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The effects of temperature on the early life history of the rocky intertidal barnacle Tesseropora rosea

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THE EFFECTS OF TEMPERATURE ON THE EARLY LIFE HISTORY OF THE ROCKY INTERTIDAL BARNACLE *TESSEROPORA ROSEA*

A thesis submitted in fulfilment of the requirements for the award of the degree

DOCTOR OF PHILOSOPHY

From the

UNIVERSITY OF WOLLONGONG

By

Justin Adam Lathlean BMarScAdv (Hons)

SCHOOL OF BIOLOGICAL SCIENCES

2012

“Great are the works of the LORD;

they are pondered by all who delight in them.”

PSALM 111:2

Sunrise at Garie Beach, New South Wales, Australia (10 March 2011)

Certification

I, Justin A. Lathlean, declare that this thesis, submitted in partial fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Justin Adam Lathlean

23 April 2012

Publications

This thesis includes chapters that have been written as the following journal articles:

Chapter 2: Lathlean JA, Ayre DJ, Minchinton TE. (2010) Supply-side biogeography: geographic patterns of settlement and early mortality for a barnacle approaching its range limit. *Marine Ecology Progress Series*. 412: 141-150

Chapter 3: Lathlean JA, Ayre DJ, Minchinton TE. (2011) Rocky intertidal temperature variability along the southeast coast of Australia: comparing data from in situ loggers, satellite-derived SST and terrestrial weather stations. *Marine Ecology Progress Series* 439**:** 83-95

Chapter 4: Lathlean JA, Minchinton TE. Manipulating thermal stress on rocky shores to predict patterns of recruitment of marine invertebrates under a changing climate. *Marine Ecology Progress Series.* Submitted for publication on 2 February 2012.

Chapter 5: Lathlean JA, Ayre DJ, Minchinton TE. Using infrared imagery to test for quadrat-level temperature variation and effects on the early life history of a rocky shore barnacle. *Limnology and Oceanography*. Submitted for publication on 9 January 2012.

As the primary supervisor, I, Associate Professor Todd E. Minchinton, declare that the greater part of the work in each article listed is attributed to the candidate, Justin Adam Lathlean. In each of the above manuscripts, Justin contributed to the study design and was primarily responsible for data collection, data analysis and data interpretation. The first draft of each manuscript was written by the candidate and Justin was then responsible for responding to the editing suggestions of his co-authors. The co-authors, Associate Professor Todd Minchinton and Professor David Ayre, were responsible for assisting in study design, interpreting data and editing all the manuscripts. Justin has been solely responsible for submitting each manuscript for publication to the relevant journals, and he has been in charge of responding to reviewers' comments, with assistance from his co-authors.

Justin Adam Lathlean	Associate Professor Todd E. Minchinton
Candidate	Principal Supervisor
23 April 2012	23 April 2012

Conferences

I have also orally presented data from this thesis at the following national and international conferences:

Lathlean JA, Ayre DJ, Minchinton TE. (2011) Novel use of infrared technology to test the effect of small scale temperature variability on early life history processes of an intertidal barnacle**. Australian Marine Science Association Annual Conference, Perth, Western Australia.**

Lathlean JA, Ayre DJ, Minchinton TE. (2010) Thermal consequences of free-space for settling larvae of the intertidal barnacle *Tesseropora rosea.* **9th International Larval Symposium, Wellington, New Zealand.**

Lathlean JA, Ayre DJ, Minchinton TE. (2010) Thermal consequences of free-space for settling larvae of the intertidal barnacle *Tesseropora rosea.* **Australian Marine Science Association Annual Conference, Wollongong, New South Wales.**

Lathlean JA, Ayre DJ, Minchinton TE. (2009) Do geographic patterns of settlement and early mortality explain adult abundance for a marine invertebrate approaching its geographic range limit? **8th International Temperate Reef Symposium, Adelaide, South Australia.**

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

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There is perhaps no other person who deserves greater recognition than my wife Elizabeth, who has been on this journey with me from the beginning. Meeting for the first time in January 2008, as I was commencing my PhD, she has always had to put up with my strange love affair with barnacles. Elizabeth has sacrificed so much on account of my PhD and there is not enough gratitude in the world for me to convey how much I appreciate all that she has done. If it weren't for her, I would not have finished this thesis. I would like to take this opportunity to formally thank Elizabeth for her sacrificial love and enduring support, even though at times it seemed I loved my PhD more than her.

And finally, this opportunity would not have been possible if God had not given it to me in the first place. Looking back over the past four years, I believe God has been incredibly gracious, generous and patient with me. I would, therefore, like to dedicate this thesis to God – the ultimate biologist.

Abstract

The rocky intertidal zone represents the interface between the marine and terrestrial environment and is considered one of the most thermally complex ecosystems on earth. Biologists have long understood that life within the intertidal zone is considerably influenced by a steep thermal gradient produced by the rising and falling tide. In recent years, however, studies have discovered that numerous small-scale processes, other than elevation in tidal height, can produce mosaic patterns of thermal stress along rocky intertidal shores. Linking this local temperature variability to the physiological and demographic patterns of intertidal invertebrates is an essential first step to understanding how climate change might be expected to influence these communities.

The early life history stages of many rocky intertidal invertebrates are particularly vulnerable to heat and desiccation stress and play a key role in structuring adult populations. Therefore, temperature variability may considerably influence important demographic processes within intertidal populations. Nevertheless, temperature measurements are often taken at large spatial scales (10 to 1000m^2) while early life history processes are typically measured at much smaller scales, such as at the quadrat-level (10 to100cm^2). Processes that operate at these different spatial scales may produce different patterns of temperature variability and consequently limit our ability to relate an organism’s physiological response to its environment and ultimately the demography of the population.

Differences between body temperatures of sessile rocky intertidal invertebrates distributed across local spatial scales (<1 to 100m) may be substantially influenced by the density and species composition of the surrounding biotic community. By contrast,

differences between body temperatures of sessile rocky intertidal invertebrates distributed across large spatial scales (100 to 1000km) most likely reflect geographical variation in temperature. Yet, the characteristics of biotic communities have been shown to vary across both regional and large spatial scales. Thus, local-scale differences in the biotic community may counteract or negate temperature variability caused by larger-scale processes. Such might be the case along the south east coast of Australia where densities of dominant space occupiers vary with latitude.

My thesis aimed to examine how large- and small-scale temperature variability influences the early life history processes of the habitat forming rocky intertidal barnacle *Tesseropora rosea* and to characterise the thermal environment at a range of scales. For the large-scale aspect of this study I investigated whether early life history processes could explain the decline in adult abundances along a latitudinal temperature gradient. I then assessed the common use of satellites and terrestrial weather stations as proxies of *in situ* rocky intertidal water and air temperatures, respectively. This was in order to determine the most appropriate method for measuring rocky intertidal temperature variability. Due to the high variability detected by loggers within a single shore, I next used infrared (IR) imagery to characterise fine-scale temperature variability relevant to recently settled larvae. By undertaking a series of manipulative experiments I investigated how this fine-scale temperature variability influences the settlement and early post-settlement growth and survival of *T. rosea.*

The large-scale component of this study initially revealed that abundances of adult *T. rosea* decline with increasing latitude, suggesting that important demographic processes, such as settlement and early mortality (i.e. recruitment), may be particularly vulnerable to changes in sea surface temperatures. However, sampling across 11 rocky shores spanning 450km over a two year period did not reveal any latitudinal gradients in

either the production, settlement or early post-settlement mortality of larvae even though *in situ* temperature measurements confirmed the existence of a latitudinal temperature gradient. Indeed, settlement and adult mortality were highly variable among locations and the original decline in adult abundance observed during February 2007 was no longer present in December 2008. These results indicate that local variation in early life-history processes and adult mortality dictate regional variability and observed latitudinal patterns of adult *T. rosea* abundance. Such local variation in early life-history processes and adult mortality may reflect high temperature variability at these local-scales. Therefore, local temperature variability may be an important factor governing biogeographic patterns of abundance.

Large-scale settlement and recruitment studies commonly use remote sensing to characterise the thermal environment of recently settled larvae. The use of these temperature measurements have yet to be validated as useful surrogates of *in situ* temperature variability. Although I found that daily and monthly average temperatures derived from satellites and terrestrial weather stations were significantly correlated, the temperatures reported were considerably different from temperatures derived from *in situ* data loggers. Daily satellite sea surface temperatures (SSTs) were up to 6.7°C, and on average 1°C, higher than *in situ* water temperatures, while daily maximum air temperatures measured by weather stations were up to 23.2°C, and on average 4.2°C, lower than *in situ* air temperatures over a 14-month period. The frequency, duration and number of days greater than 30°C, as well as rates of temperature change, were all significantly lower when measured by weather stations. These differences suggest that satellite SSTs and weather stations are ineffective at capturing extremes in intertidal water and air temperature variability, which considerably influence biological processes. Therefore, to understand the impacts of temperature variability on

populations at scales relevant to demographic processes we need to use emerging data logger and infrared technology.

Despite the fact that experimental manipulations are essential for determining causation, there are few studies that successfully manipulate temperatures on rocky intertidal shores to test for effects on early life history processes. I used different coloured settlement plates deployed within the mid shore region to experimentally alter the substratum temperatures experienced by newly settled *T. rosea* larvae. I found that maximum mean surface temperatures of black and grey plates were 5.8°C and 4.8°C warmer than white plates, respectively. Black and grey plates over the entire sampling period were on average 2.2°C and 1.6°C warmer than white plates, respectively. Importantly, cooler white plates had significantly greater settlement and early post-settlement growth of *T. rosea* than warmer black plates. However, temperature differences between black and white plates did not influence early survival and recruitment.

Substratum temperatures of unmodified areas within mid intertidal regions increased with increasing free space ($r^2=0.75$, $p<0.01$, $n=35$). This variability in free space was predominantly the result of variable densities of adult *T. rosea*. Therefore, I undertook a manipulative thermal experiment that altered mid intertidal rock temperatures (which considerably influence body temperatures of recently settled *T. rosea*) by manipulating the amount of free space, a limiting resource for benthic invertebrates. Quadrats with <25% free space were on average 4.6°C cooler than equivalent quadrats with 100% free space. However, unlike the previous manipulative experiment where substratum temperatures were manipulated using artificial plates, I did not detect a significant effect of this thermal manipulation on the settlement and

early post-settlement growth and survival of *T. rosea*. Here, I found that natural temperature variability between quadrats with 100% free space (i.e. across areas that were unmanipulated) significantly influenced the early post-settlement growth and survival of *T. rosea*. Such among-quadrat variation at the same tidal height on shore is both underappreciated and a potentially confounding factor in studies of recruitment and population dynamics.

Finally, I used IR imagery to test the hypothesis that *in situ* rocky substrates exhibit repeatable ultra fine-scale (1mm) temperature variation during aerial exposure and that this variability significantly influences early life history processes of *T. rosea*. Here, larval settlement did not vary with ultra fine-scale variation in rock temperature, but early post-settlement growth and survival were both inversely related to temperature variability at this scale. Furthermore, I found that rock temperatures decreased significantly with increasing proximity to adult *T. rosea* and that larvae that settled within 15mm of adults survived better than those that settled within 16-30mm. This is partially explained by conspecific adults shading rock and reducing rock temperatures. These results demonstrate, for the first time, that fine-scale variation in thermal stress impacts the early-life history stages of a benthic marine invertebrate.

The results of my research have broad ranging implications for understanding how rocky intertidal invertebrates will respond to increasing temperatures and extreme events associated with climate change. Firstly, the geographic distribution of *T. rosea* does not appear to be limited by a reduction in air and seawater temperatures towards its southern range limit and therefore increasing temperatures may not cause *T. rosea* to extend its southern distribution. Secondly, broad-scale temperature measurements derived from weather stations and satellites are not the most appropriate estimates of rocky intertidal temperature variability. Therefore, climate change models and

predictions should preferentially use local-scale, or better yet, estimates of temperature variability relevant to individuals. Thirdly, the thermal manipulations developed in this study may be particularly useful for simulating the effects of future temperature variability or extreme temperature events on intertidal communities because they can directly elevate body temperatures to reflect future scenarios and do not require long-term monitoring or extreme weather to simulate extreme events. Finally, the high within site temperature variability revealed by IR imaging may override the effect of large-scale temperature variability on intertidal populations and reduce our ability to predict the effects of climate change on species distributions.

In summary, numerous factors need to be considered when assessing the effect of temperature on the early life history processes of intertidal invertebrates, including consistent small-scale temperature variability. The results of this study show that for a single species, the effects of temperature not only vary during different life history stages, but also, across different spatial scales. These findings contribute to, and advance, the growing body of work that highlights the importance of small-scale temperature variability in influencing the biogeographic and physiological responses of rocky intertidal communities in the face of climate change.

List of tables

List of figures

CHAPTER 1: General Introduction

1.1 Climate change and rocky intertidal communities

The increase in greenhouse gas emissions over the past century has and will continue to change the earth's climate (IPCC 2007). Consequently, predicting how biological communities will respond to climate change has become an important environmental issue. There is mounting evidence that these climatic changes are already having dramatic impacts on ecosystems via shifts in species' range limits (Parmesan 1996, Thomas et al. 2001, Walther et al. 2002, Thomas et al. 2006), increased non-indigenous species invasions (Parmesan 2003), changes in species interactions (Poloczanska et al. 2008) and increased rates of species extinction (Thomas et al. 2004, Keith et al. 2008).

Rocky intertidal shores, and their associated biological communities, have emerged as excellent study systems to assess, monitor and predict biological responses to climate change. Firstly, the long history of scientific investigation of rocky intertidal shores not only provides a strong foundation for understanding biological processes operating across various scales and locations, but also allows us to compare contemporary and historic biogeographic distributions and relate changes to past and present climatic variability (see Sagarin et al. 1999, Mieszkowska et al. 2006, 2007, Poloczanska et al. 2008, Herbert et al. 2009, Pitt et al. 2010, Poloczanska et al. 2011). Secondly, unlike most species, rocky intertidal invertebrates have limited vertical distributions as they are restricted to the interface between the marine and terrestrial environment. Therefore, the adult life history stage of rocky intertidal invertebrates essentially have two-dimensional distributions that are ideally suited for testing predictions related to latitudinal temperature gradients (Sagarin & Gaines 2002a).

Thirdly, the heterogeneous topography of many rocky intertidal shores produces dramatic temperature variability during aerial exposure at low tide (Denny et al. 2011), and provides an effective means of examining relationships between abiotic stresses, biotic interactions and ecological patterns in nature (Connell 1972, Bertness et al. 1999a). Finally, intertidal invertebrates often live at, or close to, the upper limit of their thermal tolerance, and therefore may be particularly vulnerable to future increases in temperature (Somero 2002, 2010). Numerous studies have already documented shifts in the latitudinal distributions of several intertidal invertebrates (Sagarin et al. 1999, Herbert et al. 2003, Herbert et al. 2007, Herbert et al. 2009, Pitt et al. 2010) and algae (Lima et al. 2007, Harley & Paine 2009) due to such factors.

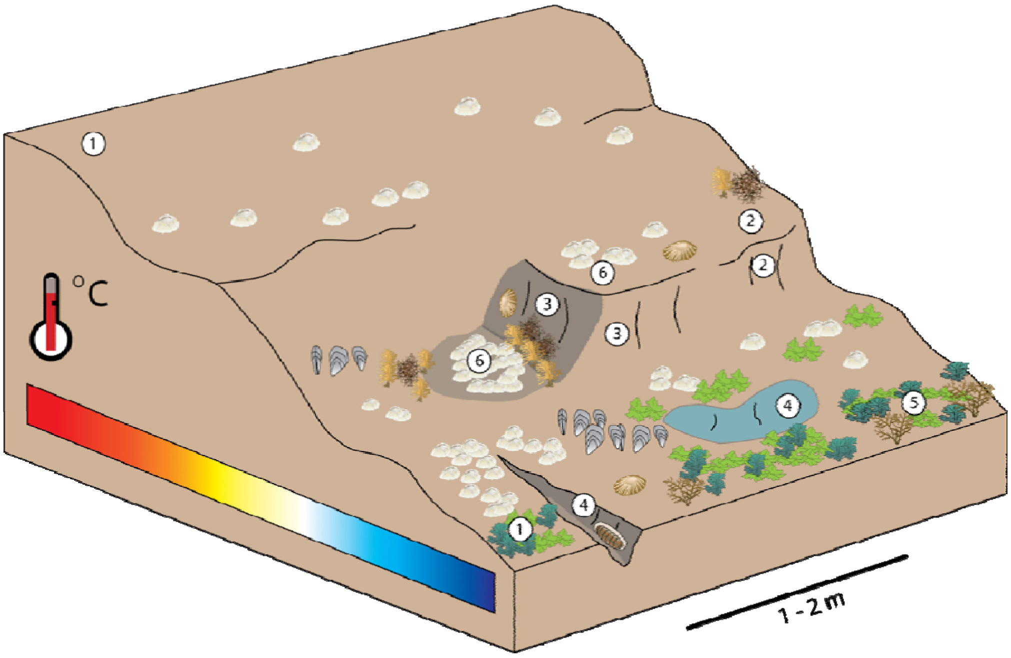
1.2 Rocky intertidal temperature variability across multiple scales

Before predictions can be made about the effects of climate change on intertidal populations from local to biogeographic scales, including changes to their distributional ranges, we must first understand how temperature influences species across multiple spatial scales. Rocky intertidal communities, and the processes affecting them, are usually categorised into local (<1 to 100m), regional (10 to 100km) and large or biogeographic (100 to >1000km) spatial scales (Broitman et al. 2001). Temperature variability is also generally categorised into these three distinct spatial scales. The majority of research to date has largely focussed on addressing processes affecting rocky shore temperature variability at local-scales (Helmuth et al. 2006b). This means much less attention has been given to larger regional and biogeographic variability. For example, temperatures at local spatial scales have been shown to vary in response to the strength and timing of the tidal cycle (Denny & Paine 1998, Harley 2008, Mislan et al. 2009), distance from shoreline or height on shore (Davenport & Davenport 2005, Denny et al. 2006), landscape topographic complexity, which includes differences in the substrate heterogeneity (O'Donnell & Denny 2008, Jackson 2010, Meager et al. 2011), aspect (Helmuth 1998, Miller et al. 2009) and orientation (Denny et al. 2006, Harley 2008, Seabra et al. 2011), and biotic factors such as adult density (Helmuth 1998, Denny et al. 2011) and community composition (Bertness & Leonard 1997, Bertness et al. 1999a) (Fig. 1.1a). In contrast, temperature variation at regional and large spatial scales has been attributed to oceanographic processes such as upwelling (Blanchette et al. 2007), wave exposure (Harley & Helmuth 2003) weather (Helmuth et al. 2006b), climatic perturbations such as El Niño-Southern Oscillation (ENSO) (Menge et al. 2011) and latitude (Helmuth et al. 2002) (Fig. 1b).

Instruments used to capture temperature variability could vary depending on the scale of interest. Local-scale *in situ* temperature variability has typically been measured through the use of thermocouples, infrared thermometers and temperature data loggers. Large-scale temperature variability has typically been measured using weather stations, oceanographic buoys and satellites (Fig. 1.1b). With recent advances in infrared technology and data logger design, techniques for measuring *in situ* temperatures on rocky intertidal shores and the body temperatures of invertebrates are becoming increasingly sophisticated, allowing us to test novel hypotheses.

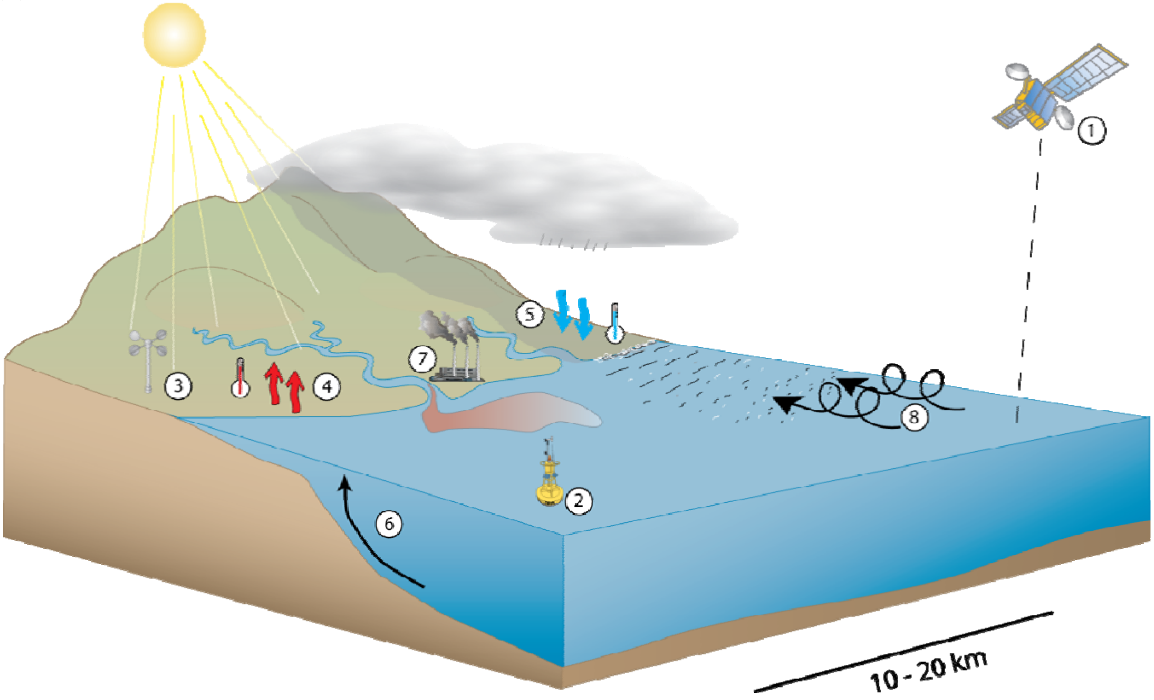
The major objective of measuring temperature across spatial hierarchies is to understand how physical processes, such as rising atmospheric temperatures and extreme temperature events, alter individual physiological processes that translate into long term shifts in the state of populations and communities (Helmuth et al. 2005, Denny & Helmuth 2009, Helmuth 2009, Helmuth et al. 2010). Assessing how

(a)



Sources of local temperature variability - 1. Intertidal height (high vs. low); **2.** Substrate aspect (vertical vs. horizontal); **3.** Substrate orientation (east vs. south); **4.** Surface heterogeneity (crevices, rock pools etc.); **5.** Proximity to macroalgae; **6.** Density of conspecifics

(b)



Instruments used for measuring temperature - 1. Satellite; **2.** Oceanographic buoy; **3.** Terrestrial weather station; **Sources of regional temperature variability 4.** High UV exposure; **5.** Low UV exposure; **6.** Oceanographic upwelling; **7**. Power station outfall; **8**. Wave exposure.

Figure 1.1 Conceptual diagrams illustrating the sources of temperature variability at (a) local and (b) regional spatial scales and the instruments commonly used to measure this temperature variability.

temperature variability influences biotic processes is essential since local factors might override regional- or large-scale temperature variability, or vice versa. At the level of the organism, studies have found that due to differences in size, colour, morphology and material properties, both within and between species, organisms subjected to similar environmental conditions may display significantly different body temperatures (Broitman et al. 2009). For example, body temperatures of the mussel *Mytilus californianus* and its dominant predator, the seastar *Pisaster ochraceus*, differed significantly even though both species occupied identical habitats (Broitman et al. 2009). Similarly, body temperatures of smaller individuals of *M. californianus* have been shown to be 5°C warmer than larger individuals exposed to identical conditions in the field (Helmuth 2002). Therefore we might expect that the impact of climate change on rocky intertidal communities to be largely species-specific, with some species being more vulnerable than others (Somero 2010).

1.3 Early life history processes and thermal stress

Due to their small size, newly settled individuals and recruits of sessile marine invertebrates are particularly vulnerable to heat and desiccation stress (Gosselin & Chia 1995, Gosselin 1997, Gosselin & Qian 1997, Hunt & Scheibling 1997). This is important because the supply of new individuals significantly contributes to the size and distribution of adult populations (Connell 1985, Gaines & Roughgarden 1985, Menge 1991, Minchinton & Scheibling 1991, Gaines & Bertness 1992, Caley et al. 1996, Menge 2000). Consequently, thermal stress during these early life history stages may disproportionately affect rocky intertidal organisms relative to thermal stress during other less susceptible life history stages.

Numerous studies have successfully demonstrated the effects of local, regional and biogeographic temperature variability on the early life history stages of rocky intertidal invertebrates. I will now briefly summarise their major findings before identifying potential limitations and areas for investigation.

1.3.1 Local-scale variability

Numerous studies have successfully demonstrated that local-scale temperature variability affects the early life history processes of intertidal invertebrates. This may be because the high spatial and temporal temperature variability commonly found within the rocky intertidal zone produces more obvious effects than other less variable habitats. Studies investigating the early post-settlement survival and recruitment of the intertidal barnacle *Semibalanus balanoides* within New England, USA have been particularly informative in demonstrating the effects of local temperature variability on the early post-settlement life-history stages (Bertness 1989, Bertness & Leonard 1997, Bertness et al. 1999a, Bertness et al. 1999b, Gedan et al. 2011). In general, these studies found that survival of recently metamorphosed *S. balanoides* was greater (i) within cooler low intertidal regions relative to warmer high intertidal regions (Bertness 1989, Bertness et al. 1999a), (ii) on boulders compared to smaller cobbles, as cobbles reach higher substrate temperatures (Bertness 1989, Gedan et al. 2011), (iii) with greater intraspecific crowding, which buffers thermal stress (Bertness 1989), and (iv) under experimental shade plots and higher macroalgae canopy cover, which reduce temperatures by 5 to 10°C (Bertness 1989, Gedan et al. 2011). Bertness et al. (1999a) also demonstrated that the early post-settlement survival of *S. balanoides* varies at regional-scales as shading and intraspecific crowding had no effect on *S. balanoides* survival within cooler sites north of Cape Cod, compared to the significant effects found within warmer sites south of Cape Cod. Early post-settlement survival of *Balanus glandula* populations within

Oregon, USA, was also shown to be influenced by local-scale temperature variability. Shanks (2009) found that survival of recently metamorphosed individuals was significantly greater on cooler ceramic tiles than warmer plexiglas settlement plates. Our capacity to apply these findings to all rocky shores may be limited, however, because they have mostly been undertaken within the northern hemisphere.

1.3.2 Regional-scale variability

Over the past decade there has been a considerable increase in the number of studies assessing regional- or meso-scale settlement and recruitment variability of rocky intertidal invertebrates (Broitman et al. 2005a, Lagos et al. 2005b, Blanchette & Gaines 2007, Menge et al. 2009, Hidas et al. 2010, Lathlean et al. 2010, Menge et al. 2011). Studies undertaken along the Pacific coasts of northern, central and southern America suggest that the settlement and recruitment of mussels and barnacles vary in response to regional-scale oceanographic processes, such as sea surface temperature (SST) variability caused by regional upwelling. For example, Broitman et al. (2005) found that barnacle and mussel recruitment was lower on the western side of Santa Cruz Island, California, and higher on the eastern side where SST was 1 to 1.5°C warmer due to less persistent upwelling. In contrast, within the same biogeographic region, Blanchette & Gaines (2007) found no difference in the recruitment of the mussel *Mytilus californianus* on either side of Point Conception, California, even though water temperatures in southern locations were significantly warmer. Further south, within central Chile, the settlement and recruitment of chthamaloid barnacles along 120km of coastline has been shown to vary significantly with meso-scale SST (Lagos et al. 2005). More recently, studies on *M. californianus* populations along 320km of the Oregon coastline, USA, indicate that the regional effects of relatively short-lived upwelling and

SST variability may be superseded by larger climatic scale processes such as the El Niño-Southern Oscillation (ENSO) or North Pacific Gyre Oscillation (NPGO) (Menge et al. 2011). Therefore, regional temperature variability needs to be considered in the context of large-scale processes which will obviously depend on the specific biogeographic region.

1.3.3 Large-scale variability

Large-scale settlement and recruitment studies encompassing numerous locations separated by 100s to 1000s of kilometres usually require extensive investment from several collaborating institutions. Although efforts to undertake such large-scale studies have intensified in recent years (see Broitman et al. 2008a, 2008b, Navarrete et al. 2008), studies of this nature remain considerably rare. To date, Broitman et al. (2008a) represents the most extensive study that directly investigates the effects of large-scale temperature variability on the recruitment of intertidal invertebrates. Broitman et al. (2008a) monitored monthly recruitment rates of mussels and barnacles at 26 rocky shore sites along the West Coast of USA (1750km) and made comparisons with monthly SST values. Patterns of recruitment were highly structured, displaying three distinct biogeographic regions with abrupt transitions around Cape Blanco (42.8°N) and Point Conception (34.6°N). Recruitment was also positively correlated with monthly SST for all species with recruitment of the barnacle *Balanus glandula* and mussels (*Mytilus* spp.) being significantly lower south of Oregon, USA (≈42°N). Other studies have also been carried out at similar spatial scales, though they do not specifically test hypotheses relating to temperature variability. Navarrete et al. (2008) made inter-hemispheric comparisons between sites spanning >900km along the coasts of Oregon-northern California (39.4° to 45.5°N) and central Chile (29.5° to 34.6°S) and found that rates of barnacle and mussel recruitment were two to three orders of magnitude higher within Oregon and northern California than within central Chile. Similarly, Connolly et al. (2001) detected a latitudinal gradient in barnacle and mussel recruitment along 17 sites within northern Oregon to central California (35.5° to 46.5°N).

