High $p\text{CO}_2$ also contributed significantly to reductions in overall skeletal deposition, as shown by high surface area to volume ratios (SA:vol) as well as reduced diameter and basal plate thickness in high $p\text{CO}_2$ corals under both temperature regimes (Figure 5.11 and Table 5.1). Furthermore, the length to width ratios of the tertiary septa were highly reduced due to malformation (i.e. incomplete extension of the septa) in the ‘High $p\text{CO}_2$’ treatment and vertical growth (height) was similarly stunted. Temperature alone appeared to have little effect, only significantly increasing tertiary septa length to width ratios. Where there were statistically significant interactions between temperature and $p\text{CO}_2$, they were positive, with elevated temperature increasing both height and tertiary septa length to width ratios under high $p\text{CO}_2$ conditions (Figure 5.11 and Table 5.1). Elevated temperature appeared to somewhat mitigate the negative effects of high $p\text{CO}_2$ on skeletal growth, particularly appearing to facilitate vertical growth at high $p\text{CO}_2$. Although there were no significant differences in corallite wall thickness between treatments, the eroded and highly porous surfaces of high $p\text{CO}_2$ corals at both temperatures demonstrate that the microstructure of the corallite wall was severely altered by high $p\text{CO}_2$, even if the larger scale structure of the wall was not.

![Figure 5.11. Quantitative output from X-ray microscopy scans of 1-month old coral skeletons under the four temperature-$p\text{CO}_2$ treatments (mean ± SE). Measurements include; (A) surface area : volume, (B) diameter, (C) height, (D) basal plate thickness (E) corallite wall thickness and (F) tertiary septa length : width. Factors (Temperature, $p\text{CO}_2$ or their interaction, Temperature * $p\text{CO}_2$) significantly contributing to differences between treatments are indicated by ★ at the top of the graph (n = 5 individuals per treatment). See Table 5.1 for detail on statistical tests.](image-url)
Table 5.1. Two-way ANOVAs testing for significant effects of temperature, $p\text{CO}_2$ and interactions between the two factors (temperature * $p\text{CO}_2$) on X-ray microscopy measurements of juvenile coral skeletons. † indicates significant effect ($p < 0.05$).

<table>
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<th>df</th>
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<th>f-value</th>
<th>p-value</th>
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</table>
5.5 Discussion

Our results indicate that coral recruits are unable to build normal calcium carbonate skeletons under high $p$CO$_2$ and low pH conditions. High $p$CO$_2$ resulted in structurally compromised skeletons that were smaller (increased SA:vol, reduced diameter and height), more fragile (thinner basal plate, pitted or porous corallite walls) and asymmetric. A higher frequency of fractures was also observed in the high $p$CO$_2$ corals. While the formation of these was likely an artefact of sample handling and processing after the experiment, it is remarkable that 50% of the individuals grown under acidified conditions had skeletal fractures, while no fractures were observed in skeletons grown under low $p$CO$_2$ conditions. Alternatively, the fractures may have occurred during the experiment while the recruits were still alive and growing their skeletons. Perhaps the increased porosity and reduced structural thickness caused fractures to form *in situ* under the mechanical strains of an actively growing skeleton. Future studies will need to examine this possibility with greater scrutiny. Consistent with the SEM data, fractures recorded in the high $p$CO$_2$ environment highlight a more fragile, porous skeleton. A recent study on adult corals similarly reports that acidification causes more fragile and porous skeletal structures, but at much higher $p$CO$_2$ than the juvenile corals studied here ($p$CO$_2$ ~ 2200 and 3800 versus 900 µatm) (Tambutté et al. 2015). Our results highlight how acutely vulnerable the growth and development of juvenile coral are to the changes in ocean chemistry expected to occur over the coming century under a ‘business as usual’ scenario (RCP 8.5) (Meinshausen et al. 2011; IPCC 2013). Although our low $p$CO$_2$ conditions were lower than present-day ambient (~250 vs 390 µatm), it is unlikely that this lower $p$CO$_2$ condition influenced the overall conclusions of this study given that 1) the impacts of the high $p$CO$_2$ treatment on the skeleton were so severe, 2) the difference in $p$CO$_2$ between present-day and the low $p$CO$_2$ treatments (~140 µatm) is much smaller than the difference between the low and high $p$CO$_2$ treatments (~650 µatm) and 3) research comparing juvenile calcification at preindustrial and current ambient conditions has shown no significant differences (Ohki et al. 2013). Nonetheless, it is possible that the more preindustrial $p$CO$_2$ levels used in our controls could have led to greater differences in skeletal deposition between the low and high $p$CO$_2$ conditions.
Corals are not the only calcifiers that experience deformation of their skeletal structure under acidified conditions. Skeletal asymmetry and microstructural abnormalities have been observed in both sea urchin juveniles and brittle star larvae exposed to acidified conditions (Kurihara and Shirayama 2004; Dupont et al. 2008; Sheppard Brennand et al. 2010; Byrne et al. 2011). One study suggested that acidification might affect brittle star larvae symmetry through the symmetry-controlling ion-flux mechanism (Hibino et al. 2006; Dupont et al. 2008). This mechanism induces left-right symmetry breakage in sea urchin larvae through asymmetrically localized control of H\(^+\) and K\(^+\) transport (Hibino et al. 2006). It is possible that similar mechanisms are responsible for the CO\(_2\)-driven skeletal asymmetry observed in the present study. In addition, features indicative of mineral dissolution (i.e. disorganized aragonite bundles and an overall pitted appearance of the skeletal surface) have also been observed in adult corals exposed to acidified conditions at natural CO\(_2\) vents (Rodolfo-Metalpa et al. 2011). However, disordered crystals were only observed in areas of exposed skeleton (i.e. parts of the skeleton not covered by tissue), while areas where a tissue layer covered the whole skeleton exhibited no such dissolution characteristics (Rodolfo-Metalpa et al. 2011). The skeletons of juvenile corals in our study were completely covered in a tissue layer throughout the experiment and yet still showed deep pitting on the skeletal surface, which could indicate dissolution. This may be due to juveniles having a much thinner tissue layer for protection (Vollmer and Edmunds 2000) compared to adult corals and further highlights the vulnerability of juvenile skeletogenesis under elevated pCO\(_2\).

