye for 4 hours during the daylight hours of 900-1600 (Lamberts 1978). Stained corals were marked with cattle tags attached to the colony base, away from the growing tips to minimise disruption to growth. In total, 240 colonies of *A. muricata*, 120 colonies of *P. damicornis* and 30 colonies of *I. palifera* were stained. Once collected, branches and colonies were placed in 10% sodium hypochlorite to remove the coral tissue and expose the skeleton (Figure 5.2).

Acropora muricata

The sampling regime for *A. muricata* encompassed four 6-month periods at each reef: summer 2012-2013 (Oct/Nov 2012-Mar/Apr 2013), winter 2013 (Apr 2013- Oct 2013), summer 2013-2014 (Oct/Nov 2013-Mar/Apr 2014), winter 2014 (Apr/May 2014-Oct-Nov 2014). Individual branches were enclosed in a 1 L plastic bag *in situ* and secured at the base with an elastic band. Alizarin red dye was injected with a needle under the elastic band into the bag. Ten colonies of *A. muricata*, with three branches per colony were stained using Alizarin red dye at each site, totalling 20 colonies and 60 branches per reef (60 colonies/180 branches total) in October 2012. In April 2013, the previously stained colonies were collected at each site and another set stained. This cycle of staining continued for two-years with 720 branches for *A. muricata* stained.

Growth measurements were determined for each branch of *A. muricata*. Linear extension (cm) was measured with venire callipers, recording the minimum distance from the

stain line to tip of the apical polyp. Branches that had died prior to final collection were excluded from analysis. In addition, 0.02 % (16/720) of branches had switched to zooxanthellae free (non-growing) tips through the course of the study that can result from interior conditions of the colony being less suitable for growth or branches growing too closely together (Oliver et al. 1984), and were excluded from analysis. To determine bulk skeletal density of the branching species *A. muricata*, corals were cut along the stain line with a geological saw using a 2 mm saw blade. The dry weight (g) of the cut branch tips was recorded. Branches were dipped in paraffin wax and the total enclosed volume was determined using water displacement technique (Oliver et al. 1983, Browne et al. 2012). Skeletal bulk density (g cm^{-3}) was then determined by dividing the dry weight by the enclosed volume. Calcification (g cm^{-2}) rates were calculated by multiplying the linear extension by the density (Lough & Barnes 2000, Browne et al. 2012). However, these calcification rates are only of the apical newly grown branch and are not a measure of whole colony calcification.

Pocillopora damicornis

The sampling regime for *P. damicornis* encompassed one year, separated into two 6-month periods at each reef: summer 2013-2014 (Oct/Nov 2013-Mar/Apr 2014) and winter 2014 (Apr/May 2014-Oct/Nov 2014). 20 colonies per location (10 at each site) were stained. Colonies (max 20 cm diameter) were removed from the substrate and put into a 70 L clear plastic bag with Alizarin dye released into the bag and remained in place for 4 hours until being reattached to the reef. For *P. damicornis*, the number of coral branches measured with callipers ranged from 10-20 (n=10 for corals 8-15 cm in diameter, n=20 for corals 15-20 cm in diameter). Branch measurements for *P. damicornis* were randomly sampled along the longest axis of growth (often the most upward projecting). Measured branches were sectioned

with a saw and the bulk density and calcification was determined as described for *A. muricata.* In addition, areas of partial mortality due to algal overgrowth or smothering due to sediment were excluded.

Isopora palifera

Growth rates of *I. palifera* were recorded for an entire year (Oct/Nov 2013-Oct/Nov 2014) at one site per location (Lizard Island, Davies Reef, Heron Island). At each location, 10 colonies were stained (30 colonies total) with 2-3 columns per colony. Columns of *I. palifer*a were enclosed in a 4 L clear plastic bag and sealed at the base with an elastic band. The dye was injected under the elastic band with a needle. To determine the linear extension of *I. palifera*, stained coral columns were sliced at 4.4 mm thickness until the maximum vertical axis of growth was determined and then photographed with a reference scale. Linear extensions were determined for each column by taking three measurements along the main vertical growth axis from the stain line to the end of the column on the digital image in Image J Fiji (Schindelin et al. 2012).

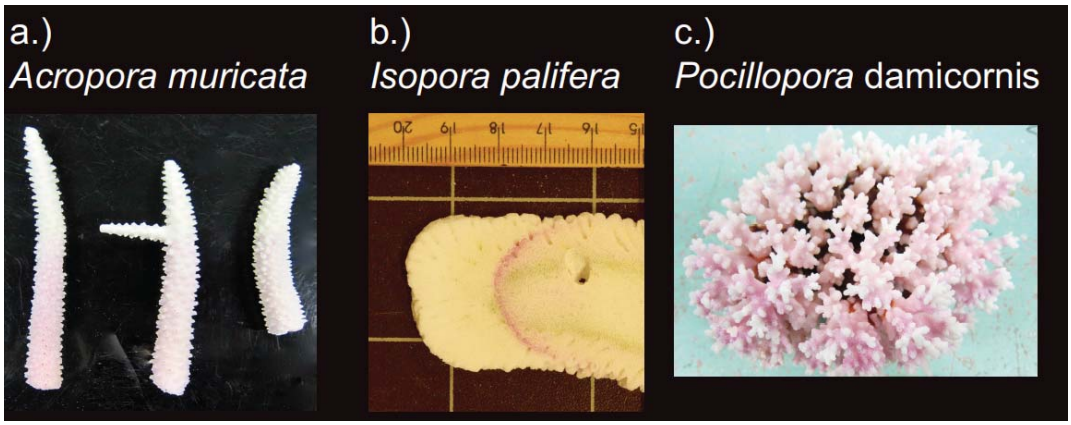

Figure 5.2. Coral species a.) *Acropora muricata*, b.) *Isopora palifera* and c.) *Pocillopora damicornis* utilised in this study. The pink portion of the skeleton is the result of the Alizard Red dye being encorporated into the skeleton from staining and the white portion is the newly accreted skeleton.

Density and calcification rates of *I. palifera* were determined from the digitised images of x-radiography (Figure 5.2), adapted from Carricart-Ganivet & Barnes (2007). In each X-ray exposure along with the coral, 6 standards made of compressed *Porites* skeleton powder, of increasing thickness (0.155-0.747 cm) and known density, determined from weight (g) and volume (cm^3) were positioned alongside the coral skeleton. X-rays were taken with a Sectional CR High Resolution Digital Imaging System 3600+ (*i*CRco 2015) and converted for analysis in Image J Fiji (Schindelin et al. 2012). A blank x-ray was subtracted to correct the background and the image was inverted for density extraction. The high quality of the scanner resulted in no further adjustments or corrections to the image. In each x-ray, the average optic density (OD) of each *Porites* standard was determined by creating a straight line of the natural log (lnOD) versus known aragonite density x step thickness. Linear fits to the lines provided correlation coefficients (R^2) better than 0.99. A standard (2.397 g cm^3) was used for quality control between consecutive x-rays producing a standard deviation of 1.6 % (0.04 g cm^3). A track 2.5 mm wide (roughly the size of a corallite) was run down the maximum vertical growth axis of each coral column and the optical density (grey-scale values of pixels ranging from 0-255) was sampled for each coral skeleton at 0.05 mm sampling interval. From the known linear relationship between the *Porites* aragonite standards, the OD (greyscale value) of each point was converted to skeletal density (g cm^{-3}). Annual density (g cm^{-3} yr^{-1}) along each column was determined from the known marked distance of annual growth from the stain line to the tip. In addition, the absolute density of the column (ranging from 3-5 cm) was determined, which constituted measuring the density from the tip to the point of obstruction in the column (e.g., boring organism). The annual nature of density banding patterns observed from the x-ray was assessed by comparing linear extension estimates calculated between major visual high density bands and the extension rate quantified from the alizarin stain line. Annual calcification (g cm^{-2}) was then calculated as the

product of the annual linear extension from the stain line (cm) and annual density (g cm^{-3}) of new growth.

5.3.4 Statistical Analysis

To assess spatial variation (among locations) in linear extension, calcification, and density of corals), the package nlme (Pinheiro et al. 2012) was used to fit linear mixed-effects (LME) models. Separate analyses were conducted for each taxa (*Acropora mucicata, Pocillopora damicornis, Isopora palifera*). For all models the fixed effect was location and as a random effect sampling period which was nested in site and then colony. Model selection was informed by AIC and the best model then fit by restricted maximum likelihood (Table 5.1). Model assumptions, including normality of errors and homogeneity of variances, were evaluated graphically. To correct for heteroscedasticity and non-normality, a square-root transformations to the models was used (Table 5.1). For each species, one-way ANOVA were used post hoc to investigate temporal variation in growth parameters within each location. Growth variables (linear extension, density and calcification) determined from the stain line in the *I. palifera* columns were compared to those determined from between consecutive high-density bands using a one-way ANOVA with nested colony and column.

Table 5.1. Linear mixed effect model results for linear extension (LE), calcification (Calc) and density (Dens) with associated transformation (Sqrt=square root) of fixed effect sector and nest random effects (Time, Site and Colony). Selected model for each response variable in bold based on lowed AIC.

Model		Response Variable	Fixed Effect	Random Effect	df	AIC
1	*Acropora muricata*	LE	Sector		4	4316
2		LE	Sector	Time	5	4298
3		LE	Sector	Time period/Site	6	4172
4		**LE**	**Sector**	**Time period /Site/Colony**	**7**	**4080**
6	*Acropora muricata*	SqrtCalc	Sector		4	569
7		SqrtCalc	Sector	Time period	5	558
8		SqrtCalc	Sector	Time period Site	6	481
9		**SqrtCalc**	**Sector**	Time period **/Site/Colony**	**7**	**466**
11	*Acropora muricata*	SqrtDens	Sector		4	-985
12		SqrtDens	Sector	Time period	5	-984
13		SqrtDens	Sector	Time period /Site	6	-994
14		**SqrtDens**	**Sector**	Time period **/Site/Colony**	**7**	**-1001**
15	*Isopora palifera*	LE	Sector		4	87
16		**LE**	**Sector**	**Colony**	5	72
17		SqrtDens	Sector			-98
18		**SqrtDens**	**Sector**	**Colony**		**-99**
19		Calc	Sector			68
20		**Calc**	**Sector**	**Colony**		**67**
21	*Pocillopora damicornis*	SqrtLE	Sector		4	2641
22		SqrtLE	Sector	Time period	5	2642
23		SqrtLE	Sector	Time period/Site	6	2471
24		SqrtLE	**Sector**	**Time period/Site/Colony**	**7**	**2022**
25	*Pocillopora damicornis*	**SqrtDens**	**Sector**		**4**	**-386**
26		SqrtDens	Sector	Time period	5	-384
27		SqrtDens	Sector	Time period/Site	6	-382
28	*Pocillopora damicornis*	**SqrtCalc**	**Sector**		4	**-229**
29		SqrtCalc	Sector	Time period	5	-227
30		SqrtCalc	Sector	Time period/Site	6	-225

5.3.5 Environmental Parameters

Sea surface temperature

Sea surface temperature (SST) throughout the study was determined from the Integrated Marine Observing System (IMOS). Data loggers instantaneously record sea temperatures every 30 minutes (AIMS 2015). At each reef, average, minimum and maximum daily and monthly SST from a sensor at 5-6 m depth was determined from Oct 2012-Nov 2014 (AIMS 2015). At the northern sector, Lizard Island SST was compiled from 3 sensors at 5-6.7 m to construct a 2-year consecutive assessment of SST taking the averages when data for multiple months was available. As the central GBR sector took place on two reefs, a t-test was performed on the average monthly SST to determine if there was significant variation between Davies Reef and Trunk Reef (closest sensor deployed to Trunk Reef was Kelso Reef, ~12 km apart). As there was no significant difference in temperature between the two central GBR sites ($t=0.126$, $df=33.9$, $p=0.815$), Davies Reef comprised a complete SST record and will be used for analysis. Two-way analysis of variance was used to determine significant variation between sector SST and monthly time period. The relationship of *A. muricata* and *P. damicornis* density, linear extension and calcification rates were compared to SST for each reef and sampling period using linear regression. As *I. palifera* was only investigated for one year at 3 sites, a statistical relationship cannot be reliably established due to limited sample size.

Historic sea surface temperature trends were determined from the Extended Reconstructed Sea Surface Temperature (ERSST) dataset (2° and monthly resolution). Satellite SST data of higher-resolution, both spatially (1/24°, ~4 km) and temporally (weekly), were also derived for the period 1985-2012 from the Pathfinder v5.2 night-only, 4 km-daily SST dataset, with gaps filled following Heron et al. (2010). However, as these data did not overlap the time periods of interest, 4 km-monthly composites were calculated and

used to bias adjust the spatially and temporally lower resolution ERSST data to ensure relevance to the study. Trends in bias-adjusted ERSST were calculated annually from 1965 to 2014. In addition, accumulated thermal stress was calculated from ERSST using the Degree Heating Months (DHM) metric (Donner et al. 2005). Values were converted to Degree Heating Weeks (DHW, Liu et al. 2003) for ease of comparison with established ecologically-relevant thresholds for significant bleaching and mortality of 4 and 8 ℃-weeks (Eakin et al. 2010, Liu et al 2003). At each reef, satellite SST during the course of the study (2012-2014) was compared to the long-term average (1965-2011) using a Welch's t-test for unequal sample size, unequal variance.

Aragonite Saturation

Within-reef aragonite saturation had previously been determined at Davies Reef (Albright et al. 2013) and Heron Island (Albright et al. 2015), but was yet to be quantified using the same methodologies in the northern sector at Lizard Island. The carbonate chemistry was determined in the summer for 9 days from Jan 23 to Feb 1, 2014, inside the lagoon on the protected back reef flat, following Albright et al. (2013, 2015). An automated water sampler was deployed for 9 days from Jan 23, 2014 to Feb 1, 2014, between South Island and Palfrey Island (14°41'52.08 S, 145°26'58.05) The water sampler was deployed to document diurnal variability in carbonate chemistry. The approximate depth of the water sampler was 1.0 m but varied with the tides. The sampler pumped water at 2-hour intervals into pre-poisoned 250 mL borosilicate bottles (0.05% $HgCl_2$ to inhibit biological activity). Bottles were filled with reef water at a flow rate of ~2 mLs^{-1}. To avoid contamination of new samples, the sampler was programmed to flush the lines for 30s between filing. Filled bottles were retrieved every 12 hr and new, prepoisoned bottles were deployed.

Water samples were analysed at the Australian Institute for Marine Science (AIMS). Total alkalinity (A_T) and dissolved inorganic carbon (C_T) were analysed using the VINTA

3C® (Versatile Instrument for Determination of Total dissolved inorganic carbon and Alkalinity, Marianda, Kiel, Germany) and a UIC CO_2 coulometer detector (UIC Inc., Joliet, USA). Accuracy was checked against certified

seawater reference material. pCO_2, pH_T (total scale), and aragonite saturation state (Ω_{arag}) were calculated as a function of the measured salinity, temperature, A_T, and C_T using the program CO2SYS (Lewis & Wallace 1998); dissociation constants for carbonate and boric acid determined by Mehrbach et al. (1973) as refit by Dickson and Millero (1987), and the dissociation constant for boric acid determined by Dickson (1990), following Albright et al. (2013).

Benthic surveys were conducted on the reef flat between South and Palfrey Island at Lizard Island to characterize the surrounding community structure of the site. Five independent transects (20 m) were conducted perpendicular to the reef crest on the back reef. Photographs were taken of 1 m^2 transects at 2 m intervals. Photos were analysed in Image J Fiji (Schindelin et al. 2012) for percentage cover of 1) live coral; (2) algae (macroalgae and turf); (3) crustose coralline algae (CCA); (4) $CaCO_3$ substrate (dead coral, rubble, sand); (5) and "other", including sponges, gorgonians, giant clams, etc.

Salinity (practical salinity units; psu) during deployment of the automated water sampler was determined from daily water samples. Samples were analysed at AIMS on a Portasal salinometer, which measure conductivity ratios and salinity.

Light

Solar radiation throughout the study was determined from the Integrated Marine Observing System (IMOS). The solar radiation sensor is an Under Water Quantum Sensor made by Licor that measures photosynthically active radiation (PAR) (AIMS 2015). At each location, the only consistent reading for solar radiation (PAR) was from the weather station relay

poles. The sensor records light intensity every 30 minutes and are exchanged and downloaded approximately every 12 months (AIMS 2015). Daily averages were then determined and summed to a monthly value for analysis. To remove bias, analyses were performed on monthly data that was present among all sectors. Two-way analysis of variance was used to determine significant variation between sector SST and monthly time period. The relationship of density, linear extension and calcification rates for *A. muricata* and *P. damicornis* with light intensity (PAR, averaged for each sampling period) for each reef then compared using linear regression. Due to the limited spatial and temporal sampling, linear regression was not performed on *I. palifera*.

5.3.6 Meta-analyses of coral growth

Linear extension is the metric most often reported in the literature for quantifying growth of branching corals (Chapter 2 - Pratchett et al. 2015). To relate measurements of linear extension from along the GBR to other measurements taken from further afield, separate meta-analyses was performed for *A. muricata* and *P. damicornis*, specifically testing for variation in linear extension with variation in local average SST during the studies, as well as latitude. Very few studies had reported growth rates on *Isopora* and this species could not be included in this analysis. A total of 13 and 16 studies that measured linear extension of *A. muricata* and *P. damicornis*, respectively, were used in these analyses. Where applicable, if additional experimental conditions were imposed in the study, we used on growth estimates from "control" corals. Daily mean SST determined from satellite imagery was quantified during the dates the study was conducted when provided, and assumed the year prior when sampling dates were not included. Study depths ranged from 0.5-15 m for *A. muricata* and 2-7 m for *P. damicornis*. However, the affect that depth had on growth was assumed to be negligible when comparing multiple studies across large temperature (annual average 21 - 29

°C) and latitudinal scales (0 - 30°). Linear regression was used to investigate the fixed effect of linear extension on the random effects of average SST and latitude. For both the *A. muricata* and *P. damicornis* data set, the models with latitude had a linear model to explain the relationship best, whereas, for SST a polynomial function provided a better relationship (based on comparison of R^2). For *P. damicornis*, the relationship of linear extension with latitude required a square root transformation to normalize the residuals.

Statistical analysis was completed in R (R Core Team 2015). All linear models were tested to meet the assumptions of linear models (homogeneity of variance, linearity, independence).

5.4 Results

Moderate levels of background coral mortality and injuries, as are common for fast growing and typically short-lived, branching corals (e.g., Pisapia et al. 2014) resulted in inevitable mortality and loss of some stained colonies and branches. Of the 720 *A. muricata* branches stained in this study, 70% (540/720) were recovered and healthy, and were used in analyses of coral growth. Of those excluded, 20 % had died since staining but were still intact, while the remainder were not relocated. For *P. damicornis*, 90% (108/120) of the colonies stained were healthy, relocated and used in this study. Of the 12 colonies not included, 7 died, 4 were not relocated and 1 did not stain well and 10% were not recovered. For *Isopora palifera*, 90 % (27/30) of stained colonies were relocated and used in the study, while the fate of the other 10 % is unknown (possibly lost due to poor tag retention).

5.4.1 Intraspecific variation in growth parameters

Acropora muricata

Average linear extension was greatest at Lizard Island (4.78 ± 0.19 cm 6-month^{-1}) compared to Davies Reef (3.81 ± 0.415 cm 6-month^{-1}) and Heron Island (2.49 ± 0.08 cm 6-month^{-1}).

Linear extension rates measured at Lizard Island were significantly greater than Heron Island (Table 5.2ai), but were not significantly different from Davies Reef. When evaluating variation among sampling periods within each reef, linear extension showed significant inter-annual variation (Table 5.3). At Lizard Island for example, the lowest (3.69 ± 0.43 cm 6-months^{-1}) and greatest (6.56 ± 0.43 cm 6-months^{-1}) average 6-month linear extension rates were in the two summer periods (Figure 5.3ai).

Table 5.2. Linear mixed effect model results for *Acropora muricata*, *Pocillopora damicornis* and *Isopora palifera* linear extension, calcification and density as the response variable for the fixed effects of sector: northern sector (Lizard Island), central sector (Davies Reef) and southern sector (Heron Island).

Species	Response variable	Fixed Effects	Value	SE	Df	t-value	p-value
a.) *A. muricata*	i.) LE	(Intercept)	4.420	0.45	302	10.10	-
		Sector: Central	-0.753	0.60	18	-1.250	0.229
		Sector: Southern	-2.010	0.59	18	-3.390	0.003
	ii.) Dens	(Intercept)	0.875	0.04	267	87.11	-
		Sector: Central	0.028	0.06	18	0.943	0.358
		Sector: Southern	-0.029	0.05	18	-1.090	0.291
	iii.) Calc	(Intercept)	3.700	0.40	271	18.42	-
		Sector: Central	-0.390	0.51	18	-0.759	0.458
		Sector: Southern	-1.500	0.49	18	-3.280	0.004
b.) *P. damicornis*	i.) LE	(Intercept)	1.040	0.08	1394	24.71	-
		Sector: Central	-0.129	0.11	8	-1.140	0.228
		Sector: Southern	-0.347	0.10	8	-3.270	0.011
	ii.) Dens	(Intercept)	1.216	0.03	90	89.59	-
		Sector: Central	-0.037	0.04	2	-1.047	0.298
		Sector: Southern	0.010	0.04	2	0.282	0.778
	iii.) Calc	(Intercept)	1.104	0.06	90	43.54	-
		Sector: Central	-0.147	0.07	2	-2.960	0.043
		Sector: Southern	-0.382	0.06	2	-5.680	0.000
c.) *I. palifera*	i.) LE	(Intercept)	1.639	0.10	80	16.31	-
		Sector: Central	-0.118	0.14	19	-0.850	0.403
		Sector: Southern	-0.281	0.14	19	-1.970	0.063
	ii.) Dens	(Intercept)	1.284	0.05	20	66.91	-
		Sector: Central	-0.115	0.06	20	-1.760	0.942
		Sector: Southern	0.041	0.07	20	0.580	0.570
	iii.) Calc	(Intercept)	2.692	0.22	20	12.21	-
		Sector: Central	-0.216	0.30	20	-1.070	0.300
		Sector: Southern	-0.209	0.31	20	-0.670	0.511

Table 5.3. Nested ANOVA results for *A. muricata* comparison of linear extension (LE), density (Dens) and calcification (Calc) for each reef comparing between sapling periods.

Species	Reef	Fixed effect	Nested ANOVA Results
A. muricata	Lizard Island	LE	$F_{3/66}$=10.59, p=0.000
		Dens	$F_{3/66}$ =0.584, p=0.628
		Calc	$F_{3/66}$=7.525, p=0.000
	Davies Reef	LE	$F_{3/45}$=4.625, p=0.005
		Dens	$F_{3/45}$=3.319, p=0.028
		Calc	$F_{3/45}$=4.145, p=0.011
	Heron Island	LE	$F_{3/73=}$4.381, p=0.007
		Dens	$F_{3/69}$=1.734, p=0.168
		Calc	$F_{3/69}$=5.850, p=0.001
P. damicornis	Lizard Island	LE	$F_{1/24}$=8.69, p=0.007
		Dens	$F_{1/24}$=0.94, p=0.334
		Calc	$F_{1/24}$=2.93, p=0.334
	Davies/Trunk Reef	LE	$F_{1/33}$=4.12, p=0.050
		Dens	$F_{1/30}$=1.06, p=0.310
		Calc	$F_{1/30}$=2.97, p=0.102
	Heron Island	LE	$F_{1/33}$=1.56, p=0.221
		Dens	$F_{1/30}$=0.05, p=0.823
		Calc	$F_{1/30}$=0.56, p=0.461

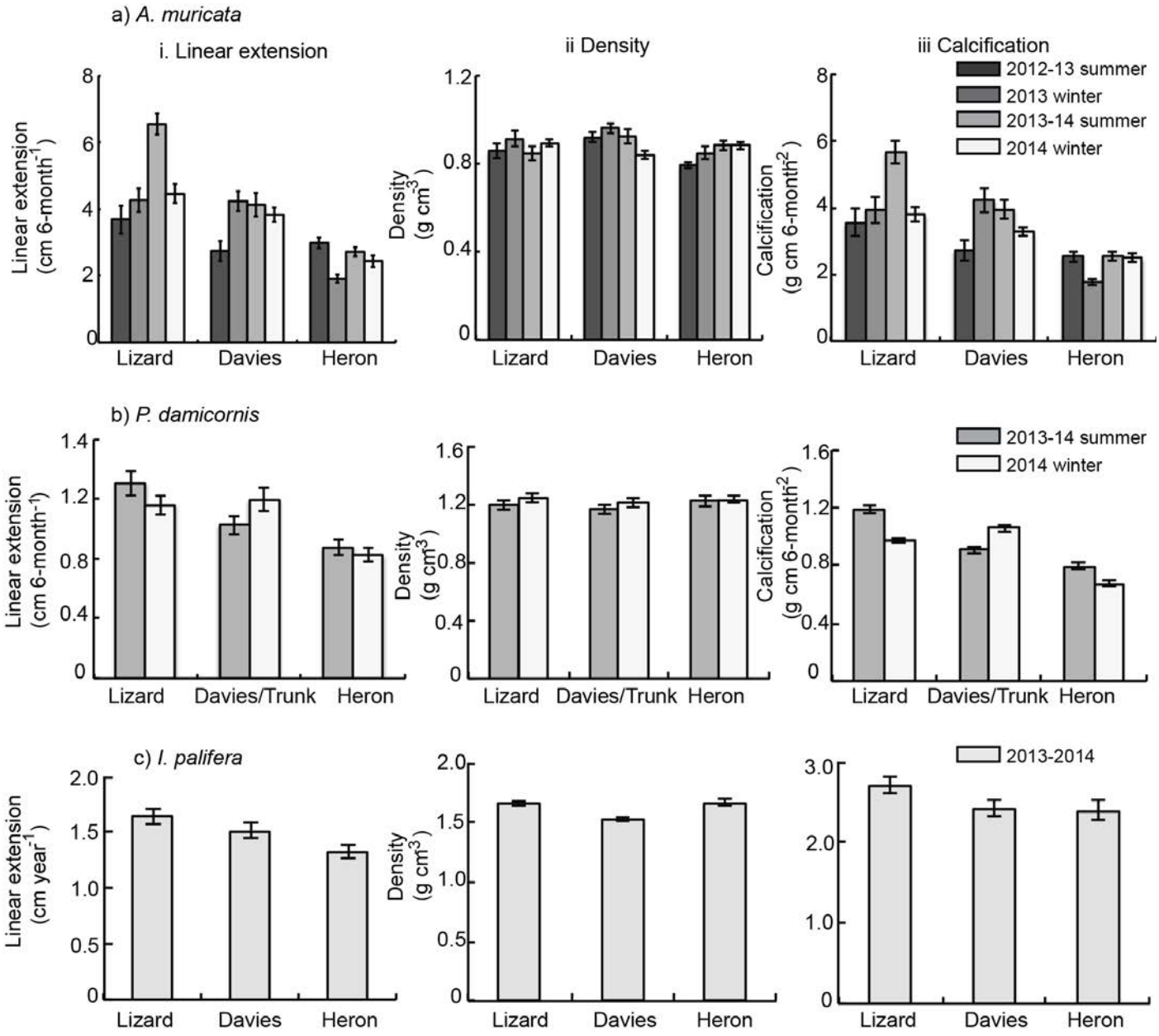

Figure 5.3. Variation in linear extension (i), density (ii) and calcification (iii) of *Acropora muricata* (a), *Pocillopora damicornis* (b) and *Isopora palifera* (c) at Lizard Island in the north, Davies and/or Trunk in the center, and Heron Island in the south of the Great Barrier Reef.

The average bulk skeletal density of *A. muricata* on the Great Barrier Reef was 0.88 ± 0.01 g cm^{-3}, and did not vary significantly among locations (Figure 5.3aii; Table 5.2aii). There was however, significant temporal variation in density of newly accreted skeleton, especially at southernmost reefs (Table 5.3). At Davies Reef and Heron Island there was significant variation in density between sampling periods (Table 5.3) but no consistent trend with respect to season (Figure 5.3aii).

Calcification rates of *A. muricata* (measured as total weight per volume of skeletal material added at growing tips) decreased along the north-south latitudinal gradient along the GBR and were largely reflective of variation in linear extension (Figure 5.4). The average 6-month calcification rate at Heron Island (2.20 ± 0.4 g cm^{-2}) was 40% less than Lizard Island (3.70 ± 0.4 g cm^{-2}) (Table 5.2aiii). Similar significant variation in calcification (34 % less) was observed between Davies Reef (3.31 ± 0.5 g cm^{-2}) and Heron Island (Figure 5.3aiii; lme, t=-2.47, p=0.024). However, calcification rates between Lizard and Davies were comparable (Table 5.2aiii). Within each reef, there was significant variation in calcification rates (Table 5.3, Figure 5.3aiii). Calculated annual rates of linear extension, density and calcification are provided in Table 5.4.

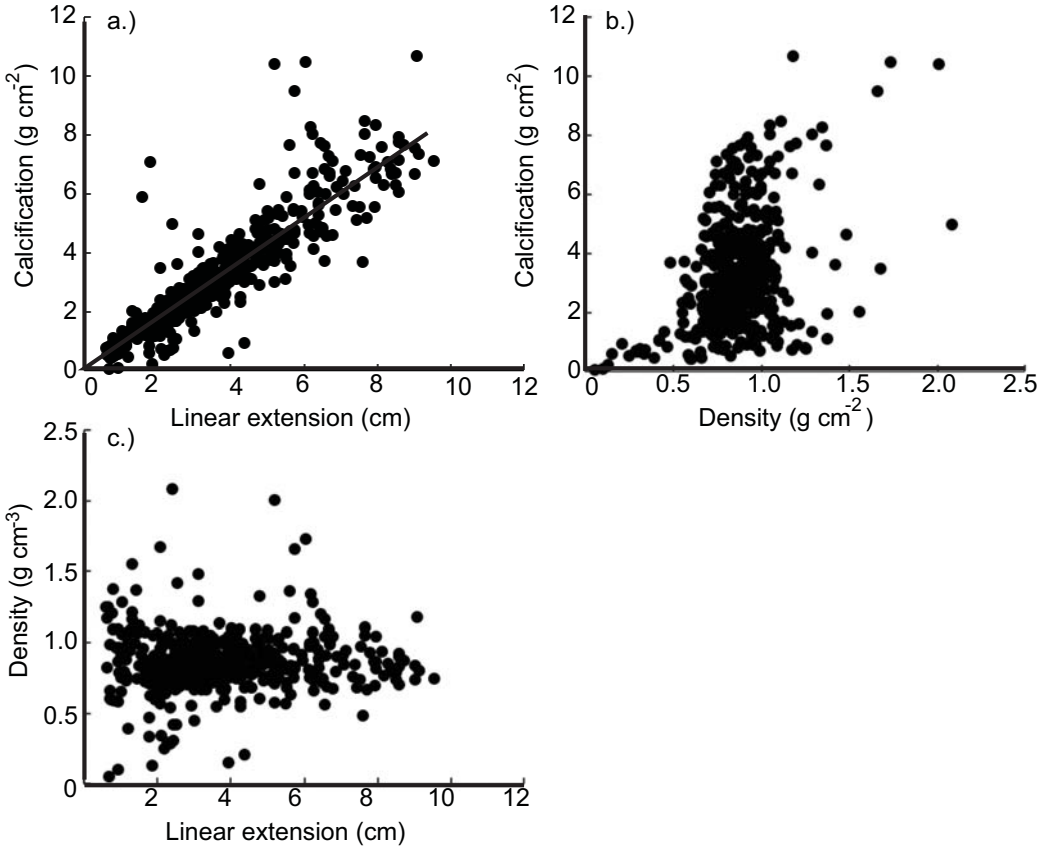

Figure 5.4. Relationship of calcification, linear extension and density of *Acropora muricata* branches during 6-month growing periods, collected along the Great Barrier Reef from Lizard Island, Davies Reef and Heron Island at 5 m depth.

Table 5.4. Summary of the linear extension (cm yr^{-1}), density (g cm^{-3}), and calcification (g cm^{-2} yr^{-1}) (Mean ± SE) for *A. muricata, P. damicornis and I. palifera* at Lizard Island, Davies Reef and Heron Island from 2012/13 and 2013/14.

Species	Location	Year	Linear Extension (cm yr^{-1})	Density (g cm^{-3})	Calcification (g cm^{-2} yr^{-1})
Acropora muricata	Lizard Island	2012/13	7.93 ± 0.29	0.89 ± 0.02	7.04 ± 0.29
		2013/14	10.8 ± 0.24	0.87 ± 0.02	9.43 ± 0.22
	Davies Reef	2012/13	7.34 ± 0.24	0.95 ± 0.02	6.95 ± 0.27
		2013/14	7.93 ± 0.21	0.89 ± 0.05	6.97 ± 0.16
	Heron Island	2012/13	4.78 ± 0.12	0.82 ± 0.02	3.93 ± 0.09
		2013/14	5.17 ± 0.21	0.88 ± 0.04	4.57 ± 0.12
Pocillopora damicornis	Lizard Island	2013/14	2.20 ± 0.17	1.22 ± 0.03	2.68 ± 0.05
	Davies Reef	2013/14	1.93 ± 0.17	1.18 ± 0.03	2.28 ± 0.05
	Heron Island	2013/14	1.50 ± 0.15	1.23 ± 0.02	1.85 ± 0.04
Isopora palifera	Lizard Island	2013/14	1.64 ± 0.35	1.66 ± 0.03	2.70 ± 0.01
	Davies Reef	2013/14	1.58 ± 0.36	1.53 ± 0.02	2.43 ± 0.10
	Heron Island	2013/14	1.43 ± 0.36	1.67 ± 0.03	2.40 ± 0.12

Pocillopora damicornis

Average linear extension of *P. damicornis* was highest at Lizard Island (1.04 ± 0.09 cm 6-month^{-1}), compared to Davies/Trunk Reefs (0.91 ± 0.11 cm 6-month^{-1}) and Heron Island (0.69 ± 0.09 cm 6-month^{-1}). There were significant differences in linear extension between Lizard and Heron Island (Figure 5.3bi; Table 5.2bi), but intermediate levels recorded at Davies Reef were not different to those recorded at Lizard Island or Heron Island (lme, t=-2.17, p=0.062). Significant variation between seasonal sampling of *P. damicornis* was observed at Lizard and Davies, but Heron had similar growth rates (Figure 5.4bi, Table 5.3). Skeletal bulk density of *P. damicornis* was not significantly different across the latitudinal gradient of the Great Barrier Reef with an average density of 1.21 ± 0.02 g cm^{-3} (Figure 5.3bii; Table 5.2bii). There was also no variation in skeletal density with respect to season (Figure 5.3bii, Table 5.3). Calcification rates per 6-months were greatest at Lizard Island (1.10 ± 0.06 g cm^{-2}), significantly greater than Davies/Trunk (1.07 ± 0.07 g cm^{-2}) and Heron Island (0.84 ± 0.06 g cm^{-2}) (Fig. 5.3biii, Table 5.2). Along the GBR, there was no significant variation in calcification between the summer 2013-2014 and winter 2014 sampling periods (Table 5.3). Calculated annual rates of linear extension, density and calcification are provided in Table 5.4.

Isopora palifera

Average linear extension across all locations for *I. palifera* was 1.49 cm yr^{-1} ± 0.03. Linear extension was greater at Lizard Island (1.64 cm yr^{-1} ± 0.06) but did not significantly vary in comparison to the Davies Reef (1.51 cm yr^{-1} ± 0.06) and Heron Island (1.33 cm yr^{-1} ± 0.06) (Table 5.2ci, Figure 5.3ci). In contrast, annual skeletal density was greatest at Heron Island (1.33 g cm^{-3}) compared to the Lizard Island and Davies Reef (Figure 5.3cii), but did not significantly vary between reefs (Table 5.2cii). Annual calcification rates were only 8%

greater at Lizard Island (2.69 cm yr^{-1} ± 0.22) compared to Davies Reef and Heron Island (Figure 5.3ciii) and were not significantly different (Table 5.2ciii).

The presence of boring organisms obstructed the internal growth patterns in many colonies and columns of *I palifera*, such that only 34 columns from 23 colonies were considered appropriate for sectioning, and of these, 68% of the columns displayed visible density-banding patterns (Table 5.5). Linear extension, calcification and density were calculated from the annual stain line and from visual consecutive high-density bands (Table 5.5). Among each reef, the distance of linear growth determined from the stain line was not significantly different from the distance between the quantified high-density bands (Table 5.6) verifying the annual nature of the high-density banding couplets. At each reef, there was a lower density at the tip of the column with increasing density down towards the base (Table 5.5). However, variation in calcification rates between the 2 most recent complete high-density bands and the annual calcification rate calculated from the stain line to the branch tip did not significantly differ (Table 5.6). In the x-rays, the appearance of fine, sub-annual banding patterns were apparent, that resembled the thickness of the dissepiment, a thin skeletal structure that supports the base of the tissue layer (Figure 5.5). In some images (10/34) the microstructures were not visible enough to quantify. The majority (75 %) of the columns deposited 25-26 micro-bands in an annual period suggesting they are formed bi-weekly. However, 5 columns deposited >30 (ranging from 30-43) microstructures during an annual period.

Table 5.5. Density, linear extension (LE) and calcification (Calc) determined for *Isopora palifera* at Lizard Island, Davies Reef and Heron Island. Values from annual nature of stain line compared to those between high-density bands.

			Alizarin stain annual values				**Density Bands**			
Reef	**Coral Column ID**	**absoulte density (g cm^{-3})**	**LE (cm yr^{-1})**	**Density (g cm^{-3})**	**Calc (g cm^{-2})**	**micro structures from stain line**	**Name**	**LE (cm)**	**Density (g cm^{-3})**	**Calc (g cm^{-2})**
Lizard Island	LIZ1A_2	1.781	1.59	1.623	2.573	26	1_2	1.15	1.768	2.033
Lizard Island	LIZ2A_2	1.704	1.39	1.548	2.145	26	1_2	1.52	1.642	2.491
							2_3	1.54	1.757	2.701
							3_4	1.68	1.789	3.009
Lizard Island	LIZ2B_3_1	1.633	1.63	1.479	2.413	26	1_2	1.56	1.581	2.470
Lizard Island	LIZ3B_02	1.771	2.28	1.631	3.711	43	1_2	2.34	1.694	3.964
							2_3	2.30	1.755	4.037
							3_4	2.46	1.899	4.672
							4_5	2.96	1.763	5.218
Lizard Island	LIZ6A_2_1	1.823	1.35	1.628	2.195	26	1_2	0.86	1.938	1.667
Lizard Island	LIZ7A_2_1	2.241	1.25	2.032	2.543	26	NA			
Lizard Island	LIZ7B_2	2.033	1.44	1.801	2.584	30	1_2	1.50	1.949	2.924
Lizard Island	LIZ8A_3	1.785	1.38	1.64	2.256	26	1_2	1.54	1.651	2.543
							3_4	1.33	1.997	2.656
							4_5	1.21	1.728	2.091
Lizard Island	LIZ8B_2	1.97	2.21	1.707	3.772	Not defined	NA			
Lizard Island	LIZ8C_1	1.927	1.89	1.604	3.032	Not defined	1_2	1.67	2.063	3.451
							2_3	1.82	2.015	3.663
Lizard Island	LIZ9B_3	1.816	1.62	1.555	2.521	26	1_2	1.20	1.893	2.272
							2_3	1.18	2.032	2.398

Davies Reef	DAV_86A_2	1.801	1.86	1.52	2.825	25	1_2	1.77	1.964	3.476
Davies Reef	DAV81A_2	1.727	1.52	1.642	2.489	26	1_2	1.28	1.809	2.316
Davies Reef	DAV82A_2	1.778	0.61	1.56	0.958	14	1_2	0.85	1.954	1.665
Davies Reef	DAV82B1_2	2.071	1.69	1.681	2.843	26	1_2	1.60	2.257	3.611
							2_3	1.60	2.25	3.600
Davies Reef	DAV82B2_2	1.466	1.82	1.4105	2.566	30	1_2	1.70	1.408	2.394
Davies Reef	DAV83A_1	1.61	1.39	1.307	1.820	26	1_2	1.22	1.42	1.732
Davies Reef	DAV84A_2	1.658	1.76	1.424	2.512	33	1_2	1.81	1.698	3.073
Davies Reef	DAV84B_1	1.969	1.45	1.4936	2.166	Not defined	NA			
Davies Reef	DAV86B_2	1.863	1.96	1.5389	3.009	26	1_2	1.78	1.721	3.063
Davies Reef	DAV87B_2	1.5633	1.81	1.534	2.781	34	NA			
Davies Reef	DAV88B_2	1.732	1.36	1.602	2.177	26	NA			
Davies Reef	DAV90A_2	1.75	1.77	1.666	2.957	26	NA			
Heron Island	HER1A_2	2.121	1.70	2.054	3.482	Not defined	NA			
Heron Island	HER3A_1	2	1.39	1.802	2.496	26	NA			
Heron Island	HER4A_1	1.77	1.64	1.589	2.608	Not defined	NA			
Heron Island	HER5B_2_1	1.807	1.70	1.611	2.746	Not defined	NA			
Heron Island	HER5C_1_1	1.736	1.84	1.656	3.050	Not defined	1_2	1.13	1.737	1.965
Heron Island	HER6A_1	1.852	1.30	1.683	2.194	Not defined	NA			
Heron Island	HER6C_02	1.642	1.99	1.569	3.123	Not defined	1_2	1.95	1.665	3.247
Heron Island	HER7A_2	1.924	1.04	1.677	1.744	26	1_2	0.99	1.801	1.790
							2_3	1.22	1.858	2.269
Heron Island	HER7B_1	1.752	0.90	1.479	1.330	Not defined	NA			
Heron Island	HER7C_2	1.825	1.11	1.57	1.740	25	1_2	1.11	1.723	1.904
							2_3	1.15	1.835	2.101
							3_4	0.96	1.909	1.831
							4_5	1.37	1.902	2.606
Heron Island	HER8A_2	1.99	1.11	1.659	1.847	25	1_2	1.26	1.73	2.182

Table 5.6. ANOVA results with nested colony for each reef comparing the linear extension (LE), density (Dens) and calcification (Calc) of the newly accreted portion of skeleton (determined from alizarin stain line) to those between adjacent high density banding patterns in *Isopora palifera* skeleton

Reef	Fixed effect	Nested ANOVA Results
Lizard Island	LE	$F_{4/14}$=1.012, p=0.435
	Dens	$F_{4/14}$=9.738, p=0.000
	Calc	$F_{4/14}$=1.957, p=0.157
Davies Reef	LE	$F_{2/7}$=0.379, p=0.698
	Dens	$F_{2/7}$=11.90, p=0.006
	Calc	$F_{2/7}$=2.684, p=0.136
Heron Island	LE	$F_{4/5}$=0.791, p=0.578
	Dens	$F_{4/5}$=34.92, p=0.000
	Calc	$F_{4/5}$=1.199, p=0.414

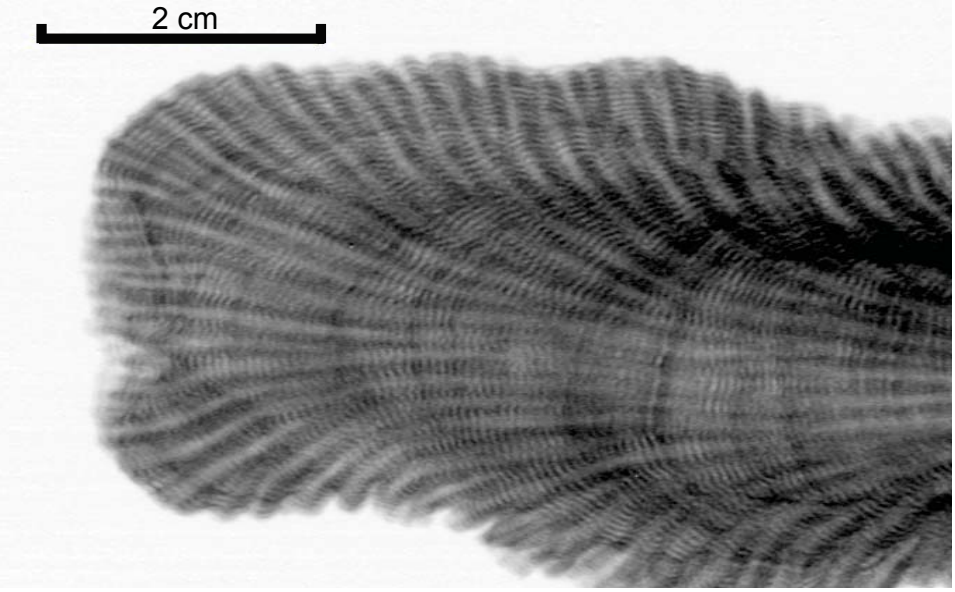

Figure 5.5. Appearance of micro-bands with high contrast x-radiography of *Isopora palifera* from Lizard Island, GBR.

5.4.2 Environmental variables along the Great Barrier Reef

Sea surface temperature

There was a significant variation in both average annual SST (Two-way ANOVA, $F_{2/76}$=196, p=0.005) and monthly average SST (Two-way ANOVA, $F_{24/76}$=36, p=0.027) among reefs. Throughout the course of the study (Oct 2012-Nov 2014), the average SST at Lizard Island was 26.8 °C (ranging from 23.2 to 30.6 °C), compared to 26.1 °C (22.5- 30.3 °C) at Davies Reef and 24.1 °C (17.4 - 28.6 °C) at Heron Island.

For *A. muricata*, linear extension (cm 6-month^{-1}) and calcification (g cm^{-2} 6-month^{-1}) was significantly related to SST (Table 5.7, Figure 5.6a); the linear extension and calcification increased 0.39 cm 6-month^{-1} and 0.35 g cm^{-2} 6-month^{-1}, respectively, for each 1 °C of SST. While linear extension and calcification of *P. damicornis* did increase with SST, the relationship was not significant (Table 5.7)

Investigating historic SST from satellite imagery at each reef, the long-term annual average at Lizard Island from 1965-2011 was 25.90 ± 0.06 (Figure 5.7a). The average SST from satellite imagery during the study (2012-2014) was 0.12 °C greater (26.02 ± 0.07 °C) but did not significantly differ (Table 5.8). Comparable SST was observed at Davies Reef and Heron Island when comparing the long-term average to the study satellite SST (Table 5.8). There was a stark contrast when comparing the rate of increase of the average SST during that time; at Lizard Island the SST rate of increase (0.108 °C per decade) was 35% greater compared to Davies Reef (0.070 °C per decade) and 47% greater compared to Heron Island (0.057 °C per decade). As well, the frequency of recorded degree heating weeks (DHWs) was markedly greater at the two lowest latitude sites in Lizard Island (35/50 years, Figure 5.7a) and Davies Reef (31/50 years, Figure 5.7b) compared to Heron Island (23/50 years, Figure 5.7c).

Table 5.7. Linear regression results for *A. muricata* and *P. damicornis* for the dependent variables (linear extension (cm 6-month^{-1}), density (g cm^{-3}) calcification (g cm^{-2} 6-month^{-1}) and independent variables, sea surface temperature (°C) and light intensity (PAR) averaged from each sampling period and reef.

Species	Independent variable	Dependent Variable	F-value	p-value	R^2
A. muricata	SST (°C)	Linear extension	$F_{1/10}$=5.058	0.048	0.34
		Density	$F_{1/10}$=0.169	0.690	0.02
		Calcification	$F_{1/10}$=5.774	0.037	0.37
P. damicornis		Linear extension	$F_{1/4}$=5.774	0.134	0.46
		Density	$F_{1/4}$=4.782	0.094	0.54
		Calcification	$F_{1/4}$=2.128	0.218	0.35
A. muricata	Light Intensity (PAR)	Linear extension	$F_{1/10}$=2.339	0.157	0.19
		Density	$F_{1/10}$=3.189	0.104	0.24
		Calcification	$F_{1/10}$=2.733	0.129	0.21
P. damicornis		Linear extension	$F_{1/4}$=0.242	0.649	0.06
		Density	$F_{1/4}$=1.791	0.252	0.31
		Calcification	$F_{1/4}$=0.651	0.465	0.14

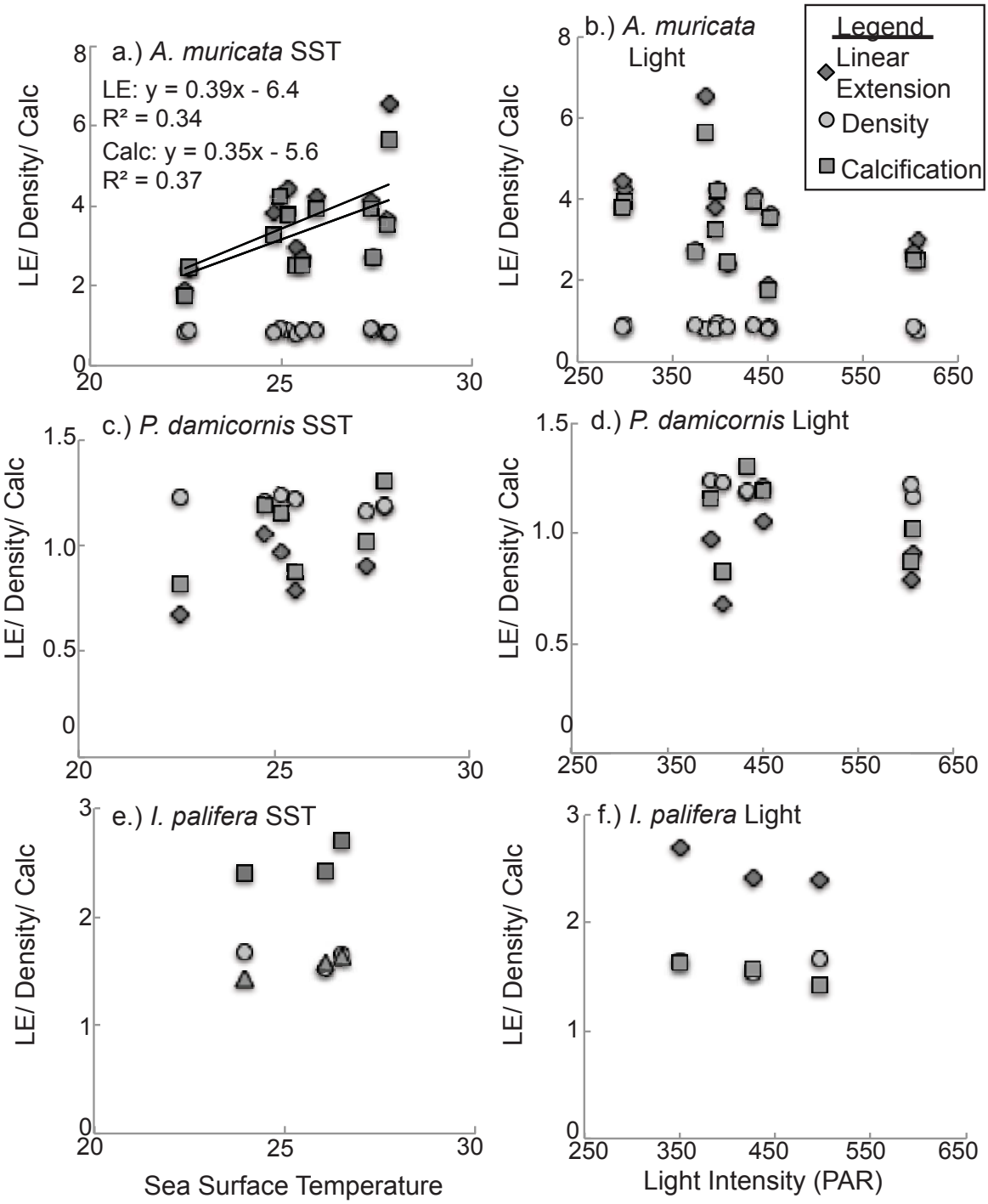

Figure 5.6. The relationship of summer and winter linear extension (cm 6-month^{-1}), density (g cm^{-3}) and calcification (g cm^{-2} 6-month^{-1}) of *Acropora muriata* (a.b.), *Pocillopora damicornis* (c.d.), *Isopora palifera* (e.f.) from 2012-2014 against average seasonal (6-month) sea surface temperature (°C) and light intensity (PAR) for all reef locations (Lizard, Davies, Heron) and sampling periods for each species. Line of best fit donates a significant relationship.

Table 5.8. Comparison of the historic annual long-term average SST (1965-2011) to the study annual average (2012-2014) from satellite imagery at Lizard Island, Davies Reef and Heron Island using Welch's t-test.

	Historic long-term average SST (°C)	Study average SST (2012-2014) (°C)	t-test
Lizard Island	25.90 ± 0.06	26.02 ± 0.07	t=-1.248, df=4.924, p=0.268
Davies Reef	25.79 ± 0.05	25.79 ± 0.04	t=-0.111, df=15.37, p=0.913
Heron Island	23.96 ± 0.05	23.96 ± 0.04	t=0.062, df=10.19, p=0.9518

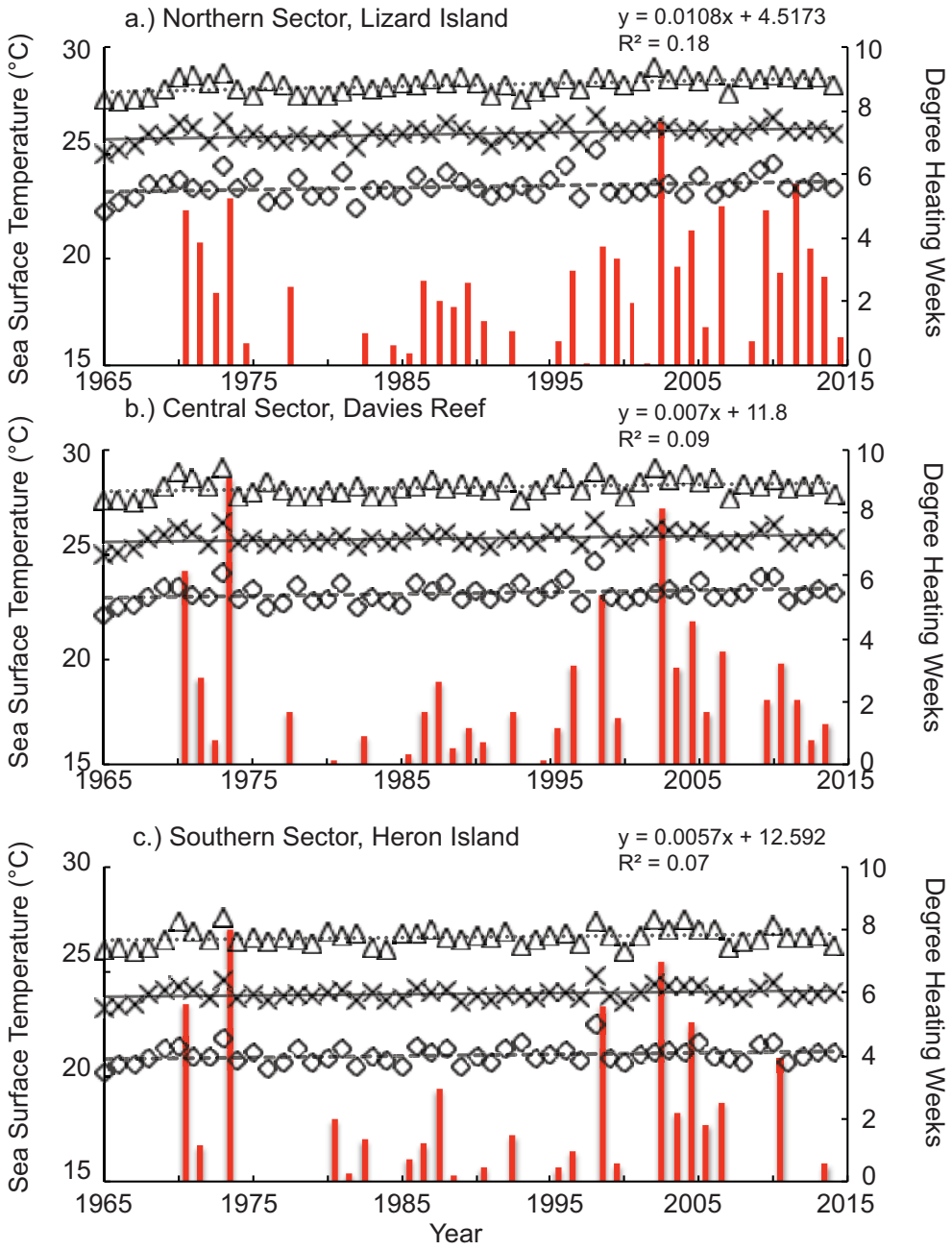

Figure 5.7. Relationship of average (X), maximum (Δ) and minimum (◇) sea surface temperature (°C) from 1965 to 2015 at the a.) northern sector, Lizard Island, b.) central sector, Davies Reef and c.) southern sector, Heron Island. Associated yearly maximum degree heating weeks (DHW) are provided.