1.3.4 Potential limitations of previous research

Previous research clearly shows that local-, regional- and large-scale temperature variability are important determinants of early life history processes for rocky intertidal invertebrates. They also reveal a bias towards northern hemisphere species and a limited number of studies that incorporate multiple scales. This may be important as recent studies suggest that local-scale temperature variability may be as great as, if not greater, than regional- or large-scale temperature variability (e.g. Denny et al. 2011, Seabra et al. 2011). My review of past studies investigating the effects of temperature on rocky intertidal invertebrates also reveals that temperature measurements are generally taken at much larger spatial scales than estimates of early life history processes. For example, satellite derived SSTs have commonly been used as proxies of temperature variability on rocky intertidal shores. Not only are satellite derived SST measurements taken at a spatial resolution of 1 to 2km^2 they also do not measure important air temperature variability that occurs during low tide. The accuracy of satellite SST and other remote sensing instruments, such as weather stations and oceanographic buoys, have yet to be empirically tested for rocky intertidal habitats (but see Smale et al. 2009).

The common use of biomimetic loggers (i.e. modified data loggers designed to mimic the shape and colour of adult invertebrates) (e.g. Helmuth 2002, Broitman et al. 2009, Szathmary et al. 2009) for measuring local-scale temperature variability is also unlikely to capture physiological relevant body temperatures of recently settled and metamorphosed juveniles as their body temperatures most likely reflect the temperature of the underlying substrate. However, few studies have either documented consistent fine-scale substratum temperature variability on rocky intertidal shores or any effects of such fine-scale temperature variability on recently settled larvae. Such information would significantly contribute to our ability to investigate the effects of heat and desiccation stress on the critical early post-settlement life history stages of benthic invertebrates.

1.4 Biotic factors and effects on local temperature variability

Biotic factors may play an important role in ameliorating heat and desiccation stress for juvenile intertidal invertebrates (see Bertness 1989, Bertness et al. 1999a). Such biotic factors include the density of conspecifics and the proximity to macroalgae or other species that produce shade or reduce evaporative water loss (Bertness & Leonard 1997). However, apart from work carried out by Bertness and others in New England, USA, there have been very few investigations into how such biotic variation influences early life history stages of rocky intertidal invertebrates.

Temperature variability caused by biotic factors, such as the percentage of unoccupied space, may be particularly important for understanding how small-scale temperature variability influences larger biogeographic temperature variability. This is because both biotic and abiotic factors vary across large spatial scales yet previous studies have typically only addressed the latter. The southeast coast of Australia represents one such region as previous research has shown that adult densities of the

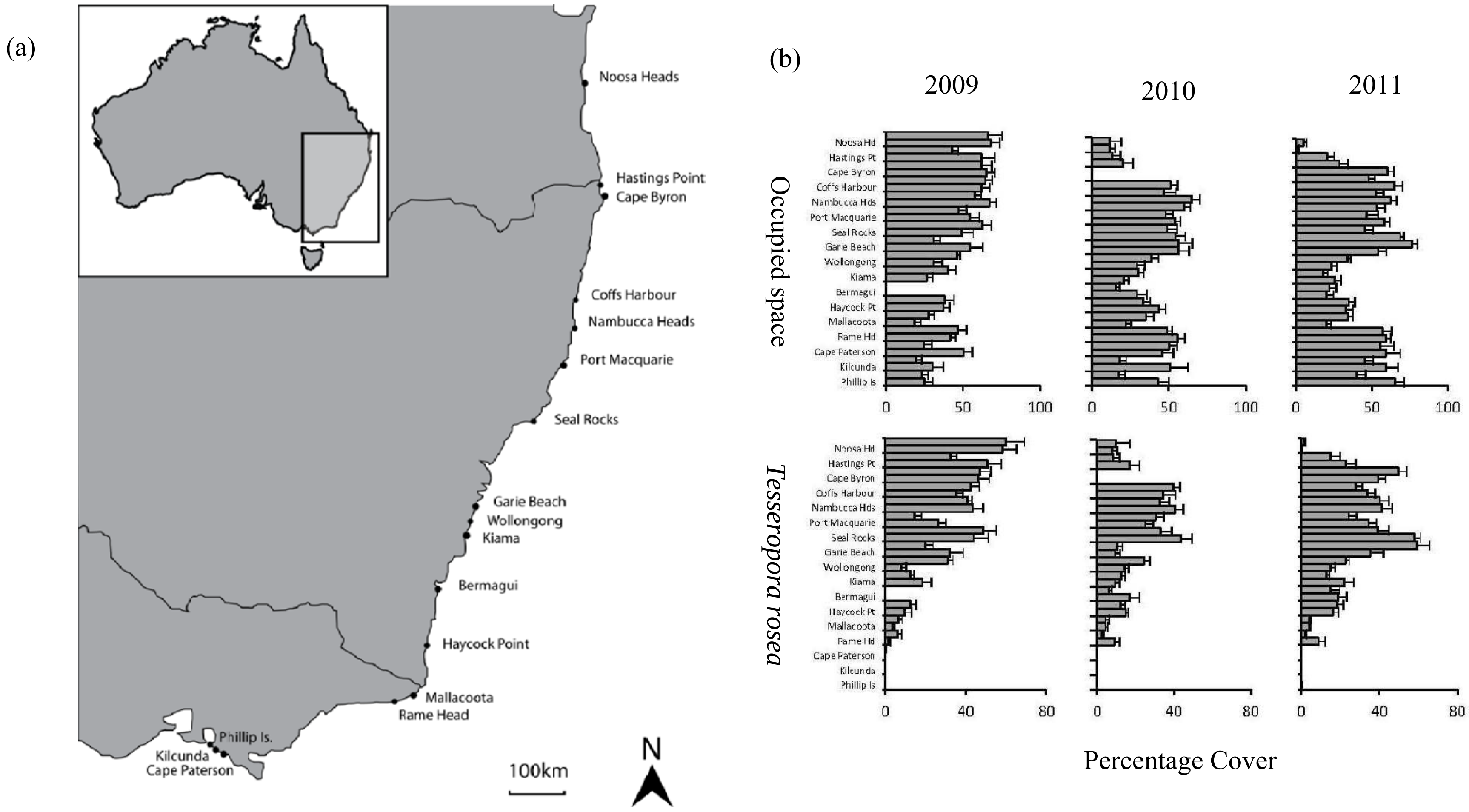


Figure 1.2. (a) (a) Map of south eastern Australia and 17 study locations; (b) Mean percentage cover (±SE) of all sessile invertebrates (occupied space) and *T. rosea* within two sites at each of the 17 locations along the south east coast of Australia across three consecutive years (Source: JA Lathlean, unpublished data)

dominant intertidal barnacle *Tesseropora rosea* decline with increasing latitudes (Hidas et al. 2010). Consequently, this latitudinal decline in densities of adult *T. rosea* significantly influences the availability of free space (see Fig. 1.2), which is a limiting resource for settling larvae (Gaines & Roughgarden 1985; Minchinton & Scheibling 1993). Such geographic variability in free space may have important consequences for large-scale patterns of larval settlement and recruitment especially if, at small spatial scales, substratum temperatures differ depending on the amount of free space. For example, if free space increases with latitude then latitude may be a poor predictor of large-scale temperature variability. However, such a relationship between the availability of free space and substratum temperatures has yet to be empirically tested.

1.5 Southeast Australian rocky intertidal communities and climate change

Marine communities within temperate regions of southern Australia are identified as being particularly vulnerable to climate change (Lough 2009, Ridgway & Hill 2009) as the Tasman Sea is warming at a rate of 2.28°C per century, which is more than three times faster than the global average (0.6±0.2 per century) (Cai et al. 2005, Ridgway 2007). Such a dramatic rise in sea surface temperature has been linked to the strengthening and increased penetration of the East Australian Current further south (Cai et al. 2005, Ridgway 2007). Recent studies have demonstrated southern range expansions for several intertidal and subtidal invertebrates (Ling et al. 2009, Pitt et al. 2010, Poloczanska et al. 2011) and coastal fish (Stuart-Smith et al. 2010, Johnson et al. 2011). For example, Pitt et al. (2010) resurveyed rocky intertidal communities along the east coast of Tasmania (40.5° to 43.5°S) from studies undertaken in the 1950s and found that the southern range limits of 15 species had shifted an average 116km further south (see Sagarin et al. 1999 for an equivalent northern hemisphere example). They found that gastropods were most affected by recent warming as six of eight species moved an average distance of 142km south. Barnacles were also affected since four of five species moved an average distance of 90km further south with an additional species, *Austromegabalanus nigrescens*, which was absent in the 1950s, being found almost along the full extent of the east Tasmanian coastline. In comparison, Poloczanska et al. (2011) resurveyed rocky intertidal communities along the east coast of southern Queensland and northern New South Wales (23° to 35°S) and found that 10 of 37 species had experienced range shifts since the 1940s/50s but only six of these shifts were consistent with expectations under climate change. Here, two temperate species retracted their northern range limits and four tropical species extended their southern range limits.

Changes in distributions represent just one type of response to climate change. Changes in abundance, physiology and phenology within single populations may also represent responses of biological communities to climate change (Walther et al. 2002). Moreover, biological changes in response to warming may not be linear over time as extreme temperature events may have long lasting impacts that are equivalent to gradual changes over time (Denny et al. 2009, Harley & Paine 2009, Mislan et al. 2009, Wethey et al. 2011b). While historical comparisons have effectively demonstrated some climatic responses of rocky intertidal communities along the southeast coast of Australia, predicting how these communities will respond to future warming may not be as simple as tracking changes in mean sea surface temperatures and may require experimental evidence. Such investigations are particularly scarce for rocky intertidal communities along the east coast of Australia though they may yield important insights into how these communities will respond to the higher than average increases in temperature associated with climate change.

1.6 Study species

The barnacle *Tesseropora rosea* is the most abundant and maybe the most studied barnacle within temperate and sub-tropical rocky intertidal shores of eastern Australia (Denley & Underwood 1979, Underwood et al. 1983). *Tesseropora rosea* is considered to be a habitat-forming species which prominently inhabits sunny emergent rock within the midshore region on exposed rocky shores from Cannonvale in northern Queensland (20°16’S) to Mallacoota in Victoria (37°34’S) (Fig. 1.2a) (Bennett & Pope 1953, Endean et al. 1956, Denley & Underwood 1979, Caffey 1985, Hidas et al. 2010). Contemporary records of *T. rosea* within mid to northern Queensland are scarce however and recent surveys suggest that the northern range limit of *T. rosea* may have contracted further south (Poloczanska et al. 2011). Within northern and southern New South Wales *T. rosea* represents the dominant occupier of space within the exposed mid shore region (Fig. 1.2b) and provides habitat for several other abundant species (Creese 1982, Underwood et al. 1983). *Tesseropora rosea* also plays an important role in the food web being the preferred prey of the predatory whelk *Morula marginalba* (Underwood et al. 1983, Fairweather 1984). Adults are commonly found alongside the surf barnacle *Catomerus polymerus*, the limpets *Cellana tramoserica* and *Patelloida latistrigata* and above the lower midshore region dominated by the tubeworm *Galeolaria caespitosa* (Denley & Underwood 1979). Thus, processes affecting populations of *T. rosea* are likely to either directly or indirectly affect numerous other species within mid intertidal communities along the east coast of Australia (Fig. 1.2c).

Tesseropora rosea has a largely distinct breeding and settlement period, which is well suited to investigating factors affecting early life history processes. Adult *T. rosea* are hermaphroditic planktivores that release planktotrophic larvae predominantly from January to June with the larvae estimated to remain within the water column for

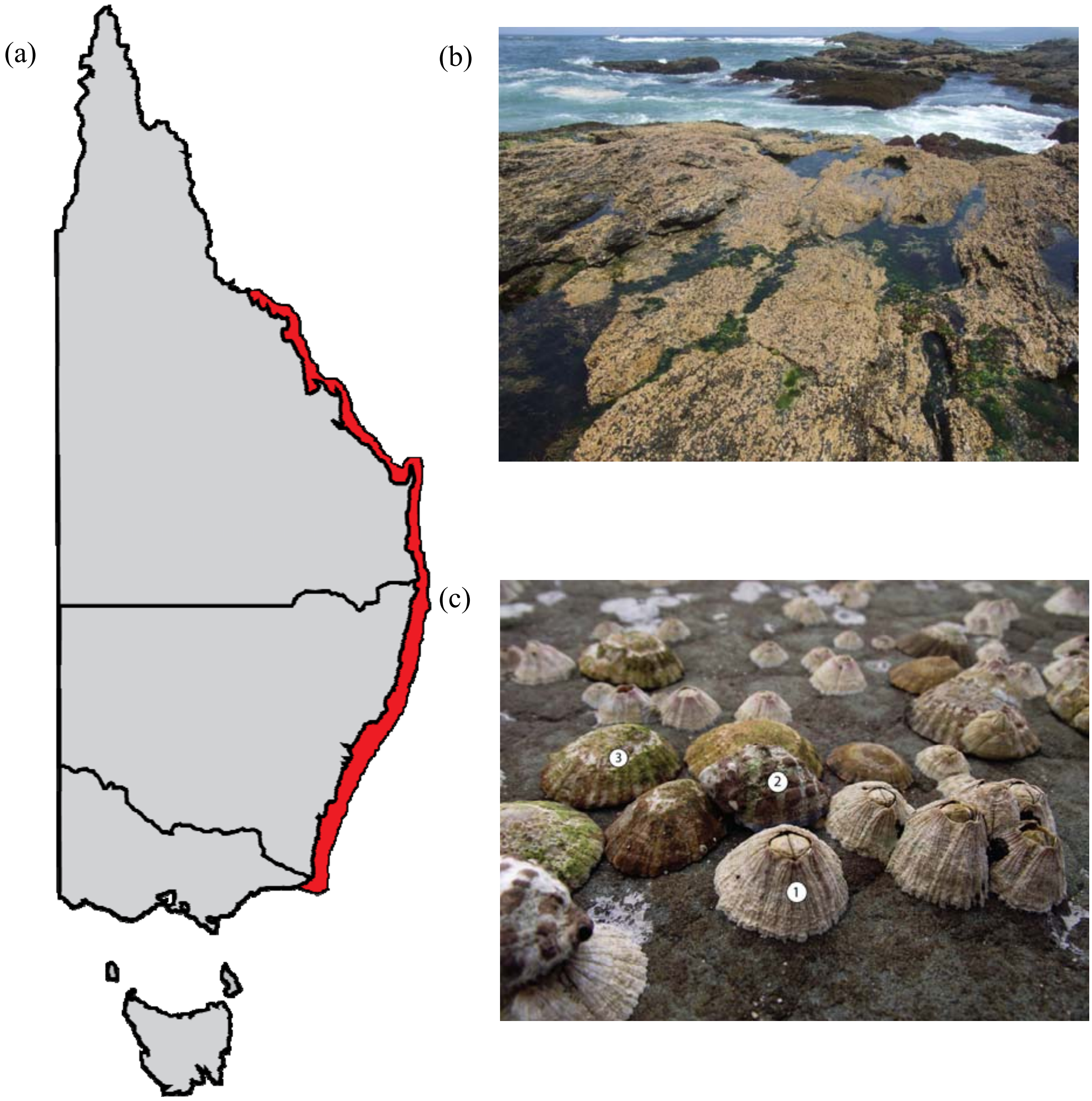


Figure 1.3. (a) Geographic distribution of *Tesseropora rosea* along the east coast of Australia; (b) rocky intertidal shore within central New South Wales dominated by *T. rosea*; (c) *T. rosea* (1) and two associated species – the predatory whelk *Morula marginalba* (2) and the limpet *Cellana tramoserica* (3).

approximately 13 days (Wisely & Blick 1964, Anderson & Buckle 1983, Egan & Anderson 1988). Although larval settlement may occur throughout the year, the vast majority settle between January and July with two peaks, one during January and February and then a second during May and June. The peak in January to February is generally more prominent at northern locations, and vice-versa for more southern locations (Caffey 1985).

Tesseropora rosea, therefore, represents an exemplary species to investigate how temperature affects early life history processes because (i) it is highly abundant and significantly influences mid-intertidal communities, (ii) has a predictable settlement period, and (iii) may be particularly vulnerable to changes in temperature within a region that is expected to experience dramatic increases in temperature due to climate change.

1.7 Thesis structure

The major objective of this study was to investigate how large- and small-scale temperature variability influences the early life history processes of a benthic marine invertebrate. I was initially interested in assessing whether reduced larval supply and recruitment within colder, southern populations could explain a latitudinal decline in the adult abundance of *T. rosea* towards its southern range limit. I then deployed *in situ* temperature data loggers within the mid shore region at several rocky intertidal shores to characterise large-scale temperature variability along the southeast coast of Australia. Since many rocky intertidal studies use satellite SST and weather station temperature data as estimates of intertidal temperature variability, I compared temperature data from *in situ* data loggers with satellites and weather stations to assess their effectiveness of capturing biological relevant temperature variability. I then began to focus on small-and fine-scale temperature variability and how this influences the settlement and early post-settlement processes of *T. rosea*. Infrared imaging of the mid rocky intertidal region revealed that temperatures of settlement plates varied depending on their colour and that rock temperatures varied depending on the availability of free space. Through these observations I developed a series of experiments that were aimed at investigating the effects of fine-scale temperature variability on recently settled *T. rosea* larvae.

Using the intertidal barnacle *T. rosea* as a model species, the specific aims of this thesis were to:

1. Test whether latitudinal gradients in several early life history processes of *T. rosea* are consistent with large-scale temperature variability, and the hypothesis that unfavourable temperatures might set species range limits (Chapter 2);
2. Determine the extent to which nearshore SSTs derived from satellites, and air temperatures derived from terrestrial weather stations, can be used as appropriate surrogates of rocky intertidal water and air temperatures, respectively (Chapter 3);
3. Develop a method for directly manipulating rocky intertidal substrate temperatures and test for effects of temperature on the early post-settlement processes of *T. rosea* (Chapter 4); and
4. Use infrared technology to measure rocky intertidal temperature variability at fine- (cm) and ultra-fine (mm) spatial scales and test for effects on the early post-settlement processes of *T. rosea* (Chapters 5 and 6).

Consequently, this study evaluates some of the current methodologies used for measuring large (Chapter 3) and local-scale (Chapters 4 and 5) rocky intertidal temperature variability and their ability in detecting effects on early life history processes of benthic invertebrates. Evaluating different methodologies for measuring temperature was necessary due to the overwhelming evidence that body temperatures of intertidal invertebrates vary significantly at the individual level (Denny et al. 2011) and that the responses of rocky intertidal communities to climate change will ultimately depend on the physiological responses of individuals (Denny & Helmuth 2009, Helmuth 2009, Helmuth et al. 2010). For the first time, estimates of early life history processes are accompanied with appropriate larval scale estimates of temperature variability (Chapter 6). This was achieved through the novel use of infrared imagery and represents the first attempt to quantify temperature variability on rocky intertidal shores at spatial scales less than 10s of centimetres. Measuring such fine scale temperatures compliments the increasing number of studies focussed on characterising biogeographic scale temperature variability. The outcomes of such studies may consequently provide important insights into climate change predictions.

CHAPTER 2: Supply-side biogeography: geographic patterns of settlement and early mortality for a barnacle approaching its range limit

A modified version of this chapter is published in *Marine Ecology Progress Series**

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*Although this chapter was conceived and initiated as part of my honours thesis in 2007, sampling continued throughout 2008 with the majority of analyses and manuscript preparations being undertaken during 2009 and 2010 as part of my PhD thesis. Other chapters within this thesis have also been published or are under review. Each chapter has been edited to reduce the inevitable repetition that this can create.

2.1 Introduction

Biogeographic theory predicts that the abundance of a species is generally greatest at the centre of its range and least at its edges (Brown 1984, Caughley et al. 1988, Sagarin & Gaines 2002a, 2002b). This 'abundant centre' hypothesis has been supported for many species of terrestrial plants, with adult abundance declining towards their geographic range limits because physiological stress reduces reproductive output and survival (Pigott & Huntley 1981, Parsons 1991, Woodward 1997, Dorken & Eckert 2001, Jump & Woodward 2003, Mathews & Bonser 2005). As for terrestrial plants, many benthic marine invertebrates have sessile adults and dispersive propagules. Consequently, their geographic patterns of abundance might be expected to conform to abundant centre distributions as a result of decreased larval supply and increased early post-settlement mortality of larvae from the centres to the edges of their range (Zacherl et al. 2003, Bahn et al. 2006, Gilman 2006b, a, Sanford et al. 2006). Dispersal in the ocean and recruitment variability into the benthic habitat is potentially much greater for benthic invertebrates than for most plants. However, the relatively few studies to date indicate that geographic patterns of adult abundance for benthic marine invertebrates generally do not reflect abundant centre distributions (Sagarin & Gaines 2002a).

For many benthic marine invertebrates with sessile adults and dispersive larvae, recruitment is a key demographic process structuring adult populations (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Caley et al. 1996, Hunt & Scheibling 1997). Recruitment integrates the arrival, settlement and early post-settlement mortality of larvae (Thorson 1950, Keough & Downes 1982) and, although these supply-side processes are often highly variable in space and time (see Underwood & Fairweather 1989, Caley et al. 1996, Hunt & Scheibling 1997), they sometimes reflect latitudinal gradients of temperature, currents, wave exposure and nutrient availability in the ocean (Connolly & Roughgarden 1998, Connolly et al. 2001, Zacherl et al. 2003, Sanford et al. 2006). Consequently, the geographic distribution of benthic marine invertebrates, particularly as a species approaches its range limit, may be strongly influenced by latitudinal gradients in the supply and early life history of larvae. Alternatively, processes operating at more local-scales in the post-recruitment environment (e.g. storm events, habitat, microclimates, predation, extreme temperature events) could override larger-scale patterns of recruitment, that might determine geographic patterns of adult abundance (Helmuth 1998). Measuring settlement and early post-settlement mortality of benthic marine invertebrates is often difficult, however, because larvae are small and often die soon after settlement. Few studies have measured these early life-history processes simultaneously across large geographic scales (but see Caffey, 1985; Connolly *et al*., 2001; Hughes *et al*., 2002), but such studies can yield important insights into the processes setting the range limits of species.

Along the linear coastline of southeast Australia, there is great potential for the population size of sessile marine invertebrates with planktonically dispersing larvae to decline with increasing latitude. First, the unidirectional East Australian Current (EAC) runs north to south along the east coast of Australia and then weakens and deflects away from the coast at the southeast corner of the mainland (Knox 1963, Huyer et al. 1988, O'Hara & Poore 2000, Oke & Middleton 2001, Roughan & Middleton 2004). Second, seawater and air temperatures decline with the transition from subtropical to temperate regions with increasing latitude. Together, these latitudinal variations in oceanographic conditions and potential physiological stresses in the benthic habitat are predicted to reduce fecundity of adults, increase early post-settlement mortality of early juveniles and diminish reliability in the supply of larvae from northern to southern populations (Barber & Blake 1983, Brey 1995, Sanford et al. 2006). Indeed, due to the absence of small individuals in southern locations, Hidas et al. (2010) suggested that recruitment events are less frequent for the intertidal barnacle *Tesseropora rosea* towards its southern range limit.

Here I investigate whether a latitudinal gradient of recruitment drives adult population structure for the intertidal barnacle *Tesseropora rosea*, a species that disperses via planktonic larvae and with adult abundances indicative of an abundant centre distribution, with declines from the middle to the southern limit of its range at the southeast corner of mainland Australia (Hidas et al. 2010). The only study to have assessed large-scale patterns of settlement and early post-settlement mortality for *T. rosea* found no latitudinal trends in recruitment, but only populations within the middle of its geographic range were examined (Caffey, 1985). I measured fecundity of adults and settlement and early post-settlement mortality of larvae (i.e. recruitment) for a cohort of *T. rosea* on rocky intertidal shores spanning 450 km of coastline to determine how geographic variation in these demographic processes were related to the patterns of abundance of individuals within the cohort surviving to adulthood at the end of that year. I predicted that a combination of reduced larval production, settlement and increased early post-settlement mortality of larvae from north to south accounts for the latitudinal decline in the abundance of *T. rosea* adults as they approach their southern range limit. For two years I also monitored recruitment into and mortality of adult populations to determine how local or geographic variation in these processes might account for the latitudinal gradient in population size.

2.2 Methods

2.2.1 Study region and species

I monitored the production, settlement, and early post-settlement mortality of larvae and mortality of adults of the intertidal barnacle *Tesseropora rosea* from February 2007 to December 2008 in mid shore regions at two sites on 11 rocky shores along the southeast coast of Australia. Rocky shore locations extended from Garie Beach south of Sydney, New South Wales (34°09'S, 151°04'E), within the middle of the geographic range of *T. rosea*, to Mallacoota, Victoria (37°34'S, 149°45'E), at its southern range limit (Bennett & Pope 1953, Edgar 2008) (Fig. 2.1). Occasionally, individuals of *T. rosea* are found in central Victoria (Jones 1990), but they do not persist, probably due to colder environmental conditions. The rocky shores were selected to have the same rock type (sandstone), degree of wave exposure (moderate to exposed), slope (gradually sloping platforms) and aspect (facing east to southeast) to ensure abiotic conditions such as substratum, hydrodynamic processes and exposure to sunlight remained equivalent amongst locations. *In situ* data loggers (Onset TidbiT v2 Temp logger), recording air and water temperatures every 10min, were deployed within the mid-shore region at both Garie Beach and Mallacoota (i.e. the most northern and southern locations, respectively) and confirmed that a temperature gradient exists across the study region, with the maximum (air: 50.8°C; water: 26.4°C) and minimum (air: 5°C; water: 14.2°C) temperatures at Garie Beach being greater than the maximum (air: 42.3°C; water: 22.4°C) and minimum (air: 3.8°C; water: 12.3°C) temperatures at Mallacoota recorded continuously between December 2007 and December 2008.

I found that recently settled *T. rosea* grow quickly and become reproductively mature two to three months after settlement, with some individuals with aperture lengths as small as 1.5mm possessing either gonads or mature or developing embryos (but see Egan & Anderson 1988). Embryos are internally fertilised and brooded within the mantle cavity until they are ready to be released. Mature embryos are recognised as eyed nauplii (embryo stage V) (Anderson 1969). From my observations embryo development in the mantle cavity is relatively synchronised so that the majority of embryos reach maturity at approximately the same time. I therefore scored individuals as being mature if eyed nauplii were present in the mantle cavity, or developing if embryos were present but immature (stages II-IV) (Anderson, 1969; see further details below).

2.2.2 Sampling design and variables

At each rocky shore location, I established two sites that extended 30m alongshore and were separated by 10 to 30m. At each site, 30, 10cm × 10cm permanent quadrats were randomly located within the mid shore region characteristically dominated by *T. rosea* (0 to 1.6m above the mean low water mark of neap tides: MLWN). Quadrats were positioned on horizontal to slightly sloping surfaces and separated by 0.5m to 1m. A stainless steel screw was drilled into the centre of each quadrat to ensure that they could be accurately resampled over time.