Since some coral reefs currently experience elevated pCO\(_2\) (and suppressed pH) relative to the open ocean (up to ~500 µatm) (Albright et al. 2013; Sutton et al. 2015), it is possible that recruits are adopting mechanisms to cope with these conditions in situ. A recent study has shown that adult coral living in highly dynamic thermal and chemical environments more rigorously controlled up-regulation of pH within the calcifying fluid; thus demonstrating a greater resilience to the effects of ocean acidification (Georgiou et al. 2015). Whether or not coral recruits that have spawned from or settled in such highly variable reef environments also
exhibit a greater degree of physiological resilience to acidification remains to be seen. Alternatively, new recruits may already be calcifying at reduced rates (relative to pre-industrial conditions) in these environments. The reduced ability to quickly produce a robust skeleton in new coral recruits can have a direct impact on survival rates. For example, reduced growth rates in 2-month old coral recruits under elevated $p$CO$_2$, led to reductions in overall survivorship due to elevated predation mortality; thus demonstrating how size-escape thresholds can shift under ocean acidification (Doropoulos et al. 2012b). However, it is possible that those individuals that do survive the smaller and more susceptible size classes, may be 1) better able to cope with high $p$CO$_2$ conditions than prior generations and 2) better able to cope with ocean acidification as they get larger (i.e. similarly porous, but larger and thus more able to cope with predation and other mechanical damage), potentially offsetting the more severe effects on the skeleton in the early post-recruitment stages.

In contrast to the effects of acidification, our results suggest that the initial effects of ocean warming (+3°C) on calcification in sub-tropical juveniles, could either be minimal or may even help to mitigate the negative impacts of elevated $p$CO$_2$; however, whether the same response is seen in other sub-tropical species is yet to be tested. This result is contrary to studies carried out in the tropics where high temperature has exacerbated reductions in calcification under high $p$CO$_2$, both in juvenile (Anlauf et al. 2011) and adult corals (Reynaud et al. 2003; Rodolfo-Metalpa et al. 2011). Tropical corals exist close to their upper thermal limit (Berkelmans and Willis 1999) and yet are presumably growing within the optimal range of temperatures for calcification. Consequently, a 3°C increase in temperature could subject them to thermal stress and depress calcification rates below optimal levels. In contrast, sub-tropical coral larvae and new recruits appear to withstand moderate (+3°C) increases in temperature (Nozawa and Harrison 2007; Foster et al. 2015). This may be a result of sub-tropical corals being acclimated to the wider annual range of temperatures experienced at higher latitude locations. Additionally, the ability of new recruits to absorb moderate temperature increases could be related to larval dispersal, where larvae must survive often for extended periods of time, over long distances and
through changing thermal environments (Treml et al. 2008; Putnam et al. 2010; Foster et al. 2015).

In conclusion, acidified conditions caused severely abnormal calcification in new coral recruits. Though the partially mitigative effect of elevated temperature is encouraging in these subtropical recruits, taller but similarly fragile skeletons will be unlikely to provide and sustain the structural support and protection required during early post-recruitment. Furthermore, this mitigative effect does not appear to be present in tropical coral recruits (Anlauf et al. 2011). Our data show that new recruits are thus highly vulnerable to acidification and indicate that near-future projections for ocean carbonate chemistry (Meinshausen et al. 2011; IPCC 2013) are likely to heavily reduce post-recruitment success. Disruptions to normal skeletal development in new recruits could compromise the ability of coral reefs to successfully migrate to more suitable thermal environments, as well as inhibiting the replenishment of existing reefs after episodic disturbances caused by storms, disease outbreaks and mass bleaching events; all of which are expected to increase over the next century if the present CO₂ trajectory is not abated.
Chapter 6: Skeletal Mineralogy of Coral Recruits Under High Temperature and $pCO_2$


6.1 Abstract

Aragonite, the polymorph of CaCO$_3$ precipitated by modern corals during skeletal formation, has a higher solubility than the more stable polymorph calcite. This higher solubility may leave animals that produce aragonitic skeletons more vulnerable to anthropogenic ocean acidification. It is therefore important to determine whether scleractinian corals have the plasticity to adapt and produce calcite in their skeletons in response to changing environmental conditions. Both high $pCO_2$ and lower Mg/Ca ratios in seawater are thought to have driven changes in the skeletal mineralogy of major marine calcifiers in the past ~540 Ma. Experimentally reduced Mg/Ca ratios in ambient seawater have been shown to induce some calcite precipitation in both adult and newly settled modern corals; however the impact of high $pCO_2$ on the mineralogy of recruits is unknown. Here we determined the skeletal mineralogy of one-month old Acropora spicifera recruits grown under high temperature (+3°C) and $pCO_2$ (~900 µatm) conditions using X-ray diffraction and Raman spectroscopy. We found that newly settled coral recruits produced entirely aragonitic skeletons regardless of the treatment. Our results show that elevated $pCO_2$ alone is unlikely to drive changes in the skeletal mineralogy of young corals. Not having an ability to switch from aragonite to calcite precipitation may leave corals and ultimately coral reef ecosystems more susceptible to predicted ocean acidification. An important area for prospective research would be to investigate the combined impact of high $pCO_2$ and reduced Mg/Ca ratio on coral skeletal mineralogy.
6.2 Introduction