Light

Comparing monthly light intensity (PAR) among sectors, there was a significant variation among sectors (two-way ANOVA, $F_{2/30}$=20.68, p=0.000) and month (two-way ANOVA, $F_{15/30}$=2.99, p=0.005, Figure 5.8). Average monthly PAR (μmol s^{-1} m^{-2}) during the study was greatest at Heron Island (539 ± 27 μmol s^{-1} m^{-2}), compared to Lizard Island (375 ± 30 μmol s^{-1} m^{-2}) and Davies Reef (371 ± 22 μmol s^{-1} m^{-2}). Linear regression was utilised to predict the calcification, density and linear extension rates based on light intensity (PAR). For all growth variables of *A. muricata* and *P. damicornis*, there was no significant relationship with solar irradiance (Table 5.7, Figure 5.6).

Conditions during deployment of the automated water sampler at Lizard Island

Physical conditions at Lizard Island during measurements of seawater chemistry were conducive to high levels of water exchange, where wind gusts up to 32.5 knots (60 km/hr) with average wind speeds of 22.5 knots (40.62 km/hr) (AIMS 2015). Moreover, the new moon was Jan 31, 2014 accompanied by the king tide causing water levels to range from 0.02 m to 3.37 m. Average sea surface temperature during the 9 days was 28.5°C (ranging from 27.4 - 29.4) (AIMS 2015). Benthic cover at Lizard Island was 17 % hard coral cover (Table 5.9). The greatest percentage of benthic cover (44.6 ± 7.4 %) consisted of $CaCO_3$ substrate due to a high proportion of sand patches and rubble on the reef flat. As well there is a large population of "other" substrate covering (29.9 ± 4.6 %), mainly gorgonians, covering the flat.

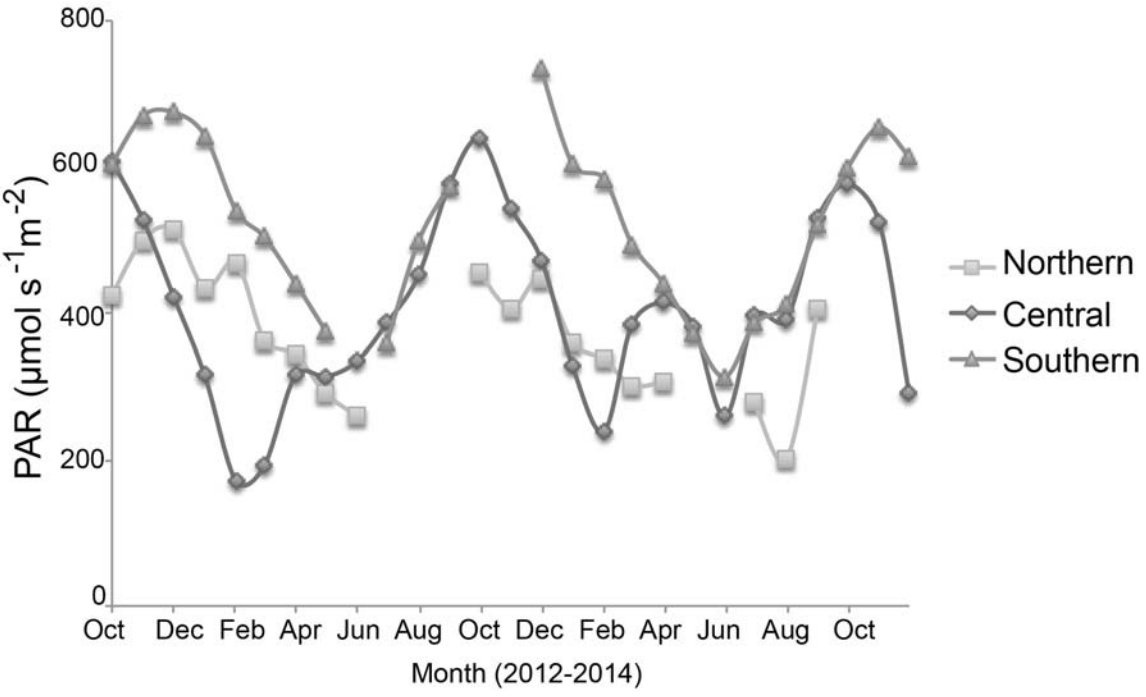

Figure 5.8. Monthly average solar irradiance (PAR) in the northern (Lizard Island), central (Davies Reef) and southern (Heron Island) sectors of the GBR. Data was determined from IMOS weather stations at each reef (AIMS 2015).

Aragonite saturation: Patterns in seawater chemistry

Aragonite saturation at Lizard Island averaged 3.3 ± 0.2 (Table 5.10) but ranged from 2.6 - 3.7 (Figure 5.9). Average aragonite saturation previously determined for Davies Reef on 17-27 January, 2012, was 3.7 ± 0.2 (Albright et al. 2013) and in Heron Island 8-18 March, 2012, was 3.3 ± 0.03 (Albright et al. 2015). Diel patterns in aragonite saturation determined for Lizard Island (Figure 5.9) follow the similar trends as observed for Davies Reef (Albright et al. 2013) and Heron Island (Albright et al. 2015). At Lizard Island, the pCO_2 and total inorganic carbon (C_T) were on average highest just before dawn (Figure 5.10), however there were two days when pCO_2 at 2:00 am was greater than 550 ppm (28/01-29/01), which coincided with a period of extensive rainfall at Lizard Island. pCO_2 levels were highly variable but followed a pattern of increasing throughout the day and were lowest around dusk. Diel patterns in pH and aragonite saturation (Ω_{arag}) were inverse to those of pCO_2 and C_T but with the highest values at dusk and lowest at dawn (Figure 5.10). All measured and calculated physical and chemical parameters are presented in Table 5.9, along with those previously determined for Davies Reef and Heron Island. Benthic cover during deployment at Lizard Island are provided in Table 5.9.

Table 5.9. Physical conditions during deployment of the automated water sampler at Lizard Island.

	Live Coral	Algae	CCA	$CaCO_3$ substrate-sand, rock, rubble	Other substrate
Mean % ±SE	16.6±2.8	8.8±3.2	1.6±0.4	44.6±7.4	29.9±4.6

Table 5.10. Comparison of within-reef carbonate chemistry at Lizard Island (northern), Davies Reef (central) and Heron Island (southern). Values for Davies Reef and Heron Island are from Albright et al (2013) and (2015), respectively. Averages and ranges of measured* and calculated physical and chemical parameters given. Carbonate chemistry for Lizard Island was determined in this study in January 2014 on the back reef inside the Lizard Island lagoon. Carbonate chemistry was determined on the back reef flat at Davies Reef in the summer January 2012. In Heron Island, values are for the combined sampling on the reef flat and crest in March 2012.

Location	T* °C	S*	A_T^* µmol kg^{-1}	C_T^* µmol kg^{-1}	$pH_{seawater}$	pCO_2 µatm	Ω_{arag}	CO_3^{2-}
Lizard Island (mean)	28.5±0.3	34.6±0.3	2230±24	1941±26	7.99±0.03	449±46	3.3±0.2	206±14
range			2165-2263	1874-2001	7.86-8.06	369-644	2.6-3.7	369-644
Davies Reef (mean)	28.5±0.2	35.0±0.1	2276±16	1954±25	8.03±0.03	404±40	3.7±0.2	228±13 227
range	28.1-28.9	34.9-35.1	2213–2304	1878–2018	7.92–8.10	325–542	2.9–4.1	181–253
Heron Island (mean)	26.6 ± 0.06	35.4 ± 0.01	2258 ± 2	1969 ± 4	7.99 ± 0.004	449 ± 6	3.3 ± 0.03	205 ± 2
range	24.2-30.4	35.2-35.5	2176-2307	1834-2059	7.83-8.14	281-669	2.3-4.2	144-261

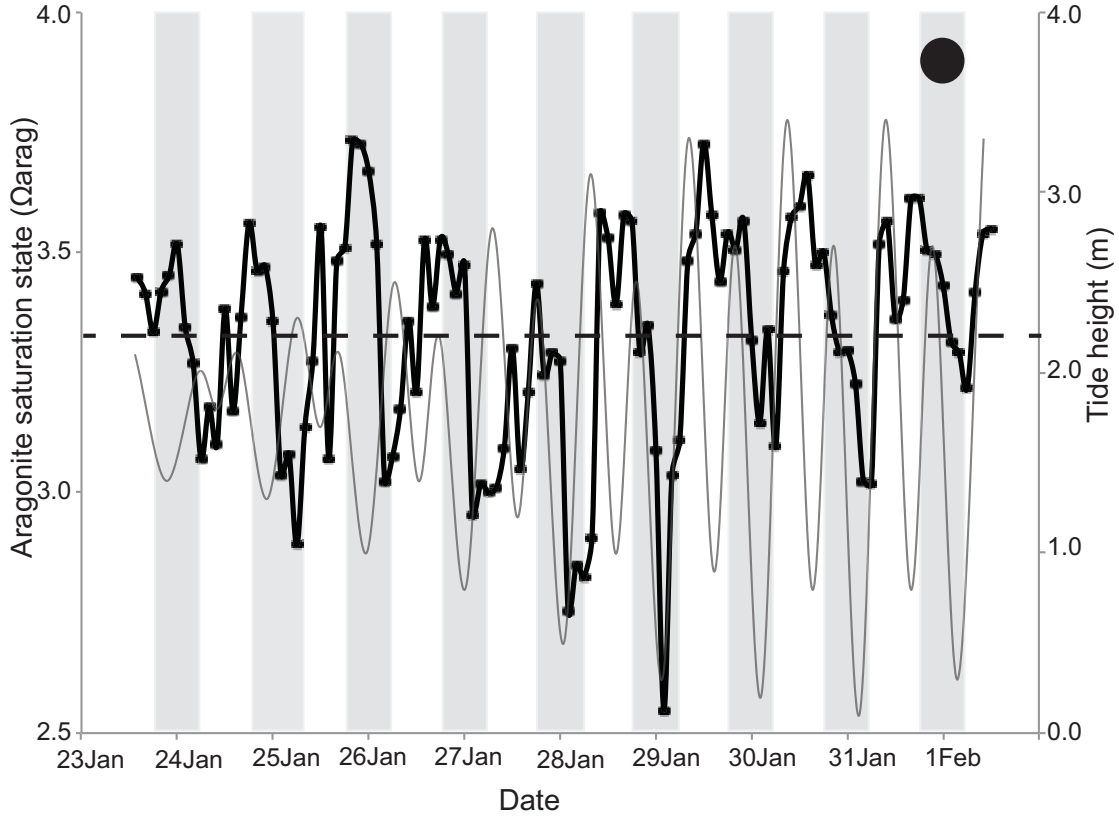

Figure 5.9. Diel variation of within reef aragonite saturation at Lizard Island from 23 January to 2 February 2014. Dark shading in the background represents night. Black lines are aragonite saturation, thin grey lines represents tide height. The horizontal black lines is the average (3.3).

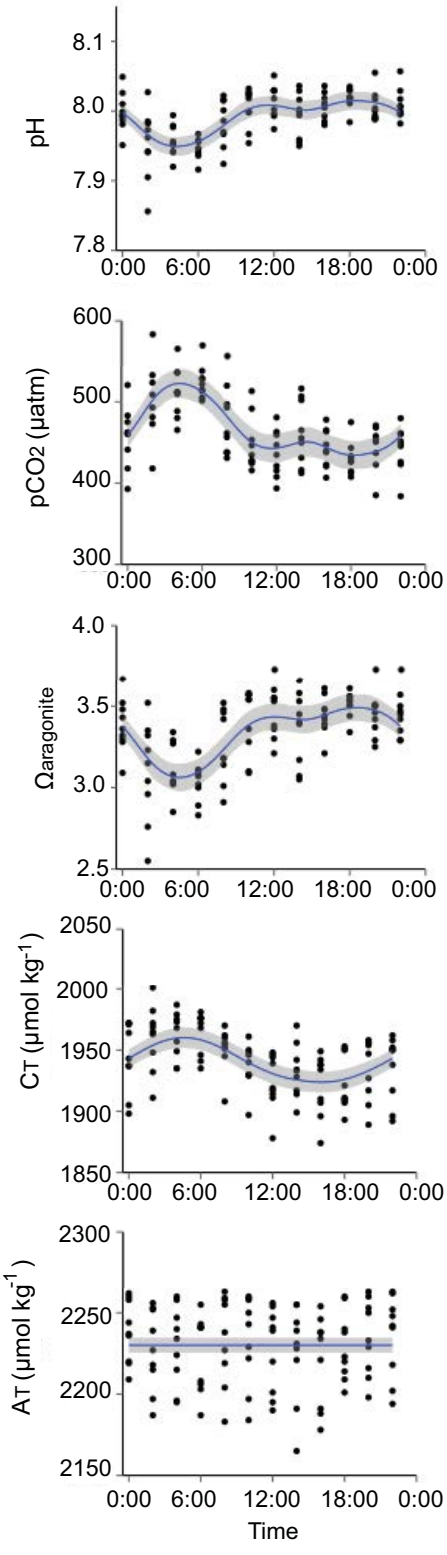

Figure 5.10. Diel curves of carbonate chemistry parameters during the summer, Jan 2014 at Lizard Island. Data points show data from 9-consecutive days with shaded lines representing 95% confidence intervals. pCO_2= partial pressure of carbon dioxide. C_T= Total carbonate. A_T= total alkalinity.

Meta-analysis of *Acropora muricata* and *Pocillopora damicornis* growth rates

From the meta-analysis on linear extension rates for *A. muricata* (Table 5.11), linear extension rates varied among locations in approximate accordance with spatial variation in annual average SST (lm, $F_{2/24}$=5.156, p=0.014, R^2=0.30, Figure 5.11). Moreover, linear extension rates of *A. muricata* decreased with increasing latitude (lm, $F_{1/25}$=5.331, p=0.030, R^2=0.18).

Pocillopora damicornis is a ubiquitous species with many estimates of growth rates published in the literature (Table 5.12). However, there is a significant difference in growth rates of linear extension rates in the Indo-Pacific (2.0 cm ± 0.3) being half of those reported for the Eastern Tropical Pacific (4.2 cm ± 0.3) (one-way ANOVA, $F_{1/33}$=27.97, p=<0.000). Therefore, the relationship between SST and latitude focused solely on data from the area of interest, the Indo-Pacific. Linear extension increased with SST to an optimal value at 26.7 °C (Figure 5.12b), however, the relationship was not significant (lm, $F_{2/19}$=2.706, p=0.093, R^2=0.22). There is a significant negative relationship of decrease linear extension with increasing latitude (Figure 5.12a, lm, $F_{1/20}$=9.83, p=0.005, R^2=0.33).

Table 5.11. Values utilised for metadata analysis on linear extension of *A. muricata*. Average linear extension was determined from mean range values when only range provided. *When the year of study was not provided, the year prior to publication was assumed

Location	Date Sampled	Latitude	Depth (m)	SST satellite	Annual extension (cm yr^{-1})	Reference
Guam	1977	13.5	3-9	27.04	3.3	Neudecker 1981
Kavaratti atoll, Lakshadweep, India	1988	10.33	2	28.30	7.9	Suresh & Mathew 1993
Kavaratti atoll, Lakshadweep, India	1989	10.33	2	27.85	8.2	Suresh & Mathew 1993
Phuket Thailand, Nai Yang	1984	8	-	28.45	11.8	Changsang et al. 1992
Phuket Thailand, S. Bangtoa	1984	8	-	28.45	9.4	Changsang et al. 1992
Phuket Thailand, Kamala	1984	8	-	28.45	14.1	Changsang et al. 1992
Phuket Marine Biological Center (PMBC)	1981	8	3	28.52	8.0	Charuchinda & Hylleberg 1984
Sri Lanka, Hikkaduwa	1997	6.14	0.5-1.5	27.86	11.8	Jinendradasa & Ekarame 2000
Sri Lanka, Roomassala	1997	6.01	0.5-1.5	27.72	12.1	Jinendradasa & Ekarame 2000
Maldives	2010	4.18	1	28.62	5.85	Morgan & Kench 2012
Middle Reef	2009	-12.5	1-3	27.04	6.3	Browne 2012
Lizard Island, GBR	1984*	-14.66	2	25.93	7.13	Oliver 1985
Lizard Island, GBR	2012-13	-14.66	5	26.01	7.93	present study
Lizard Island, GBR	2013-14	-14.66	5	26.15	10.8	present study
Davies Reef GBR	1980	-18.51	5	26.02	8	Oliver et al. 1983
Davies Reef GBR	1980	-18.51	10	26.02	12.4	Oliver et al. 1983
Davies Reef GBR	1980	-18.51	15	26.02	16.6	Oliver et al. 1983
Davies Reef GBR	2012-13	-18.51	5	26.0	7.34	present study
Davies Reef GBR	2013-24	-18.51	5	26.1	7.93	present study
Nelly Bay, GBR	1980	-19.1	-	26.13	8.82	Oliver 1987
Dampier Archipelago	1982	-20.53	-	27.04	13.7	Simpson 1988
Heron Island, GBR	2012-13	-23.44	5	23.88	3.93	present study
Heron Island, GBR	2013-14	-23.44	5	23.99	4.57	present study
Houtman Arbolhous	1979	-28.7	2-3	21.65	4	Crossland 1981
Houtman Arbolhous	1984	-28.7	10	22.14	7.6	Harriott 1998
Houtman Arbolhous	1984	-28.7	7	22.14	6.56	Harriott 1998
Houtman Arbolhous	1984	-28.7	8	22.14	5.86	Harriott 1998
Houtman Arbolhous	1984	-28.7	10	22.14	5.03	Harriott 1998

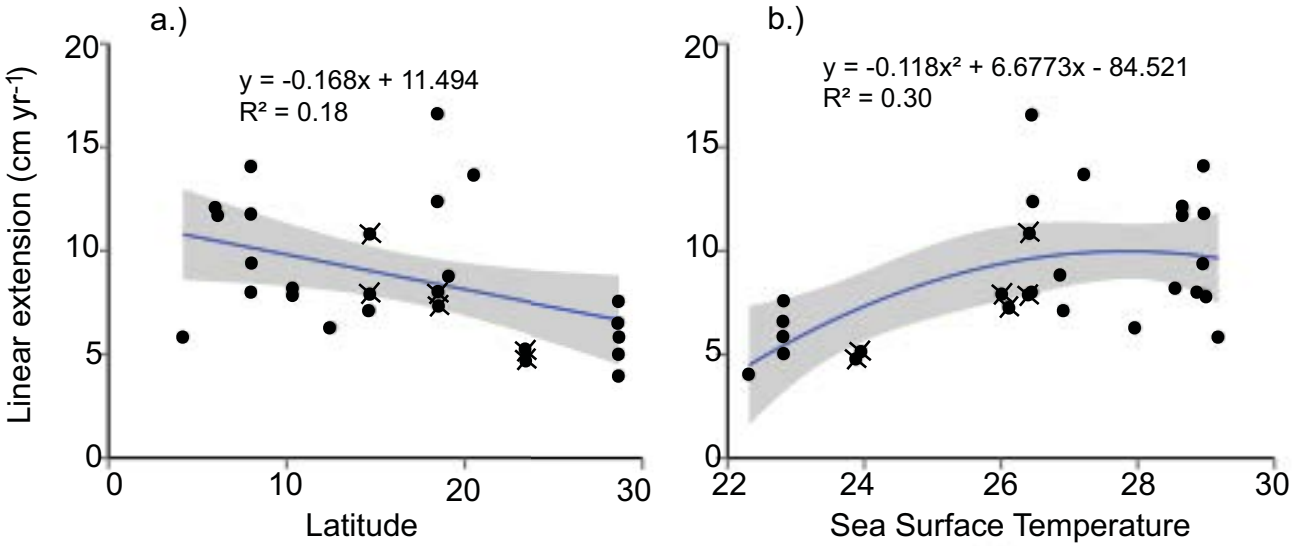

Figure 5.11. Variation in linear extension rates (cm yr^{-1}) of *A. muricata* with a.) Latitude and b.) Sea surface temperature (°C). Data points arisen from this study are dots with crosses. Values for data points are in supplementary information (Table S4). Shaded area represents 95% confidence intervals.

Table 5.12. Values utilised for meta-analysis on linear extension of *Pocillopora damicornis*. Average linear extension was determined from mean range values when only range provided. *When the year of study was not provided, the year prior to publication was assumed. ETP=Eastern Tropical Pacific

Location	Ecoregion	Year of study	Lat	Depth (m)	SST	LE (cm yr^{-1})	Reference
Na'ama Bay, Egypt	IndoPacific	1998	27.9	5	25.4	0.74	Kotb 2001
Na'ama Bay, Egypt	IndoPacific	1998	27.9	15	25.4	0.66	Kotb 2001
Kaneohe Bay, Oahu	IndoPacific	1987	21.45	-	24.6	1.64	Romano 1990
Hawaii	IndoPacific	1972	19.7	-	24.4	1.35	Maragos 1972
Guam	IndoPacific	1976	13.26	3-9	27.8	2.90	Neudecker 1981
Enewotak Atoll, Marshall Is	IndoPacific	1972	11	-	27.5	2.64	Stimson 1985
Enewotak Atoll, Marshall Is	IndoPacific	1980	11	-	27.6	2.50	Richmond 1987
Palmitas, Costa Rica	ETP	1996	10.67	3-5	27.3	5.31	Jimenez & Cortes 2003
Huevos, Costa Rica	ETP	1991	10.64	3-5	27.5	6.68	Jimenez & Cortes 2003
San Pedrito, Costa Rica	ETP	1996	10.5	3-5	27.2	3.80	Jimenez & Cortes 2003
Secas Is, Panama	ETP	1974	8.98	3	25.4	3.96	Glynn 1976
Secas Is, Panama	ETP	1974	8.98	6	25.4	3.36	Glynn 1976
Secas, Gulf of Chiriqui	ETP	1971	8.98	-	26.0	3.86	Glynn 1977
Pacific Panama	ETP	1980	8.97	-	26.4	4.80	Richmond 1987
Isla Contradora, Panama	ETP	1978	8.63	1	26.5	5.43	Wellington 1982
Isla Contradora, Panama	ETP	1978	8.63	7	26.5	4.61	Wellington 1982
Saboga Island, Gulf of Panama	ETP	1971	8.61	-	27.7	3.08	Glynn 1977
Cano Island, Costa Rica	ETP	1985	8.43	2-3	27.4	3.46	Guzman & Cortes 1989
Cano Island, Costa Rica	ETP	1985	8.43	8-10	27.4	2.98	Guzman & Cortes 1989
Pearl Island (Gulf of Panama)	ETP	1971	8.39	2-4	26.4	4.20	Glynn & Steward 1973
Uva Reef, Panama	ETP	2003	8	2-3	28.0	2.78	Manzello 2010
Ko Phuket, Thailand	IndoPacific	1983	7.53	-	28.8	1.43	Martin & Tissier 1988
Galapagos	IndoPacific	1978	- 0.49	1-4	22.5	2.24	Glynn et al. 1979
Lizard Island, GBR	IndoPacific	2013	-14.66	5	26.2	2.17	present study
Lizard Island, GBR	IndoPacific	1984	-14.68	-	25.8	3.66	Oliver 1985
Davies/Trunk Reef GBR	IndoPacific	2013	-18.51	5	25.9	1.97	present study
Palm Island, GBR	IndoPacific	1984	-18.74	-	25.3	4.32	Oliver 1985
Dampier Archipelago	IndoPacific	1982	-20.53	-	25.8	4.50	Simpson 1988
Heron Island, GBR	IndoPacific	2013	-23.44	5	24.0	1.47	present study
Houtman Arbolhous	IndoPacific	1979	-28.72	2-3	21.5	1.33	Crossland 1981
Solitary Islands	IndoPacific	1994	-30	-	22.1	1.24	Harriott 1999
Lord Howe Island	IndoPacific	2010	-31.3	4	21.7	1.16	Anderson et al. 2015
Lord Howe Island	IndoPacific	1993	-31.5	3	21.1	1.61	Harriott 1999
Rottnest Island, WA	IndoPacific	1989	-32	-	20.7	1.50	Ward 1995
Rottnest Island, WA	IndoPacific	1989	-32	-	20.7	0.90	Ward 1995

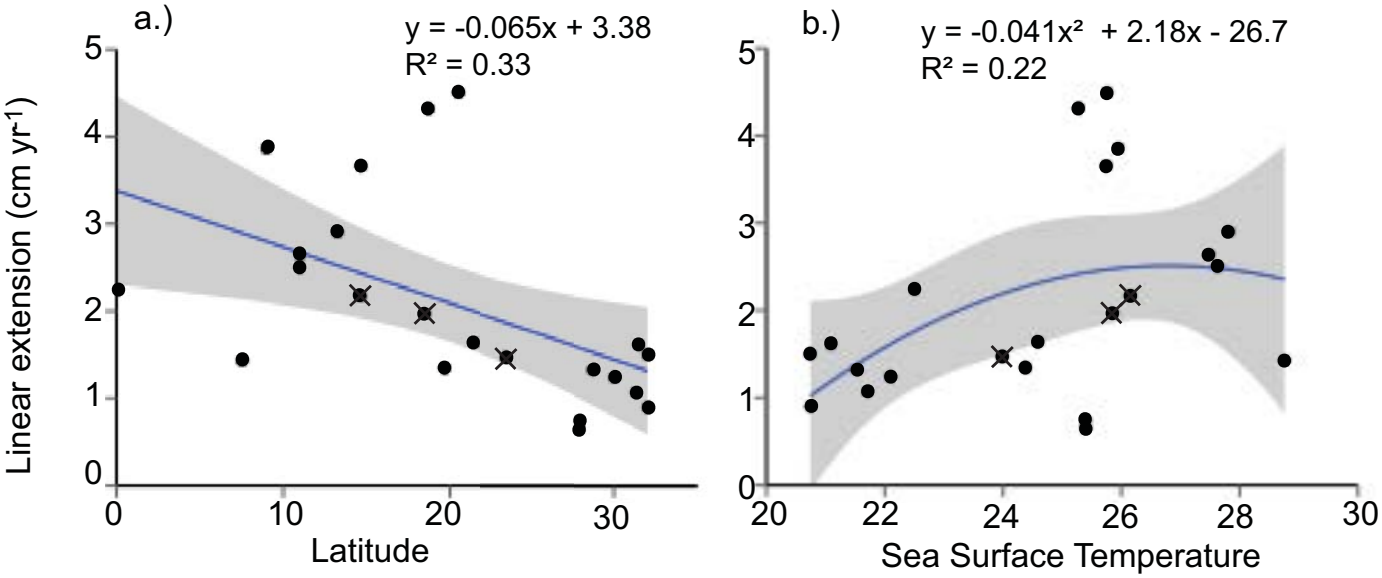

Figure 5.12. Variation in linear extension rates (cm yr^{-1}) of *P. damicornis* with a.) Latitude and b.) Sea surface temperature (°C) for corals in the Indo-Pacific. Data from this study is represented by dots with crosses. Shaded area represents 95% confidence intervals.

5.5 Discussion

This study shows that growth rates of three common coral species (*A. muricata, P. damicornis* and *I. palifera*) are consistently higher at Lizard Island (14.7 °S) compared to Heron Island (23.4 °S). Moreover, linear extension rates were intermediate at Davies Reef/Trunk Reef for both *A. muricata* and *P. damicornis* (Table 5.4a), but were not significantly different to rates recorded at Lizard Island. Trends in coral growth rates were consistent with variation in the temperature regime among locations; average annual SST at the two most northern reefs were similar (26.8 °C and 26.1 °C, at Lizard Island and Davies Reef, respectively), however SST at Heron Island was ~2 °C less (24.1 °C). Growth rates of *A. muricata* increased by 1.9 cm yr^{-1} for every 1 °C increase in average annual temperature across the three study locations. For *P. damicornis*, linear extension increased 0.3 cm yr^{-1} per 1 °C among locations. Despite contrasting morphologies, the rate of increase for *P. damicornis* was the same as that determined for massive morphologies of *Porites* (0.31 cm yr^{-1} per 1 °C) on the GBR (Lough & Barnes 2000). Growth rates of *Isopora* increased by 0.11 cm yr^{-1} per 1 °C among the three study locations.

Calcification and growth of scleractinain corals is positively related to temperature, but only within a relatively narrow range of temperatures (Lough & Barnes 2000, Carricart-Ganivet 2004), which likely accounts for increased growth rates at Lizard Island and Davies Reef, compared to Heron Island. It is increasingly apparent however, that above certain temperatures (often corresponding with local summertime maxima) increasing temperatures can have negative effects on coral growth (Jokiel & Coles 1990, Marshall & Clode 2004). Moreover, some low latitude sites are already experiencing a greater frequency and intensity of DHWs, which might be hindering growth rates at these locations. Based on the lower frequency and intensity of DHW in the southern GBR at Heron Island, the lower growth rates are likely in response to the lower annual SST at this location, rather than increased

cumulative temperature stress relative to other locations. This is corroborated by work done on massive *Porites* where along the GBR growth rates were strongly correlated with latitudinal shifts in SST (Lough & Barnes 2000).

In addition to temperature, another key environmental driver of coral reef calcification is aragonite saturation (Kleypas et al. 1999a). While we see large gradients in aragonite saturation in the open oceans (Feely et al. 2009), within-reef saturation states are driven by complex interactions of photosynthesis/respiration, tides, benthic composition and factors that affect the biological activity such as temperature, light, salinity, and nutrients (Anthony et al. 2011, Falter et al 2013, Albright et al. 2013, 2015). Heavy rainfall and large changes in tide during deployment of the water sampler at Lizard Island likely contributed to a small reduction in aragonite saturation. However, the mean value determined in this study (Ω_{arag}=3.3) is similar to that observed by Silverman et al. (2015) at Lizard Island in Oct-Nov 2008 and 2009 (Ω_{arag}=3.65 and 3.45, respectively). The average for the central sector at Davies Reef was slightly higher (Ω_{arag}=3.7) (Albright et al. 2013) than the other sectors and may reflect the variance that can be observed due to factors outlined above. Importantly, variation among locations in growth rates of the three corals species considered in this study (*A. muricata, P. damicornis* and *I. palifera*) was more consistent with differences in local temperature, rather than light or aragonite saturation.

The determined mean within-reef aragonite saturation states were comparable (Table 5: Ω_{arag}=3.3) at Lizard Island and Heron Island, despite 8.76° latitudinal separation and 2 °C difference in SST. It seems despite lower temperatures and concomitant greater solubility of calcium carbonate at Heron Island, the benthic community can buffer the reef carbonate saturation state (Anthony et al. 2013) maintaining an average aragonite similar to lower latitude sites. However the variability in available carbonate ions (Ω_{arag}) at Heron Island (range=2.1, Ω_{arag} 2.3-4.2) is almost double that of Lizard Island (range=1.1, 2.6-3.7). The reef flat of Heron Island is characterised by a greater seawater residency time that can result

in large fluctuations in carbonate chemistry (Falter et al. 2013, Kline et al. 2015). Therefore, the locally adapted corals at the southern GBR of Heron Island may be able to withstand changes in seawater chemistry, as they are naturally subjected to large intra-annual variation in temperature and pH (Albright et al. 2015, Kline et al. 2015). However, periods of anomalous temperature and pH exposure do not concur at Heron Island; the greatest diel temperature range was recorded in austral spring (October) and largest diel variability in pH occurred in the fall (June) (Kline et al. 2015). Understanding how these stressors synergistically affect coral growth and survival will be imperative for predicting persistence of the reef community.

5.5.1 Relationship of branching coral linear extension to latitude and SST

Sea surface temperatures are highly correlated with latitude, and meta-analyses of large-scale variation in growth (linear extension) for both *A. muricata* and *P. damicornis* revealed generally increasing linear extension rates with decreasing latitude, as shown previously for massive *Porites* (Lough & Barnes 2000). While temperature may be just one of several environmental parameters that vary with latitude, and thereby account for observed differences in growth (e.g., Pratchett et al. 2015 – Chapter 2), it is striking how these spatial patterns correspond to variation in local annual mean temperatures. Notably however, the best model to describe the relationship between linear extension rates of both *A. muricata* and *P. damicornis* with SST is a saturating relationship, showing that growth is largely invariant to changes in annual mean temperature between 26 and 30 ^{o}C (Figure 5.11).

5.5.2 Future impacts of climate change on growth

The effects of increasing SST on coral growth will vary spatially, depending upon the local thermal history, the extent to which corals are locally adapted, and the extent to which growth is constrained by cool winter or warm summer temperatures (Pratchett et al. 2015 – Chapter 2). Future growth rates of corals are likely to be increasingly constrained by

temperatures exceeding the optimal for coral growth and survivorship (van Hoodinck et al. 2014) and it is evident that higher latitude locations on the GBR are already experiencing a greater severity of thermal stress (Figure 5.7). Increasing temperature is the biggest threat to corals due to the predicted increase in occurrences of coral bleaching events (Donner et al. 2005). Spatial variability in bleaching events has occurred on the GBR with the central GBR experiencing the greatest impact during past widespread bleaching events in 1998 and 2002 (Berkelmans et al. 2004). With repeated bleaching events, these sites may experience shifts in the coral composition to those more thermo tolerant species, leading to declines in structural complexity which would have important consequences on fishes and mobile invertebrates associated with live coral habitats (Pratchett et al. 2008, Stella et al. 2011, Coker et al. 2014).

High latitude sites such as the southern GBR may serve initially as refugia from thermal stress. However, even high latitude sites can be affected by thermal stress or declining saturation state leading to reductions in growth rates (Chapter 3 - Anderson et al. 2015). The relative benefits of increasing temperature versus constraints imposed by declines in aragonite will play a dominant role in determining the fate of coral in the future (van Hooidonk et al. 2014). Heron Island already exhibits reduced coral calcification rates, likely driven by considerably lower annual average SSTs (50% less for staghorn *A. muricata*, 30% less for P. *damicornis* and 8% less for *I. palifera* (Figure 5.4)) compared to those at Lizard Island. Therefore, increases in temperature may have a positive effect on coral growth at the southern GBR, but there is limited understanding of the constraints imposed by ocean acidification on coral accretion at these high latitude locations. Overall, declines in aragonite saturation are expected to be less influential on calcification than rising SST (Chan & Connelly 2013, Kennedy et al. 2013) throughout this century.

In conclusion, growth rates of three dominant coral species varied spatially along the GBR, largely in conjunction with differences in average annual temperatures. Based on

limited temporal sampling of carbonate chemistry, within-reef aragonite saturation was comparable among these locations, suggesting that reef ecosystems do have considerable capacity to buffer latitudinal gradients in oceanic aragonite saturation. There was also no consistent trend in variation in solar penetration among reefs relative to observed variation in growth rates, though this may impose increased constraints on coral growth at higher latitudes (Muir et al. 2014). Linear extension rates at Heron Island, where annual SST was on average 2 °C lower, were 20 %, 33 %, and 34 % less for I. *palifera*, *P. damicornis* and *A. muricata*, respectively, compared to Lizard Island. By determining coral growth rates at multiple spatial scales, we now have a greater understanding of the key environmental drivers of branching coral growth. Continued monitoring of coral growth rates in combination with environmental conditions, such as temperature stress and within reef carbonate chemistry, will be essential to better appreciate likely impacts of climate change on corals and reef ecosystems.

Chapter 6 Synergistic effects of ocean warming and acidification on the growth and survivorship of reef-building corals

6.1 Abstract

Ongoing climate change is considered to be one of the greatest threats to the persistence of reef building corals. More specifically, ocean acidification may compound increasing increasing temperatures leading to declines in abundance and survivorship of corals. To increase our understanding of how corals will respond to the combined effects of warming and ocean acidification, two common and fast growing *Acropora* corals (*Acropra muricata* and *Acropora hyacinthus*) were used in a fully factorial experimental study using three temperature treatments (26 °C, 28.5 °C and 31 °C) crossed with three levels of pCO_2 (410 µatm, 652 µatm and 934 µatm). Temperature was increased gradually in the tanks from 26 °C (control temperature) to target temperatures after 5 week until stress was evident in the 31 °C tanks and dropped to 30 °C to assess recovery. pCO_2 was gradually changed from control values (410 µatm) to target values after 3 weeks where they remained constant until the end of then experiment at 12 weeks. Elevated temperature (31 °C) led to a 10 % decline in survivorship and over the long-term a 10-50 % decline in calcification across both coral species. End of century levels of pCO_2 reduced survivorship and over long-term lead to a 50 % reduction in calcification. Branching coral species, which are highly sensitive to temperature stress and ocean acidification, are likely to experience reduced health and survivorship, and thus be less abundant with ongoing climate change. If so, this would drastically reduce reef complexity, and likely lead to shifts in ecosystem function.

6.2 Introduction

Coral reefs are highly dynamic ecosystems affected by a multitude of disturbances (e.g., Hughes et al. 2010), which are increasingly being compounded by deleterious effects of climate change. Coral reefs are already experiencing environmental shifts due to climate change with tropical ocean sea surface temperatures (SST) increasing by 0.5 °C since instrumental records of ocean temperature began in 1880 (Lough 2012). Global temperatures are expected to increase by at least 1.8 °C (B1 scenario) to 4.0 °C (AIF1 scenario) by the end of this century depending on model predictions and carbon mitigation schemes (IPCC 2013). This would translate to an increase in SST for the tropics by at least 1.8 °C and up to 6 °C (IPCC 2007). Due to these observed and projected trends in ocean warming and since corals currently are close to their upper thermal tolerance limits, it has been predicted that major bleaching events will occur almost annually by 2030-50 (Hough-Guldberg 1999, Donner et al. 2005). Coral bleaching results from the breakdown of the symbiotic relationship between the coral host and algal dinoflagellate, *Symbiodinium* sp. (commonly referred to as zooxanthellae), following prolonged periods of thermal stress (Baker et al. 2008). The zooxanthellae are obligate to the coral host and contribute disproportionately to the energetic budgets through photosynthesis (Edmunds & Davies 1986). However, even if coral do not actually bleach, there is increasing evidence that elevated temperatures have significant sub-lethal effects, leading to declines in performance and fitness of reef-building corals (De'ath et al. 2009).

In addition to thermal stress, climate induced changes in ocean chemistry pose a major threat to marine calcifying organisms (Kleypas & Yates 2009). Since the Industrial Revolution (1760-1840), atmospheric CO_2 has increased from 280 to 400 ppm and is predicted to increase to 550 ppm (B1, "best case scenario") to 950 ppm (AIF1, "worst case scenario) by 2100 (IPCC 2013). The oceans absorb close to 30 % of the atmospheric carbon

dioxide (CO_2) (Sabine et al. 2004), which shifts ocean chemistry to a more acidic state and is termed ocean acidification. Carbon dioxide dissolves in water to form carbonic acid that readily dissociates into hydrogen and bicarbonate ions decreasing the pH and reducing the freely available carbonate ions (CO_3^{2-}) (Kleypas & Yates 2009). As a result, surface ocean pH has already declined by 0.1 units since the Industrial Revolution (Sabine et al. 2004).

Coral calcification takes place in the calicoblastic ectoderm at the base of the coral tissue where aragonite, the modern form of calcium carbonate ($CaCO_3$) produced by scleractinian corals, is precipitated (Tambutte et al 2011). Corals are able to grow aragonite crystals by elevating the saturation state of the isolated calcifying compartment (Cohen & McConnaughey 2003), but the transport of molecules to this site remains largely unknown. It has been proposed that corals use a Ca^{2+}-ATPase proton pump that requires removal of two H^+ ions from the calcifying fluid for expenditure of the ATP (energy) for calcification, which is extremely energetically costly (Cohen & McConnaughey 2003). At ambient external seawater saturation state (Ω_{arag}=3.7), the corals are able to maintain an internal calcifying fluid saturation state five-fold higher (Ω_{arag}~19) than the outside seawater (Cohen et al. 2009). But as the seawater saturation state declines, the saturation state of the internal calcifying fluid declines and the rate of $CaCO_3$ crystals growth decreases (Cohen et al. 2009). Therefore, reef-building corals are sensitive to the effects of ocean acidification as the reduced availability of carbonate ions impacts processes of calcification, which has consequences for growth and survivorship (Gattuso et al 1999, Orr et al. 2004, Langdon & Atkinson 2005, Silverman et al. 2009, Kroeker et al. 2010, Fabricius et al. 2011).

Establishing the relative and synergistic effects of increasing temperatures versus ocean acidification is one of the most fundamental steps for projecting the affects of climate change on coral reefs (Doney et al. 2009). A number of studies have investigated the effects of ocean acidification and/ or temperature on calcifying organisms (Leclercq et al. 2002, Langdon & Atkinson 2005, Anthony et al. 2008, Rodolfo-Metalpa et al. 2008, Jury et al.

2010), but few studies have looked at the effects of changes in both temperature and seawater chemistry simultaneously. Leclerq et al. (2002) and Langdon & Atkinson (2005) observed decreasing net community calcification with increasing pCO_2 at constant temperature; a decrease in calcification by 44% as Ω-aragonite decreased from 3 (460 µatm) to 1.82 (789 µatm) was observed in Langdon & Atkinson (2005), but after nutrient enrichment, there was less of an impact of decreasing Ω-aragonite on calcification (-16%). At the higher temperature of 28-29 °C and a doubling of pCO_2, Anthony et al. (2008) found calcification rates of *Acropora intermedia* and *Porites lobata* were similar and 19 % elevated, respectively. However, the lower temperature of 25-26 °C combined with a doubling of pCO_2 lead to a 19 % to 12 % reduction in calcification of *A. intermedia* and *P. lobata*, respectively (Anthony et al. 2008). Conversely, Reynaud et al. (2003) observed *Stylophora pistillata* to be insensitive to a doubled pCO_2 at 25 °C but experienced a 50% reduction in calcification at 28 °C. Due to the high variability of responses observed in experimental studies, the combined impact of ocean warming and acidification on marine organisms is largely unknown (Kroeker et al. 2013, Harvey et al. 2013). For hard corals, the effects of increasing SST may be exacerbated by ocean acidification (Reynaud et al. 2003). Alternatively, it has been predicted that the increase in temperature might increase the metabolism of coral and ameliorate the effects of ocean acidification (Kleypas & Yates 2009, McCulloch et al. 2012). Moreover, it is still unclear to what extent marine calcifiers have the capacity to upregulate their internal pH at the site of calcification and still deposit their skeleton in acidified conditions (Cohen et al. 2009, McCulloch et al. 2012, Venn et al. 2011). Therefore, there is still a lack of understanding in the physiological response (i.e., calcification) of corals under the compounded stressors of changes in carbonate chemistry and temperature. However, it is likely that the reduced physiological performance of some taxa will alter the biotic interactions within a reef, leading to a shift in community composition and ecosystem function.

Recent declines in coral growth (linear extension and calcification) have been reported in the Caribbean (Bak et al. 2009), Eastern Tropical Pacific (Manzello 2010), Thailand (Tanzil et al. 2013), the Red Sea (Cantin et al. 2010) and Australia (De'ath et al. 2013) for several species of massive corals, and these declines are generally attributed to increasing thermal stress. While branching corals (e.g., *Acropora*) are often sensitive to thermal stress (Marshall & Baird 2000, Loya et al. 2001) few studies have reported changes in the growth of these corals, largely owing to complexities in quantifying temporal patterns of growth (e.g., Anderson et al. 2015 – Chapter 3). Branching corals have the largest contribution to habitat complexity, which in turn provides a high diversity of reef-associated organisms (Coker et al. 2014). Further, branching species have the highest calcification rates and thus have the highest contribution to reef growth (Pratchett et al. 2015 - Chapter 2). Consequently, declines in growth and survivorship of branching species due to climate change will have a profound affect on the future complexity and production of coral reefs.

The aim of this study was to experimentally test the individual contributions of ocean acidification versus temperature stress on the health and performance of two fast growing coral species, *Acropora muricata* and *Acropora hyacinthus*. Field studies on Australia's Great Barrier Reef (Chapter 4) and at Lord Howe Island (Chapter 3 - Anderson et al. 2015) have revealed temporal declines in the growth rates of branching corals, but the extent to which ocean acidification or ocean warming may have contributed to these declines is unclear. This study examined growth, rates of photosynthesis, respiration, and lipid, chlorophyll, and protein abundance at three temperatures crossed with three partial pressures of CO_2, selected to reflect IPCC predictions of environmental conditions in tropical oceans in 2015 versus 2100 (IPCC 2013).

6.3 Methods

6.3.1 Field sampling

The selected study species were *Acropora hyacinthus* and *Acropora muricata.* Branching species are adversely affected by thermal stress (Marshall & Baird 2000) and ocean acidification (Fabricius et al. 2011, Edmunds et al. 2012) more than other coral types (e.g., massive corals). Both study species were collected from shallow (3-5 m) back reef habitats at Davies Reef (18°49’39’’ S, 147°38’22.56’’), a midshelf reef on the Great Barrier Reef, Australia, situated 100 km off the coast of Townsville (Figure 6.1) in May 2014. Branches of *A. muricata* were taken from 6 colonies, and 20 colonies were collected from the plate forming *A. hyacinthus*.

Corals were transported back to the Australian Institute of Marine Science, Townsville, where they initially were maintained in an outdoor flow through system, with partial shading for four weeks. Filtered seawater was pumped from Cleveland Bay through a heater/chiller unit to maintain a constant temperature of 26 °C, which corresponds with average daily temperatures at the collection site during May (AIMS 2015). One week after collection, corals were cut with bone cutters to produce experimental fragments (n = 1,100) comprising of individual branches <6 cm long for *A. muricata* and sections of anastomosed branches <3 cm diameter for *A. hyacinthus*. Coral fragments were then super glued to aragonite studs, which are flat circular bases that slide into holding trays, made out of aragonite that allow for ease in moving the fragments for sampling without direct handling of the coral. Experimental fragments were then allowed 4 weeks recovery. During this time, the tissue grew over the base of the aragonite stud, and aside from a low mortality rate consisting mostly of *A. hyacinthus* (~200 coral fragments), the majority of the coral fragments appeared visibly healthy.

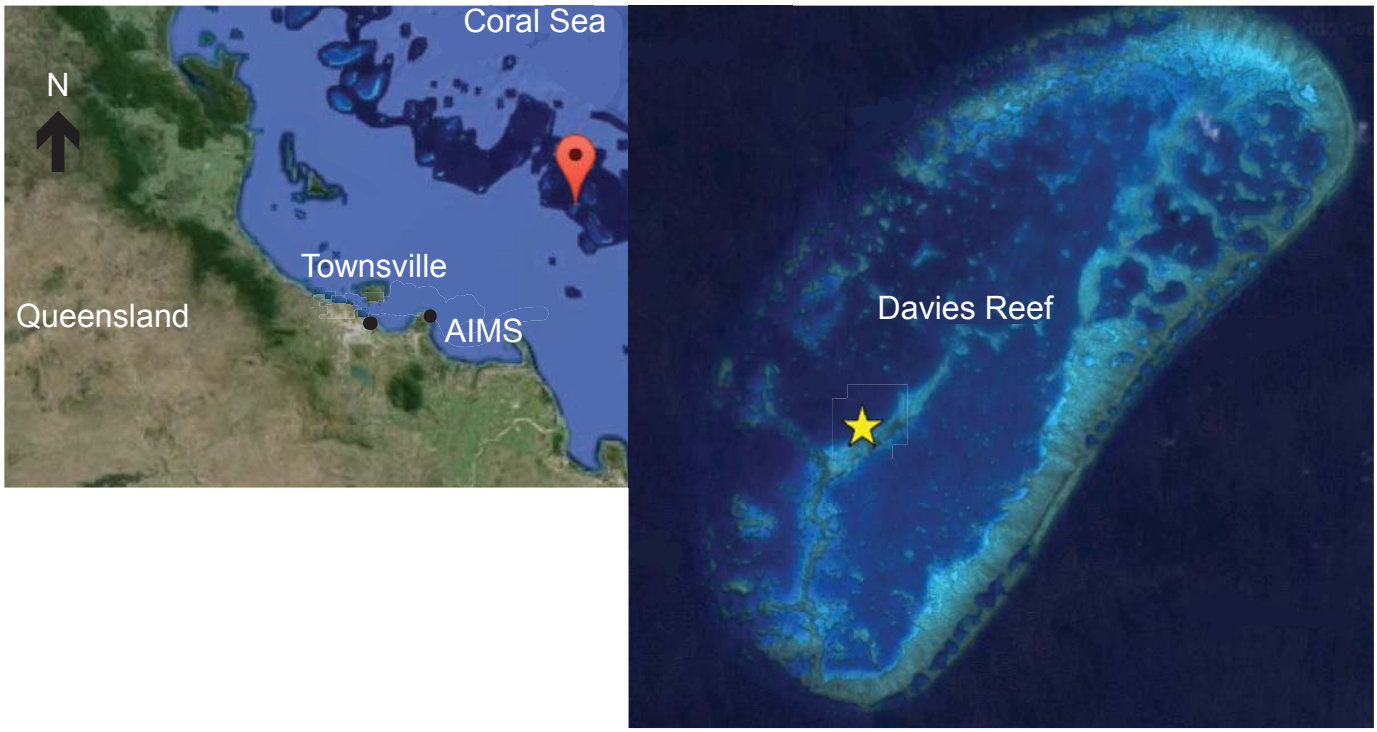

Figure 6.1. Collection site (star) of *Acropora hyacinthus* and *Acropora muricata* at Davies Reef, 100 km off the coast of Townsville, Australia. Figure adapted from Google Earth.

After four weeks, corals were moved to the indoor holding facilities of Australia's National Sea Simulator at the Australian Institute of Marine Science (AIMS). Light intensity was provided with LED lighting and carefully measured using a Li-Cor 193 spherical underwater quantum sensor to ensure a consistent level of light intensity during the experiment. Lights were set to a 12h light:12 h dark photoperiod, with a gradual five h ramping to a two h of maximum peak light intensity at midday, and five h ramp down. Maximum light intensity was chosen to be nonstressful for the corals as they initially acclimated from natural to artificial lighting. Maximum daily light intensity was initially 140 μmol s^{-1} m^{-2} and increased over four weeks to 200 μmol s^{-1} m^{-2}, which stayed constant for the remainder of the experiment. Fifteen weeks after collection, corals were moved to an indoor experimental room where maximum day light intensity was maintained at 200 μmol s^{-1} m^{-2}.

Experimental set up

This study used a fully factorial experimental study with three temperature treatments (26°C, 28.5 °C and 31 °C) crossed with three levels of pCO_2 (410 μatm, 652 μatm and 934 μatm). Experimental treatments for pCO_2 (Table 6.1) were selected to represent predicted environmental conditions at Davies Reef, central GBR, at i) present, ii) 2050, and iii) 2100. Experimental treatments for SST (sea surface temperature) represent the long-term annual average (26 °C), long-term summer maximum (28.5 °C) and a future +2.5 °C temperature stress treatment (Figure 6.2). While it is recognised that temperature and seawater chemistry will change simultaneously, the purpose of this study was to test the differential responses of temperature stress and/or ocean acidification both independently and synergistically. There were three replicate tanks for each of the 9 treatments, giving a total of 27 tanks. Coral genotypes were equally spread among treatments with a total of 397 *A. hyacinthus* and 485 *A. muricata* healthy fragments utilised in the experiment (total N=872 with ~32 nubbins per tank). They were acclimated for one week to the tanks at the

control values (26°C and 410 µatm pCO_2) prior to the commencement of the experiment. Submersible pumps ensured water circulation inside the aquaria and corals were fed three times weekly with a protein/*Artemia* food mix.

6.3.2 Temperature treatments

Temperature increases were gradual and consistent in the tanks from 26 °C at week 0 to the long-term summer max of 28.5 °C and a future +2.5 summer max treatments of 31 °C over five weeks (Figure 6.2). This represents an increase in temperature for the summer maximum treatment of 0.07 °C/day from 26 to 28.5 °C and 0.2 °C/day for the future temperature treatment from 26 to 31 °C. Once temperature stress was evident in the 31 °C treatment (40 % bleaching among tanks), temperatures in the treatments were decreased in the future +2.5 treatment to ~30 °C and in the summer maximum treatment to 27.5 °C where they remained until the end of the experiment at week 12. However, for ease of comparison through the study, the summer maximum treatment will be referred to as 28.5 °C and the high temperature stress treatment as 31 °C. Both temperature and pCO_2 were manipulated daily to increase linearly for all target treatments during the ramping periods. Temperature was controlled by mixing of 22 °C and 36 °C seawater, and heat exchangers to deliver edan accuracy of ±0.1 °C

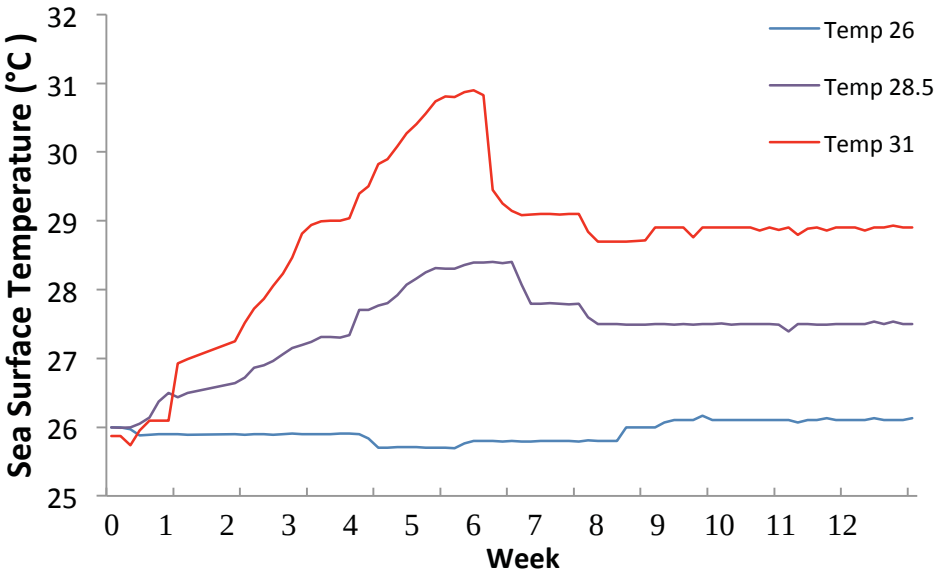

Figure 6.2. In tank probe average daily sea surface temperature profile (°C) recorded for the 12 week experiment at the long-term annual average at Davies reef (26 °C), average long-term summer maximum (28.5 °C) and a future +2.5 °C temperature stress treatment.

