Coral larval ecology and biogeography in a warming ocean

Thesis submitted by

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For the degree of Doctor of Philosophy in Marine Biology

from the ARC Centre of Excellence for Coral Reef Studies

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Statement of the contribution of authors

All of the chapters of this thesis are also manuscripts that have been published in peer-reviewed journals or are currently in preparation for submission. The author contributions are outlined below.

Chapter 2 is a manuscript published in Marine Ecology Progress Series and is co-authored by Maria Byrne (MB) and Andrew H. Baird (AHB). Experiments for this study were designed by AHB and Erika S. Woolsey (ESW) and were performed by ESW. Statistical analyses were performed by ESW under the supervision of AHB and MB. All authors contributed to writing the manuscript.

Chapter 3 is a published in the Proceedings of the 12th annual International Coral Reef Symposium. Although ESW is the sole author on this publication, AHB provided comments on the manuscript and the study uses a similar experimental design to that in Chapter 2.

Chapter 4 is in review for Coral Reefs and is co-authored by Sally Keith (SK), MB, Sebastian Schmidt-Roach (SSR) and AHB. Fieldwork was conducted by ESW, SK, SSR and AHB. Experiments were designed by AHB and ESW and performed by ESW, SK, SSR and AHB. Statistical analyses were performed by ESW under the supervision of SK, MB and AHB. All authors contributed to writing the manuscript.

Chapter 5 is in preparation for submission to the Journal of Biogeography and is co-authored by SK, MB, Joshua Madin (JM) and AHB. SK and AHB helped design the study. Fieldwork was conducted by ESW, SK and AHB. Additional data was provided by AHB and JM. SK taught ESW the technical skills to run the model and oversaw methods and analysis. All authors contributed to writing the manuscript

Fieldwork was funded by ARC grants to AHB.

Acknowledgements

I would like to express my sincere gratitude to all who guided and supported me throughout my PhD. To my primary advisor Andrew, for taking me on, teaching me so much, challenging me, and bringing me to some of the most beautiful and interesting places I will ever see. To my advisor Maria Byrne, thank you for your depth of support and guidance over the years, for introducing me to One Tree Island, and for your brilliance and encouragement. To my advisor Sally Keith, thank you for your insights, unending support, and catlike reflexes. I admire you so much and am grateful for your friendship.

Thank you to everyone that helped me get started. To Samantha de Putron, who was the first to teach me coral reef ecology. To Peter Davies, who supervised my Masters project and launched me into coral reef research. Thank you to Kate Thornborough for sharing your passion for corals, back when I couldn't tell *Pocillopora damicornis* from *Isopora palifera*. I was lucky to be stuck on boats and islands with you for prolonged periods. Tom Bridge, for introducing me to David Attenborough, for your help from the beginning, and for sharing Angus and Bonnie when I needed dogs in my life. To Miin Chua, thank you for teaching me the secrets of coral spawning work, and for your unparalleled selflessness and generosity. Thank you to the wonderful Byrne Lab family for your friendship and support: Natalie Soars, Hong Nguyen, Steve Doo, Kenny Wolfe, Shawna Foo, Dave McElroy and Paula Cisternas. Thank you to Sergio Barbosa for always giving me an ear, a shoulder and a place to crash. To Hampus Eriksson, thank you for the good times at One Tree and for welcoming me into your home for an unforgettable Midsummer.

Thank you to everyone who assisted in the field or advised on my work. Thank you to Karen Miller, who introduced me to the wonderful world of *Goniastrea favulus*. Thank you to Jen Reiffel and Russ Graham, staff of One Tree Island Research Station, for your assistance and extraordinary hospitality. Thank you to Joana Figueiredo, Viv Cumbo, and Aurelie Moya for your generous advice. You are excellent science role-models.

Thank you to my friends and colleagues in the Townsville community. To Sebastian and Alicia Schmidt-Roach for your help in the field, all of the delectable meals, and your incredible generosity and kindness when I needed it most. To Ed Roberts for your help in the field and your contagious enthusiasm for all things marine, and for trusting me with your camera. Best of luck with your thesis, Mr. Manager. Thank you to the effervescent Amelia Wenger for the hill walks and buffalo wings, and for questing for the elusive Coral Wonderfish. To the sweet and impressive Gabi Miller, I only got to know you late in my Townsville life, but am so glad I did. Thank you for all your time and attention. Jessica Nilsson, thank you for your healing presence over the years. Thank you Richard Wormald, for the guitar serenades and for sharing your space. To Johnathan Kool for being so generous with your time and so thoughtful with your advice. Thank you Kirsty Nash for your inspiring and refreshing presence in the Centre. To Daisie Ogawa, for showing me the light at the end of the tunnel and helping me transition between hemispheres. Thank you to Vera Horigue, Karen Chong-Seng and Melanie Hamel for creating a supportive and fun space filled with arts and crafts, headstands, and glitter. To Liz Tynan, for all your support and for reminding me that science extends beyond university walls. To the Centre of Excellence Student committee, and to all the students that participated in the student retreat, thank you for making it a fun and memorable experience.

Thank you to my non-scientist friends for balancing my life. To Kimberly Adolfo, for your sparkle and your unwavering friendship. To Belinda Beatty, for being such an amazing woman, for taking me in, for all our talks and adventures on both sides of the Pacific. Thank you Meagan Bridges, one of my oldest and most cherished friends. You are my prized relic from the Duke Experience and I am looking forward to seeing more of you. Thank you to Sully for trips up the hill, for ruling at Zumba, and for teaching me positivity. I hope to control the universe the way you do one day. Thank you to Nick Freeman for the talks and walks on the Strand when we were both playing injured.

To the friends I made in Sydney, thank you for inspiring me and supporting me on my path. Shanti Abedin, Adrian Davis, Emma Thompson, Geraint Hill, George Watson, Daisy Taylor, and Alex Major. I am so lucky to have met such an amazing group of people in one place. My time in Sydney was stupidly fun thanks to you.

Thank you to everyone I've worked alongside at the Centre. To Olga Bazaka for looking after me, and for offering conversation whenever I was aimlessly wandering the halls. To Janet Swanson for laughing it off whenever I made your day more difficult. Thank you to Rosemarie and Louise, for all your help and excellent organization. You made my life a lot easier. To the Powers That Be, Jenny, David and Terry, I am very grateful for your support and understanding. It's been an honour being a part of the Centre. Thank you to my funding bodies that made my PhD work and conference attendance possible: James Cook University, the ARC Centre of Excellence for Coral Reef Studies, the Graduate Research School, and the Australian Coral Reef Society.

To my amazing family, I love you so much and am eternally grateful for your unwavering support, even when I decided to run away to Australia. To my wonderful little sister Jocelyn, thank you for teaching me not to take things too seriously and for sharing your sparkle. I'm so proud of you and am deeply happy to be near you again. Thank you to my brother Matt, for always looking after me and for teaching me at the age of 4 that the world is only a speck in the whole universe. You have always been an exceptional role model and a girl couldn't ask for a better big brother. To my Aunt Karla, Uncle Chris and cousin Anna, thank you for all that you've done for me. To the Bollingers and my extended family in Vermont, Sweden, and Mexico (including mi tocayo Eric). Thank you for the support and inspiration from miles away.

Thank you to Craig for your love and encouragement. You're the most surprising discovery of my science career so far.

Finally, I would like to dedicate this thesis and associated accomplishments to my parents Brad and Kristina, who have given me unending love and support. Thank you for always encouraging me to follow my curiosities and contribute in this world. I love you so much.

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THESIS ABSTRACT

The distribution and diversity of species is changing in response to global climate change, particularly increased temperature. However, the specific response, both within and among species, is often dependent on geographical location. For instance, the greatest negative effects of global warming are predicted to occur in the tropics because low-latitude species tend to have a narrower range of thermal tolerance when compared with higher latitude species. Corals are expected to be at a particularly high risk from increased temperatures because thermal anomalies as little as 1°C above average annual summer maximums can cause mass bleaching in adult coral assemblages. Raised temperatures are also deleterious to coral larvae (the dispersive life stage), which are crucial for recruitment and replenishment of coral populations. However, studies into the effects of temperature on these early life stages have so far been limited to single locations and upper thermal limits. In addition, the effects of reduced temperature are also rarely examined. Therefore, the aims of my PhD were to 1) determine thermal tolerance breadths for the development and survival of coral larvae 2) assess the extent to which this tolerance varies across space and among species 3) test whether differences between adult coral assemblages across a dispersal barrier can be predicted by species traits, in particular larval traits including the rate of development and mode of larval nutrition. To address these aims, I combined small-scale larval experiments at three sites along the east coast of Australia, and large-scale biogeographical analyses. My major findings were that 1) raised temperatures increased the proportion of abnormal embryos, increased the rate of larval development and decreased larval lifespan, 2) lowered temperatures reduced the rate of development but did not affect larval lifespan 3) in

relation to local ambients, upper thermal thresholds were greater in coral larvae from higher latitudes 4) the rate of larval development was the best predictor for the differences in assemblage structure between the Great Barrier Reef and Lord Howe Island, with coral cover at Lord Howe Island overwhelmingly dominated by species which brood larvae that are ready to settle on release. Although local temperature ranges projected by the end of the century exceed the thermal tolerance breadths at most locations, rising temperatures pose a greater threat to low-latitude coral populations because of their narrower range of thermal tolerance. Furthermore, the effects of ocean warming are likely to vary among species. In particular, species with larvae that develop quickly may be pre-adapted to survive changing climates because they are better colonisers and therefore have a greater potential to expand their range size to track suitable climate.

CHAPTER ONE: GENERAL INTRODUCTION

1.1 Global warming and changes in species distributions

Changing temperatures are affecting the distribution of organisms throughout the world (Parmesan and Yohe 2003; Root et al. 2003; Poloczanska et al. 2007). Indeed, range shifts are a mechanism by which species persist through changing climates (Davis and Shaw 2001; Somero 2010). For example, many species of fish and marine invertebrates have recently extended their ranges pole-wards due to climate-driven ocean warming and changes in ocean circulation (Przeslawski et al. 2008; Ling et al. 2009; Figueira & Booth 2010; Feary et al. 2013). Historical data of marine invertebrate distribution and temperature records indicate a close mirroring of species' ranges and thermal regime shifts (Sagarin et al. 1999; Hellberg et al. 2001; Jones et al. 2009), a phenomenon known as climate tracking. Climate tracking has occurred in scleractinian corals on both geological and ecological timescales (geological: Veron 1992; Precht and Aronson 2004; Greenstein and Pandolfi 2008; ecological: Yamano et al. 2011, Baird et al. 2012).

Climate tracking in terrestrial environments is generally interpreted to be enabled by an expansion of area suitable for adult growth and survival. However, in marine environments, range expansion must be initiated by the dispersal of planktonic larvae (Parmesan 2006; O'Conner et al. 2007; Figueira & Booth 2010). Therefore, an alternative hypothesis to explain climate tracking in the marine environment is a breakdown in barriers to dispersal, such as waters too cool to allow larval survivorship. Dispersal-related traits, such as planktonic larval lifespan, are commonly invoked to explain aspects of organism ecology, such as geographical range size (Richmond 1987; Graham et al.

2008; Connolly and Baird 2010). However, potential impediments to dispersal of larvae have rarely been tested. For example, dispersal of corals from the Great Barrier Reef (GBR) into sub-tropical areas via the East Australian Current may be limited by the capacity of coral larvae to survive colder waters they encounter as they move south. Such environmental filters may help explain many features of scleractinian biogeography, such as the pronounced decline in species richness with increasing latitude (Wells 1955; Veron 1995). While the effects of temperatures above ambient on coral propagules are well understood, and include reduced fertilisation success, abnormal development of embryos and increased mortality with a threshold of between 2 and 5ºC above ambient (Bassim et al. 2002; Negri et al. 2007; Randall and Szmant 2009), the effects of temperatures below ambient have yet to be tested.

1.2 Variation in thermal tolerance breadth and thermal thresholds among locations and the implications for population response to global warming

Biological responses to temperature are strongly influenced by local environments (Addo-Bediako et al. 2000; Sunday et al. 2012). For example, temperatures are more stable throughout the year in the tropics compared to temperate regions (Spencer and Christy 1990) and biological responses to temperature reflect this pattern. In particular, thermal tolerance breadth, a strong indicator of an organism's potential for persistence in changing environments, increases predictably with latitude in many organisms (Janzen 1967; Chown et al. 2004; Bozinovic et al. 2011). Consequently, while tropical populations can tolerate higher absolute temperatures when compared to temperate populations, they generally possess narrower tolerance breadths, and are therefore more sensitive to small changes in temperature (Stillman 2004; Hoffmann et al. 2005). As a

result, tropical organisms, particularly ectotherms that cannot physiologically control internal temperatures, lack the flexibility required to adjust to increasing temperatures caused by global warming and are therefore considered to be under greater threat (Deutsch et al. 2008; Tewksbury et al. 2008).

In addition, the absolute temperatures at which deleterious effects are evident, known as thermal thresholds, vary predictably among locations. For example, many tropical ectotherms are living near their upper limits and are therefore at a greater risk from the effects of warming (Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009). Such patterns in spatial variation of temperature limits are also evident in reef-building corals, for which bleaching thresholds vary among regions (Coles et al. 1976; Goreau and Hayes 1994; Hoegh-Guldberg 1999). Similarly, in the planktonic stages of many marine invertebrates, thermal tolerance breadths vary among populations (Byrne et al. 2011; Hardy et al. 2014; Pecorino et al. 2014). While such variation in thermal thresholds among adult coral populations is reasonably well documented, geographical variation in thermal thresholds or tolerance breath of early life stages of corals has yet to be examined.

1.3 Effects of species traits on biogeographical distributions

Species traits such as body size, growth rates and patterns of mortality influence the ecological success and biogeographical distributions of all organisms (Brown et al. 1996). Traits that affect dispersal ability are particularly important. For example, traits related to seed dispersal have driven changes in abundance of Mediterranean plant species over a 115-year period (Lavergne et al. 2006). Species with water-dispersed seeds had the highest rates of extinction, whereas species with wind-dispersed seeds have

increased in abundance 1886-2001 (Lavergne et al. 2006). In marine environments, echinoderm species with non-feeding larvae and short pre-competency periods survive better through mass extinction events, including those associated with climate change (Valentine and Jablonski 1986, Uthicke et al. 2009, Byrne 2011).

In corals, the influence of species traits on patterns of distribution and abundance is not fully explored, partly because comprehensive records of species traits have not been available. However, recent work has shown that traits, including larval development rate and the depth range of adults, are good predictors of coral species' ability to cross faunal breaks (Keith et al. 2013). In addition, the mode of larval development appears to have affected extinction probability over geological time. For example, geological records from the Caribbean suggest that fewer species that brood larvae went extinct during the Oligocene/Miocene extinction when compared with species that broadcast spawn gametes (Edinger and Risk 1995). This is possibly because brooders are better colonisers, as brooded larvae are competent to settle on release from the parent, whereas broadcaster spawners have an obligate planktonic period of 12 to 72 hours before they become motile (Baird et al. 2009; Figueiredo et al. 2013).

1.4 Thesis aims

The general aims of this thesis are to investigate the effects of temperature on larval ecology, how these effects vary among regions, and how species traits related to larval dispersal influence biogeographical patterns.

This thesis contains four data chapters. Chapter 2 examines the effects of raised and lowered temperatures on early life stages of the species *Acropora spathulata* and *Goniastrea favulus* at One Tree Island in the southern Great Barrier Reef. This chapter has been published in the journal *Marine Ecology Progress Series* (Woolsey et al. 2013). Chapter 3 investigates whether self-fertilised embryos of the coral *Goniastrea favulus* have the same thermal tolerance breadth as out-crossed embryos. This chapter has been published in the *Proceedings of the 12th International Coral Reef Symposium* (Woolsey 2012). Chapter 4 tests how the thermal tolerance breadth of the early life stages of five coral species varies among latitudes, from Lizard Island in the northern Great Barrier Reef to Lord Howe Island, in the Tasman Sea. This paper is currently in review at *Coral Reefs*. Chapter 5 investigates whether species traits, in particular those related to dispersal, can predict changes in assemblage structure of corals across a dispersal barrier between the Great Barrier Reef and Lord Howe Island. This chapter will be submitted for review at the *Journal of Biogeography*.

Although some of the data overlap among chapters (specifically data collected at One Tree Island in 2010) these are a small subset of larger data sets used to test different hypotheses. For example, Chapter 2 compares thermal tolerance of larvae from two species at One Tree Island while Chapter 4 includes these data to explore differences in thermal thresholds among locations across a latitudinal gradient. In Chapter 4, the publication resulting from Chapter 2 is referenced.

A list of additional papers published during my candidature can be found in Appendix I.

CHAPTER TWO: The effects of temperature on embryonic development and larval survival in two scleractinian corals

This chapter has been published:

Woolsey ES, Byrne M and Baird AH (2013) The effects of temperature on embryonic development and larval survival in two scleractinian corals. Marine Ecology Progress Series 493: 179-184

2.1 ABSTRACT

Raised temperatures are deleterious to early life stages in many organisms, however, the biological effects of lowered temperatures are rarely explored. For example, the tolerance of marine invertebrate larvae to temperatures lower than ambient might affect the capacity of species to disperse from tropical to sub-tropical locations. In addition, reduced rates of development are likely to affect the proportion of larvae retained on natal reefs. Here, I explore the relationship between temperature, embryonic development and larval survival over an 8°C temperature range (-4 to +4°C around the ambient temperature at the time of spawning of 24ºC) in two reef-building corals, *Goniastrea favulus* and *Acropora spathulata* from One Tree Island (OTI) in the southern Great Barrier Reef (GBR). Rates of development were generally slower at lower temperatures: embryos of both species took longer to complete gastrulation and to become motile at temperatures below ambient. In contrast, temperatures below ambient did not affect larval survivorship in either species. *A. spathulata* larvae were more sensitive to raised temperatures than *G. favulus*, which also had higher survivorship than *A. spathulata* at all temperatures except 20°C. These results suggest that fluctuations in temperature at the

time of spawning will influence patterns of coral larval dispersal. Furthermore cold water is unlikely to prevent the dispersal of tropical corals to sub-tropical locations.