Individual barnacles were tracked in these 30 quadrats over time using digital photographs taken with a high-resolution digital camera (Fujifilm S9600), and comparisons of *in situ* counts and photographs showed this method to be accurate (J.A. Lathlean unpublished data). I photographed each quadrat monthly (February to July 2007) during the main period of settlement for *T. rosea* (see Wisely & Blick 1964, Caffey 1985) then approximately quarterly until December 2008 (i.e. August and December 2007, February, May, August and December 2008). Recently settled *T. rosea*

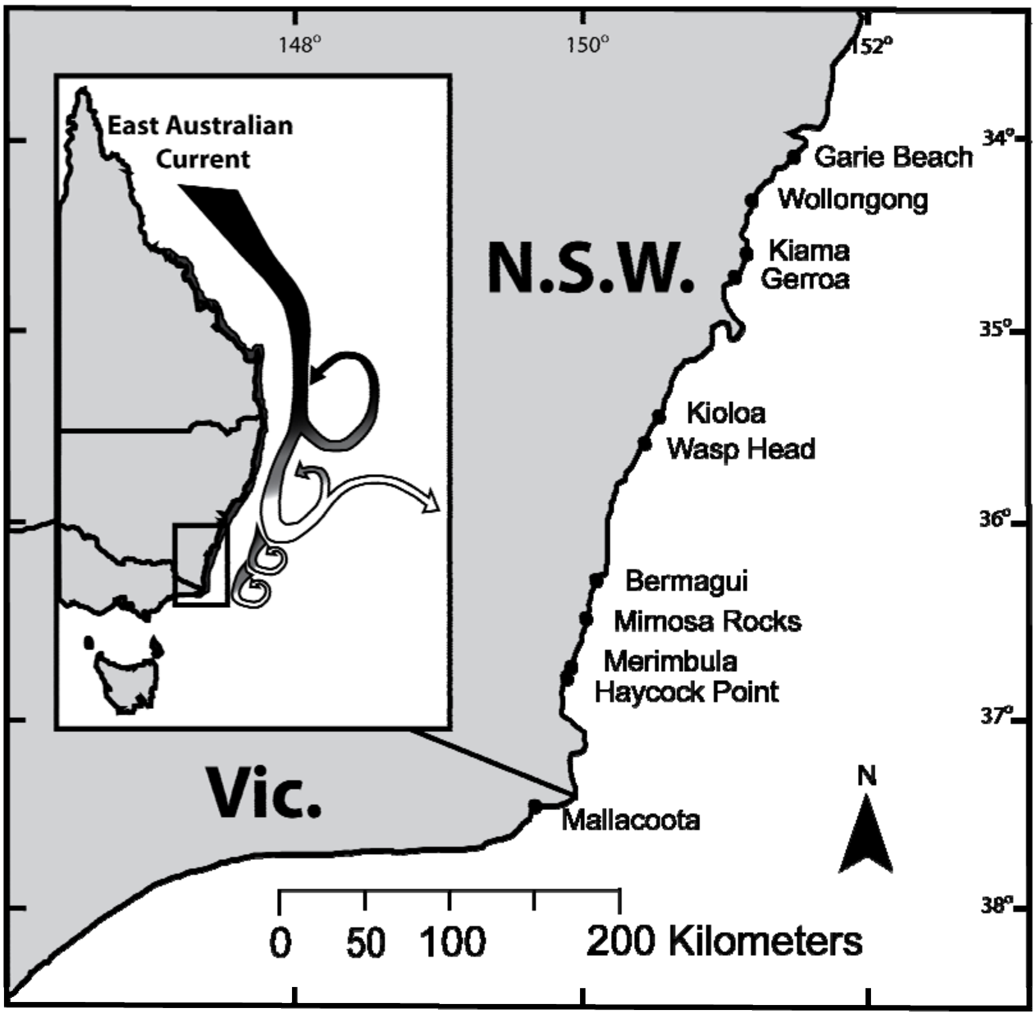

Figure 2.1. Map of the south eastern coast of Australia showing sampling locations separated by 10 to 80km. Inset shows the geographic range of *Tesseropora rosea* (shaded area) and the East Australian Current, with shading from black to white representing strong to weak influence.

(individuals < 1 week old) could not always be distinguished from recently settled individuals of the barnacle *Catomerus polymerus*, but *Catomerus polymerus* recruits (individuals greater than 1 month old) were rarely observed, and constituted < 1% of the total number of barnacle recruits; therefore, any misidentification is unlikely to influence results.

2.2.3 Geographic patterns of demography and population structure

During 2007, settlement, recruitment, and adult density at each site were determined in separate quadrats, with 10 of the 30 quadrats randomly assigned to one of three treatments: 'recleared' quadrats, were cleared of all *T. rosea* at each sampling time and used to estimate settlement, 'cumulative' quadrats, which were cleared initially and then allowed to accumulate *T. rosea* recruits and used to estimate recruitment, and 'untouched' quadrats, which were not cleared at any time and used to estimate adult density (see details below). From these estimates of abundance, mortality at each life history stage (early post-settlement mortality, post-recruitment mortality, adult mortality) was calculated (see details below). This approach differed somewhat from Caffey (1985) such that I did not alternatively clear quadrats once every two-months. In doing so I were able to estimate the percentage of recruits surviving for more than two-months and assess the likelihood that these recruits reach reproductive maturity and contribute to the size of the adult population.

Settlement at a site was estimated by counting the number of recently settled *T. rosea*, as well as any empty tests from recent deaths of settlers, in the 10 'recleared' quadrats. To ensure that I counted only recently settled individuals, recleared quadrats were cleared of all organisms at the start of the study in February 2007 and then again after each census. A metal brush was also used to remove any existing layer of visible biofilm within these recleared quadrats at each census. This may have caused us to potentially underestimate settlement, as settlement can increase with the amount and age of biofilm (Qian et al. 2003, Thiyagarajan et al. 2006 but see Olivier et al. 2000), but was necessary to remove any confounding effects of increased amounts of biofilm within southern locations where adult densities were lower. Therefore, because I sampled only once per month my ‘settlers’ could be 1 to 30 days old. Undoubtedly, at this sampling frequency some individuals that settled and died before they could be counted would have been missed, and this could have resulted in an underestimation of the absolute magnitude of settlement and early mortality (see Minchinton & Scheibling 1993a). Nevertheless, Caffey (1985) found that for this species this frequency suitably differentiated settlement from recruitment. Settlement at a site was calculated as the sum of the number of *T. rosea* that settled in each of the 10 recleared quadrats for all months between February and December 2007.

Recruitment at a site was estimated in the 10 ‘cumulative’ quadrats. These quadrats were cleared of all organisms once, in February 2007, and then settling barnacles were allowed to accumulate for the entire two-year sampling period. Recruitment at a site was calculated by summing the peak, or maximal, number of *T. rosea* recruits (i.e. individuals >30 days old) recorded within each of the 10 cumulative quadrats at any sampling interval between February and December 2007. Early post-settlement mortality was calculated as the percentage difference between settlement and recruitment. Likewise, post-recruitment mortality was calculated as the percentage difference between recruitment and the number of *T. rosea* remaining within cumulative quadrats in December 2007.

Adult density at a site was calculated as the sum of the number of *T. rosea* adults (i.e. individuals with an aperture length >1.5mm) within each of the 10 untouched quadrats in December 2007. Maximal adult density at a site was calculated as the sum of the maximal number of *T. rosea* adults recorded within each of the 10 untouched quadrats between February and December 2007. Adult mortality at a site was calculated as the percentage difference between 'maximal' adult density and adult density in December 2007.

Following the methods of Egan and Anderson (1988), the potential for larval production at each location was determined by quantifying the percentage of adults with developing (creamy to bright yellow coloured embryos) or mature ready to spawn (i.e. brown-eyed nauplii) larvae over time (Wisely & Blick, 1964; Egan & Anderson, 1988). Quantitative assessment of fecundity proved difficult because mantle cavities were often damaged when adults were prised from the substratum for examination. I collected at least 40 adult *T. rosea* (i.e. individuals with an aperture length > 1.5mm) once per month during the main breeding season (i.e. February to July, 2007), then again in August and December 2007, from areas outside the permanent quadrats and spread across both sites at each location. Adults were preserved, transported to the laboratory and the presence of developing larvae was assessed using a dissecting microscope. The proportion of adults at each location with either mature or developing larvae was calculated for all adults sampled over the entire year.

2.2.4 Changes to population structure

I monitored latitudinal changes in population structure by comparing densities of *T. rosea* within both the cumulative and untouched quadrats at each site at the beginning of the sampling period in February 2007 and again in both December 2007 and 2008. This allowed us to determine whether recruitment processes (i.e. settlement and post-settlement mortality within cumulative quadrats) would return each population to its former abundance, or whether the adult population abundance initially observed persists through time (i.e. untouched quadrats).

2.2.5 Statistical analysis

I expected substantial variation among quadrats at a site and, given that my aim here was to determine how demographic and population parameters varied with latitude, I pooled densities of settlers, recruits and adults among recleared, cumulative and untouched quadrats, respectively, to yield one estimate of each for each site (i.e. $n = 2$ sites per location). Due to extreme weather events and ephemeral algae or sand obscuring quadrats, I was unable to sample all sites in each month. For the months when sites were covered by sand, I assumed new settlers and recruits would have died and, therefore, assigned values of zero for that month (and subsequent observations showed that this was generally the case). For months when sites could not be sampled due to bad weather or were obscured by algae, I excluded the site for that month and sampled as previously described in the following month. This did not occur often, with only 7.8% of sites not sampled during the entire two-year sampling period. Larval production, settlement, recruitment, early post-settlement mortality, post-recruitment mortality, adult mortality and adult densities were correlated with latitude to test for the presence of latitudinal gradients.

I performed one-way ANOVA on (i) settlement, (ii) recruitment, (iii) early post-settlement mortality, (iv) early post-recruitment mortality, (v) adult mortality, and (vi) adult density for the 11 locations. Where significant differences were found, a Student Neuman-Keuls (SNK) test was used to determine which locations had significantly different settlement, recruitment, early post-settlement mortality, post-recruitment mortality, adult mortality or adult densities. I confirmed that data were approximately normally distributed and with equal variance using the Shapiro-Wilks and Cochran's test respectively.

2.3 Results

2.3.1 Geographic patterns of demography

The vast majority of adult *T. rosea* brooded developing and mature embryos at all locations throughout the range, but the proportion of adults with eyed nauplii did not vary across the geographic range or show any significant relationship to latitude (r^2 = 0.052, n = 10, P = 0.501) (Fig. 2.2a).

Settlement at most locations was typically derived from single large pulses of larvae settling on shore sporadically from late summer to late autumn. Indeed, although not significantly different, densities of settlers varied greatly between sites at a location and by more than an order of magnitude among locations ($F_{10,11}$ = 2.37, P = 0.086), and there was no significant relationship between settlement and latitude (r^2 = 0.013, n = 21, P = 0.613) (Fig. 2.2b).

There was great early post-settlement mortality at all locations, with an average of 79.4% of newly settled *T. rosea* dying by December 2007 (Fig. 2.2c), and as for settlement no latitudinal decline in early post-settlement mortality was detected (r^2 = 0.005, n = 21, P = 0.752). Densities of recruits varied significantly among locations ($F_{10,11}$ = 3.20, P = 0.035) with an SNK test indicating that the number of recruits at Mimosa Rocks was greater than at all other locations (Fig 2.2d). Interestingly, recruitment of *T. rosea* was largely reflective of settlement as locations that received

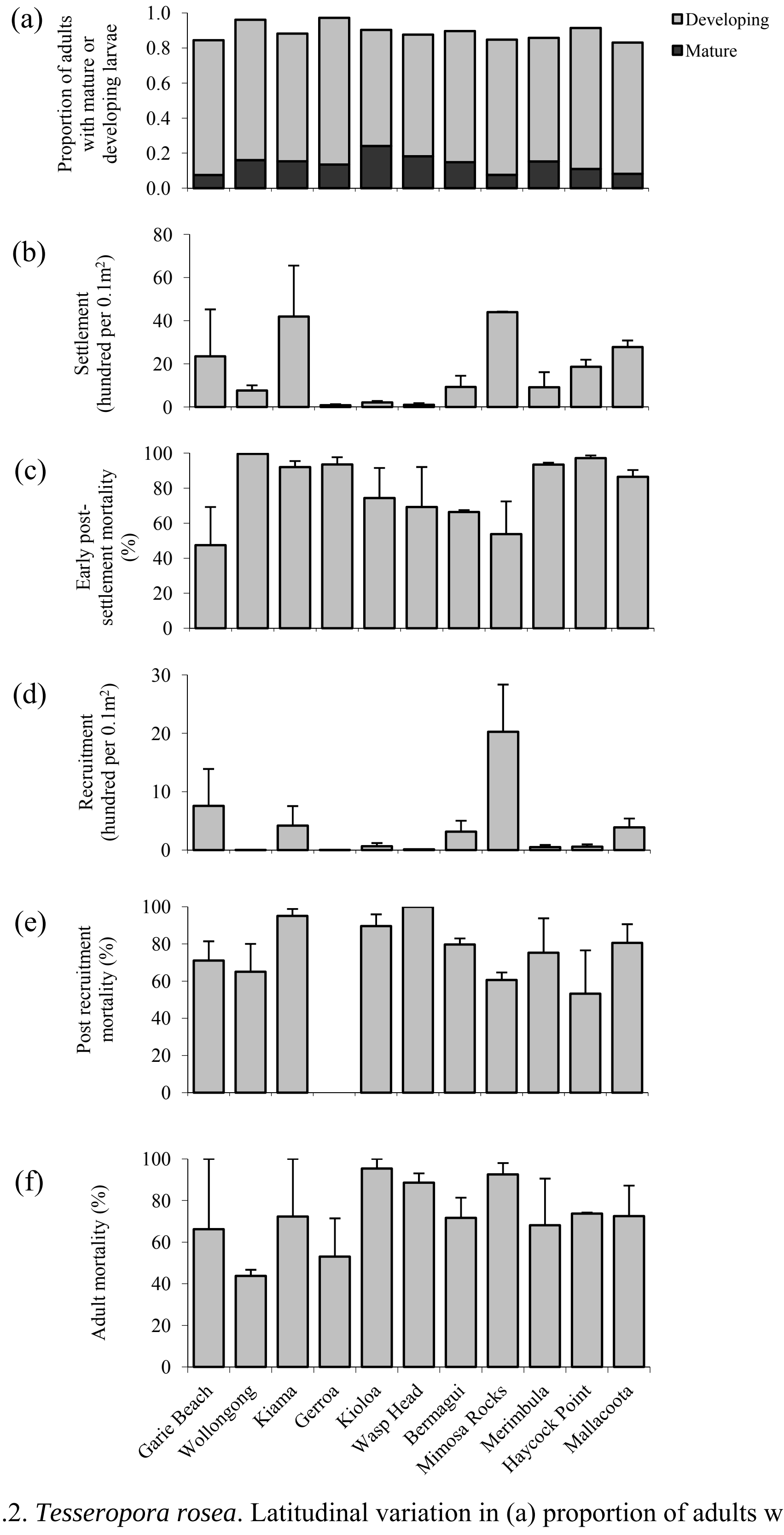

Figure 2.2. *Tesseropora rosea*. Latitudinal variation in (a) proportion of adults with either mature or developing larvae, (b) mean settlement, (c) mean percentage mortality of recently settled individuals, (d) mean recruitment, (e) mean post-recruitment mortality and (f) mean percentage of adult mortality during 2007. Error bars represent standard errors due to variation between pairs of sites at each location.

large numbers of settlers generally had a larger number of recruits. For example, Mimosa Rocks received the greatest number of settlers and subsequently had the greatest number of recruits (Fig. 2.2b and d). Additionally, though not as great as early post-settlement mortality, post-recruitment mortality was also great and varied significantly among locations ($F_{10,11} = 5.86$, $P = 0.004$), with an average of 70% of recruits dying by December 2007, with a SNK test finding substantially lower mortality at Gerroa, Haycock Point and Mimosa Rocks (Fig 2.2e).

Adult mortality was substantial at all locations, with on average 72.5% of adult barnacles dying during 2007 (Fig. 2.2f). Nevertheless, adult mortality was highly variable between sites and not significantly different among locations ($F_{10,11} = 0.857$, $P = 0.953$), being greatest at Kioloa (95.3%) and least at Wollongong (43.7%). Similar to larval production, settlement, early post-settlement mortality, recruitment and post-recruitment mortality, no latitudinal gradient was found for adult mortality ($r^2 = 0.07$, d.f. = 21, $P = 0.231$).

2.3.2 Changes to population structure

There was a significant linear relationship between the density of adult *Tesseropora rosea* and latitude at the start of sampling in February 2007, with adult abundance declining substantially from the middle to the edge of its range ($r^2 = 0.36$, $n = 21$, $P = 0.003$) (Fig. 2.3c). As a result of the consistently high and variable early post-settlement mortality, post-recruitment mortality and adult mortality, by the end of sampling in December 2008 there was no latitudinal gradient in adult abundance within either untouched ($r^2 = 0.17$, $n = 21$, $P = 0.054$) or cumulative quadrats ($r^2 = 0.028$, $n = 21$, $P = 0.455$) suggesting the original latitudinal decline in adult abundance neither persists nor becomes re-established in time (Fig. 2.3b and e). Indeed, there were no latitudinal

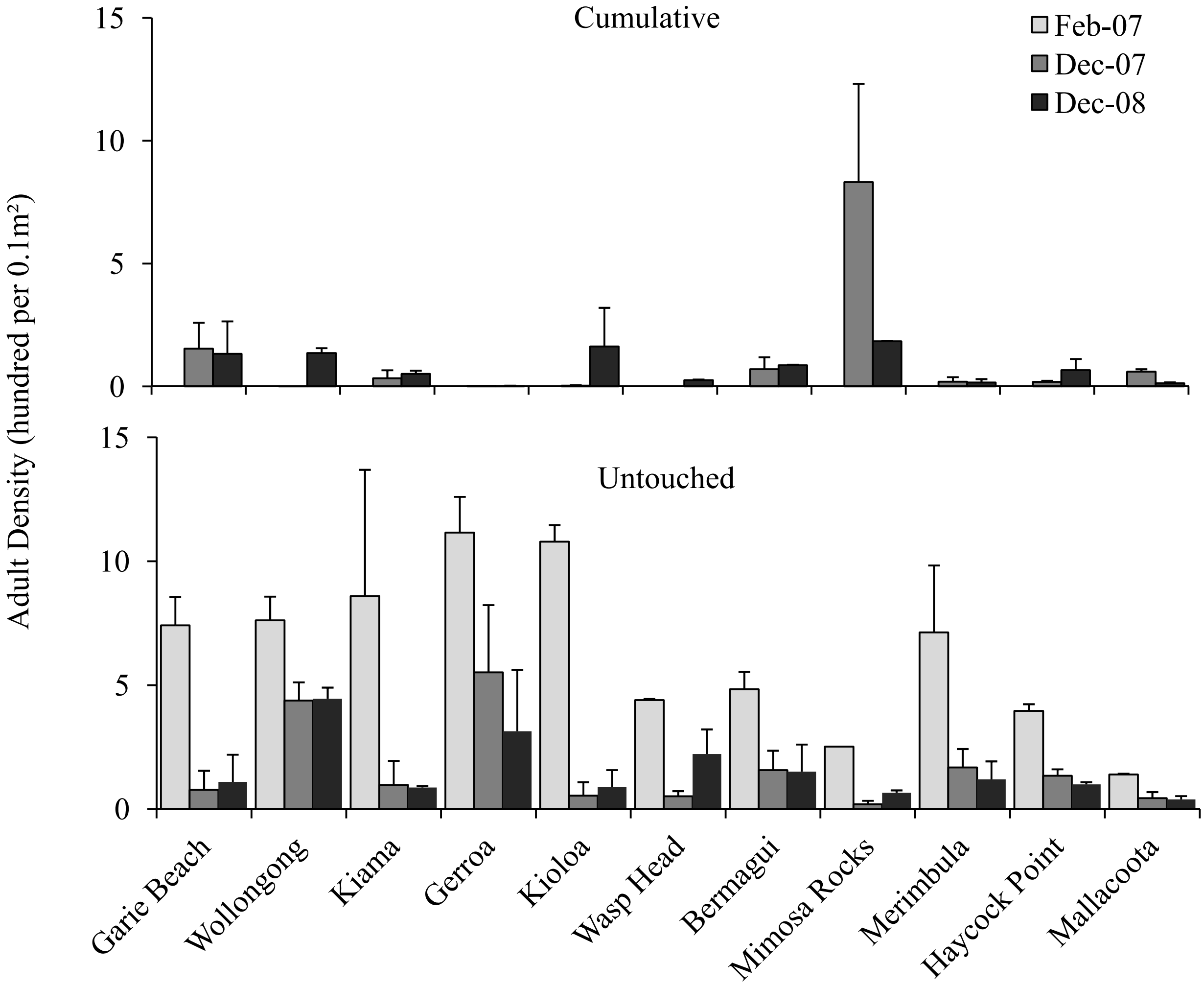

Figure 2.3. *Tesseropora rosea*. Latitudinal variation in density for both cumulative and untouched treatments in February and December 2007, and December 2008. Error bars represent standard errors due to variation between pairs at sites at each location.

patterns for any demographic process examined, with local variability in adult mortality appearing to drive geographic patterns of adult abundance.

2.4 Discussion

At the start of the study, populations of the rocky shore barnacle *Tesseropora rosea* displayed abundant-centre patterns of geographic distribution with an inverse relationship between density and latitude from the middle to the southern limits of its range. Contrary to expectations, however, I detected no latitudinal gradients in the key demographic processes expected to contribute to this pattern, including larval production, settlement, early post-settlement mortality or recruitment. Indeed, it appears that variations in recruitment and adult mortality due to local forces might make the greatest contribution to geographic patterns of abundance and apparent latitudinal trends.

Larval production was relatively uniform among locations, suggesting that the reduction in seawater and air temperatures towards the southern range limit does not limit the ability of *T. rosea* to produce larvae. This is perhaps surprising because studies have shown that such differences in seawater temperatures can influence the reproductive ability of benthic marine invertebrates (Brey 1995, Vilchis et al. 2005), and field investigations have detected reduced fecundity at range limits due to changes in seawater temperature (Barber & Blake 1983, Amaro et al. 2005). However, Helmuth *et al*. (2006) assessed body temperatures of the intertidal mussel *Mytilus californianus* across a latitudinal gradient in sea surface temperatures and found that body temperatures were often warmer or colder than was predicted from sea surface temperatures. Consequently, the lack of a latitudinal decline in larval production within the present study may reflect complex interactions between air and sea surface temperatures. Larval production has also been shown to be directly associated with food availability (Leslie et al. 2005). Therefore, more quantitative sampling of larval production could reveal differences among locations that either experience different air or sea temperatures or food concentrations. Similarly, I expected the reduction in seawater temperatures towards the southern range limit of *T. rosea* to reduce larval settlement and increase early mortality (Gaylord & Gaines 2000, Sprung 2001, Zacherl et al. 2003). Instead, settlement was largely sporadic and unpredictable, with locations separated by hundreds of kilometres simultaneously receiving large pulses of newly settled *T. rosea* while adjacent locations receiving relatively few settlers. This supports work by Caffey (1985), who found highly variable settlement of *T. rosea* at large spatial scales and no clear latitudinal trend for this species in the central region of its geographic distribution.

Early post-settlement mortality of *T. rosea* was found to be consistently high among all locations and was on average 79%, which is considerably higher than the average of 66.5% detected by Caffey (1985). Likewise, the adult mortality among all locations was extremely high for a one-year period when compared to similar studies undertaken over shorter sampling periods (Denley & Underwood 1979, Caffey 1985, Jernakoff 1985, Otway & Underwood 1987). For example, Otway & Underwood (1987) found adult mortality of *T. rosea* to vary between only 14% and 18% over 13-months, while Jernakoff and Fairweather (1985) found adult mortality to vary between 0.5% and 2.5% over a three-month period. Numerous factors such as biological and physical disturbances, thermal stress, predation and competition are known to influence the mortality of newly settled benthic marine invertebrates at small spatial scales (for review see Hunt and Scheibling, 1997). For *T. rosea* specifically, the major causes of early post-settlement mortality are algal growth, ‘bulldozing’ by grazing limpets and intraspecific competition (Denley & Underwood 1979, Underwood et al. 1983, Jernakoff 1985), with the predatory whelks *Morula marginalba* and *Dicathais orbita* being the most likely causes of adult mortality (Underwood et al. 1983, Fairweather 1984, Moran 1985). However, whether predation by *M. marginalba* and *D. orbita* continues to influence populations over large spatial scales has yet to be answered. In addition, it is unlikely that interspecific competition between *T. rosea* and *Catomerus polymerus*, another intertidal barnacle more commonly found within southern parts of Australia, contributed to the high levels of early post-settlement mortality and adult mortality of *T. rosea* documented within this study as (i) larval settlement between these two species occur at different times of the year (Wisely and Blick, 1964), (ii) *C. polymerus* abundance was generally low and (iii) free-space did not appear to be a limiting factor within southern locations where densities of *C. polymerus* were somewhat greater. However, further research is required to understand what role, if any, competition between *T. rosea* and *C. polymerus* plays in determining the southern range limit of *T. rosea.*

Latitudinal gradients in settlement and recruitment may be attributed to differential coastal upwelling, as increased upwelling reduces larval concentrations within coastal waters and subsequently reduces settlement as more larvae are transported offshore, limiting contact with their preferred substrata (Gaines et al. 1985, Roughgarden et al. 1988, Connolly et al. 2001, Menge et al. 2004). Consequently, the highly variable patterns of settlement detected within the present study could reflect variable upwelling along the southeast coast of Australia (Roughan & Middleton 2004) and geographical variation in topographic features that assist in retaining larvae (Jenkins & Hawkins 2003, Mace & Morgan 2006). However, since many oceanographic studies have revealed only weak upwelling along this coast (Roughan and Middleton, 2004), it is unlikely that variable upwelling is the only contributing factor to variable settlement. This highly variable settlement could also suggest that larval physiological condition varies significantly within the study region as recent studies have shown larval condition, which can be determined by variable temperature and food concentrations (Desai and Anil, 2004), to strongly influence the settlement (Thiyagarajan *et al*., 2002; Tremblay *et al*., 2007) and early post-settlement growth and survival (Thiyagarajan *et al*., 2005; Emlet and Sadro, 2006) of larvae. Therefore, local processes may be equally important as regional processes in setting patterns of adult abundance and potentially the geographic distribution and southern range limit of *T. rosea*.

The absence of latitudinal gradients in larval production, settlement, early post-settlement and adult mortality suggest that these life history processes are not responsible for the latitudinal decline in adult abundance or the southern range limit of *T. rosea*. However, the exceptionally high mortalities of both recently settled and adult *T. rosea* significantly reduced adult densities such that by the final census adult densities no longer declined towards the southern range limit suggesting an exceptionally large disturbance had occurred, obscuring important relationships. Indeed, the shift from an El Niño to a La Niña pattern during 2007 may have attributed to several atypical oceanographic features, including four unusually large consecutive low pressure systems crossing the Tasman Sea in June 2007, causing strong predominantly southerly swells over the study area, at times in excess of 7m (Australian Bureau of Meteorology, 2007). Increased sand scour caused by such an oceanographic regime would presumably have had a significant impact on large-scale patterns of settlement, early post-settlement and adult mortality of *T. rosea*. Such large southerly swells are seasonally common during winter along the southeast coast of Australia (Short and Trenaman, 1992). Therefore, *T. rosea* recruits may experience increased mortality during winter each year, with survival favouring earlier settling individuals that managed to reach a specific size. Alternatively, the average life expectancy of adult *T. rosea* is only four-years (Caffey, 1985). Consequently the high adult mortality detected in this study may be reflective of the senescence of a large cohort that gave rise to the initial latitudinal decline in adult abundance simultaneously dying off. However, adult mortality appeared to occur irrespective of size or age, suggesting mortality was high across several cohorts within each location. Regardless, demographic processes operating over two years have greatly influenced the population structure of *T. rosea*, suggesting that infrequent events could potentially have longer lasting impacts than patterns of settlement, early post-settlement and adult mortality combined over numerous years.

Geographic patterns of adult abundance might of course reflect environmental cycles with longer periodicity than most studies, including this one. For example, geographic patterns may develop over time due to changing environmental conditions, such as the prolonged El Niño conditions in southeast Australia from 2001 to 2006 (Australian Bureau of Meteorology, 2007), influencing demographic processes gradually. Alternatively, observed patterns of decreasing adult abundances with latitude might reflect “stored” patterns determined by a year of great recruitment combined with different environmental conditions to those observed during this study. Such large recruitment events appear common for *T. rosea* and might lock in latitudinal patterns of adult abundance for the lifespan of the species, which can be 10 years (Denley 1981, Caffey 1985). Only massive mortality such as observed in the present study might disrupt such geographic trends. Clearly longer-term observations are needed in both cases; importantly, however, results here indicate that such latitudinal patterns are dynamic. The great variability in settlement and early mortality over geographic scales observed here suggest that, for sessile marine invertebrates with planktonic dispersing larvae, factors that act at a local-scale (e.g. recruitment, mortality, natural disturbance), might be more important in setting geographic patterns of distributions than differences in larval supply, settlement and early mortality with latitude.

The remaining chapters of this thesis primarily focus on local-scale temperature variability and this variability influences the early post-settlement life history stages of *T. rosea*.

CHAPTER 3: Rocky intertidal temperature variability along the southeast coast of Australia: comparing data from *in situ* loggers, satellite-derived SST and terrestrial weather stations.