Scleractinian corals are the major reef builders, with their skeletons providing the structural basis for the habitats of many marine organisms. The skeletons of modern adult corals are comprised of aragonite, a polymorph of calcium carbonate (CaCO₃) whose stability is highly sensitive to changes in ocean pCO₂ (Orr et al. 2005; Feely et al. 2009). Interestingly, examination of a 70 million year old scleractinian coral fossil showed that some ancient corals were able to produce skeletons entirely of calcite (Stolarski et al. 2007), the most stable and least soluble polymorph of CaCO₃ (de Leeuw and Parker 1998; Boulos et al. 2014). Throughout the Phanerozoic (past 540 Ma), there have been oscillations between calcite and aragonite as the dominant polymorph precipitated by major reef building organisms. During this time period there have been three aragonite-facilitating periods or “aragonite seas” and two calcite-facilitating periods or “calcite seas”. The cause of these transitions in mineralogy has been the topic of much debate over the past 30 years. One of the most important factors affecting skeletal mineralogy is the magnesium to calcium ratio (Mg/Ca) of seawater (Sandberg 1983; Ries 2010). If the Mg/Ca ratio >2, then aragonite is predominantly precipitated (modern seawater Mg/Ca = 5.2), and if the Mg/Ca ratio <2, then calcite is predominantly precipitated (Lowenstein et al. 2001). A recent study found CaCO₃ polymorph precipitation to be a function of both Mg/Ca ratio and temperature, with aragonite precipitated at high temperature and Mg/Ca ratio and calcite precipitated at low temperature and Mg/Ca ratio (Balthasar and Cusack 2015). Changes in atmospheric pCO₂ are also thought to contribute to changes in skeletal mineralogy (Sandberg 1983; Zhuravlev and Wood 2009; Lee and Morse 2010), with rising pCO₂ and subsequent reductions in carbonate saturation state potentially favouring the precipitation of minerals with higher stability and lower Mg content, such as calcite (Morse et al. 2006; Zhuravlev and Wood 2009). If ocean acidification favours the deposition of more stable carbonate minerals such as calcite (Mackenzie et al. 1983; Morse et al. 2006; Andersson et al. 2008), then organisms producing less stable aragonite skeletons will likely be more vulnerable to changes in ocean chemistry under high pCO₂. Alternatively, organisms will be much less vulnerable if, under high pCO₂ conditions, they have the ability to switch from predominantly aragonite to calcite precipitation, especially in their early developmental stages.
It is therefore important to determine whether modern aragonitic corals, like their ancestors, are able to produce calcite in response to changing seawater chemistry. Initial work on coral skeletal mineralogy reported the presence of calcite in modern corals (Houck et al. 1975; Constantz and Meike 1990), however contamination by diagenetic recrystallization (Nothdurft and Webb 2009) and deposits from microboring organisms (Nothdurft et al. 2007) and coralline algae (Goffredo et al. 2012) were later proposed to be the source of the calcite, rather than primary calcitic formation by the coral. Adult corals grown under low Mg/Ca ratios simulating “calcite seas”, have been shown to produce significant amounts of calcite (Ries et al. 2006), however again, some of this calcite production may be due to secondary infilling of pore spaces (Ries et al. 2006; Ries 2010). Nevertheless it is accepted that modern adult corals grown under current ambient conditions have entirely aragonitic skeletons (Cuif et al. 1999).

Much less is known about the mineralogy of corals in the early post-recruitment phases. Early work on the mineralogy of new recruits reported the presence of calcite in only the very early post-settlement stages (Wainwright 1963; Vandermeulen and Watabe 1973), leading to the assumption that unlike adults, newly settled recruits were able to precipitate both calcite and aragonite under ambient conditions (Goffredo et al. 2012). However, new recruits of Acropora millepora grown under carefully controlled ambient conditions did not show any evidence of calcite in their skeleton (Clode et al. 2011) with these authors concluding that initial reports of calcite in recruits was also likely to be artefactual. Similarly, a study growing new recruits under a range of seawater Mg/Ca ratios, reported that even under the lowest Mg/Ca ratio (0.5), the skeletal mineralogy was still dominated by aragonite and under current ambient conditions (Mg/Ca = 5.3) skeletons were composed entirely of aragonite (Higuchi et al. 2014). Interestingly however, this study confirmed that coral recruits are capable of producing some primary calcite in their skeletons if the water chemistry is adjusted to “calcite sea” conditions (low Mg/Ca).
The impact of elevated $p$CO$_2$ on the skeletal mineralogy of new recruits is yet to be investigated. Here we tested whether the treatment conditions of high temperature, high $p$CO$_2$, or a combination of high temperature and high $p$CO$_2$, affected the skeletal mineralogy of newly settled corals. Specifically, we question whether high $p$CO$_2$ and reduced carbonate saturation facilitate the production of calcite within coral recruit skeletons.

6.3 Methods

6.3.1 Treatment Conditions

A detailed description of the coral culturing methods and experimental set-up is given in Chapter 3. Briefly, adult *Acropora spicifera* colonies were collected from the Houtman Abrolhos Islands in Western Australia prior to spawning and maintained under ambient conditions (~24°C and pH 8.1). Larvae were cultured and maintained under ambient conditions until they were motile, at which point they were transferred to treatment tanks. Treatment conditions were: ambient temperature and $p$CO$_2$ (Control: 24°C, ~250 µatm), high temperature and ambient $p$CO$_2$ (high temperature: 27°C, ~250 µatm), ambient temperature and high $p$CO$_2$ (high $p$CO$_2$: 24°C, ~900 µatm) and high temperature plus high $p$CO$_2$ (high temperature + $p$CO$_2$: 27°C, ~900 µatm). See Table 3.1 for more detail on the experimental conditions.

6.3.2 Processing of Skeletons

Once the coral larvae had settled, the recruits were grown for 4 weeks under treatment conditions, before the experiment was concluded. To remove organic material, polyps were immersed in 3-7% sodium hypochlorite (NaOCl) and rinsed three times in deionized water. The skeletons were then stored in 100% ethanol until further examination and analysis were possible.
6.3.3 X-ray Diffraction Analysis

Bulk analysis of the skeletal mineralogy was conducted by obtaining X-ray diffraction (XRD) patterns of the skeletal material. Subsets of 5 juvenile skeletons were randomly selected from each treatment. Skeletons were removed from the ethanol and air dried, then detached from the substrate (transparency paper) using a scalpel and gently crushed. The crushed skeletal material from each treatment was mounted on a low background holder (off angle piece of single crystal silicon) and attached to a reflection spinner stage. A PANalytical Empyrean X-ray diffractometer was used with CuK$_\alpha$ radiation to record the XRD patterns. The scanning rate was 250 seconds per step in 2 Theta ranging from 10° to 80°, with a step size of 0.006°. XRD patterns of skeletal material were compared to the XRD peaks for ICDS aragonite and calcite standards.