2.2 INTRODUCTION

The earth's environment is changing rapidly as a consequence of global warming. Rising temperatures are affecting terrestrial, marine and freshwater populations by altering processes such as growth and reproduction (Parmesan & Yohe 2003; Root et al. 2003; Poloczanska et al. 2007). However, climate change will not necessarily result in all locations becoming hotter. For example, the effects of climate change are expected to alter ocean currents, including the East Australian Current, which delivers warm waters from the tropics to higher latitudes in eastern Australia (Poloczanska et al. 2007). Such changes in circulation patterns may result in some sub-tropical locations, such as Lord Howe Island, becoming colder than at present. Consequently, it is important to investigate the effects of both raised and lowered temperatures in order to accurately predict the consequences of global warming (Addo-Bediako et al. 2000; Pörtner 2001).

The effects of raised temperature on coral larval biology are well known. Deleterious effects, such as an increase in the proportion of abnormal embryos and a decrease in larval survivorship are evident as little as 2ºC above ambient (Bassim et al. 2002). Raised temperatures also increase rates of coral larval development (Chua et al. 2013a) and coral larvae become competent to settle more quickly at higher temperatures (Nozawa & Harrison 2007; Heyward & Negri 2010). Given a strong association between rates of development and levels of self-recruitment in corals (Figueiredo et al. 2013), rising sea surface temperatures are likely to affect patterns of dispersal by reducing the levels of connectivity among populations (O'Connor et al. 2007). The effects of colder

temperatures on coral larval biology are less well known. Edmondson (1946) demonstrated that coral larvae were robust to short term exposures to temperatures as low as 0.5°C. In contrast, metamorphosis to CCA by *Stylophora pistillata* was 5 times lower at 2ºC below ambient (Putnam et al. 2008). Similarly, settlement was approximately 50% lower in *Acropora solitaryensis* larvae at 3ºC below ambient (Nozawa & Harrison 2007).

Climate-driven changes in ocean circulation are altering dispersal patterns in many marine organisms (O'Connor et al. 2007; Przeslawski et al. 2008). For example, the mussel *Mytilus edulis* (Jones et al. 2009), many reef fish species (Feary et al. 2013) and some corals (Yamano et al. 2011; Baird et al. 2012) have recently shifted their ranges pole-ward. Similarly, the fossil record indicates that scleractinian corals have been tracking climate on geological timescales (Veron 1992; Precht & Aronson 2004; Greenstein & Pandolfi 2008). This tendency of marine organisms to track changing climates strongly suggests there are environmental barriers to dispersal, although geographical ranges could also be limited indirectly, for example, by changes in competitive interactions among species (Cahill et al. 2013). Nonetheless, one potential factor limiting the dispersal of corals south from the Great Barrier Reef (GBR) into sub-tropical areas may be the capacity of coral larvae to withstand the colder waters they encounter en route.

In this study, I compared the response of the early life history stages of two species of scleractinian corals, *Goniastrea favulus* and *Acropora spathulata* to an 8ºC temperature range from -4 to +4ºC around the ambient experienced at the natal location, One Tree Island, around the time of spawning. In addition to comparing the temperature response, I tested whether cool water is a barrier to the dispersal of larvae of these species

to higher latitudes from this location. Both *G. favulus* and *A. spathulata* are common at One Tree Island (OTI), however, while OTI is the southern latitudinal limit for *A. spathulata* (Wallace 1999), *G. favulus* occurs as far south as Lord Howe Island (Veron 1993; Veron et al. 2009).

2.3 METHODS

Coral collection and culture of propagules

Six colonies of *Acropora spathulata* and five colonies of *Goniastrea favulus* were collected from the reef flat of the first lagoon at One Tree Island (23°30'S, 152°05'E) in the southern GBR, a few days prior to the predicted spawning period in 2010. Colonies were maintained in flow-through filtered seawater (FSW) in shaded outdoor aquaria. Just prior to spawning, species were placed in separate aquaria and water flow was stopped to prevent gametes being washed away. *G. favulus* spawned on the afternoon of 26 November 2010 and *A. spathulata* spawned on the night of 30 November 2010. *A. spathulata* egg and sperm bundles were collected and broken apart with gentle agitation and the density of sperm diluted to ca. 10^6 sperm ml^{-1} in order to maximize the fertilisation success (Oliver & Babcock 1992). Once cleavage was observed approximately 2 hours post-fertilisation (hpf), embryos were washed three times in 0.2 micron FSW to remove excess sperm which can cause cultures to deteriorate. In contrast to the positively buoyant egg/sperm bundles released by *A. spathulata*, *G. favulus* releases eggs and sperm separately, with the negatively buoyant eggs released approximately 30 minutes before sperm. Consequently, the eggs of *G. favulus* were collected from the base of parent colonies approximately 30 minutes after spawning was

complete. The time that eggs were spawned was considered to be the time of fertilisation in *G. favulus*.

Experimental design

To test for the effects of raised and lowered temperature on larval development and survivorship, water baths were set up in a temperature-controlled room at five temperatures (20°C, 22°C, 24ºC, 26°C, 28°C i.e. -4°C, -2°C, ambient, +2°C, +4°C). Aquarium heaters, coolers, and pumps kept treatment baths stable and within 0.5°C of the target temperatures (monitored with HOBO data loggers). Ambient average SST for the month prior to spawning (24.2°C) was determined from on-reef sensors (GBROOS, http://data.aims.gov.au/gbroos/).

The effect of temperature on embryonic development

To test the effect of temperature on embryonic development, washed embryos were transferred to 20 ml glass vials filled with 0.2 μm FSW and distributed among temperature treatments at 2 hpf (ca. 30 embryos per vial; 3 vials per treatment). The stage of development of the first 20 embryos in each vial was assessed at 8 or 9 time points depending on the species: 18, 24, 30, 36, 48, 72, 96, 120 and 144 hpf (6 days). The following five development stages were identified (following Ball et al. 2002): 4-cell blastula, multiple cell blastula, early gastrula, gastrula and planulae (motile stage). To test for differences in development time between treatments, the average time for propagules to reach gastrulation and motility was estimated following Chua et al. (2013a):

Average time to reach stage, $\overline{X}$ = Σ [time (hours) x number of propagules to reach stage]/Total number of propagules

Effect of temperature on larval survival

To test the effect of temperature on coral larval survival, 50 washed embryos were placed in 50 ml glass vials filled with 0.2 μm FSW and distributed among temperature treatments 2 hpf (50 embryos x 3 vials per treatment). Survival was measured by counting the number of embryos remaining at each of the above time points. Coral larvae lyse within 24 hours of death (Baird et al. 2006) so all larvae counted were considered to be alive at the time of census.

Data Analysis

Differences in mean time to complete gastrulation and to reach the planula stage (for *G. favulus* only) among temperature treatments (fixed, 5 levels: 20, 22, 24, 26 and 28ºC) were tested using a 1-way ANOVA for each species separately. Data were log-transformed and homogeneity of variance was confirmed by Levene's Test. Tukey's HSD post-hoc tests were used to identify which treatment levels differed. Non-parametric Kaplan-Meier product limit analyses were used to test for differences in median survivorship among temperatures for each species separately. Median survivorship (in hours) was considered significantly different when the 95% confidence intervals did not overlap. All analyses were performed using SPSS v19®.

2.4 RESULTS

Temperature had a significant effect on rates of propagule development in both species. In general, the slowest rates of development occurred at the lowest temperatures (Fig. 2.1, 2.2). Temperature had a significant effect on the mean time to complete gastrulation in both *A. spathulata* ($F_{4, 10} = 71.53$, $p < 0.001$) and *G. favulus* ($F_{4, 10} = 11.84$, $p = 0.001$) (Fig. 2.1). *A. spathulata* embryos at 28ºC took 23.1 ± 0.9 to complete gastrulation compared to 37.7 ± 2.1 hours at 20ºC. Similarly, *G. favulus* embryos required 30.4 ± 4.0 hours to complete gastrulation at 20ºC compared with 20 ± 1.0 hours at 28°C. In addition, *G. favulus* developed more rapidly than *A. spathulata* at all temperatures (Fig. 2.1). Over all temperatures pooled, the mean time to complete gastrulation was 21.6 $\pm$ 1.4 hours in *G. favulus* and 28.4 $\pm$ 1.3 hours in *A. spathulata*. Similarly, temperature had a significant effect on the mean time to reach the planula stage in *G. favulus* ($F_{4,10}=15.62$, $p=<0.001$; Fig. 2.2). The mean time to reach the planula stage was greatest at 20ºC (129.7 $\pm$ 6.3 h) and lowest at 26ºC & 28ºC (Fig. 2.2).

Only raised temperatures had a significant effect on larval survival (Fig. 2.3). In *A. spathulata,* survival was reduced at both temperatures above ambient (Fig. 2.3a). In contrast, *G. favulus* survival was reduced only at the highest temperature (Fig. 2.3b). In addition, *G. favulus* larval had higher survivorship than *A. spathulata* larvae at all temperatures, with the exception of 20ºC (Fig. 2.3).

2.5 DISCUSSION

Embryonic development was strongly affected by temperature. In general, the lower the temperature, the longer it took to complete gastrulation and for larvae to become motile. In contrast, larval survival was only reduced at temperatures above ambient. While the

response of both species to temperature was broadly similar, there were, nonetheless, differences between the species in development rate, larval survivorship and thermal tolerance.

The effect of temperature on development rates in these coral embryos is typical of most marine invertebrates (Pechenik 1987). For example, embryos of *Goniastrea australensis* in the Solitary Islands (30ºS) developed more slowly at 22ºC than at 26 and 28ºC (Wilson & Harrison 1998). This suggests that rates of embryonic development are likely to depend on the temperature conditions prevailing shortly after the time of spawning. Given that rates of self-recruitment are typically higher in larvae that develop more rapidly (Figueiredo et al. 2013), patterns of dispersal are likely to vary among years if ambient temperatures vary. In addition, patterns of dispersal might vary predictably among locations at different latitudes. In particular, high-latitude locations, are likely to have lower levels of self-recruitment than tropical locations because larvae take longer to develop. In addition, rates of predation are likely to increase the longer larvae remain in the plankton. For example, reduced levels of self-recruitment might help explain low numbers of juvenile corals at Lord Howe Island (LHI) (Latitude 33°S) when compared to many tropical locations (Hoey et al. 2011). However, the effect of low temperatures on rates of recruitment can not be discounted (Putnam et al. 2008).

Rates of embryonic development were also influenced by the size of the propagules. Across all temperatures, *G. favulus* embryos (mean diameter of 320 μm) developed more rapidly than *A. spathulata* embryos (mean diameter of 500μm; Fig. 2.1, 2.2), which can most likely be attributed to faster rates of cell division in species with smaller eggs (Berrill 1935; Marshall & Keough 2008). Similarly, in eighteen species of

broadcast spawning corals, egg size was strongly and positively correlated with time to motility (Figueiredo et al. 2013). The more rapid rate of development in *G. favulus* embryos did not come at the cost of reduced larval survival: *G. favulus* larvae survived longer that *A. spathulata* at all temperatures, except at 20°C where there was no difference between the species (Fig. 2.3).

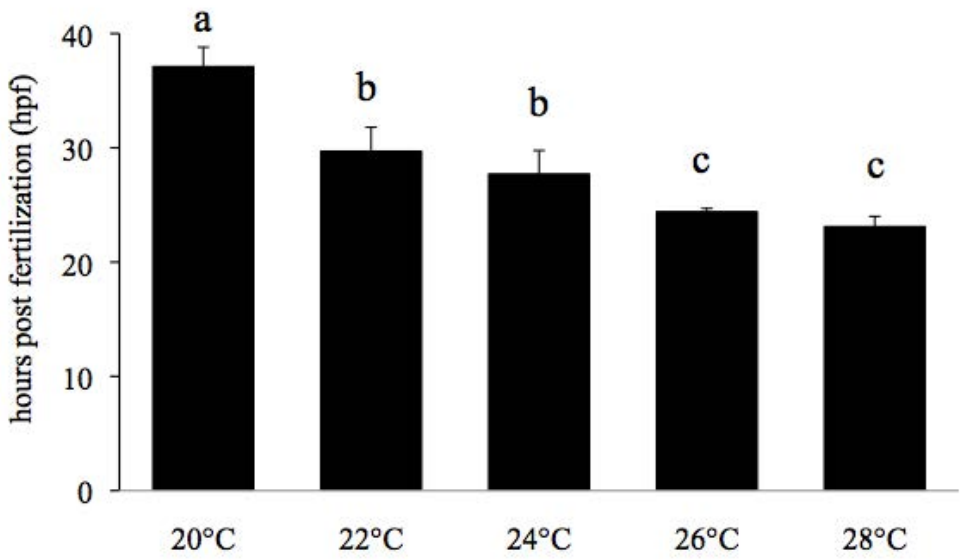
In contrast to the relationship between development and temperature, larval survival was only reduced at temperatures 2-4ºC (Fig. 2.3). These upper thermal limits (2-4ºC above ambient: Fig. 2.3) appear to be consistent over a very large geographical scale and among many different species (Bassim et al. 2002; Randall & Szmant 2009; Heyward & Negri 2010), supporting the hypothesis that many corals live very close to their upper thermal limits, In contrast, temperatures up to 4°C below ambient had no effect on larval survival (Fig. 2.3). Projections based on the speed and direction of the East Australia Current suggest that the time taken to disperse from OTI in the southern GBR to LHI takes approximately 16-33 days. Given that spawning occurs at OTI in November, larvae will arrive at LHI between late November and early January. In the course of this journey water temperatures can be as low as 19ºC (AIMS 2012). Consequently, it is unlikely that temperature is a barrier to dispersal from the southern GBR to higher latitudes for either of these species and therefore other factors must determine why *A. spathulata* is not found on LHI.

Thermal tolerance differed between the species. In particular, larval survival was reduced at 26 °C in *A. spathulata* and 28°C in *G. favulus* (Fig. 2.3). A similar difference in thermal tolerance was also observed between acroporid and merulinid embryos by Negri et al. (2007). Consistent differences in stress tolerance are also apparent between

adult colonies of these two families: adult acroporids are much more susceptible to bleaching and disease when compared to adult merulinids (Hughes & Connell 1999; Marshall & Baird 2000; Diaz & Madin 2011).

In conclusion, temperature has important effects on many aspects of coral larval biology. In particular, development rates varied predictably with temperature, suggesting that patterns of dispersal are likely to change in response to global warming. In addition, coral larvae appear to be tolerant of temperatures 2-4ºC below ambient, suggesting that cold water is unlikely to limit the dispersal of tropical species to sub-tropical locations.

a)



b)

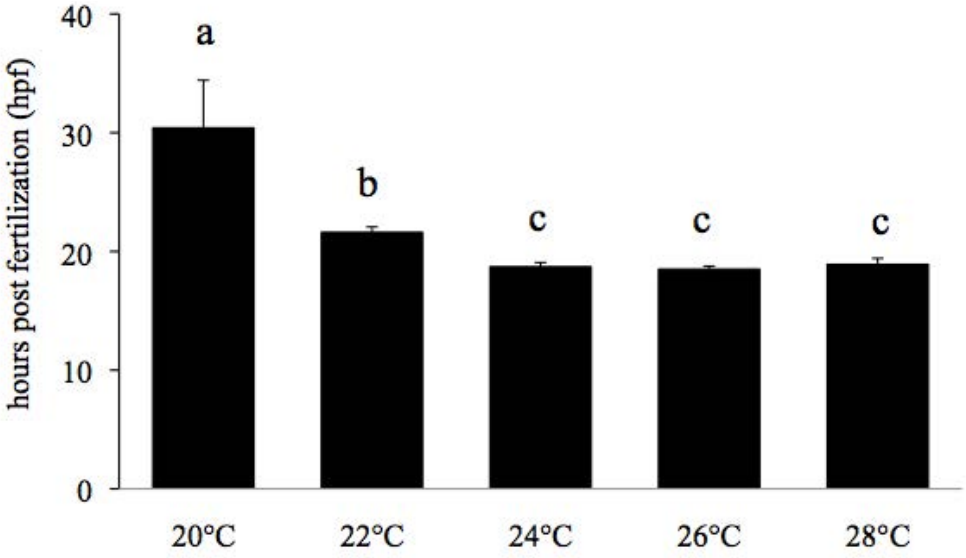


Figure 2.1 Mean time to gastrulation (hours post-fertilisation ± one SE) of a) *Acropora spathulata* and b) *Goniastrea favulus* at five temperatures (ambient = 24°C). Letters above the error bars indicate homogenous groups identified by Tukey HSD post-hoc analysis.