A modified version of this chapter is published in *Marine Ecology Progress Series.*

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3.1 Introduction

As air and sea temperatures continue to rise, remote sensing techniques, such as satellite derived sea surface temperatures (SST), are becoming increasingly important tools to assess how changes in temperature will influence the geographic distributions of species (Gilman et al. 2006, Helmuth 2009). It is well known, for example, that large-scale ocean temperature variability significantly influences physiological and demographic processes of many marine invertebrates, fish and primary producers, with shifts in species range limits associated with increased sea temperatures (Zacherl et al. 2003, Gilman 2006a, Lima et al. 2006, Herbert et al. 2007, Last et al. 2010). Invertebrates living in intertidal habitats may be particularly vulnerable to fluctuating temperatures as they have to adapt to temperature extremes in both the terrestrial and marine environment (Fields et al. 1993). However, at relatively small spatial scales, such as across the vertical extent of a rocky intertidal shore, body temperatures of sessile and sedentary invertebrates can be determined by the timing and duration of aerial exposure (Helmuth 2002), and studies have shown that air temperatures during low tide have greater effects on the physiological processes of both intertidal mussels and barnacles compared to water temperatures during high tide (Hofmann & Somero 1995, Somero 2002). Therefore, both air and water measurements are required to characterise the thermal environment of rocky intertidal shores.

Several ecological studies have previously used satellite SST to characterise the thermal environment of intertidal habitats (Barry et al. 1995, Broitman et al. 2001, Broitman et al. 2005b, Lagos et al. 2005a, Herbert et al. 2007, Blanchette et al. 2008, Broitman et al. 2008a). Studies have shown satellite derived SSTs are highly correlated with daily *in situ* measurements of SST (Keogh et al. 1999, Barton & Pearce 2008, Smale & Wernberg 2009); nevertheless, satellite derived SST are unlikely to reflect the variability of the temperature regimes experienced by the vast majority of rocky intertidal organisms (Helmuth & Hofmann 2001, Gilman et al. 2006). Indeed, Helmuth & Hofmann (2001) found that aerial body temperatures of the mussel *Mytilus californianus* varied independently of water temperatures and suggested that water temperatures by themselves should not be used as a measure of temperature stress for intertidal organisms.

Numerous factors operating across both large and small spatial scales pose difficulties when using remote sensing to estimate *in situ* temperatures on rocky intertidal shores. These include tidal dynamics and their variability among geographic locations (Helmuth et al. 2002, 2006a, Harley 2008), degree of wave exposure and height on shore (Harley & Helmuth 2003) as well as topographic orientation and slope of substratum (Helmuth & Hofmann 2001, Harley 2008). As a result of this natural variability, even hourly temperature measurements commonly recorded by terrestrial weather stations and daily composite SST produced by satellite images are unlikely to detect acute (extreme) or chronic (continually stressful) temperature events, which are more likely to influence the mortality, growth and reproduction of intertidal organisms (Denny et al. 2006, Denny et al. 2009, Harley & Paine 2009, Helmuth et al. 2010).

Southeast Australia has been identified as being particularly vulnerable to climate change (see Section 1.4) and hosts many subtropical, warm temperate and cold temperate species (Hughes 2003, Poloczanska et al. 2007, Edgar 2008). Sea surface temperatures along the southeast coast of Australia are largely influenced by the East Australian Current (EAC), which flows most strongly in the summer months and weakens during winter, usually deflecting offshore around Laurieton (31º39’S, 152º48’E) in northern NSW, producing large warm-core eddies that penetrate the coastal waters of southern NSW and eastern Victoria (Huyer et al. 1988, Roughan &

Middleton 2004). These southward flowing warm-core eddies produce latitudinal temperature gradients and are expected to increase in strength, penetrating further south under future climate change scenarios (Roughan & Middleton 2004, Lough 2009, Ridgway & Hill 2009). Many species have their northern or southern geographical range limits within this region (Knox 1963, O'Hara & Poore 2000, Hidas et al. 2007, 2010, see also Ayre et al. 2009) including *Tesseropora rosea*. Therefore, we might expect many of these species' range limits to shift with response to climate change. However, there is a significant gap in our understanding of the typical spatial and temporal temperature regimes experienced by intertidal organisms along southeast Australia, and researchers in the past have simply used satellite or buoy derived SST as a measure of large-scale temperature variability.

This chapter provides a detailed assessment of large, regional and small-scale *in situ* rocky intertidal temperature variability along the south east coast of Australia. I first determine the extent to which nearshore sea surface temperatures derived from satellites, and air temperatures derived from terrestrial weather stations can be used as appropriate surrogates of rocky intertidal water and air temperatures respectively. I expected that water and air temperatures sensed remotely would be strongly correlated with values estimated using *in situ* loggers, but that absolute values would likely differ. I then show that small-scale (i.e. local) variability in air and water temperature, measured by *in situ* data loggers, better characterises the thermal environment experienced by intertidal organisms. The objective here was to test whether temperature variability measured over both fine spatial (pairs of loggers separated by metres at three tidal heights) and fine temporal scales (10min intervals) can reveal demographically important temperature variation that cannot be estimated using remote sensing

3.2 Methods

3.2.1 Study region

The study region spanned more than 400km and included four rocky intertidal shores along the southeast coast of Australia: Garie Beach (34º10’38” S, 151º03’58”E), Kiama (34º40’08”S, 150º51’26”E), Bermagui (36º25’36”S, 150º05’02”E), and Mallacoota (37º34’40”S, 149º46’02”E), (Fig 3.1). Garie Beach and Bermagui had slightly sloping platforms (10-20°) while Kiama and Mallacoota had steeper gradients (20-30°). All locations experience a mixed semi-diurnal tidal regime with a tidal range of approximately 2m. Previous studies have shown that the degree of wave-exposure can significantly influence temperature variability at a site (Harley & Helmuth 2003, Fitzhenry et al. 2004, Denny et al. 2006); therefore, locations were chosen which have a north to northeast orientation, and all four experience similar levels of wave exposure (personal observation). All locations support similar benthic communities within the mid-shore region largely dominated by the barnacles *Tesseropora rosea* and *Catomerus polymerus*, the gastropods *Bembicium nanum, Nerita melanotragus* and *Morula marginalba*, the limpets *Cellana tramoserica* and *Patelloida latistrigata,* and the macroalgae *Hormosira banksii, Porphyra lucasii, P. columbina* and *Corallina officinalis* (Underwood et al. 1983).

3.2.2 *In situ* logger data

To determine large-scale spatial variability in air and water temperatures among the four rocky shore locations, TidbiT® v2 Temp data loggers (Onset Stowaway logger, model UTBI-001, accuracy ±0.2ºC) were deployed within the mid intertidal zone (0.8 to 1m above mean low water mark and 25 to 50cm away from biota) at each of Garie Beach, Kiama, Bermagui and Mallacoota and continuously recorded both air and water temperatures at 10min intervals from mid April 2008 until June 2009. Loggers accurately recorded temperatures within ±0.2ºC. To assess temperature variability within a single location, additional loggers were deployed at two sites separated by approximately 50m and across three intertidal heights within Garie Beach in February 2010 (i.e. n = 6). Denny et al. (2006) showed that intertidal temperatures can vary with differences in substrate aspect and orientation. Therefore, I took a conservative approach to estimating temperature variability by attaching all loggers to horizontal or slightly sloping rock surfaces with a north to northeast orientation.

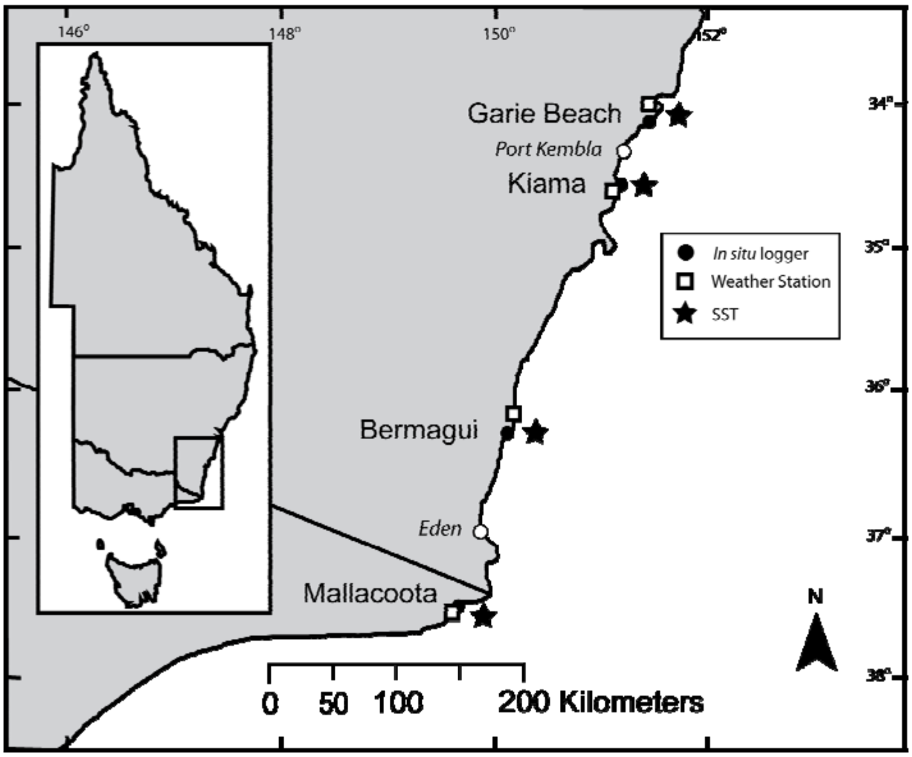


Figure 3.1. Four rocky intertidal shores along the southeast coast of Australia showing approximate locations of *in situ* logger, weather station and satellite sea surface temperature (SST) collection points. Port Kembla and Eden represent locations where tidal data was obtained.

To separate data logger temperatures into air and water temperatures I used methods of estimating ‘effective shore level’ (ESL) similar to those of Harley and Helmuth (2003). Here, a sudden drop in temperature by at least 3ºC within 20min during the daytime indicates when the logger is first inundated with the incoming tide. The time of this sudden drop is then matched with tidal heights recorded by buoys to give an ESL for each logger. Tidal data were obtained from either the Australian Bureau of Meteorology’s National Tidal Centre (www.bom.gov.au/oceanography/projects/ntc.shtml) or Manly Hydraulics Laboratory for buoys at Port Kembla (34º29’S, 150º55’E), Bermagui (36º25’S, 150º4’E) or Eden (37º4’S, 149º54’E) and hourly temperature data recorded by loggers were compared with hourly tidal data recorded by the closest of these buoys (see Fig. 3.1). Temperatures that were recorded when the tidal height was below ESL values were deemed to be air temperatures whereas temperatures recorded when the tidal height was above these values were deemed to be water temperatures. I applied a 0.3m buffer zone above and below the ESL for each logger and excluded data that were obtained within this buffer zone because wave splash may also significantly influence whether or not a logger is submerged. This approach ensured that temperatures recorded during the changing of the tides accurately represented air or water temperatures. Once logger data were separated into air and water temperatures, daily mean, maxima and minima were calculated for both air and water temperatures at each of the four locations to characterise temporal and spatial temperature variability. Additionally, air and water temperature frequency distributions were used to specifically compare temperature variability across the four locations.

3.2.3. Satellite SST and terrestrial weather station data

Comparisons were made between logger-derived *in situ* intertidal water temperatures and satellite-derived SSTs at all four locations from 16 April 2008 to 6 June 2009. Satellite SST readings recorded twice every 24 hours were obtained from the advanced very high resolution radiometer (AVHRR) taken from the NOAA series of polar orbiting satellites through the IMOS web portal (http://www.marine.csiro.au/remotesensing/imos/aggregator.html). To standardise comparisons between *in situ* loggers and satellite-derived SST across the four locations, daily SST was acquired for single fixed pixel (representing an area of ~2×2km) approximately 7km offshore for each of the four locations (Fig. 3.1). Choosing pixels 7km offshore allowed standardised SST measurements among locations and maintained an equivalent offshore distance throughout the sampling region. Several single day composites of SST were missing due to cloud cover at the time images were being taken by satellites and therefore no comparisons could be made with *in situ* loggers on these days. Using these data I correlated daily SST composites with daily mean water temperatures recorded by *in situ* temperature loggers within the mid intertidal zone. Monthly maxima, minima and mean satellite temperatures were also correlated with monthly maxima, minima and mean logger temperatures to determine whether satellite SST were capable of detecting extreme temperature events that are often more biologically relevant than daily means (Denny et al. 2009).

Comparisons between air temperatures derived from *in situ* intertidal data loggers and terrestrial weather stations were also done for all four locations. Terrestrial weather station data were obtained from the Australian Bureau of Meteorology for coastal stations closest to the 4 study locations. Consequently, logger air temperatures recorded at Garie Beach, Kiama, Bermagui and Mallacoota were correlated with weather station air temperatures at Sydney Airport (27.8km), Kiama Headland (<0.5km), Narooma (24.3km) and Mallacoota (<0.5km), respectively (distances between loggers and weather stations shown in brackets). Each weather station recorded air temperatures every three hours, which allowed daily maxima, minima and mean temperatures to be calculated and correlated with daily maxima, minima and mean logger air temperatures.

3.2.4 Biologically relevant temperature variation

Demographic patterns of rocky intertidal invertebrates can often be significantly influenced by extreme temperature events and invertebrates respond depending on the thermal characteristics leading up to and during the extreme temperature event (Denny et al. 2009, Mislan et al. 2009). Therefore, to further assess the ability of terrestrial weather stations to record biologically relevant estimates of rocky intertidal temperature, the number, duration, and frequency of extreme temperature events recorded by *in situ* loggers at all four locations were compared with the same parameters recorded by nearby weather stations during the summer of 2008/09. Here ‘number’ refers to the number of days where air temperatures reached 30°C, ‘duration’ refers to the total time temperatures stayed at or above 30°C, similar to degree heating hours (DHH) used by Helmuth et al. (2010), and ‘frequency’ (expressed as its inverse) refers to the average time between 30°C events. These parameters were chosen based on findings in Denny et al. (2006, 2009) which show that the number, duration and frequency of extreme temperature events are just as important as absolute temperatures when assessing how intertidal invertebrates respond to increased temperatures. Temperatures over 30°C were classified as extreme because previous studies have shown this temperature to be the approximate threshold for heat shock protein (Hsp) production in *Mytilus* spp. found at similar latitudes as the present study (Halpin et al. 2004).

The rates at which temperatures rise and fall are also important parameters that can influence an organism's ability to respond to thermal stress. For intertidal organisms the most rapid change in temperature is most likely to occur during the changing of the tides (Helmuth & Hofmann 2001, Harley & Helmuth 2003). Therefore I use continuous *in situ* logger data (i.e. not separated into air and water temperatures) with 10min sampling intervals to compare the frequency of rapid heating events measured by *in situ* loggers and the remote sensing methods at Garie Beach, Kiama and Bermagui during the summer of 2008/09. For *in situ* data a rapid heating event was defined as either a rise of 15°C or more within four hours, 10°C or more within three hours or 5°C or more within three hours. For equivalent comparisons to be made using remote sensing methods a rapid heating event was defined as differences of 15°C, 10°C or 5°C between daily satellite SST and daily maximum air temperatures recorded by weather stations. These rates were somewhat arbitrarily defined based on the most extreme rate of heating (i.e. 18°C within four hours) being recorded by a logger at Garie Beach during the time of interest.

3.2.5 Data analysis

Pearson's r values were used to indicate the strength of the correlation between (i) logger water temperature and satellite SST, (ii) logger air temperature and weather station air temperature and (iii) loggers at two sites within Garie Beach across the three different intertidal heights with differences being tested with paired t-tests. Correlations and paired t-tests could only be undertaken for approximately nine months at Mallacoota because the logger was damaged.

A two-way ANOVA using log (x+1) transformed data was used to test for statistically significant differences in daily mean, maxima and minima of air and water temperatures across the three rocky shore locations and time (from June 2008 to May 2009 and Mallacoota was excluded from ANOVA due to incomplete data). Where significant differences were found, Student-Neuman-Keuls (SNK) tests were used to determine which locations or seasons had significantly different temperatures. Due to natural variability in the tidal cycle some loggers remained either emerged or submerged for more than 24 hours. Consequently, several days during the sampling period did not record either air and water temperatures and were therefore excluded from analysis.

3.3 Results

3.3.1 Comparisons of temperature variability at geographic scales

Air temperatures generally declined with increasing latitude (Table 3.1). For example, daily maximum *in situ* air temperatures, averaged over the 12-month sampling period, were 24.5±7.7, 24.3±6.1 and 21.0±4.9ºC at Garie Beach, Kiama and Bermagui, respectively (Table 3.1), with maximum air temperatures ranging from 50.0, 42.3 and 37.0ºC at Garie Beach, Kiama and Bermagui, respectively (Table 3.1). Air temperatures recorded by in situ loggers also varied consistently with latitude when seasons were analysed separately (SNK test for interactions, see Table 3.2). Daily maximum air temperatures recorded by weather stations averaged for the 12-month sampling period ranged from 21.5±4.9, 20.0±3.9, 18.4±3.4 and 18.1±4.5ºC at Garie Beach, Kiama, Bermagui and Mallacoota, respectively, with maximum air temperatures ranging from 38.3, 37.5, 33 and 38.4ºC at Garie Beach, Kiama, Bermagui and Mallacoota, respectively. *In situ* logger air temperatures were highly variable across all four locations from June to November 2008 suggesting that air temperature variability does not vary with latitude (Fig. 3.2).

In contrast to air temperatures, *in situ* loggers only recorded a weak latitudinal decline in water temperatures with loggers at Garie Beach and Kiama, separated by approximately 60km, recording similar intertidal water temperatures that were both significantly different from intertidal water temperatures recorded at Bermagui, which is approximately 210km south of Kiama (Fig. 3.2, Table 3.2). For example, the annual daily mean water temperatures recorded by *in situ* data loggers at Garie Beach, Kiama and Bermagui ranged from 18.7±2.4, 18.7±2.8 and 17.4±2.2ºC, respectively (Table 3.2). However, intertidal water temperatures appeared to be consistently more variable at Garie Beach and Kiama than they were at Bermagui and Mallacoota and this was not detected by satellite SST data (Fig. 3.2 and 3.3).

3.3.2 Comparisons of temperature variability at local-scales

Comparisons between several loggers at Garie Beach showed that intertidal temperatures vary both with intertidal height and between different sites along the shore (Fig. 3.4; Table 3.3). Not surprisingly, temperatures increased and generally became more variable with increasing intertidal height. For example, maxima and minima air temperatures across both sites ranged from 52.4°C to 3.8°C within the high intertidal zone, 50.3°C to 5.8°C within the mid intertidal zone and 49.6°C to 6.7°C within the low intertidal zone. Daily air and water temperatures recorded by loggers within different sites but at equivalent intertidal heights were shown to be highly correlated, though

Table 3.1. Seasonal and annual variation in daily means, maxima and minima of air and water temperatures ±SD from *in situ* temperature data loggers within the mid intertidal

zone at the four study locations between June 2008 and May 2009. Max/Min represents the highest and lowest temperatures recorded at each location during a specific season

	2008						**2009**		**Annual**	
	Winter (June – Aug)		Spring (Sept – Nov)		Summer (Dec – Feb)		Autumn (Mar – May)		2008/09	
	Mean	Max/ Min	Mean	Max/ Min	Mean	Max/ Min	Mean	Max/ Min	Mean	Max/ Min
Air Temperatures										
Daily mean										
Garie Beach	15.4±1.8		18.2±2.8		22.3±2.7		20.4±2.5		19.1±3.6	
Kiama	14.6±1.8		17.8±2.5		21.7±2.4		20.3±2.4		18.6±3.5	
Bermagui	13.0±2.0		15.9±2.6		20.2±2.3		19.0±2.6		17.0±3.7	
Mallacoota	11.6±1.9		15.8±3.7							
Daily maxima										
Garie Beach	18.6±3.0	30.3	24.4±7.8	45.5	29.4±7.7	50.8	25.9±6.8	47.9	24.5±7.7	50.8
Kiama	19.1±2.9	28.7	25.1±6.4	40.1	27.8±5.5	42.0	25.3±5.4	42.3	24.3±6.1	42.3
Bermagui	16.8±3.1	27.9	20.4±4.9	32.5	24.2±4.4	37.0	22.6±3.5	32.6	21.0±4.9	37.0
Mallacoota	16.3±3.6	29.4	23.8±7.1	40.8						
Daily minima										
Garie Beach	12.3±2.6	7.6	14.5±2.2	8.2	18.0±1.4	14.1	17.0±2.5	10.4	15.4±3.2	7.6
Kiama	10.2±2.6	5.3	13.2±2.5	7.1	17.7±1.6	14.2	16.7±2.7	9.5	14.4±3.8	5.3
Bermagui	10.0±2.5	5.5	12.5±2.6	6.2	17.2±1.9	12.5	16.1±2.9	8.8	13.9±3.8	5.5
Mallacoota	8.4±2.1	3.8	10.6±2.7	5.8						
Water Temperatures										
Daily mean										
Garie Beach	16.8±1.5		16.7±1.3		20.2±1.5		20.9±1.5		18.6±2.4	
Kiama	16.9±2.1		16.3±1.4		19.5±1.5		21.4±2.0		18.7±2.8	
Bermagui	15.1±1.2		16.1±1.2		19.2±1.1		19.4±1.1		17.4±2.2	
Mallacoota	13.8±0.9		15.7±1.4							
Daily maxima										
Garie Beach	17.5±1.8	23.1	17.3±1.4	21.1	20.9±1.6	25.3	21.7±1.9	29.6	19.4±2.6	29.6
Kiama	17.9±2.4	22.6	17.1±1.6	22.5	20.1±1.6	27.0	22.4±2.4	29.6	19.5±2.9	29.6
Bermagui	15.2±1.2	17.5	16.3±1.2	19.4	19.5±1.1	21.5	19.6±1.1	21.8	17.6±2.3	21.8
Mallacoota	13.9±1.0	15.9	15.9±1.6	18.7						
Daily minima										
Garie Beach	16.2±1.6	13.5	16.2±1.4	12.7	19.4±1.6	16.1	20.3±1.4	17.2	18.1±2.4	12.7
Kiama	16.0±2.1	11.2	15.4±1.9	10.3	18.8±1.7	15.1	20.5±2.0	13.6	17.8±2.8	10.3
Bermagui	14.9±1.3	13.3	15.9±1.3	13.5	18.8±1.2	14.1	19.1±1.2	16.6	17.2±2.2	13.3
Mallacoota	13.7±0.9	12.3	15.4±1.3	13.3						

Table 3.2. Results of an analysis of variance (ANOVA) testing for the differences in daily mean, maximum and minimum air and water temperatures (log (x+1) - transformed) among locations across four seasons

Source	df	SS	*F*	p
Air Temps				
Daily mean				
Location	2	2.65	85.01	<0.0001
Season	3	23.28	497.91	<0.0001
Location*Season	6	0.24	2.59	0.0170
Error	1068	16.65		
Daily max				
Location	2	4.57	55.20	<0.0001
Season	3	20.92	168.28	<0.0001
Location*Season	6	0.35	1.40	0.2108
Error	1068	44.25		
Daily min				
Location	2	2.35	40.17	<0.0001
Season	3	38.39	433.42	<0.0001
Location*Season	6	0.96	5.46	<0.0001
Error	1068	31.21		
Water Temps				
Daily mean				
Location	2	0.66	53.17	<0.0001
Season	3	9.89	442.87	<0.0001
Location*Season	6	0.29	7.09	<0.0001
Error	805	4.97		
Daily max				
Location	2	1.40	99.29	<0.0001
Season	3	7.73	364.93	<0.0001
Location*Season	6	0.35	8.36	<0.0001
Error	805	5.69		
Daily min				
Location	2	0.21	13.88	<0.0001
Season	3	8.55	368.83	<0.0001
Location*Season	6	0.23	4.88	<0.0001
Error	805	6.22		

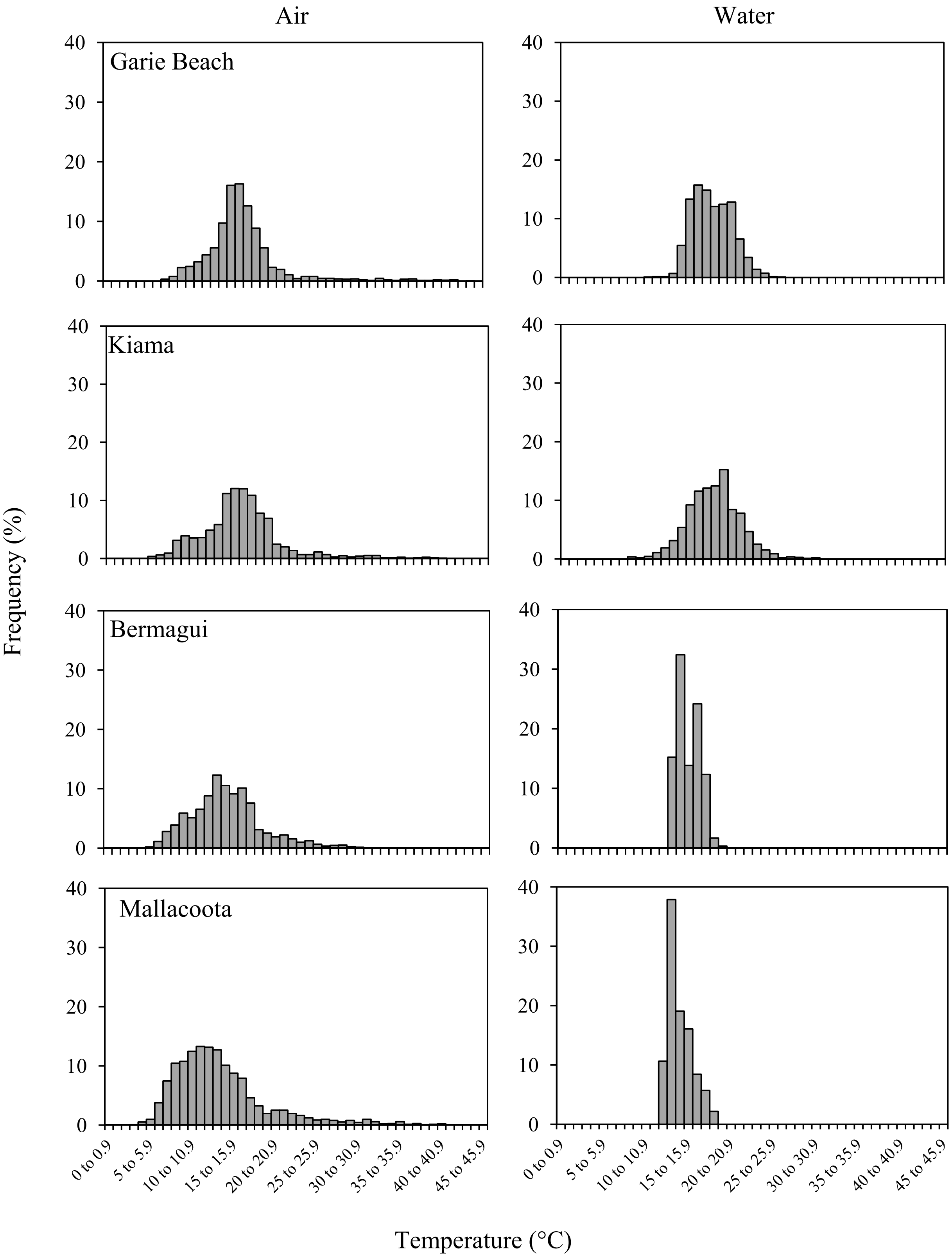


Figure 3.2. Frequency distributions of air and water temperatures measured at the four study locations using *in situ* loggers from 1 June to 30 November 2008. Locations are arranged from north to south.