6.3.4 Raman Spectroscopy

XRD provides an average analysis for the entire sample, however for calcium carbonate samples Raman spectroscopy has been shown to have lower detection limits and lower rates of errors, though only the surfaces of selected fragments can be analysed at any one time (Kontoyannis and Vagenas 2000). Therefore, complementary Raman spectroscopy was also used to check the skeletons for the presence of calcite within discreet skeletal fragments. A further 5 skeletons from each treatment were randomly selected and each skeleton was individually analysed. Raman spectra were collected from 10 random areas (~60 X 60 µm) in the crushed skeletal material of each sample, using a 633 nm red Helium neon laser. Spectra were measured every 1 µm along the gridded ~60 µm$^2$ area (Figure 6.1) for each of the 10 areas per sample (~36,000 individual spectra were taken per sample). Spectra were similarly taken of both a polished calcite standard and a biogenic aragonite standard to use as references.
Figure 6.1. (A) One month old living *Acropora spicifera* recruit, (B) a typical *Acropora spicifera* recruit skeleton with organic material removed and (C) crushed skeletal material showing a typical ~60 µm² scan area grid analysed by Raman spectroscopy. Scale bars for A and B = 500 µm and scale bar for C = 40 µm.

6.4 Results

Calcite was not detected in the XRD patterns of any of the skeletons, regardless of treatment. Prominent peaks were observed at 2 Theta ~ 26.2° and 27.2°, corresponding with the aragonite standard peaks, while no peaks were observed at 2 Theta ~ 29.4°, the location of the primary calcite peak (Figure 6.2). After analysing all of the skeletal material using XRD, the more sensitive Raman spectrometry was employed to collect spectra from random fragments of the skeleton. Similarly, no trace of calcite was detected in the spectra of any of the treatments. The calcite standard showed peaks at 154, 281, 713, and 1086 cm⁻¹ and the biogenic aragonite standard showed peaks at 154, 205, 704, and 1086 cm⁻¹, which are typical of these polymorphs of CaCO₃ (Dandeu et al. 2006). Since both calcite and aragonite peak at ~154, ~710 and ~1086 cm⁻¹, the peaks of interest were the 281 cm⁻¹ peak typical of calcite and the 205 cm⁻¹ peak typical of aragonite (Dandeu et al. 2006). All spectra from all individuals, across all treatments, exhibited peaks typical of only aragonite mineralogy (Figure 6.3), with prominent peaks at ~207 cm⁻¹ and no peaks at ~281 cm⁻¹. Both the XRD patterns and Raman spectra collected indicate that neither temperature nor pCO₂ had any effect on the skeletal mineralogy of 1-month old coral recruits, as all skeletons across treatments formed entirely aragonitic skeletons.
Figure 6.2. XRD patterns for *Acropora spicifera* coral recruit skeletons grown under (a) control, (b) high temperature, (c) high pCO$_2$ and (d) high temperature + pCO$_2$ conditions. Aragonite standard peaks occur at 26.2° and 27.2° (green bars), and the calcite standard peak occurs at 29.4° (yellow bar).
Figure 6.3. Specific Raman shift of (a) a calcite standard and (b) a biogenic aragonite standard and skeletal material from (c) control, (d) high temperature, (e) high $p$CO$_2$ and (f) high temperature + $p$CO$_2$ treated Acropora spicifera coral recruits. The ~205 peak specific to aragonite is highlighted in green and the ~281 peak specific to calcite is highlighted in yellow.
6.5 Discussion

Since aragonite is a more soluble polymorph of CaCO$_3$ than calcite, it could be advantageous for modern corals in a rapidly acidifying ocean to be able to produce calcite as their ancestors did. Production of calcite has been shown to be phenotypically plastic, with many marine calcifiers able to adjust both the proportion of calcite in their shell or skeleton as well as the Mg/Ca ratio (Ries 2010; 2011). In this study both temperature and $p$CO$_2$ were manipulated to assess their impact on skeletal mineralogy of newly settled coral recruits. Neither temperature nor $p$CO$_2$ affected mineralogy, with all coral recruits analysed producing entirely aragonitic skeletons. Although temperature has been shown to significantly affect abiotic polymorph precipitation (as a function of Mg/Ca), calcite co-precipitation with aragonite is favoured at cooler temperatures (<20°C, Balthasar and Cusack, 2015). As such, temperature treatments applied in this study (24 and 27°C), were within the range of temperatures favouring aragonite production. These temperatures were chosen because they are ecologically relevant to the subtropical corals used in this study, under both present ambient and future elevated temperature regimes.

Predicting the impact of high $p$CO$_2$ on polymorph mineralogy is more complex. The extent to which oscillations between “calcite seas” and “aragonite seas” throughout the Phanerozoic were primarily driven by $p$CO$_2$ versus Mg/Ca ratios has received a lot of attention (see review by Ries, 2010). It is well accepted that modern adult corals under current ambient conditions produce skeletons comprised entirely of aragonite (Cuif et al. 1999). Furthermore, despite initial work suggesting that new coral recruits were biminaric (producing both calcite and aragonite), more recent studies have shown that under ambient conditions recruits produce purely aragonitic skeletons (Clode et al. 2011; Higuchi et al. 2014). However, under reduced Mg/Ca ratios, both adult and newly settled corals are able to produce some calcite (Ries et al. 2006; Higuchi et al. 2014). Despite this ability to switch to a bimineralic skeleton, corals still produce skeletons comprised mainly of aragonite, even under extremely reduced Mg/Ca ratios (Higuchi et al. 2014), suggesting that the ancient ability of corals to produce entirely calcitic skeletons (Stolarski et al. 2007), is not solely controlled by the Mg/Ca ratio of seawater. The impact of
elevated $pCO_2$ on mineralogy has also been examined for a range of marine calcifiers (Ries 2011). In bimineralic animals (e.g. whelks), the proportion of calcite in the skeleton increased with increasing $pCO_2$, however in monomineralic animals precipitating entirely aragonitic skeletons, calcite was not incorporated into the skeleton as the $pCO_2$ increased. For example, a range of CO$_2$ treatments had no impact on the skeletal mineralogy of the adult temperate coral *Oculina arbuscula*, with corals in all treatments producing aragonitic skeletons (Ries et al. 2010). Our study similarly observed no change in skeletal mineralogy under elevated $pCO_2$ for newly settled corals.