6.3.3 Ocean acidification treatments

pCO_2 levels were reached after three weeks and remained stable at 410 ± 4, 653 ± 6 and 934 ± 11 µatm which corresponds to pH levels of 8.04, 7.85 and 7.71 and current, mid, and end of century pCO_2 levels, respectively (Table 6.1). A 2.3 fold increase in pCO_2 led to a 42 % decrease in CO_3^{2-} from the control treatment to the end of century treatment. pH/pCO_2 were controlled with Liqui-cel membrane contractors and mass flow controllers as CO_2 was bubbled directly into the seawater. Liqui-cel membrane contractors allow for precise control of pCO_2; 0.08 pH units variance was observed over a month long experiment (Bockmon et al. 2012). pCO_2 was monitored weekly on a LI-COR CO_2/H_20 gas analyser (Li-840A) that was standardized against 0 and 1500 ± 30 µatm nitrogen gas and confirmed with 600 µatm standard CO_2. Both pH and temperature were monitored continuously with ISFET pH probes in each of the treatments. ISFET pH probes were calibrated biweekly by determining the intank water pCO_2 and total alkalinity, which was input into CO2SYS (Lewis & Wallace 1998) and offset based on the determined pH measurement.

Table 6.1. Ocean acidification treatment values maintained after the initial three week ramping for the mid and end of century levels

Treatment	**pH_T (mean ± SD)**	**Licor $pC0_2$ (µatm)**	**Total Alkalinity (µmol/kg)**	**DIC (umol/ kg)**	**HCO_3 (umol/kg)**	**CO_3 (µmol/ kg)**	**CO_2 (µmol/ kg)**	**Ω_{arag}**
Current	8.00±0.04	410±4	2366±3	2033±3	1785±4	238±2	11±0.1	3.83±0.03
Mid century	7.85±0.05	652±6	2366±3	2129±4	1936±5	176±2	17±0.2	2.84±0.03
End century	7.71±0.1	934±11	2365±3	2193±4	2032±5	137±2	24±0.5	2.20±0.04

6.3.4 Coral health and performance

Throughout the course of the experiment, growth was measured based on changes in buoyant weight of individual coral nubbins. Buoyant weight (±1 mg) of all corals was measured at week 0 immediately before environmental conditions were changed at week five (by which time all treatment temperatures had been reached) and at week twelve, whereby fragments are weighted while suspended in seawater (Davies 1989). During buoyant weight measurements, the temperature of the water bath was changed to match the sampling temperature of each treatment, and the seawater bath was taken from each tank to ensure consistency of pCO_2. Daily calcification rate (mg cm^{-2} day^{-1}) was then calculated as the difference between initial and final weights per nubbin surface area (cm^2), divided by the number of elapsed days. Tissue area was determined from photographs using the equations of surface area of a cone ($SA = \pi r(r + s)$, were r=radius and s=side length) for *A. muricata*. Surface area for *A. hyacinthus* was determined from areal and side photos, and input into the equation of a box (SA=2(x*y + y*x+ x*z)).

The alkalinity anomaly technique was utilised to determine instantaneous calcification rates using three corals per tank per species, which were incubated in light and dark controlled conditions in the experimental room. Incubations were carried out at week 0 (T0), week five, (temp target), and week twelve (final). Coral nubbins were placed upright on the lid (held in place with a screw) of clear acrylic 0.6 L incubation chambers and then enclosed in O_2 saturated tank treatment seawater with a magnetic stirrer. The chambers were securely sealed to ensure no air was inside, and then transferred to submersible trays in flow-through bins acting as water baths to maintain consistent temperature conditions for each temperature treatment. The stands contained magnetic platforms driven by a motor unit and pullies causing the magnetic stirrers (5 cm x 0.8 cm, 202 revolutions per minute) to rotate, mixing the enclosed water to minimise boundary layer thickness. Incubation times

were roughly 90 min. In addition, blank reference (no coral present) incubation chambers were prepared of each treatment seawater (n=1-3) to provide information on potential changes in metabolic activity of microorganisms in seawater. At the end of the incubation time, oxygen concentration (mg L^{-1}) and temperature (°C) were recorded with a hand-held oxygen probe. From changes in oxygen concentration, photosynthesis and respiration rates can be determined. The water in the chambers were bottled and fixed with mercuric chloride for later analysis of alkalinity. Incubations were carried out during a "light" run, at peak light intensity, and "dark" run that started a minimum of 30 minutes after the completion of the light cycle in the experiment.

Light and dark calcification rates of the incubated corals were determined with the alkalinity anomaly technique that measures the drawdown of alkalinity over time due to precipitation of calcium carbonate. The precipitation of 1 mol of $CaCO_3$ reduces the total alkalinity of the surrounded seawater by two molar equivalents (Chisholm & Gattuso 1991). Total Alkalinity (A_T) of incubated water samples was measured following standard operational procedures (Dickson et al. 2007). The A_T of 0.06 L subsamples was determined by acid titration (0.05 M HCl) on a Methrom 885 robotic titrosampler (Methrom 855, Methrom, Switzerland) as described in Uthicke and Fabricius (2012). An in-house seawater standard was used to assess the accuracy of titrations (replicate readings were ~0.2% standard deviation of the mean) and bias of the A_T measurements, which was then used to correct for slight differences between acid batches used for the acid titration (Strahl et al. 2015). Rates of net photosynthesis/dark respiration and light/dark calcification were related to surface area and calculated in mg O_2 cm^{-2} h^{-1} and μM C cm^{-2} h^{-1}, respectively, after subtracting the values measured from the blank chambers.

Total lipid content and protein and chlorophyll concentrations were determined from randomly selected coral fragments at the commencement of the experiment (T_0 N=27 coral nubbins each species), pCO_2 target (3 *A. muricata* per tank only N=81), temperature target

(3 nubbins each tank per species N=81) and final time periods (all corals alive). A total of 439 coral fragments were frozen in liquid nitrogen and stored at –80°C prior to processing. Branches were ground into a homogeneous powder of coral tissue and skeleton with a frozen mortar and pestle, and the tissue was freeze-dried for three days prior to analysis.

Total lipid content was estimated for each coral fragment. Lipids were extracted from 1.5 g of homogenised powder with dichloromethane:methanol (2:1 v/v) following the method described by Harland et al. (1992) (adapted from Folch et al. 1957). Lipid weight was obtained following separation and evaporation of the dichloromethane. Total lipid content was normalised to coral fragment surface area.

Total protein was measured using bovine serum albumin (Bio-Rad) protein standards (0 to 1250 ug ml^{-1}) and a DC protein assay kit II (Bio-Rad Laboratories, NSW, Australia). First, 0.5 g of tissue was solubilized by sonication with 1 M NaOH and then 2 successive digestions for 30 min at 90 °C. Samples were then sonicated again and spun on low speed in a centrifuge (1500 x g for 10 min) to separate cell-debris from the solution. 200 µl of homogenate was then assayed for protein. Absorbance was measured at 750 nm wavelength in a spectrophotometer (Hewlett Packard, Agilent 8453, Agilent Technologies, Calif., USA) and compared to the standard curve for protein standards to determine concentration. Protein was normalised to coral fragment surface area.

Chlorophyll molecules were extracted from 0.5 g dry homogenised powder in 1.5 mL 95% ethanol using a sonicator in the dark (40% intensity for 30 sec) on ice. Samples were centrifuged for 5 min (10000 g) and then 200 uL was pipetted onto microplate reader. Using a mass spectrophotometer, absorbance was measured at 665nm, 649nm and 632nm. Using the blank corrected absorbance readings, Chl*a* was calculated using the equations in Ritchie (2008) for 95% ethanol:

$$Chla(\mu g/ml)=(-0.9394A_{632}) - (4.2772A_{649}) + (13.3914A_{665})$$

The equation was divided by the mean path length correction factor; Path length correction of Chl*a* standard (77.397 µg/ml) was determined by the ratio of the absorbance of the microplate measurement divided by the absorbance of the cuvette at given wavelengths (664 nm, 649 nm and 632 nm, at 200 uL=0.503329). Pigment concentrations were then standardised to surface area of the branch.

6.3.5 Data analysis

Survivorship

Probability of weekly survivorship in each treatment was evaluated using Kaplan-Meier estimate, a non-parametric statistic used to estimate survival from time interval data (May 2012). A Cox proportional hazard model was used to assess the independent and combined effects of temperature and pCO_2 on survivorship (Lin & Wei 1989).

Calcification, chlorophyll, photosynthesis and respiration

To assess caclification from the initiation of experiment until week five, when temperature targets reached, and from week five until week twelve (calculated from buoyant weight for both species), I used the package *nlme* (Pinheiro et al. 2012) to fit linear mixed-effects (LME) models. To assess net photosynthesis, dark respiration, light calcification and dark calcification (calculated with the coral incubations) at the temperature targets (week five) and end of the experiment (week twelve) for each species, I likewise used the package *nlme* (Pinheiro et al. 2012) to fit linear mixed-effects (LME) models. For all models, the fixed effects were temperature, pCO_2 and their interaction, and as a random effect, tank. To assess variation in chlorophyll *a* content, I used the package *nlme* (Pinheiro et al. 2012) to fit linear mixed-effects (LME) models with the fixed effects of temperature, pCO_2, the interaction of temperature and pCO_2, and week sampled, and as a random effect, tank. Degrees of freedom varies between the models as the sample size varies for different analyses; for example when analysing parameters from coral incubations, such as photosynthesis, only 3 corals per

tank per species were incubated, whereas, for the chlorophyll model all sampled coral fragments of each species throughout the experiment was analysed. I examined model assumptions, including normality of errors and homogeneity of variances, graphically. To correct for heteroscedasticity and non-normality, an square-root transformations was applied to calcification. For all calcification models, model selection was not performed because I were interested in the contribution of both fixed effects and their interaction. The software program R (R Development Core Team 2015) was used for all analyses.

Combined physiological response

To assess the relative support of temperature, pCO_2 and chlorophyll as a predictor for each species' calcification rates and tissue energetics (comprised of lipid and protein abundance), model averaging was used following the methods of Burnham & Anderson (2002) and Hoogenboom et al. (2011). Multi-model averaging permits an assessment of the strength of each predictor variable across a series of candidate multiple regression models that utilize all possible combinations of our explanatory variables (Hoogenboom et al. 2011). First, each variable was standardised to have a mean of zero and a standard deviation of one, then Akaike's Information Criterion (AIC) was determined for each possible model. The Akaike weight ($wAIC_i$) for each model was calculated, and the $wAIC_i$ values were then summed over all models that contained that predictor variable (i.e., temperature, pCO_2 and chlorophyll) to assess the support for a given predictor variable ($wAIC_j$). Lastly, model averaging was employed across regression parameters: each model's parameter estimate is weighted according to $wAIC_j$, which yielded the direction and magnitude of the effect of each variable (Burnham & Anderson 2002, Hoogenboom et al. 2011). For this component of the analysis, some coral fragments were not big enough to be subjected to each invasive sampling regime, so the sample size was reduced to 172 for *A. muricata* and 93 for *A. hyacinthus*. All statistical analyses were conducted with the software program R (R Development Core Team 2015).

6.4 Results

Survivorship

For *A. muricata*, survivorship of the control treatment (26 °C/410 ± 4 µatm) was 66 % with similar values (73 % and 66 %) for all treatments at 26 °C, despite corals being exposed to mid (653 ± 6) and end (934 ± 11) of century ocean acidification treatments, respectively. Elevated temperature (31 °C) had a greater influence on coral survivorship than elevated levels of pCO2. Temperature stress (31 °C) was the only factor that significantly affected survivorship (Figure 6.3a, Table 6.2), although there was some evidence of synergistic effects between temperature and pCO_2. Lowest survivorship (11 %) occurred under the combination of end-of-century pCO_2 levels and temperature stress (31 °C/ 934 µatm).

For *A. hyacinthus*, high temperature (31 °C) also resulted in poor survivorship (<5 %) regardless of pCO_2 levels (Figure 6.3b), but these were not significantly different ($p=0.077$) from survivorship levels recorded for control corals (26 °C/410 µatm) where survivorship was only 29 % (Table 6.3). Highest survivorship (64 %) for *A. hyacinthus* was in the summertime maximum temperature and mid century pCO_2 treatment (28.5 °C/653 µatm).

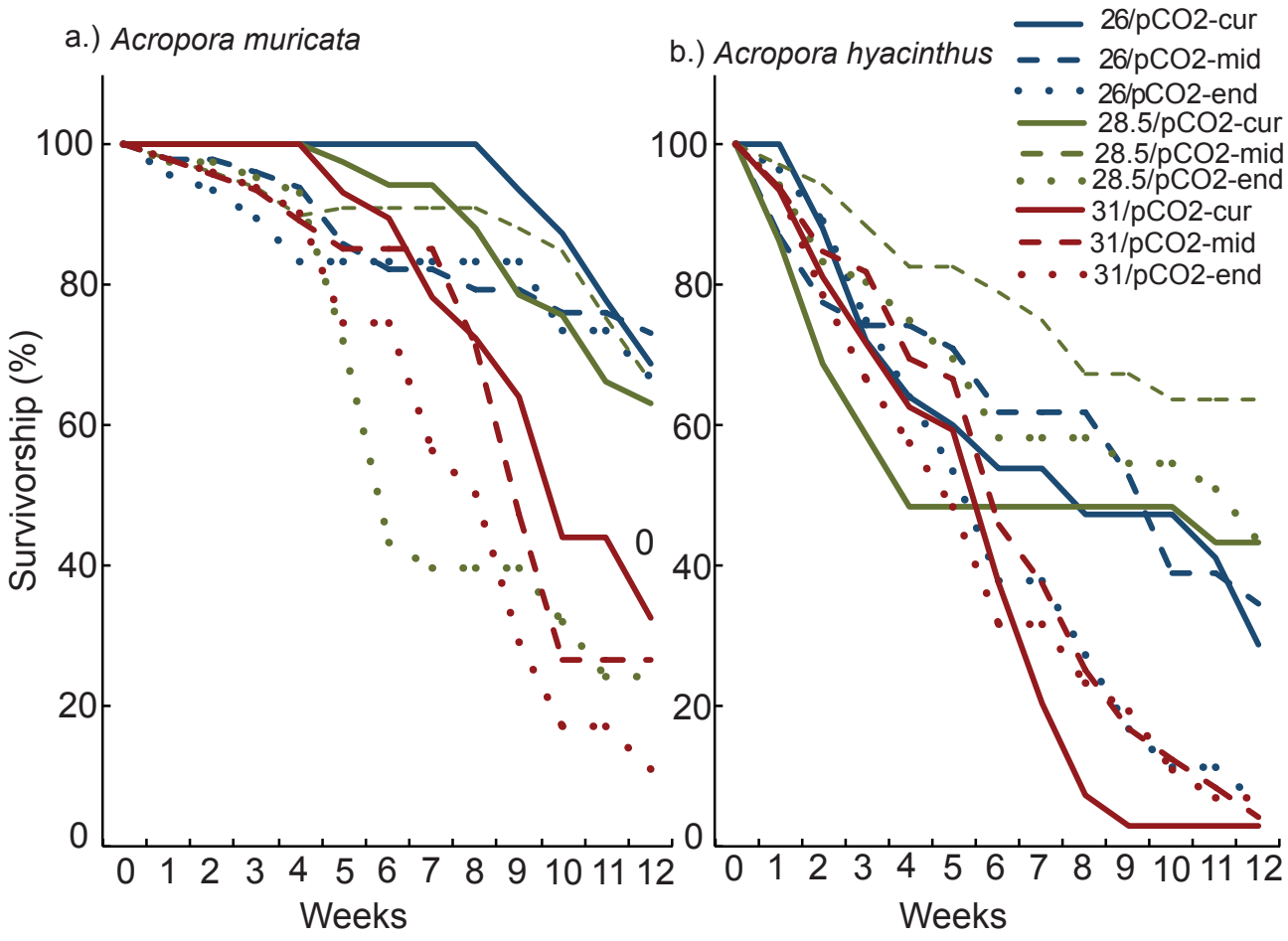

Figure 6.3. Survivorship (%) of a.) *Acropora muricata* and b.) *Acropora hyacinthus* in the nine treatments during the twelve week experiment.

Table 6.2. Results of Cox's regression to survival data for *A. muricata* compared to the control variables (long term average temp (26 °C) and current pCO_2 (410 µatm)) with pCO_2 and temperature as explanatory variables.

	Coefficient	Standard Error	P	e^b	95.0% CI for e^b
pCO_2mid	-0.420	0.43	0.326	0.657	0.28-1.52
pCO_2end	0.129	0.38	0.738	1.138	0.53-2.42
Temp28.5	-0.278	0.40	0.490	0.757	0.34-1.67
Temp31	1.371	0.32	<0.001	3.941	2.11-7.34
pCO_2mid:Temp28.5	0.639	0.59	0.280	1.895	0.59-6.05
pCO_2end:Temp28.5	0.873	0.55	0.114	2.395	0.81-7.08
pCO_2mid:Temp31	0.238	0.50	0.635	1.269	0.48-3.38
pCO_2end:Temp31	-0.013	0.45	0.977	0.987	0.40-2.41

Table 6.3. Results of Cox's regression to survival data for *A. hyacinthus* with pCO_2 and temperature as explanatory variables.

	Coefficient	Standard Error	P	e^b	95.0% CI for e^b
pCO_2mid	0.002	0.350	0.995	1.002	0.50-1.99
pCO_2end	0.472	0.336	0.160	1.603	0.83-3.01
Temp28.5	0.068	0.354	0.848	1.070	0.53-2.14
Temp31	0.563	0.318	0.077	1.756	0.94-3.28
pCO_2mid:Temp28.5	-0.745	0.503	0.138	0.474	0.18-1.27
pCO_2end:Temp28.5	-0.705	0.474	0.137	0.494	0.20-1.25
pCO_2mid:Temp31	-0.194	0.438	0.658	0.824	0.35-1.94
pCO_2end:Temp31	-0.595	0.430	0.166	0.551	0.24-1.28

Calcification by bouyant weight

For *A. muricata*, there was enhanced calcification with temperature in the current day pCO_2 (410 ± 4 µatm) treatments during the initiation of the experiment until week five. Calcification increased by 30 % (from 0.19 ± 0.02 to 0.30 ± 0.05 mg d^{-1} cm^{-2}) as temperature increased from 26 °C to +2.5 °C above the summertime maximum (31 °C), respectively. Growth rates during the first five weeks at 26 °C and 31.5 °C exposed to mid (653 ± 6 µatm) and end (934 ± 11 µatm) of century pCO_2 levels were reduced by 25-50 % compared to control pCO_2 (Figure 6.4). Bleaching caused by +2.5 °C above the summertime maximum (31 °C) caused significant reductions (10 - 50 %) in calcification in from week five to twelve (Table 6.4). Longer exposure to elevated pCO_2 at the summer maximum temperature of 28.5 °C reduced calcification by 50 % at both mid and end of century pCO_2 levels compared to that determined for weeks 0-5. At 26 °C/mid century pCO_2, longer exposure (5-12 weeks) led to further reductions in calcification when compared to control. Despite calcification rates at 26 °C/pCO_2-end of century (934±11 µatm) being 40% greater during the weeks 5-12 (0.15 ± 0.03 mg d^{-1} cm^{-2}) compared to week 0-5 (0.09 ± 0.01 mg d^{-1} cm^{-2}), the difference was not statistically significant (one-way ANOVA, $F_{1/47}$=3.683, p=0.061).

For *A. hyacinthus*, calcification rates doubled at present day pCO_2 levels (410 ± 4 µatm) with an increase in temperature to 28.5 °C (0.06 ± 0.01 to 0.11 ± 0.05 mg d^{-1} cm^{-2}, respectively) for the period of the initiation of the experiment to week 5 (Figure 6.4b). The corals during the pre-stress ramping of +2.5 °C above the summertime maximum (31 °C) did not experience temperature enhanced calcification because calcification rates were similar to the control (~0.06 mg d^{-1} cm^{-2}) for all acidification treatments. Despite lower rates of calcification in the 31 °C treatments following the bleaching stress (during weeks 5-12), calcification rates did not significantly vary compared to the control (Table 6.5, Figure 6.4b), which may be due to the limited sample size (n=5 in all 31 °C treatments). When

comparing weeks 0-5 to weeks 5-12 calcification rates, the temperature treatment of +2.5 °C above the summer maximum reduced calcification rates by 10 – 25 %. Of the *A. hyacinthus* that survived in the high temperature treatments until the end of experiment, the calcification rates were markedly reduced to close to zero.

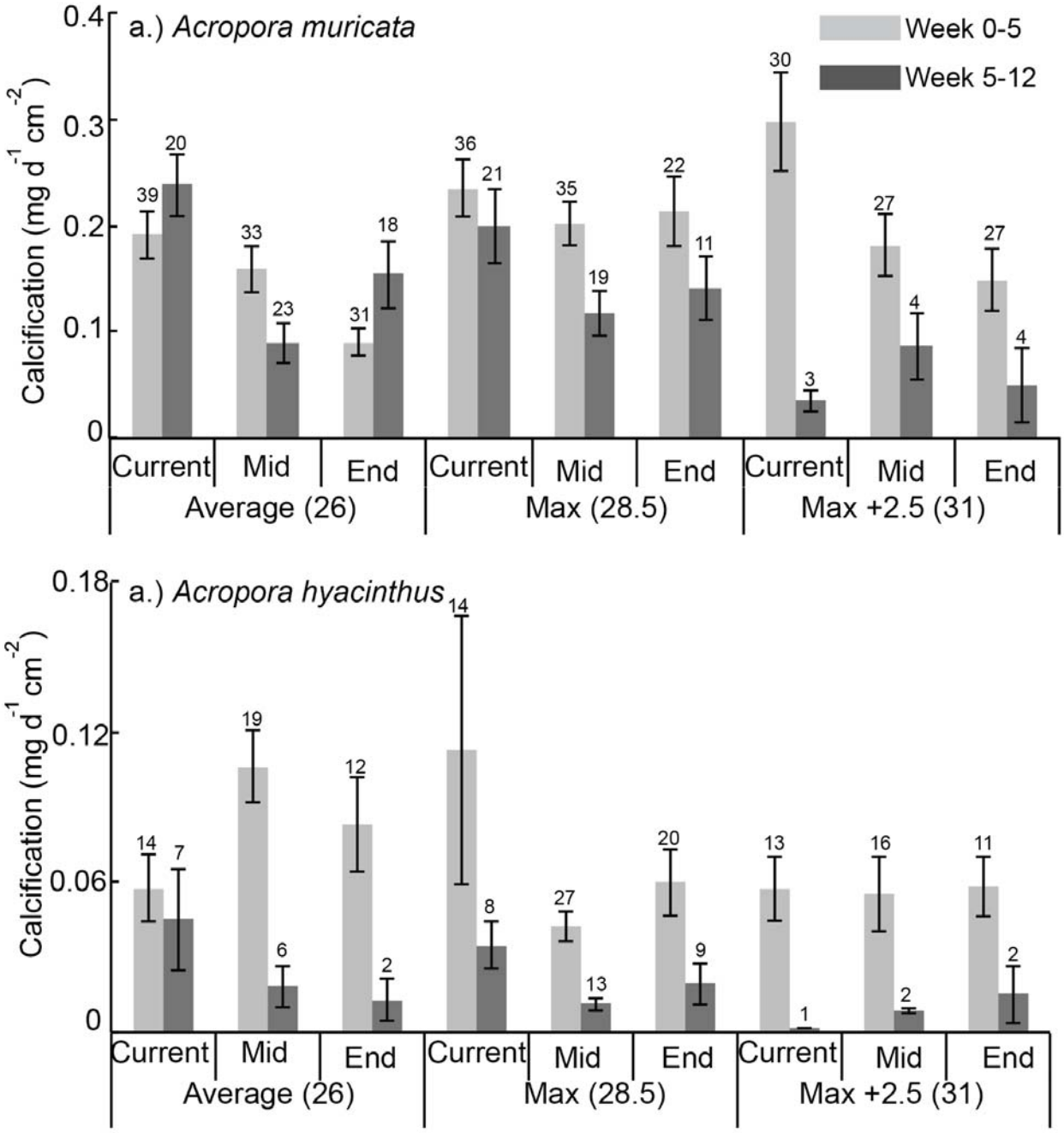

Figure 6.4. Calcification (mg d^{-1} cm^{-2}) of a.) *Acropora muricata* and b.) *Acropora hyacinthus* during the week 0 - 5 and week 5 - 12 in current (410 ± 4 µatm), mid (653 ± 6 µatm) and end (934 ± 11 µatm) of century pCO_2 levels at the long-term average SST of 26 °C, summer maximum of 28.5 °C and a future +2.5 °C stress treatment of 31 °C. Sample size of each treatment is provided above each bar.

Table 6.4. Linear mixed effects model for week 0-5 and week 5 -12 calcification rates of *A. muricata*.

	Fixed effects	**Value**	**SE**	**DF**	**t-value**	**p-value**
Weeks 0-5	(Intercept)	0.41	0.04	253	9.986	-
	Temp28.5	0.04	0.06	18	0.731	0.474
	Temp31	0.09	0.06	18	1.557	0.137
	pCO_2mid	-0.03	0.06	18	-0.573	0.574
	pCO_2end	-0.13	0.06	18	-2.241	0.038
	Temp28.5:pCO_2mid	0.01	0.08	18	0.083	0.935
	Temp31:pCO_2mid	-0.08	0.09	18	-0.949	0.355
	Temp28.5:pCO_2end	0.12	0.09	18	1.370	0.188
	Temp31:pCO_2end	-0.04	0.09	18	-0.441	0.665
Weeks 5-12	(Intercept)	0.46	0.05	97	9.474	-
	Temp28.5	-0.06	0.07	17	-0.864	0.400
	Temp31	-0.28	0.11	17	-2.490	0.023
	pCO_2mid	-0.21	0.07	17	-3.059	0.007
	pCO_2end	-0.10	0.07	17	-1.495	0.153
	Temp28.5:pCO_2mid	0.12	0.10	17	1.187	0.252
	Temp31:pCO_2mid	0.29	0.15	17	1.960	0.067
	Temp28.5:pCO_2end	0.04	0.10	17	0.413	0.685
	Temp31:pCO_2end	0.11	0.15	17	0.703	0.491

Table 6.5 Linear mixed effects model results of *A. hyacinthus* calcification for week 0 to week five and week five to week twelve periods.

	Fixed effects	Value	SE	DF	t-value	p-value
Weeks 0-5	(Intercept)	0.22	0.03	117	7.943	-
	Temp28.5	0.01	0.04	18	0.313	0.758
	Temp31	-0.01	0.04	18	-0.256	0.801
	pCO_2mid	0.09	0.04	18	2.559	0.020
	pCO_2end	0.05	0.04	18	1.133	0.272
	Temp28.5:pCO_2mid	-0.13	0.05	18	-2.637	0.017
	Temp31:pCO_2mid	-0.09	0.05	18	-1.724	0.102
	Temp28.5:pCO_2end	-0.06	0.05	18	-1.115	0.280
	Temp31:pCO_2end	-0.03	0.06	18	-0.445	0.662
Weeks 5-12	(Intercept)	0.15	0.03	27	5.254	-
	Temp28.5	0.02	0.04	13	0.655	0.524
	Temp31	-0.11	0.07	13	-1.500	0.158
	pCO_2mid	-0.03	0.04	13	-0.772	0.454
	pCO_2end	-0.04	0.06	13	-0.742	0.472
	Temp28.5:pCO_2mid	-0.05	0.05	13	-0.954	0.358
	Temp31:pCO_2mid	0.09	0.09	13	0.922	0.374
	Temp28.5:pCO_2end	-0.01	0.07	13	-0.221	0.828
	Temp31:pCO_2end	0.12	0.10	13	1.156	0.269

Chlorophyll

A. muricata average chlorophyll *a* (chl*a*) abundance at the start of the experiment was 21.0 ± 1.3 μg cm^{-2}. Temperature treatment of 31.0 °C led to significant declines in Chl*a* by 16 – 33 % compared to control values (Table 6.6, Figure 6.5) as would be expected due to severe bleaching at the time when temperature stress was reached (week 5) and the end of the experiment (week 12). Across all treatments, there was a significant decline in concentration of Chl*a* at week 5 when the maximum temperature targets were reached and at the end of the experiment at week 12, in comparison to initial sampling time point (Table 6.6).

The average Chl*a* abundance of *A. hyacinthus* at the start of the experiment was 8.9 ± 1.3 μg cm^{-2}. Similar to *A. muricata*, 31.0 °C temperature treatments had significant reductions in Chl*a* by 50 % compared to the initial time point (Table 6.7, Figure 6.5). As well, as the corals were sampled throughout the experiment, the average abundance of Chl*a* per coral fragments declined (Table 6.7).

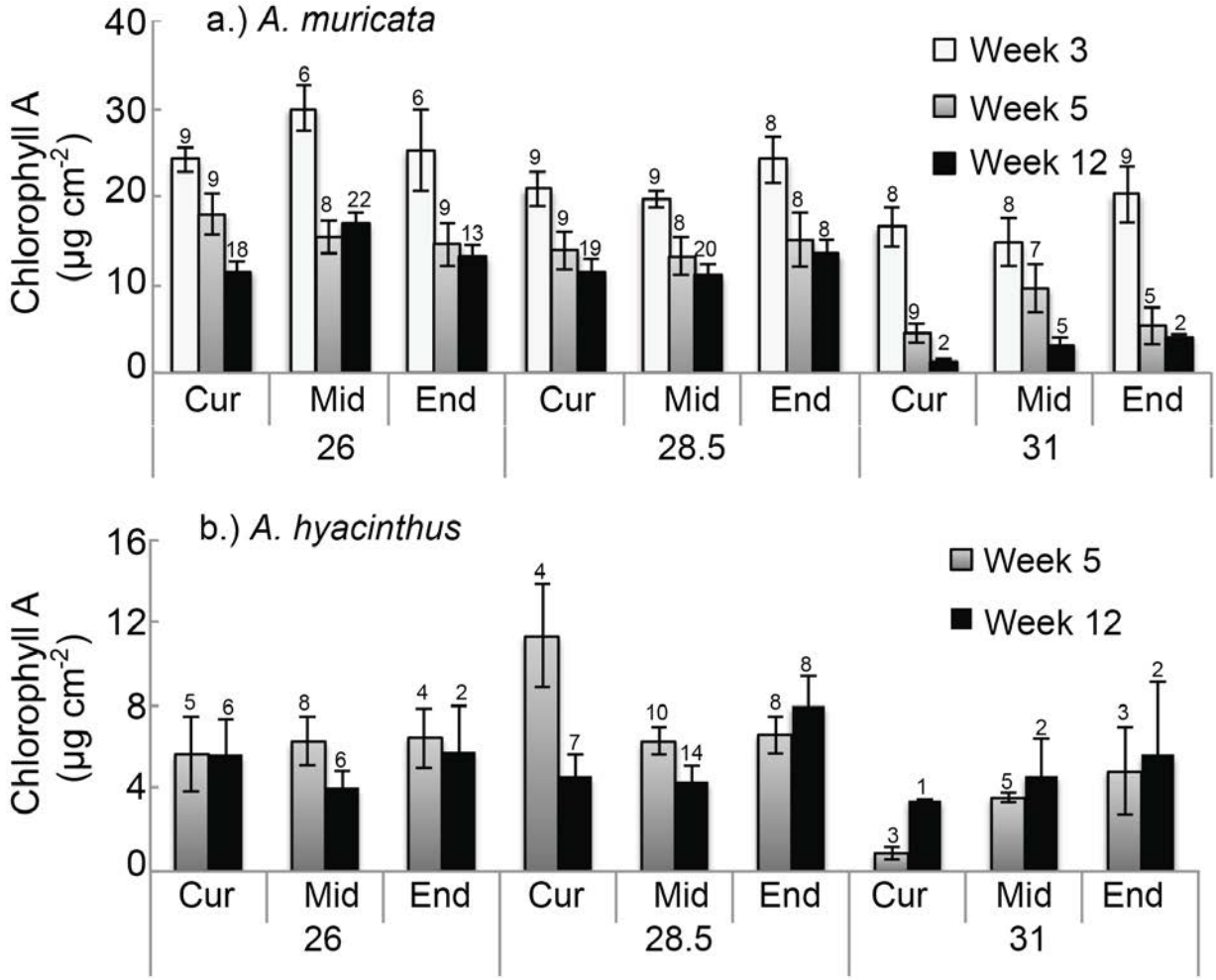

Figure 6.5. Chlorophyll *a* concentration in coral fragments of a.) *A. muricata* and b.) *A. hyacinthus* when the ocean acidification targets were reached (Week 3), temperature targets reached (Week 5) and the final sampling (Week 12) were completed. Treatments are the three temperatures of 26 °C, 28.5 °C, 31 °C at current (Cur=410 ± 4 µatm), mid (653 ± 6 µatm)) and end of century (934 ± 11 µatm) pCO_2 levels.

Table 6.6. Linear mixed effects model results for chlorophyll *a* of *A. muricata* with fixed effects of pCO_2 (mid and end of century) and temperature (28.5 °C and 31.0 °C) and period when the coral frags were sampled at week 3 (ocean acidification targets reached), week 5 (temperature targets reache), week 12 (end of experiment) compared to the control (26.0 °C/current pCO_2 and start of experiment freezing time point) .

	Value	SE	DF	t-value	p-value
(Intercept)	21.05	1.21	243	17.347	-
pCO_2mid	3.37	1.63	243	2.060	0.041
pCO_2end	0.12	1.72	243	0.070	0.944
Temp28.5	-1.93	1.62	243	-1.194	0.234
Temp31.0	-9.75	1.93	243	-5.042	<0.001
Week 3	3.49	1.79	243	1.957	0.051
Week 5	-5.81	1.77	243	-3.280	0.001
Week 12	-7.99	1.71	243	-4.683	<0.001
pCO_2mid:Temp28.5	-4.06	2.30	243	-1.766	0.079
pCO_2end:Temp28.5	1.70	2.48	243	0.685	0.494
pCO_2mid:Temp31.0	-1.90	2.68	243	-0.708	0.480
pCO_2end:Temp31.0	2.91	2.84	243	1.025	0.306

Table 6.7. Linear mixed effects model results for chlorophyll *a* of *A. hyacinthus* with fixed effects of pCO_2 (mid and end of century) and temperature (28.5 °C and 31.0 °C) and the two period through the experiment when the coral frags were sampled at the temperature targets reached (Week 5), and the end of experiment at (Week 12) compared to the control (26.0 °C/current pCO_2 and start of experiment freezing time point)

	Value	SE	DF	t-value	p-value
(Intercept)	8.56	0.75	87	23.362	-
pCO_2mid	-0.59	1.71	87	-0.359	0.720
pCO_2end	0.26	2.18	87	0.128	0.899
Temp28.5	1.60	2.00	87	0.874	0.384
Temp31.0	-5.87	1.43	87	-3.302	0.001
Week 5	-2.64	1.28	87	-1.961	0.053
Week 12	-3.72	1.15	87	-2.927	0.004
pCO_2mid:Temp28.5	-1.46	2.25	87	-0.664	0.509
pCO_2end:Temp28.5	0.23	2.85	87	0.089	0.929
pCO_2mid:Temp31.0	6.43	4.17	87	1.874	0.064
pCO_2end:Temp31.0	7.21	4.78	87	1.861	0.066

6.4.1 Calcification Incubations

For *A. muricata*, the average dark and light calcification rate (μM C cm^{-2} h^{-1}) at the initiation of the experiment was 6.34 ± 0.53 and 14.35 ± 1.03, respectively, and the average dark and light respiration rate (mg O_2 cm^{-2} h^{-1}) for was -0.21± 0.01 and 0.89 ± 0.05, respectively. At week 5, net photosynthesis was significantly enhanced by end of century pCO_2 levels (934 ± 11 μatm) (Figure 6.6, Table 6.7a). However, after longer exposure (to week 12), there was no significant variation among pCO_2 and temperature treatments (Table 6.7a), but the photosynthesis rates in the 31 °C /end of century pCO_2 (934 ± 11 μatm) treatment were double the rate of all other treatments. This variation was likely due to the robustness of the few surviving coral fragments; two of the four coral fragments that survived remained pigmented and did not severely bleach under these stressful temperature and acidification conditions. Dark respiration rates of *A. muricata* at both time points were unaffected by pCO_2 and temperature (Figure 6.6; Table 6.8b). Similarly, light calcification rates were all positive and did not significantly vary due to temperature or pCO_2 across all treatments. However, average light calcification within the 31°C /end of century pCO_2 treatment had negative calcification rates (-1.1 μM C cm^{-2} h^{-1}), indicating dissolution under high stress conditions. Dark calcification rates were significantly impacted by end of century pCO_2, summer max temperature treatment (28.5 °C), and max +2.5 temperature treatment (31.0 °C) (Figure 6.6g; Table 6.8d) at week 5. However, at week 12, the surviving corals' dark calcification rates were not significantly impacted by pCO_2 or temperature as compared to the control (Figure 6.6h; Table 6.8d).

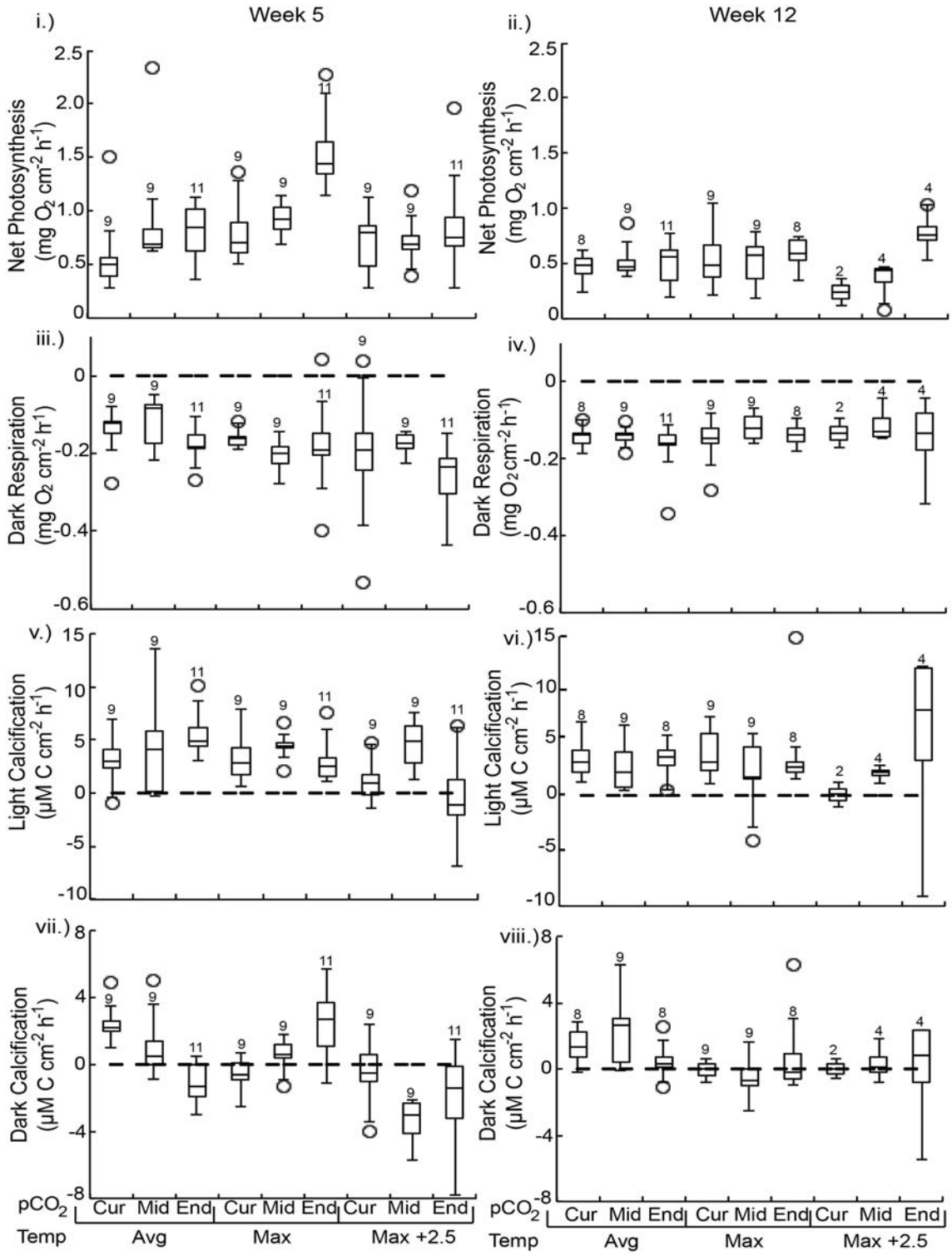

Figure 6.6. Net photosynthesis (mg O_2 cm^{-2} h^{-1}) (a,b), dark respiration (mg O_2 cm^{-2} h^{-1}) (c,d), light (e,f) and dark calcification (µM C cm^{-2} h^{-1}) (g,h) for *A. muricata* at week five when the temperature targets were reached (a,c,e,g), and at the end of the experiment (week twelve) (b,d,f,h). All nine treatments are presented with the three temperatures (Avg=longterm average of 26 °C, Max=longterm summer max of 28.5 °C, Max +2.5= summer max +2.5 of 31 °C) crossed with the three pCO_2 (Cur=current at 410 ± 4 µatm, Mid=mid-century predictions at 653 ± 6 µatm, End=end of century predictions at 934 ± 11 µatm).

Table 6.8. Linear mixed effects model results for the alkalinity anomaly technique for *A. muricata* photosynthesis (a), dark respiration (b), light calcification (c) and dark calcification (d) at week 5 when the temperature targets were reached and week 12. Significant ($p<0.05$) p-values are in bold.

a.) *A. muricata* Photosynthesis

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	0.49	0.10	57	4.882	-	0.47	0.09	37	5.099	-
pCO_2mid	0.28	0.14	18	1.983	0.063	0.05	0.13	17	0.389	0.702
pCO_2end	0.32	0.14	18	2.338	**0.031**	0.04	0.13	17	0.279	0.784
Temp28.5	0.28	0.14	18	2.021	0.059	0.07	0.13	17	0.570	0.576
Temp31	0.21	0.14	18	1.545	0.140	-0.23	0.17	17	-1.371	0.188
pCO_2mid:Temp28.5	-0.13	0.20	18	-0.645	0.527	-0.08	0.18	17	-0.420	0.680
pCO_2end:Temp28.5	0.45	0.19	18	2.353	**0.030**	0.03	0.18	17	0.171	0.866
pCO_2mid:Temp31	-0.26	0.20	18	-1.306	0.208	0.05	0.22	17	0.227	0.823
pCO_2end:Temp31	-0.28	0.19	18	-1.467	0.160	0.52	0.22	17	2.392	**0.029**

b.) *A. muricata* dark respiration

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	-0.15	0.04	59	-4.154	-	-0.15	0.01	37	-9.790	-
pCO_2mid	0.03	0.05	18	0.561	0.581	0.00	0.02	17	0.142	0.889
pCO_2end	-0.03	0.05	18	-0.653	0.522	-0.01	0.02	17	-0.315	0.756
Temp28.5	-0.02	0.05	18	-0.365	0.720	0.01	0.02	17	0.590	0.563
Temp31	-0.07	0.05	18	-1.367	0.189	0.01	0.03	17	0.423	0.677
pCO_2mid:Temp28.5	-0.07	0.07	18	-0.993	0.334	0.01	0.03	17	0.428	0.674
pCO_2end:Temp28.5	0.01	0.07	18	0.176	0.863	0.01	0.03	17	0.204	0.841
pCO_2mid:Temp31	0.01	0.07	18	0.120	0.906	0.02	0.04	17	0.595	0.560
pCO_2end:Temp31	-0.01	0.07	18	-0.077	0.939	0.02	0.04	17	0.478	0.639

c) *A. muricata* light calcification

AM light calc	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	3.10	1.05	59	2.947	-	3.98	2.02	37	1.967	-
pCO_2mid	0.19	1.51	18	0.125	0.902	-1.00	2.85	17	-0.351	0.730
pCO_2end	2.62	1.45	18	1.802	0.088	-0.32	2.84	17	-0.113	0.912
Temp28.5	0.56	1.49	18	0.380	0.709	0.39	2.85	17	0.136	0.894
Temp31	-1.96	1.49	18	-1.319	0.204	-3.77	3.36	17	-1.121	0.278
pCO_2mid:Temp28.5	0.62	2.12	18	0.290	0.775	-0.94	4.02	17	-0.234	0.818
pCO_2end:Temp28.5	-3.23	2.06	18	-1.571	0.134	2.52	4.04	17	0.624	0.541
pCO_2mid:Temp31	3.26	2.12	18	1.536	0.142	2.99	4.47	17	0.669	0.513
pCO_2end:Temp31	-3.96	2.06	18	-1.926	0.070	9.16	4.48	17	2.044	0.057

Table 6.8 (continued). Linear mixed effects model results for the alkalinity anomaly technique for *A. muricata* photosynthesis (a), dark respiration (b), light calcification (c) and dark calcification (d) at week 5 when the temperature targets were reached and week 12. Significant ($p<0.05$) p-values are in bold.

d.) *A. muricata* dark calcification

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	2.46	0.57	60	4.307	-	1.44	0.91	39	1.576	-
pCO_2mid	-1.43	0.81	18	-1.777	0.092	0.93	1.29	17	0.721	0.481
pCO_2end	-3.56	0.77	18	-4.629	**<0.001**	-0.97	1.28	17	-0.753	0.462
Temp28.5	-3.05	0.81	18	-3.784	**0.001**	-1.49	1.29	17	-1.157	0.263
Temp31	-2.84	0.81	18	-3.514	**0.003**	-1.42	1.55	17	-0.920	0.370
pCO_2mid:Temp28.5	2.65	1.14	18	2.325	**0.032**	-1.42	1.83	17	-0.779	0.447
pCO_2end:Temp28.5	6.49	1.09	18	5.968	**<0.001**	2.82	1.83	17	1.538	0.143
pCO_2mid:Temp31	-1.63	1.14	18	-1.431	0.170	-0.40	2.05	17	-0.195	0.848
pCO_2end:Temp31	1.96	1.09	18	1.802	0.088	1.59	2.05	17	0.778	0.447

For *A. hyacinthus*, the average dark and light calcification rate (μM C cm^{-2} h^{-1}) at the initiation of the experiment was 3.23 ± 0.38 and 5.11 ± 0.46, respectively, and the average dark respiration and photosynthesis rates (mg O_2 cm^{-2} h^{-1}) were -0.15 ± 0.01 and 0.49 ± 0.02, respectively. By week 5, the end of century pCO_2 (932 ± 11 μatm) treatments had significantly greater photosynthesis rates (Figure 6.7a; Table 6.9a). This increase in photosynthesis may have stemmed from the increased pool of dissolve inorganic carbon. Even after twelve weeks of acclimation, the remaining five fragments in the high temperature treatments had significantly higher photosynthesis rates (Figure 6.7b; Table 6.9a). By the end of the experiment at week 12, dark respiration rates were significantly reduced in the end of century pCO_2 and high temperature treatments compared to the control (Figure 6.7c; Table 6.9b). At week 12, following temperature stress at 31 °C, dark respiration rates remained significantly reduced compared to the controls (Figure 6.7d; Table 6.9b). Light calcification rates of *A. hyacinthus* were significantly greater at mid-century pCO_2 levels compared to the control. The high-temperature treatment and both mid and end of century pCO_2 levels had negative calcification rates compared to all other treatments (Figure 6.7e; Table 6.9c). However, by week 12, there was no significant variation among the remaining coral fragments for light calcification rates (Table 6.9c). Dark calcification rates were highly variable by week 12 with the greatest values in the 28.5 °C /mid century pCO_2 (653 ± 6) treatments and lowest values in the 31 °C /mid century pCO_2 (653 ± 6) (Figure 6.7g, Table 6.9d).

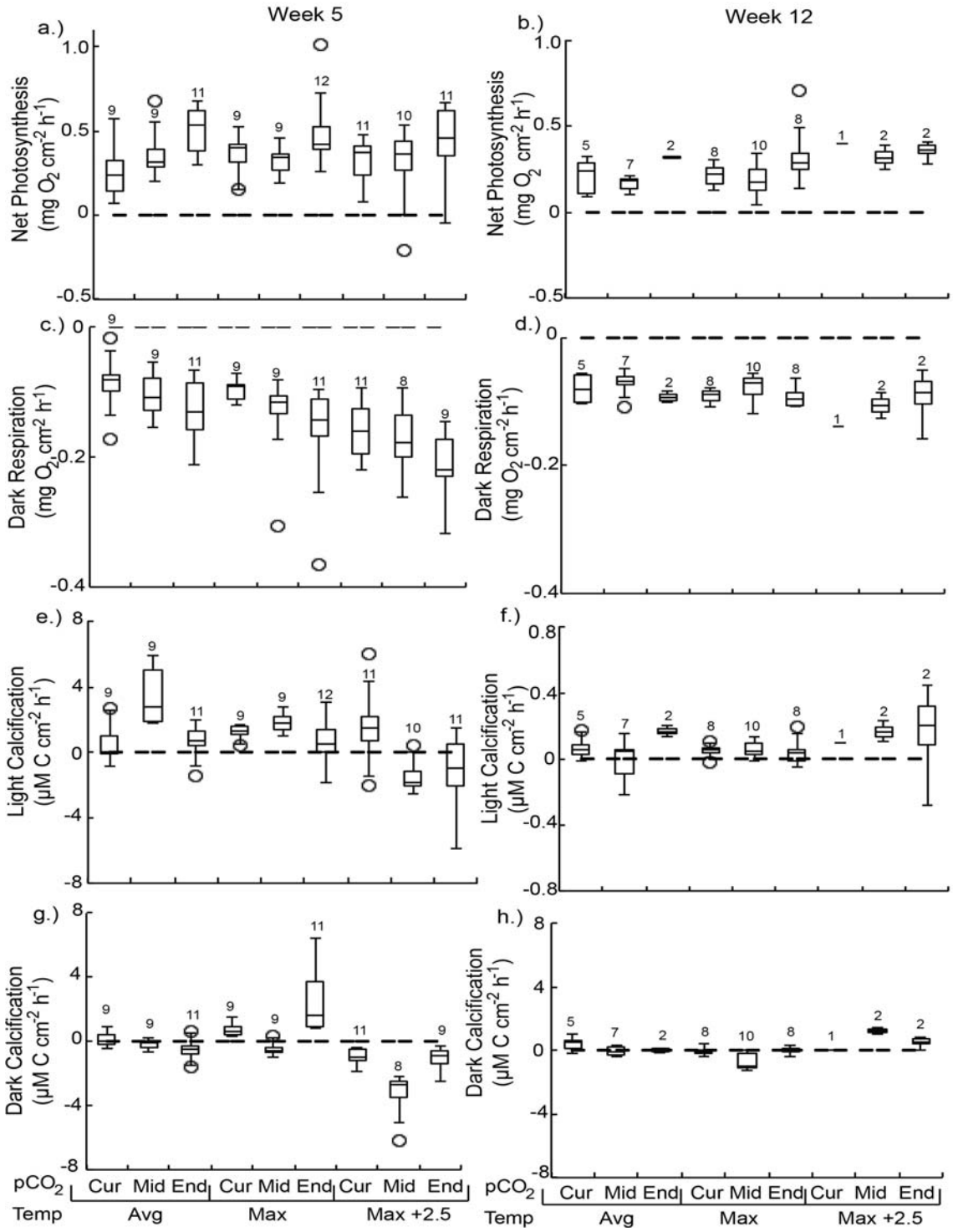

Figure 6.7. Net photosynthesis (mg O_2 cm^{-2} h^{-1}) (a,b), dark respiration (mg O_2 cm^{-2} h^{-1}) (c,d), light (e,f) and dark calcification (µM C cm^{-2} h^{-1}) (g,h) for *A. hyacinthus* at week five when the temperature targets were reached (a,c,e,g), and at the end of the experiment (week twelve) assessing post-temperature stress recovery (b,d,f,h). All nine treatments are presented with the three temperatures (Avg=longterm average of 26 °C, Max=longterm summer max of 28.5 °C, Max +2.5= summer max +2.5 of 31 °C) crossed with the three pCO_2 (Cur=current at 410 ± 4 µatm, Mid=mid-century predictions at 653 ± 6 µatm, End=end of century predictions at 934 ±11 µatm).