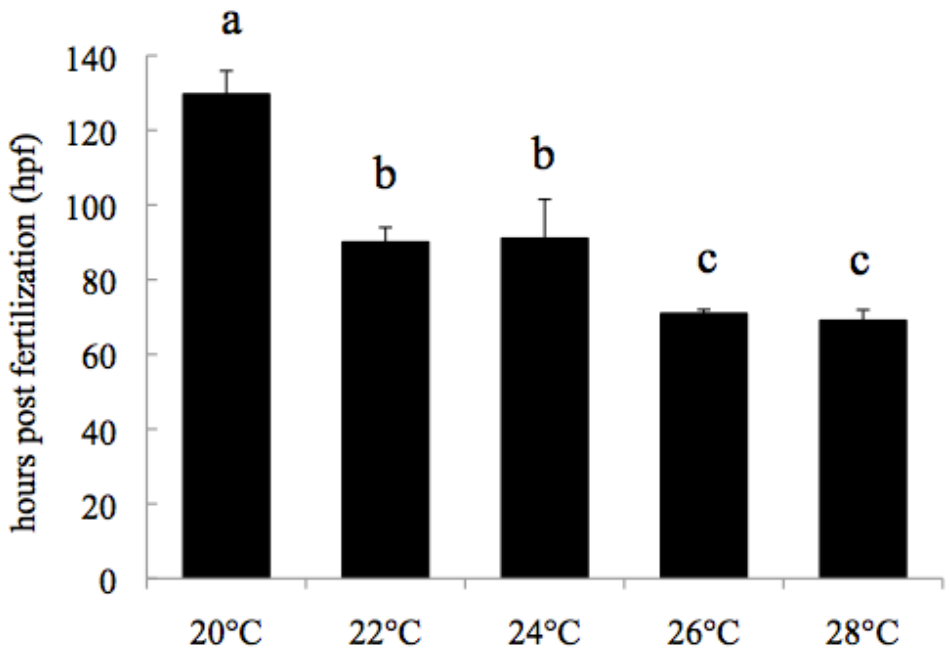
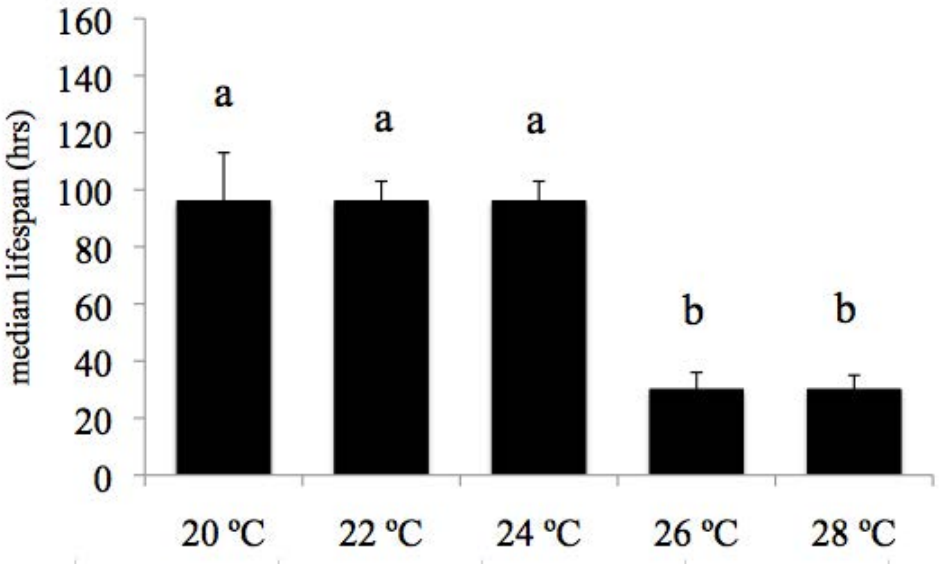


Figure 2.2 Mean time to the planula stage (hours post-fertilisation ± one SE) in *Goniastrea favulus* at five temperatures (ambient = 24°C). Letters above the error bars indicate homogenous groups identified by Tukey HSD post-hoc analysis.

a)



b)

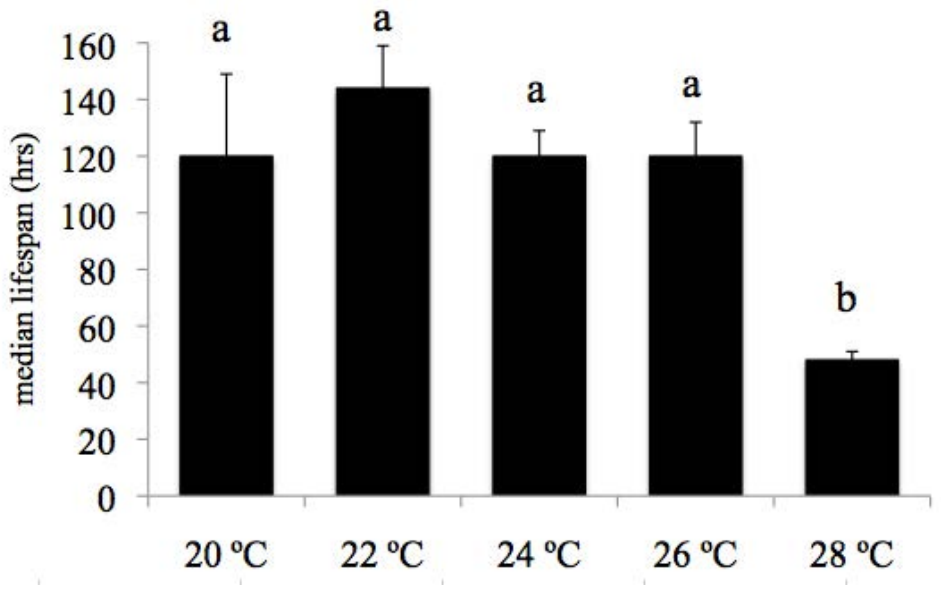


Figure 2.3 Kaplan-Meier median survivorship estimates for a) *Acropora spathulata* and b) *Goniastrea favulus* at five temperatures (ambient = 24°C). Error bars show 95% confidence intervals and letters indicate homogenous groups determined by the overlap of confidence intervals.

CHAPTER THREE: Self-fertilisation suppresses thermal tolerance in embryos of reef-building coral.

This chapter has been published:
Woolsey E (2012). Self-fertilisation suppresses thermal tolerance in embryos of reef-building coral. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012.

3.1 ABSTRACT

Self-fertilisation is unusual in most animals but common in some scleractinian corals, in particular, the family Merulinidae. High levels of self-fertilisation in many merulinids may contribute to their large latitudinal range size and their domination of some isolated, high-latitude coral assemblages in eastern Australia. In this study, conducted at One Tree Island in the southern Great Barrier Reef, the thermal tolerance of self-fertilised *G. favulus* embryos was compared to outcrossed embryos across five temperature treatments (20ºC, 22ºC, 24ºC, 26ºC, and 28ºC). Response variables were fertilisation success, development rate, and larval survivorship. Fertilisation was high (85-100%) across all treatments in cross-fertilised embryos. In self-fertilised *G. favulus* fertilisation was low in treatments below ambient (27 and 60 % at -4 and -2 ºC, respectively), though the effects on fertilisation were not significant among the treatments. Development rates (i.e., mean times to the planula stage) were similar in selfed and outcrossed embryos. Development occurred more rapidly at raised temperatures for both groups. High mortality occurred at raised temperatures, at +4ºC especially, for both self and crossed-fertilised *G. favulus*. Survivorship curves, median lifespans, and overlaps in 95% confidence intervals suggest

reduced survivorship in selfed embryos. These results suggest self-fertilisation has a negative effect on dispersal potential in reef-building corals.

3.2 INTRODUCTION

Self-fertilisation, involving male and female gametes from a single individual, yields ecological benefits as well as costs. Selfing is generally rare, but common in some animals (Jarne and Auld 2006). For instance, the reef-building coral family Merulinidae (formerly Faviidae) exhibits high selfing success (Miller and Babcock 1997; Knowlton et al. 1997). This reproduction method ensures genetic transmission, especially in animals with limited mobility, and is thought to be an evolutionary strategy enabling species persistence in conditions of low densities (Tomlinson 1966; Crow 1994; Jarne and Auld 2006). Like asexual reproduction, selfing maintains a genotype known to be successful in the maternal environment. However, the main associated cost is reduced fitness from lower genetic variation within a population (Jarne 1995; Trouvé et al. 2003; Jarne and Auld 2006).

This study tests the hypothesis that self-fertilised coral embryos are less thermally tolerant than crossed-fertilised embryos. The test species, *Goniastrea favulus*, is a merulinid that has a wide geographical distribution from Japan to southern Australia and exhibits high rates of self-fertilisation (Stoddart et al. 1998; Miller and Mundy 2005). It displays an unusual spawning method where eggs are discharged in mucous and sperm is subsequently released in multiple pulses (Kojis and Quinn 1981). Eggs of *G. favulus* are negatively buoyant and retained close to the parent colony during fertilisation (Heyward and Babcock 1986; Miller and Mundy 2005). In the marine environment, many species rely on a planktonic life stage for recruitment and dispersal (Strathmann 1985; Cowen

and Sponaugle 2009; Connolly and Baird 2010). In scleractinian corals, planula larvae are transported in the water column before settling, metamorphosing, and growing into adult corals. Spawning and dispersal are therefore crucial for reef recruitment and replenishment. Larval ecology may help explain biogeography of marine organisms. For example, *Parvulastra exigua*, a cross and self-fertilizing sea-star lacks dispersive larvae and yet is widely distributed in Australia. The combination of fertilisation methods may account for this paradox (Barbosa et al. 2012).

Thermal stress is known to affect many aspects of larval ecology (Hughes et al. 2003; O'Connor et al. 2007). However, there are often significant differences in response among species. In *Acropora millepora* (Family Acroporidae) fertilisation success decreases with temperatures 2-4°C above ambient and ceases at +6°C (Negri et al. 2007). In merulinids and pectiniids, high fertilisation rates as well as normal development occur at temperatures 5°C above ambient (Bassim et al. 2002, Negri et al. 2007). Indeed, merulinids are particularly tolerant to warm and cold temperature stressors, as survivorship in *G. favulus* embryos was found to be significantly greater than in *Acropora spathulata* across multiple temperature treatments (Woolsey et al. 2013). Poleward migration with increasing temperatures has been observed in corals and other marine animals (Greenstein and Pandolfi 2008; Figueira and Booth 2010; Yamano 2011) and thermal tolerance in dispersed propagules could promote range expansion in corals (Woolsey 2007).

It is necessary to understand phenotypic responses to temperature because larvae dispersed over long distances are likely to encounter temperature fluctuations. In addition, these responses may provide insight into long-term adaptive capacity to

projected temperature changes in eastern Australia (Poloczanska et al. 2007; Lough 2008) that are expected to alter patterns of larval dispersal in many coral species (Ayre and Hughes 2004, Heyward and Negri 2010).

This study compares the thermal response of self-fertilised and crossed progeny of *G. favulus* to determine if early developmental success differs with fertilisation type. It addresses the hypothesis that self-fertilisation lowers environmental tolerance in coral embryos.

3.3 METHODS

Study location and collection

Six adult colonies of *Goniastrea favulus* (Family Faviidae) were collected from the southern coral flats of One Tree lagoon (23°30'S, 152°05'E), Australia. Colonies were collected at least 10 m apart to reduce the chance of genetic similarity. Corals were maintained in flow-through filtered seawater (FSW) in shaded outdoor aquaria at ambient light and temperature. Before spawning, 3 colonies were separated into 3 tubs for self-fertilisation experiments while the remaining 3 colonies were kept in a separate tub for cross-fertilisation experiments. Cross-fertilisation was assumed in embryos collected from the tub with multiple colonies.

Sperm and eggs were released asynchronously over a half hour, and time of fertilisation was taken as 1.5 hours after all spawning was complete. At this time (0 hours), embryos were transferred to 20 ml glass vials and distributed among temperature treatments (approximately 20 embryos in each vial x 3 replicates per treatment). Embryos in these vials were used to confirm fertilisation at 2 hours post fertilisation (hpf), by

observing cleavage under the microscope. Once fertilisation was confirmed, embryos remaining in the culture were distributed among temperature treatments.

Temperature treatments

Ambient temperature was defined as 24 °C, the average SST reading from on-reef sensors for the month prior to spawning (GBROOS, http://data.aims.gov.au/gbroos/). Water baths were set up in a temperature-controlled room at One Tree Island Research Station at 5 temperatures (20°C, 22°C, 24ºC, 26°C, 28°C i.e. -4°C, -2°C, ambient, +2°C, +4°C). Aquarium heaters, coolers, and pumps kept treatment baths stable and within 0.5°C of the target temperatures (monitored with HOBO data loggers). Larvae were maintained in UV-C treated, 0.2 µm FSW to prevent bacterial contamination. Water was changed daily after being heated or cooled to the appropriate temperature.

Response variables

Glass vials (50ml) were filled with 30-50 embryos and transferred among treatments. There were 3 replicates for each of the 5 temperatures. These vials were used to monitor development stage throughout the experiment. Fertilisation data was collected at 6 hpf, using cleavage as an estimate of fertilisation success.

The stage of development of 20 embryos in each 50 ml vial was recorded at 9 time points: 18, 24, 30, 36, 48, 72, 96, 120 and 144 hpf. The stages used were: 2-cell, 4-cell, multicell/morula, blastula, gastrula, pre-planula and planula.

To test the effect of temperature on *G. favulus* larval survival, I followed the methods described in Chapter 2 of this thesis (and Woolsey et al. 2013).

Data Analysis

A fully factorial 2-way ANOVA was used to test for differences in mean fertilisation success at 6 hpf and development rates among temperature treatments (fixed, 5 levels: -4, -2, ambient, +2, and +4 °C) and fertilisation mode (fixed, 2 levels: crossed and selfed). After graphical analysis of the residuals, development data was log transformed and fertilisation data was arcsine transformed to remove bias. Levene's Tests were used to confirm homogeneity. Tukey HSD post-hoc analysis determined differences among treatment levels. Analyses were completed using R and SPSS v19.

Survivorship

Non-parametric Kaplan-Meier product limit analyses were used to test for differences in median survivorship among temperatures and fertilisation modes. Median survivorship (in hours) was considered significantly different when the 95% confidence intervals did not overlap. Analyses were completed using SPSS v19.

3.4 RESULTS

Fertilisation success did not differ significantly among temperatures or among the larval groups (Table 3.1). In crossed embryos, fertilisation was high in all treatments ranging from 85 $\pm$ 7.6% at 22ºC to 100% at 28ºC (Fig. 3.1). In self-fertilised embryos, mean fertilisation rates were $\geq$ 80% treatment at and above ambient (Fig. 3.1). There was more variation in self-fertilised embryos, with low fertilisation success at temperatures below ambient (27 $\pm$ 24.2% at 20ºC and 60 $\pm$ 27.8 % at 22ºC).

Time to planula was shorter at higher temperatures but not affected by fertilisation method (Table 3.2). Mean time to the free-swimming planula stage among crossed and selfed embryos was 124 hrs at 20°C, 91 hrs at 22°C, 82 hrs at 24°C, 73 hrs at 26°C and 72 hrs at 28°C (Fig. 3.2).

For both fertilisation types, survivorship was low at +4ºC (28ºC). The 28ºC median lifespan was 48 hrs in both crossed and self-fertilised embryos (Fig. 3.3). In cross-fertilised *G. favulus*, all temperature treatments besides 28ºC show overlap in confidence intervals, meaning there are no significant differences in median survival time among treatments (Fig. 3.3, Fig. 3.4). In self-fertilised *G. favulus* however, median survivorship and confidence intervals indicate significant differences among treatments (Fig. 3.3, Fig. 3.5).

3.5 DISCUSSION

Neither development rate nor fertilisation success was affected by fertilisation type. Development rate was faster at higher temperatures, which is consistent with metabolic theory, and mean time to the free-swimming planula stage did not vary among larval groups. Although there was greater variation in self-fertilised embryos, fertilisation success was also not significantly affected by fertilisation method.

Survivorship data, however, indicate suppressed thermal tolerance in self-fertilised *G. favulus*. This suggests that self-fertilisation, while potentially promoting growth on isolated or disturbed reefs, produces less healthy larvae and therefore reduces dispersal capabilities.

Table 3.1 Results of 2-way analysis of variance (ANOVA), testing for significant differences between mean fertilisation rates. Factors of the model were temperature (fixed, 5 levels) and fertilisation method (fixed, 2 levels). Data arcsine transformed. df error= 20.

Factor	*df*	F	*p*
Temperature	4	2.49	0.076
Method	1	3.45	0.059
Temperature * Method	4	2.74	0.060

Table 3.2 Results of 2-way analysis of variance (ANOVA), testing for significant differences between mean time to planula among treatments. Factors of the model were temperature (fixed, 5 levels) and fertilisation method (fixed, 2 levels). Data log transformed. df error= 20. Treatment order from Tukey HSD post-hoc test.

Factor	*df*	F	*p*	Treatments (°C)
Temperature	4	32.3	<0.001	20>22=24>26=28
Method	1	0.792	0.384	
Temperature* Method	4	2.44	0.081	

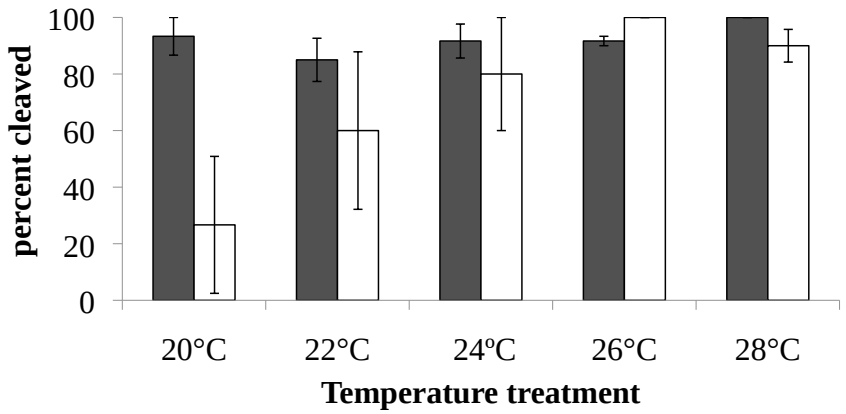


Figure 3.1 Fertilisation success (mean proportion of eggs cleaved ± one SE) of crossed (dark bars) and self-fertilised (light bars) *G. favulus* embryos at temperatures above and below ambient. Fertilisation success was measured by percent cleavage at 6 hpf.

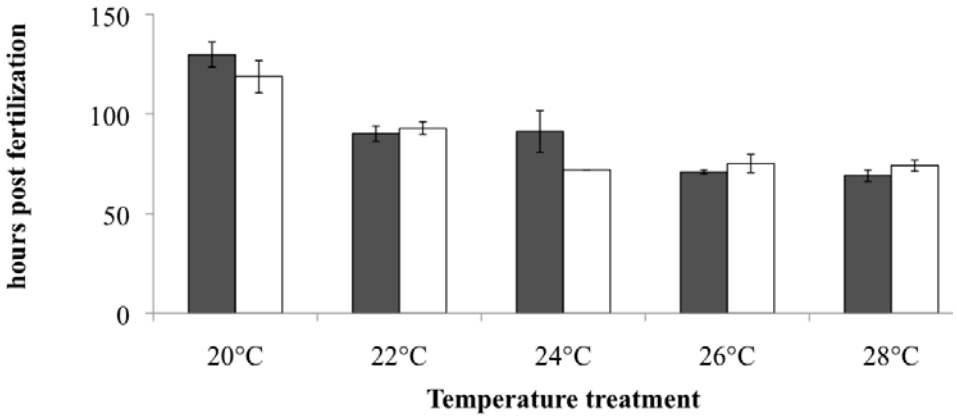


Figure 3.2 Time to the free-swimming planula stage (mean hours post-fertilisation ± one SE) in crossed (dark bars) and self-fertilised (light bars) *G. favulus*.