This study is part of a growing body of evidence that indicates that corals do not produce calcite under current ambient or predicted future high $pCO_2$ scenarios, regardless of their life stage. While coral recruits exposed to extremely reduced Mg/Ca ratios still produced predominantly aragonite skeletons (Higuchi et al. 2014), the combined impact of elevated $pCO_2$ and reduced Mg/Ca ratio on the skeletal mineralogy of new recruits is yet to be tested. Since $pCO_2$ and Mg/Ca ratio have varied approximately inversely proportionally to one another over geological time (Ries 2010; 2011), this would be an interesting direction for future research. Certainly if elevated $pCO_2$ and concomitant reductions in Mg/Ca ratio are driving the ocean towards “calcite sea” conditions (Andersson et al. 2008), then it will be necessary to examine the simultaneous impact of both acidified and low Mg/Ca ratio conditions on coral skeletal mineralogy.
Chapter 7: General Discussion

7.1 Range Expansion and the Abrolhos Islands

With warming ocean temperatures, there has been a growing interest in the potential for tropical organisms to expand their ranges into what are currently temperate reefs. In the late Pleistocene coral species in WA existed ~500 km further south than the current limits to their distribution (Kendrick et al. 1991). Critical to this expansion is not only successful dispersal and recruitment, but also the distribution of sub-tropical reefs that can provide a geographical connection between tropical and temperate reefs (Ayre and Hughes 2004; Greenstein and Pandolfi 2008). The periodic dispersal and recruitment of tropical organisms into temperate regions is already occurring along the east coast of Australia to the temperate reefs of the Solitary Islands (30°S) (Harriott et al. 1995) and Lord Howe Island (31°S) (Harriott and Banks 2002), and down the Western Australian coastline to Jurien Bay (30°S) (Wernberg et al. 2013) and Rottnest Island (32°S) (Marsh 1993). The sub-tropical Houtman Abrolhos Islands (28°S) are critical to connecting tropical and temperate reefs in WA, as they support extensive and diverse communities of broadcast spawning corals. The high coral cover and species diversity at the Abrolhos Islands is relatively unique given their high latitude, with up to 70% of the 184 species of scleractinian corals at the Abrolhos occurring at the southernmost limit of their distribution (Veron and Marsh 1988). These unusually dense and diverse communities are maintained by the southward-flowing waters of the Leeuwin Current, which bathe the Abrolhos in warm water year round. The Leeuwin Current is predicted to continue to warm and weaken in the coming years (Feng et al. 2009), which will have important consequences for the larval biology of coral at the Abrolhos as well as their ability to recruit to temperate reefs further south. Determining how corals at the Abrolhos Islands are able to cope with climate stressors will also be fundamental in gauging their ability to both facilitate range expansion into higher latitudes and act as refuges as conditions change. This thesis aimed to address some of these issues by examining the impacts of warmer water temperatures and ocean acidification on corals in various stages of their lifecycle at the Abrolhos Islands.
7.2 Reduced Adult Calcification Rates Under High Temperature

The first experimental chapter (Chapter 2) of this thesis examined baseline coral calcification rates for a range of latitudes, seasons and morphologies. For the duration of the two-year study, summer temperatures were warmer than normal and followed record-high water temperatures during a marine heat wave in the summer of 2010-2011. Our findings suggested that elevated summer temperatures prior to and during the study period likely caused sub-bleaching temperature stress; reducing summer calcification rates in all species and across all latitudes. The effect was particularly pronounced in temperature-sensitive branching morphologies and at the high latitude locations (the Abrolhos Islands and Marmion), where seasonal differences in light and temperature should normally cause summer growth rates to be higher than growth rates in winter. This study, in conjunction with observations of coral bleaching during the heat wave and in the following two years, showed that adult corals at the Abrolhos Islands are sensitive to increases in temperature. An increase in temperature of 3-4°C above average for a prolonged period of time (weeks to months) resulted in widespread bleaching during the summer of 2011. The following two years saw temperatures ~2°C above average and some bleaching was observed as well as reduced calcification in the summer of 2012. While corals at the Abrolhos did recover to an extent following the heat wave (Moore et al. 2012), the extended monitoring undertaken in this study (Chapter 2) indicated that they still showed signs of stress as reflected by their reduced growth rates. Although these coral communities may be able to withstand or recover from rare episodic temperature events, the cumulative impact of warmer water events occurring repetitively would likely lead to a change in community dynamics, with hardier massive coral species out-competing more temperature sensitive branching species (Marshall and Baird 2000). Along the Western Australian coastline this scenario is likely to occur particularly during prolonged or extreme La Niña events, whose frequency will likely increase with global warming (Zinke et al. 2015).
7.3 Resilience to Temperature in the Early Life Stages

In contrast to adult corals at the Abrolhos, larvae and newly settled recruits appeared to be able to withstand an ~3°C increase in water temperature, as seen in the laboratory experiments described in Chapter 3. This was evident in both the lack of a temperature effect on settlement and post-settlement survival as well as the partially mitigative effect of elevated temperature on skeletal formation under high $pCO_2$. Corals in their early life stages may be pre-equipped to withstand temperature fluctuations in order to survive long dispersal distances in the highly variable top 1 m of the water column (Treml et al. 2008; Putnam et al. 2010). Similarly, following dispersal, larvae could potentially settle in locations with vastly different temperature regimes from their source location and may require the ability to cope with changes in temperature. Some studies have reported reduced bleaching in young corals (Loya et al. 2001; Depczynski et al. 2013) while other work has shown that coral larvae prefer a fluctuating temperature environment to a constant one (Putnam et al. 2010).