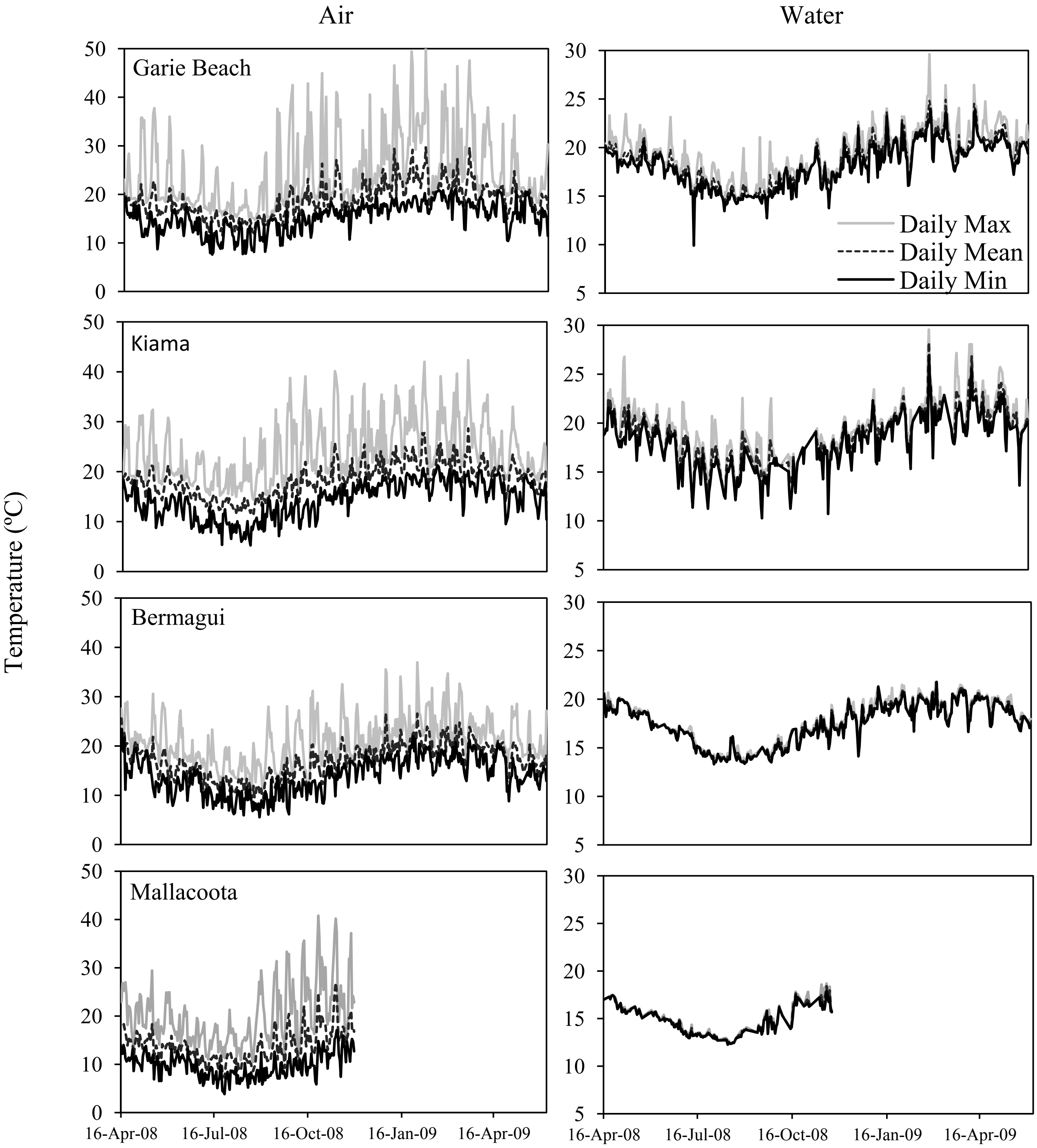


Figure 3.3. Daily mean, maximum and minimum air and water temperatures recorded at the four study locations using *in situ* data loggers from 16 April 2008 to 6 June 2009 (Mallacoota data only until 10 December 2008). Note different scales on y-axis.

paired t-tests generally revealed that temperatures were significantly different between sites across all three intertidal heights (Fig. 3.4, Table 3.3). For example, maximum air temperatures within the high and mid intertidal zones were on average 2.3°C and 2.7°C greater respectively in site one compared to site two. In comparison, differences in air temperatures between sites were smallest within the low intertidal zone, where on average daily mean, maxima and minima air temperatures differed by no more than 0.2°C (Table 3.3). Therefore, depending on intertidal height, intertidal invertebrates within equivalent microhabitats separated by 10's of metres may experience dramatically different temperatures. Not surprisingly, water temperatures varied less across the different intertidal heights and were generally more highly correlated between the two sites in comparison to air temperatures.

3.3.3. Satellite versus *in situ* logger water temperatures

Comparison of SST and *in situ* logger estimates of water temperature revealed that, although the two sets of measures were always significantly correlated, they typically produced significantly different estimates of absolute temperatures. For example, at all four study locations daily satellite SSTs 7km offshore were significantly correlated with daily mean water temperatures recorded by *in situ* loggers within the mid intertidal zone, although the correlation co-efficient varied substantially among locations, ranging from 0.50 at Kiama to 0.77 at Bermagui (Fig. 3.5, Table 3.4). Similarly, means, maxima and minima of monthly satellite SST were significantly correlated with water temperatures estimated by intertidal loggers, except for the most southerly location, Mallacoota (Fig. 3.5, Table 3.4). The strength of correlations between monthly measures varied considerably more among locations than correlations between daily means (Table 3.4).

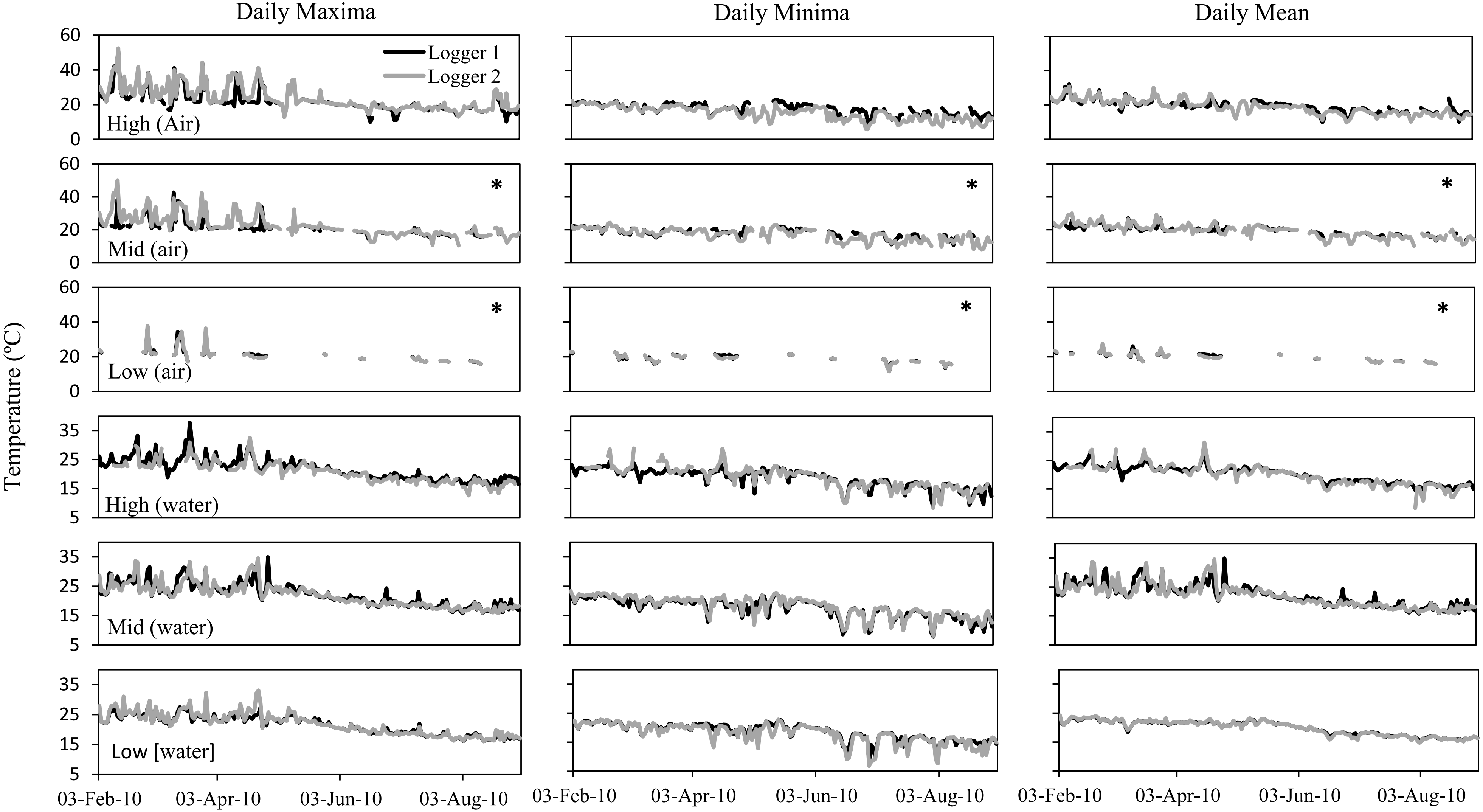


Figure 3.4. Comparisons of the air and water temperatures at two sites at Garie Beach and across high, mid and low intertidal heights from 3 February to 31 August 2010. Daily maxima, minima and mean temperatures were calculated from *in situ* temperature logger data recorded every hour.
(*) Incomplete data – see Methods.

Table 3.3. Summary of paired t-tests and Pearson correlations comparing daily mean, maxima and minima of air and water temperatures measured using *in situ* loggers across two sites within the high, mid and low intertidal zones, at Garie Beach from 3 February to 5 October 2010 (Fig. 3.2). Mean and max difference refers to the average and maximum differences between temperatures measured by loggers within each of the two sites, respectively. (*) p-value <0.001

	df	Difference (ºC)		t-value	p-value	Pearson's correlation (r)
		Mean	Max			
Air temperatures						
High						
Mean	168	0.41	7.10	2.72	0.007	0.784*
Max	168	2.28	20.05	6.96	<0.0001	0.660*
Min	168	2.10	10.78	11.21	<0.0001	0.609*
Mid						
Mean	115	0.38	9.5	1.93	0.057	0.712*
Max	115	2.67	22.56	5.86	<0.0001	0.524*
Min	115	1.12	7.69	6.15	<0.0001	0.664*
Low						
Mean	63	0.16	2.28	2.04	0.046	0.932*
Max	63	0.13	4.65	1.09	0.280	0.954*
Min	63	0.18	2.09	2.04	0.046	0.908*
Water temperatures						
High						
Mean	209	0.29	5.24	3.04	0.003	0.880*
Max	209	0.33	7.25	1.47	0.142	0.545*
Min	209	0.02	7.09	0.16	0.873	0.759*
Mid						
Mean	209	0.32	4.62	6.73	<0.0001	0.951*
Max	209	0.21	9.99	1.67	0.096	0.790*
Min	209	0.47	5.53	5.75	<0.0001	0.876*
Low						
Mean	209	0.04	1.86	2.07	0.040	0.987*
Max	209	0.35	7.87	4.54	<0.0001	0.920*
Min	209	0.62	7.45	7.00	<0.0001	0.861*

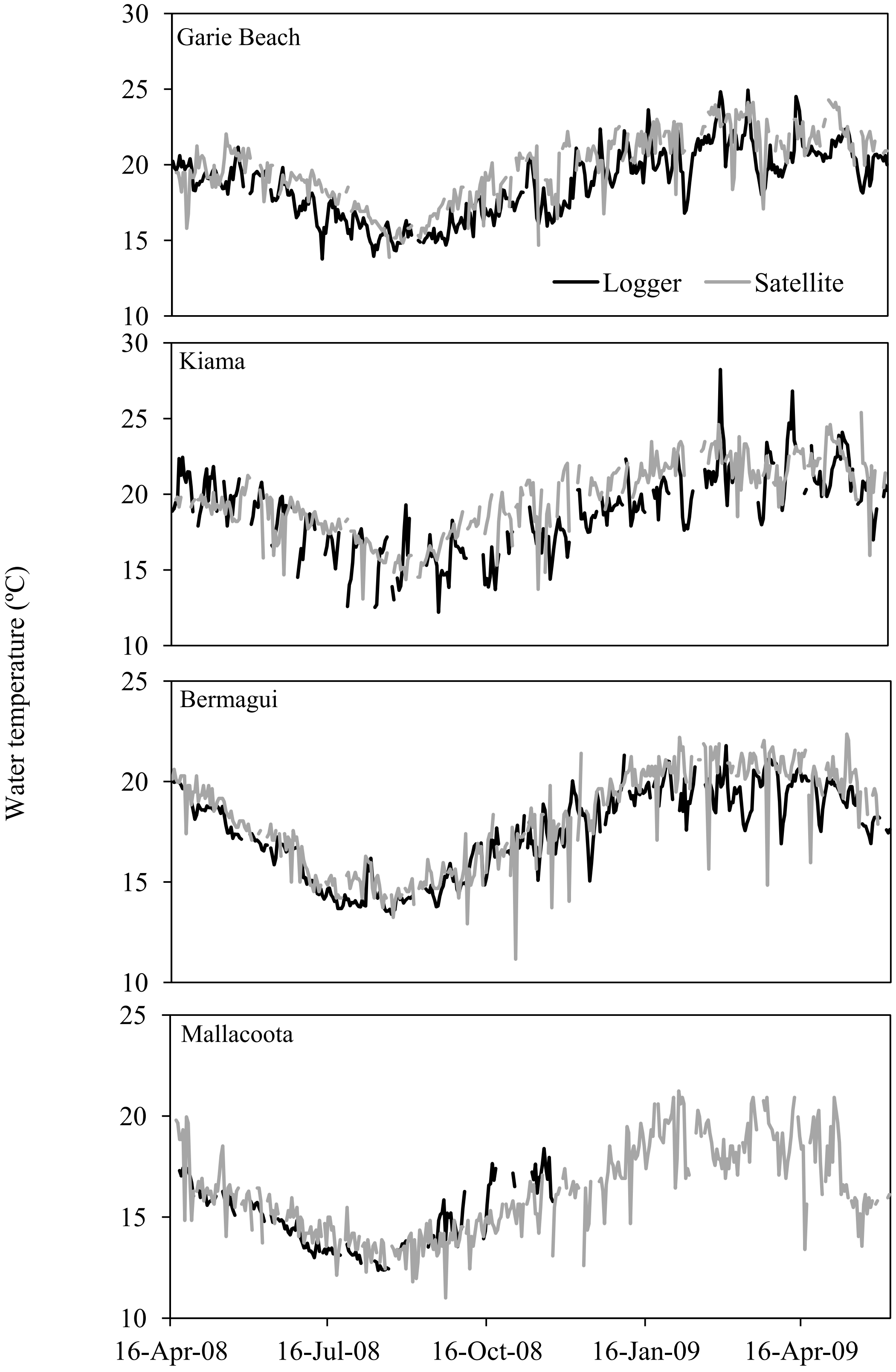


Figure 3.5. Daily mean water temperatures recorded by *in situ* loggers within the mid intertidal zone at each of the four study locations and satellite sea-surface temperatures (SST) approximately 7km offshore of each of the four study locations from 16 April 2008 to 6 June 2009 (Mallacoota data only until 10 December 2008). Note different scale on y-axis for Bermagui and Mallacoota.

Table 3.4. Summary of paired t-tests and Pearson correlations comparing daily means and monthly means, maxima and minima of water temperatures derived from *in situ* loggers within the mid intertidal zone at the four study locations with satellite SST approximately 7km offshore of each location from 16 April 2008 to 6 June 2009 (Fig. 3.3). Mallacoota data only extends to 10 December 2008. Mean and max difference refers to the average and maximum differences between water temperatures measured by *in situ* loggers and satellites, respectively. (*) p-value <0.05 (**) p-value <0.001

	df	Difference (ºC)		t-value	p-value	Pearson's correlation (r)
		Mean	Max			
Daily means						
Garie Beach	363	1.03	4.98	13.55	<0.001	0.64**
Kiama	266	0.81	6.67	6.75	<0.001	0.50**
Bermagui	341	0.64	6.24	10.07	<0.001	0.77**
Mallacoota	147	0.04	3.20	0.40	0.655	0.58**
Monthly means						
Garie Beach	12	1.19	1.80	10.95	<0.001	0.97**
Kiama	12	1.05	2.68	3.61	0.004	0.80**
Bermagui	12	0.59	1.28	5.50	<0.001	0.98**
Mallacoota	6	0.20	1.31	0.59	0.578	0.63**
Monthly maxima						
Garie Beach	12	0.49	1.90	1.73	0.110	0.89**
Kiama	12	0.05	4.44	0.08	0.941	0.55*
Bermagui	12	0.78	2.20	4.44	0.001	0.93**
Mallacoota	6	0.06	1.90	1.06	0.919	0.41
Monthly minima						
Garie Beach	12	0.63	3.15	1.94	0.077	0.68**
Kiama	12	1.29	6.03	2.51	0.027	0.53*
Bermagui	12	1.02	2.72	2.68	0.020	0.52*
Mallacoota	6	1.26	2.70	3.33	0.016	0.36

Although daily satellite SST and daily logger water temperatures were strongly correlated, absolute estimates of water temperature were significantly different from each other, with the exception of temperatures recorded at Mallacoota (Table 3.4). Daily satellite SST were generally greater than logger water temperatures with maximum differences at times reaching 6.7°C, but on average these differences were less than ≈1°C across all four locations and decreased with increasing latitude (Fig. 3.5, Table 3.4). Paired t-tested also revealed that loggers often recorded significantly higher monthly mean, maxima and minima temperatures compared to satellites with maximum and mean differences reaching 6°C and 1.3°C respectively (Table 3.4).

3.3.4 Weather station versus *in situ* logger air temperature

At all four locations, daily means, maxima and minima of air temperature recorded by *in situ* loggers and weather stations were all significantly correlated (Fig. 3.6, Table 3.5), although these correlations were substantially weaker than those between daily satellite SST and intertidal water temperatures (compare Table 3.4 and 3.5). With the exception of minimum and mean air temperatures at Kiama and Bermagui respectively, *in situ* loggers consistently recorded significantly higher daily air temperatures than weather stations (Fig. 3.6), with differences most pronounced for daily maximum air temperatures (Table 3.5). For example, across the four locations daily maximum air temperatures recorded by *in situ* loggers were on average 2.6°C to 4.2°C higher than daily maximum air temperatures recorded by weather stations (Fig. 3.6, Table 3.5). In contrast, daily minimum air temperatures recorded by *in situ* loggers were on average only 0.1°C to 1.5°C higher than daily minimum air temperatures recorded by weather stations. Maximum differences in mean, maxima and minima air

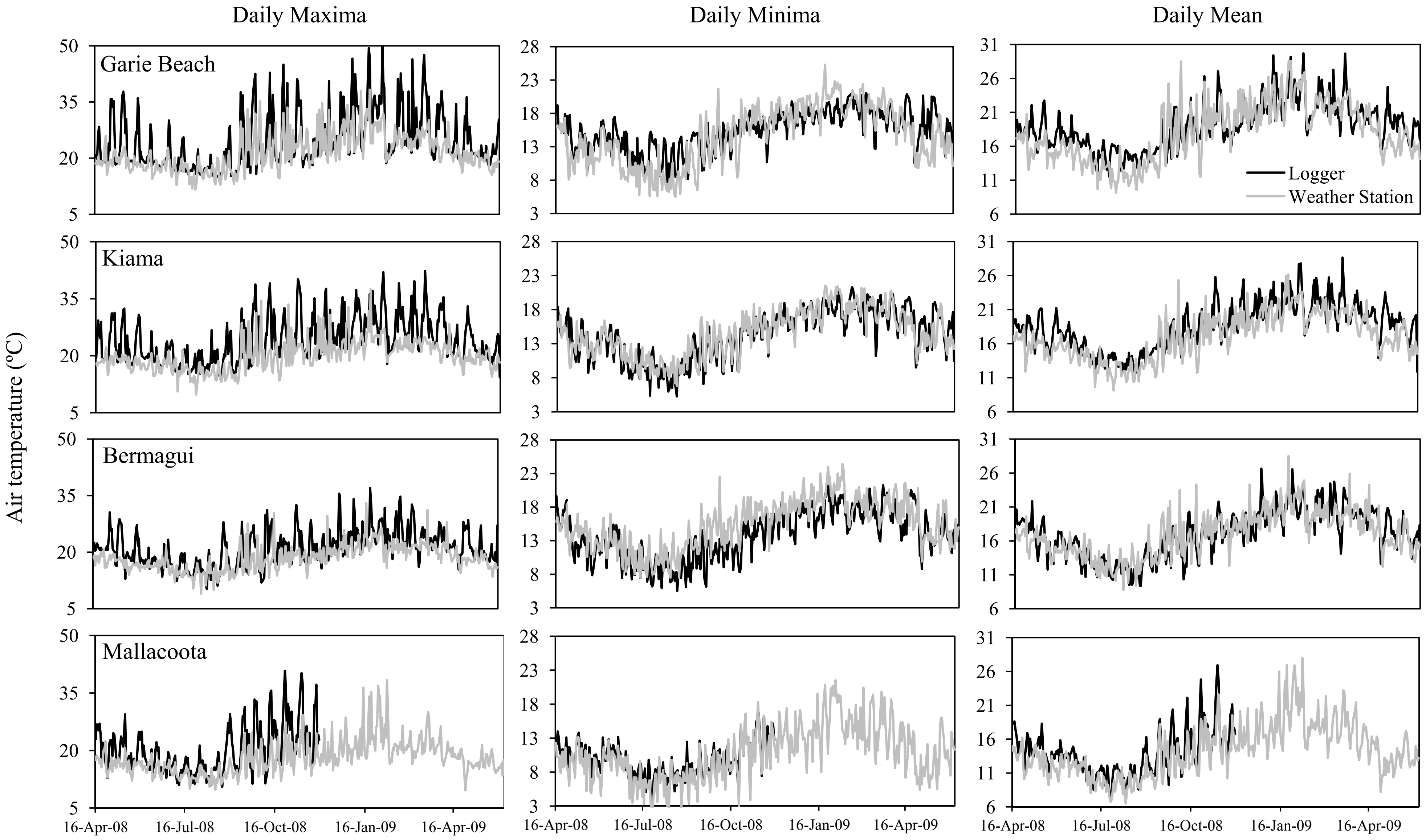


Figure 3.6. Daily air temperatures recorded within the mid intertidal zone using *in situ* loggers and weather station temperatures at each of the four study locations from 16 April 2008 to 6 June 2009 (Mallacoota data only until 10 December 2008). Note different scales on y-axis.

Table 3.5. Summary of paired t-tests and Pearson correlations comparing daily means, maxima and minima of air temperatures derived from *in situ* loggers within the mid intertidal zone at the four study locations with air temperatures obtained by terrestrial weather stations no more than 28km away from 16 April 2008 to 6 June 2009 (Fig. 4). Mallacoota data only extends to 10 December 2008. Mean and max difference refers to the average and maximum differences between air temperatures measured by *in situ* loggers and weather stations, respectively. (*) p-value <0.001

	df	Difference (ºC)		t-value	p-value	Pearson's correlation (r)
		Mean	Max			
Daily means						
Garie Beach	416	1.02	9.56	7.84	<0.0001	0.60*
Kiama	416	1.47	7.44	13.69	<0.0001	0.62*
Bermagui	410	0.08	19.20	0.73	0.4671	0.60*
Mallacoota	228	1.53	7.71	12.41	<0.0001	0.69*
Daily maximum						
Garie Beach	416	2.98	23.19	10.34	<0.0001	0.39*
Kiama	416	4.23	18.77	16.70	<0.0001	0.27*
Bermagui	410	2.59	21.00	12.46	<0.0001	0.26*
Mallacoota	228	3.90	18.17	12.82	<0.0001	0.49*
Daily minimum						
Garie Beach	416	0.73	10.32	5.02	<0.0001	0.54*
Kiama	416	0.10	7.42	1.11	0.2688	0.73*
Bermagui	410	1.50	18.40	12.53	<0.0001	0.61*
Mallacoota	228	1.03	8.30	10.72	<0.0001	0.76*

temperatures recorded by *in situ* loggers and weather stations ranged from 19.2, 23.2 and 18.4°C respectively, which are considerably greater than similar comparisons of *in situ* logger water temperatures and satellite SST (compare Table 3.4 and 3.5).

3.3.5. Biologically relevant temperature variation

Regardless of latitude, *in situ* loggers recorded a considerably greater number, frequency and duration of extreme temperature events compared to nearby weather stations (Table 5). For example, the *in situ* logger at Garie Beach recorded 29 and 44 days where temperatures reached 35°C and 30°C respectively, in comparison weather stations detected only two and 19 days reaching 35°C and 30°C respectively. The

Table 3.6. Comparison of biologically important temperature measurements recorded by an *in situ* data logger within the mid intertidal zone at each of Garie Beach, Kiama and Bermagui with nearby terrestrial weather stations during the summer of 2008/09. *30°C temperature events were classified as any day where air temperatures reached 30°C. Data from Mallacoota were only available until 10 December 2008 and therefore were not included in the analysis.

	Number of days max temp		Duration (hours spent above 30°C)	Frequency (average time between 30°C events* - hours ±SD)
	>35°C	>30°C		
Garie Beach				
In situ data logger	29	44	111	42.8±55.7
Weather station	2	19	105	86.3±99.6
Kiama				
In situ data logger	15	44	95	43.2±45.9
Weather station	1	6	24	255±206.6
Bermagui				
In situ data logger	3	17	29	123.1±105
Weather station	0	1	3	-

Table 3.7. Number of rapid heating events recorded by *in situ* data loggers and remote sensing devices among 3 of the study locations during the summer of 2008/09.*Heating rates were determined by the difference in daily satellite SST and daily maximum air temperatures recorded by weather stations. Data from Mallacoota were only available until 10 December 2008 and therefore were not included in the analysis.

	Number of days when temperature increased by more than		
	15°C within 4 hrs	10°C within 3 hrs	5°C within 3 hrs
Garie Beach			
In situ data logger	24	40	62
Weather station and satellite*	2	15	45
Kiama			
In situ data logger	10	34	74
Weather station and satellite*	1	5	12
Bermagui			
In situ data logger	5	16	50
Weather station and satellite*	0	2	11

number, frequency and duration of extreme temperature events also increased with decreasing latitude, indicating that northern locations maybe more thermally stressful for intertidal invertebrates. For example, the number of days where temperatures reached 35°C decreased from 29, 15 to three and the total number of hours spent above 30°C decreased from 111, 95 and 29 at Garie Beach, Kiama and Bermagui, respectively. *In situ* loggers also recorded a considerably greater number of rapid heating events compared to those recorded by weather stations and satellites across all locations (Table 6). For example, at Garie Beach the *in situ* logger recorded 24 days where temperatures increased by over 15°C within four hours whereas weather stations and satellites only recorded two. Logger data reveal that heating rates also vary with latitude (Table 6). For example, the number of days where temperatures increased by more than 15°C within 4 hours decreased from 24, 10 and five at Garie Beach, Kiama and Bermagui, respectively.

3.4 Discussion

The strong correlations that I detected between daily or monthly temporal variation in temperatures estimated by both satellite and weather station data and *in situ* intertidal temperature loggers provides superficial validation of the use of remote sensing to characterise the intertidal environment. However, even estimating variation at these coarse scales, remotely sensed and *in situ* estimates of air and water temperature at times differed by up to 23.2 and 6.7 degrees respectively. The results also show that the use of satellites and weather stations as proxies of intertidal temperatures significantly underestimates biologically important extreme temperature events.

3.4.1 Temperature variability at geographic scales

Excluding the most southern location, *in situ* temperature variability among locations was shown to be highly variable, with average air and water temperatures generally declining with latitude. However, *in situ* air temperatures recorded at Mallacoota, the most southern location, appeared greater and more variable than temperatures recorded at Bermagui, suggesting that intertidal air temperatures along the southeast coast of Australia may not necessarily decline with increasing latitude. This might explain why I previously did not find early life history processes of *T. rosea* to decline with latitude (see Chapter 2).

Helmuth et al. (2006a) similarly reported that among site variation in the body temperatures of mussels were not well correlated with latitude. This unexpected lack of correlation with latitude most likely reflects differences among sites with respect to wave exposure (Harley & Helmuth 2003, Fitzhenry et al. 2004, Davenport & Davenport 2005), even though wave exposure was subjectively quantified and standardised by choosing locations with similar aspects. Indeed, Jackson (2010) demonstrated that the degree of wave exposure on rocky intertidal shores influences air temperatures within crevices. However, further research is needed to understand the role of wave exposure on latitudinal patterns of intertidal air temperature within this region. Poloczanska et al. (2011) used a regional wave-fetch model to show that a biogeographic discontinuity of rocky intertidal species within southern Queensland was most likely due to differences in the degree of wave-exposure.

3.4.2. Satellite and weather station data versus logger data

The results of this study show that although strongly correlated, *in situ* intertidal water temperatures are significantly different to those estimated by satellites, with *in situ* loggers generally recording lower water temperatures than satellites. This strong correlation between satellite SST and intertidal water temperature supports an equivalent study undertaken within the subtidal where nearshore benthic water temperatures and satellite SST were highly correlated to, yet 1 to 2°C lower than, satellite SST within temperate regions of Western Australia (Smale & Wernberg 2009). As I observed when comparing *in situ* and satellite water temperatures, air temperatures recorded by *in situ* loggers and weather stations were both strongly correlated and significantly different. Nonetheless, correlations between weather stations and loggers were considerably weaker than correlations between satellites and loggers, and *in situ* air temperatures were generally warmer than weather station air temperatures. The consistently higher air temperatures recorded by *in situ* loggers may reflect differences in microclimates. For example, *in situ* loggers in the present study were exposed to full UV light while weather station temperature readings were taken within shaded housings (information from the Australian Bureau of Meteorology, www.bom.gov.au).