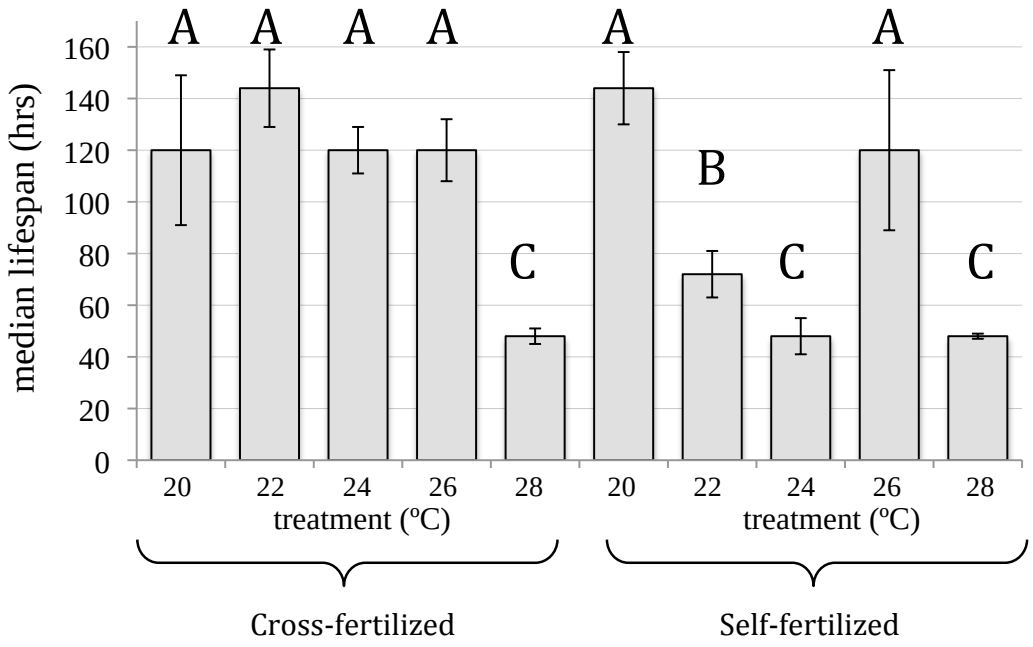


Figure 3.3 Kaplan-Meier median survivorship estimates for cross and self-fertilised *G. favulus*, n=150. Error bars show 95% Confidence Intervals. Treatments with overlap in Confidence Intervals are labeled as groups A, B, or C.

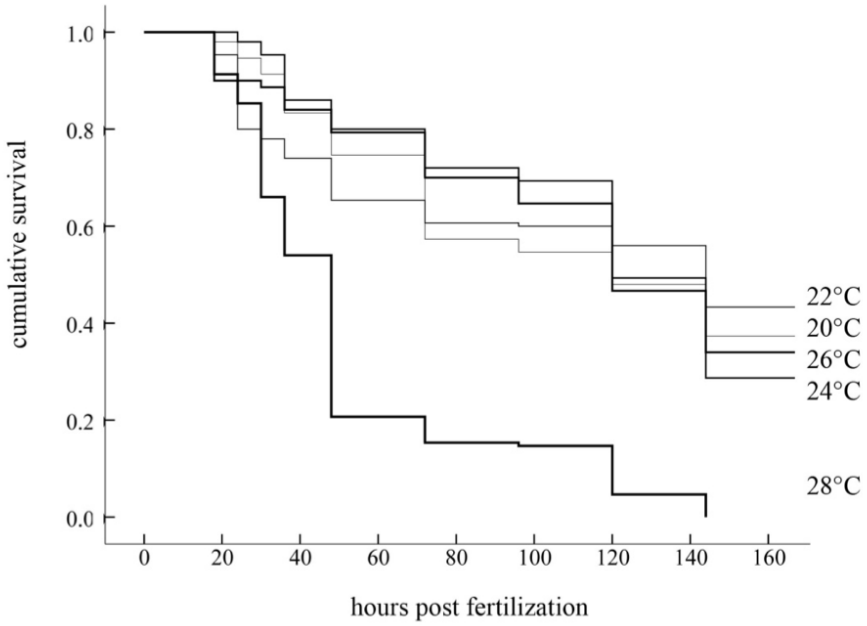


Figure 3.4 Kaplan-Meier median survivorship curves for crossed-fertilised *G. favulus* at temperatures above and below ambient (24°C), n=150.

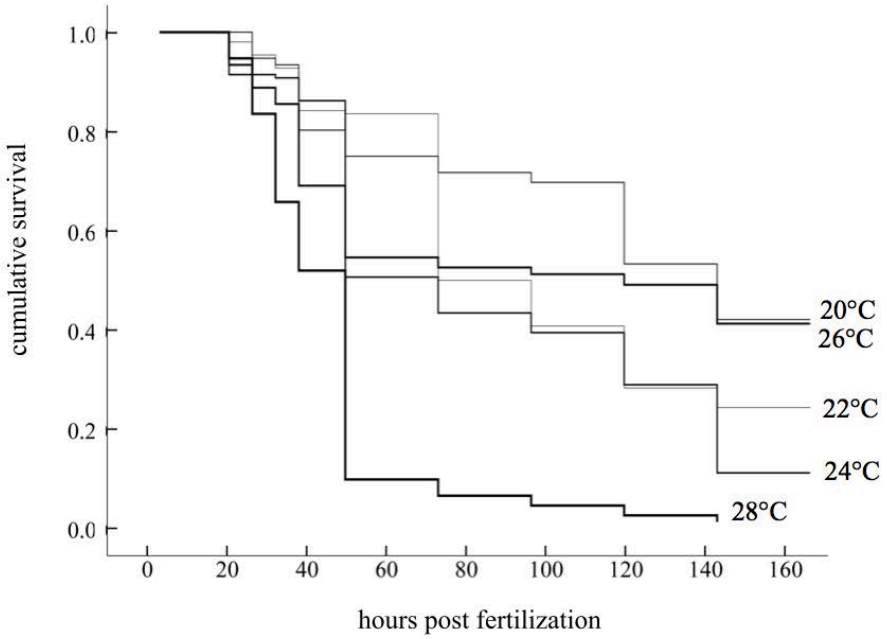


Figure 3.5 Kaplan-Meier median survivorship curves for self-fertilised *G. favulus* at temperatures above and below ambient (24°C), n=150.

CHAPTER FOUR: Latitudinal variation in thermal tolerance thresholds of early life stages of corals

This chapter is in review:

Woolsey ES, Keith SA, Byrne M, Schmidt-Roach S and Baird AH (in review) Latitudinal variation in thermal tolerance thresholds of early life stages of corals. Coral Reefs.

4.1 ABSTRACT

Organisms living in habitats characterised by a marked seasonal temperature variation often have a greater thermal tolerance than those living in more stable habitats. To determine the extent to which this hypothesis applies to reef corals, I compared thermal tolerance of the early life stages of five scleractinian species from three locations spanning 17 degrees of latitude along the east coast of Australia. Embryos were exposed to an 8ºC temperature range around the local ambient temperature at the time of spawning. Upper thermal thresholds, defined as the temperature treatment at which the proportion of abnormal embryos or median lifespan was significantly different to ambient controls, varied predictably among locations. At Lizard Island, the northern-most site with the least annual variation in temperature, the proportion of abnormal embryos increased and lifespan decreased 2°C above ambient in the two species tested. At two southern sites, One Tree Island and Lord Howe Island, where annual temperature variation was lower, upper temperature thresholds were generally 4°C or greater above ambient for both variables in the four species tested. The absolute upper thermal threshold temperature also varied among locations: 30°C at Lizard Island; 28°C at One Tree Island; 26°C at Lord Howe Island. These results support previous work on adult

corals demonstrating predictable differences in upper thermal thresholds with latitude. With projected ocean warming these temperature thresholds will be exceeded in northern locations in the near future, adding to a growing body of evidence indicating that climate change is likely to be more detrimental to low latitude than high latitude corals.

4.2 INTRODUCTION

Rising temperatures, as a result of climate change are altering species distributions and causing reductions in global biodiversity (Thomas et al. 2004; Pereira et al. 2010). Although proximate causes of local extinction vary (Cahill et al. 2012), thermal tolerance is often a good predictor of the potential of a population to persist as temperature increase (Sorte et al. 2011). Consequently, it is important to consider the thermal tolerance of species when projecting the potential effects of increased temperatures on biodiversity.

At the global scale, temperatures are more stable throughout the year in tropical regions compared to temperate regions (Spencer and Christy 1990) and consequently, the thermal tolerance of organisms is generally greater at higher latitudes (Janzen 1967; Stevens 1989, Chown et al. 2004; Bozinovic et al. 2011). This phenomenon is especially relevant in ectotherms because these organisms rely on the environment to regulate internal temperatures. Indeed, many tropical ectotherms (e.g. insects, lizards) are already living close to their upper thermal limits and are thus more likely to be adversely affected by projected temperature rises as a consequence of climate change (Deutsch et al. 2008; Tewksbury et al. 2008; Huey et al. 2009).

Similar systematic differences in temperature thresholds have been observed for adult corals. The temperature at which bleaching is induced varies predictably among regions (Coles et al. 1976; Goreau and Hayes 1994), although the correlation between

bleaching thresholds and latitude can be complicated by the type of algal symbiont hosted by the coral (Ulstrup et al. 2006). Bleaching thresholds decreased with increasing latitude during the 1998 bleaching event on the Great Barrier Reef (GBR): 30.0ºC in the northern GBR, 29.2ºC in the central GBR and 28.3ºC in the southern GBR (Hoegh-Guldberg 1999). These thermal threshold are reasonably well understood for adult corals, however, there is a paucity of data on temperature thresholds on crucial stages in the early life history of corals.

To test the hypothesis that thermal tolerance thresholds varied among latitudes, I exposed developing gametes of five species of scleractinian corals to a temperature range of 8ºC around the ambient at the time of spawning for each of three locations. Locations spanned 17° of latitude along the east coast of Australia, from Lizard Island in the north to Lord Howe Island, the world's southernmost coral reef. Specifically, larvae from higher latitude reefs were predicted to have a greater upper thermal tolerance limit relative to ambient than those from lower latitude reefs.

4.3 METHODS

Collection of adult coral colonies and larvae

The effects of temperature on the early life stages of coral were tested at three locations in eastern Australia: Lizard Island (LI, 14.7ºS), One Tree Island (OTI, 23.5°S) and Lord Howe Island (LHI, 31.5 ºS). Six colonies each of *Acropora millepora*, *A. spathulata*, and *Goniastrea favulus* were collected from LI lagoon in November 2011. Six colonies of *A. spathulata* and five colonies of *G. favulus* were collected from OTI lagoon in November 2010. Five colonies of *G. australensis* and six colonies of *Cyphastrea microphthalma* were collected from LHI lagoon in January 2012. It was not possible to use the same

coral species at each location because of difference in the distribution and abundance of species amongst these widely separated locations. Colonies were maintained in flow-through filtered seawater (FSW) in shaded outdoor aquaria at all locations except LHI, where colonies were kept below a pier in the lagoon for a maximum of three days. Immediately prior to spawning, colonies were placed in separate aquaria with no water flow to capture the gametes. At LI, *G. favulus*, *A. spathulata* and *A. millepora* spawned on the night of November 15, 2011. At OTI, G. favulus spawned on 26 November 2010 and *A. spathulata* spawned on 30 November 2010. At LHI, *G. australensis* and *C. microphthalma* spawned on 20 January 2012.

Egg and sperm bundles were collected and broken apart with gentle agitation. Sperm was diluted to a density of approximately 10^6 sperm ml^{-1} by eye, a technique that regularly results in close to 100% fertilization success (Baird pers obs). Eggs were mixed with the sperm stock at the local ambient temperature. Once cleavage was observed, approximately 2 h post-fertilization (hpf), embryos were washed three times in 0.2 μm FSW to remove excess sperm and placed in the experimental treatments. The reproductive ecology of *Goniastrea favulus* necessitated a different collection method. *G. favulus* releases clusters of negatively buoyant eggs followed by sperm. The eggs of *G. favulus* were collected with a pipette from the base of parent colonies approximately 30 min after sperm was released.

Temperature treatments and temperature profiles for each location

To investigate the effects of temperature on embryonic development and survivorship, water baths were set up in a temperature-controlled room at five temperatures (-4°C, -

2°C, ambient, +2°C, +4°C). Ambient temperatures (Table 4.1) were defined as the mean temperature in the month prior to spawning obtained from the on-reef sensor network of the Great Barrier Reef Ocean Observing System and the Australian Institute of Marine Science (GBROOS 2013, AIMS 2013). Temperature profiles for treatments and each of the three locations are provided in Supplemental Materials at the end of this chapter. Aquarium heaters, coolers, and pumps kept treatment baths within ca. 0.5°C of the target temperatures (Table 4.S1). Temperature profiles for Lizard, One Tree, and Lord Howe Islands are presented in Fig. 4.S1. Temperature regimes were predictably more variable at higher latitudes. For example, the average difference between average monthly maximum sea surface temperature (SST) and average monthly minimum SST for each month between 2010 and 2013 were 4.2 ± 0.21ºC at Lizard Island, 5.7 ± 0.20ºC at One Tree Island and 7.0 ± 0.36ºC at Lord Howe Island (Table 4.2). Similarly, the temperature range (i.e. the difference between the average monthly maximum and average monthly minimum SST, from 2010 to 2013) during the month of spawning was greater at higher latitudes: 4.0ºC (26.0-29.9ºC) at Lizard Island, 6.0ºC (22.4-28.3ºC) at One Tree Island, and 9.0ºC (19.7-28.4ºC) at Lord Howe Island (Table 4.2).

The effect of temperature on development on embryonic development

To investigate the effect of temperature on development, embryos raised at ambient temperature were transferred to 20 ml glass vials containing UV-C treated, 0.2 μm FSW and distributed among temperature treatments (ca. 30 embryos per vial; 3 vials per treatment) following Chua et al. (2013a,b) and Woolsey et al. (2013). The proportion of abnormal embryos was counted at 18 hpf. Abnormal embryos are easily identified

because they deviate strongly from the regular and predictable pattern of development described by Ball et al. (2002).

The effect of temperature on larval survival

To test the effect of temperature on larval survival, I followed the methods described in Chapter 2 of this thesis (and Woolsey et al. 2013).

Statistical analysis

Differences in the mean proportion of abnormal embryos among treatments were tested using 1-way ANOVA with temperature as a fixed factor (5 levels: -4°C, -2°C, ambient, +2°C, +4°C). Proportional data were arcsine-transformed and homogeneity of variance was confirmed by Levene's Test. Tukey's HSD post-hoc tests were used to identify which treatment levels differed. To test for differences in larval survivorship among temperatures, I followed the methods for data analysis described in Chapter 2 of this thesis (and Woolsey et al. 2013). Analyses were performed using SPSS v19® (IBM Corp. 2010). Threshold temperatures were defined as the temperature relative to ambient at which the response variable differed significantly to the control temperature (i.e. ambient). Finally, to estimate the potential effects of projected increase in SST as a result of global warming on the embryonic development and survival I compared the experimentally determined temperature thresholds to projected average annual maximum SST at these locations in 2100, taken from Lough (2008).

4.4 RESULTS

The effect of temperature on larval development

The proportion of abnormal embryos was high (50-90%) in elevated temperature treatments in all assays (Table 4.1; Fig. 4.1), with the exception of *G. favulus* at OTI where there was no effect of temperature (Table 4.1; Fig. 4.1d). Temperatures below ambient had no effect on the proportion of abnormal embryos in any assays (Table 4.1; Fig. 4.1). Threshold temperatures varied predictably among locations (Table 4.2). At LI, the proportion of abnormal embryos increased significantly at +2 ºC above ambient in all three species (Table 4.2; Fig. 4.2). At OTI and LHI the threshold temperature was +4 ºC or greater in all assays (Table 4.2; Fig. 4.2).

The effect of temperature on lifespans

Lifespans were reduced by temperatures above ambient except for the two species from LHI where there was no effect of temperature (Fig. 4.2). Temperatures below ambient did not affect lifespan, with the exception of *A. millepora* at LI where lifespan was reduced at -4ºC (Fig. 4.2a). Threshold temperatures varied predictably among locations (Table 4.2). At LI, lifespans were significantly reduced at +2 ºC above ambient in all three species (Table 4.2; Fig. 4.2 a, b, c). At OTI and LHI the threshold temperature was +4 ºC or greater in all assays except for *A. spathulata* at OTI where the threshold was +2 ºC (Table 4.2; Fig. 4.2).

The effects of projected changes in SST on embryonic development and survival

Average annual SSTs in 2100 are projected to exceed the upper thresholds for normal development and survival in *Acropora* and *Goniastrea* at LI (Table 4.3). Similarly, projected average annual SST in 2100 will exceed the upper thresholds for survival in *Acropora* and *Goniastrea* at OTI (Table 4.3). In contrast, at LHI, thermal thresholds are not projected to be exceeded within this time frame (Table 4.3).

4.5 DISCUSSION

Temperatures above ambient increased the percentage of abnormal development and reduced survival. Moreover, as predicted, the temperature at which the effects were evident varied among locations. At LI, the lowest latitude location, thresholds were generally 2ºC above the local ambient in all species whereas at the higher latitude locations, OTI and LHI, thresholds were 2-4ºC above ambient in most species (Table 4.2). In addition, the absolute threshold temperature also varied predictably among locations: 30°C at LI; 28°C at OTI; 26°C at LHI (Table 4.2).