Corals living at high versus low latitude locations are also exposed to a broader annual range in temperatures. If corals in the sub-tropics are acclimated to a broader range of temperatures, then they may be able to tolerate temperature fluctuations and elevations more readily than corals in the tropics that are generally exposed to a narrower range of temperatures. This idea is supported by work comparing coral colonies from different reef zones, with corals in the highly variable thermal environments of nearshore reef zones found to have higher thermal tolerances than conspecifics in more stable temperature environments at fore reef zones (Castillo et al. 2012). Corals at higher latitude reefs also have the benefit of not having to be exposed to the absolute high temperatures (>30°C) observed at low latitude reef environments during anomalously warm periods and heat waves. The ability to tolerate a fluctuating temperature environment and the overall cooler temperatures at high latitude locations (i.e. temperatures that do not approach the upper thermal limits of tropical corals; Berkelmans and Willis, 1999) could provide a buffer to temperature elevations for corals in temperate and sub-tropical regions and suggests that high latitude locations have the potential to act as refuges under future ocean warming scenarios.
The results of this thesis suggest that any resilience to temperature elevations in high latitude corals is apparent only during the early life stages. Nonetheless, it is possible that the capacity for larvae to endure higher temperatures may be carried on into adulthood, even if the temperature resistance of the existing adult coral population (which settled and acclimated to local conditions years if not decades earlier) is not particularly strong. This particular species (*Acropora spicifera*) may also be relatively resilient to sub-tropical level temperature elevations at all stages of its life cycle. While widespread bleaching, slow recovery and reduced summer calcification rates have been reported for adult corals at the Abrolhos under ~3°C temperature elevations (Moore et al. 2012; Abdo et al. 2012; Foster et al. 2014), none of the studies specifically investigated *Acropora spicifera* and it is unknown whether this species bleached. *A. spicifera* at the Abrolhos also likely has tropical origins, with transport to the sub-tropics occurring via the Leeuwin Current (Cresswell 1996). Thus although *A. spicifera* has been established at the Abrolhos for at least half a century (Veron and Marsh 1988) and is currently self-seeding, particularly in the southern group of the islands (Thomas et al. 2015), its genetic legacy may enable it to still withstand tropical temperatures (~27-28°C). Whether this lack of response to elevated temperature is common in other species in the sub-tropics (particularly those not commonly found in the tropics) remains to be seen. Certainly further work is required to confirm the ‘sub-tropical refuge hypothesis’ presented here. However regardless of whether the response is universal, it is a ‘good news story’ for the Abrolhos and for WA, with an abundant and important habitat provider showing signs of resilience to future changes in temperature.

### 7.4 Larval Attraction to Red Settlement Substrates

Another important observation of this work suggested that while sub-tropical larvae and new recruits may not be directly affected by initial temperature elevations, there could be indirect impacts of high temperature. Larvae exhibited a preference for red settlement substrates indicating that they are able to detect and respond to both spectral and chemical settlement cues
in order to locate their preferred crustose coralline algae (CCA) settlement substrate. However, settlement rates reduced significantly when the substrate appeared white, simulating the spectral signal of bleached CCA. CCA bleaches when exposed to both high temperature and high $p$CO$_2$, disrupting both chemical (Webster et al. 2011; 2013a; 2013b) and spectral settlement cues. At the Abrolhos, spawning occurs during the warmest months of the year (February and March), thus the chances of a bleaching event coinciding with coral spawning are relatively high. Although our data show that larvae are able to withstand and possibly even benefit from elevated temperature (once settled), they may be unable to locate the reef for settlement if warmer water causes CCA bleaching, thereby reducing overall recruitment success.

### 7.5 Reduced Skeletal Deposition Under Acidification

Elevated $p$CO$_2$ did not affect larval settlement rates or post-settlement survival, but severely reduced mineral deposition in the skeletons of new recruits. Coral recruits from high $p$CO$_2$ treatments had both reduced calcification rates and overall smaller skeletons (as determined by a range of 3D X-ray microscopy measurements of overall deposition and individual structures). High $p$CO$_2$ skeletons also had pitted and porous surfaces and a range of deformities disrupting their symmetry, with malformations of the skeleton ranging from small gaps in the structure to large sections not forming. The increased porosity and loss of major structural elements likely increased the overall fragility of the skeleton, with fractures observed in half of the high $p$CO$_2$ corals and none of the low $p$CO$_2$ corals. These findings highlight that newly settled recruits are highly vulnerable to acidification and will struggle to build their skeletons under near-future $p$CO$_2$ conditions. Interestingly however, elevated temperature did not further exacerbate the problem, instead appearing to mitigate the negative effects of high $p$CO$_2$ on skeletal development.

While post-settlement survival was not affected by elevated $p$CO$_2$ under laboratory conditions, slower calcification rates as well as smaller and more porous skeletons will likely reduce overall chances of survival \textit{in situ}, where tiny new recruits are immediately faced with the pressures of an adult coral. In particular, newly settled recruits are highly vulnerable to being outcompeted
by other benthic organisms, including the CCA on which they settle (Dunstan and Johnson 1998). Coral recruits require high growth rates and robust skeletons to not only maintain their position on the substrate, but also to rapidly move out of the smallest size class. Post-settlement survival rates are positively correlated with size (Babcock and Mundy 1996); coral recruits with the slowest growth rates are subsequently in the smallest size classes and generally have the highest mortality (Babcock 1991; Babcock and Mundy 1996). Higher mortality in small size classes is probably due to increased risk of overgrowth (Dunstan and Johnson 1998) and predation by corallivores or herbivores (Penin et al. 2010; Doropolous et al. 2012b). Reduced growth rates are therefore highly likely to cause reductions in overall survival of new recruits and subsequently reduce recruitment success.

High rates of recruitment are important because 1) they provide an influx of new young corals to a reef and can aid in recovery after damaging events, and 2) the sexual reproduction of mass spawning events helps to maintain the genetic diversity of a reef thereby boosting its resilience to environmental change (van Oppen and Gates 2006). Successful recruitment is therefore essential to the long-term health and survival of coral reefs, particularly under rapid climate change. What may eventuate in a warmer and more acidic ocean is reduced overall recruitment success, but also an offset effect of elevated temperature in sub-tropical and temperate locations. This might be evident particularly in processes such as calcification, where initial temperature increases in these cooler waters could act to help mitigate the negative effects of acidification on mineral deposition. Although the architecture and formation rate of recruit skeletons diminished when exposed to high $p$CO$_2$, there was also variability observed between individuals in the larger-scale structure of the skeleton. For example, some high $p$CO$_2$ individuals maintained the same diameter or height as low $p$CO$_2$ individuals, particularly under elevated temperature conditions. This variability in response suggests that under high $p$CO$_2$ conditions, some individuals may maintain required sizes, albeit with more porous skeletal structures, and also highlights the value of high latitude reefs, where there may initially be a positive impact of temperature elevations on calcification.
7.6 Skeletal Mineralogy