Importantly, this study showed that the effectiveness of satellite derived SST and weather station air temperatures as proxies of intertidal water and air temperatures varied across geographic locations. This geographic variation in the accuracy of satellite SST in estimating intertidal water temperatures may reflect differences in nearshore water circulation across the four study locations. For instance, at large spatial scales sea surface temperatures in this region are mostly influenced by large warm-core eddies that move in an anti-clockwise direction from north to south (Huyer et al. 1988, Roughan & Middleton 2002, 2004). However, at relatively small spatial scales the movement of nearshore water may also be influenced by subtidal topography, including islands (see Mace & Morgan 2006), and localised atmospheric conditions. Therefore, the association between intertidal and offshore water temperatures may vary among locations because offshore water may not always move shoreward.

The effectiveness of weather stations as estimates of intertidal air temperatures also varied among locations. Surprisingly, however, correlations between weather stations and *in situ* loggers at Kiama and Mallacoota, where loggers were located within several hundred metres of weather stations, were no stronger than correlations for Garie Beach and Bermagui where loggers were up to 28km from weather stations. This suggests that the value of weather station data as surrogates for values estimated by *in situ* loggers could not be improved by standardised usage of weather stations in close proximity to rocky shores of interest.

3.4.3 Biologically relevant temperature variability

The physiological performance of many marine and terrestrial organisms has long been understood to be strongly influenced by short term extremes and rapid fluctuations in temperature (Easterling et al. 2000, Underwood & Chapman 2000, Denny et al. 2009). Consequently thermal limits are often used to estimate the vulnerability of a particular species to *in situ* heat stress (Denny et al. 2006, Dong et al. 2008). My results show that weather station data are unlikely to detect acute changes in intertidal air temperatures or accurately characterise temperature extremes relevant to organisms. Since air temperatures are believed to play a significant role in the physiological processes of intertidal organisms (Schiel et al. 2004) this is a major discrepancy that may have important implications when using weather station data to model past and future affects of temperature variability on species distributions and range limits. For instance, Denny et al. (2006) used weather station data to create a model of predicted body temperatures for the intertidal limpet *Lottia gigantea* and found that over a five-year period, body temperatures only reached lethal limits (34-38ºC) on three days. My results would suggest that this might be a serious underestimation of extreme intertidal temperature events.

Mortality caused by heat stress depends not only on the frequency of high temperature events but also on the rate of heating and cooling experienced by organisms (Denny et al. 2006), which in the absence of behavioural avoidance will be determined by the timing of low tides, the degree of wave exposure and weather (Harley & Helmuth 2003, Harley 2008, Mislan et al. 2009). In the present chapter I show that satellite SST and weather station air temperatures are unlikely to detect the majority of rapid heating events within the mid intertidal zone. Therefore, I argue that attempts to predict the effect of temperature change on intertidal taxa require *in situ* measurements and should focus on biologically relevant variation.

The following chapters utilise fine-scale temperature measurements and thermal manipulations across a single rocky shore to test whether local temperature variability influences the early post-settlement life history stages of *T. rosea.*

CHAPTER 4 Manipulating thermal stress on rocky shores to predict patterns of recruitment of marine invertebrates under a changing climate

This chapter has been accepted for publication within the journal *Marine Ecology Progress Series.*

4.1 Introduction

As increases in global temperatures are expected to alter the physiology, ecology and biogeography of organisms worldwide it is not surprising that climate change research has increased rapidly over the past two decades (Harley et al. 2006; Helmuth et al. 2006b). At the heart of this research is an attempt to understand how physical parameters, such as rising atmospheric temperature and extreme temperature events, alter physiological processes that translate into long term shifts in the demography of populations and assembly of communities (Denny & Helmuth 2009, Helmuth et al. 2010). This is particularly true for rocky intertidal organisms where factors such as the tidal cycle, micro-topography, wind speed, air temperature and solar radiation cause body temperatures to fluctuate by more than 20°C within a few hours and differ significantly between individuals only centimetres apart (Denny et al. 2011, Helmuth et al. 2011). This thermal variability makes wave-swept rocky shores excellent systems to test and model the predicted biological impacts of increased temperatures associated with climate change (Pitt et al. 2010, Helmuth et al. 2011, Wethey et al. 2011b). In common with most species, it is the early life history stages of benthic invertebrates that are most vulnerable to changes in temperature (Gosselin & Qian 1997, Hunt & Scheibling 1997). Despite this,' few studies have measured the responses of newly settled larvae or recruits to temperature manipulations in the field (see Table 4.1).

In reviewing the literature I found 76 studies that have examined the effects of temperature on rocky intertidal invertebrates in the field (Table 4.1). The majority of field based experimental studies investigating the role of temperature on intertidal invertebrates do so by indirectly manipulating temperatures. Moreover, only 23 include an experimental component that manipulates temperature and, of these, 16 manipulated temperature indirectly by either shading or transplanting individuals across intertidal heights. Such indirect manipulations typically do not control for other potentially confounding factors, for example, levels of UV exposure that can vary with intertidal height (Harley & Helmuth 2003, Gosselin & Jones 2010). Additionally, only 23 studies assessed the effect of temperature on early life history stages of invertebrates and only five of these included an experimental component. In these five studies, temperatures altered by manipulating shade (Bertness 1989, Bertness et al. 1999b), macroalgae (Bertness et al. 1999a), substrate size (Gedan et al. 2011) and substrate type (Shanks 2009) influenced the early life history processes of barnacles (Table 4.1). Only one study directly manipulated temperature and this was achieved through the use of propane heaters and assessed the relationship between macroalgae diversity and resilience (Allison 2004).

The finding that field studies have rarely assessed the effect of temperature variation on the early life history stages of intertidal invertebrates is surprising because settlers and recruits are known to be particularly vulnerable to heat and desiccation stress (Gosselin & Qian 1997, Hunt & Scheibling 1997) and early life history processes play important roles in structuring the size and distribution of adult populations (Connell 1985, Minchinton & Scheibling 1991, Caley et al. 1996, Menge 2000). This gap in research is most likely due to a combination of difficulties, including teasing apart multiple factors that influence body temperatures of intertidal invertebrates (Helmuth et al. 2006b), undertaking field measurements of early life history processes (Keough & Downes 1982, Minchinton & Scheibling 1993b), and measuring temperature variability at a scale relevant to individual settlers.

Studies examining early life history processes and quantifying patterns of recruitment of intertidal invertebrates have often used, with great success, artificial settlement surfaces, such as ceramic tiles and PVC plates covered in Safety Walk® tape

(SWT) (Farrell et al. 1991, Lagos et al. 2005b, Broitman et al. 2008b). This research has shown that differences in substrate temperature, texture, etc. between artificial and natural rock surfaces can influence early mortality and recruitment (e.g. Raimondi 1988a, McGuinness 1989, Herbert & Hawkins 2006, Shanks 2009, Menge et al. 2010). For example, Shanks (2009) found that plexiglas plates covered in grey SWT were significantly warmer and caused higher early post-settlement mortality in comparison to cooler, ceramic tiles, and Menge et al. (2010) discovered that barnacle settlement was greater on plates covered in SWT compared to natural rock. These studies suggested that plates covered with SWT could be a useful way of manipulating temperature at a single intertidal height on rocky shores and to test for effects on early life history processes. Such an experimental manipulation would also benefit from recently developed infrared imaging techniques used to quantify fine-scale variation in both physical and biological characteristics of rocky intertidal shores (Murphy et al. 2006, Underwood & Murphy 2008, Chapperon & Seuront 2011, Cox & Smith 2011). The advantage of such infrared sensing is that temperature variability can be assessed at spatial scales relevant to newly settled benthic marine invertebrates.

The primary aim of this chapter was to use artificial settlement plates covered with SWT of different colours to manipulate substrate temperatures at a single tidal height on a rocky shore and to examine the effects on settlement, early post-settlement growth, survival and recruitment of the barnacle *Tesseropora rosea.* A secondary objective was to investigate whether the thermal properties of settlement plates covered in SWT are similar to those of natural rock. I achieved this by comparing settlement, early post-settlement growth, survival and recruitment of *T. rosea* on natural rock to the artificial settlement plates.

Table 4.1. Summary of key methodologies used in field studies measuring temperature and its effects on rocky intertidal organisms. Search excluded laboratory or modelling studies without a field component, as well as studies that did not directly compare temperature variability to biological processes.*Safety-Walk Tape

Was temperature manipulated?	How was temperature manipulated?	How was temperature measured?	Taxa	Substrate type	Life-history stage	Ecological process	Geographic region	Study
Yes	Propane heater	Thermometer	Macroalgae	Rock	Adult	Resilience	Oregon, USA	Allison 2004
Yes	Shading, substrate size	Thermistor	Barnacle	Rock	Juvenile-adult	Intraspecific competition	Rhode Is., USA	Bertness 1989
Yes	Shading, adult density	*Not specified*	Macroalgae, mussels	Rock	Adult	Positive interactions	Rhode Is., USA	Bertness & Leonard 1997
Yes	Removal of macroalgae	Data loggers	Numerous	Rock	Juvenile-adult	Positive interactions	Maine, USA	Bertness et al. 1999a
Yes	Shading, recruit density, transplants	Weather station	Barnacle	Rock	Juvenile	Climate	Maine, USA	Bertness et al. 1999b
Yes	Shading, macroalgae density	Data logger, thermocouple	Chiton	Rock	Adult	Positive interactions	Washington, USA	Burnaford 2004
Yes	Painted shells black and white	Thermocouple	Gastropod	Rock	Adult	Aggregation	NSW, Australia	Chapman & Underwood 1996
Yes	Shading	Thermocouple	Macroalgae	Rock	Adult	Thermal stress	Washington, USA	Dethier et al. 2005
Yes	Substrate size	Data logger	Barnacle	Rock	Juvenile	Thermal stress	Rhode Is., USA	Gedan et al. 2011
Yes	Shading	Infrared surface thermometer	Mussel	Vexar panel	Adult	Adult growth	Québec, Canada	Guichard et al 2001
Yes	Transplant	*Not specified*	Mussel	Rock	Adult	Thermal stress	Oregon, USA	Halpin et al. 2004
Yes	Transplant	Data logger	Macroalgae	Rock	Adult	Range limits	Washington, USA	Harley 2003
Yes	Shading	*Not specified*	Barnacles	Rock	Adult	Parasitism	Washington, USA	Harley & Lopez 2003
Yes	Shading	Thermocouple	Limpets	Black slate	Adult	Methodology	California, USA	Hayworth & Quinn 1990
Yes	Transplant	Data loggers	Mussel	Slate tiles	Adult	Range limits	North Carolina, USA	Jones et al. 2009
Yes	Transplant	Data loggers	Mussel	Slate tiles	Adult	Range shifts	Atlantic Coast, USA	Jones et al. 2010
Yes	Shading	Radiant thermometer, thermo-hygrometer	Mussel, barnacle	Ceramic tiles	Adult	Facilitation	Pacific Coast, Japan	Kawai & Tokeshi 2004
Yes	Shading	Data logger	Limpet, macroalgae	Rock	Adult	Herbivory	California, USA	Morelissen & Harley 2007
Yes	Transplant	Data logger	Mussels	Rock	Adult	Growth, survival	Pacific Coast, NZ	Petes et al 2007
Yes	Outfall of Power Station	Data logger	Numerous	Rock	Adult	Biodiversity	California, USA	Schiel et al. 2004
Yes	Shading, transplant	Biomimetic data logger	Mussels	Rock	Adult	Invasions	California, USA	Schneider & Helmuth 2007

Table 4.1. (continued)

Was temperature manipulated?	**How was temperature manipulated?**	**How was temperature measured?**	**Taxa**	**Substrate type**	**Life-history stage**	**Ecological process**	**Geographic region**	**Study**
Yes	Substrate type	Infrared surface thermometer	Barnacles	Plexiglas plates covered in grey SWT*, ceramic tiles	Juvenile	Recruitment	Oregon, USA	Shanks 2009
Yes	Outfall of Power Station	Data logger	Numerous	Rock	Adult	Biodiversity	California, USA	Steinbeck et al. 2005
Yes	Shading	*Not specified*	Macroalgae	Rock	Adult	Regulation	Isle of Man, UK	Thompson et al. 2004
No		Satellite SST	Mussels	Rock, Plastic mesh	Juvenile-adult	Recruitment	California, USA	Blanchette & Gaines 2007
No		Satellite SST	Numerous	Rock	Juvenile-adult	Biogeography	Pacific, USA	Blanchette et al. 2008
No		Buoy SST, data loggers	Mussel	Rock	Adult	Growth	California, USA	Blanchette et al. 2007
No		Satellite SST	Numerous	Rock	Juvenile-adult	Biogeography	Central Chile	Broitman et al. 2001
No		Satellite SST	Barnacles, mussels	Ceramic plates, plastic mesh	Larva-juvenile	Recruitment	California, USA	Broitman et al. 2005
No		Satellite SST	Barnacles, mussels	PVC plates covered in SWT*, plastic mesh	Juvenile	Recruitment	Pacific Coast, USA	Broitman et al. 2008
No		Satellite SST	Barnacle	Rock	Juvenile-adult	Biogeography	Scotland	Burrows et al. 2010
No		Thermal imaging	Gastropod	Rock	Adult	Thermal stress	South Australia	Caddy-Retalic et al. 2011
No		Data logger	Mussel	Rock	Adult	Thermal stress	Rhode Is., USA	Carrington et al. 2009
No		Thermocouple	Barnacle	Rock	Adult	Mortality	Hong Kong, China	Chan et al. 2006
No		Infrared imagery	Gastropod	Rock	Adult	Thermoregulation	South Australia	Chapperon & Seuront 2011
No		*Not measured*	Anemone	Rock	Adult	Growth	Mediterranean	Chomsky et al. 2004
No		Thermocouple	Mussel	Rock Plastic mesh	Adult	Positive interactions	NSW, Australia	Cole 2010
No		Biomimetic data logger	Mussel	Aluminium plate	Adult	Thermal stress	California, USA	Denny et al. 2011
No		Biomimetic data logger	Mussels	Rock	Adult	Thermal stress	Oregon, USA	Fitzhenry et al. 2004
No		Data logger	Limpet	Rock	Juvenile-adult	Biogeography	California, USA	Gilman 2006
No		Biomimetic data logger	Mussel, barnacle	Rock	Adult	Vertical distribution	Washington, USA	Harley & Helmuth 2003
No		Biomimetic data logger	Mussels, limpets	Rock	Adult	Mortality	California, USA	Harley 2008
No		*Not specified*	Numerous	Rock	Adult	Predation	Pacific Coast, USA	Harley 2011
No		Thermocouple, data logger	Numerous	Rock	Adult	Amelioration	California, USA	Harley & O'Riley 2011
No		Biomimetic data logger	Mussels	Rock	Adult	Thermal stress	California, USA	Helmuth & Hofmann 2001
No		Biomimetic data logger	Mussels	Rock	Adult	Thermal stress	Washington, USA	Helmuth 1998
No		Thermocouple	Mussels	Rock	Adult	Thermal stress	Washington, USA	Helmuth 1999
No		Biomimetic data logger	Mussels	Rock	Adult	Thermal stress	Pacific Coast, USA	Helmuth et al. 2006
No		Data logger (SST only)	Barnacle	Rock	Juvenile-adult	Recruitment	English Channel	Herbert et al. 2007

Table 4.1. (continued)

Was temperature manipulated?	How was temperature manipulated?	How was temperature measured?	Taxa	Substrate type	Life-history stage	Ecological process	Geographic region	Study
No		Thermocouple	Mussel	Rock	Adult	Thermal stress	Washington, USA	Hofmann & Somero 1995
No		Weather station	Macroalgae	Rock	Juvenile-adult	Disturbance	Hong Kong, China	Hutchinson & Williams 2003
No		*Not specified*	Chitons	Rock	Adult	Vertical distribution	Pacific coast, Costa Rica	Jorger et al. 2008
No		Data logger (SST only)	Barnacle	White PVC pipe	Juvenile	Settlement	Baja California	Ladah et al. 2005
No		Data logger (SST only)	Barnacles	Plexiglas plates covered in grey SWT*	Juvenile	Settlement, recruitment	Central Chile	Lagos et al. 2005
No		Data logger (SST only)	Numerous	Plexiglas plates covered in grey SWT*, plastic mesh	Juvenile	Recruitment	Central Chile	Lagos et al. 2007
No		Biomimetic data logger	Limpets	Rock	Adult	Methodology	Washington, USA	Lima & Wethey 2009
No		Infrared thermometer	Numerous	Rock	Adult	Habitat structure	Qld, Australia	Meager et al. 2011
No		Data logger	Mussels	Rock	Adult	Climate	Oregon, USA	Menge et al. 2008
No		Satellite SST	Mussels	Plastic mesh	Juvenile	Recruitment	Oregon, USA	Menge et al. 2009
No		ENSO, PDO, NPGO Oceanographic data	Barnacles, mussels	PVE plates covered in SWT*, plastic mesh	Juvenile	Recruitment	Oregon, USA	Menge et al. 2011
No		Thermocouple	Gastropod	Rock	Adult	Thermal stress	California, USA	Miller & Denny 2011
No		Data logger	Crab	Rock	Adult	Biogeography	Pacific Coast, Chile	Monaco et al. 2010
No		Thermocouple	Periwinkle	Rock	Adult	Aggregations	Central Chile	Munoz et al 2008
No		Data logger	Barnacles	Rock	Juvenile	Recruitment	Pacific Coast, Japan	Munroe & Noda 2010
No		Thermocouple	Gastropod	Rock	Adult	Resource use	Québec, Canada	Pardo & Johnson 2004
No		Biomimetic data logger	Sea star	Rock	Adult	Thermal stress	California, USA	Pincebourde et al. 2008
No		*Not measured*	Mussel	Rock	Adult	Thermal stress	Pacific Coast, USA	Place et al. 2008
No		*Not measured*	Barnacles	Rock	Adult	Thermal stress	Atlantic Coast	Power et al. 2011
No		*Not specified*	Whelk	Rock	Adult	Foraging	Mediterranean	Rilov et al. 2005
No		Buoy SST	Numerous	Rock	Juvenile-adult	Range shift	Central Chile	Rivadeneira & Fernandez 2005
No		Data logger	Sea star	Rock	Adult	Foraging	Oregon, USA	Sanford 2002
No		Buoy SST, Weather station	Numerous	Rock	Adult	Biogeography	Pacific Coast, USA	Schoch et al. 2006
No		Biomimetic data logger	Limpet	Rock	Adult	Thermal stress	Atlantic Coast	Seabra et al. 2010
No		Biomimetic data logger	Sea star	Rock	Adult	Thermal stress	British Columbia, Canada	Szathmary et al 2009
No		Data logger (SST only)	Barnacles	Plexiglas plates covered in SWT*	Juvenile	Settlement	Central Chile	Tapia & Navarrete 2010
No		Satellite SST	Numerous	Rock	Juvenile-adult	Range shift	Portugal-France	Wethey et al. 2011

4.2 Methods

4.2.1 Study region and species

This chapter focussed on the barnacle *T. rosea* on an exposed rocky intertidal shore at Garie Beach (34°10’38.1S, 151°03’57.8E) near Sydney in south eastern Australia. The rocky platform at Garie Beach is primarily composed of siltstone and is grey in colour. The platform has an east to north easterly aspect and an overall slight to moderate (10-20°) inclination. *In situ* measurements show that mid-intertidal air temperatures at Garie Beach (across both day and night) varied between 11.9°C and 38.6°C and were on average 20.8°C during the sampling period (8 March to 20 April 2011; see Appendix I). Wave heights in this region are greatest and most variable during February, March and June and at times may exceed 4m (Short & Trenaman 1992). East to south easterly waves are the most common and occur year round, with easterly waves peaking in March and November and south easterly waves peaking in May and November (Short & Trenaman 1992). *Tesseropora rosea* on this headland is abundant and populations have been continuously monitored over the past five years (Hidas et al. 2010, Lathlean et al. 2010). I have observed a distinct breeding and settlement period between January and June each year with larvae usually arriving in three distinct pulses, once in January, then from late February to early April and then again in May (Denley & Underwood 1979, Lathlean et al. 2010).

4.2.2 Manipulation of substratum temperatures

After preliminary investigations, I developed four treatments to manipulate substratum temperatures and investigate effects on the early life history processes of *T. rosea*. The first three treatments were artificial surfaces (10×10×0.5cm) of different colour: (1) grey PVC plates covered with black Safety Walk Tape (SWT) (3M™ Safety-Walk™ Slip-Resistant Material General Purpose 600 series); (2) grey PVC plates covered with clear SWT, and (3) white Acrylic plates covered with clear SWT (Fig. 4.1a, b, c). The fourth treatment was natural rock (10×10cm quadrats) that was initially cleared of all invertebrates and biofilm using a chisel and metal brush (hereafter referred to as rock) (Fig. 4.1d). Minor chemical differences do exist between black SWT, which is made of polyurethane coated with a solvent, and clear SWT, which is made of polyethylene without a solvent (3M, personal communication). Note that a simpler choice of materials, such as black, grey and white SWT on grey PVC plates, proved difficult due to time constraints and the unavailability of all three coloured SWT of equivalent textures.

The first three treatments were used to manipulate temperature and test for effects on settlement, early post-settlement growth, survival and recruitment of *T. rosea.* One advantage of using plates with SWT to manipulate substrate temperature is that all substrata have equivalent surface textures. Differences in colour among artificial surfaces would therefore not be expected to influence processes after barnacle settlement, other than by influencing substrate temperatures. Moreover, Caffey (1982) has shown that there was no influence of differently coloured rock on settlement of *T. rosea* and larvae are, therefore, unlikely to respond to the differently coloured surfaces at settlement. The fourth treatment allowed comparisons between natural rock and artificial surfaces.

Fifteen plates (five per treatment) were allocated haphazardly and screwed onto horizontal emergent rock, 1 to 2m apart, at mid intertidal heights characterised by moderate to high adult densities at Garie Beach on 7 March 2011. Five permanent quadrats of natural rock were also established at the same tidal height and interspersed amongst the 15 settlement plates. These areas of rock were horizontal to moderately sloping with at least 400cm^2 area of flat surface without crevices or depressions that could retain water during low tide.

To minimise any differences in chemical properties of differently coloured plates and SWT, I thoroughly cleaned plates using freshwater and allowed them to soak for 24 hrs before applying SWT. Once SWT was applied plates were further conditioned in the field for three-weeks before measuring settlement and early post-settlement processes, allowing natural biofilms to accumulate on all artificial surfaces and natural rock (Qian et al. 2003). I monitored plates daily and no barnacles were observed to have settled on plates or rock during this conditioning period. Therefore, I did not need to remove any settlers before the start of the experiment.

4.2.3 Measuring substratum temperatures using infrared imaging

To measure rock temperatures, infrared (IR) images were taken using a digital IR camera (Forward-looking Infrared S65 ThermaCAM, FLIR®) fitted with a germanium coated lens, which captures wavelengths between 7.5-13μm using a focal plane array uncooled microbolometer detector. Images were taken of quadrats 10 × 10cm in size, from 50cm above the substratum with each laser beam producing an arc length of 1.3 milliradians (mrad) when camera is held 1m away from the point of contact. Therefore, each IR image had a spatial resolution less than 1mm^2 /pixel. Measurements at these scales allowed comparison of rock temperature variability both within and among plates and quadrats. Importantly, measurements of rock temperature at this extremely fine (mm) scale should reflect the thermal stresses experienced by recently settled barnacles.

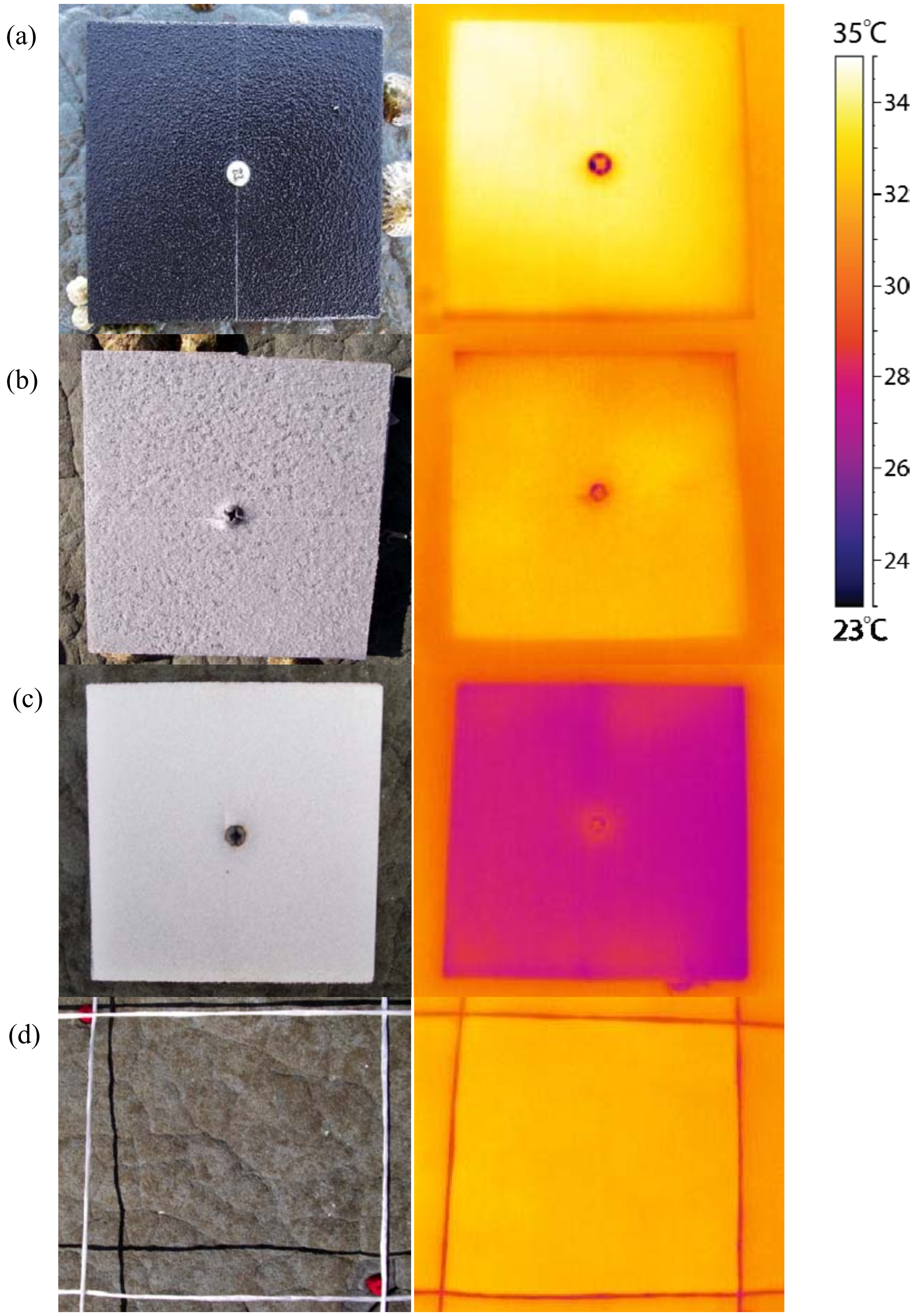


Figure 4.1. Photographs and infrared images of (a) black, (b) grey, and (c) white settlement plates and (d) natural quadrat. Infrared images were taken between 11:00am and 12:00pm (low tide: 11:45am) on 16 March 2011 when ambient air temperatures were on average 31.7°C.

The thermal resolution of the IR camera is 0.08°C at 30°C, with an accuracy of ±0.2°C (*see* below). This accuracy of the FLIR S65 ThermaCAM is superior to most other models that typically produce accuracies of ±2°C, or 2% of the reading. This is largely due to the camera's ability to automatically recalibrate measurements as frequently as once every 2 minutes (FLIR, personal communication). Emissivity (□) was set at 0.95 as previous studies demonstrate that emissivity values of rocky substrata and invertebrates on intertidal shores typically vary between 0.95 and 1.00 (Helmuth 1998, Denny & Harley 2006, Chapperon & Seuront 2011, Cox & Smith 2011). The plates used in this study are likely to have similar emissivity values to that of the natural substratum (personal observation). To avoid the potential effects of reflectance on estimates of rock and plate temperature, all quadrats and plates were shaded while IR images were being taken. Nevertheless, because variations in emissivity and reflectance can influence the accuracy of IR temperature measurements, ground-truthing was undertaken comparing rock temperatures from IR images and a digital thermocouple (Dick Smith Electronics™ Digital Multimeter, P/N: Q-1574). Both instruments were used to record rock temperatures within the mid shore region at Garie Beach during low tide. Rock temperatures during this ground-truthing period ranged from 19°C to 31°C, which was similar to the range of temperatures experienced during the study period. A linear regression confirmed a strong and direct relationship between temperatures measured with the IR camera and the digital thermocouple ($r^2=0.84$, $p<0.001$, $n=40$). This significant linear regression between temperatures recorded by the IR camera (T_{IR}) and the digital thermocouple (T_C) can be represented as $T_{IR} = 0.904 \times T_C + 2.625$. Rock temperatures recorded by the IR camera were on average 0.2°C higher than rock temperatures recorded by the digital thermocouple.