The temperature thresholds for embryos and larvae differed predictably among locations (Table 4.2). For instance, in *G. favulus* temperatures 2ºC above ambient reduced lifespan from lower latitude Lizard Island populations, whereas at the higher latitude One Tree Island temperatures 4ºC above ambient were required to produce an effect. These results are consistent with work on adult corals indicating that thermal thresholds for bleaching vary predictably among locations (Hoegh-Guldberg 1999) and suggest that thermal tolerance breadth might be greater at locations that experience greater fluctuations in temperature (McClanahan et al. 2007). These data add to a growing body of evidence suggesting that low latitude corals are living close to the upper

thermal limit for many critical life history stages. Therefore, in the absence of acclimatization or adaptation projected temperature rises are likely to be more detrimental to tropical corals than those at higher latitudes.

Thermal thresholds did not vary greatly among species within locations. However, at OTI embryos and larvae of the acroporid *A. spathulata* were more sensitive to temperature increase than the merulinid *G. favulus*. Similarly, temperatures 4ºC above ambient increased the proportion of abnormal embryos in *A. millepora* but not in the merulinids *Favites chinensis* and *Mycedium elephantotus* (Negri et al. 2007). These finding are consistent with previous observations that adult acroporids are less thermally tolerant than merulinids (Loya et al. 2001; Baird and Marshall 2002) and suggests that acroporids are therefore at greater risk than merulinids from increased ocean temperatures caused by climate change.

Larval lifespans were uniformly low at LHI, with median lifespans of 24 ± 2 h compared to greater than 80 h at ambient in all species at the other locations (Fig. 4.2). In addition, none of the larvae in cohorts from 6 other species of coral cultivated at LHI in 2011 survived beyond 48 h (Baird et al. unpublished data), suggesting that the gametes of these sub-tropical corals were either highly sensitive to handling or of poor quality. Indeed, the marginal conditions for coral growth, for example, winter temperatures as low as 14.4ºC (AIMS 2013), might have a detrimental effect on gamete quality. Low larval survivorship is consistent with low rates of recruitment at LHI (Noreen et al. 2009; Hoey et al. 2011) and suggests that isolated margin habitats, such as LHI, will be highly susceptible to disturbance.

Climate change is likely to have profound effects on patterns of dispersal and population dynamics of reef corals. Our results suggest that coral populations in tropical regions are likely to be more seriously affected by increased sea temperatures than those in the subtropics because they are living at temperatures closer to the maximum values that various life history stages can tolerate.

Table 4.1 ANOVA results, testing for difference among temperatures in the proportion of abnormal embryos 18 hours post-fertilisation at Lizard Island (LI), One Tree Island (OTI) and Lord Howe Island (LHI). Data were arcsine transformed. Treatment order from Tukey's HSD post-hoc test (p = 0.05)

Location	Species	*df*	F	*p*	Treatment order (°C)
LI	*Acropora millepora*	4	11.48	0.001	24=26=28<30=32 (-4=-2=ambient<+2=+4)
LI	*Acropora spathulata*	4	10.98	0.001	24=26=28<30=32 (-4=-2=ambient<+2=+4)
LI	*Goniastrea favulus*	4	4.15	0.031	24=26=28<30=32 (-4=-2=ambient<+2=+4)
OTI	*Acropora spathulata*	4	27.60	<0.001	20=22=24=26<28 (-4=-2=ambient=+2<+4)
OTI	*Goniastrea favulus*	4	0.99	0.458	NS
LHI	*Goniastrea australensis*	4	6.04	0.010	18=20=22=24<26 (-4=-2=ambient=+2<+4)
LHI	*Cyphastrea microphthalma*	4	4.98	0.018	18=20=22=24<26 (-4=-2=ambient=+2<+4)

Table 4.2 The upper thermal threshold temperature for each species at each location and ambient temperature at each location in the month prior to experiments. The threshold temperature was defined as the temperature at which median larval lifespan was significantly lower and the proportion of abnormal embryos significantly higher than at ambient. Monthly sea surface temperature (SST) ranges were calculated by subtracting average minimum SST from average maximum SST of that month, collected from on-reef AIMS and GBROOS sensors, 2010-2013 (see Supplementary Materials at the end of this chapter). Spawning months are November at Lizard and One Tree Islands, and January at Lord Howe Island.

Location (latitude)	Ambient	Average monthly SST range (± SE)	SST range during spawning month	Species	Threshold for normal development (treatment)	Threshold for normal development (temperature)	Threshold for survival (treatment)	Threshold for survival (temperature)
Lizard Island	28ºC	4.2 ± 0.21ºC	3.9ºC	*Acropora millepora*	+2ºC	30ºC	+2ºC	30ºC
(14.7ºS)			(26.0-29.9ºC)	*Acropora spathulata*	+2ºC	30ºC	+2ºC	30ºC
				Goniastrea favulus	+2ºC	30ºC	+2ºC	30ºC
One Tree Island	24ºC	5.7 ± 0.20ºC	5.9ºC	*Acropora spathulata*	+4ºC	28ºC	+2ºC	26ºC
(23.5ºS)			(22.4-28.3ºC)	*Goniastrea favulus*	>+4ºC	>28ºC	+4ºC	28ºC
Lord Howe Island	22ºC	7.0 ± 0.36ºC	8.7	*Goniastrea australensis*	+4ºC	26ºC	>+4ºC	>26ºC
(31.5ºS)			(19.7-28.4ºC)	*Cyphastrea microphthalma*	+4ºC	26ºC	>+4ºC	>26ºC

Table 4.3 Current (1950-2007) and projected (2100) average annual sea surface temperatures (SST) and average annual maximum SST, after Lough (2008). Thresholds of early life stages in *Goniastrea* and *Acropora* spp are the temperature treatments at which there was a significant increase in the proportion of abnormal embryos or decrease in larval lifespan. Dashes indicate a threshold was not observed over the 8ºC experimental range. (na = no data).

	Current (1950-2007)		**Projected by 2100**		**Observed threshold of early life stages of *Goniastrea* spp (ºC)**		**Observed threshold of early life stages of *Acropora* spp (ºC)**	
Location	**Average annual SST (ºC)**	**Average annual maximum (ºC)**	**Average annual SST (ºC)**	**Average annual maximum (ºC)**	**Normal Development**	**Survival**	**Normal Development**	**Survival**
Northern GBR (14.5ºS)	28.8	30.0	29.5	30.4	30	30	30	30
Southern GBR (23.5ºS)	24.0	26.6	25.4	27.9	---	28	28	26
High latitude (29.5ºS)	21.2	23.2	22.5	24.6	26	---	na	na

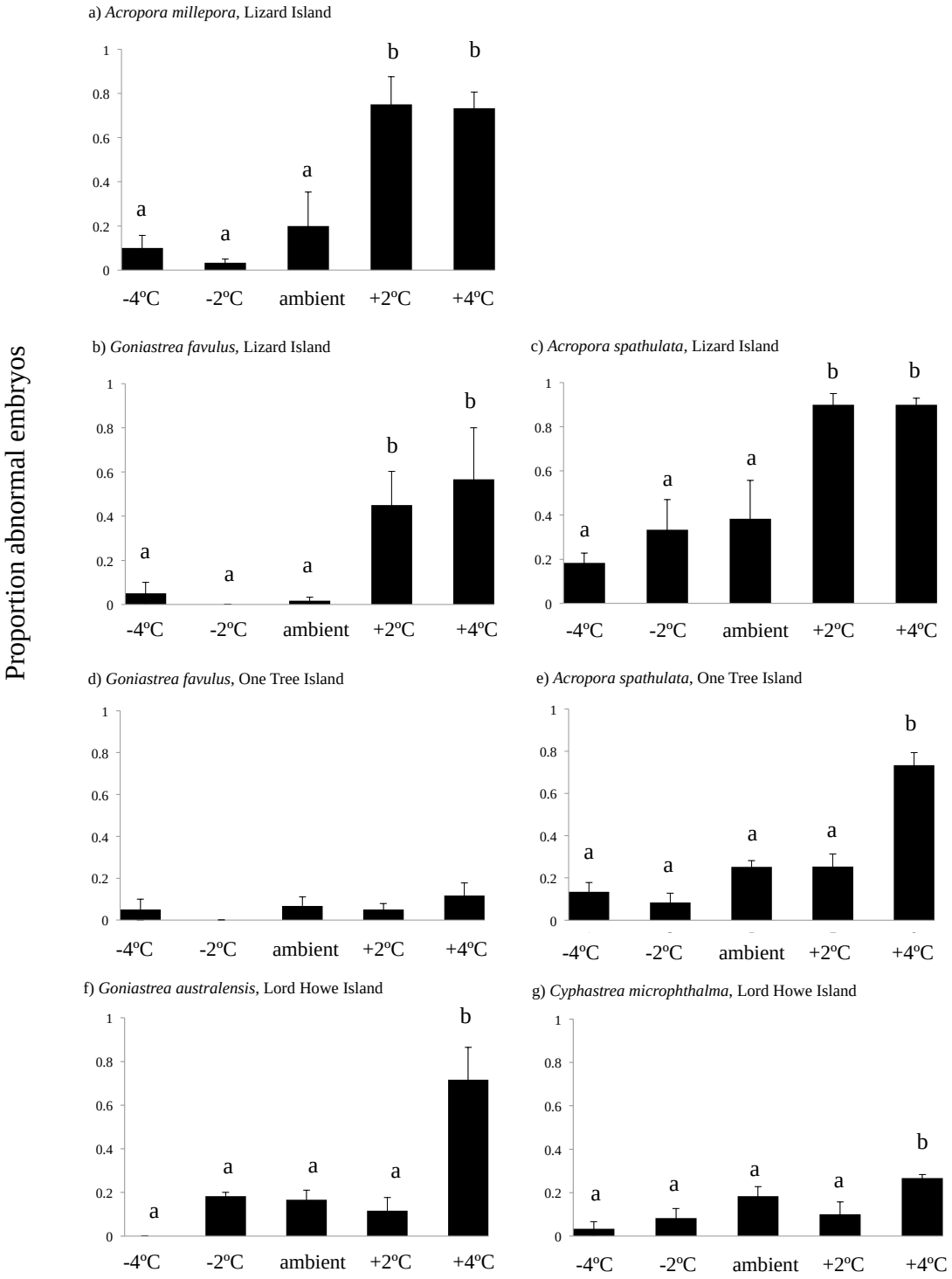


Figure 4.1 The proportion of abnormal embryos (± 1 SE) 18 hpf of *Acropora millepora* (a), *Goniastrea favulus* (b, d), *A. spathulata* (c, e), *G. australensis* (f) and *Cyphastrea microphthalma* (g) in treatments 2-4ºC above and below the ambient temperature: 28ºC at Lizard Island, 24ºC at One Tree Island, and 22ºC at Lord Howe Island. Letters above the error bars indicate groups identified by Tukey's HSD post-hoc test.

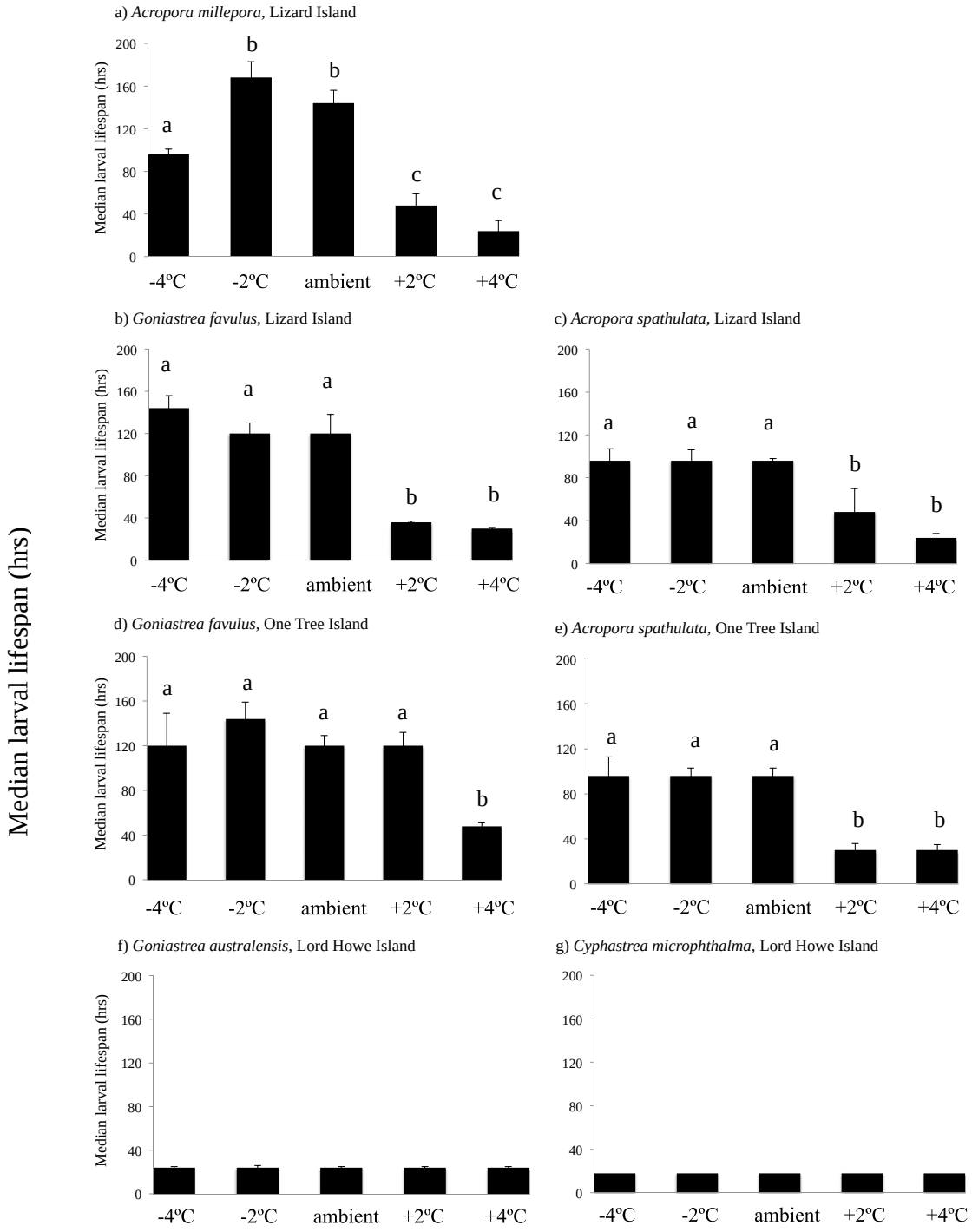


Figure. 4.2 Larval lifespan (hours) of *Acropora millepora* (a), *Goniastrea favulus* (b, d), *A. spathulata* (c, e), *G. australensis* (f) and *Cyphastrea microphthalma* (g) in treatments 2-4ºC above and below the local ambient temperature: 28ºC at Lizard Island, 24ºC at One Tree Island, and 22ºC at Lord Howe Island. Error bars show 95% confidence intervals and letters indicate homogenous groups determined by the overlap of confidence intervals.

Chapter 4 Supplementary Materials (referenced in Methods)

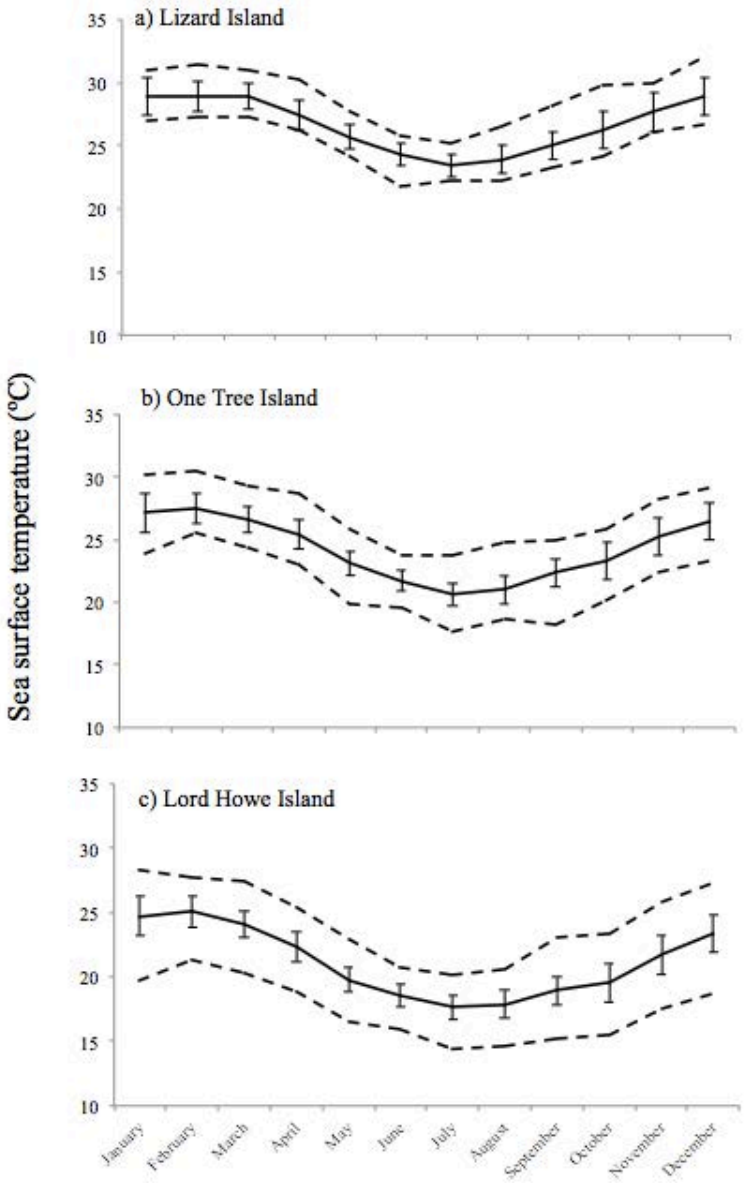


Figure 4.S1 Lagoonal sea surface temperatures (SST) 2010-2013 at a) Lizard Island (14.7ºS), b) One Tree Island (23.5ºS) and c) Lord Howe Island (31.5ºS). Solid lines represent average SST for each month, 2010-2013. Vertical bars show standard deviation. Dashed upper lines represent average maximum SST for each month. Dashed lower lines represent average minimum SST for each month. Monthly differences between average maximum and average minimum ranged from approximately 3-5ºC at Lizard Island, 4-7ºC at One Tree Island and 5-9ºC at Lord Howe Island. Data were collected from the Australian Institute of Marine Science (AIMS) and Great Barrier Reef Ocean Observing System (GBROOS) websites.