Table 6.9. Linear mixed effects model results for the alkalinity anomaly technique for *A. hyacinthus* photosynthesis (a), dark respiration (b), light calcification (c) and dark calcification (d) at the temperature targets (week 5) and week 12. Significant ($p<0.05$) p-values are in bold.

a.) *Acropora hyacinthus* photosynthesis

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	0.26	0.06	62	4.220	-	0.21	0.04	22	5.925	-
pCO_2mid	0.13	0.09	20	1.461	0.160	-0.04	0.05	13	-0.887	0.391
pCO_2end	0.25	0.08	20	3.015	**0.004**	0.11	0.07	13	1.656	0.122
Temp28.5	0.11	0.09	20	1.305	0.207	0.01	0.05	13	0.206	0.840
Temp31	0.06	0.08	20	0.668	0.512	0.19	0.09	13	2.207	**0.046**
pCO_2mid:Temp28.5	-0.18	0.12	20	-1.455	0.161	0.01	0.06	13	0.186	0.855
pCO_2end:Temp28.5	-0.11	0.11	20	-0.955	0.343	-0.06	0.08	13	-0.761	0.460
pCO_2mid:Temp31	-0.13	0.12	20	-1.114	0.278	-0.04	0.11	13	-0.361	0.724
pCO_2end:Temp31	-0.08	0.12	20	-0.704	0.489	-0.14	0.12	13	-1.219	0.245

b.) *Acropora hyacinthus* dark respiration

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	-0.09	0.01	56	-6.594	-	-0.08	0.01	23	-8.632	-
pCO_2mid	-0.01	0.02	20	-0.782	0.443	0.01	0.01	13	0.721	0.484
pCO_2end	-0.04	0.02	20	-2.132	**0.037**	-0.01	0.02	13	-0.761	0.460
Temp28.5	-0.01	0.02	20	-0.381	0.707	-0.01	0.01	13	-1.000	0.336
Temp31	-0.07	0.02	20	-4.019	**0.001**	-0.06	0.02	13	-2.645	**0.020**
pCO_2mid:Temp28.5	0.00	0.03	20	-0.009	0.993	0.00	0.02	13	0.248	0.808
pCO_2end:Temp28.5	0.00	0.03	20	-0.001	0.999	0.01	0.02	13	0.597	0.561
pCO_2mid:Temp31	0.00	0.03	20	0.163	0.872	0.02	0.03	13	0.889	0.390
pCO_2end:Temp31	-0.02	0.03	20	-0.747	0.464	0.07	0.03	13	2.167	**0.049**

c.) *Acropora hyacinthus* light calcification

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	0.65	0.59	62	1.094	-	0.60	0.70	23	0.867	-
pCO_2mid	2.78	0.83	20	3.344	**0.003**	-0.68	0.98	13	-0.694	0.500
pCO_2end	0.13	0.81	20	0.162	0.872	1.06	1.13	13	0.945	0.362
Temp28.5	0.63	0.82	20	0.765	0.453	-0.18	0.97	13	-0.180	0.860
Temp31	1.00	0.81	20	1.236	0.231	0.37	1.43	13	0.256	0.802
pCO_2mid:Temp28.5	-2.22	1.17	20	-1.905	0.071	0.79	1.37	13	0.579	0.573
pCO_2end:Temp28.5	-0.66	1.10	20	-0.600	0.551	-1.10	1.48	13	-0.742	0.471
pCO_2mid:Temp31	-5.92	1.15	20	-5.145	**<0.001**	1.38	1.82	13	0.757	0.463
pCO_2end:Temp31	-2.75	1.13	20	-2.426	**0.025**	-0.01	1.90	13	-0.003	0.998

Table 6.9 (continued). Linear mixed effects model results for the alkalinity anomaly technique for *A. hyacinthus* photosynthesis (a), dark respiration (b), light calcification (c) and dark calcification (d) at the temperature targets (week 5) and at the end of the experiment at week 12. Significant ($p<0.05$) p-values are in bold.

d.) *Acropora hyacinthus* dark calcification

	Week 5 (temperature targets)					Week 12				
	Value	SE	DF	t	p	Value	SE	DF	t	p
(Intercept)	0.11	0.50	59	-	0.821	0.32	0.21	23	1.494	-
pCO_2mid	-0.28	0.71	20	-0.395	0.697	-0.30	0.30	13	-1.001	0.335
pCO_2end	-0.63	0.70	20	-0.902	0.371	-0.33	0.35	13	-0.935	0.367
Temp28.5	0.66	0.70	20	0.941	0.358	-0.35	0.30	13	-1.169	0.263
Temp31	-1.04	0.70	20	-1.488	0.152	-0.35	0.45	13	-0.782	0.448
pCO_2mid:Temp28.5	-0.96	1.00	20	-0.955	0.351	-0.45	0.42	13	-1.075	0.302
pCO_2end:Temp28.5	1.86	0.94	20	1.985	0.052	0.33	0.46	13	0.731	0.478
pCO_2mid:Temp31	-2.07	1.01	20	-2.063	0.052	1.56	0.57	13	2.733	**0.017**
pCO_2end:Temp31	0.47	0.98	20	0.483	0.634	0.92	0.60	13	1.539	0.148

6.4.2 Combined physiological response

The response of calcification to temperature, pCO_2, and Chla

For *A. muricata*, pCO_2, protein and then temperature were the strongest predictors of calcification rates at week 5 (Figure 6.8ai). Based on the model averaged regression coefficients, corals sampled at week 5 (subjected to five weeks of temperature ramping and two weeks at target pCO_2 levels) showed that increasing temperatures from 26°C to 28.5 °C and 31 °C, respectively, positively enhanced calcification compared to the control (Figure 6.8aii). Similarly, by week 5, mid century pCO_2 levels (653 ± 6 µatm) did not negatively impact calcification rates (Figure 6.8aii). In comparison, pCO_2 concentrations projected for the end of century (934 ± 11) negatively impacted calcification. However, Chl*a* and pCO_2 were the strongest predictors of calcification (Figure 6.8bi). Both mid and end of century pCO_2 negatively impacted calcification after twelve weeks compared to the control. Further, the temperature treatment of 28.5 °C still positively correlated with calcification after twelve weeks; however, at 31.0 °C the effect was not significant (Figure 6.8bii).

For *A. hyacinthus*, all three predictor variables (temperature, pCO_2 and chlorophyll *a*) were important drivers of calcification at week 5 (Figure 6.8ci). However, both temperature treatments of 28.5 °C and 31.0 °C negatively impacted calcification (Figure 6.8cii). Over the first five weeks, calcification under mid-century pCO_2 (653 ± 6 µatm) targets remained positive, whereas end of century pCO_2 (934 ± 11 µatm) negatively impacted the calcification of *A. hyacinthus*. However, after twelve weeks both temperature and pCO_2 treatments negatively impacted calcification compared to controls (Figure 6.8dii).

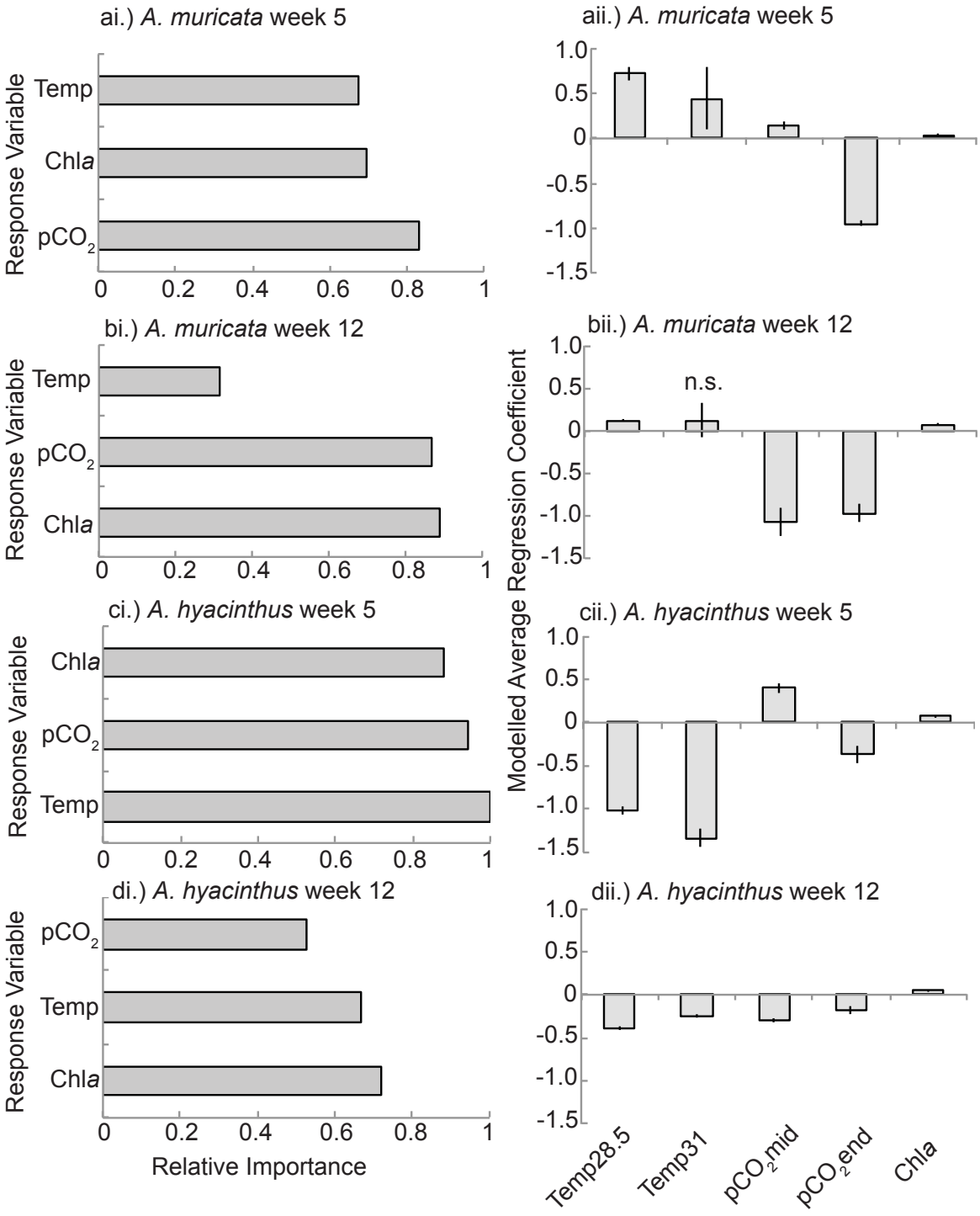

Figure 6.8. The relative importance of each predictor variable on calcification rates (left-hand column) and the model averaged regression coefficients (right-hand column) of a) *A. muricata* after week 5, b) *A. muricata* after week 12, c) *A. hyacinthus* after week 5, and d) *A. hyacinthus* after week 12. Variable importance was calculated as the sum of Akaike weights over all candidate models that included each predictor. Model averaged regression coefficients show the effect of each predictor variable on calcification. Error bars show 95% confidence intervals, and n.s. indicates non-significant values.

Coral tissue energetics

For *A. muricata*, the concentration of Chl*a* was the most important predictor variable in determining the protein and lipid concentrations after week 5 as well as after week 12 (Figure 6.9). During weeks 0 - 5, pCO_2 was the second best predictor of protein and lipid concentrations in the models; however, following bleaching at 31°C by week 12, temperature was the greatest predictor variable. There was also variability in the magnitude and direction of regression coefficients between the weeks 0-5 and weeks 5-12. For example, after five weeks, protein and lipid abundances were negatively impacted by high temperatures (28.5 °C and 31 °C). However, at week 12, the protein and lipid abundances of the surviving coral fragments in the higher temperature treatments did not significantly differ from the control (Figure 6.9bii,dii).

Likewise, for *A. hyacinthus*, Chl*a* concentration was the most important predictor variable in determining the protein and lipid concentrations after week 5 as well as after week 12 (Figure 6.10). Temperature and pCO_2 had relatively equal importance as predictor variables for protein and lipid at both sampling periods. The magnitude and direction changed for some variables from the weeks 0-5 to weeks 5-12 periods. For example, at both pCO_2 levels the direction in the response of protein concentration changed from positive at week 5 (short term exposure) to negative at week 12 (longer exposure). However, temperatures of 28.5 °C and 31 °C negatively impacted lipid concentration throughout the experiment in comparison to the control.

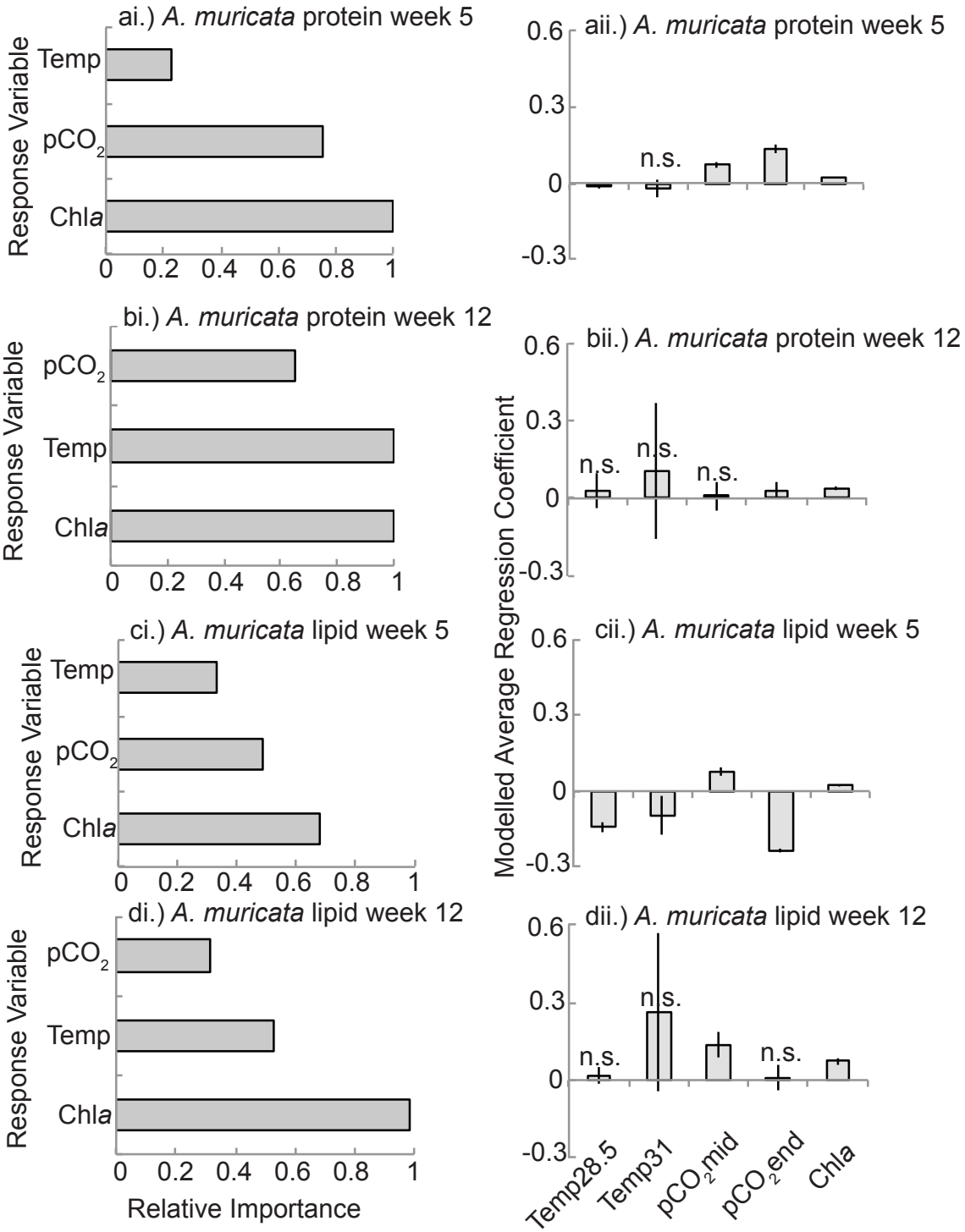

Figure 6.9. The relative importance of each predictor variable on *A. muricata* tissue energetics (left-hand column) and the model averaged regression coefficients (right-hand column) of a) *A. muricata* protein content after week 5, b) *A. muricata* protein content after week 12, c) *A. muricata* lipid content after week 5, and d) *A. muricata* lipid content after week 12.Variable importance was calculated as the sum of Akaike weights over all candidate models that included each predictor. Model averaged regression coefficients show the effect of each predictor variable on tissue energetics. Error bars show 95% confidence intervals, and n.s. indicates non-significant values.

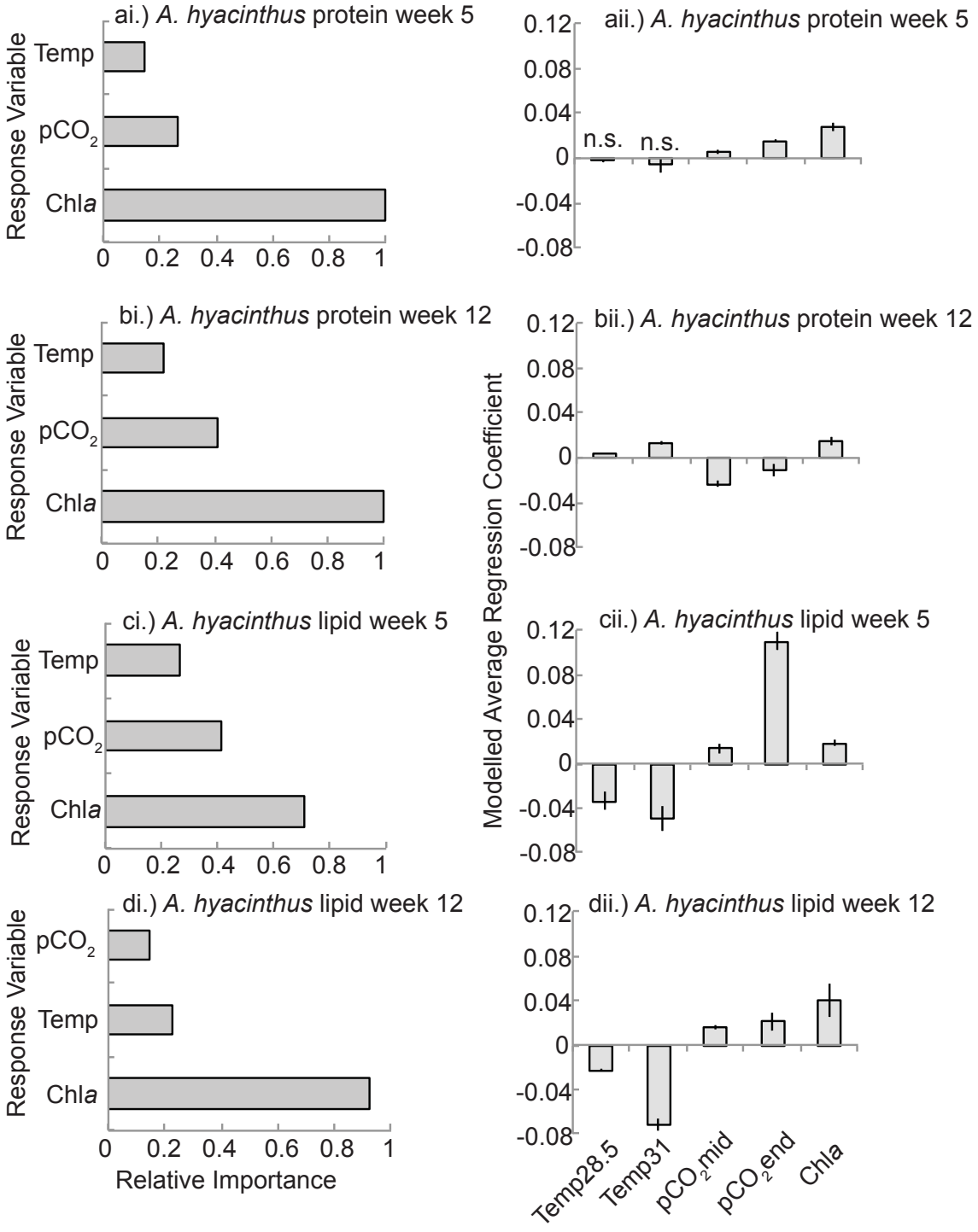

Figure 6.10. The relative importance of each predictor variable on *A. hyacinthus* tissue energetics (left-hand column) and the model averaged regression coefficients (right-hand column) of a) *A. hyacinthus* protein content after week 5, b) *A. hyacinthus* protein content after week 12, c) *A. hyacinthus* lipid content after week 5, and d) *A. hyacinthus* lipid content after week 12.Variable importance was calculated as the sum of Akaike weights over all candidate models that included each predictor. Model averaged regression coefficients show the effect of each predictor variable on tissue energetics. Error bars show 95% confidence intervals, and n.s. indicates non-significant values.

6.5 Discussion

Reef-building corals are purportedly extremely vulnerable to the persistent and accumulative stress of global climate change due to the combined effects of increasing temperature and ocean acidification (e.g., Hoegh-Guldberg et al. 2007). While there have been numerous studies that have demonstrated negative effects of both increasing temperature (Jokiel & Coles 1990) and ocean acidification (Leclerq et al. 2002) on corals, there is limited experimental tests of the synergistic effects of increasing temperature and pCO_2 enriched ocean acidification (but see Reynaud et al. 2003, Anthony et al. 2008, Edmunds et al. 2012). Our fully factorial experiment tested the effects of increasing temperature and elevated pCO_2 and it suggests that at least for *A muricata* and *A. hyacinthus*, temperature stress outside their adapted range (+2.5 °C above the long term summer maximum) will have the strongest negative affect on survivorship and calcification.

6.5.1 Temperature and pCO_2 effects on calcification

This study displayed temperature-enhanced calcification trends as previously observed for other coral species (e.g., Clausen & Roth 1975, Marshall & Clode 2004, Reynaud et al. 2007, Cooper et al. 2008). Calcification of *A. muricata* increased by 57 % from 26 °C to 31 °C prior to any observed bleaching during the prestress (week 0-week 5) temperature ramping period at present day pCO_2 concentrations. Reynaud et al. (2007) observed a 5.7 fold increase in the calcification rate of *Acropora* sp. during a four-week study with an 8 °C (21-29 °C) increase in temperature. *A. hyacinthus* was more sensitive to elevated temperature during the experiment compared to *A. muricata*; calcification rates doubled at present day pCO_2 in the 26 °C to 28.5 °C during the pre-stress period, but calcification rates were not enhanced in the highest temperature treatment (31 °C) compared to the control. Similarly, model averaging demonstrated that for *A. hyacinthus*, the high temperature treatment had a negative impact on calcification. Conversely, for *A. muricata*, the high

temperature treatment had a positive impact on calcification. Indeed, the thermal sensitivity of *A. hyacinthus* has been well documented in field observations (Marshall & Baird 2000).

Short-term exposure to ocean acidification conditions (including three weeks ramping and two weeks at targets values) at the long-term summer maximum temperature (28.5 °C) displayed similar calcification rates regardless of pCO_2 for *A. muricata*. Therefore, the increase in thermodynamic activity, at least over short term, may be able to alleviate the effects of ocean acidification (McCulloch et al 2012). This phenomenon may be corroborated by the coral incubations at week 5, where the coral fragments in 28.5 °C and end of century pCO_2 treatment had significantly greater photosynthetic and dark calcification rates compared to the other treatments. However, a short-term study may underestimate the true impacts of future ocean acidification conditions. For *A. muricata,* longer exposure (until week 12) to both mid and end of century pCO_2 levels at 28.5 °C lead to a 50 % reduction in calcification compared to the pre-stress period. Within the high stress treatment that suffered bleaching at 31 °C combined with end of century pCO_2 concentrations, at the end of the experiment there were a few coral fragments (50 %) that maintained high rates of photosynthesis and calcification, which suggests that there potential for some tolerant individuals to persist under future climate change scenarios.

At the end of the experiment, calcification rates were negatively impacted by both mid and end of century ocean acidification treatments. Declines in calcification due to ocean acidification (reduced pH, high pCO_2 and low CO_3) have been reported in other *Acropora* species (Marubini et al. 2003, Schneider & Erez 2006, Anthony et al. 2008, Albright et al. 2010, Chauvin et al. 2011). In a short-term experiment (8 days) coral nubbins of *A. verwayi* had 18 % lower calcium carbonate deposition at pH 7.76 (~860 µatm) compared to pH 8.06 (~410 µatm) (Marubini et al. 2003). Similar to other studies (Reynaud et al. 2003, Kroeker et al. 2013), in the present experiment, both *A. muricata and A. hyacinthus* displayed enhanced sensitivity to acidification when exposed to elevated seawater temperatures. Light

calcification rates in 31 °C temperature and end of century pCO_2 treatment at week five for both species were negative during the coral incubations, which demonstrates that calcification may have halted for some coral fragments in this high stress treatment. This physiological impairment may be due to temperature stress, which causes a breakdown to the photosystem of the *Symbiodinium* and leads to reductions in energy, in addition to ocean acidification, which stresses the site of calcification (Cohen & Holcomb 2009, Tambutte et al. 2011).

6.5.2 Climate change effects on coral health

Symbiodinium sp. can provide up to 95 % of the energy required to meet daily metabolic requirements (Muscatine et al. 1981, Grottoli et al. 2006). Lower survivorship in the 31 °C high temperature stress treatment was likely due to decreased photosynthesis and increased respiration (Figure 6.7a,c) of the coral fragments. *Symbiodinium* photosynthesis had been shown to decrease above 30 °C (Iglesias-Prieto et al. 1992), leading to less energy available for growth and maintenance. Greater respiration rates suggest an increase in metabolic activity that will deplete energy stores.

Rates of photosynthesis were enhanced under mid and end-of century pCO_2 treatments. This may have occurred due to the increase in dissolved inorganic carbon for the symbiotic zooxanthellae; other studies have found increased photosynthetic activity under high pCO_2 (Langdon & Atkinson 2005, plants reviewed by Ainsworth & Long 2005). However, observable paling of the coral pigment and reductions in chlorophyll *a*, which are symptomatic of coral bleaching, clearly demonstrate that corals suffer from temperature stress +2.5 °C above the long-term summertime maximum (31° C). However, the photosynthetic and light calcification rates of *A. muricata* at the end of the experiment in the 31° C/end of century pCO_2 treatment (n=4) were 37-61 % greater than the controls, respectively, despite the temperature stress. McCulloch et al. (2012) suggests that the

enhanced kinetics associated with increasing temperature may counter the effects of ocean acidification, which may have been the case for the surviving *A. muricata* in the high stress treatment (31° C/934 ± 11 µatm).

Protein and lipid concentration are key indicators of tissue energetics and a metabolic source of stored energy reserves within a coral (Rodrigues & Grottoli 2007). Corals with a surplus energy budget will contain higher levels of stored energy in the form of lipid and protein (Stimson 1987, Grottoli et al. 2004, Rodrigues & Grottoli 2007). Temperature ramping (28.5 and 31° C) for both species at week 5 negatively correlated with lipid concentrations compared to the controls likely due to increased metabolic demands at higher temperatures, which is typical in ectotherms (Deutsch et al. 2008). As corals start to bleach and the photosynthetic symbiotic relationship breaks down, they must rely on an alternative source of energy to meet daily cellular metabolic demands. If heterotrophic feeding is insufficient, corals will metabolize their stored lipid reserves as an energy source to survive (Porter et al. 1989, Grottoli et al 2004, Rodrigues & Grottoli 2007). Lipid levels declined by 50 % after two weeks of temperature stress associated with the 1982-83 El Nino in *Pocillopora damicornis* (Glynn et al. 1985). However, reductions to coral energy stores are not always observed. For example, colonies of *Montastraea franksi* showed no reductions in glycerol, protein and tissue biomass when bleached (Edmunds et al. 2003). Nonetheless, the authors noted that collection occurred only four weeks post bleaching, and the physiological consequence of bleaching may develop slowly in these colonies and may not coincide with the visible discolouration of bleaching (Edmunds et al. 2003).

Protein concentration was positively associated with increases in pCO_2 for both species at week 5. However, by the end of the experiment, *A. hyacinthus* protein concentrations were negatively impacted by pCO_2. An increase in protein concentrations at reduced pH levels of 7.19 (compared to 8.09 and 7.49) was observed in *Stylophora pistillata* after a 14-month exposure (Krief et al. 2012). This increase in protein was potentially an

increase to protect from corrosive seawater (Rodolfo-Metalpa et al. 2011). Krief et al. (2012) also found increased chlorophyll concentration per cell at reduced pH levels, but zooxanthellae density and skeletal growth were significantly reduced at pH 7.19 compared to 8.09. Thus, they suggest the potential for coral acclimation in a high CO_2 environment (Krief et al. 2012), but ocean acidification and ocean warming are unlikely to occur independently. The present study reveals that temperature stress and ocean acidification will synergistically cause a negative impact to coral physiology and growth in two common branching corals.

The coral fragments that tolerated the severe temperature stress (31 °C treatment) likely had physiological traits that allowed survival. The surviving corals may have contained greater tissue biomass and energetic reserves prior to temperature stress (Thornhill et al. 2011), which allowed them to survive. At the end of the experiment, model average regression coefficients of *A. muricata* lipids in the 31 °C treatment were not significantly different (but displayed a positive directionality) to the control despite suffering a +2.5 °C thermal stress event. This may suggest that these corals contained a surplus of lipids prior to bleaching, which provided a high-energy reserve for coral maintenance and survival during and after thermal stress. Another explanation for the temperature stress survivors may be that the corals were composed of the thermo-tolerant *Symbiodinium* clade D, which would allow them to survive the thermal stress, despite being not as productive (Cantin et al. 2009). However, the corals in the high temperature stress treatment were visibly bleached and contained less *Symbiodinium* (reduced Chl*a* abundance), suggesting that these coral fragments survived because they were able to maintain higher tissue biomass parameters of lipid and protein during the stress event as opposed to thermal tolerance.

Experimental duration is critical in assessing the effects of climate change scenarios on corals. Short-term experiments may not capture the ability of corals to acclimate to

acidification conditions. For example, the cold water coral *Lophelia pertusa* showed reduced calcification by 26-29 % for a pH decrease of 0.1 units over a one-week exposure to high CO_2 (Form & Reibesell 2012). However, after six months exposure, these corals displayed slightly enhanced calcification rates suggesting an ability to acclimate (Form & Reibesell 2012). In the present experiment, longer exposure (up to twelve weeks) to mid and end of century pCO_2 at the average long-term summer maximum temperature (28.5 ° C) showed reductions in calcification compared to the short term calcification rates (taken at five weeks). However, measuring net calcification from buoyant weight does not reveal whether corals are decreasing their rates of calcification or if the skeletons are in a state of dissolution. Further work needs to be done to investigate the saturation state when coral skeletons are in a state of dissolution and the consequence of long-term exposure of acidification to the skeletal structures.

This study also highlights a differential response in two Acroporid corals to experimental manipulation. *A. hyacinthus* survivorship in the controls was 30-50 % whereas for *A. muricata* survivorship was 70 % after 12 weeks. *A. hyacinthus* have plate morphologies that collect nutrients as water pushes up through the branches and it is unlikely that the single circulating motor at the back of each tank was able to create the currents needed for this species. As well, the fragmenting process of breaking the plate often causing skeletal exposure on three sides may have caused too much damage for the tissue to recover before experimental manipulation *A. hyacinthus* may also be more sensitive to changes in carbonate chemistry, for example only 2 coral fragments survived the 26° C/end of century pCO_2 treatment, compared to 18 *A. muricata*. Therefore, this difference may highlight the inherent variability of each species to different temperature and ocean acidification threshold as a result of exposure and adaptation. Moreover, the differential response may be due to other factors such as genetics that could be determining the stress tolerance of corals (Yin et al. 2016). Future work should look at integrating multiple factors

such as genetics, physiology, and the role of *Symbiodinium* type in survival of both *A. hyacinthus* and *A. muricata.*

In conclusion, this study assessed the combined responses of two dominant Indo-Pacific corals to ocean acidification and increasing temperature. Temperature stress led to marked reductions in survivorship and calcification of both *A. muricata* and *A. hyacinthus*. With predicted increases in SST for tropical oceans by 1.8 – 6.0 ° C at the end of the century (IPCC 2013), corals will likely experience chronic thermal stress, diminishing their ability for growth and maintenance. It is predicted that annual bleaching events may be occurring on reefs by 2030-2050 (Donner et al. 2005), and branching *Acropora* are particularly sensitive to thermal stress (Marshall & Baird 2000). Moreover, coral reefs are continuously affected by other disturbances (De'ath et al. 2012), limiting the opportunity for coral recovery. Temperature stress will occur synergistically with changing carbonate chemistry, and these coupled effects may be exacerbated when combined (Kroeker et al. 2013, Harvey et al. 2013). However, this study found there is potential for some corals to survive these stressful conditions and be more resilient with climate change. But without adaptation or acclimation of the majority of the population to thermal stress, declines in the growth and survivorship of two dominant fast-growing corals, *A. muricata* and *A. hyacinthus*, will have a profound effect on future reef growth and complexity.

Chapter 7 General Discussion

There has been extensive research on coral growth (e.g., Buddemeier & Kinzie 1976, Glynn 1977, Lough & Barnes 2000, Dullo 2005, Foster et al. 2014), initially focussed on links between coral growth and reef accretion (Darwin 1874), but more recently motivated by apparent affects of climate change on coral growth (e.g., De'ath et al. 2009, Cantin et al. 2010, Manzello et al. 2010). However, most of this research has focussed on massive and robust coral species (e.g., *Porites* sp., Cooper et al. 2008, De'ath et al. 2009, Cantin et al. 2010, Tanzil et al. 2013, Cantin & Lough 2014) largely owing to the relative ease with which to reconstruct the growth history of such corals (Barnes & Lough 1989). For example, Cantin & Lough (2014) found a 13-18 % decline in calcification of massive *Porites* on two inshore reefs of the Great Barrier Reef as a result of the 1998-bleaching event, which led to suppressed growth for up to four years. For branching corals, there are a plethora of data from short-term and direct measurements of growth rates (e.g., *Acropora*: Shinn 1966, Gladfelter et al. 1978, Oliver et al. 1983, Suresh & Mathew 1995, Brown 2012), but very limited insight as to whether such corals are growing more slowly as a consequence of increasing ocean warming and/or ocean acidification (but see Bak et al. 2009 & Anderson et al. 2015 – Chapter 3).

Declines in growth rates of corals will have potentially severe consequences for coral reef ecosystems. In the first instance, change is growth may have limited apparent effects on coral cover or abundance of corals, but it is clear that any declines in key demographic rates will undermine resilience to ever-increasing disturbances (e.g., Gilmour et al. 2013). Notably, growth rates are fundamental in determining rates of recovery (specifically, increases in abundance, cover and size structure of coral populations) following major disturbances that cause extensive coral loss (Gilmour et al. 2013). Moreover, declines in coral growth will likely lead to declines in abundance of very large colonies, which make disproportionate contribution to reproduction and population

replenishment (Wood 1998). Also, declines in rates of coral growth, and corresponding declines in abundance of very large colonies, are likely to lead to reduced structural complexity, which has been linked with declines in fish biodiversity and abundance (Jones et al. 2004, Graham et al. 2015) that directly undermine the fisheries productivity and economic value of reef ecosystems.

Up until the research presented in this thesis, temporal declines in growth rates of branching corals had been reported only in the Caribbean and Eastern Pacific Panama (Bak et al. 2009, Manzello 2010). In the Caribbean, linear extension rates of *Acropora palmata* declined by 0.23-0.35 % yr^{-1} from 1971/73 to 2002/04 (Bak et al. 2009). Similarly, in Pacific Panama, linear extension of *Pocillopora damicornis* declined by 0.9 % yr^{-1} from 1974 to 2006 (Manzello 2010). In this study, we showed that contemporary growth rates of branching corals (specifically *Acropora* and *Pocillopora* spp.) on the east coast of Australia were significantly lower than had been reported 15-30 years previously (Chapter 3 & 4). At Lord Howe Island, a subtropical location off Australia's eastern coast, linear extension rates of *Acropora yongei* and *Pocillopora damicornis* declined by >30 % from 1994/95 to 2010/11 (Anderson et al. 2015 - Chapter 3). At Davies Reef, average annual linear extension of *A. muricata* significantly decreased by 5 % at 5 m, 54 % at 10 m, and 58 % at 15 m from 1980/82 to 2012/14 (Chapter 4).

The mechanistic basis of apparent temporal declines in growth rates of massive and branching corals is generally unclear, but variously attributed to increasing temperature and/ or ocean acidification (De'ath et al. 2009, Cantin et al. 2010, Tanzil et al. 2013). In the Caribbean, declines in growth rates of *A. palmata* were attributed to declines in carbonate saturation state (Bak et al. 2009) that can impede calcification, as it becomes more energetically costly to form a calcium carbonate skeleton (Cohen & McConnaughey 2003). This process is due to corals upregulating the saturation state at the internal site of calcification to precipitate a coral skeleton (Venn et al. 2011). In ambient seawater, the

saturation state at the site of calcification can be 5-fold higher than that of the surrounding waters (Cohen et al. 2009). As corals acquire the carbonate minerals from the surrounding seawater, reductions in the calcium carbonate concentrations translate into greater energy expenditure for the corals to increase the internal saturation state for calcification to take place (Cohen et al. 2009). Moreover, ocean acidification decreases the available carbonate but corals can acquire the abundant bicarbonate ion (HCO_3^-) for calcification (Jokiel 2013) but it is a more energetically costly process to split the hydrogen ion. *In situ* measurements of the carbonate chemistry at Lizard Island, Davies Reef and Heron Island on the GBR (Great Barrier Reef) reveal that these reefs are supersaturated with respect to aragonite; Saturation states quantified had a daily mean saturation state (Ω_{arag}) of 3.7 at Davies Reef (Albright et al. 2013) to 3.3 at both Lizard Island (Chapter 5) and Heron Island (Albright et al. 2015). Because of similar mean saturation states, it is unlikely that carbonate chemistry is currently limiting growth rates along the Great Barrier Reef.

Increasing temperatures (linked to climate change) are the most likely explanation for apparent declines in coral growth and calcification (Chapter 6), due to either suppressed growth after periods of bleaching (Cantin & Lough 2014) or sustained declines in rates of calcification at higher temperatures (Marshall & Clode 2004, Pratchett et al. 2015 – Chapter 2). Coral bleaching may result when sea surface temperatures are 1 °C above the thermal maximum for an extended period, which is often associated with the long-term summertime temperature (Jokiel & Coles 1990). Coral bleaching results from the breakdown of the symbiotic relationship between the zooxanthellae and coral host (Baker et al. 2008). The zooxanthellae provide a disproportionate contribution to the energy budget of the coral host through photosynthesis (Edmunds & Davies 1986). When the zooxanthellae become stressed, the photosystem breaks down and the corals can no longer supply energy (Hoegh-Guldberg 1999). As a result, severe bleaching and long-term, persistent environmental stress results in coral mortality (Hough-Guldberg 2011). However, even if the corals don't visibly

bleach, there are likely to be sublethal effects, such as declines in growth. At Lord Howe Island, declines in growth of *A. yongei* and *P. damicornis* were quantified the year following a major bleaching event (Anderson et al. 2015 - Chapter 3). Bleaching events can lead to suppression of growth rates up to 4 years post bleaching, at least in massive *Porites* (Cantin & Lough 2014). But is seems branching species (such as *Acropora*) are more sensitive to thermal stress than massive species such as *Porites* (Marshall & Baird 2000). The differential loss of coral species from bleaching events may have a disproportionate affect on the coral reef ecosystem through alterations in fish species abundance (Pratchett et al. 2008) or coral community dominance (Pratchett et al. 2011).

Besides climate change, there may be other pervasive effects limiting coral growth such as declines in water quality (turbidity, sedimentation) (Carricart-Ganivet et al. 2000, Crabbe & Smith 2005), shuffling of zooxanthellae symbionts (Cantin et al. 2009), and competition with space competitors such as macroalgae (Crabbe 2010). For example, Crabbe & Smith (2005) found growth rates of *Porites lutea* to be 3.8 fold greater at a site with low turbidity and human activity (1.53 cm yr^{-1} ± 0.48) (mean ± SD) compared to a high turbid and human activity site (0.40 cm yr^{-1} ± 0.13). Moreover, the acquisition of the thermo-tolerant clade D of zooxanthellae had been shown to reduce growth rates of host corals (Cantin et al. 2009). In addition, competition of *Acropora cervicornis* with *Dictyota* species of macroalgae led to growth rates 38 % lower at sites where the colonies came into contact with the macroalgae (8.75 cm yr^{-1}) compared to sites with no competition (12.7 cm yr^{-1}). There may be a greater abundance of macroalgal-coral competitions in the future due to reductions in herbivorous fish as a result of increasing fishing pressures (Hughes 1994, Pandolfi et al. 2003). Therefore, direct effects of climate change on corals growth are likely to be increasingly compounded by other local stressors.

Given the scarcity of studies that have directly tested for temporal changes in the growth of branching corals at time scales (years to decades) relevant to assessing the

potential impact of global climate change, we have compiled extensive meta-data on growth rates of well-studied coral species *Acropora muricata* and *Pocillopora damicornis* (see Chapter 5) to test for evidence of long-term declines in reported growth rates, as might be expected based on results from Bak et al (2009), Manzello (2010) and Anderson et al. (2015) – Chapter 3. However, the data was compiled from a range of locations and we do not know to what extent variation in local environment conditions (e.g., temperature (Lough & Barnes 2000), turbidity (Crabbe & Smith 2005)) may be controlling growth rates for these species (reviewed in Pratchett et al. 2015 - Chapter 2). However, data points were all taken from the control sites and therefore can assume optimal growth in the local environment. Moreover, studies utilised to assess changes in linear extension were restricted to those from tropical locations (latitude $<26^{o}$ North or South), as growth rates can be limited in subtropical locations during colder winter months (Crossland 1984), and the IndoPacific to rule out any major geographic variation in environmental regimes. Having compiled data from 24 locations on *Acropora muricata* and *Pocillopora damicornis* in addition to this thesis, a linear regression was used to investigate the relationship of the fixed effect, linear extension, on the random effect, year of study, for both species. The linear regression of *P. damicornis* required a square root transformation to normalise the residuals.

Linear extension rates vary significantly with year of study when aggregating across all studies that have quantified growth rates for *A. muricata* (lm $F_{1/20}$=8.356, p=0.009, R^2=0.29), but not for *P. damicornis* (lm, $F_{1/12}$=1.47, p=0.249, R^2=0.11) (Figure 7.1a). There is however, a significant trend (decline) in published growth rates for *P. damicornis* (lm, $F_{1/5}$=50.7, p=0.0082, R^2=0.92) when constraining the dataset to only those studies conducted on Australia's GBR. Here, mean linear extension of *P. damicornis* was 4.2 cm (± 0.3SE) in the early 1980's and decreased by 40 % to 2.5 cm ± 0.07 in 2013-2014 (3 reefs, Chapter 5)(Figure 7.1b).

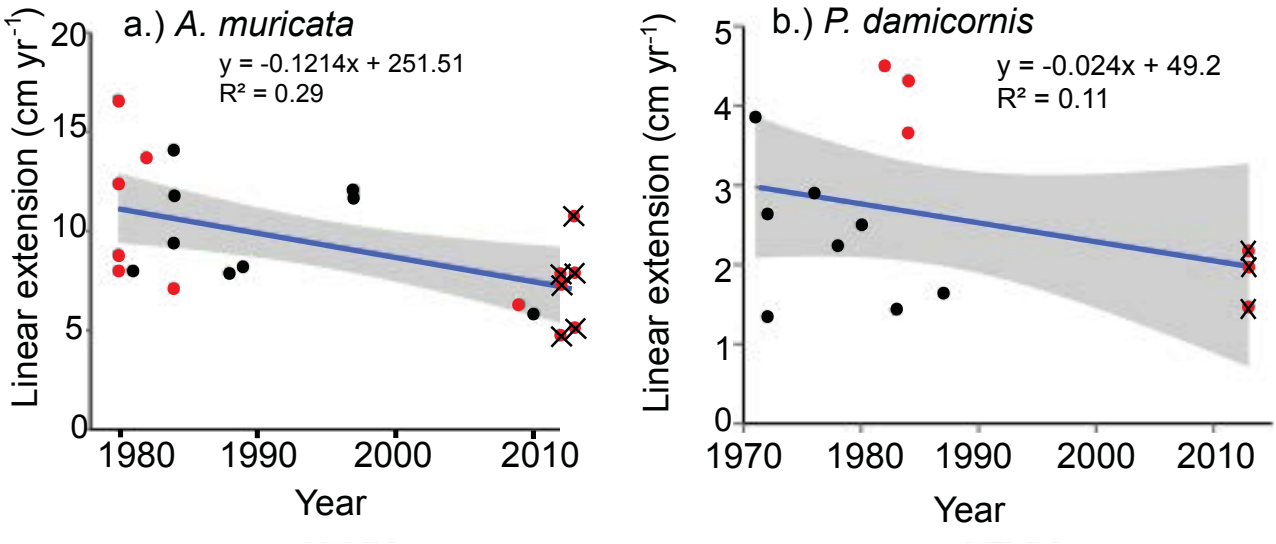

Figure 7.1. Linear extension (cm yr^{-1}) of a.) *A. muricata* and b.) *P. damicornis* against year of study with data points utilised from meta-analysis in Chapter 4. Data points with X through them represent values from this thesis. Red dots represent studies on the Great Barrier Reef.

Extrapolation of absolute declines in the growth rates of branching corals (e.g., 1.2 cm per decade for *A. muricata*; Figure 7.1a) would suggest that coral growth may cease by ~2070 (*sensu* Cantin et al. 2010). However, sustained declines in coral growth rates are unlikely as the future frequency and intensity of disturbances are predicted to accelerate with climate change (IPCC 2013). At least on the GBR, we have seen a preponderance of more frequent and intense degree heating weeks, a measure of accumulative thermal stress, in the last two decades (see Chapter 5). Without global mitigation schemes to keep global warming to a minimum, the frequency and intensity of bleaching events are likely to get worse which would have disastrous consequences for those thermal sensitive corals. Moreover, we are only beginning to understand the extent to which corals may be able to adapt to environmental change (Putnam & Gates 2015). An increase in thermo tolerance of 0.2 - 1.0 °C per decade was determined to allow persistence of coral reefs with modelled predicted increases in bleaching events based on IPCC predictions (Donner et al. 2005).

Current growth rates of dominant corals on the Great Barrier Reef showed that calcification is strongly correlated with SST (Chapter 5). Similar to massive *Porites* (Lough & Barnes 2000), calcification increased with higher annual average SST at lower latitudes. Despite 1,187 km of spatial separation on the GBR, other environmental variables that are known to contribute to spatial variation in reef growth such as light irradiance and aragonite saturation (Kleypas et al. 1999a) were similar among the reefs (Chapter 5). Therefore, variations in SST are likely to be the dominant environmental variable to control branching coral growth on the GBR, similar to massive species. However, the relationship of coral growth to SST is not linear, and past the thermal optimum we are likely to see declines in coral growth (Marshall & Clode 2004), especially when extrapolating to temperatures projected to occur due to climate change (Chapter 6).

The importance of sea surface temperature was demonstrated when assessing the response of branching corals *A. muricata* and *A. hyacinthus* to future climate change

scenarios (Chapter 6). For both species, we observed temperature-enhanced calcification for the first five weeks of temperature ramping. After twelve weeks exposure, survivorship and calcification were markedly affected by high temperature stress of +2.5 °C above the long-term average summer maximum. The projected increases to mid and end of century pCO_2 levels led to a 50 % reduction in calcification with longer exposure across all temperature treatments. The synergistic effects of temperature and ocean acidification led to further declines in survivorship and calcification of *Acropora*, predominantly when subjected to end of century pCO_2 (934 ± 11 µatm) (Chapter 6).

The effects of increasing temperature are generally exacerbated when combined with ocean acidification for a range of marine taxa (Kroeker et al. 2010). For the hard coral *Stylophora pistillata,* Reynaud et al. (2003) observed it to be insensitive to a doubled pCO_2 at 25 °C but experienced a 50 % reduction in calcification at 28 °C. The effects of climate change are unlikely to occur independently and more studies are needed to assess the responses of corals to both temperature and ocean acidification. The 60 % increase in pCO_2 from present day (410 µatm ± 4) to mid century predictions (653 µatm ± 6) led to similar survivorship in the absence of heat stress (26 °C and 28.5 °C) (Chapter 6) suggesting corals will be able to cope with a declining saturation state. McCulloch et al. (2012) suggest that the increase in kinetics associated with increasing temperature will be able to alleviate the effects of climate change, as corals internally upregulate the site of calcification (Cohen & Holcomb 2009). Therefore, it seems future temperature stress is the greatest threat to the survival and persistence of coral reefs, at least in the short term, and will affect the survival and calcification of *Acropora muricata* and *Acropora hyacinthus* without adaptation or acclimation.

7.1 Future directions

There is increasing recognition of the need for direct and comparable measurements of coral growth (Pratchett al. 2015 – Chapter 2), especially for branching corals that lack a historic record of growth in their skeleton (Roch et al. 2010). While recent studies (e.g., Bak et al. 2009, Manzello 2010, Anderson et al. 2015 - Chapter 3) indicate that there are sustained declines in the growth rates of branching corals, consistent with the emerging affects of global climate change (Chapter 6), it is unclear to what extent these results are driven by chronic or acute changes in seawater temperature, changes in carbonate chemistry, and/or chronic changes in environmental conditions that are independent of global climate change. To resolve this, we need more studies of temporal changes in the growth rates of branching corals across a wide range of different locations and environmental settings. Continual assessment of inter-annual variation in growth rates across a large spatial scale will be necessary to separate out the effects of temperature anomalies versus the localised changes in baseline conditions.

Climate change will invoke simultaneous changes in a number of different environmental parameters (e.g., temperature, seawater chemistry, current speed, salinity and light penetration; IPCC 2013) and we are only just beginning to understand the complex relationships among these parameters, e.g., how within-reef carbonate chemistry varies with other environmental conditions (Albright et al. 2013, 2015). However, *in situ* exposure of corals to high CO_2 at carbon seeps has shown to reduce the abundance and physical performance of sensitive species, such as branching corals (Fabricius et al. 2011). Therefore, it is likely that both ocean acidification and sustained increases in baseline temperatures, as well as increasing frequency of extreme temperature anomalies, represent the greatest threat to coral growth and abundance.

In conclusion, this thesis demonstrates that increasing temperature is the foremost threat to reef-building corals from sustained and ongoing climate change, and likely to lead to ongoing reductions in coral growth across a wide range of locations and habitats in the near future. Despite apparent and projected declines in aragonite saturation, it seems corals have the ability to continue calcification to some degree, albeit at a reduced rate, whereas, thermal stress led to reduced survivorship and ceased calcification (Chapter 6). However, ocean acidification is clearly compounding effects of increasing temperature (Reynaud et al. 2003, Chapter 6) and it is unclear the stress involved in maintaining growth in acidified condition but this will become increasingly important in the future. There is however, increasing evidence that corals vary greatly in their susceptibility to increasing temperature and ocean acidification (Edmunds et al. 2012, Chan & Connelly 2013), necessitating further work on a much wider range of different corals, in different geographical setting, and in different habitats to better understand the vulnerability/ resilience of corals to ongoing changes in environmental conditions.

References

Adjeroud, M., Augustin, D., Galzin, R. & Salvat, B. 2002. Natural disturbances and interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia): 1991 to 1997. *Marine Ecology Progress Series* **237**, 121-131.

Ainsworth, E.A. & Long, S.P. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytology* **165**:351-371.

Albright, R., Benthuysen, J., Cantin, N., Caldeira, K. & Anthony, K. 2015. Coral reef metabolism and carbon chemistry dynamics of a coral reef flat. *Geophysical Research Letters* **42**:doi:10.1002/ 2015GL063488.

Albright R., Caldeira L., Hosfelt J., Kwiatkowski L., Maclaren J.K., Mason B.M., Nebuchina Y., Ninokawa A., Pongratz J., Ricke K.L., Rivlin T., Schneider K., Sesboüé M., Shamberger K., Silverman J., Wolfe K., Zhu K., Caldeira K. (2016) Reversal of ocean acidification enhances net coral reef calcification. *Nature* 531:362-365

Albright, R., Langdon, C. & Anthony, K.R.N. 2013. Dynamics of seawater carbonate chemistry, production, and calcification of a coral reef flat, central Great Barrier Reef. *Biogeosciences* **10**:6747-6758.

Albright, R., Mason, B. & Langdon, C. 2008. Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. *Coral Reefs* **27**, 485-490.

Albright, R., Mason, B., Miller, M. & Langdon, C. 2010. Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. *Proceedings of the National Academy of Sciences of the United States of America* **107**:20400-20404.

Al-Hammady, M.A.M. 2013. The effect of zooxanthellae availability on the rates of skeletal growth in the Red Sea coral *Acropora hemprichii*. *The Egyptian Journal of Aquatic Research* **39**, 177-183.

Al-Horani, F.A., Tambutté, É. & Allemand, D. 2007. Dark calcification and the daily rhythm of calcification in the scleractinian coral, *Galaxea fascicularis*. *Coral Reefs* **26**, 531-538.

Alibert, C. & McCulloch, M.T. 1997. Strontium/calcium ratios in modern *Porites* corals from the Great Barrier Reef as a proxy for sea surface temperature: Calibration of the thermometer and monitoring of ENSO. *Paleoceanography* **12**, 345-363.

Allemand, D., Tambutté, E., Zoccola, D. & Tambutté, S. 2011. Coral calcification, cells to reefs. In *Coral Reefs: An Ecosystem in Transition*, Z. Dubinsky & N. Stambler (eds). Amsterdam, The Netherlands: Springer, 119-150.

Aller, R.C. & Dodge, R.E. 1974. Animal-sediment relations in a tropical lagoon: Discovery Bay, Jamaica. *Journal of Marine Research* **32**, 209-232.

Allison, N., Tudhope, A.W. & Fallick, A.E. 1996. Factors influencing the stable carbon and oxygen isotopic composition of *Porites lutea* coral skeletons from Phuket, South Thailand. *Coral Reefs* **15**, 43-57.

Al-Rousan, S., Al-Moghrabi, S., Patzold, J. & Wefer, G. 2002. Environmental and biological effects on the stable oxygen isotope records of corals in the northern Gulf of Aqaba, Red Sea. *Marine Ecology Progress Series* **239**, 301-310.

Al-Rousan, S. & Felis, T. 2013. Long-term variability in the stable carbon isotopic composition of *Porites* corals at the northern Gulf of Aqaba, Red Sea.