To compare differences in substratum temperatures of the four substratum types I took a single IR image of each replicate (n=5 quadrats/plates) on each sampling date (n=16 dates) during low tide and haphazardly sub-sampled and averaged the temperatures of 30 pixels within each image using the software package ThermaCAM Researcher PRO 2.9. Mean temperatures of replicates were then used to calculate the mean temperatures of treatments for each sampling date.

4.2.4 Early life history processes

To test the effect of temperature and artificial surfaces on the early life history processes of *T. rosea*, settlement, early post-settlement growth, survival and recruitment were estimated by tracking individual barnacles. Using a high resolution digital camera (Fujifilm S9600) photographs of plates and rock were taken daily between 7 March and 2 April and then weekly from 3 to 20 April 2011. The first pulse of settlers arrived after several days of strong wave action on 24 March, with numbers of settlers gradually decreasing through to 2 April. Using daily images of plates and rock, newly settled larvae and metamorphosed individuals were identified and individually tracked by digitally mapping their positions and orientations as they settled on a given day during the ten day period of settlement. Settlement was therefore calculated as the total number of recently settled cyprids or metamorphosed *T. rosea* larvae observed on settlement plates or rock from 24 March to 2 April 2011, including empty tests of individuals that had settled, metamorphosed and died.

For three daily cohorts of settlers I calculated early post-settlement survival as the percentage of 30 randomly selected individuals that settled on plates or rock on 28, 29 and 31 March that were still alive on 14 April. These three cohorts comprised 52% of total settlement during the 10-day settlement period and, therefore, are representative of the majority of individuals that settled during the sampling period. Similarly, to measure early post-settlement growth, the maximum test length of individuals from three daily cohorts that settled on 28, 29 and 31 March were measured on 14 April (between 10 and 25 individuals were measured on each plate, depending on availability, to obtain a single growth estimate for each replicate plate). Because all individuals within a cohort settled and metamorphosed on the same day, differences in maximum test length were attributed to differential growth not age. Maximum test length was measured instead of aperture length because at this early age the apertures of *T. rosea* settlers are often difficult to distinguish from the test. Finally, recruitment, the end product of larval settlement and early post-settlement survival, was estimated by counting the total number of *T. rosea* that settled on plates and rock between the 24 March and 2 April (i.e. during the period when settlement was recorded) that were still alive on 14 April.

4.2.5 Data analysis

Two-way ANOVA was used to test whether the four substrata (three differently coloured settlement plates and natural rock) experienced different temperatures, and whether these differences varied depending on the date measurements were taken. One-way ANOVA was used to test for differences in settlement, early post-settlement growth, survival and recruitment of *T. rosea* amongst the four substrata. Because estimates of growth and survival for the three different daily cohorts were measured across different durations we undertook separate one-way ANOVAs and post-hoc comparisons for each of the three daily cohorts. Where significant differences were found with ANOVA, Student-Neuman-Keuls (SNK) tests were used to determine which treatments experienced significantly different temperatures and early life history processes. Differences among the three artificial surfaces were also tested separately (i.e. excluding natural rock), but statistical comparisons among plates were the same regardless of whether rock was included as a treatment, so analyses including rock are presented here. Data were confirmed to be normally distributed and showed equal variance using the Shapiro-Wilks' test for normality and Cochran's test, respectively, and therefore data were not transformed.

4.3 Results

4.3.1 Manipulation of substratum temperatures

Substrate temperatures were significantly different amongst the four treatments, but differences varied depending on the temperature on the date measurements were taken (interaction of treatment × sampling date: $F_{45,240}=7.17$, $p<0.001$). Over the entire sampling period, black and white plates differed by up to 5.8°C, with an average difference of 2.2°C, confirming the hypothesis that plate colour alters substratum temperatures.

When substratum temperatures were analysed separately for each day, significant differences were detected among treatments for 11 of the 16 sampling dates, with warmer dates showing greater differences among substrata than cooler days (Fig. 4.2, SNK tests). In general, black and grey plates and rock were consistently warmer than white plates, and these differences were most obvious on 15, 16, 17, 29 and 30 March when low tides fell between 10:53am and 12:32pm and ambient air temperatures varied between 22°C and 32°C (Fig. 4.2, SNK tests). The most pronounced temperature differences occurred on 17 March as the temperatures of black, grey, and white plates and rock were on average 31.4°C, 29.6°C, 25.6°C and 27.2°C respectively (Fig. 4.2). Interestingly, the thermal properties of natural rock were most similar to those of grey plates.

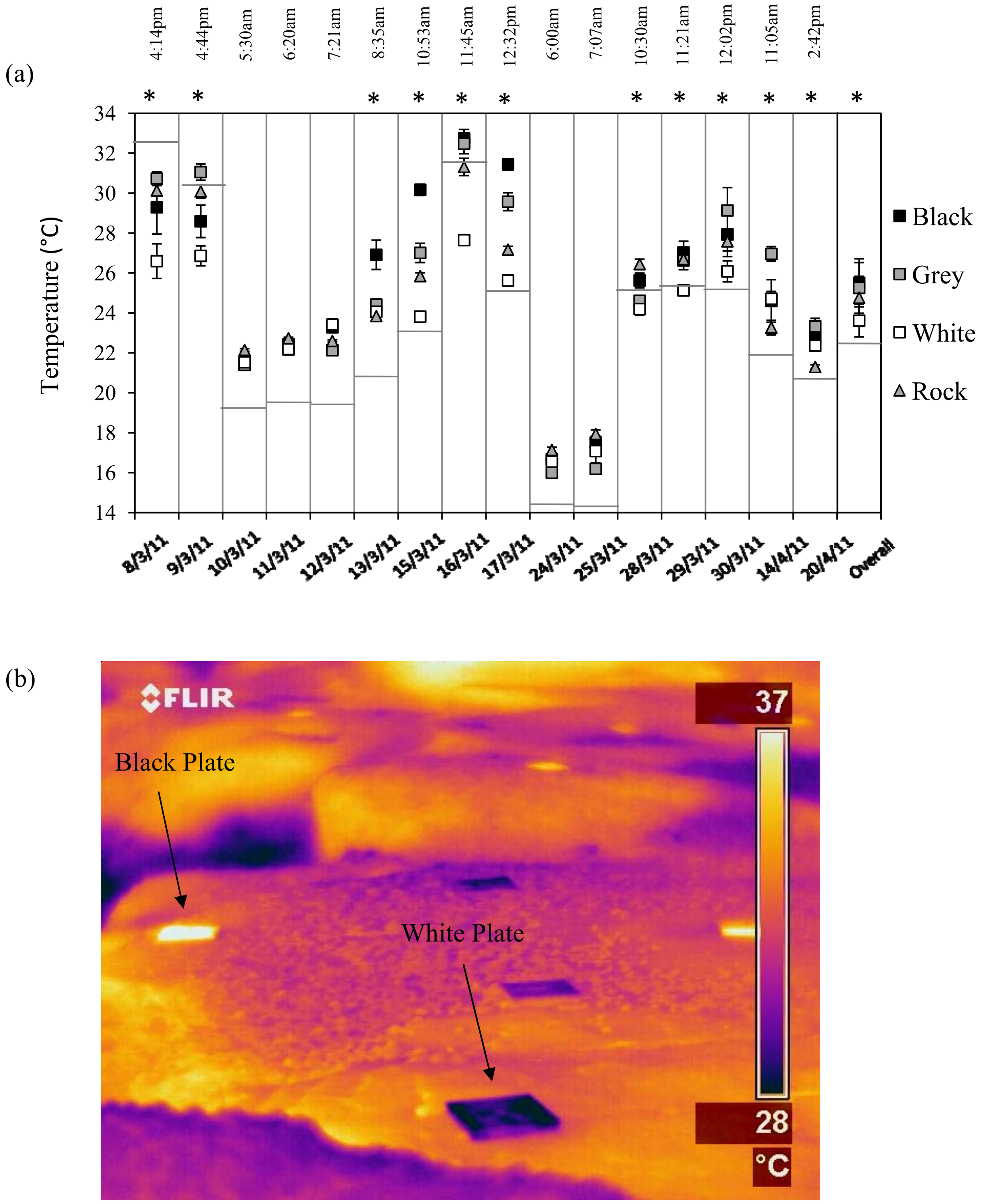


Figure 4.2. (a) Mean (±SE) temperature of black, grey and white settlement plates and natural rock measured from infrared images taken at low tide between 8 March and 20 April 2011. Horizontal lines indicate the mean air temperatures recorded by *in situ* data loggers during the time of sampling. Timing of low tide for each sampling date is indicated at the top of each column. Sampling dates marked with an asterisk indicate dates with significant differences between treatments; (b) IR image of plates in the field on 16 March 2011.

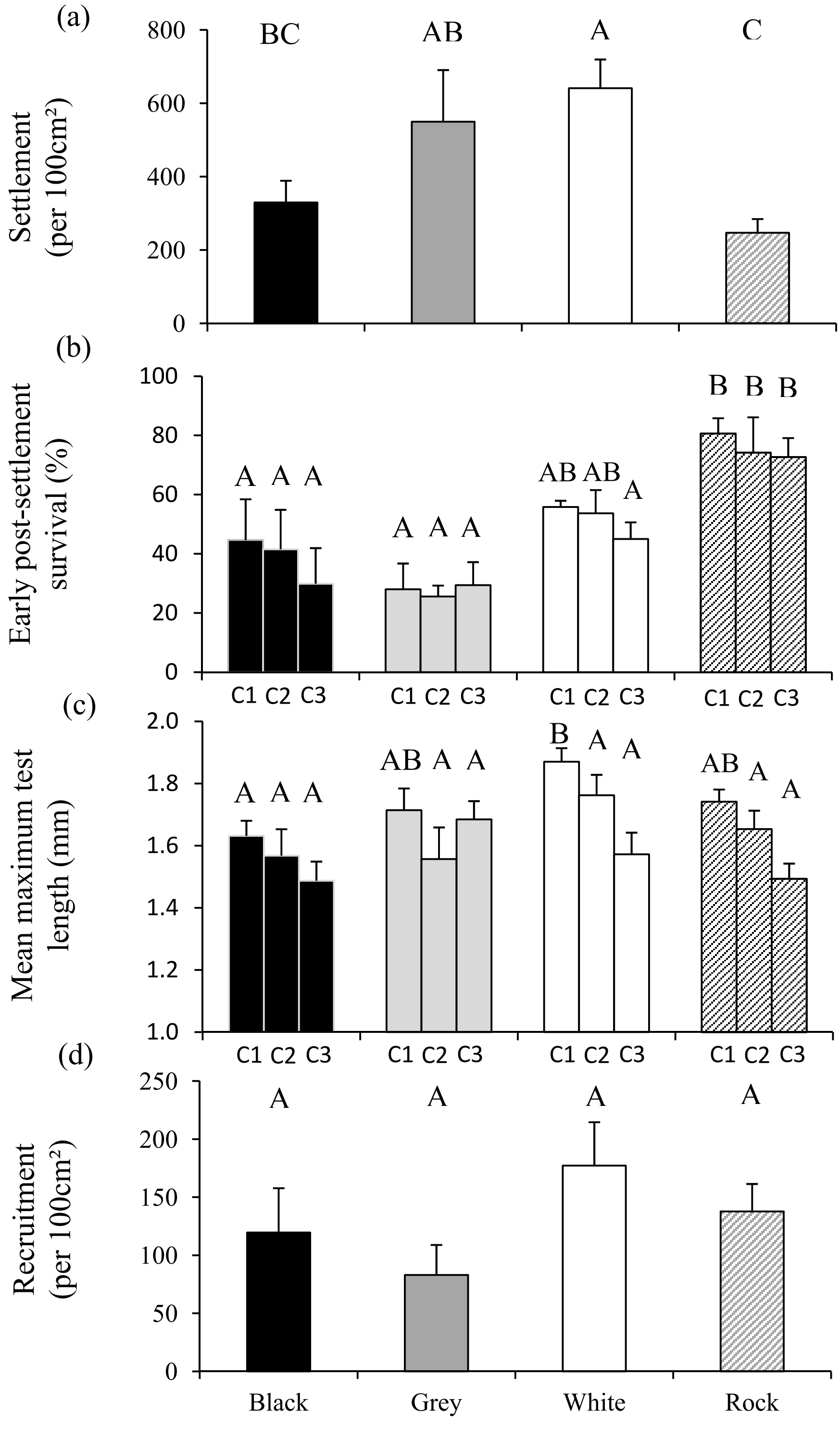


Figure 4.3. Mean (±SE) (a) settlement of *T. rosea* from 24 March to 2 April (n=5), (b) percentage of daily cohorts that settled on 28 (C1), 29 (C2) and 31 (C3) March surviving to 14 April (n=5), (c) final maximum test length of daily cohorts that settled on 28 (C1), 29 (C2) and 31 (C3) March on 14 April (n=5), and (d) number of *T. rosea* recruits on the 14 April (n=5) on settlement plates (black, grey and white) and natural rock. In each graph, bars with different letters denote statistically significant differences according to SNK tests. For graphs b and c letters only denote differences between the four substratum types within each cohort (and do not indicate differences among cohorts).

4.3.2 Early life history processes

From 24 March to 2 April, settlement of barnacle larvae varied significantly amongst substrata and was greatest on white settlement plates and least on natural rock ($F_{3,17}$=3.75, p=0.036) (Fig. 4.3a). Larval settlement on white plates varied significantly from larval settlement on black plates and natural rock. For example, white plates received almost double the number of settlers as black plates, and nearly three times as many settlers than natural rock (Fig. 4.3a). Larval settlement on both white and grey plates was also significantly greater than the number of *T. rosea* larvae settling on natural rock (Fig. 4.3a).

Early post-settlement survival varied significantly amongst treatments and was consistent amongst all three daily cohorts (28 March: $F_{3,18}$= 6.20, p= 0.006; 29 March: $F_{3,18}$= 4.23, p= 0.024; 31 March: $F_{3,18}$= 5.70, p= 0.008) (Fig. 4.3b). Mean survival of all three cohorts was greatest for larvae that settled on natural rock (~76%) and least for larvae that settled on grey plates (~28%) (Fig. 4.3b). Surprisingly, the thermal manipulation did not have a significant effect on early post-settlement survival of settlers on artificial surfaces of different colour (Fig. 4.3b). In contrast, early post-settlement survival was significantly lower on artificial surfaces compared to natural rock, with survival on black and grey plates were almost 2 to 3 times lower than survival on rock (Fig. 4.3b). This difference between natural rock and plates suggests that plates might not be appropriate in providing absolute estimates early post-settlement survival for *T. rosea* on natural rock.

For individuals that settled on 28 March growth varied significantly amongst the four substrata ($F_{3,18}$=4.26, p=0.006) (Fig. 4.3c). Here, individuals that settled on cooler, white plates were 15% larger than those on warmer, black plates (Fig. 4.3c). By contrast, no significant difference in growth was found when estimates were made using daily cohorts that settled on either the 29 or 31 March. Furthermore, unlike settlement and early post-settlement survival, no significant difference was found in the size of settlers on either black plates, grey plates and rock, indicating that early growth of *T. rosea* on these artificial substrata is equivalent to the early growth on natural rock.

Recruitment was variable but did not vary significantly among substrata with different temperatures ($F_{3,18}$=1.38, p=0.287) (Fig. 4.3d). Although not statistically significantly, white plates had almost twice the number of recruits compared to grey plates (Fig. 4.3d). Similar patterns of recruitment among substrata most likely reflect differences in the number of settlers and their subsequent survival. For example, although settlement on rock was relatively low (246±38 settlers/quadrat), early post-settlement survival was high (80%) and thus resulted in considerable recruitment (138±24 recruits/quadrat). In comparison, settlement on grey plates was considerably higher (550±141 settlers/plate), but due to low survival (28%), recruitment was moderate (83±26 recruits/ plate). The slightly greater number of recruits on white plates (177±37 recruits/plate) may be largely attributed to greater settlement (641±78 settlers/ plate) and moderate early post-settlement survival (56%). Furthermore, comparison of plates with rock indicates that artificial substrata produce similar estimates of recruitment in comparison to rock.

4.4 Discussion

This successful manipulation of temperature in the field represents a novel approach to experimentally investigating the effect of temperature on rocky intertidal invertebrates. By deploying differently coloured settlement plates coated with clear or black SWT average substratum temperatures were manipulated by up to 6°C, with differences being most obvious on hot days. The magnitude of temperature differences obtained by this thermal manipulation is comparable to that reported by Gedan et al.

(2011) who, by insulating cobbles into the bedrock, reduced substratum temperature within the mid intertidal zone by 8°C, as well as with Bertness and Leonard (1997) who reduced substratum temperatures by 6 to 9°C through shading. Most importantly, I demonstrate that this thermal manipulation significantly influences early post-settlement growth of the intertidal barnacle *T. rosea* and although not statistically significant patterns of early survival and recruitment were generally greater on cooler white plates.

4.4.1 Manipulating rocky intertidal temperatures

Apart from the present study, only Shanks (2009) and Gedan et al. (2011) have successfully manipulated the temperatures of rocky intertidal invertebrates without the use of shade or transplantations (but see Allison 2004 for macroalgae). Shanks (2009) discovered that plexiglas settlement plates covered in grey SWT are more thermally stressful than ceramic tiles, while Gedan et al. (2011) demonstrated that cobbles insulated within the bedrock were cooler than equivalent exposed cobbles. It is difficult, however, to manipulate the thermal environment without the outcome being confounded by factors that could influence the variable being measured. For instance, ceramic tiles typically have different rugosity or surface texture than settlement plates covered in SWT, and several studies have found that surface texture significantly influences rates of larval settlement and survival (Shanks 2009, Menge et al. 2010, Savoya & Schwindt 2010). Likewise, small-scale hydrodynamics around cobbles imbedded within the underlying substrate may differ significantly from exposed cobbles (Guichard et al. 2001), and this in turn may also influence larval settlement (Wright & Boxshall 1999, but see O'Donnell & Denny 2008). In the present study, the use of differently coloured plates and SWT on emergent rock in the mid shore region ensured that differences in early life history processes among these artificial surfaces were not due to differences in shade, tidal height, substratum texture or small-scale hydrodynamics. Nevertheless, this manipulation of the thermal environment with plates may also be potentially confounded by differences in plate colour and associated properties (see Discussion below).

4.4.2 Early life history processes

The effect of temperature and artificial plates on larval settlement, growth, survival and recruitment of *T. rosea* varied depending on the life history process being measured. For example, the three thermal treatments significantly influenced larval settlement and growth but not survival and recruitment, whereas only larval settlement and survival were significantly different between natural rock and plates. It is unlikely that substrate temperatures influenced larval settlement directly since larvae arrive during high tide when substrate temperatures are less variable and unlikely to reflect the temperature variability that occurs during low tide. Alternatively, differences in biofilm composition produced by the different thermal regimes may be indirectly responsible for differences in larval settlement (Olivier et al. 2000; Qian et al. 2003; but see Keough and Raimondi 1996). In a similar fashion, Hung et al. (2005) demonstrated that variation in UV exposure influences biofilm composition, which in turn influenced the larval settlement of the polychaete *Hydroides elegans*. However, whether or not thermal variability indirectly influences larvae settlement by altering biofilm communities has yet to be empirically tested.

Substratum colour can also be an important factor influencing settlement of benthic marine invertebrates (Pawlik 1992). Although barnacle cyprids do not possess colour vision, their simple median eyes are thought to be capable of detecting light direction and intensity (Brusca & Brusca 2003; but see Visscher & Luce 1928). Therefore, *T. rosea* larvae may settle in response to colour, not temperature or biofilm, as the intensity of light associated with different colours can be a particularly strong visual cue. Marine invertebrate larvae use light intensity to differentiate microhabitats that are either exposed or sheltered from damaging UV light (see review by Pawlik 1992). For example, coral and ascidian larvae preferentially settle in dark-shaded areas as a result of negative phototaxis immediately before settlement (Thorson 1964, Young & Chia 1984, Kuffner 2001). In the present study, however, darker coloured black plates were more thermally stressful than lighter coloured grey and white plates. Therefore, greater settlement on white plates suggest that larvae of *T. rosea* preferentially settle in areas perceived to be exposed to high levels of ambient light, which is what we might expect since adults are found predominantly on emergent rock exposed to full sunlight (Denley & Underwood 1979). In areas exposed to high levels of ambient light Caffey (1982) found no difference in the number of *T. rosea* settling on different coloured natural rock substrata. This suggests that *T. rosea* discriminates shaded from sunny areas but not between rocky types exposed to full sunlight. Differences in larval settlement in the present study could also be due to different chemical properties of plates and SWT. I believe this to be unlikely because I used materials that are relatively inert, cleaned the plates before placing them in the field, and conditioned them *in situ* for three weeks prior to experimentation. Nevertheless, the necessity for such caveats indicates the difficulty of such manipulations in the field.

The greater number of larvae settling on artificial plates covered in SWT in comparison to the natural substrata supports Menge et al. (2010) who demonstrate that the greater textual complexity of SWT increases settlement and recruitment of the barnacle *Balanus glandula* in comparison to natural rock. In the present study, plates covered in SWT had surface textures (600-700 µm grain size) coarser than the natural siltstone (4-60 µm grain size). However, Caffey (1982) found no difference in the amount of *T. rosea* settling on light-brown sandstone and dark-grey mudstone, two naturally occurring rock types with equivalent grain sizes to SWT and siltstone, respectively. Alternatively, potential differences in settlement between natural and artificial surfaces detected in the present study may be due to differences in biofilm composition (Faimali et al. 2004). Regardless, differences between natural and artificial surfaces detected in this study suggest a cautionary approach should be taken when interpreting the results of studies that use settlement plates covered in SWT to estimate early life history processes. Artificial plates may provide useful comparisons to patterns with natural substrata, provided that the temperature and texture of plates are similar to those of the natural rock substrata.

For marine invertebrate larvae the transition from the water column to the intertidal zone is usually characterised by high levels of mortality due to increased heat and desiccation stress (Gosselin 1997, Hunt & Scheibling 1997). In the present study, however, I found no effect of our thermal manipulation on early post-settlement survival of *T. rosea* even though white plates were up to 5.8°C cooler than black plates. Interestingly, the 28% survival of larvae on grey plates with SWT reported within the present study was higher than Shanks (2009) who found ≈10% survival of newly settled *Balanus glandula* on settlement plates covered in grey SWT. However, I also report unusually high (80%) early post-settlement survival of *T. rosea* on natural rock. At times, plates were observed to be dryer than underlying substratum. Therefore, desiccation stress may have been substantially lower on natural rock compared to plates because (i) siltstone is more permeable to water than SWT, and (ii) plates were not insulated by surrounding substrata. Previous work confirms that *T. rosea* populations at Garie Beach typically experience high rates of early post-settlement survival (≈50%) in comparison to other populations along the southeast coast of Australia (0 to 20%) (see Lathlean et al. 2010). However, this does not explain why there was no difference in early post-settlement survival among the three differently coloured plates. Apart from thermal stress, bulldozing by the common intertidal limpet *Cellana tramoserica* might also be a likely source of early mortality for intertidal barnacles within the study region (Jeffery 2003), but this explanation is unlikely because these limpets were rarely observed on plates.

Along with increased thermal stress the transition from the water column to the benthos is also metabolically expensive as larvae typically undergo metamorphosis and rapidly increase in size within the first few weeks after settlement. Like many physiological processes, I found early post-settlement growth of *T. rosea* to be significantly influenced by temperature as individuals on white plates grew significantly more than individuals on warmer grey and black plates. In contrast, laboratory experiments carried out by Findlay et al. (2010a, b) show that temperature has no effect on the early post-settlement growth of the intertidal barnacles *Semibalanus balanoides* and *Elminius modestus,* while field studies on intertidal mussels have found higher temperatures to either increase (Blanchette et al. 2007) or decrease adult growth (Petes et al. 2007). My results suggest that for newly settled *T. rosea* increased temperatures prolong the time it takes for juveniles to reach a particular size whereby they may be no longer as vulnerable to environmental stress or predation.

Although this thermal manipulation successfully influenced several important early life history processes, it is unclear whether these manipulations reflect the natural variability of rocky intertidal substrata and their associated effects on settlement, growth and recruitment. Therefore, in the following chapter I quantify small-scale rock temperature variability to investigate whether this natural variability significantly influences the early post-settlement processes of *T. rosea*.

CHAPTER 5: Using infrared imagery to test for quadrat-level temperature variation and its effects on the early life history of a rocky shore barnacle

This chapter is currently under review with the journal *Limnology and Oceanography*.

5.1 Introduction

Rocky intertidal shores are perhaps one of the most extensively studied ecosystems worldwide (Paine 1994) and provide us with our earliest experimental and theoretical work on community dynamics and species interactions (Grinnell 1917, Orton 1929, Connell 1961a, 1972). More recently, however, rocky intertidal communities have been used to measure biological responses to climate change by linking range shifts to climatic variability (e.g. Mieszkowska et al. 2006, Poloczanska et al. 2008, Pitt et al. 2010). Consequently there has been a rapid increase in the number of intertidal studies attempting to understand how large-scale temperature variability translates into local variability in abundance of rocky shore species (e.g. Helmuth et al. 2006a, Menge et al. 2011).

The success of rocky intertidal studies as model systems can be largely attributed to their amenity in allowing extensive replication of discrete sampling units (typically quadrats), and the allocation of experimental treatments to quadrats within areas of the shore that are assumed to experience relatively uniform conditions. However, such studies have rarely tested the assumption that quadrat-scale replicates are thermally homogeneous and temperature is usually measured at much coarser scales (Blanchette & Gaines 2007, Broitman et al. 2008a, Lathlean et al. 2011). Nevertheless, numerous biotic factors on rocky intertidal shores have exceptionally high levels of spatial variability (Underwood & Chapman 1996, Miller & Ambrose 2000, Denny et al. 2004) and much of this variation may be due to undetected temperature variability (Denny et al. 2011).

Quadrat scale temperature variation could result from subtle physical differences in the substratum including composition, colour, orientation and aspect (e.g. Denny et al. 2006, Harley 2008, Meager et al. 2011). The occupancy of the substratum by different biological communities may also contribute to natural temperature variability on rocky intertidal shores (Bertness & Leonard 1997). In particular, species that form habitat, such as ecosystem engineers, may alter physical parameters and ameliorate stresses on other organisms or conspecific juveniles (Jones et al. 1994). For example, intertidal macroalgae reduce thermal stress for understorey invertebrates by lowering temperatures and evaporative water loss (Bertness et al. 1999b). Shading effects of the goose barnacle *Capitulum mitella* ameliorates heat stress for the mussel *Septifer virgatus* by lowering body temperatures and increasing interstitial humidity within patches (Kawai & Tokeshi 2004). Consequently, areas characterised by low adult densities may be more thermally stressful than areas with high adult densities due to conspecifics buffering neighbours from harsh environmental conditions (Bertness & Leonard 1997). Indeed, Bertness et al. (1999a) demonstrate that when exposed to thermal stress recruits of the barnacle *Semibalanus balanoides* survive better at higher densities. In contrast, Gaines and Roughgarden (1985) found that the survival of newly settled *Balanus glandula* larvae increased with increasing amounts of free space (inverse of density) (see also Minchinton & Scheibling 1993a).

Free space has often been considered a limiting resource within benthic communities as larval settlement and survival is often directly proportional to the availability of free space (Gaines & Roughgarden 1985, Minchinton & Scheibling 1993a). Nevertheless, for rocky intertidal invertebrates, larvae that settle in areas with more free space may experience higher mortality due to increased thermal stress during low tide. Due to the difficultly of measuring and manipulating temperature variability at small spatial scales, this relationship between early post-settlement survival, thermal stress and free space remains untested. Recently developed infrared (IR) imaging techniques for rocky intertidal habitats could provide an effective method of capturing not only the temperature variability caused by variable free space but also variability among replicate quadrats (Murphy 2006, Chapperon & Seuront 2011, Cox & Smith 2011).

Here I use IR imaging to quantify rock temperature variability at the quadrat level within the midshore region dominated by the intertidal barnacle *Tesseropora rosea* (see Fig. 1.2), which provides habitat for several other species (Creese 1982; Underwood et al. 1983, Hidas et al. 2010). I first test whether natural variability in free space is related to variability in rock temperature among quadrats, and whether this variability in rock temperature, a proxy for thermal stresses experienced by recent barnacle settlers, influences the early life history processes of *T. rosea.* I then manipulate the cover of adult *T. rosea* to determine how free space influences rock temperature variability and early life history processes of *T. rosea*, and how this compares to free space on the rocky shore not occupied by *T. rosea*.