Table 4.S1 Mean temperatures in each of the temperature treatments (-4°C, -2°C, ambient, +2°C, +4°C) ± Standard Deviation at Lizard Island (ambient=28ºC), One Tree Island (ambient=24ºC) and Lord Howe Island (ambient=22ºC). Data were collected by HOBO temperature loggers every 10 minutes throughout the duration of the experiments.

	Lizard Island	**One Tree Island**	**Lord Howe Island**
-4 treatment (ºC)	23.90 ± 0.24	20.37 ± 0.43	18.32 ± 0.18
-2 treatment (ºC)	26.12 ± 0.42	22.21 ± 0.63	20.10 ± 0.37
Ambient treatment (ºC)	**27.89 ± 0.28**	**23.92 ± 0.61**	**22.19 ± 0.23**
+2 treatment (ºC)	30.16 ± 0.61	26.30 ± 0.40	24.24 ± 0.33
+4 treatment (ºC)	31.79 ± 0.46	28.14 ± 0.68	26.10 ± 0.30

CHAPTER FIVE: Species colonisation potential predicts changes in coral assemblage structure across a biogeographic barrier

This chapter is in preparation for the Journal of Biogeography

5.1 ABSTRACT

Life history traits of plants and animals that describe survival, growth and reproduction influence spatial distribution patterns and potential for long-term survival. Here, I investigated the relationship between coral life history traits and assemblage structure of coral reefs across the dispersal barrier between reefs on the Great Barrier Reef and Lord Howe Island in eastern Australia. For 120 species of corals observed in surveys, data on life history traits including larval nutrition, sexuality, depth range, corallite size, modularity, colony size and rate of larval development were assimilated. To assess whether these traits influence changes in coral assemblage across the dispersal barrier, non-metric multidimensional scaling, multiple regression, linear mixed models, and model averaging were applied. Rate of larval development and mode of larval nutrition were identified as the best predictors for changes in coral assemblage structure between locations on the Great Barrier Reef and the high-latitude coral communities at Lord Howe Island. Biological traits related to dispersal may therefore have a greater influence on large-scale patterns of abundance in reef-building corals than traits associated with morphology and environmental tolerance. Specifically, brooding species with larvae that are immediately competent to settle and therefore have high colonisation capacity are more likely to be successful in isolated, marginal habitats and survive the effects of climate change.

5.2 INTRODUCTION

Understanding mechanisms that determine the spatial distribution patterns of plant and animal species is a central goal in ecology (Brown et al. 1996; Roy and Whitman 2009; Valentine 2009) and due to the effects of contemporary warming (IPCC 2014) it is essential to understand the drivers of biogeographic patterns to anticipate and better manage the effects of climate change on biodiversity (Thomas et al. 2004; Clarke 2009; Sunday et al. 2011). One of the most prominent spatial patterns is the decline in species richness with increasing latitude. This pattern occurs in numerous taxa (Gaston 2000; Willig et al. 2003), including reef-building corals (Stehli and Wells 1971; Veron 1993; Keith et al. 2013).

In reef-building corals, the latitudinal attenuation of species has been attributed to a number of factors including reduced temperature and light availability (Dana 1843; Wells 1955; Banks and Harriott 1995; Kleypas et al. 1999), low aragonite saturation (Crossland 1981; Grigg 1982; Harriott 1999), reduced habitat availability (Bellwood and Hughes 2001), competition with other organisms, in particular macro-algae (Coles 1988; Johannes et al. 1983) and patterns of larval dispersal (Veron and Done 1979; Kleypas and Burrage 1994). However, the role of species-specific characteristics in determining this latitudinal attenuation of species has not been fully explored. Traits related to dispersal have been linked to the persistence of organisms during periods of environmental change. For example, Mediterranean plant species with wind-dispersed seeds increased in abundance over a 115-year period in parallel with rising temperatures and wetland destruction, while species with water-dispersed seeds experienced high rates of extinction (Lavergne et al. 2006). Similarly, in the marine environment, traits associated with

dispersal have been linked to extinction probability. For example, echinoderm species with planktonic non-feeding larval stages went extinct less often than species with feeding larvae (Valentine & Jablonski 1986, Uthicke et al. 2009, Byrne 2011). In scleractinian corals, both depth range and rate of larval development were good predictors of whether a species was able to cross faunal breaks (Keith et al. 2013). In addition, mode of larval development may predict persistence over geological time, as fewer brooding species with high colonisation capacity went extinct in the Caribbean during the Oligocene/ Miocene extinction compared to corals that broadcast spawn their gametes (Edinger and Risk 1995). Examining the traits of species that dominate assemblages at the limits of their environmental tolerance can also provide insight into future composition of global biodiversity in response to climate change (Guinotte et al. 2003). For example, high-latitude reefs are dominated by stress-tolerant, brooding species with small corallites and massive or horizontal growth forms (Harriott & Banks 2002; Sommer et al. 2014). Similarly, reefs degraded by human disturbances and thermal stress often resemble high-latitude reefs, being composed of suites of species with similar life history strategies (Sommer et al. 2014; Darling et al. 2012).

Lord Howe Island (31.5ºS) is a high-latitude reef located approximately 1,000 km south of the Great Barrier Reef (GBR) and 600 km east of the mainland Australian coast. It is a marginal reef at the southernmost limit of coral reef growth with approximately 85 species (Harriott et al. 1995). The coral assemblages include many tropical species at the limits of their distribution, as well as a small number of temperate species that are rare or absent on the GBR (Harriott et al. 1995). Although Lord Howe Island is at the limit of reef formation in the southern hemisphere and has fewer species, coral cover is similar to

many sites on the GBR (Dalton and Roff 2013). Population genetic and hydrodynamic studies indicate that Howe Island populations are highly isolated from the nearest source of propagules on the southern GBR (Ayre & Hughes 2004; Noreen et al. 2009; Patterson & Swearer 2007; Wood et al. 2014). Consequently, it is an ideal location at which to explore the potential effects of species traits in contributing to the latitudinal decline in species richness down the east coast of Australia crossing this dispersal barrier.

The aim of this study was to test whether coral species traits can predict the difference in coral assemblage structure between the GBR and Lord Howe Island. Coral assemblage structure was documented at Lord Howe Island and at two sites on the GBR, Lizard Island in the north and One Tree Island in the south. Coral species traits were obtained from an online database (see Methods) and used to test the hypothesis that species traits influence the capacity of species to cross and establish populations across this dispersal barrier.

5.3 METHODS

Difference in coral assemblage structure among locations

Coral assemblage structure was quantified using line intercept transects (LIT) at Lizard Island (14.7ºS) in the northern GBR in November 2011, One Tree Island (23.5°S) in the southern GBR in March 2012, and Lord Howe Island (31.5 ºS) in January 2012. At each location six sites were surveyed: 3 lagoon sites and 3 crest sites. At each site we conducted 12 x 10 m LIT at 1-2 metres depth. The intercepts of coral colonies greater than 5 cm maximum diameter and lying directly under transects were measured to the nearest centimetre. Colonies were identified to the species level either in the field or

using photographic images captured in the field following Wallace (1999) and Veron (2000).

Differences in coral assemblage structure among habitats and locations were explored with non-metric multidimensional scaling (NMDS). NMDS collapses multidimensional data into fewer dimensions, making them easier to visualise and interpret (Gower 1966). In addition, NMDS is designed specifically for ecological abundance data that are rarely normally distributed, and is recognized as the most robust ordination method for community data (Minchin 1987). Unlike other techniques that rely on Euclidian distances, NMDS uses rank orders and is therefore more flexible (Shaw 2003). Differences in assemblage structure between habitats and locations were tested using Analysis of Similarity (ANOSIM, Clarke 1993; Clarke and Warwick 1994) with 999 permutations and Bray-Curtis ordination. Species driving differences in coral assemblage structure among habitats and locations were identified using Similarity Percentage analysis (SIMPER, Clarke 1993; Warton et al. 2012). The five species with the greatest contributions to dissimilarities between locations (Lizard, One Tree and Lord Howe Islands) and habitats (crest and lagoon) are presented (Theis et al. 2012). All analyses were run in R (v. 3.0.1; R Core Team 2013) with the vegan (Oksanen et al. 2013), visreg (Breheny and Burchett 2013) and car (Fox and Weisberg 2011) packages.

Species traits

Species traits were collated from the Coral Traits database (Madin and Baird 2014, http://coraltraits.org/). Traits used included mode of larval nutrition, sexuality, depth range, corallite size, modularity, maximum colony size and rate of larval development. All coral larvae are non-feeding, however, some species have eggs or larvae that contain

photosynthetic symbiotic algae on release and are likely to be autotrophic (Richmond 1987) while the remainder can be described as lecithotrophic (Baird et al. 2009). Autotrophic larvae would be expected to have a great capacity to disperse given they have an additional source of nutrition (Richmond 1987). Sexuality in corals is either hermaphroditic or gonochoric (Kerr et al. 2011). Hermaphrodites might be more effective colonisers because of a, albeit limited, capacity to self-fertilise. Depth range is a proxy for environmental tolerance; species with a broader depth range are able to tolerate a wider variety of habitats and for this reason might be expected to be better colonisers (Addo-Bediako et al. 2000; Keith et al. 2013; Laube et al. 2013), in particular, of locations at the limits of coral ranges. Corallite size is often used as a proxy for degree of autotrophy (Porter 1976; Houlbrèque and Ferrier-Pagès 2009) or competitive ability (Lang 1973) in adult corals and therefore is likely to have a strong effect on species ecology (e.g. Sommer et al. 2014). Body size is also likely to have strong effects on species distributions. For example, maximum colony size was correlated with extinction probability in Neogene reef corals (Johnson et al. 1995). In this study, rate of larval development was classified into four categories based on the time taken for propagules to become motile. Species that brood larvae that are motile on release were classified as 1; species that broadcast spawn gametes were classified into three categories based on egg size, category 2 = 1-200µm; category 3 = 201-400µm; category 4 = > 400µm. Egg size is a strong predictor of the time taken to reach motility in broadcast spawning coral species (Figueiredo et al. 2013) and rates of development are highly correlated with rates of self-retention and therefore colonisation potential in corals species (Figueiredo et al. 2013, 2014).

Species traits as drivers of differences among coral assemblages

The extent to which species traits could explain differences in coral assemblages along the locations were tested using multiple linear regression, which models the relationship between two or more explanatory variables and a response variable (Logan 2010). To ensure the response variable was tractable, we used axis scores generated by NMDS, which reduced the multi-dimensional assemblage data to a single value for each species (Diaz et al. 2013). NMDS axis scores for each species used in the analysis are presented in Table 5.S1 at the end of this chapter. Statistical assumptions were tested following Logan (2010). The shape of the relationship between each predictor variable and the response variable was determined by selecting the polynomial order (linear, quadratic or cubic) that produced the lowest Akaike Information Criterion value corrected for small sample size (AICc) in regression of each predictor variable independently. Non-independence of evolutionary history was accounted for by incorporating coral clade as a random effect. The strength of this effect was assessed visually with caterpillar plots and statistically by calculating the variance partition coefficient. The best combination of species traits to predict differences in assemblage structure among habitats and location was determined using model selection and averaging (Bartoń 2013). Models that were within three ΔAICc units of the best model were chosen and then this model set was averaged (Bolker 2008). Partial coefficients of the model-averaged predictors were generated to describe the influence of each species trait on differences in coral assemblage structure.

5.4 RESULTS

Differences in coral assemblage structure among locations and between habitats

Coral assemblage structure differed significantly between locations and among habitats. The first axis of the NMDS clearly separated Lord Howe Island sites from sites at Lizard Island and One Tree Island (Fig. 5.1). The second axis separated most reef crest sites from lagoon sites, except at Lord Howe Island were there was little difference among the coral assemblages between habitats (Fig. 5.1). These results were supported by ANOSIM that indicated significant differences in assemblage structure between Lord Howe Island and both GBR sites, but not between the GBR sites (Table 5.1). Similarly, significant differences between habitats were only evident at Lizard Island and One Tree Island but not at Lord Howe Island (Table 5.2).

Species that exerted the greatest influence on the differences in assemblage structure among locations are listed in Table 5.1. In particular, Lizard Island was distinguished from the other two locations by high cover of *Acropora hyacinthus* and *A. formosa*; One Tree Island was distinguished by high cover of *Isopora palifera* and *Goniopora tenuidens* and Lord Howe Island by high cover of *Isopora cuneata*, *Porites heronensis* and *Pocillopora damicornis* (Table 5.1; Fig. 5.1). Species that exerted the greatest influence on the differences in assemblage structure among habitats within locations are listed in Table 5.2. The reef crest at Lizard Island was distinguished by high cover of *A. hyacinthus* and *A. digitata* and the lagoon by high cover of *A. formosa* and *A. horrida* (Table 5.2; Fig. 5.1). The reef crest at One Tree Island was distinguished by high cover of *A. nasuta* and *Pavona decussata* and the lagoon by higher cover of *Goniopora tenuidens* and *Porites lichen* (Table 5.2; Fig. 5.1). As mentioned above, there was no significant difference in the habitats at Lord Howe Island.

Traits that predict assemblage structure across a dispersal barrier

Of the traits tested, rate of larval development (coefficient: −0.76; $p < 0.001$) and mode of larval nutrition (coefficient: -1.19; $p = 0.028$) were both significant predictors of changes in coral assemblage structure among locations as captured by Axis 1 of the NMDS (Table 5.3; Fig. 5.2). Specifically, species with rapidly developing, autotrophic larvae were significantly more abundant at Lord Howe Island than on the GBR. The proportion of coral cover made up of species with rapidly developing larvae increased from less than 10% at Lizard Island to over 80% at Lord Howe Island (Fig. 5.3a). Similarly, the proportion of coral cover made up of species with autotrophic larvae increased from 19% (± 3.9) at Lizard Island to 50% (± 6.5) at Lord Howe Island (Fig. 5.3b).

5.5 DISCUSSION

Coral assemblage structure changed markedly between the Great Barrier Reef and Lord Howe Island, and traits related to larval dispersal were the best predictors of this difference. Specifically, Lord Howe Island assemblages were dominated by species with larvae that develop rapidly and species with larvae that are autotrophic. These results suggest that isolated corals assemblages, such as Lord Howe Island, are dominated by species that have both the capacity to cross the dispersal barrier (i.e. larvae that derive nutrition from photosymbionts) and to establish populations once they arrive (i.e. larvae that develop rapidly and are therefore more likely to be retained on the natal reef).

Lord Howe Island assemblages were overwhelmingly dominated by species that brood their larvae (i.e. development rate category 1), which make up an extraordinary 80% of coral cover (Fig. 5.3a). In contrast, Lizard Island was dominated by species with slower-developing larvae, such as the *Acropora* (development category 4; Fig. 5.3a). This

finding is consistent with previous work on Lord Howe Island documenting the abundance of brooders in both the adult and recruit assemblages (Harriott 1992). Similarly, in many marine invertebrates, brooders are, in general, more prevalent at high latitudes (Thorson 1950; Mileikovsky 1971; Marshall et al. 2012). We hypothesize that the dominance of brooders is most likely related their rapid rates of larval development: brooded larvae are ready to settle on, or shortly after, release compared with an obligate planktonic period of 12 to 36 hours in broadcast spawners (Baird et al. 2009; Figueiredo et al. 2013). Rapid rates of development will lead to greater rates of retention on the reef of origin (Figueiredo et al. 2014), a strategy that is likely to be highly correlated with colonisation ability, particularly on isolated reefs such as Lord Howe Island. However, species that brood larvae have also been suggested to be more tolerant of environmental extremes, for example, brooding species were less likely to go extinct during the Neogene in the Caribbean, a period of environmental turbulence that included regional cooling (Edinger and Risk 1995). Consequently, brooding species may be pre-adapted to locations at the boundaries of habitat suitable for corals, such as Lord Howe Island. However, the other proxy for environmental tolerance, depth range, was not as significant predictor of differences in assemblage structure between the Great Barrier Reef and Lord Howe Island. This is surprising because depth generalists are typically more successful at higher latitudes (Stevens 1989) and a broad depth range is a good predictor of a species ability to cross faunal breaks on a biogeographic scale (Keith et al. 2013). One possible reason that depth was not a useful predictor is that surveys only included shallow water corals (surveys were conducted at 1-2 meters depth). Clearly, the relationship between

depth range, environmental tolerance, and geographical range size needs to be examined more fully.

Species with autotrophic larvae were also much more abundant at Lord Howe Island than on the GBR, making up almost 50% of total coral cover compared to less than 20% at GBR locations (Fig. 5.3b). We attribute this success to the superior dispersal ability conferred by translocation of energy from the photosymbiotic algae in the propagules of these species. However, there is also a very strong correlation between rates of larval development and mode of larval nutrition. Indeed, all brooded larvae (development category 1), with the exception of those species from the genus *Isopora*, are autotrophic (Baird et al. 2009). Indeed, the most abundant species at Lord Howe Island, which makes up 28% of total coral cover *Isopora cuneata* is a lecithotrophic brooder. This relationship suggests that the rate of larval development is more important than the mode of larval nutrition in determining the structure of Lord Howe Island corals assemblages.