Palaeogeography, Palaeoclimatology, Palaeoecology **381**, 1-14.
Alvarez-Filip, L., Dulvy, N.K., Côté, I.M., Watkinson, A.R. & Gill, J.A. 2011. Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications* **21**, 2223-2231.
Anderson, K. Heron, S.F. & Pratchett, M.S. 2015. Species-specific declines in the linear extension of branching corals at a sub-tropical reef, Lord Howe Island. *Coral Reefs* **34**:479-490.
Anderson, K., Pratchett, M.S. & Baird, A.H. 2012. Summer growth rates of corals at Lord Howe Island, Australia. *Proceedings of the Twelfth International Coral Reef Symposium* **4C**, 1-5.
Andersson, A.J., Mackenzie, F.T. & Bates, N.R. 2008. Life on the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers. *Marine Ecology Progress Series* **373**, 265-273.
Angilletta, M.J. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. New York, USA: Oxford University Press.
Anthony, K.R.N. 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* **19**, 59-67.
Anthony, K.R.N, Diaz-Pulido, G., Verlinden, N., Tilbrook, B. & Andersson, A.J. 2013. Benthic buffers and boosters of ocean acidification on coral reefs. *Biogeosciences* **10**:4897-4909.
Anthony, K.R.N. & Fabricius, K.E. 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology* **252**, 221-253.
Anthony, K.R.N., Hoogenboom, M.O. & Connolly, S.R. 2005. Adaptive variation in coral geometry and the optimization of internal colony light climates. *Functional Ecology* **19**, 17-26.
Anthony, K.R.N., Kline, D.I., Diaz-Pulido, G., Dove, S. & Hoegh-Guldberg, O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 17442-17446.
Anthony, K.R.N., Maynard, J.A., Diaz-Pulido, G., Mumby, P.J., Marshall, P.A., Cao, L. & Hoegh-Guldberg, O. 2011. Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* **17**, 1798-1808.
Antonov, J.I., Seidov, D., Boyer, T.P., Locarnini, R.A., Mishonov, A.V., Garcia, H.E., Baranova, O.K., Zweng, M.M. & Johnson, D.R. 2010. World Ocean Atlas: Salinity. In: *NOAA Atlas NESDIS 69*, Levitus S (ed). Washington, D.C: Government Printing Office.
Atkinson, M.J., Carlson, B. & Crow, G.L. 1995. Coral growth in high-nutrient, low-pH seawater: a case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs* **14**, 215-223.
Atkinson, M.J. & Grigg, R.W. 1984. Model of a coral reef ecosystem. II Gross and net benthic primary production at French Frigate Shoals, Hawaii. *Coral Reefs* **3**, 13-22.
Australian Institute of Marine Science (AIMS). 2014. Graph generated 3 April, 2014 using North Bay water temperatures Temperature logger and Data Centre, AIMS. Viewed 3rd April, 2014. http://data.aims.gov.au/aimsrtds/datatool.xhtml?site=1115&param=water%20temperature
Australian Institute of Marine Science (AIMS). 2015. Temperaure and light loggers data. Data sourced from AIMS Data Centre. http://www.aims.gov.au/docs/data/data.html.
Babcock, R.C. 1988. Age-structure, survivorship and fecundity in populations of massive corals. *Proceedings of the Sixth International Coral Reef Symposium* **2**, 625-633.
Babcock, R.C. 1991. Comparative demography of three species of scleractinian corals using

age-and size-dependent classifications. *Ecological Monographs* **61**, 225-244.
Babcock, R.C. & Mundy, C. 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *Journal of Experimental Marine Biology and Ecology* **206**, 179-201.
Baird, A.H., Guest, J.R. & Willis, B.L. 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* **40**, 551-571.
Baird, A.H. & Marshall, P.A. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* **237**, 133-141.
Bak, R.P.M. 1973. Coral weight increment in situ. A new method to determine coral growth. *Marine Biology* **20**, 45-49.
Bak, R.P.M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research* **10**, 285-337.
Bak, R.P.M. 1983. Neoplasia, regeneration and growth in the reef-building coral *Acropora palmata*. *Marine Biology* **77**, 221-227.
Bak, R.P.M. & Meesters, E.H. 1999. Population structure as a response of coral communities to global change. *American Zoologist* **39**, 56-65.
Bak, R.P.M., Nieuwland, G. & Meesters, E.H. 2009. Coral growth rates revisited after 31 years: what is causing lower extension rates in *Acropora palmata*? *Bulletin of Marine Science* **84**, 287-294.
Baker, A.C., Glynn, P.W. & Riegl, B. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* **80**, 435-471.
Baker, P.A. & Weber, J.N. 1975. Coral growth rate: variation with depth. *Physics of the Earth and Planetary Interiors* **10**, 135-139.
Barnes, D.J. 1970. Coral skeletons: an explanation of their growth and structure. *Science* **170**, 1305-1308.
Barnes, D.J. 1972. The structure and formation of growth-ridges in scleractinian coral skeletons. *Proceedings of the Royal Society of London Series B: Biological Sciences* **182**, 331-350.
Barnes, D.J. 1973. Growth in colonial scleractinians. *Bulletin of Marine Science* **23**, 280-298.
Barnes, D.J. 1983. Profiling coral reef productivity and calcification using pH and oxygen electrodes. *Journal of Experimental Marine Biology and Ecology* **66**:149-161.
Barnes, D.J. 1988. Seasonality in community productivity and calcification at Davies Reef, Central Great Barrier Reef. *Proceedings of the 6th International Coral Reef Symposium, Australia* **2**:521-527.
Barnes, D.J. & Chalker, B.E. 1990. Calcification and photosynthesis in reef-building corals and algae. In *Coral Reefs. Ecosystems of the World.*, Z. Dubinsky (ed.). Amsterdam, The Netherlands: Elsevier, 109-131.
Barnes, D.J. & Crossland, C.J. 1980. Diurnal and seasonal variations in the growth of a staghorn coral measured by time-lapse photography. *Limnology and Oceanography* **25**, 1113-1117.
Barnes, D.J. & Devereux, M.J. 1988. Variations in skeletal architecture associated with density banding in the hard coral *Porites*. *Journal of Experimental Marine Biology and Ecology* **121**, 37-54.
Barnes, D.J. & Lough, J.M. 1989. The nature of skeletal density banding in scleractinian corals: fine banding and seasonal patterns. *Journal of Experimental Marine Biology and Ecology* **126**, 119-134.

Barnes, D.J. & Lough, J.M. 1993. On the nature and causes of density banding in massive coral skeletons. *Journal of Experimental Marine Biology and Ecology* **167**, 91-108.

Barnes, D.J. & Lough, J.M. 1999. *Porites* growth characteristics in a changed environment: Misima Island, Papua New Guinea. *Coral Reefs* **18**, 213-218.

Barnes, D.J. & Taylor, D.L. 1973. In situ studies of calcification and photosynthetic carbon fixation in the coral *Montastrea annularis*. *Helgoländer wissenschaftliche Meeresuntersuchungen* **24**, 284-291.

Barry, C.K. 1965. *Ecological study of the decapod crustaceans commensal with the branching coral* Pocillopora meandrina *var.* nobilis *Verrill*. M.Sc. thesis, University of Hawaii, Honolulu, USA.

Bates, N.R. 2002. Seasonal variability of the effect of coral reefs on seawater CO_2 and air-sea CO_2 exchange. *Limnology and Oceanography* **47**, 43-52.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L. & Depczynski, M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* **12**, 1587-1594.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. 2004. Confronting the coral reef crisis. *Nature* **429**, 827-833.

Berkelmans, R., De'ath, G., Kininmonth, S., Skirving, W.J. 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. *Coral Reefs* **23**:74-83.

Berkelmans, R. & Oliver, J.K. 1999. Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs* **18**:55-60.

Berkelmans, R. & Van Oppen, M.J.H. 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London Series B: Biological Sciences* **273**, 2305-2312.

Berumen, M.L. & Pratchett, M.S. 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* **25**, 647-653.

Bessat, F. & Buigues, D. 2001. Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of ocean-atmosphere variability from south central Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* **175**, 381-392.

Birkeland, C. 1976. An experimental method of studying corals during early stages of growth. *Micronesica* **12**, 319-322.

Blanchon, P., Granados-Corea, M., Abbey, E., Braga, J.C., Braithwaite, C., Kennedy, D.M., Spencer, T., Webster, J.M. & Woodroffe, C.D. 2014. Postglacial Fringing-Reef to Barrier-Reef conversion on Tahiti links Darwin's reef types. *Scientific Reports* **4**, 4997.

Bode, M., Connolly, S.R. & Pandolfi, J.M. 2012. Species differences drive nonneutral structure in Pleistocene coral communities. *American Naturalist* **180**, 577-588.

Bongiorni, L., Shafir, S., Angel, D. & Rinkevich, B. 2003. Survival, growth and gonad development of two hermatypic corals subjected to in situ fish-farm nutrient enrichment. *Marine Ecology Progress Series* **253**, 137-144.

Bosscher, H. 1993. Computerized tomography and skeletal density of coral skeletons. *Coral Reefs* **12**, 97-103.

Bosscher, H. & Meesters, E.H. 1992. Depth related changes in the growth rate of *Montastrea annularis*. *Proceedings of the Seventh International Coral Reef Symposium* **1**, 507-512.

Boto, K. & Isdale, P.J. 1985. Fluorescent bands in massive corals result from terrestrial fulvic acid inputs to nearshore zone. *Nature* **315**, 396-397.

Boyer, T.P., Antonov, J.I., Baranova, O.K., Garcia, H.E., Johnson, D.R., Locarnini, R.A., Mishonov, A.V., O'Brien, T.D., Seidov, D., Smolyar, I.V. & Zweng, M.M. 2009. World Ocean Database. In: NOAA Atlas, Levitus S (ed). Washington, D. C: NESDIS. U.S. Gov. Pringing Office, pp216.

Brachert, T.C., Reuter, M., Kroeger, K.F. & Lough, J.M. 2006. Coral growth bands: A new and easy to use paleothermometer in paleoenvironment analysis and paleoceanography (late Miocene, Greece). *Paleoceanography* **21**, PA4217.

Brooke, S. & Young, C.M. 2009. In situ measurement of survival and growth of *Lophelia pertusa* in the northern Gulf of Mexico. *Marine Ecology Progress Series* **397**, 153-161.

Brown, B.E., Sya'Rani, L. & Le Tissier, M. 1985. Skeletal form and growth in *Acropora aspera* (Dana) from the Pulau Seribu, Indonesia. *Journal of Experimental Marine Biology and Ecology* **86**, 139-150.

Browne, N.K. 2012. Spatial and temporal variations in coral growth on an inshore turbid reef subjected to multiple disturbances. *Marine Environmental Research* **77**, 71-83.

Bruno, J.F. & Edmunds, P.J. 1997. Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. *Ecology* **78**, 2177-2190.

Bruno, J.F. & Selig, E.R. 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS ONE* **2**, e711.

Buddemeier, R.W. 1974. Environmental controls over annual and lunar monthly cycles in hermatypic coral calcification. *Proceedings of the Second International Coral Reef Symposium* **2**, 259-267.

Buddemeier, R.W. & Kinzie, R.A. III 1976. Coral growth. *Oceanography and Marine Biology: An Annual Review* **14**, 183-225.

Buddemeier, R.W., Maragos, J.E. & Knutson, D.W. 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. *Journal of Experimental Marine Biology and Ecology* **14**, 179-199.

Burgess, S.N., McCulloch, M.T., Mortimer, G.E. & Ward, T.M. 2009. Structure and growth rates of the high-latitude coral: *Plesiastrea versipora*. *Coral Reefs* **28**, 1005-1015.

Burnham, K. & Anderson, D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York: The University of Chicago Press.

Bythell, J.C., Gladfelter, E.H. & Bythell, M. 1993. Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* **12**, 143-152.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48**, 1079-1087.

Caldeira, K. & Wickett, M.E. 2003. Anthropogenic carbon and ocean pH. *Nature* **425**:365-365.

Caley, M.J. & St John, J. 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology*, 414-428.

Camoin, G.F., Seard, C., Deschamps, P., Webster, J.M., Abbey, E., Braga, J.C., Iryu, Y., Durand, N., Bard, E. & Hamelin, B. 2012. Reef response to sea-level and environmental changes during the last deglaciation: Integrated Ocean Drilling Program Expedition 310, Tahiti Sea Level. *Geology* **40**, 643-646.

Cantin, N.E., Cohen, A.L., Karnauskas, K.B., Tarrant, A.M. & McCorkle, D.C. 2010. Ocean warming slows coral growth in the central Red Sea. *Science* **329**, 322-325.

Cantin, N.E. & Lough, J.M. 2014. Surviving coral bleaching events: *Porites* growth anomalies on the Great Barrier Reef. *PLoS ONE* **9**, e88720.

Cantin, N., van Oppen, M., Willis, B., Mieog, J. & Negri, A. 2009. Juvenile corals can acquire more carbon from high-performance algal symbionts. *Coral Reefs* **28**:405-414.

Carilli, J.E., Donner, S.D. & Hartmann, A.C. 2012. Historical temperature variability affects coral response to heat stress. *PLoS ONE* **7**, e34418.

Carilli, J.E., Norris, R.D., Black, B.A., Walsh, S.M. & McField, M. 2009. Local stressors reduce coral resilience to bleaching. *PLoS ONE* **4**, e6324.

Carilli, J.E., Norris, R.D., Black, B.A., Walsh, S.M. & McField, M. 2010. Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Global Change Biology* **16**, 1247-1257.

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortés, J., Delbeek, J.C., DeVantier, L., Edgar, G.J., Edwards, A.J., Fenner, D., Guzmán, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J.E.N., Wallace, C., Weil, E. & Wood, E. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* **321**, 560-563.

Carricart-Ganivet, J.P. 2004. Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis*. *Journal of Experimental Marine Biology and Ecology* **302**, 249-260.

Carricart-Ganivet, J.P. & Barnes, D.J. 2007. Densitometry from digitized images of X-radiographs: Methodology for measurement of coral skeletal density. *Journal of Experimental Marine Biology and Ecology* **344**, 67-72.

Carricart-Ganivet, J.P., Beltrán-Torres, A.U., Merino, M. & Ruiz-Zárate, M.A. 2000. Skeletal extension, density and calcification rate of the reef building coral *Montastraea annularis* (Ellis and Solander) in the Mexican Caribbean. *Bulletin of Marine Science* **66**, 215-224.

Carricart-Ganivet, J.P., Cabanillas-Teran, N., Cruz-Ortega, I. & Blanchon, P. 2012. Sensitivity of calcification to thermal stress varies among genera of massive reef-building corals. *PLoS ONE* **7**, e32859.

Carricart-Ganivet, J.P. & Merino, M. 2001. Growth responses of the reef-building coral *Montastraea annularis* along a gradient of continental influence in the southern Gulf of Mexico. *Bulletin of Marine Science* **68**, 133-146.

Castillo, K.D., Ries, J.B. & Weiss, J.M. 2011. Declining coral skeletal extension for forereef colonies of *Siderastrea siderea* on the Mesoamerican Barrier Reef System, Southern Belize. *PLoS ONE* **6**, e14615.

Castillo, K.D., Ries, J.B., Weiss, J.M. & Lima, F.P. 2012. Decline of forereef corals in response to recent warming linked to history of thermal exposure. *Nature Climate Change* **2**, 756-760.

Chadwick-Furman, N.E., Goffredo, S. & Loya, Y. 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. *Journal of Experimental Marine Biology and Ecology* **249**, 199-218.

Chalker, B.E. & Barnes, D.J. 1990. Gamma densitometry for the measurement of skeletal density. *Coral Reefs* **9**, 11-23.

Chalker, B.E., Barnes, D.J. & Isdale, P.J. 1985. Calibration of X-ray densitometry for the measurement of coral skeletal density. *Coral Reefs* **4**, 95-100.

Chan, N.C.S. & Connolly, S.R. 2013. Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Global Change Biology* **19**, 282-290.

Chansang, H., Phongusuwan, N. & Boonyanate, P. 1992. Growth of corals under the effect of sedimentation along the northwest coast of Phuket, Thailand. *Proceedings of the Seventh International Coral Reef Symposium* **1**, 241-248.

Charuchinda, M. & Chansang, H. 1985. Skeleton extension and banding formation of

Porites lutea of fringing reefs along the south and west coasts of Phuket Island (Thailand). *Proceedings of the Fifth International Coral Reef Symposium* **6**, 83-87.
Charuchinda, M. & Hylleberg, J. 1984. Skeletal extension of *Acropora formosa* at a fringing reef in the Andaman Sea. *Coral Reefs* **3**, 215-219.
Chauvin, A., Denis, V. & Cuet, P. 2011. Is the response of coral calcification to seawater acidification related to nutrient loading? *Coral Reefs* **30**:911-923.
Chisholm, J.R.M. & Gattuso, J.-P. 1991. Validation of the alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities. *Limnology and Oceanography* **36**, 1232-1239.
Chornesky, E.A. & Peters, E.C. 1987. Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. *Biological Bulletin* **172**, 161-177.
Christensen, J.H., Kanikicharla, K.K., Marshall, G. & Turner, J. 2013. Climate phenomena and their relevance for future regional climate change. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T.F. Stocker et al. (eds). Cambridge, UK: Cambridge University Press, 1217-1308.
Clark, S. & Edwards, A.J. 1995. Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. *Coral Reefs* **14**, 201-213.
Clausen, C.D. & Roth, A.A. 1975. Effect of temperature and temperature adaptation on calcification rate in the hermatypic coral *Pocillopora damicornis*. *Marine Biology* **33**:93-100.
Cobb, K.M., Charles, C.D. & Hunter, D.E. 2001. A central tropical Pacific coral demonstrates Pacific, Indian, and Atlantic decadal climate connections. *Geophysical Research Letters* **28**, 2209-2212.
Cohen, A.L. & Holcomb, M. 2009. Why corals care about ocean acidification: Uncovering the mechanism. *Oceanography* **22**:118-127.
Cohen, A.L. & McConnaughey, T.A. 2003. Geochemical perspectives on coral mineralization. In: *Biomineralization*, Dove PM, DeYoreo JJ, Weiner S (eds), pp151-187.
Cohen, A.L., McCorkle, D.C., de Putron, S., Gaetani, G.A. & Rose, K.A. 2009 Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into the biomineralization response to ocean acidification. *Geochemistry, Geophysics, Geosystems* **10**:Q07005.
Coker, D.J., Pratchett, M.S. & Munday, P.L. 2009. Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology* **20**, 1204-1210.
Coker, D.J., Wilson, S.K. & Pratchett, M.S. 2014. Importance of live coral habitat for reef fishes. *Reviews in Fish Biology and Fisheries* **24**, 89-126.
Cole, A.J., Pratchett, M.S. & Jones, G.P. 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries* **9**, 286-307.
Comeau, S., Edmunds, P.J., Spindel, N.B. & Carpenter, R.C. 2013. The responses of eight coral reef calcifiers to increasing partial pressure of CO_2 do not exhibit a tipping point. *Limnology and Oceanography* **58**, 388-398.
Comeau, S., Edmunds, P.J., Spindel, N.B. & Carpenter, R.C. 2014. Fast coral reef calcifiers are more sensitive to ocean acidification in short-term laboratory incubations. *Limnology and Oceanography* **59**, 1081-1091.
Connell, J.H. 1973. Population ecology of reef-building corals. In *Biology and Geology of Coral Reefs*, O.A. Jones & R. Endean (eds). New York, USA: Academic Press, 247-268.
Connell, J.H., Hughes, T.P. & Wallace, C.C. 1997. A 30- year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecological*

Monographs **67**, 461-488.
Connell, J.H., Hughes, T.P., Wallace, C.C., Tanner, J.E., Harms, K.E. & Kerr, A.M. 2004. A long-term study of competition and diversity of corals. *Ecological Monographs* **74**, 179-210.
Cooper, T.F., De'ath, G., Fabricius, K.E. & Lough, J.M. 2008. Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology* **14**, 529-538.
Cooper, T.F., O'Leary, R.A. & Lough, J.M. 2012. Growth of Western Australian corals in the Anthropocene. *Science* **335**, 593-596.
Corrège, T., Gagan, M.K., Beck, J.W., Burr, G.S., Cabioch, G. & Le Cornec, F. 2004. Interdecadal variation in the extent of South Pacific tropical waters during the Younger Dryas event. *Nature* **428**, 927-929.
Couce, E., Ridgwell, A. & Hendy, E.J. 2012. Environmental controls on the global distribution of shallow-water coral reefs. *Journal of Biogeography* **39**:1508-1523.
Cox, E.F. 1986. The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. *Journal of Experimental Marine Biology and Ecology* **101**, 161-174.
Crabbe, M.J.C. 2009. Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. *Marine Environmental Research* **67**, 189-198.
Crabbe, M.J.C. 2010. Topography and spatial arrangement of reef-building corals on the fringing reefs of North Jamaica may influence their response to disturbance from bleaching. *Marine Environmental Research* **69**, 158-162.
Crabbe, M.J.C. 2013. Coral reef populations in the Caribbean: Is there a case for better protection against climate change? *American Journal of Climate Change* **2**, 97-105.
Crabbe, M.J.C. & Smith, D.J. 2005. Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. *Coral Reefs* **24**, 437-441.
Crabbe, M.J.C., Wilson, M.E.J. & Smith, D.J. 2006. Quaternary corals from reefs in the Wakatobi Marine National Park, SE Sulawesi, Indonesia, show similar growth rates to modern corals from the same area. *Journal of Quaternary Science* **21**, 803-809.
Crain, C.M., Kroeker, K. & Halpern, B.S. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* **11**, 1304-1315.
Crook, E.D., Cohen, A.L., Rebolledo-Vieyra, M., Hernandez, L. & Paytan, A. 2013. Reduced calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 11044-11049.
Crossland, C.J. 1981. Seasonal growth of *Acropora* cf. *formosa* and *Pocillopora damicornis* on a high latitude reef (Houtman Abrolhos, Western Australia). *Proceedings of the Fourth International Coral Reef Symposium* **1**, 663-667.
Crossland, C.J. 1984. Seasonal-variations in the rates of calcification and productivity in the coral *Acropora formosa* on a high-latitude reef. *Marine Ecology-Progress Series* **15**:135-140.
Cruz-Piñón, G., Carricart-Ganivet, J.P. & Espinoza-Avalos, J. 2003. Monthly skeletal extension rates of the hermatypic corals *Montastraea annularis* and *Montastraea faveolata*: biological and environmental controls. *Marine Biology* **143**, 491-500.
Custodio, H.M. III & Yap, H.T. 1997. Skeletal extension rates of *Porites cylindrica* and *Porites* (*Synaraea*) *rus* after transplantation to two depths. *Coral Reefs* **16**, 267-268.
Dana, J.D. 1890. *Corals and Coral Islands*. New York: Dodd, Mead and Company.
Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R. & Côté, I.M. 2012. Evaluating life-history strategies of reef corals from species traits. *Ecology Letters* **15**, 1378-1386.

Darwin, C. 1874. *The Structure and Distribution of Coral Reefs*. London: Smith, Elder & Co.

Dávalos-Dehullu, E., Hernández-Arana, H. & Carricart-Ganivet, J.P. 2008. On the causes of density banding in skeletons of corals of the genus *Montastraea*. *Journal of Experimental Marine Biology and Ecology* **365**, 142-147.

Davies, P.S. 1989. Short-term growth measurements of corals using an accurate buoyant weighing technique. *Marine Biology* **101**, 389-395.

De'ath, G., Fabricius, K.E. & Lough, J.M. 2013. Yes – coral calcification rates have decreased in the last twenty-five years! *Marine Geology* **346**, 400-402.

De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 17995-17999.

De'ath, G., Lough, J.M. & Fabricius, K.E. 2009. Declining coral calcification on the Great Barrier Reef. *Science* **323**, 116-119.

Dennison, W.C. & Barnes, D.J. 1988. Effect of water motion on coral photosynthesis and calcification. *Journal of Experimental Marine Biology and Ecology* **115**, 67-77.

Descombes, P., Wisz, M.S., Leprieur, F., Parravicini, V., Heine, C., Olsen, S.M., Swingedouw, D., Kulbicki, M., Mouillot, D. & Pellissier, L. 2015. Forecasted coral reef decline in marine biodiversity hotspots under climate change. *Global Change Biology*:DOI:10.1111/gcb.12868.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 6668-6672.

Diaz, M. & Madin, J. 2011. Macroecological relationships between coral species' traits and disease potential. *Coral Reefs* **30**, 73-84.

Dickson, A.G. & Millero, F.J. 1987. A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. *Deep-Sea Research* **34**:1733-1743.

Dickson, A.G., Sabine, C.L. & Christian, J.R. 2007. *Guide to Best Practices for Ocean CO2 Measurements*. Sidney, British Columbia: North Pacific Marine Science Organization. p.191.

Dikou, A. 2009. Skeletal linear extension rates of the foliose scleractinian coral *Merulina ampliata* (Ellis & Solander, 1786) in a turbid environment. *Marine Ecology* **30**, 405-415.

Dizon, R.M. & Yap, H.T. 2005. Coral responses in single-and mixed-species plots to nutrient disturbance. *Marine Ecology Progress Series* **296**, 165-172.

Dodds, L.A., Black, K.D., Orr, H. & Roberts, J.M. 2009. Lipid biomarkers reveal geographical differences in food supply to the cold-water coral *Lophelia pertusa* (Scleractinia). *Marine Ecology Progress Series* **397**, 113-124.

Dodge, R.E., Aller, R.C. & Thomson, J. 1974. Coral growth related to resuspension of bottom sediments. *Nature* **247**, 574-576.

Dodge, R.E. & Brass, G.W. 1984. Skeletal extension, density and calcification of the reef coral, *Montastrea annularis*: St. Croix, US Virgin Islands. *Bulletin of Marine Science* **34**, 288-307.

Dodge, R.E. & Thomson, J. 1974. The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. *Earth and Planetary Science Letters* **23**, 313-322.

Dodge, R.E., Wyers, S.C., Frith, H.R., Knap, A.H., Smith, S.R., Cook, C.B. & Sleeter, T.D. 1984. Coral calcification rates by the buoyant weight technique: effects of alizarin staining. *Journal of Experimental Marine Biology and Ecology* **75**, 217-232.

D'Olivo, J.P., McCulloch, M.T. & Judd, K. 2013. Long-term records of coral calcification

across the central Great Barrier Reef: assessing the impacts of river runoff and climate change. *Coral Reefs* **32**, 999-1012.

Domart-Coulon, I.J., Traylor-Knowles, N., Peters, E., Elbert, D., Downs, C.A., Price, K., Stubbs, J., McLaughlin, S., Cox, E. & Aeby, G. 2006. Comprehensive characterization of skeletal tissue growth anomalies of the finger coral *Porites compressa*. *Coral Reefs* **25**, 531-543.

Donati, V. 1751. New discoveries relating to the history of coral. *Philosophical Transactions* **47**, 95-108.

Doney, S.C., Fabry, V.J., Feely, R.A. & Kleypas, J.A. (2009) Ocean Acidification: The Other CO2 Problem. *Annual Review of Marine Science,* pp169-192.

Donner, S.D. 2009. Coping with commitment: projected thermal stress on coral reefs under different future scenarios. *PLoS ONE* **4**, e5712.

Donner, S.D., Heron, S.F. & Skirving, W.J. 2009. Future Scenarios: a Review of Modelling Efforts to Predict the Future of Coral Reefs in an Era of Climate Change. In *Coral Bleaching*, M.H. Van Oppen & J. Lough (eds). Berlin Heidelberg: Springer, 159-173.

Donner, S.D., Skirving, W.J., Little, C.M., Oppenheimer, M. & Hoegh-Guldberg, O. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology* **11**:2251-2265.

Dove, S.G., Kline, D.I., Pantos, O., Angly, F.E., Tyson, G.W. & Hoegh-Guldberg, O. 2013. Future reef decalcification under a business-as-usual CO_2 emission scenario. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 15342-15347.

Draschba, S., Pätzold, J. & Wefer, G. 2000. North Atlantic climate variability since AD 1350 recorded in $\delta^{18}O$ and skeletal density of Bermuda corals. *International Journal of Earth Sciences* **88**, 733-741.

Dubinsky, Z. & Falkowski, P. 2011. Light as a source of information and energy in zooxanthellate corals. In *Coral Reefs: An Ecosystem in Transition*, Z. Dubinsky & N. Stambler (eds). Netherlands: Springer, 107-118.

Dubinsky, Z., Stambler, N., Ben-Zion, M., McCloskey, L.R., Muscatine, L. & Falkowski, P.G. 1990. The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. *Proceedings of the Royal Society of London Series B: Biological Sciences* **239**, 231-246.

Dullo, W.-C. 2005. Coral growth and reef growth: a brief review. *Facies* **51**:33-48.

Duprey, N., Boucher, H. & Jiménez, C. 2012. Digital correction of computed X-radiographs for coral densitometry. *Journal of Experimental Marine Biology and Ecology* **438**, 84-92.

Dustan, P. 1975. Growth and form in the reef-building coral *Montastrea annularis*. *Marine Biology* **33**, 101-107.

Eakin, C.M., Feingold, J.S. & Glynn, P.W. 1994. Oil refinery impacts on coral reef communities in Aubra. In *Proceedings of the Colloquium on Global Aspects of Coral Reefs, Health, Hazards and History*, R.N. Ginsburg (ed.). Florida: Rosenstiel School of Marine and Atmospheric Science, University of Miami, 139-145.

Eakin, C.M., Morgan, J.A., Heron, S.F., Smith, T.B., Liu, G., Alvarez-Filip, L., Baca, B., Bartels, E., Bastidas, C., Bouchon, C., Brandt, M., Bruckner, A.W., Bunkley-Williams, L., Cameron, A., Causey, B.D., Chiappone, M., Christensen, T.R.L., Crabbe, M.J.C., Day, O., de la Guardia. E., Diaz-Pulido, G., DiResta, D., Gil-Agudelo, D.L., Gilliam, D.S., Ginsburg, R.N., Gore, S., Guzman, H.M., Hendee, J.C., Hernandez-Delgado, E.A., Husain, E., Jeffrey, C.F.G., Jones, R.J., Jordan-Dahlgren, E., Kaufman, L.S., Kline, D.I., Kramer, P.A., Lang, J.C., Lirman, D., Mallela, J., Manfrino, C., Marechal, J.P., Marks, K., Mihaly, J., Miller, W.J.,

Mueller, E.M., Muller, E.M., Toro, C.A.O., Oxenford, H.A., Ponce-Taylor, D., Quinn, N., Ritchie, K.B., Rodriguez, S., Ramirez, A.R., Romano, S., Samhouri, J.F., Sanchez, J.A., Schmahl, G.P., Shank, B.V., Skirving, W.J., Steiner, S.C.C., Villamizar, E., Walsh, S.M., Walter, C., Weil, E., Williams, E.H., Roberson, K.W. & Yusuf, Y. 2010. Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. *Plos One* **5**:9.

Ebeid, M.L., Hassan, M.H. & Geneid, Y.A. 2009. Response to increased sediment load by three coral species from the Gulf of Suez (Red Sea). *Journal of Fisheries and Aquatic Science* **4**, 238-245.

Edinger, E.N., Limmon, G.V., Jompa, J., Widjatmoko, W., Heikoop, J.M. & Risk, M.J. 2000. Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health? *Marine Pollution Bulletin* **40**, 404-425.

Edmondson, C.H. 1929. Growth of Hawaiian corals. *Bishop Museum Bulletins* **58**, 1-38.

Edmunds, P.J. 2005. The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. *Oecologia* **146**, 350-364.

Edmunds, P.J. 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. *Marine Ecology Progress Series* **341**, 1-13.

Edmunds, P.J., Brown, D. & Moriarty, V. 2012. Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. *Global Change Biology* **18**:2173-2183.

Edmunds, P.J. & Davies, P.S. 1986. An energy budget for *Porites porites* (Scleractinia). *Marine Biology* **92**:339-347.

Edmunds, P.J. & Elahi, R. 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastraea annularis*. *Ecological Monographs* **77**, 3-18.

Edmunds, P.J., Gates, R.D. & Gleason, D.F. 2003. The tissue composition of Montastraea *franksi* during a natural bleaching event in the Florida Keys. *Coral Reefs* **22**:54-62.

Edmunds, P.J., Putnam, H.M., Nisbet, R.M. & Muller, E.B. 2011. Benchmarks in organism performance and their use in comparative analyses. *Oecologia* **167**, 379-390.

Edmunds, P.J., Burgess, S.C., Putnam, H.M., Baskett, M.L., Bramanti, L., Fabina, N.S., Han, X., Lesser, M.P., Madin, J.S. & Wall, C.B. 2014. Evaluating the causal basis of ecological success within the scleractinia: an integral projection model approach. *Marine Biology* **161**, 2719-2734.

Einbinder, S., Mass, T., Brokovich, E., Dubinsky, Z., Erez, J. & Tchernov, D. 2009. Changes in morphology and diet of the coral *Stylophora pistillata* along a depth gradient. *Marine Ecology Progress Series* **381**, 167-174.

Elizalde-Rendón, E.M., Horta-Puga, G., González-Diaz, P. & Carricart-Ganivet, J. 2010. Growth characteristics of the reef-building coral *Porites astreoides* under different environmental conditions in the Western Atlantic. *Coral Reefs* **29**, 607-614.

Emanuel, K.A. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* **436**, 686-688.

Evans, G.C. 1972. *The Quantitative Analysis of Plant Growth*. Berkley and Los Angeles, California: University of California Press.

Fabricius, K.E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* **50**, 125-46.

Fabricius, K.E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M.S. & Lough, J.M. 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nature Climate Change* **1**, 165-169.

Fagerstrom, J.A. 1991. Reef-building guilds and a checklist for determining guild membership. *Coral Reefs* **10**, 47-52.

Fallon, S.J., McCulloch, M.T., van Woesik, R. & Sinclair, D.J. 1999. Corals at their latitudinal limits: laser ablation trace element systematics in *Porites* from Shirigai Bay, Japan. *Earth and Planetary Science Letters* **172**, 221-238.

Falter, J.L., Lowe, R.J., Zhang, Z. & McCulloch, M. 2013. Physical and biological controls on the carbonate chemistry of coral reef waters: effects of metabolism, wave forcing, sea level, and geomorphology. *PLoS ONE* **8**:e53303.

Feely, R.A., Doney, S.C. & Cooley, S.R. 2009. Ocean acidification: present conditions and future changes in a high-CO2 world. *Oceanography* **22**:36-47.

Feely, R.A., Sabine, C.L., Byrne, R.H., Millero, F.J., Dickson, A.G., Wanninkhof, R., Murata, A., Miller, L.A. & Greeley, D. 2012. Decadal changes in the aragonite and calcite saturation state of the Pacific Ocean. *Global Biogeochemical Cycles* **26**:GB3001.

Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J. & Millero, F.J. 2004. Impact of Anthropogenic CO2 on the CaCO3 System in the Oceans. *Science* **305**:362-366.

Feng, M., McPhaden, M.J., Xie, S.-P. & Hafner, J. 2013. La Niña forces unprecedented Leeuwin Current warming in 2011. *Scientific Reports* **3**, 1277.

Ferrier-Pagès, C., Gattuso, J.P., Dallot, S. & Jaubert, J. 2000. Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* **19**:103-113.

Ferrier-Pagès, C., Hoogenboom, M.O. & Houlbrèque, F. 2011. The role of plankton in coral trophodynamics. In *Coral Reefs: An Ecosystem in Transition*, Z. Dubinsky & N. Stambler (eds). Netherlands: Springer, 215-229.

Ferrier-Pagès, C., Witting, J., Tambutté, E. & Sebens, K.P. 2003. Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. *Coral Reefs* **22**, 229-240.

Finckh, A.E. 1904. Biology of the reef-forming organisms at Funafuti Atoll. In *The Atoll Funafuti: borings into a coral reef and the results. Report of the Coral Reef Committee of the Royal Society of London*. London, UK: The Royal Society of London, 125-150.

Flannery, J.A. & Poore, R.Z. 2013. Sr/Ca proxy sea-surface temperature reconstructions from modern and Holocene *Montastraea faveolata* specimens from the Dry Tortugas National Park, Florida, U.S.A. *Journal of Coastal Research* **SI63**, 20-31.

Folch, J., Lees, M. & Sloane-Stanley, G. 1957. A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biology Chemistry* **226**:497-509.

Folke, C., Carpenter, S.R., Walker, B.H., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* **35**, 557-581.

Form, A.U. & Riebesell, U. 2012. Acclimation to ocean acidification during long-term CO2 exposure in the cold-water coral *Lophelia pertusa*. *Global Change Biology* 18:843-853.

Forster, P., Ramaswamy, V., Artaxo, P., Berntsen, T., Betts, R., Fahey, D.W., Haywood, J., Lean, J., Lowe, D.C. & Myhre, G. 2007. Changes in atmospheric constituents and in radiative forcing. Chapter 2. In *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, S. Solomon et al. (eds). Cambridge, UK: Cambridge University Press, 129-234.

Foster, T., Short, J.A., Falter, J.L., Ross, C. & McCulloch, M.T. 2014. Reduced calcification in Western Australian corals during anomalously high summer water temperatures. *Journal of Experimental Marine Biology and Ecology* **461**:133-143.

Franzisket, L. 1970. The atrophy of hermatypic reef corals maintained in darkness and their subsequent regeneration in light. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **55**, 1-12.

Furla, P., Galgani, I., Durand, I. & Allemand, D. 2000. Sources and mechanisms of inorganic carbon transport for coral calcification and photosynthesis. *Journal of Experimental Biology* **203**:3445-3457.

Gardiner, J.S. 1901. On the rate of growth of some corals from Fiji. *Proceedings of the Cambridge Philosophical Society* **11**, 214-219.

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**, 958-960.

Garzón-Ferreira, J., Zea, S. & Díaz, J.M. 2005. Incidence of partial mortality and other health indicators in hard-coral communities of four southwestern Caribbean atolls. *Bulletin of Marine Science* **76**, 105-122.

Gateno, D., León-Campos, A., Barki, Y., Cortés-Núñez, J. & Rinkevich, B. 2003. Skeletal tumor formations in the massive coral *Pavona clavus*. *Marine Ecology Progress Series* **258**, 97-108.

Gattuso, J.-P., Allemand, D. & Frankignoulle, M. 1999. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. *American Zoologist* **39**, 160-183.

Gattuso, J.-P., Frankignoulle, M. & Wollast, R. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* **29**, 405-434.

Gattuso, J.-P., Pichon, M., Delesalle, B., Canon, C. & Frankignoulle, M. 1996. Carbon fluxes in coral reefs. I. Lagrangian measurement of community metabolism and resulting air-sea CO_2 disequilibrium. *Marine Ecology Progress Series* **145**, 109-121.

Ghiold, J. & Enos, P. 1982. Carbonate production of the coral *Diploria labyrinthiformis* in south Florida patch reefs. *Marine Geology* **45**, 281-296.

Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H. & Pratchett, M.S. 2013. Recovery of an isolated coral reef system following severe disturbance. *Science* **340**, 69-71.

Gischler, E. 2008. Accretion patterns in Holocene tropical coral reefs: do massive coral reefs in deeper water with slowly growing corals accrete faster than shallower branched coral reefs with rapidly growing corals? *International Journal of Earth Sciences* **97**, 851-859.

Gladfelter, E.H. 1982. Skeletal development in *Acropora cervicornis*: I. Patterns of calcium carbonate accretion in the axial corallite. *Coral Reefs* **1**, 45-51.

Gladfelter, E.H. 1984. Skeletal development in *Acropora cervicornis*. *Coral Reefs* **3**, 51-57.

Gladfelter, E.H. & Gladfelter, W.B. 1979. Growth and total carbonate production by *Acropora palmata* on a windward reef. In *Environmental Studies of Buck Island Reef National Monument St. Croix, USVI II. Report for the National Park Service, US Department of Interior*, E.H. Gladfelter et al. (eds). St. Croix, US Virgin Islands: West Indies Laboratory of Fairleigh Dickinson University, III, 1-8.

Gladfelter, E.H., Monahan, R.K. & Gladfelter, W.B. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. *Bulletin of Marine Science* **28**, 728-734.

Gledhill, D.K., Wanninkhof, R., Millero, F.J. & Eakin, M. 2008. Ocean acidification of the Greater Caribbean Region 1996–2006. *Journal of Geophysical Research: Oceans* **113**, C10031.

Glynn, P.W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. In *Biology and Geology of Coral Reefs*, O.A. Jones & R. Endean (eds). New York, USA: Academic Press, 271-324.

Glynn, P.W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs* **46**, 431-456.

Glynn, P.W. 1977. Coral growth in upwelling and non-upwelling areas off the Pacific coast of Panama. *Journal of Marine Research* **35**, 567-585.
Glynn, P.W., Perez, M. & Gilchrist, S.L. 1985. Lipid decline in stressed corals and their crustacean symbionts. *The Biological Bulletin* **168**:276-284.
Glynn, P.W. & Stewart, R.H. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. *Limnology and Oceanography* **18**, 307-379.
Glynn, P.W., Wellington, G.M. & Birkeland, C. 1979. Coral reef growth in the Galapagos: limitation by sea urchins. *Science* **203**, 47-49.
Goffredo, S., Caroselli, E., Mattioli, G., Pignotti, E., Dubinsky, Z. & Zaccanti, F. 2009. Inferred level of calcification decreases along an increasing temperature gradient in a Mediterranean endemic coral. *Limnology and Oceanography* **54**, 930-937.
Goldberg, W.M. 2002. Feeding behavior, epidermal structure and mucus cytochemistry of the scleractinian *Mycetophyllia reesi*, a coral without tentacles. *Tissue & Cell* **34**, 232-245.
Goreau, T.F. 1959. The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biological Bulletin* **116**, 59-75.
Goreau, T.F. 1961. Problems of growth and calcium deposition in reef corals. *Endeavour* **20**, 32-39.
Goreau, T.F. 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef-builders. *Annals of the New York Academy of Sciences* **109**, 127-167.
Goreau, T.F. & Goreau, N.I. 1959. The physiology of skeleton formation in corals. II. Calcium deposition by hermatypic corals under various conditions in the reef. *Biological Bulletin* **117**, 239-250.
Goreau, T.F., Goreau, N.I. & Yonge, C.M. 1971. Reef corals: autotrophs or heterotrophs? *Biological Bulletin* **141**, 247-260.
Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**:94-97.
Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. & Robinson, J. 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 8425-8429.
Greenstein, B.J. & Pandolfi, J.M. 2008. Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. *Global Change Biology* **14**:513-528.
Grigg, R.W. 1981. Coral reef development at high latitudes in Hawaii. *Proceedings of the Fourth International Coral Reef Symposium* **1**, 687-693.
Grigg, R.W. 1982. Darwin Point: a threshold for atoll formation. *Coral Reefs* **1**, 29-34.
Grigg, R.W. 1998. Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history. *Coral Reefs* **17**, 263-272.
Grigg, R.W. 2006. Depth limit for reef building corals in the Au'au Channel, SE Hawaii. *Coral Reefs* **25**, 77-84.
Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169-1194.
Grime, J.P. & Hunt, R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**, 393-422.
Grottoli, A.G. 1999. Variability of stable isotopes and maximum linear extension in reef-coral skeletons at Kaneohe Bay, Hawaii. *Marine Biology* **135**, 437-449.
Grottoli, A.G., Rodrigues, L.J. & Juarez, C. 2004. Lipids and stable carbon isotopes in two

species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Marine Biology* **145**:621-631.
Grottoli, A.G., Rodrigues, L.J. & Palardy, J.E. 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature* **440**, 1186-1189.
Grove, C.A., Nagtegaal, R., Zinke, J., Scheufen, T., Koster, B., Kasper, S., McCulloch, M.T., van den Bergh, G. & Brummer, G.J.A. 2010. River runoff reconstructions from novel spectral luminescence scanning of massive coral skeletons. *Coral Reefs* **29**, 579-591.
Guest, J.R., Baird, A.H., Maynard, J.A., Muttaqin, E., Edwards, A.J., Campbell, S.J., Yewdall, K., Affendi, Y.A. & Chou, L.M. 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE* **7**, e33353.
Guinotte, J.M., Buddemeier, R.W. & Kleypas, J.A. 2003. Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* **22**:551-558.
Guinotte, J.M., Fabry, V.J. 2008. Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* **1134**:320-342.
Guzmán, H.M., Cipriani, R. & Jackson, J.B.C. 2008. Historical decline in coral reef growth after the Panama Canal. *Ambio* **37**, 342-346.
Guzmán, H.M. & Cortés, J. 1989. Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). *Bulletin of Marine Science* **44**, 1186-1194.
Guzmán, H.M., Jackson, J.B.C. & Weil, E. 1991. Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* **10**, 1-12.
Guzmán, H.M. & Tudhope, A.W. 1998. Seasonal variation in skeletal extension rate and stable isotopic (13C/12C and 18O/16O) composition in response to several environmental variables in the Caribbean reef coral *Siderastrea siderea*. *Marine Ecology Progress Series* **166**, 109-118.
Halford, A., Cheal, A.J., Ryan, D. & Williams, D.M. 2004. Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* **85**, 1892-1905.
Hall, V.R. & Hughes, T.P. 1996. Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* **77**, 950-963.
Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D. & Buia, M.-C. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* **454**, 96-99.
Harland, A., Davies, P.S. & Fixter, L. 1992. Lipid content of some Caribbean corals in relation to depth and light. *Marine Biology* **113**:357-361.
Harriott, V.J. 1998. Growth of the staghorn coral *Acropora formosa* at Houtman Abrolhos, Western Australia. *Marine Biology* **132**, 319-325.
Harriott, V.J. 1999. Coral growth in subtropical eastern Australia. *Coral Reefs* **18**, 281-291.
Harriott, V.J., Harrison, P.L & Banks, S.A. 1995. The coral communities of Lord Howe Island. *Marine and Freshwater Research* **46**:457-465.
Harrison, P., Dalton, S. & Carroll, A. 2011. Extensive coral bleaching on the world's southernmost coral reef at Lord Howe Island, Australia. *Coral Reefs* **30**:775-775.
Hart, D.E. & Kench, P.S. 2007. Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia. *Coral Reefs* **26**, 53-68.
Hartmann, D.L., Klein Tank, A.M.G., Rusicucci, M., Alexander, L.V., Broenniman, B., Charabi, Y., Dentener, F.J., Dlugokencky, E.J., Easterling, D.R., Kaplan, A., Soden, B.J., Thorne, P.W., Wild, M., Zhai, P.M. & Kent, E. 2013. Observations: Atmosphere and surface. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the*

Intergovernmental Panel on Climate Change, T.F. Stocker et al. (eds). Cambridge, UK: Cambridge University Press, 159-254.
Harvey, B.P., Gwynn-Jones, D. & Moore, P.J. 2013. Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecology and Evolution* **3**:1016-1030.
Hassan, R.M., Scholes, R. & Ash, N. (eds). 2005. *Ecosystems and Human Well-Being: Current State and Trends: Findings of the Condition and Trends Working Group*. Washington DC, USA: Island Press.
Hata, H., Kudo, S., Yamano, H., Kurano, N. & Kayanne, H. 2002. Organic carbon flux in Shiraho coral reef (Ishigaki Island, Japan). *Marine Ecology Progress Series* **232**, 129-140.
Heiss, G.A. 1995. Carbonate production by scleractinian corals at Aqaba, Gulf of Aqaba, Red Sea. *Facies* **33**, 19-34.
Heiss, G.A. 1996. Annual band width variation in *Porites* sp. from Aqaba, Gulf of Aqaba, Red Sea. *Bulletin of Marine Science* **59**, 393-403.
Helmle, K.P. & Dodge, R.E. 2011. Sclerochronology. In *Encyclopedia of Modern Coral Reefs*, D. Hopley (ed.). Dordrecht, The Netherlands: Springer, 958-966.
Helmle, K.P., Dodge, R.E. & Ketcham, R.A. 2002. Skeletal architecture and density banding in *Diploria strigosa* by X-ray computed tomography. *Proceedings of the Ninth International Coral Reef Symposium* **1**, 365-371.
Helmle, K.P., Dodge, R.E., Swart, P.K., Gledhill, D.K. & Eakin, C.M. 2011. Growth rates of Florida corals from 1937 to 1996 and their response to climate change. *Nature Communications* **2**, 215.
Hendy, E.J., Gagan, M.K. & Lough, J.M. 2003. Chronological control of coral records using luminescent lines and evidence for non-stationary ENSO teleconnections in northeast Australia. *The Holocene* **13**, 187-199.
Henry, L.-A. & Hart, M. 2005. Regeneration from injury and resource allocation in sponges and corals - a review. *International Review of Hydrobiology* **90**, 125-158.
Herler, J. & Dirnwöber, M. 2011. A simple technique for measuring buoyant weight increment of entire, transplanted coral colonies in the field. *Journal of Experimental Marine Biology and Ecology* **407**, 250.
Heron, S.F., Willis, B.L., Skirving, W.J., Eakin, C.M., Page, C.A. & Miller, I.R. (2010) Summer hot snaps and winter conditions: modelling white syndrome outbreaks on Great Barrier Reef corals. *PLoS ONE* **5**:e12210.
Heyward, A.J. & Collins, J.D. 1985. Growth and sexual reproduction in the scleractinian coral *Montipora digitata* (Dana). *Marine and Freshwater Research* **36**, 441-446.
Highsmith, R.C. 1979. Coral growth rates and environmental control of density banding. *Journal of Experimental Marine Biology and Ecology* **37**, 105-125.
Highsmith, R.C., Lueptow, R.L. & Schonberg, S.C. 1983. Growth and bioerosion of 3 massive corals on Belize barrier-reef. *Marine Ecology Progress Series* **13**, 261-271.
Hoegh-Guldberg, O. 1999 Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839-866.
Hoegh-Guldberg, O. 2004. Coral reefs in a century of rapid environmental change. *Symbiosis* **37**, 1-31.
Hoegh-Guldberg, O. (2011) Coral reef ecosystems and anthropogenic climate change. *Regional Environmental Change* **11**:S215-S227.
Hoegh-Guldberg, O. & Bruno, J.F. 2010. The Impact of Climate Change on the World's Marine Ecosystems. *Science* **328**:1523-1528.
Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A. & Hatziolos, M.E. 2007.

Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737-1742.
Hoeke, R.K., Jokiel, P.L., Buddemeier, R.W. & Brainard, R.E. 2011. Projected changes to growth and mortality of Hawaiian corals over the next 100 years. *PLoS ONE* **6**, e18038.
Hoey, A.S., Pratchett, M.S. & Cvitanovic, C. 2011. High macroalgal cover and low coral recruitment undermines the potential resilience of the world's southernmost coral reef assemblages. *Plos One* **6**:e25824
Holbrook, S.J., Brooks, A.J. & Schmitt, R.J. 2002. Predictability of fish assemblages on coral patch reefs. *Marine and Freshwater Research* **53**, 181-188.
Holbrook, S.J., Forrester, G.E. & Schmitt, R.J. 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* **122**, 109-120.
Holbrook, S.J. & Schmitt, R.J. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* **83**, 2855-2868.
Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. 2008. Resistance and resilience of a coral reef fish community to changes in coral cover. *Marine Ecology Progress Series* **371**, 263-271.
Holcomb, M., Cohen, A.L. & McCorkle, D.C. 2013. An evaluation of staining techniques for marking daily growth in scleractinian corals. *Journal of Experimental Marine Biology and Ecology* **440**, 126-131.
Hoogenboom, M.O., Connolly, S.R. & Anthony, K.R.N. 2009. Effects of photoacclimation on the light niche of corals: a process-based approach. *Marine Biology* **156**, 2493-2503.
Hoogenboom, M.O., Connolly, S.R. & Anthony, K.R.N. 2011. Biotic and abiotic correlates of tissue quality for common scleractinian corals. *Marine Ecology Progress Series* **438**:119-128.
Hoogenboom, M.O., Rodolfo-Metalpa, R. & Ferrier-Pagès, C. 2010. Co-variation between autotrophy and heterotrophy in the Mediterranean coral *Cladocora caespitosa*. *Journal of Experimental Biology* **213**, 2399-2409.
Hooper, D.U., Chapin, F.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M. & Naeem, S. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3-35.
Horta-Puga, G. & Carriquiry, J.D. 2014. The last two centuries of lead pollution in the southern Gulf of Mexico recorded in the annual bands of the scleractinian coral *Orbicella faveolata*. *Bulletin of Environmental Contamination and Toxicology* **92**, 567-573.
Houlbrèque, F. & Ferrier-Pagès, C. 2009. Heterotrophy in tropical scleractinian corals. *Biological Reviews* **84**, 1-17.
Houlbrèque, F., Tambutté, E., Allemand, D. & Ferrier-Pagès, C. 2004. Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *Journal of Experimental Biology* **207**, 1461-1469.
Houlbrèque, F., Tambutté, E. & Ferrier-Pagès, C. 2003. Effect of zooplankton availability on the rates of photosynthesis, and tissue and skeletal growth in the scleractinian coral *Stylophora pistillata*. *Journal of Experimental Marine Biology and Ecology* **296**, 145-166.
Hubbard, D.K. 2009. Depth-related and species-related patterns of Holocene reef accretion in the Caribbean and Western Atlantic: A critical assessment of existing models. In *Perspectives in Carbonate Geology: A Tribute to the Career of Robert Nathan Ginsburg*, P.K. Swart et al. (eds). West Sussex, UK: John Wiley & Sons Ltd, 1-18.
Hubbard, D.K. & Scaturo, D. 1985. Growth rates of seven species of scleractinean corals

from Cane Bay and Salt River, St. Croix, USVI. *Bulletin of Marine Science* **36**, 325-338.

Hubbard, J.A.E.B. & Pocock, Y.P. 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. *Geologische Rundschau* **61**, 598-626.

Hudson, J.H. 1981. Growth rates in *Montastraea annularis*: a record of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. *Bulletin of Marine Science* **31**, 444-459.

Hudson, J.H. 1985. Long-term growth rates of *Porites lutea* before and after nuclear testing: Enewetak Atoll, Marshall Islands. *Proceedings of the Fifth International Coral Reef Symposium* **6**, 179-185.

Hudson, J.H. & Goodwin, W.B. 1997. Restoration and growth rate of hurricane damaged pillar coral (*Dendrogyra cylindrus*) in the Key Largo National Marine Sanctuary, Florida. *Proceedings of the Eighth Internatioinal Coral Reef Symposium* **1**, 567-570.

Hudson, J.H., Hanson, K.J., Halley, R.B. & Kindinger, J.L. 1994. Environmental implications of growth rate changes in *Montastrea annularis*: Biscayne National Park, Florida. *Bulletin of Marine Science* **54**, 647-669.

Hudson, J.H. & Robbin, D.M. 1980. Effects of drilling mud on the growth rate of the reef-building coral, *Montastrea annularis*. In *Marine Environmental Pollution, 1 – Hydrocarbons*, A.G. Richard (ed.). Amsterdam, The Netherlands: Elsevier, 455-470.

Hudson, J.H., Shinn, E.A., Halley, R.B. & Lidz, B. 1976. Sclerochronology: a tool for interpreting past environments. *Geology* **4**, 361-364.

Hughes, T.P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *American Naturalist* **123**, 778-795.

Hughes, T.P. 1987. Skeletal density and growth form of corals. *Marine Ecology Progress Series* **35**, 259-266.

Hughes, T.P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean Coral Reef. *Science* 265:1547-1551.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B. & Roughgarden, J. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929-933.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J. & Steneck, R.S. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution* **25**:633-642.

Hughes, T.P. & Jackson, J.B.C. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. *Science* **209**, 713-715.

Hughes, T.P. & Jackson, J.B.C. 1985. Population dynamics and life histories of foliaceous corals. *Ecological Monographs* **55**, 141-166.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., Moltschaniwskyj, N., Pratchett, M.S., Steneck, R.S. & Willis, B.L. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**, 360-365.

Hughes, T.P. & Tanner, J.E. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**, 2250-2263.

Huston, M. 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* **4**, 19-25.

Idjadi, J.A., Lee, S.C., Bruno, J.F., Precht, W.F., Allen-Requa, L. & Edmunds, P.J. 2006. Rapid phase-shift reversal on a Jamaican coral reef. *Coral Reefs* **25**, 209-211.

Iglesias-Prieto, R., Matta, J.L., Robins, W.A. & Trench, R.K. 1992. Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium*

microadriaticum in culture. *Proceedings of the National Academy of Sciences of the United States of America* **89**:10302-10305.

IPCC. 2007. Climate Change 2007: the physical science basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Solomon, S., D. Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L. (eds) Cambridge, United Kingdom, New York: Cambridge University Press.

IPCC. 2013. Summary for Policymakers. In *Climate Change 2013: The Physical Science Basis*, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M. (eds) Cambridge, United Kingdom, New York: Cambridge University Press.

Isdale, P. 1984. Fluorescent bands in massive corals record centuries of coastal rainfall. *Nature* **310**:578-579.

Isdale, P.J. & Daniel, E.E. 1989. The design and deployment of lightweight submarine fixed drilling system for the acquisition of coral cores. *Marine Technology Society Journal* **23**, 3-8.

Jackson, J.B.C. 1979. Morphological strategies of sessile animals. In *Biology and Systematics of Colonial Organisms*, G. Larwood & B. Rosen (eds). London, UK: Academic Press, 499-555.

Jackson, J.B.C. 1991. Adaptation and diversity of reef corals. *BioScience* **41**, 475-482.

Jackson, J.B.C., Donovan, M.K., Cramer, K.L. & Lam, V.V. 2014. *Status and Trends of Caribbean Coral Reefs: 1970–2012*. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN.

Jackson, J.B.C. & Hughes, T.P. 1985. Adaptive strategies of coral-reef invertebrates. *American Scientist* **73**, 265-273.