Another way that coral could cope with increasing ocean $p$CO$_2$ could be through changing their mineralogy from aragonite to calcite, a less soluble polymorph of calcium carbonate. Major marine calcifiers have adjusted their polymorph precipitation based on changes to ocean chemistry, with the main drivers thought to be oscillations in magnesium to calcium ratio (Mg/Ca) and changes in ocean $p$CO$_2$ (Sandberg 1983; Zhuravlev and Wood 2009; Ries 2010; Lee and Morse 2010). Ancient corals were able to produce calcitic skeletons under “calcite sea” conditions (low Mg/Ca) while recent experiments on modern marine calcifiers have shown that changes in both Mg/Ca and $p$CO$_2$ can drive changes in mineralogy (Ries et al. 2006; Ries 2011). This experiment (Chapter 6) examined the ability of new coral recruits to adjust their mineralogy under high $p$CO$_2$. There was no evidence that recruits were able to switch to calcite precipitation under high $p$CO$_2$ conditions, with all recruits producing entirely aragonitic skeletons regardless of the treatment. Thus it is unlikely that corals will be able to adjust their mineralogy in order to cope with ocean acidification, at least not without a substantial reduction in seawater Mg/Ca (Ries et al. 2006; Higuchi et al. 2014).

7.7 Conclusions

This thesis has highlighted how important it is to analyse the interactive effects of multiple stressors and constraints on corals, to look at different stages of the life cycle and to examine different physiological, biological and ecological processes - as any one of these stressors, stages or processes (or their interactions) could cause a bottleneck in the overall success of a reef in the coming years. For example, even if larvae prove to be resilient to increases in temperature at high latitude locations, if adults are sensitive and bleach when there is a warm water event such as the 2011 heat wave, then the chances of them producing larvae are slim (Baird et al. 2006). Similarly, if juveniles are able to settle, metamorphose and calcify under elevated temperature, but the architecture of their skeleton is compromised under acidification, they may be vulnerable to predation, damage from storms or be out-competed in the battle for
substrate space. The relative contributions and interactive effects of latitude dependent
environmental constraints are also important. Although temperatures are increasing in high
latitude locations allowing for the survival of tropical species, these increases are not consistent.
Occasional ‘cold snaps’ could disrupt poleward migrations by killing populations that have
managed to settle there. Furthermore, light and pH both decrease with increasing latitude and
are also important constraints on coral growth, thus there will be limits to how far corals can
move poleward with increasing water temperatures.

It is not only critical to determine the bottlenecks to success, but also the outliers that may be
immune to those bottlenecks, as it is often the outliers that become key when conditions change.
In this thesis sub-tropical juvenile corals have been identified as a group that should be
investigated further and may prove to be such outliers. This work adds to a growing body of
evidence that juvenile marine species in temperate and sub-tropical regions can withstand or
even benefit from temperature elevations under high $pCO_2$ conditions, particularly if the species
has a wide tropical-temperate distribution (Byrne and Przeslawski 2013). For example, in
temperate sea urchin larvae from the southeast coast of Australia (~33°S), warming (+4°C)
mitigated the impact of acidification on growth (Byrne et al. 2013). Similar observations were
made in brittlestar (~30°S, +3°C) (Sheppard Brennand et al. 2010) and oyster (~32-34°S, +4°C)
(Parker et al. 2010) larvae. Newly settled corals from Lord Howe Island (~31°S) also benefited
from an increase in temperature, with elevated post-settlement survival rates recorded at +3°C
(Nozawa and Harrison 2007). These findings are in contrast to the majority of studies carried
out in the tropics where similar temperature elevations (+1-4°C) have had largely negative
impacts on coral larvae and recruits (Bassim and Sammarco 2003; Randall and Szmant 2009;
Anlauf et al. 2011; Albright and Mason 2013). This thesis examined the larvae and recruits of
the coral *Acropora spicifera*, one of the most dominant reef-building species at the Abrolhos
and at many other reefs throughout WA. The response to elevated temperature ranged from no
effect to a positive effect (particularly on early calcification), which indicated that future
generations of one of the most dominant and important habitat-forming coral species at the
Abrolhos may have some level of resilience to predicted temperature elevations.
Coral reefs on the margins of their distribution have been recognized as hotspots for hybridization and evolutionary potential (Budd and Pandolfi 2010). Additionally, it is likely that corals will expand or shift their ranges into higher latitudes in response to global warming (Precht and Aronson 2004). Thus high latitude reefs have already been identified as important areas to protect under future climate scenarios; however the findings of this thesis further highlight the importance of sub-tropical reefs. If corals in the sub-tropics are more resilient to future elevations in temperature, they may become important refuges for many species, particularly providing the ‘breathing time’ for tropical species to move poleward. That is, if temperate and sub-tropical reefs are able to maintain a predominantly coral reef environment, (as opposed to shifting to a more algal dominated community), then they will be more likely to facilitate a range expansion or shift for tropical corals. The wider range of temperatures experienced in the temperate regions as well as the tropical origins of many high latitude species may be key to their resilience to future temperature elevations and their potential to act as temperature refuges. However more research is needed to determine if a similar pattern is seen across species, life stage and location. Specifically future work should focus on comparing the responses to temperature-$p\text{CO}_2$ regimes in: 1) the same species across latitudes and at other high latitude locations, 2) sub-tropical species that are commonly found in the tropics versus those specific to sub-tropical and temperate latitudes, and 3) across life history stages including adulthood. The impact of elevated atmospheric CO$_2$ and subsequent ocean acidification is a global threat to coral reefs as well as many other marine organisms that use calcium carbonate to build their shells and skeletons. As with temperature, there is variability in species responses to acidification and consequently there will likely be changes in community composition and dynamics as the climate and ocean chemistry changes (Hughes et al. 2003; Doney et al. 2009). These differences in species and life stage susceptibility to climatic stressors, as well as their interaction with local scale stressors, have the potential to cause fundamental changes to the overall structure of a reef.
7.8 Outlook for the Future