One other interesting pattern in species composition among the assemblages was the apparent replacement of species within some genera or morphological groups. For example, *Pocillopora edouxi, P. meandrina,* and *P. verrucosa* were all abundant on the GBR but absent from Lord Howe Island where *P. damicornis* is the only member of the genus present (Fig. 5.1). Similarly, *Isopora cuneata* replaces *I. palifera* at higher latitudes. The arborescent coral *A. formosa* was adundant at Lizard Island but was replaced by *A. yongei* at Lord Howe Island and the tabular *A. hyacinthus* on Lizard Island was replaced by *A. clathrata* on Lord Howe. This suggests a very different pattern of species turnover than the nested structure recently identified in scleractinian coral

assemblages (Keith et al. 2013) and the traditional view of high-latitude coral species as being a subset of the tropical species pool (Veron 1995). Another general trend in species composition was a decrease in the relative abundance of *Acropora* with increasing latitude, which is consistent with other recent work along the east coast of Australia (Dalton and Roff 2013).

In conclusion, species traits related to dispersal strongly most strongly influenced the difference in assemblage structure of corals between the GBR and Lord Howe Island. In particular, the rate of larval development was the best predictor of a species' ability to cross this dispersal barrier, a feature attributed to the superior colonising ability of species with larvae that can settle soon after release.

Table 5.1 Results of ANOSIM and SIMPER analyses among locations, including the five most important species causing differences in coral assemblage structure between Lizard, One Tree, and Lord Howe Island.

Comparison (A vs B)	ANOSIM	SIMPER: Overall Average Dissimilarity	Five most influential species	Percent contribution to difference	Average percent cover at A	Average percent cover at B
Lizard Island vs One Tree Island	R=0.012 p=0.396	81.20	*Isopora palifera*	10.71	4.0	21.0
			Acropora hyacinthus	7.64	13.0	3.0
			Acropora formosa	7.24	12.0	0.0
			Goniopora tenuidens	4.02	0.0	7.0
			Pavona decussata	3.92	0.0	6.0
Lizard Island vs Lord Howe Island	R=0.37 p=0.001	92.02	*Isopora cuneata*	15.14	0.0	28.0
			Porites heronensis	12.99	0.0	24.0
			Pocillopora damicornis	7.67	3.0	17.0
			Acropora hyacinthus	7.05	13.0	1.0
			Acropora formosa	6.37	12.0	0.0
One Tree Island vs Lord Howe Island	R=0.21 p=0.001	90.15	*Isopora cuneata*	15.40	0.0	28.0
			Porites heronensis	13.21	0.0	24.0
			Isopora palifera	11.65	21.0	0.0
			Pocillopora damicornis	6.73	6.0	17.0
			Goniopora tenuidens	3.62	7.0	0.0

Table 5.2 Results of ANOSIM and SIMPER analyses among habitats (lagoon and crest) within each location, including the five most important species causing differences in coral assemblage structure between habitats.

Comparison	ANOSIM	SIMPER: Overall Average Dissimilarity	Five most influential species	Percent contribution to difference	Average percent abundance (Lagoon)	Average percent abundance (Crest)
Lizard Island Lagoon vs Lizard Island Crest	R=0.33 p=0.001	85.93	*Acropora hyacinthus*	13.26	2.0	24.0
			Acropora formosa	13.14	23.0	1.0
			Acropora digitifera	4.47	0.0	8.0
			Acropora horrida	3.83	7.0	0.0
			Isopora palifera	3.34	2.0	6.0
One Tree Island Lagoon vs One Tree Island Crest	R=0.33 p=0.001	73.61	*Isopora palifera*	12.24	28.0	14.0
			Goniopora tenuidens	8.68	13.0	0.0
			Porites lichen	7.78	12.0	0.0
			Acropora nasuta	6.39	1.0	10.0
			Pavona decussata	5.55	6.0	7.0
Lord Howe Island Lagoon vs Lord Howe Island Crest	R=0.11 p=0.20	53.39	*Isopora cuneata*	20.91	20.0	36.0
			Porites heronensis	18.50	27.0	21.0
			Pocillopora damicornis	13.83	11.0	22.0
			Acropora clathrata	6.94	8.0	2.0
			Acropora yongei	5.87	6.0	0.0

Table 5.3 Model-averaged partial coefficients from the best linear models for location, describing the relationship between coral species traits and Axis 1, which represents the distinction between the Great Barrier Reef and Lord Howe Island.

Predictor	Coefficient	Standard error	p
Rate of larval development	-0.76	0.18	0.000020
Mode of larval nutrition	-1.19	0.53	0.028
Corallite size (quadratic)	0.19	0.35	0.58
Sexuality	0.12	0.17	0.51
Depth range	-0.00092	0.0056	0.87
Colony size	-0.00035	0.00032	0.28

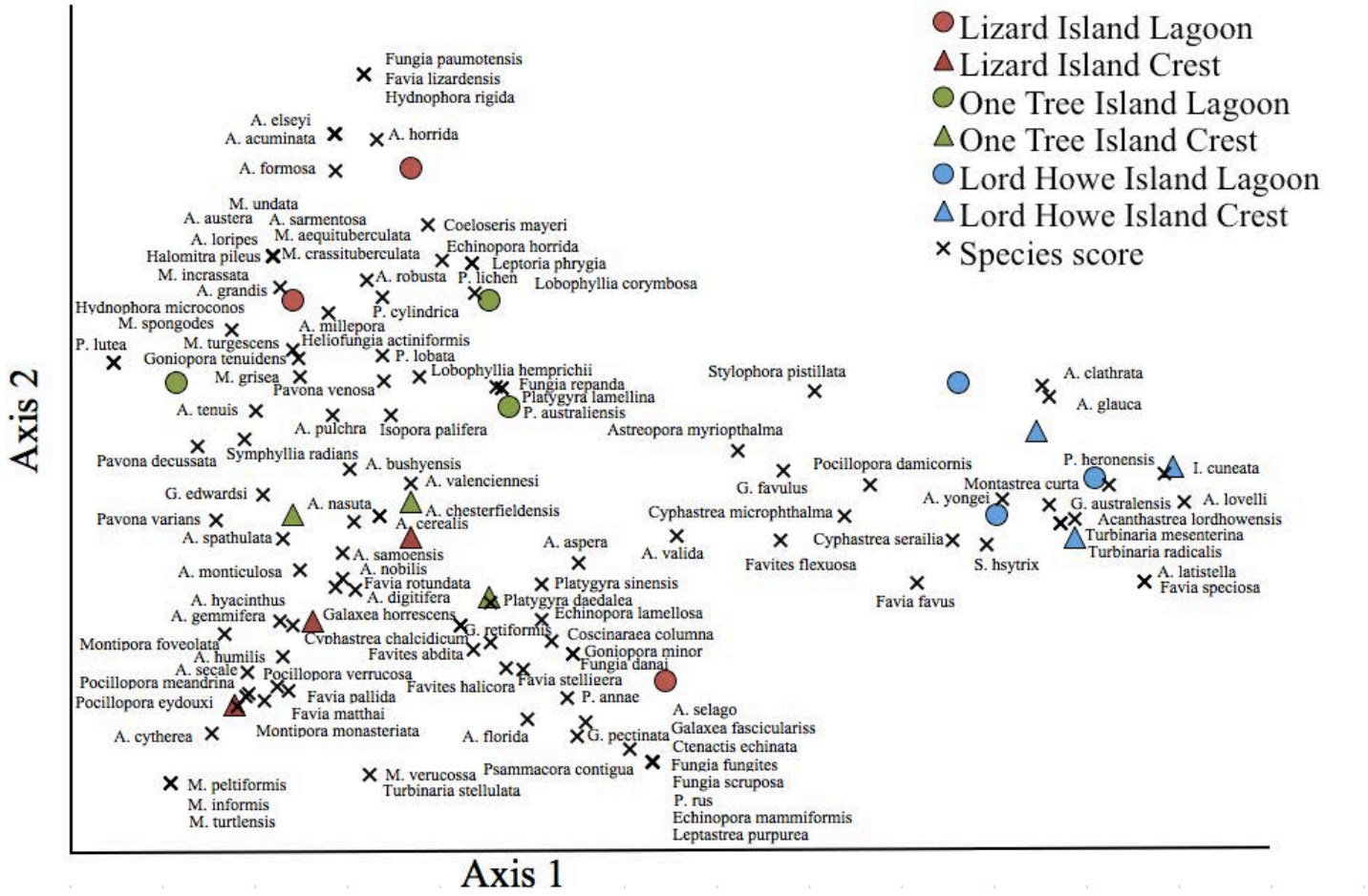


Figure 5.1 Similarity in coral assemblage (abundance) at 18 sites off the east coast of Australia based on NMDS (two-dimensional stress: 0.15). Circles = lagoon sites, triangles = crest sites, red = Lizard Island, green = One Tree Island, blue = Lord Howe Island, crosses = 120 observed species. Distance between points represents relative difference in coral assemblage. ANOSIM (at the transect level) suggests there is a significant difference in assemblage between the Great Barrier Reef (Lizard and One Tree Islands) and Lord Howe Island (R= 0.34, p=0.001), which is captured by Axis 1.

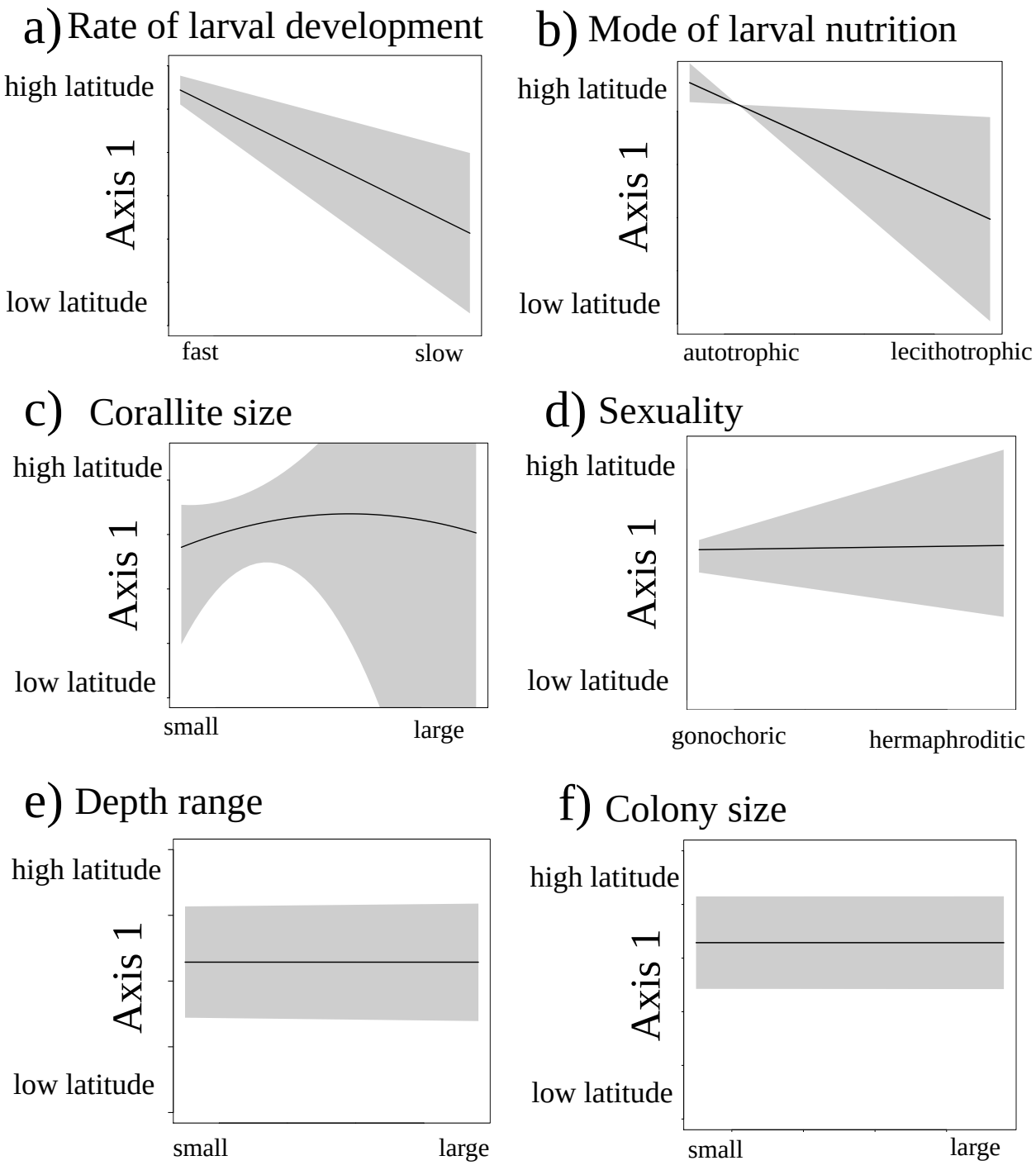
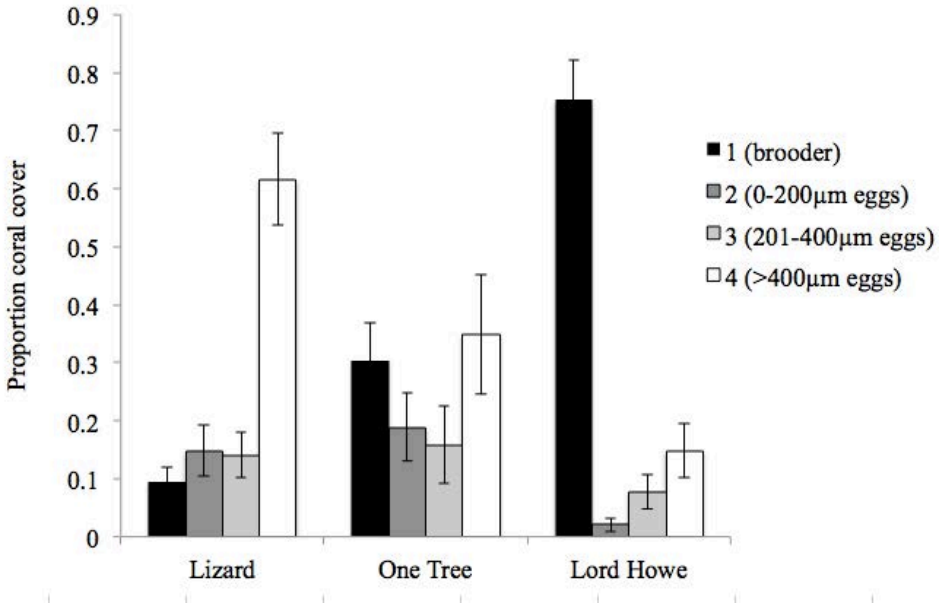


Figure 5.2 Partial coefficients from the averaged best models describing the relationship between each life history trait and Axis 1, which describes distinction in coral assemblage along a latitudinal gradient, for a) Rate of larval development, b) Mode of larval nutrition, c) Corallite size, d) Sexuality, e) Depth range and f) Colony size. 95% confidence intervals are shown in grey.

a) Rate of larval development



b) Mode of larval nutrition

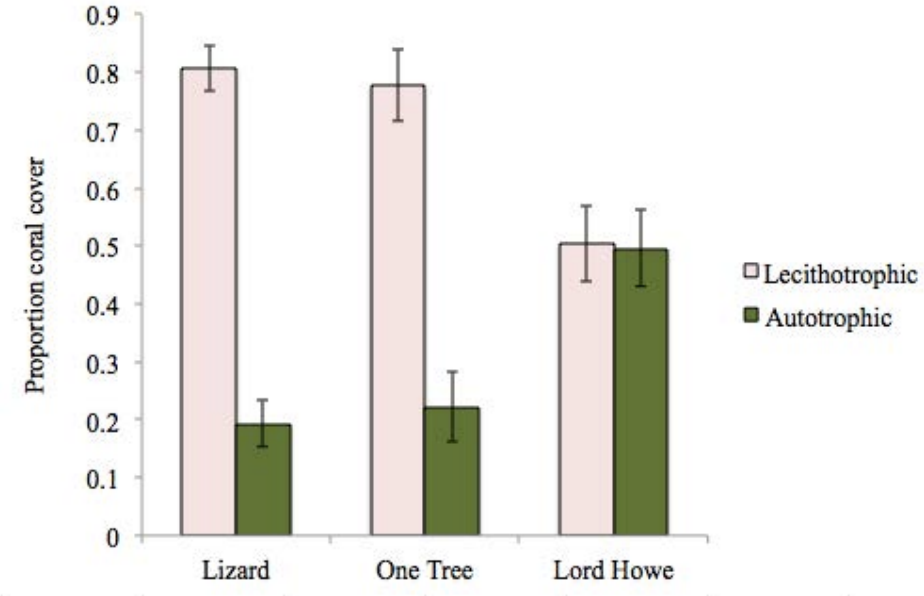


Figure 5.3 Average proportion coral cover of species, presented by a) rate of larval development b) larval nutrition at Lizard, One Tree, and Lord Howe Islands. Bars show standard error.

Table 5.S1(referenced in Methods) Species list and associated axis 1 scores generated by non-metric multidimensional scaling (NMDS). Axis 1 of the NMDS represents differences in coral assemblage structure between the Great Barrier Reef and Lord Howe Island (see Fig. 5.1, and note that, while there are negative values in the table, axis lines were shifted in the figure for simplification).