Jiménez, C. & Cortés, J. 2003. Growth of seven species of scleractinian corals in an upwelling environment of the eastern Pacific (Golfo de Papagayo, Costa Rica). *Bulletin of Marine Science* **72**, 187-198.

Jin YK, Lundgren P, Lutz A, Raina J-B, Howells EJ, Paley AS, Willis BL, van Oppen MJH (2016) Genetic markers for antioxidant capacity in a reef-building coral. *Science Advances* 2:e1500842

Jinendradasa, S.S. & Ekarame, S.U.K. 2000. Linear extension of *Acropora formosa* (Dana) at selected reef locations in Sri Lanka. *Proceedings of the Ninth International Coral Reef Symposium* **1**, 537-540.

Johnson, K.G., Jackson, J.B.C. & Budd, A.F. 2008. Caribbean reef development was independent of coral diversity over 28 million years. *Science* **319**, 1521-1523.

Jokiel, P.L. 2013. Coral reef calcification: carbonate, bicarbonate and proton flux under conditions of increasing ocean acidification. *Proceedings of the Royal Society B: Biological Sciences* **280**:20130031.

Jokiel, P.L. & Coles, S.L. 1977. Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology* **43**, 201-208.

Jokiel, P.L. & Coles, S.L. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* **8**:155-162.

Jokiel, P.L., Maragos, J.E. & Franzisket, L. 1978. Coral growth: buoyant weight technique. In *Coral Reefs: Research Methods*, D.R. Stoddart & R.E. Johannes (eds). Paris, France: UNESCO, 529-541.

Jokiel, P.L. & Tyler, W.A. 1992. Distribution of stony corals in Johnston Atoll lagoon. *Proceedings of the Seventh International Coral Reef Symposium* **2**, 683-692.

Jones, A. & Berkelmans, R. 2010. Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS ONE* **5**,

e10437.
Jones, G.P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **123**, 115-126.
Jones, G.P., McCormick, M.I., Srinivasan, M. & Eagle, J.V. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 8251-8253.
Jury, C.P., Whitehead, R.F. & Szmant, A.M. 2010. Effects of variations in carbonate chemistry on the calcification rates of *Madracis auretenra* (= *Madracis mirabilis* sensu Wells, 1973): bicarbonate concentrations best predict calcification rates. *Global Change Biology* **16**:1632-1644.
Kaniewska, P., Anthony, K.R.N. & Hoegh-Guldberg, O. 2008. Variation in colony geometry modulates internal light levels in branching corals, *Acropora humilis* and *Stylophora pistillata*. *Marine Biology* **155**, 649-660.
Kaniewska, P., Magnusson, S.H., Anthony, K.R.N., Reef, R., Kühl, M. & Hoegh-Guldberg, O. 2011. Importance of macro- versus microstructure in modulating light levels inside coral colonies. *Journal of Phycology* **47**, 846-860.
Karlson, R.H. & Hurd, L.E. 1993. Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs* **12**, 117-125.
Kiessling, W., Simpson, C., Beck, B., Mewis, H. & Pandolfi, J.M. 2012. Equatorial decline of reef corals during the last Pleistocene interglacial. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 21378-21383.
Kikuchi, R.K.P., Oliveira, M.D.M. & Leão, Z.M.A.N. 2013. Density banding pattern of the south western Atlantic coral *Mussismilia braziliensis*. *Journal of Experimental Marine Biology and Ecology* **449**, 207-214.
Kinzie, R.A. III & Sarmiento, T. 1986. Linear extension rate is independent of colony size in the coral *Pocillopora damicornis*. *Coral Reefs* **4**, 177-181.
Kissling, D. 1977. Population structure characteristics for some Paleozoic and modern colonial corals. *Second International Symposium on Corals and Fossil Coral Reefs, Paris*, September 1975:497-506
Klein, R. & Loya, Y. 1991. Skeletal growth and density patterns of two *Porites* corals from the Gulf of Eilat, Red Sea. *Marine Ecology Progress Series* **77**, 253-259.
Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L. & Klimešová, J. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* **96**, 1266-1274.
Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J.-P., Langdon, C. & Opdyke, B.N. 1999b. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**, 118-120.
Kleypas, J.A., Castruccio, F.S., Curchitser, E.N. & McLeod, E. 2015. The impact of ENSO on coral heat stress in the western equatorial Pacific. *Global Change Biology*:doi: 10.1111/.
Kleypas, J.A. & Langdon, C. 2013. Coral reefs and changing seawater carbonate chemistry. In *Coral Reefs and Climate Change: Science and Management*, J.T. Phinney et al. (eds). Washington DC, USA: American Geophysical Union, 73-110.
Kleypas, J.A., McManus, J.W. & Meñez, L.A.B. 1999a. Environmental limits to coral reef development: where do we draw the line? *American Zoologist* **39**, 146-159.
Kleypas, J.A. & Yates, K.K. 2009. Coral reefs and ocean acidification. *Oceanography* **22**:108-117.
Kline, D.I., Teneva, L., Hauri, C., Schneider, K., Miard, T., Chai, A., Marker, M., Dunbar, R., Caldeira, K., Lazar, B., Rivlin, T., Mitchell, B.G., Dove, S. & Hoegh-Guldberg,

O. 2015. Six month in situ high-resolution carbonate chemistry and temperature study on a coral reef flat reveals asynchronous pH and temperature anomalies. *PLoS ONE* **10**:e0127648.

Klotzbach, P.J. 2006. Trends in global tropical cyclone activity over the past twenty years (1986–2005). *Geophysical Research Letters* **33**, L10805.

Knittweis, L., Jompa, J., Richter, C. & Wolff, M. 2009. Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia. *Coral Reefs* **28**, 793-804.

Knowlton, N., Weil, E., Weigt, L.A. & Guzmán, H.M. 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. *Science* **255**, 330-333.

Knutson, D.W., Buddemeier, R.W. & Smith, S.V. 1972. Coral chronometers: seasonal growth bands in reef corals. *Science* **177**, 270-272.

Koch, M., Bowes, G., Ross, C. & Zhang, X.-H. 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Global Change Biology* **19**:103-132.

Kotb, M.M.A. 2001. Growth rates of three reef-building coral species in the northern Red Sea, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries* **5**, 165-185.

Krief, S., Hendy, E.J., Fine, M., Yam, R., Meibom, A., Foster, G.L. & Shemesh, A. 2010. Physiological and isotopic responses of scleractinian corals to ocean acidification. *Geochimica et Cosmochimica Acta* **74**:4988-5001.

Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L., Singh, G.S., Duarte, C.M. & Gattuso, J.-P. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* **19**, 1884-1896.

Kroeker, K.J., Kordas, R.L., Crim, R. & Singh, G.G. 2010 Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* **13**:1419-1434.

Kružić, P., Sršen, P. & Benković, L. 2012. The impact of seawater temperature on coral growth parameters of the colonial coral *Cladocora caespitosa* (Anthozoa, Scleractinia) in the eastern Adriatic Sea. *Facies* **58**, 477-491.

Kuffner, I.B., Hickey, T.D. & Morrison, J.M. 2013. Calcification rates of the massive coral *Siderastrea siderea* and crustose coralline algae along the Florida Keys (USA) outer-reef tract. *Coral Reefs* **32**, 987-997.

Lamberts, A.E. 1978. Coral growth: alizarin method. In *Coral Reefs: Research Methods*, D.R. Stoddart & R.E. Johannes (eds). Paris, France: UNESCO, 523-527.

Langdon, C. & Atkinson, M.J. 2005. Effect of elevated pCO2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research* **110**:C09S07.

Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H. & Atkinson, M.J. 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* **14**, 639-654.

Larcom, E.A., McKean, D.L., Brooks, J.M. & Fisher, C.R. 2014. Growth rates, densities, and distribution of *Lophelia pertusa* on artificial structures in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* **85**, 101-109.

Lauvset, S., Gruber, N., Landschützer, P., Olsen, A. & Tjiputra, J. 2015. Trends and drivers in global surface ocean pH over the past 3 decades. *Biogeosciences* **12**:1285-1298.

Lawton, J.H. 1999. Are there general laws in ecology? *Oikos* **84**, 177-192.

Leclercq, N., Gattuso, J.-P. & Jaubert, J. 2002. Primary production, respiration, and

calcification of a coral reef mesocosm under increased CO2 partial pressure. *Limnology and Oceanography* **47**:558-564.
Lee, K., Tong, L.T., Millero, F.J., Sabine, C.L., Dickson, A.G., Goyet, C., Park, G.-H., Wanninkhof, R., Feely, R.A. & Key, R.M. 2006. Global relationships of total alkalinity with salinity and temperature in surface waters of the world's oceans. *Geophysical Research Letters* **33**:L19605.
Leuzinger, S., Anthony, K.R.N. & Willis, B.L. 2003. Reproductive energy investment in corals: scaling with module size. *Oecologia* **136**, 524-531.
Leuzinger, S., Willis, B.L. & Anthony, K.R.N. 2012. Energy allocation in a reef coral under varying resource availability. *Marine Biology* **159**, 177-186.
Lewis, J.B., Axelsen, F., Goodbody, I., Page, C. & Chislett, G. 1968. *Comparative Growth Rates of Some Reef Corals in the Caribbean. Marine Sciences Manuscript Report No. 10*. Montreal, Canada: Marine Sciences Centre, McGill University.
Lewis, J.B. & Price, W.S. 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. *Journal of Zoology* **176**, 527-544.
Lewis, E. & Wallace, D.W.R. 1998. Program Developed for CO2 System Calculations. In: Carbon Dioxide Information Analysis Center. Oakridge, Tennessee: Oak Ridge National Laboratory, U S Department of Energy.
Liberman, T., Genin, A. & Loya, Y. 1995. Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. *Marine Biology* **121**, 741-746.
Lin, D.Y. & Wei, L.-J. 1989. The robust inference for the Cox proportional hazards model. *Journal of the American Statistical Association* **84**:1074-1078.
Linares, C., Pratchett, M.S. & Coker, D.J. 2011. Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* **438**, 97-104.
Lirman, D. 2000. Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. *Journal of Experimental Marine Biology and Ecology* **251**, 41-57.
Little, A.F., Van Oppen, M.J.H. & Willis, B.L. 2004. Flexibility in algal endosymbioses shapes growth in reef corals. *Science* **304**, 1492-1494.
Liu, G., Strong, A.E., & Skirving, W. 2003. Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. *Eos, Transactions American Geophysical Union* **84**:137-141
Liu, G., Rauenzahn, J., Heron, S.F., Eakin, C.M., Skirving, W.J., Christensen, T., Strong, A.E. & Li, J. 2013. NOAA Coral Reef Watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management. In *NOAA Technical Report NESDIS* **143**. College Park, MD:NOAA/NEDIS.
Logan, A. & Anderson, I.H. 1991. Skeletal extension growth rate assessment in corals, using CT scan imagery. *Bulletin of Marine Science* **49**, 847-850.
Logan, A. & Tomascik, T. 1991. Extension growth rates in two coral species from high-latitude reefs of Bermuda. *Coral Reefs* **10**, 155-160.
Logan, A., Yang, L. & Tomascik, T. 1994. Linear skeletal extension rates in two species of *Diploria* from high-latitude reefs in Bermuda. *Coral Reefs* **13**, 225-230.
Lough, J.M. 2008. Coral calcification from skeletal records revisited. *Marine Ecology Progress Series* **373**, 257-264.
Lough, J.M. 2010. Climate records from corals. *Wiley Interdisciplinary Reviews: Climate Change* **1**, 318-331.
Lough, J.M. 2011. Measured coral luminescence as a freshwater proxy: comparison with visual indices and a potential age artefact. *Coral Reefs* **30**:169-182
Lough, J.M. 2012. Small change, big difference: Sea surface temperature distributions for

tropical coral reef ecosystems, 1950-2011. *Journal of Geophysical Research-Oceans* **117**:C09018.
Lough, J.M. & Barnes, D.J. 1992. Comparisons of skeletal density variations in *Porites* from the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* **155**, 1-25.
Lough, J.M. & Barnes, D.J. 2000. Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* **245**, 225-243.
Lough, J.M., Barnes, D.J., Devereux, M.J., Tobin, B.J. & Tobin, S. 1999. Variability in growth characteristics of massive *Porites* on the Great Barrier Reef. Technical Report No. 28. Townsville: CRC Reef Research Centre Ltd.
Lough, J.M., Barnes, D.J. & McAllister, F. 2002. Luminescent lines in corals from the Great Barrier Reef provide spatial and temporal records of reefs affected by land runoff. *Coral Reefs* **21**, 333-343.
Lough, J.M. & Cantin, N.E. 2014. Perspectives on massive coral growth rates in a changing ocean. *Biological Bulletin* **226**, 187-202.
Lough, J.M. & Cooper, T.F. 2011. New insights from coral growth band studies in an era of rapid environmental change. *Earth-Science Reviews* **108**, 170-184.
Lough, J.M., Lewis, S.E. & Cantin, N.E. 2015. Freshwater impacts in the central Great Barrier Reef: 1648-2011. *Coral Reefs* **34**:739-751.
Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H. & van Woesik, R. 2001. Coral bleaching: the winners and the losers. *Ecology Letters* **4**, 122-131.
Ma, T.Y.H. 1933. On the seasonal change of growth in some Palaeozoic corals. *Proceedings of the Imperial Academy (Tokyo)* **9**, 407-409.
Ma, T.Y.H. 1934. On the seasonal change of growth in a reef coral, *Favia speciosa* (Dana), and the water-temperature of the Japanese Seas during the latest geological times. *Proceedings of the Imperial Academy (Tokyo)* **10**, 353-356.
Ma, T.Y.H. 1937. On the growth rate of reef corals and its relation to sea water temperature. *Palaeontologia Sinica* **16**, 426.
Macintyre, I.G. 1975. A diver-operated hydraulic drill for coring submerged substrates. *Atoll Research Bulletin* **185**, 21-26.
Macintyre, I.G. & Glynn, P.W. 1976. Evolution of modern Caribbean fringing reef, Galeta Point, Panama. *AAPG Bulletin* **60**, 1054-1072.
Madin, J.S., Baird, A.H., Dornelas, M. & Connolly, S.R. 2014. Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecology Letters* **17**, 1008-1015.
Madin, J.S. & Connolly, S.R. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* **444**, 477-480.
Madin, J.S., Hoogenboom, M.O. & Connolly, S.R. 2012. Integrating physiological and biomechanical drivers of population growth over environmental gradients on coral reefs. *Journal of Experimental Biology* **215**, 968-976.
Madin, J.S., O'Donnell, M.J. & Connolly, S.R. 2008. Climate-mediated mechanical changes to post-disturbance coral assemblages. *Biology Letters* **4**, 490-493.
Maier, C., Felis, T., Pätzold, J. & Bak, R.P.M. 2004. Effect of skeletal growth and lack of species effects in the skeletal oxygen isotope climate signal within the coral genus *Porites*. *Marine Geology* **207**, 193-208.
Manton, S.M. 1932. On the growth of the adult colony of *Pocillopora bulbosa*. *Great Barrier Reef Expedition (1928–1929) Scientific Reports* **3**, 157-166.
Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. 1997. A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production. *Bulletin of the American Meteorological Society* **78**:1069-1079.
Manzello, D.P. 2010. Coral growth with thermal stress and ocean acidification: lessons from the eastern tropical Pacific. *Coral Reefs* **29**, 749-758.

Manzello, D.P., Kleypas, J.A., Budd, D.A., Eakin, C.M., Glynn, P.W. & Langdon, C. 2008. Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO_2 world. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 10450-10455.

Maragos, J.E. 1972. *A study of the ecology of Hawaiian reef corals*. Ph.D. thesis, University of Hawaii, Honolulu, USA.

Maragos, J.E. 1978. Coral growth: geometrical relationships. In *Coral Reefs: Research Methods*, D.R. Stoddart & R.E. Johannes (eds). Paris, France: UNESCO, 543-550.

Marsh, L.M. 1992. The occurrence and growth of *Acropora* in extra-tropical waters off Perth, Western Australia. *Proceedings of the Seventh International Coral Reef Symposium* **2**, 1233-1238.

Marshall, A.T. & Clode, P. 2004. Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. *Coral Reefs* **23**, 218-224.

Marshall, P.A. & Baird, A.H. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **19**, 155-163.

Martin, D.A. & Le Tissier, A. 1988. The growth and formation of branch tips of *Pocillopora damicornis* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **124**, 115-131.

Marubini, F., Barnett, H., Langdon, C. & Atkinson, M.J. 2001. Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Marine Ecology Progress Series* **220**:153-162.

Marubini, F., Ferrier-Pages, C. & Cuif, J.-P. 2003. Suppression of skeletal growth in scleractinian corals by decreasing ambient carbonate-ion concentration: A cross-family comparison. *Proceedings: Biological Sciences* **270**:179-184.

Mass, T. & Genin, A. 2008. Environmental versus intrinsic determination of colony symmetry in the coral *Pocillopora verrucosa*. *Marine Ecology Progress Series* **369**, 131-137.

Matson, E.G. 2011. Core Plugs. In *Encyclopedia of Modern Coral Reefs*, D. Hopley (ed.). Dordrecht, The Netherlands: Springer, 294-296.

May, W. 2012. Kaplan-Meier Survival Analysis. In: *Encyclopedia of Cancer*, Schwab, M. (eds). Berlin Heidelberg:Springer, pp1934-1937.

Mayor, A.G. 1924. Growth rate of Samoan corals. *Papers from the Department of Marine Biology of the Carnegie Institute of Washington* **19**, 51-72.

McClanahan, T.R., Ateweberhan, M. & Omukoto, J. 2008. Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Marine Biology* **153**, 755-768.

McClanahan, T.R., Baird, A.H., Marshall, P.A. & Toscano, M.A. 2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. *Marine Pollution Bulletin* **48**, 327-335.

McClanahan, T.R., Weil, E. & Maina, J. 2009. Strong relationship between coral bleaching and growth anomalies in massive *Porites. Global Change Biology* **15**:1804-1816.

McCulloch, M.T., Fallon, S.J., Wyndham, T., Hendy, E.J., Lough, J.M. & Barnes, D.J. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* **421**, 727-730.

McCulloch, M.T., Falter, J., Trotter, J. & Montagna, P. 2012. Coral resilience to ocean acidification and global warming through pH up-regulation. *Nature Climate Change* **2**, 623-627.

McGill, B.J. 2006. A renaissance in the study of abundance. *Science* **314**, 770-772.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**, 178-185.

Meesters, E.H., Wesseling, I. & Bak, R.P.M. 1996. Partial mortality in three species of reef-building corals and the relation with colony morphology. *Bulletin of Marine Science* **58**, 838-852.

Mehrbach, C., Culberson, C. H., Hawley, J. E. & Pytkowicz, R. M. 1973. Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. *Limnology and Oceanography* **18**, 897–907.

Mendes, J.M. 2004. Timing of skeletal band formation in *Montastraea annularis*: Relationship to environmental and endogenous factors. *Bulletin of Marine Science* **75**, 423-437.

Mendes, J.M. & Woodley, J.D. 2002. Effect of the 1995-1996 bleaching event on polyp tissue depth, growth, reproduction and skeletal band formation in *Montastraea annularis*. *Marine Ecology Progress Series* **235**, 93-102.

Messmer, V., Jones, G.P., Munday, P.L., Holbrook, S.J., Schmitt, R.J. & Brooks, A.J. 2011. Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology* **92**, 2285-2298.

Meyer, J.L. & Schultz, E.T. 1985. Tissue condition and growth-rate of corals associated with schooling fish. *Limnology and Oceanography* **30**, 157-166.

Mitsuguchi, T., Matsumoto, E. & Uchida, T. 2003. Mg/Ca and Sr/Ca ratios of *Porites* coral skeleton: Evaluation of the effect of skeletal growth rate. *Coral Reefs* **22**, 381-388.

Moberg, F. & Rönnbäck, P. 2003. Ecosystem services of the tropical seascape: interactions, substitutions and restoration. *Ocean & Coastal Management* **46**:27-46.

Montaggioni, L.F. 2005. History of Indo-Pacific coral reef systems since the last glaciation: development patterns and controlling factors. *Earth-Science Reviews* **71**, 1-75.

Moore, J.A.Y., Bellchambers, L.M., Depczynski, M.R., Evans, R.D., Evans, S.N., Field, S.N., Friedman, K.J., Gilmour, J.P., Holmes, T.H. & Middlebrook, R. 2012. Unprecedented mass bleaching and loss of coral across 12 of latitude in Western Australia in 2010–11. *PLoS ONE* **7**, e51807.

Moore, W.S. & Krishnaswami, S. 1972. Coral growth rates using ^{228}Ra and ^{210}Pb. *Earth and Planetary Science Letters* **15**, 187-190.

Morgan, K.M. & Kench, P.S. 2012. Skeletal extension and calcification of reef-building corals in the central Indian Ocean. *Marine Environmental Research* **81**, 78-82.

Mortensen, P.B., Rapp, H.T. & Båmstedt, U. 1998. Oxygen and carbon isotope ratios related to growth line patterns in skeletons of *Lophelia pertusa* (L.) (Anthozoa, Scleractinia): Implications for determination of linear extension rate. *Sarsia* **83**, 433-446.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., Van Vuuren, D.P., Carter, T.R., Emori, S., Kainuma, M. & Kram, T. 2010. The next generation of scenarios for climate change research and assessment. *Nature* **463**, 747-756.

Müller, A., Gagan, M.K. & Lough, J.M. 2004. Effect of early marine diagenesis on coral reconstructions of surface-ocean $^{13}C/^{12}C$ and carbonate saturation state. *Global Biogeochemical Cycles* **18**, GB1033.

Muir, P.R., Wallace, C.C., Done, T. & Aguirre, J.D. 2015. Limited scope for latitudinal extension of reef corals. *Science* **348**:1135-1138.

Munday, P.L. 2000. Interactions between habitat use and patterns of abundance in coral-dwelling fishes of the genus *Gobiodon*. *Environmental Biology of Fishes* **58**, 355-369.

Munday, P.L. 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* **128**, 585-593.

Murdoch, T.J.T. 2007. *A functional group approach for predicting the composition of hard coral assemblages in Florida and Bermuda*. Ph.D. thesis, University of South Alabama, Mobile, USA.

Muscatine, L. 1973. Nutrition of corals. In *Biology and Geology of Coral Reefs*, O.A. Jones & R. Endean (eds). New York, USA: Academic Press, 77-115.

Muscatine, L., McCloskey, L. & Marian, R. 1981. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnology and Oceanography* **26**:601-611.

Nakamura, T. & Yamasaki, H. 2005. Requirement of water-flow for sustainable growth of pocilloporid corals during high temperature periods. *Marine Pollution Bulletin* **50**, 1115-1120.

Naumann, M.S., Orejas, C. & Ferrier-Pagès, C. 2014. Species-specific physiological response by the cold-water corals *Lophelia pertusa* and *Madrepora oculata* to variations within their natural temperature range. *Deep Sea Research Part II: Topical Studies in Oceanography* **99**, 36-41.

Neudecker, S. 1977. Transplant experiments to test the effect of fish grazing on coral distribution. *Proceedings of the Third International Coral Reef Symposium* **1**, 317-323.

Neudecker, S. 1981. Growth and survival of scleractinian corals exposed to thermal effluents at Guam. *Proceedings of the Fourth International Coral Reef Symposium* **1**, 173-180.

Oliver, J.K. 1984. Intra-colony variation in the growth of *Acropora formosa*: extension rates and skeletal structure of white (zooxanthellae-free) and brown-tipped branches. *Coral Reefs* **3**, 139-147.

Oliver, J.K. 1985. Recurrent seasonal bleaching and mortality of corals on the Great Barrier Reef. *Proceedings of the Fifth International Coral Reef Symposium* **4**, 201-206.

Oliver J (1987) *Aspects of skeletal growth in the Indo-Pacific Staghorn coral Acropora formosa*. Doctoral Thesis. Townsville: James Cook University, p1-178.

Oliver, J.K., Chalker, B.E. & Dunlap, W.C. 1983. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. I. Long-term growth responses of *Acropora formosa* (Dana 1846). *Journal of Experimental Marine Biology and Ecology* **73**, 11-35.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A. & Joos, F. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**, 681-686.

Osborne, M.C., Dunbar, R.B., Mucciarone, D.A., Sanchez-Cabeza, J.-A. & Druffel, E. 2013. Regional calibration of coral-based climate reconstructions from Palau, West Pacific Warm Pool (WPWP). *Palaeogeography, Palaeoclimatology, Palaeoecology* **386**, 308-320.

Palardy, J.E., Grottoli, A.G. & Matthews, K.A. 2005. Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. *Marine Ecology Progress Series* **300**, 79-89.

Palardy, J.E., Rodrigues, L.J. & Grottoli, A.G. 2008. The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. *Journal of Experimental Marine Biology and Ecology* **367**, 180-188.

Pandolfi, J.M. 2002. Coral community dynamics at multiple scales. *Coral Reefs* **21**, 13-23.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R. & Jackson, J.B.C. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955-958.

Pandolfi, J.M. & Budd, A.F. 2008. Morphology and ecological zonation of Caribbean reef corals: the *Montastraea* '*annularis*' species complex. *Marine Ecology Progress Series* **369**, 89-102.

Pandolfi, J.M., Connolly, S.R., Marshall, D.J. & Cohen, A.L. 2011. Projecting coral reef

futures under global warming and ocean acidification. *Science* **333**, 418-22.
Pätzold, J. 1984. Growth rhythms recorded in stable isotopes and density bands in the reef coral *Porites lobata* (Cebu, Philippines). *Coral Reefs* **3**, 87-90.
Pelejero, C., Calvo, E. & Hoegh-Guldberg, O. 2010. Paleo-perspectives on ocean acidification. *Trends in Ecology & Evolution* **25**, 332-344.
Pellissier, L., Leprieur, F., Parravicini, V., Cowman, P.F., Kulbicki, M., Litsios, G., Olsen, S.M., Wisz, M.S., Bellwood, D.R. & Mouillot, D. 2014. Quaternary coral reef refugia preserved fish diversity. *Science* **344**:1016-1019.
Penin, L., Michonneau, F., Baird, A.H., Connolly, S.R., Pratchett, M.S., Kayal, M. & Adjeroud, M. 2010. Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology Progress Series* **408**, 55-64.
Perry, C.T., Murphy, G.N., Kench, P.S., Smithers, S.G., Edinger, E.N., Steneck, R.S. & Mumby, P.J. 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature Communications* **4**, 1402.
Perry, C.T., Spencer, T. & Kench, P.S. 2008. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* **27**, 853-866.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-124, http://CRAN.R-project.org/package=nlme.
Pisapia, C., Anderson, K. & Pratchett, M.S. 2014. Intraspecific variation in physiological condition of reef-building corals associated with differential levels of chronic disturbance. *PLoS ONE* **9**, e91529.
Pollock, F.J., Lamb, J.B., Field, S.N., Heron, S.F., Schaffelke, B., Shedrawi, G., Bourne, D.G. & Willis, B.L. 2014. Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. *PLoS ONE* **9**, e102498.
Porter, J.W. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. *American Naturalist* **110**, 731-742.
Porter, J.W., Fitt, W.K., Spero, H.J., Rogers, C.S. & White, M.W. 1989. Bleaching in reef corals: Physiological and stable isotopic responses. *Proceedings of the National Academy of Sciences* **86**:9342-9346.
Pörtner, H.-O. 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **132**, 739-761.
Poulsen, A., Burns, K., Lough, J., Brinkman, D. & Delean, S. 2006. Trace analysis of hydrocarbons in coral cores from Saudi Arabia. *Organic Geochemistry* **37**, 1913-1930.
Pratchett, M.S., Anderson, K.D., Hoogenboom, M.O., Widman, E., Baird, A.H., Pandolfi, J.M., Edmunds, P.J. & Lough, J.M. 2015. Spatial, temporal and taxonomic variation in coral growth: Implications for the structure and function of coral reef ecosystems. *Oceanography and Marine Biology: An Annual Review* **53:**215-295.
Pratchett, M.S., Caballes, C.F., Rivera Posada, J.A. & Sweatman, H.P.A. 2014. Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). *Oceanography and Marine Biology: An Annual Review* **52**, 133-200.
Pratchett, M.S., McCowan, D., Maynard, J.A. & Heron, S.F. 2013. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS ONE* **8**, e70443.
Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V.C. & Mcclanahan, T.R. 2008. Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences.

Oceanography and Marine Biology: An Annual Review **46**, 251-296.
Pratchett, M.S., Trapon, M., Berumen, M. & Chong-Seng, K. 2011. Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs* **30**:183-193
Pratchett, M.S., Wilson, S.K., Graham, N.A.J., Munday, P.L., Jones, G.P. & Polunin, N.C. (2009) Coral Bleaching and Consequences for Motile Reef Organisms: Past, Present and Uncertain Future Effects. In: *Ecological Studies: Analysis and Synthesis*, VanOppen M, Lough J (eds). Berlin, Germany Townsville: Springer-Verlag Berlin, Heidelberger Platz 3, D-14197, pp139-158.
Preiss, K., Thomassin, B.A., Heiss, G.A., Dullo, W.-C. & Camoin, G. 1995. Varibility in growth-rate of massive *Porites* in the coral reefs of Mayotte Island. *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la Vie* **318**, 1147-1154.
Putnam, H.M. & Gates, R.D. (2015) Preconditioning in the reef-building coral *Pocillopora damicornis* and the potential for trans-generational acclimatization in coral larvae under future climate change conditions. *Journal of Experimental Biology* **218**:2365-2372
R Core Team. 2014/2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.
Reed, J.K. 1981. In situ growth rates of the scleractinian coral *Oculina varicosa* occurring with zooxanthellae on 6-m reefs and without on 80-m banks. *Proceedings of the Fourth International Coral Reef Symposium* **2**, 201-206.
Reynaud, S., Ferrier-Pagès, C., Meibom, A., Mostefaoui, S., Mortlock, R., Fairbanks, R. & Allemand, D. 2007. Light and temperature effects on Sr/Ca and Mg/Ca ratios in the scleractinian coral *Acropora sp*. *Geochimica et Cosmochimica Acta* **71**:354-362.
Reynaud, S., Leclercq, N., Romaine-Lioud, S., Ferrier-Pages, C., Jaubert, J. & Gattuso, J.P. (2003) Interacting effects of CO2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biology* **9**:1660-1668.
Rinkevich, B., & Loya, Y. 1986. Senescence and dying signals in a reef building coral. *Experientia* **42**, 320-322.
Richardson, A.J. 2008. In hot water: zooplankton and climate change. *ICES Journal of Marine Science* **65**, 279-295.
Riegl, B.M. & Purkis, S.J. 2009. Model of coral population response to accelerated bleaching and mass mortality in a changing climate. *Ecological Modelling* **220**, 192-208.
Ritchie, R.J. 2008. Universal chlorophyll equations for estimating chlorophylls a, b, c, and d and total chlorophylls in natural assemblages of photosynthetic organisms using acetone, methanol, or ethanol solvents. *Photosynthetica* **46**:115-126.
Roberts, L.G. & Harriott, V.J. 2003. Can environmental records be extracted from coral skeletons from Moreton Bay, Australia, a subtropical, turbid environment? *Coral Reefs* **22**, 517-522.
Roche, R.C., Abel, R.A., Johnson, K.G. & Perry, C.T. 2010. Quantification of porosity in *Acropora pulchra* (Brook 1891) using X-ray micro-computed tomography techniques. *Journal of Experimental Marine Biology and Ecology* **396**, 1-9.
Rodgers, K.u., Cox, E. & Newtson, C. 2003. Effects of mechanical fracturing and experimental trampling on Hawaiian corals. *Environmental Management* **31**, 0377-0384.
Rodolfo-Metalpa, R., Hoogenboom, M.O., Rottier, C., Ramos-Esplá, A., Baker, A.C., Fine, M. & Ferrier-Pagès, C. 2014. Thermally tolerant corals have limited capacity to acclimatize to future warming. *Global Change Biology* **20**, 3036-3049.
Rodolfo-Metalpa, R., Houlbreque, F., Tambutte, E., Boisson, F., Baggini, C., Patti, F.P., Jeffree, R., Fine, M., Foggo, A., Gattuso, J.P. & Hall-Spencer, J.M. 2011 Coral and

mollusc resistance to ocean acidification adversely affected by warming. *Nature Climate Change* **1**:308-312.
Rodolfo-Metalpa, R., Peirano, A., Houlbrèque, F., Abbate, M. & Ferrier-Pagès, C. 2008 Effects of temperature, light and heterotrophy on the growth rate and budding of the temperate coral *Cladocora caespitosa*. *Coral Reefs* **27**:17-25.
Rodrigues, L.J. & Grottoli, A.G. 2007. Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnology and Oceanography* **52**:1874-1882.
Rogers, A., Blanchard, J.L. & Mumby, .PJ. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* **24**:1000-1005.
Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* **62**, 185-202.
Romano, S.L. 1990. Long-term effects of interspecific aggression on growth of the reef-building corals *Cyphastrea ocellina* (Dana) and *Pocillopora damicornis* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **140**, 135-146.
Rosenfeld, M., Bresler, V. & Abelson, A. 1999. Sediment as a possible source of food for corals. *Ecology Letters* **2**, 345-348.
Rosenfeld, M., Yam, R., Shemesh, A. & Loya, Y. 2003. Implication of water depth on stable isotope composition and skeletal density banding patterns in a *Porites lutea* colony: results from a long-term translocation experiment. *Coral Reefs* **22**, 337-345.
Rotjan, R.D. & Lewis, S.M. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* **367**, 73-91.
Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Wallace, D.W.R., Tilbrook, B., Millero, F.J., Peng, T.-H., Kozyr, A., Ono, T. & Rios, A.F. (2004) The Oceanic Sink for Anthropogenic CO2. *Science* **305**:367-371.
Sabine, C., Hankin, S., Koyuk, H., Bakker, D.C., Pfeil, B., Olsen, A., Metzl, N., Kozyr, A., Fassbender, A. & Manke, A. 2012. Surface Ocean CO2 Atlas (SOCAT) gridded data products. *Earth System Science Data Discussions* **5**:781-804.
Saenger, C., Cohen, A.L., Oppo, D.W., Halley, R.B. & Carilli, J.E. 2009. Surface-temperature trends and variability in the low-latitude North Atlantic since 1552. *Nature Geoscience* **2**, 492-495.
Saenger, C., Cohen, A.L., Oppo, D.W. & Hubbard, D. 2008. Interpreting sea surface temperature from strontium/calcium ratios in *Montastrea* corals: Link with growth rate and implications for proxy reconstructions. *Paleoceanography* **23**, PA3102.
Sano, M., Shimizu, M. & Nose, Y. 1987. Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series* **37**, 191-199.
Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S. & Schmid, B. 2012. Fiji: an open-source platform for biological-image analysis. *Nature methods* **9**:676-682.
Schlager, W. 1981. The paradox of drowned reefs and carbonate platforms. *Geological Society of America Bulletin* **92**, 197-211.
Schmidt-Roach, S., Miller, K.J., Lundgren, P. & Andreakis, N. 2014. With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zoological Journal of the Linnean Society* **170**:1-33.
Schneider, K. & Erez, J. 2006. The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnology and Oceanography* **51**:1284-1293.
Schutter, M., Crocker, J., Paijmans, A., Janse, M., Osinga, R., Verreth, A. & Wijffels, R.H. 2010. The effect of different flow regimes on the growth and metabolic rates of the

scleractinian coral *Galaxea fascicularis*. *Coral Reefs* **29**, 737-748.
Scoffin, T.P., Tudhope, A.W., Brown, B.E., Chansang, H. & Cheeney, R.F. 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral Reefs* **11**, 1-11.
Seo, I., Lee, Y.I., Watanabe, T., Yamano, H., Shimamura, M., Yoo, C.M. & Hyeong, K. 2013. A skeletal Sr/Ca record preserved in *Dipsastraea* (*Favia*) *speciosa* and implications for coral Sr/Ca thermometry in mid-latitude regions. *Geochemistry, Geophysics, Geosystems* **14**, 2873-2885.
Shaish, L., Levy, G., Katzir, G. & Rinkevich, B. 2010. Employing a highly fragmented, weedy coral species in reef restoration. *Ecological Engineering* **36**, 1424-1432.
Shi, Q., Yu, K.F., Chen, T.R., Zhang, H.L., Zhao, M.X. & Yan, H.Q. 2012. Two centuries-long records of skeletal calcification in massive *Porites* colonies from Meiji Reef in the southern South China Sea and its responses to atmospheric CO_2 and seawater temperature. *Science China Earth Sciences* **55**, 1-12.
Shinn, E.A. 1966. Coral growth-rate, an environmental indicator. *Journal of Paleontology* **40**, 233-240.
Silverman, J., Lazar, B., Cao, L., Caldeira, K. & Erez, J. (2009) Coral reefs may start dissolving when atmospheric CO2 doubles. *Geophysical Research Letters* **36**: L05606.
Simberloff, D. 2004. Community ecology: is it time to move on? *American Naturalist* **163**, 787-799.
Simpson, C.J. 1988. Ecology of scleractinian corals in the Dampier Archipelago, Western Australia. *Technical Series No. 23*, Perth, Australia: Environmental Protection Authority.
Smith, L.W., Barshis, D. & Birkeland, C. 2007. Phenotypic plasticity for skeletal growth, density and calcification of *Porites lobata* in response to habitat type. *Coral Reefs* **26**, 559-567.
Smith, S.V. 1973. Carbon dioxide dynamics: a record of organic carbon production, respiration, and calcification in the Eniwetok reef flat community. *Limnology and Oceanography* **18**, 106-120.
Smith, S.V. 1981. The Houtman Abrolhos Islands: carbon metabolism of coral reefs at high latitude. *Limnology and Oceanography* **26**, 612-621.
Smith, S.V. & Buddemeier, R.W. 1992. Global Change and Coral Reef Ecosystems. *Annual Review of Ecology and Systematics* **23**:89-118.
Smith, S.V. & Kinsey, D.W. 1978. Calcification and organic carbon metabolism as indicated by carbon dioxide. In *Coral Reefs: Research Methods*, D.R. Stoddart & R.E. Johannes (eds). Paris, France: UNESCO, 469-484.
Sowa, K., Watanabe, T., Kan, H. & Yamano, H. 2014. Influence of land development on Holocene *Porites* coral calcification at Nagura Bay, Ishigaki Island, Japan. *PLoS ONE* **9**, e88790.
Sowa, K., Watanabe, T., Nakamura, T., Sakai, S. & Sakamoto, T. 2013. Estimation of uncertainty for massive *Porites* coral skeletal density. *JAMSTEC Report of Research and Development* **16**, 31-39.
Spalding, M.D., Ravilious, C. & Green, E.P. 2001. World Atlas of Coral Reefs. Berkeley, USA:University of California Press.
Stafford-Smith, M.G. & Ormond, R.F.G. 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Marine and Freshwater Research* **43**, 683-705.
Stearn, C. W., & Colassin, C. 1979. A simple underwater pneumatic hand drill. *Journal of Paleontology* **53**, 1257-1259.
Stearn, C.W., Scoffin, T.P. & Martindale, W. 1977. Calcium carbonate budget of a fringing

reef on the west coast of Barbados. Part I—Zonation and Productivity. *Bulletin of Marine Science* **27**, 479-510.
Stehli, F.G. & Wells, J.W. 1971. Diversity and age patterns in hermatypic corals. *Systematic Biology* **20**, 115-126.
Stella, J.S., Pratchett, M.S., Hutchings, P.A. & Jones, G.P. 2011. Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology: An Annual Review* **49**, 43-104.
Stephenson, T.A. & Stephenson, A. 1933. Growth and asexual reproduction in corals. *Great Barrier Reef Expedition (1928–1929) Scientific Reports* **3**, 167-217.
Stimson, J. 1985. The effect of shading by the table coral *Acropora hyacinthus* on understory corals. *Ecology* **66**, 40-53.
Stimson, J. 1987. Location, quantity and rate of change in quantity of lipids in tissue of Hawaiian hermatypic corals. *Bulletin of Marine Science* **41**:889-904.
Stimson, J. 1996. Wave-like outward growth of some table- and plate-forming corals, and a hypothetical mechanism. *Bulletin of Marine Science* **58**, 301-313.
Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M. (eds). 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
Storz, D. & Gischler, E. 2011. Coral extension rates in the NW Indian Ocean I: reconstruction of 20th century SST variability and monsoon current strength. *Geo-Marine Letters* **31**, 141-154.
Strahl, J., Stolz, I., Uthicke, S., Vogel, N., Noonan, S.H.C. & Fabricius, K.E. 2015. Physiological and ecological performance differs in four coral taxa at a volcanic carbon dioxide seep. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **184**:179-186.
Strong, C. & Magnusdottir, G. 2009. The role of tropospheric rossby wave breaking in the Pacific decadal oscillation. *Journal of Climate* **22**:1819-1829,1831-1833.
Suresh, V.R. & Mathew, K.J. 1993. Skeletal extension of staghorn coral *Acropora formosa* in relation to environment at Kavaratti atoll (Lakshadweep). *Indian Journal of Marine Sciences* **22**, 176-179.
Suresh, V.R. & Mathew, K.J. 1995. Growth of staghorn coral *Acropora aspera* (Dana)(Scleractinia: Acropridae) in relation to environmental factors at Kavaratti atoll (Lakshadweep Islands), India. *Indian Joumal of Marine Sciences* **24**, 175-176.
Suzuki, A., Kawahata, H., Tanimoto, Y., Tsukamoto, H., Gupta, L. & Yukino, I. 2000. Skeletal isotopic record of a *Porites* coral during the 1998 mass bleaching event. *Geochemical Journal (Japan)* **34**, 321-329.
Tambutté, S., Holcomb, M., Ferrier-Pagès, C., Reynaud, S., Tambutté, É., Zoccola, D. & Allemand, D. 2011. Coral biomineralization: from the gene to the environment. *Journal of Experimental Marine Biology and Ecology* **408**, 58-78.
Tanner, J.E. 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* **190**, 151-168.
Tanner, J.E. 1997. Interspecific competition reduces fitness in scleractinian corals. *Journal of Experimental Marine Biology and Ecology* **214**, 19-34.
Tanzil, J.T.I., Brown, B.E., Dunne, R.P., Lee, J.N., Kaandorp, J.A. & Todd, P.A. 2013. Regional decline in growth rates of massive *Porites* corals in Southeast Asia. *Global Change Biology* **19**, 3011-3023.
Tanzil, J.T.I., Brown, B.E., Tudhope, A.W. & Dunne, R.P. 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and

2005. *Coral Reefs* **28**, 519-528.
Tentori, E. & Allemand, D. 2006. Light-enhanced calcification and dark decalcification in isolates of the soft coral *Cladiella* sp. during tissue recovery. *Biological Bulletin* **211**, 193-202.
Thornhill, D.J., Rotjan, R.D., Todd, B.D., Chilcoat, G.C., Iglesias-Prieto, R., Kemp, D.W., LaJeunesse, T.C., Reynolds, J.M., Schmidt, G.W., Shannon, T., Warner, M.E. & Fitt, W.K. 2011. A connection between colony biomass and death in Caribbean reef-building corals. *PLoS ONE* **6**:e29535.
Tomascik, T. 1990. Growth rates of two morphotypes of *Montastrea annularis* along a eutrophication gradient, Barbados, WI. *Marine Pollution Bulletin* **21**, 376-381.
Tomascik, T. & Sander, F. 1985. Effects of eutrophication on reef-building corals. *Marine Biology* **87**, 143-155.
Tomascik, T., Suharsono & Mah, A.J. 1993. Case histories: a historical perspective of the natural and anthropogenic impacts in the Indonesian Archipelago with a focus on the Kepulauan Seribu, Java Sea.In *Proceedings of the Colloquium on Global Aspects of Coral Reefs, Health, Hazards, and History*, R.N. Ginsburg (compiler). Florida, USA: Rosenstiel School of Marine and Atmospheric Science, University of Miami, 304-310.
Torres, J.L., Armstrong, R.A., Corredor, J.E. & Gilbes, F. 2007. Physiological responses of *Acropora cervicornis* to increased solar irradiance. *Photochemistry and Photobiology* **83**, 839-850.
Tremblay, P., Grover, R., Maguer, J.-F., Hoogenboom, M. & Ferrier-Pagès, C. 2014. Carbon translocation from symbiont to host depends on irradiance and food availability in the tropical coral *Stylophora pistillata*. *Coral Reefs* **33**, 1-13.
Tudhope, A.W., Allison, N., Le Tissier, M.D.A. & Scoffin, T.P. 1992. Growth characteristics and susceptibility to bleaching in massive *Porites* corals, South Thailand. *Proceedings of the Seventh International Coral Reef Symposium* **1**, 64-69.
Tunnicliffe, V. 1983. Caribbean staghorn coral populations: pre-Hurricane Allen conditions in Discovery Bay, Jamaica. *Bulletin of Marine Science* **33**, 132-151.
United Nations Education, Scientific and Cultural Organization (UNESCO). 2014. Lord Howe Island Group. Accessed 25 June 2014. http://whc.unesco.org/en/list/186.
Uthicke, S. & Fabricius, K.E. 2012. Productivity gains do not compensate for reduced calcification under near-future ocean acidification in the photosynthetic benthic foraminifer species *Marginopora vertebralis*. *Global Change Biology* **18**:2781-2791.
van Hooidonk, R., Maynard, J.A., Manzello, D. & Planes, S. 2014. Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. *Global Change Biology* **20**, 103-112.
van Hooidonk, R., Maynard, J.A. & Planes, S. 2013. Temporary refugia for coral reefs in a warming world. *Nature Climate Change* **3**, 508-511.
van Veghel, M.L.J. & Bosscher, H. 1995. Variation in linear growth and skeletal density within the polymorphic reef building coral *Montastrea annularis*. *Bulletin of Marine Science* **56**, 902-908.
Venn, A., Tambutté, E., Holcomb, M., Allemand, D. & Tambutté, S. 2011. Live tissue imaging shows reef corals elevate pH under their calcifying tissue relative to seawater. *PLoS ONE* **6**:e20013.
Venn, A.A., Tambutté, E., Holcomb, M., Laurent, J., Allemand, D. & Tambutté, S. 2013. Impact of seawater acidification on pH at the tissue–skeleton interface and calcification in reef corals. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 1634-1639.
Wallace, C.C. 1999. *Staghorn Corals of the World: a Revision of the Coral Genus* Acropora. Collingwood, Australia: CSIRO publishing.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* **416**, 389-395.

Ward, S. 1995. The effect of damage on the growth, reproduction and storage of lipids in the scleractinian coral *Pocillopora damicornis* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* **187**, 193-206.

Waterhouse, J., Brodie, J., Tracey, D., Lewis, S.E., Hateley, L., Brinkman, R., Furnas, M., Wolff, N., da Silva, E., O'Brien, D. & McKenzie, L. 2014. Assessment of the relative risk of water quality to ecosystems of the Wet Tropics Region, Great Barrier Reef. A report to Terrain NRM, Innisfail TropWATER Report 14/27, Townsville, Australia.

Weber, J.N. & White, E.W. 1974. Activation energy for skeletal aragonite deposited by the hermatypic coral *Platygyra* spp. *Marine Biology* **26**, 353-359.

Weber, J.N. & White, E.W. 1977. Caribbean reef corals *Montastrea annularis* and *Montastrea cavernosa* - long-term growth data as determined by skeletal X-radiography. In *Reefs and Related Carbonates: Ecology and Sedimentology*, S.H. Frost et al. (eds). Oklahoma, USA: American Association of Petroleum Geologists, 171-179.

Wellington, G.M. 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. *Oecologia* **52**, 311-320.

Wellington, G.M. & Glynn, P.W. 1983. Environmental influences on skeletal banding in eastern Pacific (Panama) corals. *Coral Reefs* **1**, 215-222.

Wells, J.W. 1957. Corals. *Geological Society of America Memoirs* **67**, 1087-1104.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S. & Rousseaux, C.S. 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change* **3**, 78-82.

Whitfield, R.P. 1898. Notice of a remarkable specimen of the West India coral *Madrepora palmata*. *Bulletin of the American Museum of Natural History* **10**, 463-465.

Wijgerde, T., Diantari, R., Lewaru, M.W., Verreth, J.A.J. & Osinga, R. 2011. Extracoelenteric zooplankton feeding is a key mechanism of nutrient acquisition for the scleractinian coral *Galaxea fascicularis*. *Journal of Experimental Biology* **214**, 3351-3357.

Wilkinson, C. 2008. *Status of Coral Reefs of the World: 2008*. Townsville, Australia: Global Coral Reef Monitoring Network and Rainforest Research Centre.

Wilson, S., Dolman, A., Cheal, A., Emslie, M., Pratchett, M. & Sweatman, H. 2009. Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs* **28**:3-14.

Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P. & Polunin, N.V.C. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* **12**, 2220-2234.

Wood, R. 1998. The ecological evolution of reefs. *Annual Review of Ecology and Systematics* **29**, 179-206.

Veron, J.E.N. 1986 Corals of Australia and the Indo-Pacific. North Ryde, N.S.W.: Angus & Robertson.

Yap, H.T. & Gomez, E.D. 1981. Growth of *Acropora pulchra* (Brook) in Bolinao, Pangasinan, Philippines. *Proceedings of the Fourth International Coral Reef Symposium* **2**, 207-213.

Yap, H.T. & Gomez, E.D. 1985. Growth of *Acropora pulchra*. *Marine Biology* **87**, 203-209.

Zhao, M.X., Yu, K.F., Zhang, Q.M., Shi, Q. & Roff, G. 2014. Age structure of massive *Porites lutea* corals at Luhuitou fringing reef (northern South China Sea) indicates recovery following severe anthropogenic disturbance. *Coral Reefs* **33**, 39-44.

Appendix A. Supplementary Tables

Table A1. *A. muricata* (*A. formosa*) growth data from May 1980-Jan 1981 at Davies Reef published in Oliver (1987), PhD Thesis, "Aspects of skeletal growth in the Indo-Pacific Staghorn coral *Acropora formosa*", James Cook University, p 1-178. Data was provided for the (a) 5 m, (b) 10 m and (c) 15 m.

a) 5 m site extension for cm/30 days

Sample	Date	Count	Mean	Stdev	se	min	max
1	May-80	56	0.5957	0.354	0.047	0	1.2171
2	Jul-80	56	0.5381	0.281	0.038	0	0.9512
3	Sep-80	33	0.2479	0.183	0.032	0	0.624
4	Oct-80	53	0.6318	0.247	0.034	0.065	1.0864
5	Dec-80	43	0.6761	0.326	0.050	0	1.2371
6	Feb-81	39	0.8036	0.357	0.057	0	1.6424
7	Apr-81	39	0.9518	0.394	0.063	0.073	1.5523
8	Jun-81	36	0.8212	0.365	0.061	0.063	1.3858
9	Sep-81	36	0.7863	0.228	0.038	0.33	1.2717
10	Nov-81	32	0.6503	0.232	0.041	0.183	0.9667
11	Jan-81	26	0.8248	0.327	0.064	0.084	1.4745

b) 10 m site extension for cm/30 days

Sample	Date	Count	Mean	Stdev	se	min	max
1	May-80	46	1.214	0.225	0.033	0.6496	1.5818
2	Jul-80	49	0.948	0.319	0.046	0.1743	1.4629
3	Sep-80	32	0.843	0.277	0.049	0.1286	1.1633
4	Oct-80	75	1.045	0.313	0.036	0.2107	1.5698
5	Dec-80	35	1.135	0.322	0.054	0.3067	1.6989
6	Feb-81	32	0.543	0.486	0.086	0.0234	1.442
7	Apr-81	31	1.341	0.340	0.061	0.0809	1.9965
8	Jun-81	53	1.2	0.297	0.041	0.4257	1.6403
9	Sep-81	44	1.124	0.261	0.039	0.5346	1.5969
10	Nov-81	37	1.04	0.253	0.042	0.49	1.4717
11	Jan-81	34	0.861	0.355	0.061	0.1042	1.3942

c) 15 m site extension for cm/30 days

Sample	Date	Count	Mean	Stdev	se	min	max
1	May-80	39	1.541	0.395	0.063	0.3739	2.1054
2	Jul-80	45	1.389	0.374	0.056	0.3781	1.9465
3	Sep-80	55	1.165	0.344	0.046	0.1861	1.7192
4	Oct-80	60	1.332	0.451	0.058	0	1.867
5	Dec-80	36	1.505	0.484	0.081	0.1276	2.0945
6	Feb-81	36	1.173	0.608	0.101	0	2.1498
7	Apr-81	33	1.36	0.457	0.079	0.0617	1.9363
8	Jun-81	40	1.206	0.618	0.098	0.411	1.9085
9	Sep-81	35	1.05	0.649	0.110	0.144	1.9238
10	Nov-81	32	1.246	0.342	0.060	0.3667	1.975
11	Dec-81	29	0.899	0.674	0.125	0	2.0626

Appendix B. Other scientific contributions during candidature

Anderson, K.D., Pratchett, M.S. & Baird, A.H. 2012. Summer growth rates of corals at Lord Howe Island, Australia. *Proceedings of the Twelfth International Coral Reef Symposium* **4C**, 1-5.

Anderson, K. & Pratchett, M. 2014. Variation in size-frequency distributions of branching corals between a tropical versus sub-tropical reef. *Marine Ecology Progress Series* **502**:117-128.

Pisapia, C., Anderson, K. & Pratchett, M.S. 2014. Intraspecific Variation in Physiological Condition of Reef-Building Corals Associated with Differential Levels of Chronic Disturbance. *Plos One* **9**:e91529.

Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012
4C Coral reef response to multiple stresses: organisms to ecosystems

Summer growth rates of corals at Lord Howe Island, Australia

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Abstract. Spatial, temporal and taxonomic differences in coral growth play an important role in the ecology and dynamics of coral reef ecosystems, affecting reef productivity, heterogeneity, and growth. Moreover, climate change poses an increasing risk to the future status of coral reefs with increasing ocean temperature and acidification causing reductions in growth of reef-building corals, if not survivorship. The purpose of this study was to measure the growth rate of six scleractinian corals, *Acropora yongei*, *Isopora cuneata*, *Pocillopora damicornis*, *Porites heronensis, Seriatopora hystrix* and *Stylophora pistillata,* at Lord Howe Island, Australia's southernmost coral reef environment, during the 2010-11 summer growing season. Measurements were taken to compare growth rates of corals from other sub-tropical locations, and greatly increase understanding of the effects of climate change on coral growth. At high latitude locations (subtropical reefs), coral growth is currently limited by the cool winter temperatures and climate related increases in ocean temperature may extend the summer growing period. Conversely, aragonite saturation declines with increasing latitude and climate-induced ocean acidification may further reduce the capacity for growth of calcifying organisms at the latitudinal limits of reef growth. Coral growth (specifically, linear extension) was measured at North Bay and Horseshoe Reef using i) Alizarin staining, and ii) changes in length of individually tagged branches. *Acropora* displayed at least two fold higher growth rates, significantly greater than other genera, whereas *Pocillopora* had the lowest growth rate. There was limited evidence of recent increases in growth rates of corals, rather growth rates of *Pocillopora* were much lower than expected. While very preliminary, these findings suggest that declining aragonite saturation, which will have most pronounced effects on high latitude reefs, are already offsetting any positive effect of increasing temperature.