In 2015 and 2016 we have witnessed the third global coral bleaching event unfolding, with devastating impacts on affected reefs. This has drawn the spotlight to the immediate impacts of climate change on one of the world’s most diverse and important ecosystems. Recent research has also shown that ocean acidification has already caused reductions in calcification on the reef scale and that returning the water chemistry to pre-industrial levels would increase calcification (Albright et al. 2016), while further increases in $pCO_2$ (doubling expected by the end of the century) will likely change the architecture of reefs as they are pushed towards net dissolution as opposed to net accretion (Silverman et al. 2009). Wealthy countries such as Australia have an obligation to lead the way in reducing CO$_2$ (and other greenhouse gas) emissions and changing the trajectory for ocean temperature and $pCO_2$. Currently Australia is one of the largest producers and exporters of fossil fuels (World Coal Association, 2013) and has an economy that is heavily reliant on extractive industries. Also, unlike other developed nations such as the United States and countries of the European Union, where land clearing slowed or stabilised decades or centuries ago (Kauppi et al. 2006), Australia still clears land for agriculture at an alarming rate (Lindenmayer and Burgman 2005; Taylor, 2015). Australia’s fossil fuel emission-based economy and low emissions reduction target (5-25% compared to the 40% target of the EU and 26-28% of the US) similarly leaves much room for improvement, and unfortunately Australia has now also been ranked as the developed nation with the lowest Climate Change Performance Index (Burck et al. 2016). If Australia is to be ‘in step’ with the rest of the developed world on climate targets, a change in both outlook and strategy is required at the federal level.

In addition to national and global level changes, local scale management can provide additional protection to help buffer the effect of global scale stressors. For coral reef organisms, this protection is often provided through the establishment of Marine Protected Areas (MPAs). The protection from local disturbances, such as pollution, sedimentation and overfishing provided by MPAs, allows reefs to ‘bounce back’ from global climate related disturbances such as bleaching events (Lubchenco et al. 2003; Mumby and Harborne 2010; Gilmour et al. 2013).
Locations like the Abrolhos Islands will need to be managed carefully under future emissions scenarios, given their strategic importance to the whole coastline (i.e. as ‘stepping stones’ in facilitating range expansion). Currently in WA there are a number of authorities managing the marine environments of an exceptionally vast (~13,000 km) coastline. To the north of the Abrolhos Islands is the Ningaloo Marine Park and to the south is the Jurien Bay Marine Park; both are managed by the state conservation agency, the Department of Parks and Wildlife. The Abrolhos have a 3 nautical mile state waters jurisdiction surrounding them and are therefore managed by the Western Australian Department of Fisheries. The Islands are managed as ‘Fish Habitat Protection Areas’ (FHPAs), with a strong focus in management on commercially important species, particularly the western rock lobster. There are currently four ‘No Take Areas’ at the Abrolhos Islands, which are important for the recovery and maintenance of both the coral reef and fish stocks. However, since the Islands are managed as FHPAs and not as a Marine Park, these ‘No Take Areas’ do not protect against all extractive activity, including mining or oil and gas exploration and development. In addition to providing a higher level of protection for the Abrolhos ecosystems (i.e. truly non-extractive no take areas), it would be extremely valuable to have a network of ‘No Take’ sanctuaries down the WA coastline. High connectivity between reefs increases resilience to disturbances, while fragmentation and isolation of reef habitats have been shown to reduce it (Jones et al. 2007; Almany et al. 2009), thus a network approach could be critical not only in facilitating the movement of species southwards, but also in boosting resilience in an era of rapid global change. This thesis has highlighted the important role that the Abrolhos could play in facilitating range expansion under future climate scenarios. For the Islands to act in this capacity however they will need to be protected against both current and potential human induced pressures and further, their connectivity to other reefs along the coastline will need to be considered.
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Appendix

First page of the publication arising from Chapter 2:

Effect of ocean warming and acidification on the early life stages of subtropical Acropora spicifera

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Abstract This study investigated the impacts of acidified seawater (pCO\(_2\) ~ 900 μatm) and elevated water temperature (+3 °C) on the early life history stages of Acropora spicifera from the subtropical Houtman Abrolhos Islands (28°S) in Western Australia. Settlement rates were unaffected by high temperature (27 °C, ~250 μatm), high pCO\(_2\) (24 °C, ~900 μatm), or a combination of both high temperature and high pCO\(_2\) treatments (27 °C, ~900 μatm). There were also no significant differences in rates of post-settlement survival after 4 weeks of exposure between any of the treatments, with survival ranging from 60 to 70 % regardless of treatment. Similarity, calcification, as determined by the skeletal weight of recruits, was unaffected by an increase in water temperature under both ambient and high pCO\(_2\) conditions. In contrast, high pCO\(_2\) significantly reduced early skeletal development, with mean skeletal weight in the high pCO\(_2\) and combined treatments reduced by 60 and 48 %, respectively, compared to control weights. Elevated temperature appeared to have a partially mitigative effect on calcification under high pCO\(_2\); however, this effect was not significant. Our results show that rates of settlement, post-settlement survival, and calcification in subtropical corals are relatively resilient to increases in temperature. This is in marked contrast to the sensitivity to temperature reported for the majority of tropical larval and recruits in the literature. The subtropical corals in this study appear able to withstand an increase in temperature of 3 °C above ambient, indicating that they may have a wider thermal tolerance range and may not be adversely affected by initial increases in water temperature from subtropical 24 to 27 °C. However, the reduction in skeletal weight with high pCO\(_2\) indicates that early skeletal formation will be highly vulnerable to the changes in ocean pCO\(_2\) expected to occur over the twenty-first century, with implications for their longer-term growth and resilience.

Keywords Coral · Climate change · Acidification · Juveniles · Subtropical

Introduction

Increases in atmospheric CO\(_2\) are driving the two major global threats to coral reefs: ocean warming and acidification (Hoegh-Guldberg et al., 2007; Veron et al., 2009). Consequently, coral reefs are currently facing unprecedented rates of change in both seawater temperature and carbonate chemistry. Many coral reefs around the world have already shown declines in overall coral cover and species diversity in response to a combination of local and climatic disturbances (Bak et al. 2008; Hughes et al. 2010; De’ath et al. 2012; McClanahan et al. 2014). Successful sexual reproduction is critical to sustaining genetic variability and filling damaged areas as well as maintaining genetic diversity (Richmond 1997; Ayre...