Species	Axis score	Species	Axis score	Species	Axis score
Acanthastrea lordhowensis	1.20	*Coeloseris mayeri*	-0.46	*Lobophyllia hemprichii*	-0.48
Acropora acuminata	-0.70	*Coscinaraea columna*	-0.14	*Montastrea curta*	1.13
Acropora aspera	-0.07	*Ctenactis echinata*	0.12	*Montipora aequituberculata*	-0.85
Acropora austera	-0.85	*Cyphastrea chalcidicum*	-0.37	*Montipora crassituberculata*	-0.85
Acropora bushyensis	-0.66	*Cyphastrea microphthalma*	0.61	*Montipora foveolata*	-0.98
Acropora cerealis	-0.58	*Cyphastrea serailia*	0.89	*Montipora grisea*	-0.78
Acropora chesterfieldensis	-0.58	*Echinopora horrida*	-0.42	*Montipora incrassata*	-0.85
Acropora clathrata	1.12	*Echinopora lamellosa*	-0.17	*Montipora informis*	-1.11
Acropora cuneata	1.43	*Echinopora mammiformis*	0.12	*Montipora monasteriata*	-0.87
Acropora cytherea	-1.01	*Favia favus*	0.79	*Montipora peltiformis*	-1.11
Acropora digitifera	-0.64	*Favia lizardensis*	-0.62	*Montipora spongodes*	-1.26
Acropora elseyi	-0.69	*Favia matthaii*	-0.91	*Montipora turgescens*	-0.80
Acropora florida	-0.20	*Favia pallida*	-0.81	*Montipora turtlensis*	-1.11
Acropora formosa	-0.69	*Favia rotundata*	-0.68	*Montipora undata*	-0.85
Acropora gemmifera	-0.80	*Favia speciosa*	1.38	*Montipora verrucosa*	-0.60
Acropora glauca	1.13	*Favia stelligera*	-0.21	*Pavona decussata*	-1.05
Acropora grandis	-0.83	*Favites abdita*	-0.34	*Pavona varians*	-1.00
Acropora horrida	-0.59	*Favites flexuosa*	0.45	*Pavona venosa*	-0.57
Acropora humilis	-0.83	*Favites halicora*	-0.25	*Platygyra daedalea*	-0.30
Acropora hyacinthus	-0.84	*Fungia danai*	-0.09	*Platygyra lamellina*	-0.27
Acropora latistella	1.38	*Fungia fungites*	0.12	*Platygyra sinensis*	-0.16
Acropora loripes	-0.85	*Fungia paumotensis*	-0.62	*Pocillopora damicornis*	0.68
Acropora lovelli	1.48	*Fungia repanda*	-0.28	*Pocillopora eydouxi*	-0.94
Acropora millepora	-0.71	*Fungia scruposa*	0.12	*Pocillopora meandrina*	-0.92
Acropora monticulosa	-0.78	*Galaxea fascicularis*	0.12	*Pocillopora verrucosa*	-0.84
Acropora nasuta	-0.64	*Galaxea horrescens*	-0.37	*Porites annae*	-0.10
Acropora nobilis	-0.69	*Goniastrea australensis*	1.16	*Porites australiensis*	-0.27
Acropora palifera	-0.55	*Goniastrea edwardsi*	-0.88	*Porites cylindrica*	-0.57
Acropora pulchra	-0.70	*Goniastrea favulus*	0.46	*Porites heronensis*	1.29
Acropora robusta	-0.61	*Goniastrea pectinata*	-0.08	*Porites lichen*	-0.34
Acropora samoensis	-0.68	*Goniastrea retiformis*	-0.30	*Porites lobata*	-0.57
Acropora sarmentosa	-0.85	*Goniopora minor*	-0.09	*Porites lutea*	-1.26
Acropora secale	-0.92	*Goniopora tenuidens*	-0.79	*Porites rus*	0.12
Acropora selago	0.12	*Halomitra pileus*	-0.85	*Psammocora contigua*	0.06
Acropora spathulata	-0.83	*Heliofungia actiniformis*	-0.96	*Seriatopora hystrix*	0.97
Acropora tenuis	-0.90	*Hydnophora microconos*	-1.26	*Stylophora pistillata*	0.53
Acropora valenciennesi	-0.50	*Hydnophora rigida*	-0.62	*Symphyllia radians*	-0.92
Acropora valida	0.18	*Leptastrea purpurea*	0.12	*Turbinaria mesenterina*	1.16
Acropora yongei	1.01	*Leptoria phrygia*	-0.34	*Turbinaria radicalis*	1.16
Astreopora myriophthalma	0.34	*Lobophyllia corymbosa*	-0.34	*Turbinaria stellulata*	-0.05

CHAPTER SIX: GENERAL DISCUSSION

This thesis provides new information on coral larval ecology and biogeography in eastern Australia. In general, I found that raised temperatures lower the amount of viable larval stock (Chapters 2-4) and that heat tolerance of early life stages varies among species (Chapter 2), modes of fertilisation (Chapter 3) and latitudes (Chapter 4). In addition, I discovered that traits related to dispersal are likely to influence changes in assemblage structure of adult corals among locations (Chapter 5).

In the first data chapter (Chapter 2), I found that water temperatures 2-4ºC above the local ambient (24ºC) reduced larval lifespan and sped development in *Acropora spathulata* and *Goniastrea favulus* at One Tree Island in the southern Great Barrier Reef (GBR). Thermal tolerance differed between the species however, as 26°C (+2ºC) treatments reduced larval lifespan in *A. spathulata* and 28°C (+4ºC) treatments reduced lifespans of *G. favulus*. This finding that merulinids have greater tolerance to raised temperatures than acroporids is supported by previous work in adult corals as well as early life stages (Hughes & Connell 1999; Marshall & Baird 2000; Negri et al. 2007). Temperatures 2-4ºC below ambient meanwhile did not affect larval survival. This new finding suggests that colder waters are unlikely to prevent dispersal of coral propagules from the tropics to cooler, higher-latitude reefs. In fact, slower development from colder temperatures would increase time in the plankton, possibly enhancing potential for long-distance dispersal. Indeed, temperature also affected rate of larval development in all species and locations. As temperatures increased, development sped up and at lower temperatures, embryos and larvae took longer to reach gastrulation and become motile, respectively. Rates of embryonic development were also influenced by the size of the

propagules. *G. favulus* embryos (~ 320 µm) developed more rapidly than the larger *A. spathulata* embryos (~500µm) at all temperatures. Indeed, egg size is negatively correlated with rate of larval development (Marshall and Bolton 2007; Figueiredo et al. 2013).

In Chapter 3, I compared thermal tolerance between self and cross-fertilised *G. favulus* embryos and found that self-fertilised embryos were more sensitive to raised temperatures than outcrossed embryos. Specifically, larval lifespans of self-fertilised embryos were shorter than lifespans of cross-fertilised embryos at raised temperatures. *G. favulus* has the unique ability to self-fertilise, which is likely to be advantageous in isolated and low-density areas. However, results of this chapter show that this reproductive strategy comes at a cost because self-fertilisation is likely to result in reduced dispersal potential in warming oceans.

I extended the spatial scale of my study in Chapter 4 and examined the effects of temperature on early life stages of coral across latitudes. At Lizard Island, the lowest latitude study location, thresholds (i.e., the temperature treatments at which we observed at effect) for larval lifespan and proportion of abnormally developing embryos were 2ºC above the local ambient (28ºC) for all species. Whereas at the higher latitude locations, One Tree and Lord Howe Islands, thresholds were generally 2-4ºC above ambient, or there was no threshold observed at all. These results support the hypothesis that thermal tolerance is greater in organisms from higher latitude regions that experience a greater annual temperature range (Janzen 1967; Chown et al. 2004; Bozinovic et al. 2011).

While the first three chapters focused on the effects of temperature on early life stages of corals and how these effects vary through space, the final thesis data chapter (Chapter 5) investigated how characteristics of the entire coral life stages influence spatial

distribution. I found that traits related to dispersal are the best predictors for changes in coral assemblage structure across the hypothesized dispersal barrier between the Great Barrier Reef and Lord Howe Island. Species with larvae that are immediately competent to settle and have autotrophic larvae- both are traits related to brooding species- appear to have an advantage in high-latitude marginal environments. The finding that rate of larval development influences changes in abundance among locations supports observations of latitudinal patterns in other marine invertebrates (Thorson 1950; Marshall et al. 2012) and is consistent with the dominance of brooding species at high latitudes (Harrison and Wallace 1990; Harriott et al. 1992).

Implications

Findings reported here can help form projections of future distributions of coral reefs. Most notably, species with larvae that have broad thermal tolerance and spend short periods in the plankton are more likely to survive as coral habitats become more fragmented and degraded. This includes spawning species with fast-developing eggs and high tolerance to temperature, such as merulinids, and brooding species that release fully formed larvae that are immediately competent to settle. Acroporid species, in contrast, have larvae with narrow thermal tolerances that develop slowly in the plankton and so are more vulnerable to the prolonged effects of fluctuating temperatures. Indeed, present compositions of adult corals support these predictions, as merulinids and brooding species are more tolerant to bleaching and are more abundant in variable high-latitude environments than acroporids (Hughes & Connell 1999; Dalton and Roff 2013).

The effects of ocean warming are likely to impact coral populations differently across latitudes. Coral populations in low latitudes appear to be living closer to their upper thermal limits and, in the absence of adaptation, these populations are therefore more vulnerable to the effects of ocean warming (Chapter 4). Higher latitude coral populations, in contrast, are less vulnerable to rising temperatures, as projected temperature changes still sit within their wider tolerance breadths (Chapter 4). This is despite the fact that higher latitude regions are warming at a greater rate. Indeed, the effects of warming rely on level of tolerance as well as the amplitude of environmental change (Tewksbury et al. 2008; Sunday et al. 2011). For instance, in subtropical coral communities of eastern Australia, e.g. Flinders Reef, Cook Island, Solitary Islands and South West Rocks, sea surface temperatures (SST) are rising 0.19-0.24 °C per decade (Lima and Wethey 2012; Dalton and Roff 2013), more rapidly than on the Great Barrier Reef (GBR), where SST are rising 0.08ºC per decade in the northern GBR and 0.16ºC per decade in the southern GBR (Lough 2008). Despite smaller amplitudes of change, ocean warming is impacting tropical coral communities more strongly, as evidenced by regular bleaching events (Hoegh-Guldberg 1999; Baker et al. 2008). However a recent observation of coral bleaching at Lord Howe Island suggests sub-tropical communities are not immune to the effects of warming (Harrison et al. 2011). Nonetheless, high-latitude coral populations are expected to have broader thermal tolerance breadths than lower latitude corals, which would corroborate findings of this thesis and other latitudinal patterns of thermal tolerance among marine and terrestrial organisms (Tewksbury et al. 2008; Sorte et al. 2011; Sunday et al. 2011).

Continued ocean warming may result in loss of coral biodiversity around the equator and poleward extension of species ranges, as occurred during the last Pleistocene

interglacial (Kiessling et al. 2012). Indeed, coral species in eastern Australia may currently be migrating southward as temperature regimes shift down the coast and higher latitudes become warmer. Four acroporid species that have not been previously observed in higher latitudes have recently been recorded in the Solitary Islands (30ºS) (Baird et al. 2012). Similarly, in Japan coral species have recently extended their ranges pole-ward over an 80 year period that coincided with rising temperatures (Yamano et al. 2011). Such range shifts suggest there have previously been cold thermal barriers to larval dispersal to high latitudes. However, results from this thesis suggest that colder waters are unlikely to reduce dispersal capacity and so thermal barriers are more likely to be associated with annual temperatures experienced by the adult stage.

The persistence of coral reef environments under contemporary climate change is uncertain and, as tropical coral populations continue to be subjected to thermal stress, higher latitude habitats may provide refuge to coral species that extend their ranges (Hughes et al. 2010; Woodroffe et al. 2010; Dalton and Roff 2013). However, the potential of high-latitude reefs for providing stable habitats for thermal refugia remains unknown. Some evidence suggests high-latitude reefs in eastern Australia are more vulnerable to the disturbances due to isolation and low recruitment (Harriott 1999; Noreen et al. 2009; Hoey et al. 2011), whereas other observations describe sub-tropical reef communities as stable and resilient and thereby possible habitats for refugia. Indeed, long-term comparisons of subtropical reefs in eastern Australia found that these assemblages remained relatively stable, with 75% similarity over a 15-20 year period (Dalton and Roff 2013). Additionally, communities in marginal environments may predict the future states of tropical communities (Guinotte et al. 2003), so investigating species traits associated with success

at the edges of species distributions may therefore anticipate future distributions to better manage global biodiversity. As brooding species and species with thermally tolerant larvae are most successful at high latitudes, they are most likely to survive climate change and persist in degraded, variable environments.

Climate change will likely have profound effects on patterns of dispersal and population dynamics in corals and other marine invertebrates. Our findings suggest that rising temperatures are affecting marine invertebrates across life stages and the impacts of ocean warming will vary among species and populations. In addition, species traits related to dispersal are important for investigating distributions and long-term survival of marine invertebrate species. Results of this thesis encourage further investigation and special management consideration of reefs at higher latitudes and in marginal habitats, as these regions may give insight into the future states of lower latitude reefs and provide important refuge for species that extend their ranges in response to ocean warming.

Future work

Findings from this thesis illustrate the importance of considering multiple species and locations as well as early life history stages in addition to adults. Future work could therefore measure the effects of temperature at more locations using more species, including those that brood larvae. This would help further understand latitudinal patterns in thermal tolerance of early life stages and identify differences in thermal tolerance among species with different modes of larval development. For instance, the effects of temperature on larval ecology in subtropical transition zones such as Flinders Reef, the Solitary Islands and Elizabeth and Middleton Reefs, with particular focus on species that are dominant in

these environments, should be further investigated. In addition, conducting transplant or common garden experiments of adult colonies prior to spawning would give greater insight into genetic effects and long-term adaptive capacity to ocean warming.

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APPENDIX I: Additional publications during PhD candidature, including brief descriptions of my contributions. Final published versions of first authored manuscripts are included in the following pages.

1. Baird AH, Gudge S, Keith S, Tan C-H, **Woolsey ES** (*in preparation*) Coral reproduction on a high latitude reef: Lord Howe Island, Australia.

   ESW contribution: Assisted with fieldwork and data collection.

2. de Bérigny Wall C, Gough P, Faleh M, and **Woolsey E** (2014) Tangible user interface design for climate change education in interactive installation art. Leonardo (MIT Press).

   ESW contribution: Scientific advisor to the artists, provided content as well as access to field stations on the Great Barrier Reef, wrote large sections of the manuscript.

3. **Woolsey E,** Byrne M, Beaman R, Williams S, Pizarro O, Bridge T, Thornborough K, Davies P and Webster J. (2013) *Ophiopsila pantherina* beds on subaqueous dunes off the Great Barrier Reef. In Echinoderms in a Changing World. C. Johnson et al (eds).

   ESW contribution: Led data collection, analysis, and manuscript preparation. See published version in the following pages.

4. Schmidt-Roach S, Miller K, **Woolsey E**, Gerlach G and Baird A (2012) Spawning by *Pocillopora* species on the Great Barrier Reef. PlosOne 7(12): e50847. doi:10.1371/journal.pone.0050847.

   ESW contribution: Assisted with fieldwork and data collection.

5. **Woolsey E**, Bainbridge S, Kingsford M and Byrne M (2012) Impacts of Cyclone Hamish at One Tree Reef: integrating environmental and benthic habitat data. Marine Biology 159: 793-803.

   ESW contribution: Led data analysis and manuscript preparation. See published version in the following pages.

6. Schneider K, Silverman J, **Woolsey E**, Eriksson H, Byrne M and Caldeira K (2011) Potential influence of sea cucumbers on coral reef $CaCO_3$ budget: a case study at One Tree Reef. Journal of Geophysical Research – Biogeosciences. Vol. 116, Issue G4.

ESW contribution: Conducted surveys of holothurian populations at One Tree Island, assisted with manuscript preparation.

7. Byrne M, Selvakumaraswamy P, Ho MA, **Woolsey E** and Nguyen HD (2011) Sea urchin development in a global change hotspot, potential for southerly migration of warm adapted propagules. *Deep Sea Research II* 58: 712-719.

ESW contribution: Processed and presented sea surface temperature data.

Mar Biol (2012) 159:793–803
DOI 10.1007/s00227-011-1855-8

ORIGINAL PAPER

Impacts of cyclone Hamish at One Tree Reef: integrating environmental and benthic habitat data

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Received: 6 June 2011 / Accepted: 7 December 2011 / Published online: 30 December 2011

Abstract The southern Great Barrier Reef (GBR), a region that rarely experiences cyclones, was impacted by tropical cyclone (TC) Hamish in March 2009. We documented on-reef physical and habitat conditions before, during and after the cyclone at One Tree Reef (OTR) using data from environmental sensor instrumentation and benthic surveys. Over 5 years of monitoring, ocean mooring data revealed that OTR experienced large swells (4–8 m) of short duration (10–20 min) not associated with a cyclone in the area. These swells may have contributed to the physical disturbance of benthic biota and decline in coral cover recorded prior to and after TC Hamish. During the cyclone, OTR sustained southeasterly gale force winds (>61.2 km h^{-1}) for 18.5 h and swells >6 m in height for 4 h. Benthic surveys of exposed sites documented a 20% drop in live coral cover, 30% increase in filamentous algae cover and the presence of dislodged corals and rubble after the storm. Leeward sites were largely unaffected by the cyclone. Benthic cover did not change in the lagoon sites. Significant rubble movement and infill of the lagoon occurred. Two years after the cyclone, algal cover remained high and laminar corals had not recovered. Total coral cover at impacted sites had continued to decline. Environmental conditions and habitat surveys supported Puotinen's (Int J Geogr Inf Sci 21:97–120, 2007) model for cyclone conditions that cause reef destruction. While TC Hamish had a major impact on the reef, change in benthic cover over several years was due to multiple stressors. This on-reef scale integration of physical and biological data provided a rare opportunity to assess impacts of a major storm and other disturbances, showing the importance of considering multiple stressors (short-lived and sustained) in assessing change to reef habitats.

Communicated by F. Bulleri.

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Ophiopsila pantherina beds on subaqueous dunes off the Great Barrier Reef

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ABSTRACT: An autonomous underwater vehicle (AUV) was used to generate images of an *Ophiopsila pantherina* population on subaquous dunes at Hydrographers Passage, 200 km off the Australian mainland. High-resolution stereo images captured by the AUV were used to determine population structure of the aggregations, which consisted of adults at a mean density of 418 animals m^{-2} at depths of 65-70 m. *Ophiopsila pantherina* (8-15 mm dd) takes advantage of their elevated position on the lee side of the dunes for suspension feeding. On contact stimulation, the arms emit visible light as a bright green flash that travels down the arm. These aggregated ophiuroid communities in dune fields may be a specialized natural feature for consideration in managing common inter-reefal sandy habitats within the Great Barrier Reef Marine Park.