Key words: Coral reef, Linear extension, Subtropics

Introduction

Climate change poses a significant and increasing risk to the distribution and survival of reef-building corals (Hoegh-Guldberg 1999), as many reef-building corals are extremely sensitive to sustained and ongoing increases in ocean temperatures (Hughes et al. 2003), as well as emerging effects of ocean acidification (Hoegh-Guldberg et al. 2007). Most corals are adapted to local environmental temperature (Hughes et al. 2003), and typically bleach and die if the local temperature exceeds the normal summer maxima by >1°C for 3 to 4 weeks (Hoegh-Guldberg 1999). Even if climate change does not significantly and directly alter the survivorship of reef building corals, there are likely to be significant consequences for individual growth rates (e.g., Cooper et al. 2008, Cantin et al. 2010). Cooper et al. (2008) for example showed that calcification, a proxy for growth, of massive *Porites* on Australia's Great Barrier Reef has declined by 21% from 1988 to 2003.

Recent declines in growth rates have also been demonstrated for branching corals, including *Pocillopora* from Pacific Panama (Manzello 2010) and *Acropora palmata* in the Caribbean (Bak et al. 2009). However, both these studies were conducted in locations where aragonite saturation is expected to limit coral growth, rather than temperature. Branching corals are generally considered to be much more susceptible to extreme temperatures (Marshall and Baird 2000) and ocean acidification (Fabricius et al. 2011), compared to massive coral species. However, measuring specific responses of branching corals to changing environmental conditions requires direct measurements because annual density bands, used to hindcast growth rates of massive corals, are rarely present (Gladfelter 1982). For branching corals, any effects of declining calcification on linear extension may also be offset by reductions in skeletal density (Lough 2008).

Changes in environmental conditions may have both positive and negative effects on coral growth. At some subtropical reefs, coral growth is currently limited by cool winter temperatures (Harriott 1999, Crossland 1981), whereby coral growth is negligible

during winter months. Consequently, increasing temperatures due to climate change may greatly extend the growing period, leading to overall to increases in annual growth rates (Cooper et al. 2012). However, positive effects of increasing temperature at subtropical locations may be offset by declines in carbonate saturation. Aragonite saturation declines with increasing latitude and climate-induced ocean acidification may further reduce the capacity for growth of calcifying organisms at the latitudinal limits of reef growth (Kleypas et al. 1999).

The aim of this study was to quantify summer growth rates for a range of scleractinian corals, especially, branching species, at Lord Howe Island. Lord Howe, located at 31.5˚S, represents eastern Australia's southernmost coral reef formation (Harriott et al. 1995). Coral assemblages at this location are relatively depauperate, comprising approximately 83 species (Harriott et al. 1995).

Material and Methods

This study was conducted in December 2010 to March 2011 at Lord Howe Island, located 600 kilometres off the coast of New South Wales, Australia. Sampling for this study was conducted at North Bay (S31°31.273, E159°2.773) and Horseshoe Reef (S31°32.554, E159°3.704), located 1.5 kilometres apart within the extensive lagoon system that extends along the northwest coastline of Lord Howe Island. At each site, a 20 metre long permanent transect was established at 4 m depth, marked using 50 cm stainless steel stakes hammered into the reef.

Study species

Growth rates were measured for 6 species of scleractinian corals: *Acropora spp., Porites heronensis, Pocillopora damicornis, Isopora cuneata, Stylophora pistillata* and *Seriatopora hystrix.* Measurements of growth rates for *Acropora* spp. were mostly conducted using large and distinctive colonies of *Acropora yongei*, but given the relatively low number of colonies of clear taxonomic identity and atypical morphologies of *Acropora* at Lord Howe Island (A. Baird, unpublished data), a wide range of different *Acropora* species of uncertain species identity were sampled.

Coral growth rates were quantified by comparing changes in size over the 15 week summer growth period, from December 12-15, 2010 to March 24-31, 2011. Linear extension of corals was measured using two methods: i) directly measuring changes in the length of branches or columns from a fixed reference point, marked using plastic cable ties; ii) recording the extent of new skeletal growth by staining corals with Alizarin-red, following Lamberts (1978) and Harriott (1999). A total of three branches per colony were selected and tagged using small plastic cable ties. Cable ties were secured 10-30 mm from the tip of each branch, then recording the exact distance from the top of the tie buckle to the branch tip on each sampling occasion (Fig. 1). Corals selected for staining (Table 1), were completely enclosed within a plastic bag, and exposed to 10 mg/L of Alizarin Red. Given limited success in staining corals on subtropical reefs (e.g., Harriott 1999) the exposure time was increased from 3-4 hours (which is commonly used at tropical locations) to 7-8 hours, accounting for slow rates of calcification. After 15 weeks, stained corals were sacrificed to measure the linear extent of new growth above well-defined staining bands. Linear extension was measured on 20-34 branches per colony (Table 1), depending on colony size.

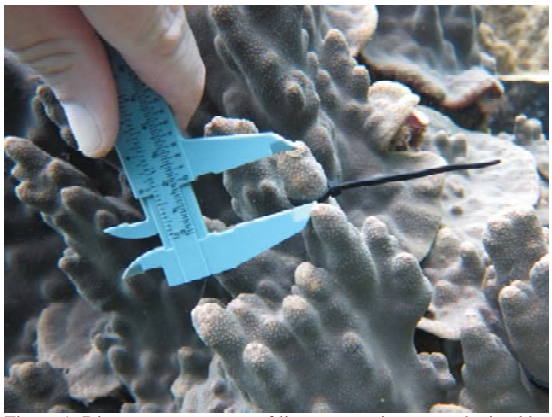

Figure 1: Direct measurements of linear extension were obtained by recording the distance from the cable tie to the branch tip, using callipers, on each sampling occasion.

Table 1: Number of colonies (C) and branches (Br) used for direct tagged linear extension, and stained linear extension.

	Direct		Stained	
	C	Br	C	Br
Acropora	28	67	4	110
Isopora	22	65	4	78
Pocillopora	23	67	3	224
Porites	24	70	4	89
Seriatopora	21	49	4	175
Stylophora	20	51	4	135

Statistical Analysis

Variation in linear extension was analysed using a mixed-model analysis of variance (ANOVA), testing for differences among locations, among genera, and among colonies (within genera). Due to the limited number of colonies stained using Alizarin red, analyses were conducted to first confirm that there was no significant ($p>0.05$) effect of location, and then data from both locations was pooled to test for differences among genera, and among colonies

(within genera). Tukey's' HSD post hoc tests were used to identify specific differences among genera, following ANOVA.

Results

Direct Tagging

Linear extension, measured as change in length for individually tagged branches (or columns), was quantified for 394 branches, on 138 colonies from 6 genera. Of the 394 branches that were tagged in December 2010, 93.7% (369/394) were alive and growing in March 2011. Estimates of linear extension obtained using direct tagging were consistent between sites for all genera except *Acropora* where the linear extension at Horseshoe Reef was 14.76 ± 1.45 mm (mean ± SE) and North Bay was 18.53 ± 2.47 mm. The linear extension varied significantly within and among coral genera (Table 2). *Acropora* had the greatest mean linear extension (16.62 ± 1.43 mm) (Fig. 2). The slowest growing coral was *Pocillopora* with a branch mean linear extension of 2.15 ± 0.27 mm.

Table 2: Mixed-model ANOVA to test for differences in linear extension of corals measured using direct measurements of branch length, at Lord Howe Island.

Effect	SS	df	F	p
Location	24.11	1	1.14	0.29
Genus	9492.09	5	89.74	0.00
Location*Genus	389.46	5	3.68	0.00
Colony(Genus)	5286.32	71	3.52	0.00
Error	6050.34	286		

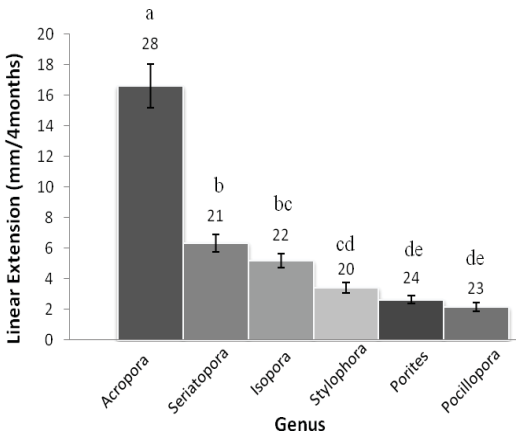

Figure 2: The direct linear extension of coral genera over the summer growth period (early Dec-end Mar). Each coral colony had 3 cable ties secured over the summer for the direct measurement. The number of colonies measured (N) and Tukey's grouping is provided. Data was combined from Horseshoe Reef and North Bay.

Alizarin Stain

Alizarin red was incorporated relatively uniformly into the skeleton across all areas of coral colonies that were stained at Lord Howe Island, providing a clear reference to measure subsequent coral growth. Estimates of linear extension from stained corals were significantly different within and among genera (Table 3). *Acropora* had the fastest mean growth rate (13.59 ± 0.59 mm) (Fig. 3). Again, *Pocillopora* had the least growth (4.81 ± 0.12 mm).

Table 3: Nested ANOVA for Alizarin stained to test for differences in linear extension of corals, measured following staining with Alizarin Red, at Lord Howe Island. Data was pooled across study locations (North Bay and Horseshoe Bay) to increase sample size and statistical power.

Effect	SS	Df	F	p
Genus	4793.28	5	109.64	0.00
Colony(Genus)	772.15	17	5.19	0.00
Error	6872.82	786		

The extension rates recorded from colonies stained using Alizarin red were generally lower than estimates obtained using direct tagging. For *Acropora*, for example, average linear extension recorded using direct tagging was 4.15 mm/month, compared to 3.40 mm/month for corals stained using Alizarin Red. The taxonomic differences in growth rates of corals were much better resolved using direct tagging. However, the approximate rankings, where *Acropora* has the fastest growth rates, *Pocillopora* the slowest, and limited differences between *Seriatopora, Isopora, Stylophora* and *Porites* were consistent for both techniques.

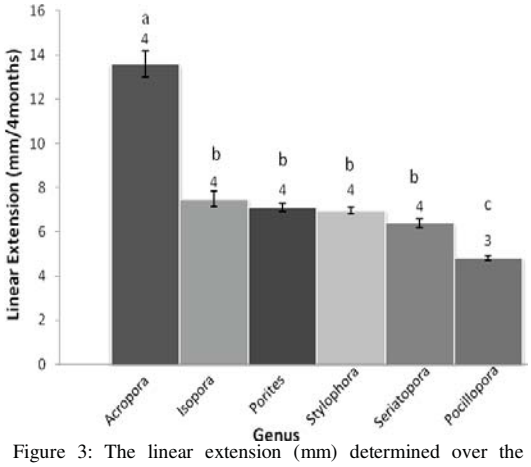

Figure 3: The linear extension (mm) determined over the summer growth period at Lord Howe Island using Alizarin Red stain. All branches from each colony or portion of colony collected were measured to the nearest millimeter. The number of colonies measured (N) is provided along with Tukey's grouping

Discussion

Growth rates of scleractinian corals have a fundamental influence on all aspects of their biology and ecology (Connell 1973). It is also known that growth rates are inherently variable among different corals species, partly in accordance with differences in gross morphology, skeletal structure and polyp size (Hall and Hughes 1996). In general, branching corals are characterised by their rapid linear extension (Buddemeier and Kinzie 1976), though growth is sometimes moderated by the need to increase skeletal density to withstand hydrodynamic forces (Hughes 1987). In contrast, massive corals, especially massive *Porites* tend to grow much more slowly (Connell 1973). At Lord Howe Island, there were marked inter-specific differences in summertime growth rates, but these differences were not related to colony morphology. Both *Isopora cuneata* and *Porites heronensis*, which have columnar growth forms, had higher growth rates compared to *Pocillopora damicornis*, but grew more slowly when compared to *Acropora*.

Growth rates of *Acropora* corals recorded at Lord Howe Island (4.15-3.40 mm/month) in the present study, were much greater than have been documented for comparable subtropical locations, such as the Solitary Islands. Harriott (1999) quantified summertime growth rates of 0.46 mm/month for *A. cytherea* and 0.80 mm/month for *A. valida* at the Solitary Islands, in the mid 1990's using Alizarin stain. These differences may be partly attributable to the specific species of coral considered, whereby most *Acropora* colonies at Lord Howe were staghorn corals (mostly, *A. yongei*), which are known to have faster growth rates compared to tabular (*A. cytherea*) or corymbose (*A. valida*) corals. However, the sea surface temperature (SST) in the current study ranged from 23.35-25.4°C (http://data.aims.gov.au/), remarkably higher than the SST (20.5°C) recorded by Harriott (1999) at the Solitary Islands, which may be contributing to greater growth rates. However, the summer growth rate determined at Lord Howe Island is still much lower compared to tropical locations, such as Davies Reef on the Great Barrier Reef where the summer SST reaches 30°C. At Davies Reef the linear extension of staghorn *Acropora* was determined using Alizarin stain to be 6.66 mm/month at 5 metres depth (Oliver et al. 1983), 38% greater than the current study.

Aside from *Acropora*, *Pocillopora* is often considered to be among the fastest growing scleractinian corals (Buddemeier and Kinzie 1976). At Lord Howe Island, however, *P. damicornis* was the slowest growing of all corals studied. The current rate 0.54-1.20 mm/month (direct and staining methods, respectively) is comparable to growth rates of *P. damicornis* determined using Alizarin stain at Rottnest Island, Western Australia (0.75-1.25 mm/month); these figures were extrapolated from six months growth during Dec 1988 to June 1989 (Ward 1995). Our estimates of linear extension for *P. damicornis* were 29-68% lower when compared to the summer growth rates at the Solitary Islands determined using Alizarin stain in 1994/1995 (Harriott 1999). Possibly *P. damicornis* is allocating most of its energy for reproduction in the summer accounting for the reduced summer growth. It remains to be seen whether these corals continue to grow over winter at Lord Howe, but if not, the current growth rates is also much lower than total annual growth estimates for this species at Lord Howe in the mid 1990's (Harriott 1999).

Understanding how climate change will affect corals in subtropical locations requires a better understanding of temperature performance of corals plus experimental studies to test whether corals in subtropical locations have higher or lower sensitivity to increasing temperatures compared to their tropical counterparts. Temperature-growth response curves are well established for scleractinian corals (Buddemeier and Kinzie 1976). As greater skeletal elongation with increasing temperature is observed seasonally in the subtropics (Crossland 1981), rising global temperatures could support greater subtropical coral growth rates. However, elevated temperatures have been shown to have a greater affect on branching species, such as *Acropora* and *Pocillopora* (Marshall and Baird 2000), which is a cause of concern for high latitude reef corals where their upper thermal limits are lower than for their low latitude counterparts (Cook et al. 1990).

Growth rates of corals in sub-tropical locations are clearly limited by temperature (Kleypas et al. 1999), but any increases in temperature will not necessarily lead to increased growth. In the south Pacific, the ocean is undersaturated with aragonite (Kleypas et al. 1999), and aragonite saturation is expected to continue to decrease throughout this century (Orr et al. 2005). Projected changes in the seawater chemistry, specifically ocean acidification, are expected to lead to major contractions in the geographical extent of areas that are amenable to calcification (Hoegh-Guldberg et al. 2007). The first and worst affected areas are likely to be locations at the current geographic limits of coral growth, especially high latitude reefs. The slow and seemingly reduced growth of *P. damicornis* at Lord Howe Island may reflect initial effects of ocean acidification, though it is unclear why such affects would disproportionately affect *Pocillopora* and not *Acropora* (Langdon and Atkinson 2005).

This study increases knowledge of coral growth and interspecific variation in responses of corals to environmental change at high latitude reefs. An explicit resolution of recent changes in growth rates for common coral genera will be apparent when the annual sampling is completed, allowing direct comparison to annual estimates of coral growth by Harriott (1999). However, our data suggest that sub-tropical reefs are not necessarily going to provide adequate refuges from sustained and ongoing climate change, as these environments are likely to be the first and worst affected due to climate change, especially given ocean acidification is likely to constrain coral growth regardless of increases in sea surface temperature.

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References

Bak RPM, Nieuwland G, and Meesters EH (2009) Coral growth rates revisted after 31 years: What is causing lower extension rates in *Acropora palmata*? Bull Mar Sci 84:287-294

Buddemeier RW, Kinzie RA (1976) Coral growth. Oceanogr Mar Biol Ann Rev 14: 183-225

Cantin NE, Cohen AL, Karnauskas KB, Tarrant AM, McCorkle DC (2010) Ocean warming slows coral growth in the central Red Sea. Science 329: 322-325

Connell JH (1973) Population ecology of reef building corals. In, Jones OA, Endean RE (eds) Biology and geology of coral reefs. Academic Press, New York, pp 205-245

Cook CB, Logan A, Ward J, Luckhurst B, Berg CJ (1990) Elevated temperatures and bleaching on a high latitude coral reef: the 1988 Bermuda event. Coral Reefs 9: 45-49

Cooper TF, De'ath G, Fabricius KE, Lough JM (2008) Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. Global Change Biol 14: 529-538

Crossland CJ (1981) Seasonal growth of *Acropora cf. formosa* and *Pocillopora damicornis* on a high latitude reef (Houtman Abrolhos, Western Australia). Proc 4th Int Coral Reef Sym 1:663-667

Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, De'ath G, Okazaki R, Muehllehner N, Glas M, Lough JM (2011) Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nature Climate Change 1: 165-169

Gladfelter EH (1982) Skeletal development in *Acropora cervicornis* I. Patterns of calcium carbonate accretion in the axial corallite. Coral Reefs 1(1): 45-51

Hughes TP (1987) Skeletal density and growth forms of corals. Mar Ecol Prog Ser 35: 259-266

Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77: 950-963

Harriott VJ (1999) Coral growth in subtropical eastern Australia. Coral Reefs 18: 281-291

Harriott VJ, Harrison PL, Banks SA (1995) The coral communities of Lord Howe Island. Mar Freshw Res 46: 457-465

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50: 839-866

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737-1742

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301: 929-933

Kleypas JA, Langdon C (2006) Coral reefs and changing seawater carbonate chemistry. in Phinney JT, Hoegh-Guldberg O, Kleypas J, Skirving W, Strong A (eds) Coastal and Estuarine Studies 61: Coral reefs and climate change: science and management. American Geophysical Union, Washington DC: pp 73-110

Kleypas JA, McManuc JW, Menez LAB (1999) Environmental limits to coral reef development: where do we draw the line? Am Zool 39: 146-159

Langdon C, Atkinson MJ (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. J Geophys Res 110: C09S07

Lamberts AE (1978) Coral growth: alizarin method. in Stoddart A, Johannes RE (eds) Coral Reefs: research methods. UNESCO, Paris: pp 523-527

Lough JM (2008) Coral calcification from skeletal records revisited. Mar Eco Prog Ser 373: 257-264

Manzello DP (2010) Coral growth with thermal stress and ocean acidification: lessons from the eastern tropical Pacific. Coral Reefs 29: 749-758

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19: 155-163

Oliver JK, Chalker BE, Dunlap WC (1983) Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. Long-term growth-responses of *Acropora formosa* (Dana 1846). J Exp Mar Biol Ecol 73: 11-35

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key R M, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner GK, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig MF, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437: 681-686

Ward S (1995) Two patterns of energy allocation for growth, reproduction and lipid storage in the scleractinian coral *Pocillopora damicornis*. Coral Reefs 14: 87-90

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Variation in size-frequency distributions of branching corals between a tropical versus sub-tropical reef

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ABSTRACT: Diversity in the life history of corals plays a critical role in shaping coral assemblages and reef habitats. Given difficulties in quantifying key demographic rates, valuable insights into life histories of corals are often inferred based on size-frequency distributions. The present study compares size-frequency distributions of branching coral taxa between Lord Howe Island, a sub-tropical reef, and Heron Island, in the southern Great Barrier Reef. Size-frequency distributions were markedly different among coral species but also varied among locations. Log-transformed size-frequency distributions of the majority of species were negatively skewed, reflecting the high levels of mortality among the smaller size classes and the persistence of the larger colonies. Among species, there were marked differences in kurtosis, reflective of fundamental variation in coral life histories; *Acropora yongei* had the lowest kurtosis, indicative of fast growth and high population turnover. Between locations, there was a higher proportion of smaller colonies at Heron Island, which was consistent across all coral taxa, suggesting a greater incidence of mortality at Heron Island. Size-frequency distributions provide important insights on the life-history dynamics of coral species and should be monitored over time to test how coral populations and communities will respond to global climate change, especially at high-latitude reefs.

KEY WORDS: Population · Life-history traits · Growth · Mortality · Colony size

INTRODUCTION

The structure and dynamics of coral populations and communities vary greatly in time and space (Done 1999), and improved understanding of the causes of this variation is critically important in projecting effects of climate change and other anthropogenic disturbances on coral assemblages and reef habitats. Inherent differences in the life-history characteristics of different coral species (e.g. the mode of reproduction, recruitment, growth and longevity) have an important role in shaping coral assemblages and structuring reef habitats. Fast-growing branching corals play an important role as the primary habitat-forming species (e.g. Coker et al. 2014). However, branching corals (e.g. *Acropora*, *Pocillopora* and *Stylophora*) are also the most susceptible to severe disturbances (Hughes & Connell 1999, Marshall & Baird 2000) but are nonetheless very common because they are able to rapidly colonise reef habitats following disturbance (Highsmith 1982, Tunnicliffe 1983, Hughes et al. 1992, Hall & Hughes 1996). In contrast, other growth forms such as massive and columnar are far less dynamic, having slower growth and lower rates of population turnover, but are also more resistant to most major disturbances (Connell 1973). As a consequence, it is unclear how coral communities might change due to increasing incidence of disturbances (Pandolfi et al. 2011), including climate change.

The resilience of coral species to sustained and ongoing disturbances, incorporating both resistance

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and recovery potential, is fundamentally dependent on key life-history characteristics, including the mode of reproduction and rates of recruitment as well as size-specific growth and survival (Hughes & Tanner 2000). Moreover, any changes in demographic rates brought about by changes in environmental conditions and/or disturbance regimes will directly affect the vulnerability and local persistence of individual species (Bak & Meesters 1999, Gilmour et al. 2013). However, there is a paucity of demographic data for individual coral species and populations, largely due to the effort required to directly quantify key demographic rates (Connell et al. 2004). An alternative method of inferring spatial, temporal or taxonomic differences in life histories is to simply assess size- and/or age-structure. For scleractinian corals (like all colonial organisms), demographic rates (e.g. fecundity, growth and mortality) are strongly dependent on colony size (Connell 1973, Hughes 1984, Hughes & Jackson 1985, Soong 1993), as opposed to age. Consequently, there is an increasing number of studies reporting on the size-structure of coral populations in a range of geographic locations (e.g. Persian Gulf [Bauman et al. 2013] and Chagos [Pratchett et al. 2013]).

Size-frequency distributions can be highly variable within and among coral populations (Adjeroud et al. 2007). Interspecific differences in size structure reflect inherent differences in life-history characteristics, especially growth and mortality (e.g. Adjeroud et al. 2007). However, variability in size-frequency distributions essentially results from disparities in the rates of recruitment, the subsequent persistence within a given size class, or growing into a larger size class, in addition to shrinking into a smaller size class due to partial mortality, or whole colony mortality (Bak & Meesters 1998). In addition, fragmentation can move colonies back in a size class, resulting in a preponderance of smaller colonies (Highsmith 1982, Wallace 1985). For colonial organisms, the growth of the colony is potentially indeterminate (Jackson 1977, Jackson & Hughes 1985). However, extrinsic factors such as available space, competition, disturbances, sedimentation and high temperatures can limit the capacity for growth and thus the advance to the next size classes or, in the case of significant partial mortality, actually lead to negative growth (Connell 1973, 1978). Therefore, factors that influence coral growth, such as light, carbonate saturation and available substrate, are counteracted by factors inhibiting growth (Vermeij & Bak 2003).

In general, the size-frequency distributions of coral populations are positively skewed, with the populations composed mainly of smaller colonies and relatively few large colonies (Hughes & Jackson 1985, Babcock 1991, Soong 1993, Bak & Meesters 1998). Log-transforming the size distribution thus results in a more normally distributed size-frequency distribution and increases resolution among smaller size classes (Meesters et al. 2001). However, not all coral populations exhibit a normally distributed log-transformed size structure; high levels of mortality will especially alter the population structure, reflected in changes in the coefficient of variation (CV), skewness and kurtosis of the frequency distribution (Bak & Meesters 1998). For example, following bleaching on Australia's Great Barrier Reef (GBR), fast-growing *Acropora* had negatively skewed size-frequency distributions, dominated by larger colonies (Linares et al. 2011).

Coral demographics will change with spatial and temporal gradients in environmental conditions, which should be reflected in contrasting size-frequency distributions among distinct populations (Bak & Meesters 1998). Knowledge of disturbance regimes can greatly increase the ability to infer demographic processes and contrast life histories, although background disturbances may cause unknown variation in the size-frequency distribution. At Lord Howe Island (off New South Wales), the 2 main processes known to structure the coral communities are the seasonal proliferation of macroalgae (Hoey et al. 2011) and a temperature-induced bleaching (Harrison et al. 2011). Macroalgae can cause fine-scale partial mortality to big colonies and whole colony mortality to small colonies, whereas bleaching is a large-scale disturbance that adversely affects branching morphologies (Marshall & Baird 2000, Loya et al. 2001) and larger colonies (McClanahan et al. 2008), as smaller colonies are less susceptible (Brandt 2009). In addition, on the GBR, disturbances such as tropical cyclones and crown-of-thorn starfish outbreaks cause the majority of coral mortality (Osborne et al. 2011).

The aim of the present study was to compare the size-frequency distributions of 5 species of branching corals between a tropical location, Heron Island, and a subtropical location, Lord Howe Island. At Lord Howe Island, growth rates of corals are lower than their tropical conspecifics (Harriott 1999). Therefore, the coral populations should be more peaked and centralized, resulting in a positive kurtosis, due to lower probability of transitioning through the size classes. In addition, the frequent disturbance regime at Heron Island would result in smaller colonies compared to Lord Howe Island. Subtropical locations

have been proposed as refugia in the face of climate change (Greenstein & Pandolfi 2008), and understanding variations between locations and among species will allow us to understand which species and what locations are likely to be most resilient to ongoing effects of climate change.

MATERIALS AND METHODS

Study sites

Subtropics: Lord Howe Island

The present study was conducted at Lord Howe Island, which is close to the southern limit of coral reef formation in the Pacific Ocean (Kleypas et al. 1999). Lord Howe Island is located 700 km south from the GBR, and local coral assemblages comprise only a fraction (83 of 356) of coral species that are found on the GBR (Harriott et al. 1995). To explore the size-frequency distributions of common coral species at Lord Howe Island, sampling was conducted at 2 sites, Horseshoe Reef (31° 32.554′ S, 159° 3.704′ E) and North Bay (31° 31.273′ S, 159° 2.773′ E), both of which are situated within the extensive lagoon on the western side of the island (Fig. 1). The lagoon encompasses the highest coral cover (40%) around Lord Howe Island, and both sites are relatively shallow (<4 m) (Harriott et al. 1995). Despite low species diversity, the reefs have complex physical structures dominated by branching and column-forming species. Due to the homogenous depth in the lagoon, the spatial comparisons are restricted to between sites as opposed to among depths.

Southern GBR: Heron Island

To facilitate a spatial comparison between Lord Howe Island and the GBR, sampling took place at Wistari Reef. Wistari Reef is in the Capricorn and Bunker region of the southern GBR on the leeward side of Heron Island, Queensland (Fig. 1). It is situated 67 km northeast of Gladstone and 1137 km from Lord Howe Island. Heron Island comprises 72% of coral species found on the GBR (NOAA 2013). To match the topography of Lord Howe Island, sampling was restricted to 4 m depth at 2 sites (Wistari East: 23° 26.1′ S, 151° 53.12′ E; Wistari West: 23° 26.35′ S, 151° 52.01′ E), located 1 km apart running east west along the northern crest of the lagoonal platform. Both sites are similar in topography comprised of interconnecting reefs and bombooras (shallow submerged reefs, shallow rocks or sand banks).

Disturbance regimes

Heron Island is much more exposed to cyclones than Lord Howe Island. On average, the Capricorn Bunker Group is affected by one major cyclone every 4 yr (Flood 1986). Analyzing the database of past tropical cyclone tracks from the Australia Bureau of Meteorology (2013), 34 cyclone tracks were recorded from 1904 to the present within 50 km of Heron Island. The last cyclone reported within that distance was in 1994. In contrast, only 18 cyclones have

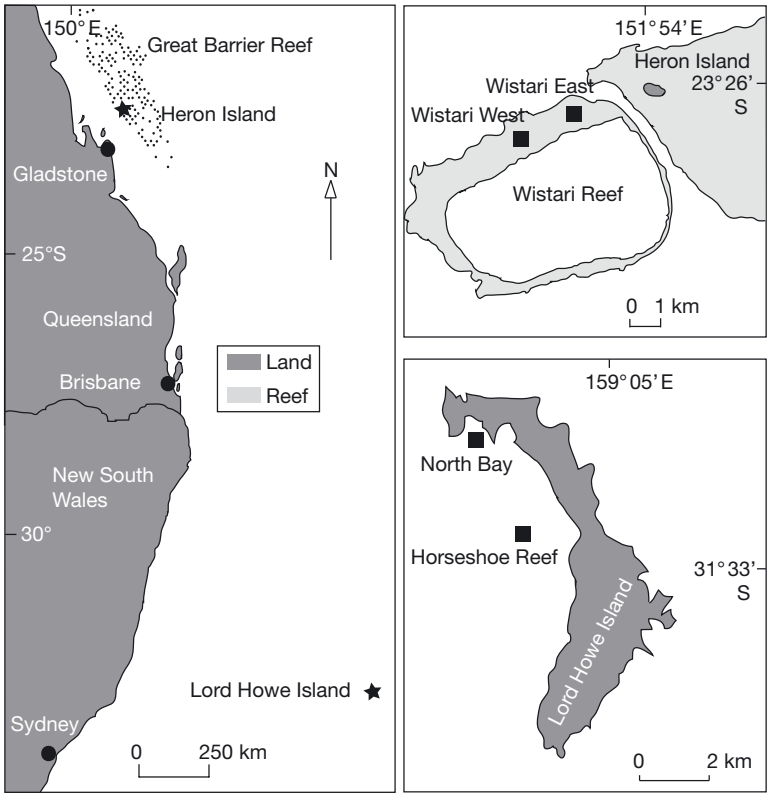

Fig 1. Study sites (■) at 2 sampling locations in Australia: subtropical Lord Howe Island and tropical Heron Island

passed within 50 km of Lord Howe Island during that same time period, with the last one occurring in 1967 (Australia Bureau of Meteorology 2013).

Another major disturbance to directly affect coral reefs is mass bleaching, which is increasing in frequency, extent and severity with ocean warming (Hoegh-Guldberg 1999). The first major bleaching recorded on the GBR was in 1998 (Baird & Marshall 1998), which affected Heron Island. Since then, bleaching has been documented in 2002 (Franklin et al. 2006), August 2003 (Hoegh-Guldberg et al. 2005), 2004 (Fine et al. 2005), a mild bleaching event in January to May 2006 (Ortiz et al. 2009) and February 2009 (MacKellar & McGowan 2010). In contrast, the only bleaching events at Lord Howe Island were documented by Harrison et al. (2011), who stated that coral bleaching did occur in 1998 but was most severe in 2010.

Study species

Lord Howe Island

At the subtropical location, we sampled *Acropora yongei, Pocillopora damicornis*, *Isopora cuneata*, *Stylophora pistillata* and *Seriatopora hystrix*. Species were identified using Veron & Stafford-Smith (2000). These species were selected based on their relatively high local abundance and contrasting morphologies, which are likely related to changes in their inherent life-history characteristics (Bak & Meesters 1998). Most of the species are branching, except *I. cuneata* which forms blades with laterally compressed extensions. The size-frequency distributions of *I. cuneata*, *S. hystrix* and *S. pistillata* have never before been examined.

Sampling was undertaken from 24 to 30 March 2011. Three researchers swam in a uniform direction parallel to the shore sampling every colony encountered in an area encompassing 100 m^2. All visible colonies were sampled. Colony diameter ranged from 1 to 810 cm, i.e. both adults and juveniles are included in the size-frequency distributions. In total, 1200 colonies were sampled: 585 at Horseshoe Reef and 615 at North Bay. For every colony sampled, the longest diameter and the perpendicular diameter of the coral colonies were recorded. Individual colonies were defined as autonomous, freestanding coral skeletons with live tissue (Bak & Meesters 1998). If the colony tissue was separate (e.g. because of partial mortality) but the colony remained one morphological entity, it was considered a single colony. Measurements of colony dimensions were taken based on the maximal extent of intact and recognisable skeleton. The percentage of partial mortality was estimated *in situ* and subtracted from the total surface area to determine the amount of live tissue on each colony.

Heron Island

At the tropical location, we sampled *Pocillopora damicornis*, *Isopora cuneata, Stylophora pistillata* and *Seriatopora hystrix*. *Acropora yongei* does not occur at Heron Island, so the staghorn coral *A. muricata* was chosen for comparison. *A. muricata* often forms large monospecific thickets making size structure analysis difficult. However, these fragmented thickets at Wistari Reef are on the sand at >4 m outside of the depth chosen to match the study site at Lord Howe Island. Therefore, the size-frequency distribution of *A. muricata* is unreflective of the breadth of coral cover of these large thickets at the deeper depths.

Sampling was undertaken from 22 to 26 April 2013. The same sampling methodology performed at Lord Howe Island was implemented at Heron Island. At Wistari North and Wistari South, 444 and 435 corals were sampled, respectively, totalling 879 colonies. The relative density of colonies for each study species were quantified along replicate (n = 5) 10 × 2 m belt transects at each site and location.

Statistical analysis

Estimates of average diameter were used to approximate the 2-dimensional surface area of every coral colony, following Linares et al. (2011). Size-frequency distributions were then constructed based on the estimated living surface area for each coral species at each site. The intervals for the size-frequency distributions were chosen to encompass the largest breadth of colonies for direct comparison among the species and locations. Due to the large variation in colony size, the colonies of *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* that did not attain the large size of *Acropora* spp. or *Isopora cuneata* were grouped for comparison, allowing a more in-depth comparison among species. The size-frequency distributions of the smaller corals ranged for the untransformed data from 100 to >2000 cm^2. *Acropora* spp. and *I. cuneata* size-frequency distributions ranged for the untransformed

data from 500 to >10 000 cm^2. The colony size data were log_{10} transformed to normalize the distribution and increase the resolution of the highly abundant smaller size classes, following Bak & Meesters (1998). The intervals for the log-transformed data ranged from 0.0 to 6.0 log-transformed colony size (cm^2). The size-structure for each species was directly compared between each species and each site, then between locations, using a 2-sample Kolmogorov-Smirnov (KS) test. In addition, the percentage of average partial mortality was calculated for each size class. A Student's *t*-test was used to look for variation in partial mortality. A 2-way ANOVA was used to assess variation in colony size between sites and locations. To determine specific differences among species from the ANOVA results, a Tukey's post hoc test was utilized. To compare the coral species' mean colony size between locations, a Student's *t*-test was performed

Descriptive statistics

Variation in the size structure of corals (within and among species) was compared based on (1) geometric mean, (2) CV, (3) skewness (g_1) and (4) kurtosis (g_2) following Bak & Meesters (1998). The geometric mean provides relative measures of colony size providing information on reproductive output (Hall & Hughes 1996). The CV describes the variation in the data set and allows for comparisons irrespective of the mean. Skewness describes the proportion of individuals in the population that are smaller or larger than the mean. If the skewness is negative, the population is skewed to the left, with a relatively larger proportion of colonies in the larger size classes than in the smaller size classes (Bak & Meesters 1998). Conversely, if the skewness if positive, then the population is skewed to the right, containing a large number of individuals in the smaller size classes than in the large size classes. Kurtosis describes whether the data is peaked or flat relative to the normal distribution and may reflect the transition through the size classes. If kurtosis is positive, the distribution is leptokurtic, which is peaked and highly centralized around the mean, indicative of slower population growth (Adjeroud et al. 2007). If kurtosis is negative, the distribution is platikurtic with a wide peak around the mean.

RESULTS

A total of 1856 corals were sampled during the present study (Table 1). Mean densities of corals were generally higher at Heron Island compared to Lord Howe Island, except for *Isopora cuneata* (Table 1).

While all coral populations had a large number of colonies in the smaller size classes, there were differences in the size-frequency distributions among species and between locations (Figs. 1 & 2). Given the prevalence of smaller colonies, all size-frequency distributions were positively skewed using the untransformed data. All distributions had the largest drop in numbers through the smallest size classes. By log-transforming the data, the size-frequency distributions became more normally distributed compared to the untransformed data.

Table 1. Statistical summary of the size-frequency distributions (using log-transformed colony size) for 6 coral species sampled at tropical (Heron Island) and/or subtropical (Lord Howe Island) locations. The sample size (n), density, log-transformed mean colony size, coefficient of variation (CV), skewness (g_1), kurtosis (g_2), and probability of being normally distributed (Kolmogorov-Smirnov p-value) are specified. For *Isopora cuneata*, statistics are given for each site at Lord Howe Island (HS: Horseshore Reef, NB: North Bay), since there were significant site effects (2-sample KS test, $p < 0.05$)

Species	Location	n	No. per m^2	Mean colony size (cm^2)	CV	g_1	g_2	p
Acropora yongei	Lord Howe	146	0.04	3.23	78	0.23	−0.50	<0.01
Acropora muricata	Heron Island	173	0.21	3.26	78	0.92	0.61	<0.01
Isopora cuneata	Lord Howe HS	100	0.20	3.06	57	−1.24	1.92	<0.01
	Lord Howe NB	100	0.21	2.72	76	−0.66	−0.15	ns
	Heron Island	153	0.19	2.51	26	−0.50	0.48	<0.05
Pocillopora damicornis	Lord Howe	236	0.27	2.49	29	−0.84	0.78	<0.01
	Heron Island	182	0.43	1.79	22	−0.31	−0.47	<0.05
Seriatopora hystrix	Lord Howe	240	0.18	2.05	27	−0.54	0.51	ns
	Heron Island	155	0.23	1.85	21	−0.03	0.08	<0.05
Stylophora pistillata	Lord Howe	177	0.13	2.17	34	−0.87	0.49	<0.01
	Heron Island	194	0.33	1.89	22	−0.38	−0.04	ns

For all species at Lord Howe Island, there was no significant effect of site, except for *Isopora cuneata* (2-sample KS test, $p < 0.05$). A few larger colonies of *I. cuneata* were observed at Horseshoe Reef, leading to a larger mean colony size and resulting in the significant variation between the sites. To display the variation among species and locations, the data were pooled between sites (Figs. 2 & 3). At Heron Island, there was no significant effect of site (2-sample KS test, $p > 0.05$) for all species, and the data were pooled between sites. Comparing between Lord Howe Island and Heron Island, there was a significant variation in the size-frequency distributions for each species (2-sample KS test, $p < 0.05$).

The staghorn *Acropora* spp. were the largest corals recorded for each site. There was a significant difference in colony size among species at Lord Howe Island (2-Way ANOVA, $F_{4,989} < 0.01$, $p < 0.01$) but not between sites (2-way ANOVA, $F_{1,989} = 0.17$, $p = 0.683$). Based on the Tukey's post hoc test, the colony size of *A. yongei* for both Horseshoe Reef and North Bay was significantly greater than that of all other species. Similarly at Heron Island, there was a significant difference in colony size among species (2-way ANOVA, $F_{4,847} = 4.52$; $p = 0.001$) but not between sites (2-way ANOVA, $F_{1,847} = 1.791$, $p = 0.181$). Based on Tukey's post hoc test, the colony size of *A. muricata* was significantly greater than that of all other species. Comparing between locations, the mean

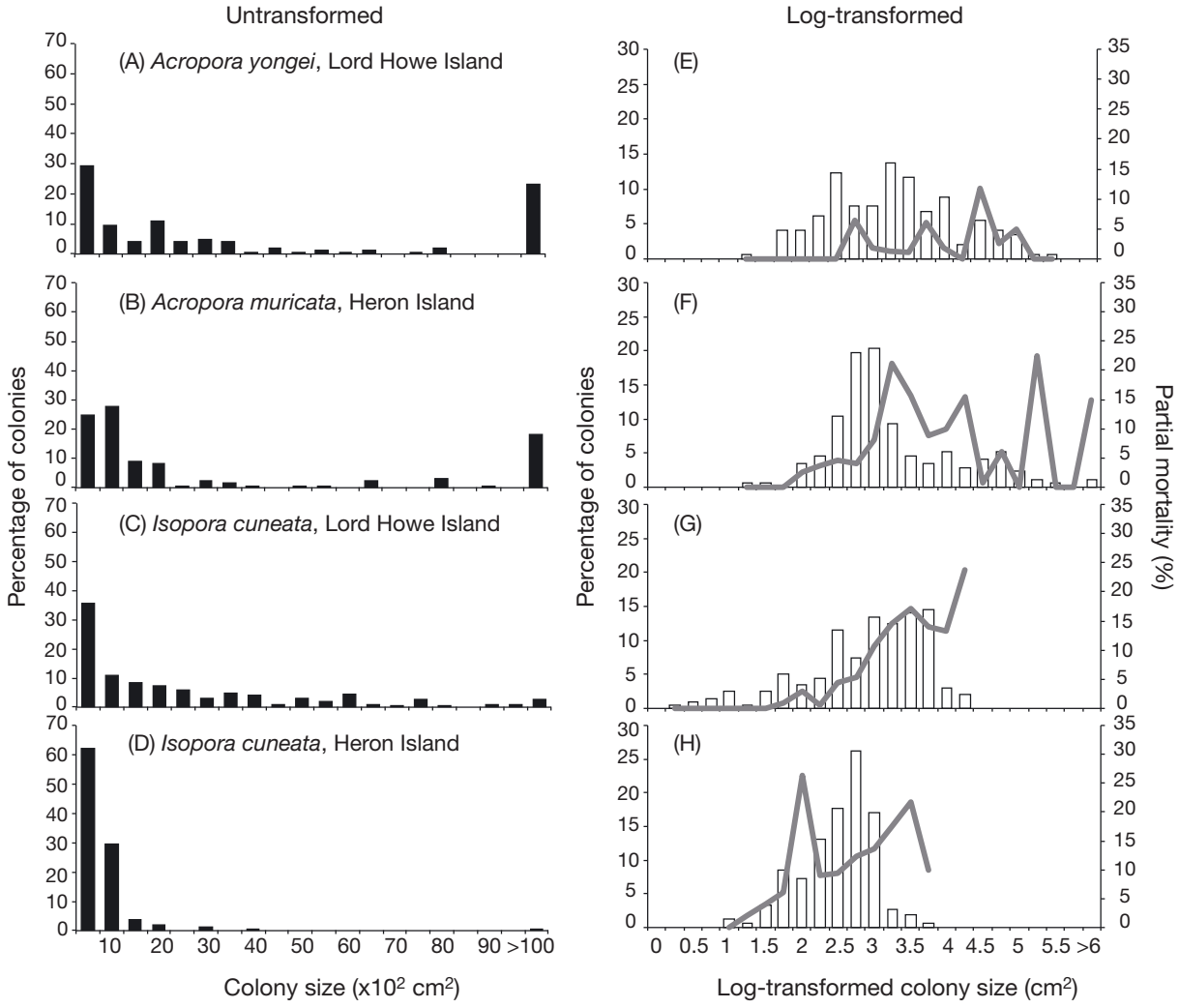

Fig. 2. (A–D) Untransformed and (E–H) log-transformed size-frequency distributions of (A,E) *Acropora yongei*, (B,F) *Acropora muricata* and (C,D,G,H) *Isopora cuneata* at (A,C,E,G) Lord Howe Island and (B,D,F,H) Heron Island. The grey line indicates average partial mortality (%) for each size class

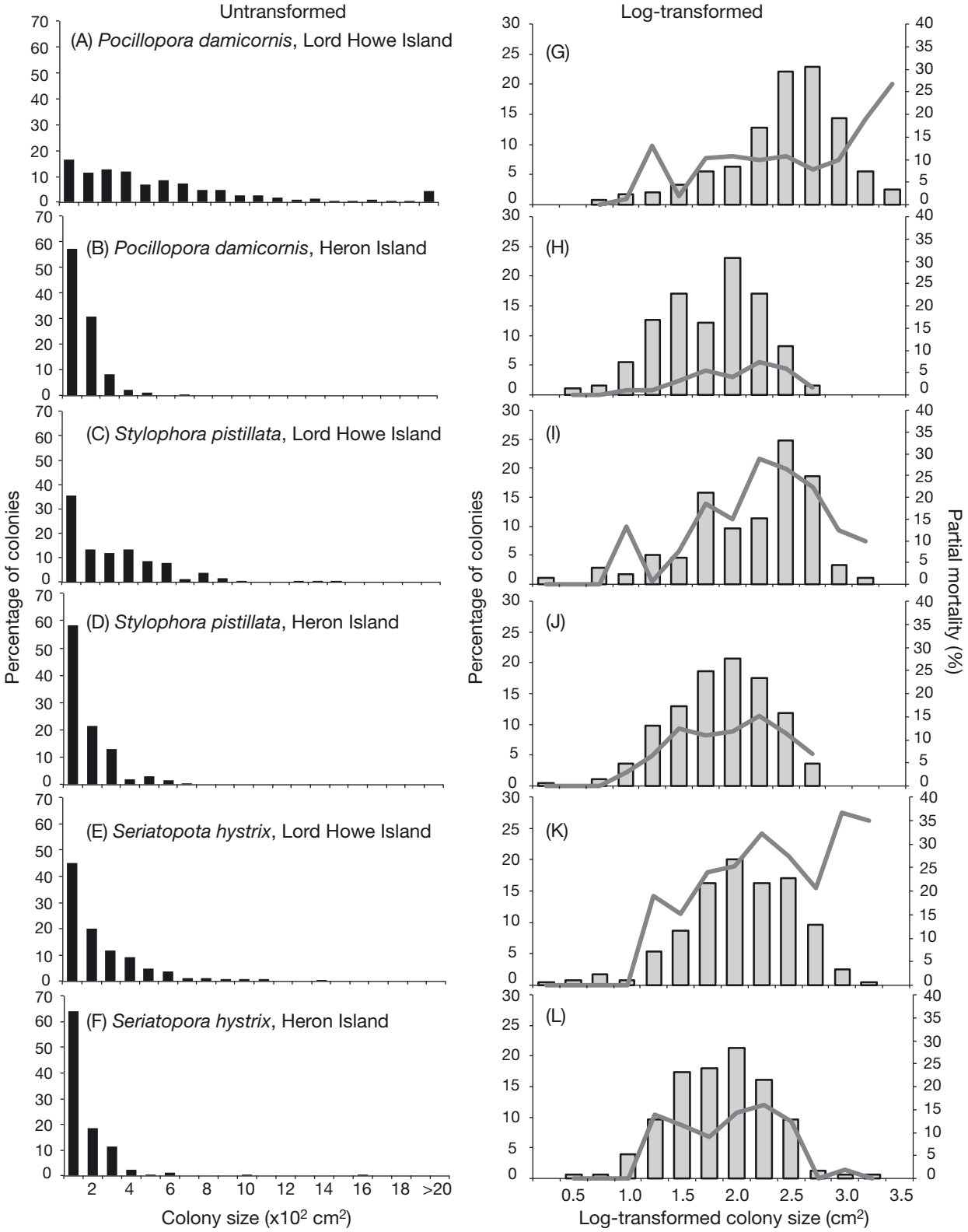

Fig. 3. (A–F) Untransformed and (G–L) log-transformed size-frequency distributions of (A,B,G,H) *Pocillopora damicornis*, (C,D,I,J) *Stylophora pistillata* and (E,F,K,L) *Seriatopora hystrix* at (A,C,E,G,I,K) Lord Howe Island and (B,D,F,H,J,L) Heron Island. The grey line indicates average partial mortality (%) for each size class

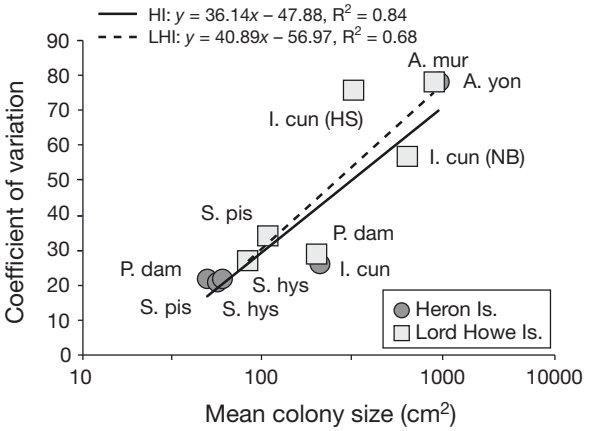

Fig. 4. Comparison of coefficient of variation (CV) and mean colony size for both Lord Howe Island (LHI) and Heron Island (HI) corals, *Acropora muricata* (A. mur), *Acropora yongei* (A. yon), *Isopora cuneata* (I. cun), *Stylophora pistillata* (S. pis), *Seriatopora hystrix* (S. hys), and *Pocillopora damicornis* (P. dam). *I. cuneata* had significant variation at Lord Howe Island, and therefore, the CV was plotted for both Horseshoe Reef (HS) and North Bay (NB)

colony size for *A. muricata* at Heron Island and *A. yongei* at Lord Howe Island did not differ significantly (Student's *t*-test, $p > 0.05$). However for all other species, the colony size was significantly larger at Lord Howe Island (Student's *t*-test within species, $p < 0.05$).

Acropora muricata and *A. yongei* both had a larger percentage (23 and 18%, respectively) of colonies in the largest class size (>10 000 cm^2) compared to the other species (Fig. 2). *Isopora cuneata* at Lord Howe Island and Heron Island had a few colonies (1 to 2%) in the largest size class. The largest discrepancy between locations comes from the percentage of colonies in the smallest size class; *I. cuneata* at Heron Island had almost twice (62%) as many colonies in the smallest size class (500 cm^2) compared to the same species at Lord Howe Island (35%). For *Pocillopora damicornis* at Lord Howe Island, 16% of the colonies were in the smallest size class (100 cm^2) compared to 57% at Heron Island, a 3-fold increase (Fig. 3). Similarly for *Stylophora pistillata*, there was almost double the number of colonies in the smallest size class at Heron Island (58%) compared to Lord Howe Island (35%). Colonies of *Seriatopoa hystrix* were the smallest ones recorded at both locations, and not surprisingly this species had the greatest number of colonies in the smallest size class (64% at Heron Island, and 45% at Lord Howe Island).

Predominantly, the percentage of partial mortality increased as the colonies became larger. Partial mortality significantly varied between Lord Howe Island and Heron Island (Student's *t*-test within species, $p < 0.05$) for all species except *Isopora cuneata* (Student's *t*-test, $p > 0.05$). Partial mortality in the staghorn *Acropora* species was greater at Heron Island than at Lord Howe Island (Student's *t*-test, $t = 3.824$, $p < 0.01$) (Fig. 2E,F). Conversely, partial mortality was greater at Lord Howe Island compared to Heron Island for *Pocillopora damicornis* ($t = -3.988$, $p < 0.01$), *Stylophora pistillata* ($t = -3.966$, $p < 0.01$) and *Seriatopora hystrix* ($t = -5.019$, $p < 0.01$) (Fig. 3G–L).

To further analyse the distributions, the descriptive statistics of the log-transformed colony size data were evaluated among species and between locations (Table 1). The first descriptive statistic, the geometric mean, significantly varied among species (ANOVA, $F_{5,6} = 8.51$, $p < 0.05$): *Acropora muricata* had the greatest mean colony size (3.26 cm^2), similar to that of *A. yongei* (3.23 cm^2), and *Seriatopora hystrix* at Heron Island had the smallest mean colony size (1.85 cm^2). The geometric mean size was greater at Lord Howe Island for all species except *Isopora cuneata.* The CV varied greatly, ranging from 21 for *S. hystrix* at Heron Island, to 78 for both *Acropora* species (Fig. 4). There was a positive correlation of the CV and mean colony size (Fig. 4). With the log-transformed data, all coral species were negatively skewed or skewed to the left, except *A. yongei* and *A. muricata*. The total range of skewness (g_1) was −1.24 (for *I. cuneata* at Horseshoe Reef) to 0.92 (for *A. muricata*). Kurtosis (g_2) displayed the greatest range, being negative for *A. yongei* (−0.50) and highly positive (1.92) for *I. cuneata* at Horseshoe Reef. In addition, the KS test for normality was significant ($p < 0.05$) for all species after log-transformation except for *I. cuneata* at North Bay, *S. hystrix* at Lord Howe Island and *Stylophora pistillata* at Heron Island. Therefore, the hypothesis that the distributions are normally distributed was only accepted for these latter 3 coral populations.

DISCUSSION

The present study is the first to explicitly compare size-frequency distributions of corals between a subtropical and tropical reef. Untransformed size-frequency distributions for all coral species, regardless of location, were strongly and positively skewed, reflecting a preponderance of smaller size classes (Figs. 2 & 3). Similar positively skewed size-frequency distributions are apparent for virtually all coral species and all study locations (e.g. Hughes &

Jackson 1985, Meesters et al. 2001). However, equivalent coral taxa exhibit more strongly skewed size-frequency distributions at Heron Island, on the GBR, than at the subtropical location, Lord Howe Island. Assuming a constant supply of recruits to the population (i.e. no recruitment failure), strong positively skewed size-frequency distributions are generally considered to reflect higher mortality, especially among smaller colonies (Babcock 1991, Hughes & Tanner 2000). Accordingly, changes in the abundance of colonies between successive size classes were much greater for small colonies than for larger colonies. The trend of high mortality among the smaller size classes is consistent with known declines in the probability of whole colony mortality with increases in colony size (Hughes et al. 1992).

Growth is strongly temperature-dependent (e.g. Lough & Barnes 2000) and is likely to lead to variation in size-frequency distributions along large-scale latitudinal gradients. Compared to tropical locations, coral growth at Lord Howe Island is slower (Harriott 1999), and this may be reflected in the size-frequency distributions. Highly centralized, peaked distributions may represent a slower transition through the size classes as a result of slower growth rates (Adjeroud et al. 2007). However, for most coral taxa in our study, the size-frequency distributions were more peaked at Heron Island than at Lord Howe Island. This suggests that high mortality of the small and large colonies may be more dominant in structuring the size-frequency distributions at tropical locations than growth rates.

The magnitude of differences in the growth rates among coral species contributed to the variation in size-frequency distributions; *Acropora yongei* grew at least 2-fold faster than all other corals at Lord Howe Island during the summer (Anderson et al. 2012). These differences demonstrate apparent life-history trade-offs whereby fast-growing corals, such as *A. yongei,* that easily fragment have a high rate of mortality, especially in smaller size classes. Fragmentation causes corals to regress in size classes, contributing to a large number of corals in the smaller size classes (Wallace 1985). Similar trends of partial mortality were observed for *A. muricata* at Heron Island. The fast growth of *Acropora* spp. allows fast population turnover and persistence of larger colonies as they escape the risk of whole colony mortality (Hughes et al. 1992). Growth rates of corals are slower on Lord Howe Island compared to tropical reefs (Harriott 1999). However, the variations in life histories among corals are preserved between temperate and tropical reefs, despite this difference in growth rate.

Partial mortality is crucial in determining the size of coral colonies, as death of part of the living tissue can cause colonies to regress in size (Hughes 1984), similar to fragmentation (Wallace 1985). In our study, partial mortality increased with increasing size classes, supporting results from other studies and locations (e.g. Babcock 1991, Bak & Meesters 1998). The increase in partial mortality in relation to colony size was similar among the species suggesting the factors causing partial mortality (e.g. sedimentation, predation) are similar regardless of locations. However, partial mortality of *Pocillopora damicornis*, *Stylophora pistillata* and *Seriatopora hystrix* was greater at Lord Howe Island than at Heron Island. Despite the reduced partial mortality at Heron Island, colonies were generally smaller at Heron Island, suggesting a greater incidence of whole colony mortality. These results are similar to those of Bauman et al. (2013), who recorded a smaller mean colony size in the southern Persian Gulf than in the northern Gulf, which experiences greater chronic and acute disturbances.

The increased frequency of partial mortality with increasing size reflects an increased frequency of exposure to disturbances at both locations, despite their very different regimes of disturbance. The similarity suggests that there is a comparable frequency of disturbances affecting colonies at small scales on both temperate and tropical reefs, such as predation, fragmentation, sediment accumulation and competitive interactions, but the frequency is likely to be greater at Lord Howe Island as indicated by the greater partial mortality among the majority of corals. At temperate locations, seasonal competition with macroalgae can lead to mortality in small corals and cause partial mortality in larger corals. However, it is unclear if the macroalgae directly colonised the colonies causing mortality, or if the colony bleaches (Harrison et al. 2011), killing a portion of the colony which is then invaded by its space competitor (Crossland 1984, Hoey et al. 2011). At Heron Island, increased frequency of cyclones and crown-of-thorn-starfish outbreaks (Osborne et al. 2011) can lead to increased incidence of whole colony mortality.

Once log-transformed, the size-frequency distributions of all coral species were negatively skewed, and the majority of the corals had positive kurtosis, displaying over-centralized, peaked distributions. Skewness was reflective of the variation in disturbance regimes between a subtropical and tropical location, in addition to partial mortality. *Isopora cuneata, Pocillopora damicornis, Seriatopora hystrix* and *Stylophora pistillata* were negatively skewed at

both locations. However, the degree of skewness was less at Heron Island compared to Lord Howe Island, suggesting a lower probability of transitioning to the larger size classes (Adjeroud et al. 2007) due to a higher disturbance regime at the tropical location.

Positive kurtosis indicates high mortality of small and large colonies or slow transitioning through the size classes as a result of slow colony growth (Adjeroud et al. 2007). The flat size-frequency distribution of *Acropora yongei* at Lord Howe Island is characteristic of the genus' fast growth and high population turnover, as reported for *A. hemprichii* in the Red Sea (Guzner et al. 2007). Interestingly, kurtosis was positive at Heron Island for *A. muricata*. At Heron Island, increased incidence of disturbance is likely causing greater mortality to the smaller size classes, leading to the peaked distribution. A negative kurtosis was observed in *Acropora* spp. following a bleaching event in Kenya, where the size-frequency distribution shifted from positive to negative kurtosis (McClanahan et al. 2008). At Lord Howe Island, the first reported mass-bleaching of corals was recorded in 2010 and caused only moderate (up to 25%) coral mortality (Harrison et al. 2011, Hoey et al. 2011). There is limited evidence of any other major disturbances which typically affect tropical locations (e.g. outbreaks of crown-of-thorns starfish and severe tropical storms; Osborne et al. 2011) affecting these coral assemblages. Therefore, the characteristic fast growth of *A. yongei* is likely structuring its size-frequency distribution at Lord Howe Island, as opposed to disturbances.

The CV displayed marked variation among the coral species relative to colony size (Fig. 4). The present study contradicts that of Bak & Meesters (1998), who found the CV to be negatively related to the mean size of the coral species, whereas for the coral species in the present study, the CV was positively related (Fig. 4). However, a major difference between the studies was the species used: Bak & Meesters (1998) analysed massive or encrusting species. In the present study, the CV was similar among locations when compared to mean colony size, as evident in the similar slopes between Heron Island and Lord Howe Island, suggesting similar variance among coral populations at each location as the colonies increase in size. A higher CV has been associated with a very high proportion of very small corals (Bak & Meesters 1998), suggestive of large fluctuations in recruitment and mortality of the smaller size classes. At Lord Howe Island, however, the coral populations are sustained by very low and presumably fairly constant levels of recruitment (Hoey et al. 2011). Recruit assemblages at Lord Howe Island tend to be dominated by the Family Pocilloporidae, Family Poritidae and sub-genus *Isopora* (Harriott 1992, Hoey et al. 2011), which all release brooded planulae (Harriott 1992). This is a stark contrast to the GBR where mass-spawning corals recruit in much higher abundances than brooding corals (Hughes et al. 1999). However, such shifts in the predominant reproductive strategies (towards brooding) of corals at peripheral locations have been well documented (Baird et al. 2009).

In conclusion, the size-frequency distributions of corals at Lord Howe Island and Heron Island varied greatly among species, yet they were all mostly negatively skewed and flattened distributions. The major exceptions were the fast-growing *Acropora* spp. The variations in the size-frequency distributions between locations were strongly suggestive of variation in local disturbance regimes. Smaller mean colony size at Heron Island demonstrated the more severe disturbance regime at this location. Recorded incidence of partial mortality was greatest at Lord Howe Island, but this may reflect the longer time to repair injuries due to slower coral growth at tropical locations (Harriott 1999) rather than increased rates of injury. These results strengthen our understanding of inter-specific variation in size-frequency distribution as a result of inherent life-history strategies. Ongoing research to investigate the size-structure at Lord Howe Island over time, thus analyzing changes in the coral communities, will be vital in determining the fate of corals at this high-latitude reef. This will help to identify whether subtropical reefs will provide important refugia for tropical reef corals subject to increasing effects of global climate change.

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LITERATURE CITED

Adjeroud M, Pratchett MS, Kospartov MC, Lejeusne C, Penin L (2007) Small-scale variability in the size structure of scleractinian corals around Moorea, French Polynesia: patterns across depths and locations. Hydrobiologia 589:117–126

Anderson KD, Pratchett MS, Baird AH (2012) Summer growth rates of corals at Lord Howe Island, Australia.

Proc 12th Int Coral Reef Symp, Cairns. www.icrs2012.com/proceedings/manuscripts/ICRS2012_4C_1.pdf

Australia Bureau of Meteorology (2013) The Australian Tropical Cyclone Database. www.bom.gov. au/cyclone/history/index.shtml (accessed 4 Nov 2013)

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age-dependent and size-dependent classification. Ecol Monogr 61:225–244

Baird AH, Marshall PA (1998) Mass bleaching of corals on the Great Barrier Reef. Coral Reefs 17:376

Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. Annu Rev Ecol Evol Syst 40: 551–571

Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size-frequency distributions. Mar Ecol Prog Ser 162:301–306

Bak RPM, Meesters EH (1999) Population structure as a response of coral communities to global change. Am Zool 39:56–65

Bauman AG, Pratchett MS, Baird AH, Riegl B, Heron SF, Feary DA (2013) Variation in the size structure of corals is related to environmental extremes in the Persian Gulf. Mar Environ Res 84:43–50

Brandt ME (2009) The effect of species and colony size on the bleaching response of reef-building corals in the Florida Keys during the 2005 mass bleaching event. Coral Reefs 28:911–924

Coker D, Wilson S, Pratchett M (2014) Importance of live coral habitat for reef fishes. Rev Fish Biol Fish 24:89–126

Connell JH (1973) Population ecology of reef building corals. In: Jones OA, Endean R (eds) Biology and geology of coral reefs, Vol II, Biology 1. Academic Press, New York, NY, p 205–245

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Connell JH, Hughes TE, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity of corals. Ecol Monogr 74:179–210

Crossland CJ (1984) Seasonal variations in the rates of calcification and productivity in the coral *Acropora formosa* on a high-latitude reef. Mar Ecol Prog Ser 15:135–140

Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. Am Zool 39:66–79

Fine M, Meroz-Fine E, Hoegh-Guldberg O (2005) Tolerance of endolithic algae to elevated temperature and light in the coral *Montipora monasteriata* from the southern Great Barrier Reef. J Exp Biol 208:75–81

Flood PG (1986) Sensitivity of coral cays to climatic variations, southern Great-Barrier-Reef, Australia. Coral Reefs 5:13–18

Franklin DJ, Cedres CMM, Hoegh-Guldberg O (2006) Increased mortality and photoinhibition in the symbiotic dinoflagellates of the indo-pacific coral *Stylophora pistillata* (Esper) after summer bleaching. Mar Biol 149: 633–642

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Greenstein BJ, Pandolfi JM (2008) Escaping the heat: range shifts of reef coral taxa in coastal Western Australia. Glob Change Biol 14:513–528

Guzner B, Novoplansky A, Chadwick NE (2007) Population dynamics of the reef-building coral *Acropora hemprichii* as an indicator of reef condition. Mar Ecol Prog Ser 333: 143–150

Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950–963

Harriott VJ (1992) Recruitment patterns of scleractinian corals in an isolated sub-tropical reef system. Coral Reefs 11:215–219

Harriott VJ (1999) Coral growth in subtropical eastern Australia. Coral Reefs 18:281–291

Harriott VJ, Harrison PL, Banks SA (1995) The coral communities of Lord Howe Island. Mar Freshw Res 46:457–465

Harrison P, Dalton S, Carroll A (2011) Extensive coral bleaching on the world's southernmost coral reef at Lord Howe Island, Australia. Coral Reefs 30:775

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Prog Ser 7:207–226

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866

Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S, Strong A (2005) Coral bleaching following wintry weather. Limnol Oceanogr 50:265–271

Hoey AS, Pratchett MS, Cvitanovic C (2011) High macroalgal cover and low coral recruitment undermines the potential resilience of the world's southernmost coral reef assemblages. PLoS ONE 6:e25824

Hughes TP (1984) Population dynamics based on individual size rather than age: a general model with a reef coral example. Am Nat 123:778–795

Hughes TP, Connell JH (1999) Multiple stressors on coral reefs: a long-term perspective. Limnol Oceanogr 44: 932–940

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. Trends Ecol Evol 7:292–295

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63

Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am Nat 111:743–767

Jackson JBC, Hughes TP (1985) Adaptive strategies of coral-reef invertebrates. Am Sci 73:265–274

Kleypas JA, McManuc JW, Menez LAB (1999) Environmental limits to coral reef development: Where do we draw the line? Am Nat 39:146–159

Linares C, Pratchett MS, Coker DJ (2011) Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 438:97–104

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites.* J Exp Mar Biol Ecol 245:225–243

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: winners and losers. Ecol Lett 4:122–131

MacKellar MC, McGowan HA (2010) Air-sea energy exchanges measured by eddy covariance during a localised coral bleaching event, Heron Reef, Great Barrier Reef,

Australia. Geophys Res Lett 37:L24703, doi:10.1029/2010GL045291

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

McClanahan TR, Ateweberhan M, Omukoto J (2008) Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. Mar Biol 153: 755–768

Meesters EH, Hilterman M, Kardinaal E, Keetman M, de Vries M, Bak RPM (2001) Colony size-frequency distributions of scleractinian coral populations: spatial and interspecific variation. Mar Ecol Prog Ser 209: 43–54

NOAA (National Oceanic and Atmospheric Administration) (2013) PMEL Carbon Program: Heron Island. www.pmel.noaa.gov/co2/story/Heron+Island (accessed 15 November 2013)

Ortiz JC, Gomez-Cabrera MD, Hoegh-Guldberg O (2009) Effect of colony size and surrounding substrate on corals experiencing a mild bleaching event on Heron Island reef flat (southern Great Barrier Reef, Australia). Coral Reefs 28:999–1003

Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). PLoS ONE 6:e17516

Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333:418–422

Pratchett MS, Pisapia C, Sheppard CRC (2013) Background mortality rates for recovering populations of *Acropora cytherea* in the Chagos Archipelago, Central Indian Ocean. Mar Environ Res 86:29–34

Soong K (1993) Colony size as a species character in massive reef corals. Coral Reefs 12:77–83

Tunnicliffe V (1983) Caribbean staghorn coral populations: pre-hurricane Allen conditions in Discovery Bay, Jamaica. Bull Mar Sci 33:132–151

Vermeij MJA, Bak RPM (2003) Species-specific population structure of closely related coral morphospecies along a depth gradient (5-60 m) over a Caribbean reef slope. Bull Mar Sci 73:725–744

Veron JEN, Stafford-Smith M (2000) Corals of the world. Australian Institute of Marine Science, Townsville

Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora.* Mar Biol 88:217–233

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Intraspecific Variation in Physiological Condition of Reef-Building Corals Associated with Differential Levels of Chronic Disturbance

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Abstract

Even in the absence of major disturbances (e.g., cyclones, bleaching), corals are subject to high levels of partial or whole-colony mortality, often caused by chronic and small-scale disturbances. Depending on levels of background mortality, these chronic disturbances may undermine individual fitness and have significant consequences on the ability of colonies to withstand subsequent acute disturbances or environmental change. This study quantified intraspecific variations in physiological condition (measured based on total lipid content and zooxanthellae density) through time in adult colonies of two common and widespread coral species (*Acropora spathulata* and *Pocillopora damicornis*), subject to different levels of biological and physical disturbances along the most disturbed reef habitat, the crest. Marked intraspecific variation in the physiological condition of *A. spathulata* was clearly linked to differences in local disturbance regimes and habitat. Specifically, zooxanthellae density decreased ($r^2 = 26$, df = 5,42, $p < 0.02$, B = −121255, $p = 0.03$) and total lipid content increased ($r^2 = 14$, df = 5,42, $p = 0.01$, B = 0.9, $p = 0.01$) with increasing distance from exposed crests. Moreover, zooxanthellae density was strongly and negatively correlated with the individual level of partial mortality ($r^2 = 26$, df = 5,42, $p < 0.02$, B = −7386077, $p = 0.01$). Conversely, *P. damicornis* exhibited very limited intraspecific variation in physiological condition, despite marked differences in levels of partial mortality. This is the first study to relate intraspecific variation in the condition of corals to localized differences in chronic disturbance regimes. The next step is to ascertain whether these differences have further ramifications for susceptibility to periodic acute disturbances, such as climate-induced coral bleaching.

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Introduction

Coral reefs are very dynamic ecosystems, impacted by a variety of natural and anthropogenic processes, which may vary in scale, frequency, and intensity [1]. Even in the absence of major disturbances (e.g., cyclones, bleaching or outbreaks of crown-of-thorns starfish), corals are still subject to a range of chronic, often small-scale disturbances that cause relatively high rates of background mortality (annual background mortality rates can generally vary from 1 to 30%: [2–5]). These background mortality agents (such as predation, competition and disease) are a normal part of the natural dynamics and turnover in coral populations and communities [6–8]. However, increases in prevalence and impact of chronic disturbances undermine the resilience of coral colonies and populations [4,5,8,9,10], which are subject to ever-increasing threats from climate change and other more direct anthropogenic disturbances [11,12].

Background mortality agents can trigger complex responses in corals that may affect colony physiological condition, alter demographic performance, especially growth [13–15] and reproduction [15,16,17] and they can therefore have significant consequences on the ability of colonies to withstand and survive periodic acute disturbances and environmental changes [18]. Intraspecific competition, for example, can substantially reduce fitness and growth rates of colonies engaged in competitive interactions [14]. Tanner 1997 documented a reduction in growth rates from 120 to 35% in *Acropora hyacinthus* when engaged in competitive interactions, and a decrease in growth from 45 to −16% in *Pocillopora damicornis*. Similarly, chronic predation can inflict a significant energetic cost to prey corals and may accelerate rates of coral decline following a disturbance [19]. Coral grazing fishes are a potentially important source of background coral mortality [19], even when they do not leave any visible signs of damage on coral colonies [20]. Rates of tissue removal from individual coral colonies can be considerable (16.75±0.30 bites per 20 min, [19]) and this chronic removal of live tissue can have potentially important consequences for colony fitness. Similarly, sedimentation can affect coral physiological condition by exerting significant energetic costs due to the removal of particles from colonies and limit energy availability due to reduced light and photosynthetic activity [15,21]. *Siderastrea siderea* reduced linear extension rates from 3.5 mm to 3 mm three years following an oil spill, which caused increased sedimentation levels [21].

The physiological condition of a colony is largely determined by the energy available and by the partitioning of energy reserves

among maintenance, growth, and reproduction [22]. Energy within a colony is a limited resource and it is distributed among costly life history processes. If a coral invests heavily in repairing tissues damaged by chronic predation or sedimentation, or is investing heavily in interspecific competition, then this will reduce resources available for growth and reproduction. Evidences of energy trade-offs have been widely documented in corals, with injury often causing a decline in growth [23,24] or fecundity [25]. Moreover, diversion of essential energy reserves may undermine the capacity of corals to withstand periodic acute disturbances, such as anomalous temperatures that cause widespread bleaching [22]. When injured, corals often divert energy towards regeneration of lost tissue, and species with high regenerative capacity (such as *Acropora* spp) being able to fully heal the injury in less than 80 days [23]. However, environmental stresses, large lesions and competition may impair regeneration and hence compromise survival [23,26]. The bare skeleton resulting from tissue loss can be colonized by algae, pathogens or bioeroders, which may undermine the integrity of the colony [27,28]. These organisms may later compete with the coral for food and space, or cause structural damage to the coral skeleton [27,28].

The capacity of corals to withstand ongoing disturbances is strongly size-dependent, with small colonies being more vulnerable to whole-colony mortality than larger ones [6]. Corals as modular organisms are made up of repeated units (polyps), each of which can function and survive as physiologically independent entities. However, partial mortality and the consequent decline in the total number of polyps that make up a colony can greatly reduce individual fitness and resilience [6,17,29]. A reduction in size results in fewer polyps available to support colony vital processes and will generally reduce survivorship [6,30], growth [23,24], reproduction and regeneration [15]. Large colonies have greater regenerative abilities [6,8], growth [31], are more fecund [17] and have lower rates of total mortality compared to smaller colonies [6,17]. Likelihood of survival in larger colonies is greater than smaller ones because there is a higher probability that part of the colony may remain unaffected [32]. Particularly, following a disturbance, big colonies can make a disproportionate contribution to population as they produce more eggs per unit area [17].

Intra-specific variation of corals in responses to stresses is largely due to genotypic and phenotypic variation among both corals and their zooxanthellae [33–35], however the disturbance history and current physiological condition of individual colonies may also play a critical role. The exhaustion of energy available to maintain vital processes represents a physiologically critical threshold for survival [36]. During a bleaching event for instance, a key determinant for survival and recovery of a coral is its amount of lipid reserves [22], as they can. When bleaching occurs the energy acquisition by the zooxanthellae stops, hence the coral must use its energy reserves accumulated in the form of lipids in order to survive [38–41]. So colonies in good physiological conditions, with a great magnitude of lipid reserves, are more likely to survive and recover from a bleaching event, than colonies with lower level of lipid reserves [22,42]. Also colonies which survived a previous disturbance and are potentially in good physiological condition, can substantially contribute to community recover through their growth and through their reproductive output [17,43,44].

The purpose of this study is to quantify intra-specific variation in physiological condition (specifically, total lipid content and zooxanthellae density) through time in adult colonies exposed to several biological and environmental factors. Variation in colony condition among individuals may account for differences in susceptibility to disturbances. Many studies have documented significant variation in the capacity of corals to withstand and recover from major disturbances [4,8,45,46], but the underlying basis of this variation is still poorly understood. Most of these studies have focused on among-species variability for stress resistance. Hoegh-Guldberg [47] suggested that in the aftermath of climate change some coral species are more likely to adapt and survive better than others. But still little is known on intraspecific variability to environmental changes.

Methods

Ethics Statement

The activities for this study were conducted under permission from the Great Barrier.

Reef Marine Park Authority (Permit Number G12/35017.1). Visual censuses of fishes and benthic communities were conducted during this study; one coral branch per colony was collected in May and one in October.

Chronic Disturbances

This study was conducted at Lizard Island (14°40′S, 145°27′E) in the northern Great Barrier Reef, Australia. 24 colonies, ranging in size from 9 cm up to 35 cm diameter, of *Pocillopora damicornis* and *Acropora spathulata* were individually tagged and sampled in May and October 2012 to test for intraspecific differences in physiological condition. At the same time, detailed observations were undertaken to quantify intra-specific differences in background disturbance regimes (NB. There were no major bleaching events or other acute disturbances during the conduct of this study). Colonies at the same depth were selected from the reef crest in two different sites, one sheltered and one in the windward side of the island. For each coral colony we measured the distance from the reef crest (presumed to reflect colony physical position in respect of local hydrodynamic regime), proportional tissue loss attributable to coral competition and/or coral disease, and also rates of predation by corallivorous fishes. Variation in the level of predation among individual coral colonies was documented using GoPro cameras, deployed to record the total number of bites taken by all corallivorous fishes within replicate one-hour periods. The fish species and size were also recorded. Partial mortality was measured by quantifying the exact proportion of dead versus living tissue within the overall physical extent of each coral colony, using the software Image J. Growth rates were also calculated comparing colony surface area from pictures in May and in October for each individual colony.

Colony Physiological Condition

Colony condition was assessed based on total lipid content and zooxanthellae density. The size of lipid reserves is a good measure of colony condition because it represents an alternative source of fixed carbon, which can be allocated to vital processes such as growth or reproduction. Lipid reserves can also allow the host to meet its daily metabolic energy needs in absence of endosymbionts, such as during a bleaching event [42]. Similarly, the symbiotic relationship between the coral colonies and the symbionts makes zooxanthellae density a good proxy of coral condition [48]. Zooxanthellae density has been shown to decrease in response to chronic stresses such as exposure to both low and high temperature [49], sedimentation [50], disease [51], and water quality [52,53], and has been widely measured to assess coral condition in response to stimulants, as well as natural variation in environmental factors [52,53,54,55]. To measure both total lipid content and zooxanthellae density, one branch was collected from each of the tagged colony in May and October. To minimize

within-branch variability in lipids, only central inner branches were collected [56].

Branches were fixed in 10% formalin seawater and decalcified in 5% Formic acid for 1 day followed by 10% formic acid for 5 days and then stored in 70% ethanol. To extract total lipids, coral branches were dried in the oven at 55°C for 24 h, weighed and placed in a solution of chloroform: methanol (2:1, v:v) to dissolve the lipids [57]. The tissues were redried at 55°C overnight and reweighed. The difference in weight was due to lipids loss, with total lipid content then expressed as percentage of dry weight. Total lipid content was analysed instead of lipid classes because of the total lipids, triacylglycerol and wax esters are the main storage lipids in corals, and can account for 40–73% of total lipids [58–60].

Zooxanthellae density (per unit surface area (cells/cm^2)) was quantified for each coral based on samples (5 mm×5 mm) from the collected branch (4 replicates per branch). Each sample was homogenized and the ground solution was examined on a glass slide under a microscope and counts were normalized to coral surface area, following McCowan et al. [61].

Data were deposited on Figshare and are available at http://dx.doi.org/10.6084/m9.figshare.928440.

Data Analyses

To test whether there were significant differences in partial mortality, in total lipid content, in zooxanthellae density, in competition and in the number of fish bites, between May and October, a series of paired t-tests were carried out for each variable. Proportional mortality of individual coral colonies was Arcsin transformed prior to analyses. A One-Way ANOVA was carried out to further investigate whether colonies exposed to predation had lower lipid content than colonies that did not receive any bite. To test whether physiological condition of coral colonies relates to biological and physical disturbance regimes, we used a stepwise Multiple Regression model, testing the extent to which i) partial mortality, 2) mean number of fish bites, 3) extent of coral competition, 4) colony size, 5) distance from crest, and 6) Site, explained intraspecific variation in either total lipid content or zooxanthelae density for each coral species. Separate analyses were carried out for total lipid content and zooxanthellae density. Bivariate correlations were also used to test for any relationship between zooxanthellae density and total lipid content in each coral species.

Results

Chronic Disturbances

Competitive interactions and partial mortality were constant between May and October in both coral species (Fig. 1). Only the number of fish bites differed significantly with time, being 23 times higher in October than in May for *P. damicornis* (paired t-test, $p < 0.05$). Some colonies received few bites in May (from 0 to 4 bites per hour) while they were exposed to high predation pressure in October (163 and 392 bites per hour). In *A. spathulata*, overall predation pressure was two times higher in October, but given marked intra-specific variation this was not statistically significant (Fig. 1). Bite rate varied among colonies in *P. damicornis*, ranging from 0 to >100 bites per hour among colonies. In both coral species, the colonies that received most bites in May were not the same ones that received most bites in October, while some colonies did not receive any bite in either May or October.

In *P. damicornis* the majority of the colonies were smaller than 1000 cm^2, with colony surface area ranging from 161 cm^2 to 679 cm^2, while in *A. spathulata* colony surface area ranged from 160 cm^2 up to 1.830 cm^2. Colony growth (expressed as changes in colony surface area) from May to October in *A. spathulata* was 118.3 cm^2, while *P. damicornis* showed a negative growth rate (−10.3 cm^2) due to partial mortality.

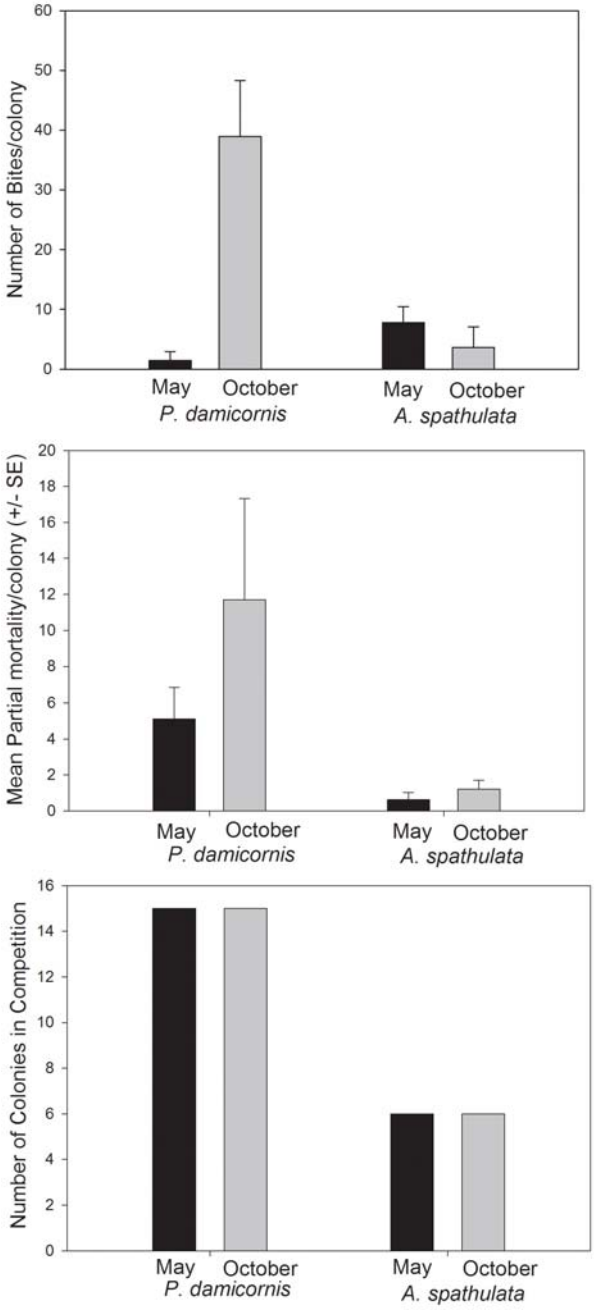

Figure 1. Chronic disturbance regimes in May and October in the two reef-building corals *P. damicornis* and *A. spathulata*. A) Predation – mean no. of bites taken per colony in replicate three-minute observations, where Go Pro cameras were used to record the total number of bites taken by all corallivorous fishes (mostly, butterflyfishes), B) Partial mortality –proportional of dead versus living tissue within the overall physical extent of each coral colony, C) – number of colonies engaged in competitive interactions.
doi:10.1371/journal.pone.0091529.g001

Intraspecific Variation in Colony Condition

All the sampled corals survived the entire study period. Colony condition was found to vary between May and October in both coral species (Fig. 2). Specifically, a significant decline in total lipid content was observed in October compared to May (Table 1, 2; Fig. 2). In *A. spathulata* energy reserves in October were almost half compared to May (declined from 13.7 (±7.5) % to 7.8 (±1.8) %), while in *P. damicornis* the decline was two-fold during the same time (Fig. 2). Zooxanthellae density on the other hand, remained constant and did not change significantly between sampling periods in either coral species (Fig. 2). For *P. damicornis*, intraspecific variation in total lipid content was strongly correlated with zooxanthellae density ($r = 99$, $df = 5,42$, $p<0.001$), but no such relationship was found for *A. spathulata*.

P damicornis showed a high variation within colonies in partial mortality (between 0 and 20%), number of fish bites (between 0 and 392 bites per hour) and total lipid content (between 1.5 and 80% dw). By comparison, intraspecific variation in partial mortality and disturbance rates for *A. spathulata* were much smaller (Fig. 1).

In *P damicornis*, partial mortality, number of fish bites, competition, distance from crest and size were poor predictors of both lipid content (Multiple Regression total lipid content $r^2 = 11$, $df = 5,42$, $p = 0.27$; Table 1); and zooxanthellae density ($r^2 = 25$, $df = 5, 42$, $p = 0.3$; Table 1): the regressions explained only a very small proportion of the total variation (<12%). Conversely in *A. spathulata*, partial mortality and distance from crest were found to have a significant effect on both total lipid content and zooxanthellae density (Multiple Regression total lipid content *A. spathulata* $r^2 = 14$, $df = 5,42$, $p = 0.2$; zooxanthellae density $r^2 = 26$, $df = 5,42$, $p = 0.02$; Table 2). In particular, total lipid content increased with distance from crest, while zooxanthellae density declined with increasing partial mortality and distance from crest (Table 2).

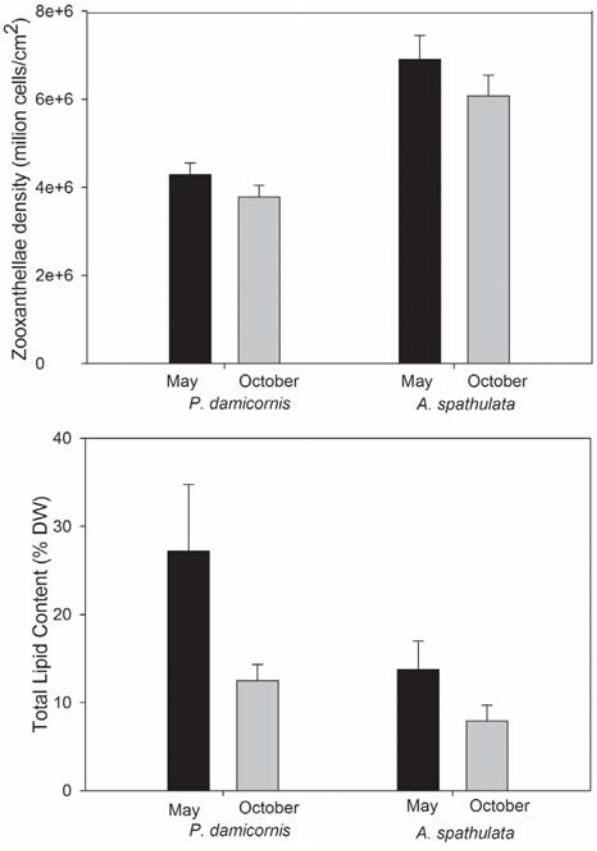

Figure 2. Physiological condition, specifically A) total lipid content and B) zooxanthellae density, in May and October in the two reef-building corals *P. damicornis* and *A. spathulata*.
doi:10.1371/journal.pone.0091529.g002

Discussion

This is the first study that attempts to relate intraspecific variation in physiological condition of scleractinian corals to small-scale differences in chronic disturbances, such as fish predation. It is well known that coral colonies living in close proximity may exhibit vastly different demographic rates [6,8,45,62], possibly reflective of differences in their disturbance history and subsequent energy allocation [27,63]. The difficulty in making this link is that very subtle differences in disturbance regimes, operating at any time in the lifetime of each coral, may lead to marked differences in contemporary condition and fitness of individual coral colonies. We acknowledge that the current study provides very limited insights on lifetime differences among closely positioned colonies, mainly due to the limited observational periods, and the range of factors that may be impacting on individual coral colonies. However, it is interesting that we saw no significant temporal shifts in rates of partial mortality, competition and predation between the two observational periods. The high degree of constancy in background mortality may be evidence that there is a high stability in terms of routine mortality.

Under low levels of background mortality, demographic models of scleractinian corals predict constant growth and fecundity of individual colonies, enabling rapid recovery following major acute disturbance [4,36,64]. However, in the present study, even within relatively constant rates of biological and physical disturbances, the incidence of injuries still varied among colonies. For instance, some coral colonies did not receive any fish bites in either May or October. Similarly, some colonies of *P. damicornis* that were not injured in May showed partial mortality in October, while some colonies never showed partial mortality. In the long term, these differences among colonies may likely be responsible for important inter-colony differences in condition and fitness. Importantly, variation in the disturbance history of individual colonies may have important ramifications for their long-term fate, especially during major disturbances (e.g., climate-induced coral bleaching).

Not unexpectedly, this study revealed marked intraspecific variation in the physiological condition of both *A. spathulata* and *P. damicornis*. However, these differences were only partially explained by inter-colony differences in rates of partial mortality, competition, predation, colony size or the position of the colony relative to the reef crest. Comparing to other studies, which documented a lipid level of 35% in tissue of *P. damicornis* [56,65], this study found a lower lipid content (27% dw). Conversely, zooxanthellae density was found to be higher (3.0 cells/cm^2 in May) than what reported in the literature (3.0 cells/cm^2, [66]). Also differences in colony condition, specifically in total lipid content, were greater among adjacent colonies of *P. damicornis* than when compared to colonies of *A. spathulata*, revealing intraspecific differences in physiological condition and in susceptibility to chronic disturbances. These differences suggest that coral physiological condition can be more variable than predicted with the outcome depending, in part, on flow, partial mortality, and position of the colony.

Predation rates on coral colonies were higher in October than in May in both coral species, especially in *P. damicornis*. Similarly,

Table 1. Multiple Regression for zooxanthellae density and total lipid content in *P. damicornis*.

Zooxanthellae	**B**	**StdErr of B**	**t(42)**	**p**
Intercept				
Partial Mortality	−14	834221	−1.7	0.08
Competition	−44	312617	−1.4	0.1
Number of bites	1632	2745	0.5	0.5
Size	174	1044	0.16	0.8
Site	2338	374570	0.06	0.9
Distance from crest	68	61603	1.1	0.2
Lipid content	**B**	**StdErr of B**	**t(42)**	**p**
Intercept				
Partial Mortality	−23	13.7	−1.7	0.09
Competition	−3.6	5.1	−0.7	0.4
Number of bites	0.008	0.04	0.1	0.8
Size	0.003	0.01	−1.7	0.8
Site	3.96	6.14	0.64	0.5
Distance from crest	−1.6	1.01	−1.5	0.1

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coral grazing parrotfishes have been shown to exhibit higher feeding rates in October compared to April on the GBR [67]. For parrotfishes, temporal differences in feeding rates have been previously attributed to differences the nutritional quality of colonies associated with gametogenesis [68]. For butterflyfishes, which tend to take very shallow bites [69], it is unlikely that gametogenesis of the corals would influence feeding behavior, but changes in the nutritional content may still occur within and among coral colonies. For instance mucus production can drive feeding preferences in butterflyfishes [70,71]. In October, colonies may have released more mucous as a stress response to environmental changes [72] and this discharge may have increased their desirability as food source. The observed differences in bite rates could also be due to seasonal differences in the metabolic rate of food demands of the fishes themselves.

Chronic disturbances were found to affect physiological condition only in. *A. spathulata*, which exhibited strong intraspecific variation that was explained to a large extent by inter-colony differences in biological disturbances and physical position, however these differences were not observed in *P. damicornis*. Even though both study species (*A. spathulata* and *P. damicornis*) are shallow, fast-growing, branching corals, they have slightly different

Table 2. Multiple Regression for zooxanthellae density and total lipid content in *A. spathulata*.

Zooxanthellae	**B**	**StdErr of B**	**t(18)**	**p**
Intercept				
Partial Mortality	−7386077	2909017	−2.5	0.01
Competition	−543263	551519	−0.98	0.3
Number of bites	22837	19454	1.17	0.24
Size	−487	643	−0.75628	0.4
Site	−510264	500279	−1.019	0.3
Distance from crest	−121255	55915	−2.16854	0.03
Lipid content	**B**	**StdErr of B**	**t(42)**	**p**
Intercept				
Partial Mortality	−2.1	18.5127	−0.11	0.9
Competition	0.7522	3.5098	0.21	0.8
Number of bites	−0.04	0.1238	0.33	0.7
Size	0	0.004	−0.05	0.9
Site	−1.87	3.2105	−0.58	0.5
Distance from crest	0.9	0.3558	2.57	0.01

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life-histories strategies, which can explain observed differences. *P. damicornis* is a brooding, opportunistic coral which colonizes very disturbed habitats and it is one of the most resilient corals [46]. These characters may explain why *P. damicornis* was more resilient to chronic background disturbances than *A. spathulata*, which instead seems to dominate communities in relatively stable environments [46]. *A. spathulata* showed higher lipid reserves with increasing distance from the crest and lower symbiont density with increasing partial mortality and distance from crest. The observed increase in total lipid content with distance from crest may be due to the higher energetic cost of this reef habitat.

The reef crest is a shallow wave-exposed habitat, where water flow strongly influences organisms mechanically and physiologically with important consequences on community structure [73]. To avoid hydrodynamic dislodgment, colonies on the crest may need to invest more resources in growth to reach the dislodgment threshold [73], but since energy is limited within a colony, if more resources are allocated to increase colony size, less energy will be available to store. The findings from this study suggest that colonies in intermediate position between reef crest and reef flat have a better performance than conspecific on the crest. However, even though the reef crest is an energetic costly habitat, the high flow can positively affect colonies as they can benefit from it for feeding and escretion [74]. Together with light, flow is a critical abiotic factor affecting colony condition [74]. Colonies exposed to high flow generally have higher skeletal density, higher protein concentration, zooxanthellae density, chlorophyll content, and higher number and size of oocytes compared to colonies exposed to lower flow conditions [74]. Flow enhances zooxanthellae density and photosynthesis due to the enhanced nutrient supply [75], and can explain the decreasing zooxanthellae density with distance from crest found in this study.

The symbiotic relationship between the zooxanthellae and the host may be affected by a variety of internal and external factors and processes, the composition of which still has not been fully investigated [54,76]. Findings from this study suggest that increasing partial mortality and distance from crest may lead to a decline in density of *Symbiodinium*. Not many studies have shown differences in zooxanthellae density among reef habitats regardless of depth. For instance Strickland [76] did not find any difference in zooxanthellae density with increasing distance from the reef crest or location along the reef. Conversely, zooxanthellae within the same reef habitat have been shown to vary with environmental fluctuations and season cycles [54,77,78].

Despite consistency in levels of routine or background mortality, the lipid content within coral tissues consistently declined across all coral colonies between May and October in both *P. damicornis* and *A. spathulata*. The decline in total lipid content observed in October in both coral species may partly be explained by sustained and ongoing rates of background mortality, though the declines in may also reflect limited productivity during winter months, due to both reduced temperature and reduced day length [79]. Zooxanthellae supply corals with an excess of lipids and a limitation in their activity can results in a decline in lipid reserves [56,80]. Stimson [56] documented a decrease in total lipid content following about one month in *P. damicornis* due to light limitation. Corals tend to consume their lipid reserves when maintenance costs of a colony exceed carbon acquisition [22], during environmental unfavourable conditions such as limited light [6,58,81], during reproductive events [82–84] or whenever an increase in energy demand occurs such as the development of a tumor in coral tissue [85].

Large colonies generally have greater regenerative abilities [6,8], greater growth [31], are more fecund [17] and have lower rates of total mortality compared to smaller colonies [6,15]. Consequently we were expecting larger colonies to be more resilient to chronic background disturbances than smaller ones. Conversely, in the present study chronic disturbances had a similar effect on physiological condition of colonies regardless of the size, suggesting that larger colonies are not necessary more resilient than smaller colonies. Similar incidence of chronic disturbances on coral colonies regardless of the size also suggests a lack of size-specific susceptibility to agents of coral mortality [86]. Other studies documented a lack of differences in resilience between small and large colonies [87,88]. For instance *S. siderea* exposed to partial mortality continued to dedicate resources to reproduction even after the colony had shrunk below their size of maturation while larger colonies reduced their fecundity [88]. Often recent injuries play a bigger role than size in predicting colony fate [89]. Large colonies with higher partial mortality may die before small colonies with no injuries [89].

Extensive research effort has focused on understanding the ability of reef corals to withstand and absorb disturbances, thereby contributing to the persistence and resilience of coral colonies, populations and species [1,3,12,42,49,90,91]. Quantifying the effects of essentially routine and ongoing disturbances on colony condition and assess intraspecific differences in colony condition added to this understanding and it is critical because background mortality influences recovery capacity, time and vulnerability to future disturbances.

This study documented significant effects of partial mortality and distance from crest on zooxanthellae density in *A. spathulata* with important ecological consequences for recovery capacity in the aftermath of climate change. A reduction in performances arising from these sub-lethal stressors, is likely to reduce colony resilience and hence increase chances of whole-colony mortality so that colonies suffering from partial mortality may not survive a subsequent acute disturbance. The approach used here, investigating drivers of colony-condition and their energetic consequences for colony resilience, provides a strong framework for predicting resistance, recovery capacity and resilience of reef-building corals. If colonies in poor physiological conditions (e.g. less resilient) are more susceptible to bleaching, disease and other stressors, colonies capable of maintaining a higher physiological condition may have a distinct ecological advantage [22,92]. Consequently, colonies of *A. spathulata*, with high partial mortality rates and located on the reef crest, may have a lower potential to withstand and recover from environmental changes compared to conspecific with lower rates of partial mortality and located in intermediate habitats. The observed differences in physiological conditions could have a strong bearing on the selectivity of major disturbances and the capacity of corals to withstand major disturbances, and thereby adapt to changing conditions.

This study is the first to document significant intra-specific variation in background mortality and colony condition, the next step is to investigate whether this variation impacts individual vulnerability of corals. If so, this will provide strong incentive to reduce background levels of stresses (e.g. control all the factors that routinely injure colonies such as predation or anchoring) as a sure way to increase resilience of corals subject to inevitable increases in acute disturbances in association with global climate change.

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Author Contributions

Conceived and designed the experiments: CP KA MSP. Performed the experiments: CP KA MSP. Analyzed the data: CP KA MSP. Contributed reagents/materials/analysis tools: CP KA MSP. Wrote the paper: CP KA MSP.

References

1. Karlson RH, Hurd LE (1993) Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs 12: 117–125.
2. Stimson J (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory corals. Ecology 66: 40–53.
3. Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16 Suppl: S101– S113.
4. Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27: 1−13.
5. Pratchett MS, Pisapia C, Sheppard C (2013) Background mortality rates for recovering populations of *Acropora cytherea* in the Chagos Archipelago, central Indian Ocean. Mar Environ Res 86: 29–34.
6. Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55: 141–166.
7. Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Washington: Smithsonian Institution Press.
8. Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. Coral Reefs 12: 143–152.
9. Bak RPM, Luckhurst BE (1980) Constancy and change in coral reef habitats along depth gradients at Curaçao. Oecologia 47: 145–155.
10. Harriot VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. Mar Ecol Prog Ser 21: 81–88.
11. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, et al. (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301: 929−93.
12. Déath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci 109: 17995–17999.
13. Cox EF (1986) The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. J Exp Mar Biol Ecol 101: 161–174.
14. Tanner JE (1997) Interspecific competition reduces fitness in scleractinian corals. J Exp Mar Biol Ecol 214: 19–34.
15. Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals– a review. Int Rev Hydrobiol 90: 125–158.
16. Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14: 179–185.
17. Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77: 950–963.
18. Rotjan RD, Dimond JL, Thornhill DJ, Leichter JJ, Helmuth B, et al. (2006) Chronic parrotfish grazing impedes coral recovery after bleaching. Coral Reefs 25: 361–368.
19. Cole AJ, Lawton RJ, Pratchett MS, Wilson SK (2011) Chronic coral consumption by butterflyfishes. Coral Reefs 30: 85–93.
20. Hourigan TF, Tricas TC, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel GS, editors. Marine Organisms as Indicators. New York: Springer Verlag. 107–135.
21. Guzman HM, Burns KA, Jackson JBC (1994) Injury, regeneration and growth of Caribbean reef corals after a major oil spill in Panama. Mar Ecol Prog Ser 105: 231–241.
22. Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Funct Ecol 23: 539–550.
23. Bak RPM (1983) Neoplasia, regeneration and growth in the reef-building coral *Acropora Palmata*. Mar Biol 77: 221–227.
24. Meesters EH, Noordeloos M, Bak RPM (1994) Damage and regeneration: links to growth in the reef-building coral *Montastrea annularis*. Mar Ecol Prog Ser 112: 119–128.
25. Kojis BL, Quinn NJ (1985) Puberty in *Goniastrea favulus* age or size limited? Proc 5th Int Coral Reef Congr 4: 289–293.
26. Meesters EH, Bos A, Gast GJ (1992) Effects of sedimentation and lesion position on coral tissue regeneration. Proc 7th Int Coral Reef Symp 2: 681–688.
27. Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. Proc 3rd Int Coral Reef Symp 143–148.
28. Titlyanov EA, Titlyanova TV, Yakovleva IM, Nakano Y, Bhagooli R (2005) Regeneration of artificial injuries on scleractinian corals and coral/algal competition for newly formed substrate. J Exp Mar Biol Ecol 323: 27–42.
29. Bruckner AW, Hill RL (2009) Ten years of change to coral communities off Mona and Desecheo Islands, Puerto Rico, from disease and bleaching. Dis Aquat Organ 87: 19–31.
30. Babcock RC (1991) Comparative demography of three species of scleractinian corals using age and size-dependent classifications. Ecol Monogr 61: 225–244.
31. Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209: 713−715.
32. Jackson JBC (1979) Morphological strategies of sessile animals. In: Larwood G, Roser BR, editors. Biology and systematics of colonial organisms. London: Academic Press. 499–555.
33. Black NA, Voellmy R, Szmant AM (1995) Heat shock protein induction in *Montastrea faveolata* and *Aiptasia pallida* exposed to elevated temperatures. Biol Bull 188: 234–240.
34. Baker AC, Rowan R (1997) Diversity of symbiotic dinoflagellates (zooxanthellae) in scleractinian corals of the Caribbean and eastern Pacific. Proc 8th Int Coral Reef Symp 2: 1301–1306.
35. D'Croz L, Maté JL (2004) Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. Coral Reefs 23: 473–483.
36. Gurney WSC, Middleton DAJ, Nisbet RM, McCauley E, Murdoch WM, et al. (1996) Individual energetics and the equilibrium demography of structured populations. Theor Popul Biol 49: 344–368.
37. Spencer-Davies P (1991) Effect of daylight variations on the energy budgets of shallow-water corals. Mar Biol 108: 137–144.
38. Szmant AM, Gassman NJ (1990) The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8: 217–224.
39. Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol Oceanogr 45: 677–685.
40. Grottoli AG, Rodrigues LJ, Juarez C (2004) Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. Mar Biol 145: 621–631.
41. Rodrigues LJ, Grottoli AG (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr 52: 1874–1882.
42. Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440: 1186–1189.
43. Halford A, Cheal AJ, Ryan D, Williams D (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85: 1892–1905.
44. Connell JH, Hughes TP, Wallace CC, Tanner JE, Harms KE, et al. (2004) A long-term study of competition and diversity of corals. Ecol Monogr 74: 179–210.
45. Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237: 133–141.
46. Darling ES, Alvarez-Philip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15: 1378–1386.
47. Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshwater Res 50: 839–66.
48. Sheppard CRC, Davy SK, Pilling GM (2009) The biology of coral reefs. Oxford New York: Oxford University Press.
49. Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf S 80: 435–471.
50. Peters EC, Pilson MEQ (1985) A comparative study of the effects of sedimentation on symbiotic and asymbiotic colonies of the coral *Astrangia danae* Milne-Edwards and Haime 1849. J Exp Mar Biol Ecol 92: 215–230.
51. Cervino J, Goreau TJ, Nagelkerken I, Smith GW, Hayes R (2001) Yellow band and dark spot syndromes in Caribbean corals: distribution, rate of spread, cytology, and effects on abundance and division rate of zooxanthellae. Hydrobiologia 460: 53–63.
52. Cooper TF, Gilmour JP, Fabricius KE (2009) Bioindicators of changes in water quality on coral reefs: review and recommendations for monitoring programmes. Coral Reefs 28: 589–606.
53. Cooper TF, Ulstrup KE (2009) Mesoscale variation in the photophysiology of the reef building coral *Pocillopora damicornis* along an environmental gradient. Estuar Coast Shelf S 83: 186–196.
54. Fagoonee I, Wilson HB, Hassell MP, Turner JR (1999) The dynamics of zooxanthellae populations: a long-term study in the field. Science 283: 844–845.
55. Ferrier-Pagès C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O (2001) Response of a scleractinian coral, *Stylophora pistillata*, to iron and nitrate enrichment. J Exp Mar Biol Ecol 259: 249–261.
56. Stimson JS (1987) Location, quantity and rate of change in quantity of lipids in tissue of Hawaiian hermatypic corals. Bull Mar Sc 41: 889–904.
57. Barnes DJ, Blackstock J (1973) Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophospho- vanillin method for 'total' lipids. J Exp Mar Biol Ecol 112: 103–118.
58. Harland AD, Navarro JC, Spencer Davies P, Fixter LM (1993) Lipids of some Caribbean and Red Sea corals: total lipid, wax esters, triglycerides and fatty acids. Mar Biol 117: 113–117.

59. Patton JS, Abraham S, Benson AA (1977) Lipogenesis in the intact coral *Pocillopora capitata* and its isolated zooxanthellae: evidence for a light-driven carbon cycle between symbiont and host. Mar Biol 44: 235–247.
60. Oku H, Yamashiro H, Onaga K, Sakai K, Iwasaki H (2003) Seasonal changes in the content and composition of lipids in the coral *Goniastrea aspera*. Coral Reefs 22: 83–85.
61. McCowan DM, Pratchett MS, Paley AS, Seeley M, Baird AH (2011) A comparison of two methods of obtaining densities of zooxanthellae in *Acropora millepora*. Galaxea Journal of Coral Reef Studies 13: 29–34.
62. Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551.
63. Hall VR (1997) Interspecific differences in the regeneration of artificial injuries on scleractinian corals. J Exp Mar Biol Ecol 212: 9–23.
64. Done TJ (1988) Simulation of recovery of pre-disturbance size structure in populations of *Porites* spp. damaged by the crown of thorns starfish *Acanthaster planci*. Mar Biol 100: 51–61.
65. Ward S (1995) Two patterns of energy allocation for growth, reproduction and lipid storage in the scleractinian coral *Pocillopora damicornis*. Coral Reefs 14: 87–90.
66. Stimson JS (1997) The annual cycle of density of zooxanthellae in the tissues of field and laboratory-held *Pocillopora damicornis* (Linnaeus). J Exp Mar Biol Ecol 214: 35–48.
67. Bonaldo RM, Welsh JQ, Bellwood DR (2012) Spatial and temporal variation in coral predation by parrotfishes on the GBR: evidence from an inshore reef. Coral Reefs 31: 263–272.
68. Rotjan RD, Lewis SM (2009) Predators selectively graze reproductive structures in a clonal marine organism. Mar Biol 156: 569–577.
69. Motta PJ (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): An ecomorphological approach. Environ Biol Fish 22: 39–67.
70. Cole A, Pratchett MS, Jones GP (2009) Effects of coral bleaching on the feeding response of two species of coral-feeding fish. J Exp Mar Biol Ecol 373: 11–15.
71. Pisapia C, Cole AJ, Pratchett MS (2012) Changing feeding preferences of butterflyfishes following coral bleaching. Proc 12th Int Coral Reef Sym 13: 1–5.
72. Reigl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J Exp Mar Biol Ecol 186: 259–275.
73. Madin JS, Dell AI, Madin EMP, Nash MC (2013) Spatial variation in mechanical properties of coral reef substrate and implications for coral colony integrity. Coral Reefs 32: 173–179.
74. Mass T, Brickner I, Hendy E, Genin A (2011) Enduring physiological and reproductive benefits of enhanced flow for a stony coral. Limnol Oceanogr 56: 2176–2188.
75. Muscatine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. Proc R Soc Lond B 236: 311–324.
76. Strickland D (2010) Variations in coral condition within the hydrodynamic regime at Sandy Bay, Ningaloo Reef, Western Australia. Thesis University Western Australia.
77. Rowan R, Knowlton N, Baker AC, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388: 265–269.
78. Jones RJ (1997) Zooxanthellae loss as a bioassay for assessing stress in corals. Mar Ecol Prog Ser 149: 163–171.
79. Cooper T, Lai M, Ulstrup KE, Saunders SM, Flematti GR, et al. (2011) Symbiodinium genotypic and environmental controls on lipids in reef building corals. PLOSONE 6(5): e20434.
80. Crossland CJ, Barnes DJ, Borowitzka MA (1980) Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. Mar Biol 60: 81–90.
81. Hoogenboom M, Rodolfo-Metalpa R, Ferrier-Pagès C (2010) Co-variation between autotrophy and heterotrophy in the Mediterranean coral *Cladocora caespitosa*. J Exper Biol 213: 2399–2409.
82. Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93: 527–533.
83. Pernet V, Gavino V, Gavino G, Anctil M (2002) Variations of lipid and fatty acid contents during the reproductive cycle of the anthozoan *Renilla koellikeri*. J Comp Physiol B 172: 455–465.
84. Leuzinger S, Anthony K, Willis B (2003) Reproductive energy investment in corals: scaling with module size. Oecologia 136: 524–531.
85. Yamashiro H, Oku H, Onaga K, Iwasaki H, Takara K (2001) Coral tumors store reduced level of lipids. J Exp Mar Biol Ecol 265: 171–179.
86. Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony-size frequency distribution. Mar Ecol Prog Ser 162: 301–306.
87. Nugues MM, Roberts CM (2003) Partial mortality in massive reef corals as an indicator of sediment stress on coral reefs. Mar Pollut Bull 46: 314–323.
88. Graham JE, van Woesik R (2013) The effects of partial mortality on the fecundity of three common Caribbean corals. Mar Biol 160: 2561–2565.
89. Cumming (2002) Tissue injury predicts colony decline in reef-building corals. Mar Ecol Prog Ser 242: 131–141.
90. Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19: 155–163.
91. Linares C, Pratchett MS, Coker DJ (2011) Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 438: 97–104.
92. Bachok Z, Mfilinge P, Tsuchiya M (2006) Characterization of fatty acid composition in healthy and bleached corals from Okinawa, Japan. Coral Reefs 25: 545–554.