5.2 Methods

5.2.1 Temperature variability and early life history processes

Throughout this chapter I measure rock temperatures and early life history processes within areas either with a biotic community dominated by *T. rosea* (see Fig. 5.1d) or in areas at the same tidal height on shore without a biotic community and therefore, with a high natural abundance of free space on the rock (see Fig. 5.1a). Areas with a biotic community had variable amounts of free space, which was typically inversely related to the density and cover of adult *T. rosea*. I present spatial and

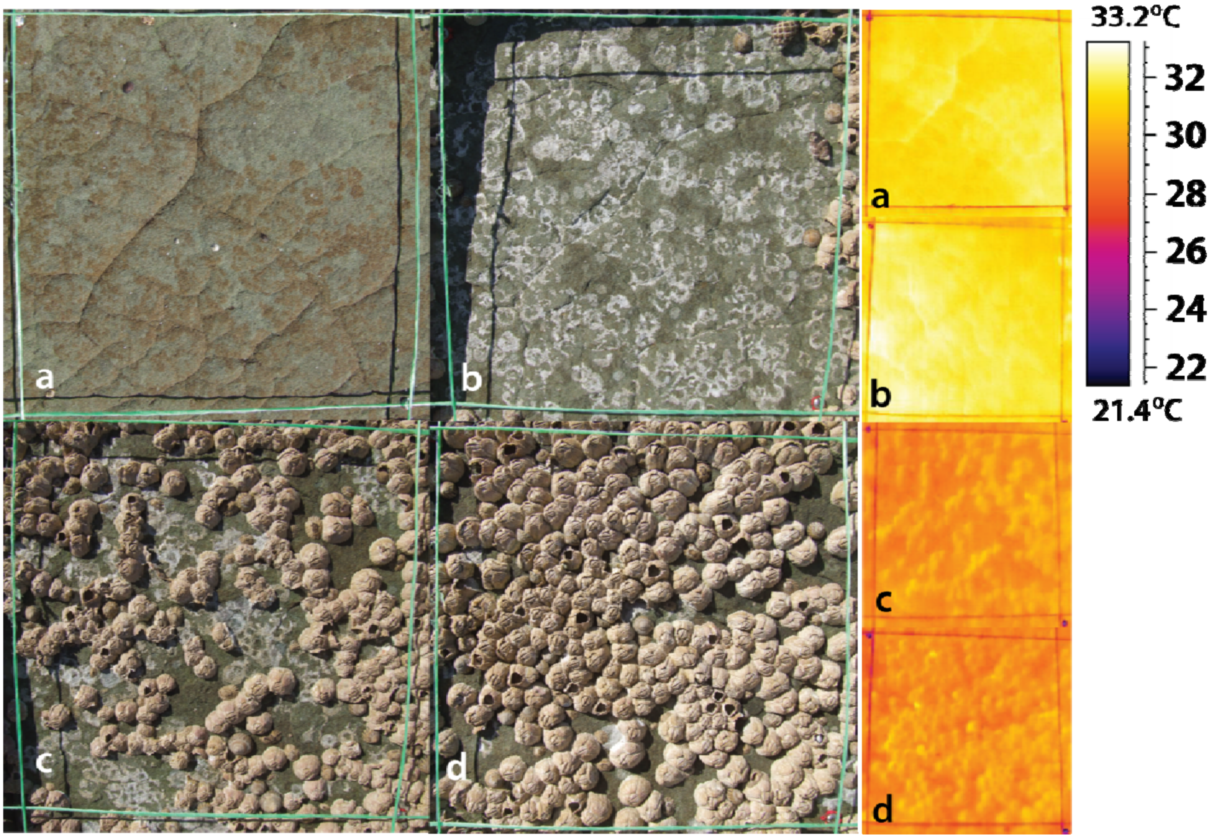


Figure 5.1. Photographs and infrared images of (a) unmanipulated 100% free space, (b) manipulated treatment with 100% free space, (c) manipulated treatment with 25-50% free space and (d) manipulated treatment with less than 25% free space. Note strong differences in temperature between areas with (c, d) or without (a, b) a biotic community dominated by the barnacle *T. rosea*.

temporal rock temperatures for two relationships: areas with variable amounts of free space, and areas with or without a biotic community. All sampling was carried out at Garie Beach (see section 4.2.1 for site description) using IR imaging techniques described in Chapter 4.

5.2.1.1 Relationship between free space and rock temperature

To test the hypothesis that rock temperatures vary with the amount of free space on the rocky shore, I haphazardly took IR images of 20cm × 20cm quadrats with variable amounts of free space at Garie Beach on 29 November 2009, 9 January and 9 March 2010 (n=23 to 35 quadrats per sampling event). All quadrats were: (1) within the mid shore region dominated by the barnacle *Tesseropora rosea* (0.8 to 1.6m above the mean low water mark of neap tides: MLWN); (2) were within an area of at least $400cm^2$ flat, emergent rock without crevices, depressions or macroalgae that could retain water during low tide; and (3) had horizontal to moderately sloping surfaces (<20°). Because there are many factors that could influence intertidal rock temperature (Helmuth et al. 2011), I standardised tidal and climatic conditions by taking IR images on days where low tide fell between 10am and 1pm, air temperatures were greater than 30°C, wave height was less than 0.5m, and cloud cover was minimal to absent.

The percentage of free space within each quadrat was calculated using a point-intercept method, whereby an evenly distributed, 100 point matrix was overlaid onto a high resolution digital image of each quadrat (Fujifilm S9600) and points that fell on areas not occupied by sessile invertebrates or macroalgae were counted as free space. This percentage of free space was then compared with the mean rock temperature for each quadrat, which was calculated by selecting and averaging the temperatures of 30 points within each IR image known to be areas of free space (using the ThermaCAM

Research Pro 2.9 software package) which was sufficient to get a representative sample of rock temperature within quadrats.

5.2.1.2 Consistency of thermal variation

To test the hypothesis that rock temperatures vary consistently among quadrats with or without biotic communities, I established twenty permanent 20cm × 20cm quadrats within the mid shore region at Garie Beach on 8 February 2010. Ten of these quadrats were established in areas with high adult cover with less than 50% free space (hereafter referred to as <50% free space) and 10 in areas without adult *T. rosea* and with 100% free space (hereafter referred to as 100% free space). Consequently, these comparisons represent the most extreme differences between areas with or without a biotic community. Importantly, these quadrats were interspersed naturally at the same mid shore tidal heights across the rocky shore. Infrared images of these quadrats were taken on 25 and 26 February, and 2, 9 and 16 March 2010 during low tides that fell between 10:30am and 3:40pm. Differences in the time of sampling would have had a minimal affect on rock temperature variability because on each day the mid shore region had sufficient time (at least 3 h) to heat up with little variation in the incidence of sunlight. Differences between sampling events are more likely to differ due to daily variability in weather (see Appendix II). I determined rock temperatures at the scale of the quadrat by calculating the mean temperature of 30 to 49 evenly spaced pixels representing free space within each quadrat using IR images taken for each of the five sampling events. I then ranked mean quadrat temperatures to test the hypothesis that relative rock temperatures were highly correlated in space over time (see Table 1). Here, if rock temperatures vary consistently in areas with or without *T. rosea* over time, then I might expect to see this variability influence early life history processes.

5.2.1.3 Effects of thermal variation on early life history processes

To test whether temperature variation among quadrats with naturally variable free space influences early life history processes of *T. rosea* I measured settlement, early post-settlement growth and survival within 25 permanent quadrats with 15 to 100% free space. As a comparison I also measured the same early life history processes within 20 permanent quadrats with 100% free space (i.e. without a biotic community) to test whether temperature variation among quadrats influences the early life history processes of *T. rosea* independently of free space.

Newly settled individuals were identified and tracked within all quadrats every two to four days from 9 February to 23 March 2010 using a high resolution digital camera (Fujifilm S9600). I identified newly settled barnacles by digitally mapping the location and size of individuals within each quadrat and counting the number of newly metamorphosed *T. rosea,* including empty tests of individuals that had settled, metamorphosed and died, since the previous census. The first significant settlement pulse was not detected until 5 March and it continued through to the 16 March. Therefore, I calculated settlement for each quadrat by summing the number of newly settled barnacles recorded at each census from 2 to 16 March. The association between temperature and settlement was estimated by comparing this total number of settlers per quadrat with mean quadrat temperatures measured by IR images taken on 2, 9 and 16 March. The effect of variable free space on settlement was calculated by comparing the total number of settlers within a quadrat (divided by the unit area of free space) with the percentage of free space within each quadrat on 9 March.

Settlement was greatest between 5 and 7 of March and individuals that were first detected on 7 March were subsequently audited on 9, 16 and 23 March to produce three estimates of early post-settlement survival for the same individuals (i.e. 7 to 9 March, 9 to 16 March and 16 to 23 March). Due to highly variable settlement amongst quadrats, early post-settlement survival was calculated as the percentage of five to 30 haphazardly chosen individuals that settled within each quadrat between 5 and 7 March that were still alive on 9, 16 and 23 March. I used Pearson correlations to compare estimates of early survival for each quadrat to the average temperature of the 30 individuals within each quadrat calculated from IR images taken on 9 and 16 March. Similarly, I used Pearson correlations to compare estimates of early survival to the percentage of free space within a quadrat. I had to reduce the sample size when estimating early post-settlement survival because some quadrats received less than five individuals (i.e. n=14 to 19 quadrats).

Early post-settlement growth was estimated for individuals that settled between 5 and 9 March by measuring the maximum test length of three to 10 individuals per quadrat on 9 and 16 March and calculated growth as the percentage increase in test length by 16 and 23 March respectively. Maximum test length was used instead of aperture length because it was difficult to distinguish the aperture from the test of newly metamorphosed settlers. Additionally, to avoid the potentially confounding effects of crowding, individuals that were in contact with one another at any stage of the sampling period were not included for estimates of growth or survival. Using IR images taken on 9 and 16 March, I undertook Pearson correlations to compare mean growth per quadrat to mean temperature of the three to 10 individuals within each quadrat. I also compared estimates of early survival to the percentage of free space within a quadrat using Pearson correlations. Due to high mortality within quadrats estimates of early post-settlement growth were based on even further reduced sample sizes (i.e. n= 11 to 18 quadrats).

5.2.2 Experimental manipulation of free space

To test whether experimental manipulation of free space influences rock temperatures, I haphazardly established an additional 30 permanent 20cm × 20cm quadrats within the mid shore region on 8 February 2010. These quadrats were established in areas with greater than 75% adult barnacle cover (i.e. <25% free space) and then randomly allocated into three experimental treatments: (i) 100% free space, (ii) 25 to 50% free space, and (iii) 0 to 25% free space (see Fig. 1). I achieved this by using a chisel and metal brush to clear all invertebrates and biofilm within quadrats assigned to the first treatment, creating 25 to 50% free space within quadrats assigned to the second treatment and leaving the remaining 10 quadrats assigned to the third treatment untouched. I also compared these 30 manipulated quadrats with the 10 unmanipulated quadrats with 100% free space described in the previous subsection 'temperature variability among areas with or without biotic community'. Here, I expected rock temperatures (and early life history processes) within the unmanipulated 100% free space treatment to be similar to those in quadrats of the first treatment, which were completely cleared of all invertebrates.

Infrared images were taken of all 40 quadrats during times of aerial exposure on 25 and 26 February, and 2, 9 and 16 March 2010. I randomly selected 30 points within each IR image that represented free space and pooled points within all 10 replicates to produce temperature-frequency distributions for each treatment (i.e. n=300). To determine whether experimental manipulation of free space significantly alters rock temperatures, I used non-parametric two-sample Kolmogorov-Smirnov (KS) tests to compare the temperature-frequency distributions across all four treatments.

To test whether experimental manipulation of free space influences early life history processes of *T. rosea*, I measured settlement, early post-settlement growth and survival within the four experimental treatments previously outlined for unmanipulated quadrats (see ‘Early life history processes’ section above). Consequently I have parallel measures of settlement, early post-settlement growth and survival for both natural and manipulated areas on the rocky shore with and without biotic communities dominated by *T. rosea*. I used 1-way ANOVA to test for differences in settlement, early post-settlement growth and survival of *T. rosea* amongst the four experimental treatments. Where significant differences were found, a Student-Neuman-Keuls (SNK) post-hoc comparisons were made to determine the location of differences among treatments. I confirmed that the data were normally distributed and showed equal variance using the Shapiro-Wilks’ and Cochran’s test, respectively.

5.3 Results

5.3.1 *Temperature variability and early life history processes*

5.3.1.1 Relationship between free space and rock temperature

In quadrats with variable barnacle cover, rock temperatures increased significantly with increasing availability of free space (Fig. 5.2). Mean rock temperatures varied by as much as 8°C among haphazardly chosen quadrats when differences in the level of free space ranged from 10 to 100% (Fig. 5.2). Rock temperatures and free space were also correlated significantly and strongly across all three sampling events (Fig. 5.2).

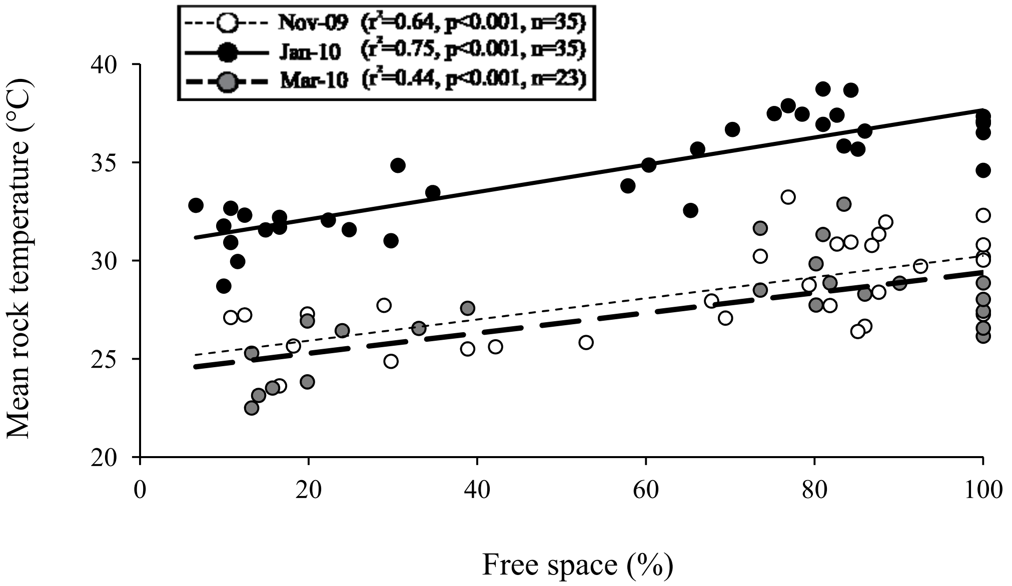


Figure 5.2. The relationship between percentage free space and mean rock temperatures, within the mid intertidal zone, at Garie Beach on 29 November 2009 (low tide: 12:00pm), 9 January 2010 (low tide: 10:00am) and 9 March 2010 (low tide: 10:26am).

5.3.1.2 Consistency of thermal variation

Rock temperatures were highly variable among quadrats with differences being as great as 5.7°C and 8.2°C among quadrats with <50% and 100% free space, respectively (see 9 March in Fig. 5.3). Nevertheless, variation in mean temperatures among quadrats was often but not universally consistent over time (Table 5.1). For example, mean temperatures of quadrats with <50% free space recorded on 25 February were positively correlated with mean quadrat temperatures recorded on 26 February and 2 and 16 March (Table 5.1). Similarly, the mean temperatures of quadrats with 100% free space recorded on 25 and 26 February were positively correlated with mean quadrat temperatures recorded on 2 March (Table 5.1). This demonstrates that, at the quadrat scale, particular areas on the shore with or without adult barnacles are consistently hot or cold. Similar to previous results (i.e. Fig. 5.2), mean rock temperatures were consistently lower within quadrats with <50% free space compared to quadrats with 100% free space (Fig. 5.3).

5.3.1.3 Effects of thermal variation on early life history processes

Several strong relationships were found between the early life history processes of *T. rosea* and rock temperature variability, with most pronounced effects in areas with 100% free space (compare Figs. 4, 5 and 6).

For quadrats with naturally variable free space, larval settlement increased significantly with increasing mean rock temperatures of quadrats (Fig. 5.4a). This positive relationship between larval settlement and rock temperature reflects the positive relationship between larval settlement and free space (r^2=0.20, p=0.020, n=25) and the positive relationship between free space and rock temperatures (r^2=0.65, p<0.001, n=25). In contrast, for quadrats with 100% free space no relationship was detected between mean rock temperatures of quadrats and larval settlement (Fig. 5.4b). This suggests that the strong positive relationship between larval settlement and mean rock temperature of quadrats with variable free space reflects the relationship between larval settlement and the availability of free space, not rock temperature variability.

Early post-settlement growth was highly variable although it was not significantly associated with temperature variation among quadrats with variable free space (Fig. 5.5a,c). In comparison, early post-settlement growth was inversely related to rock temperatures within 100% free space quadrats when individuals were measured from 9 to 16 March (Fig. 5.5b), but not when individuals were measured from 16 to 23 March (Fig. 5.5d).

Early post-settlement survival was also highly variable among quadrats with different amounts of free space but survival did not vary significantly with mean rock temperatures regardless of whether estimates were made from 7 to 9, 9 to 16 or 16 to 23 March (Fig. 5.6a,c,e). In contrast, higher mean rock temperatures significantly decreased early post-settlement survival when estimates were made from 9 to 16 and 16 to 23 March within quadrats with 100% free space (Fig. 5.6b,d,f).

Table 5.1. Summary of outcomes for the rank correlation (r^2) between the mean rock temperature of individual quadrats with either 100% or less than 50% free space for five separate sampling events. Bold font indicates significant positive relationships with p-value <0.05 (n=10 quadrats).

Among quadrats with less than 50% free space					Among quadrats with 100% free space			
	25 Feb	**26 Feb**	**2 March**	**9 March**	**25 Feb**	**26 Feb**	**2 March**	**9 March**
26 Feb	**0.73**				0.07			
2 March	**0.72**	**0.93**			**0.51**	**0.46**		
9 March	<0.01	0.03	<0.01		0.08	0.03	<0.01	
16 March	**0.63**	0.30	0.36	<0.01	0.12	**0.56**	**0.66**	<0.01

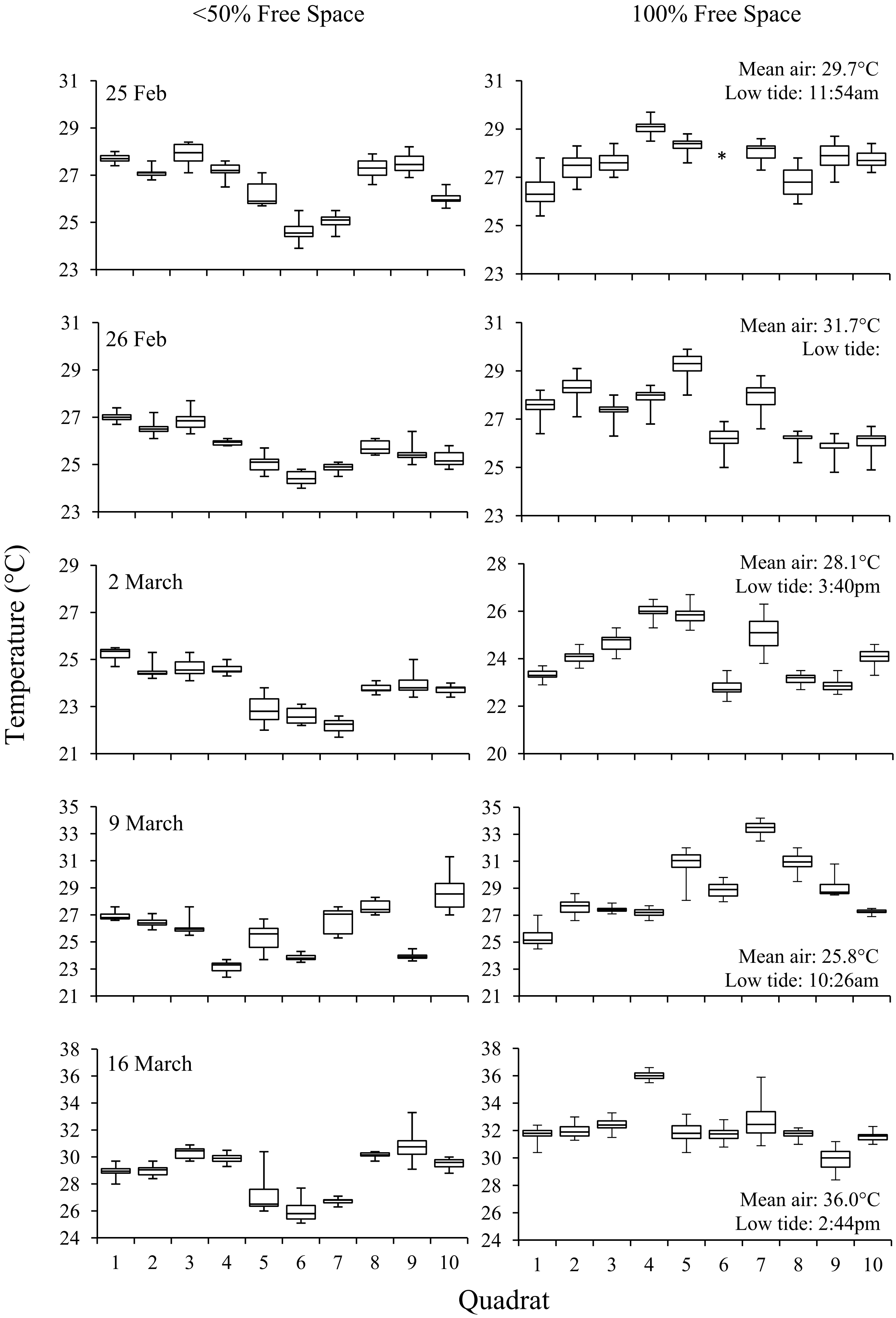


Figure 5.3. Small-scale temperature variability within and among quadrats with less than 50% free space (left) and 100% free space (right) at low tide on 25 and 26 February, 2, 9 and 16 March 2010. Box plots represent median, interquartile range, maximum and minimum. Mean air is the mean air temperature recorded by *in situ* data loggers at the time of sampling. Low tide is the approximate time of low tide. Note different scale on y-axis'.* Infrared image unavailable.

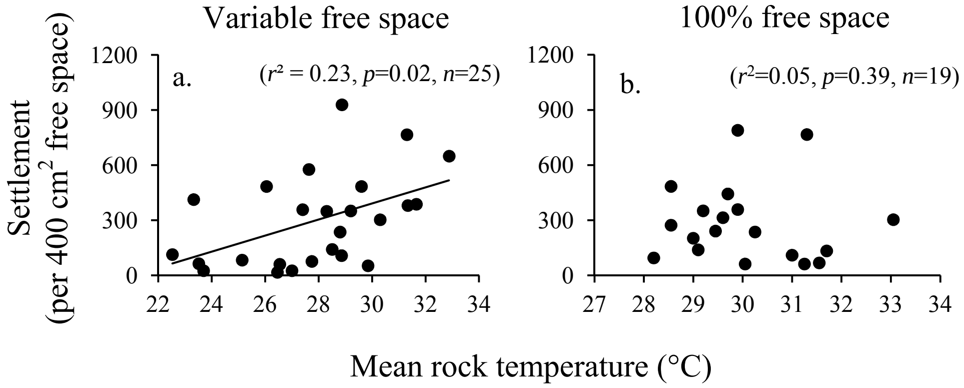


Figure 5.4. The influence of mean rock temperature of quadrats with (a) variable (15% to 100%) free space, and (b) 100% free space on settlement of *T. rosea* from 2 to 16 March 2010.

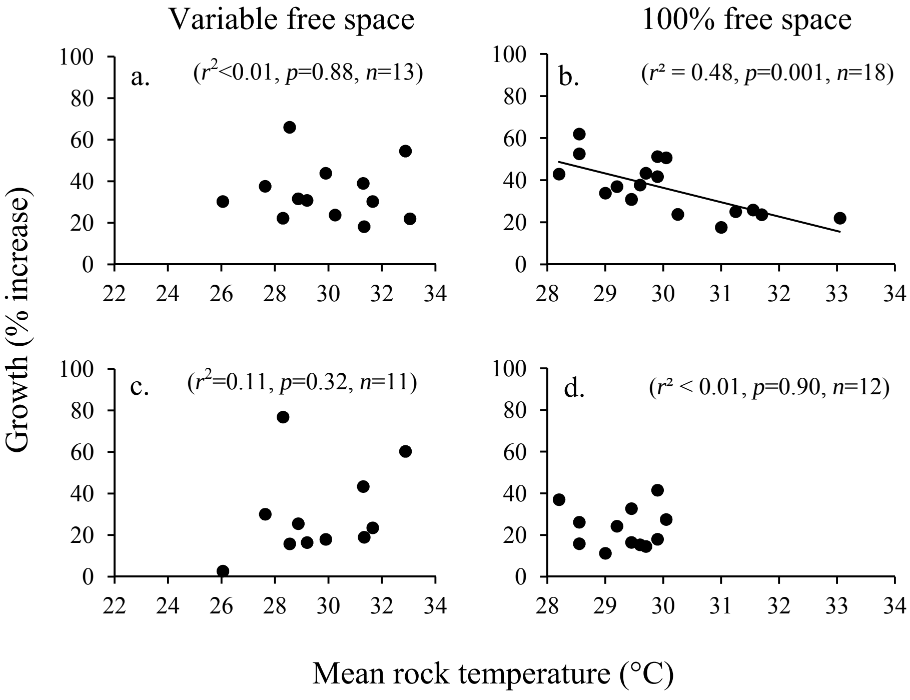


Figure 5.5. The influence of mean rock temperature of quadrats with (a,c) variable (15% to 100%) free space, and (b,d) 100% free space on early post-settlement growth of *T. rosea* from (a,b) 9 to 16 and (c,d) 16 to 23 March 2010.

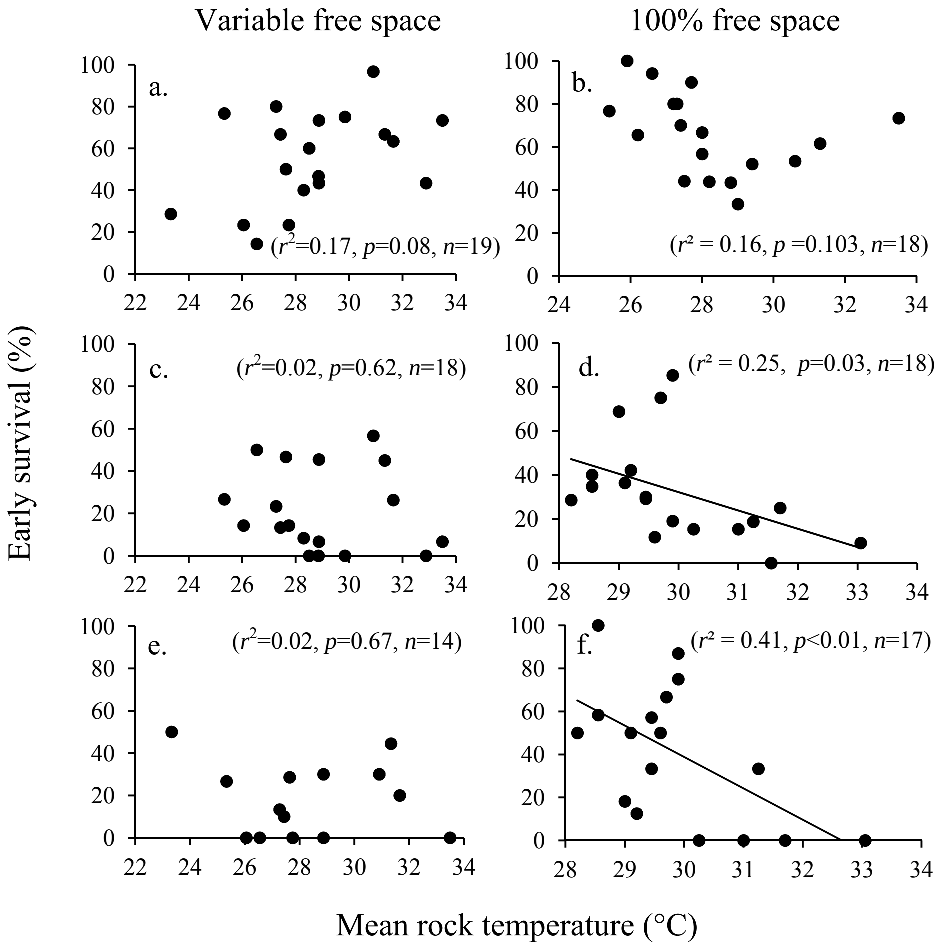


Figure 5.6. The influence of mean rock temperature of quadrats with (a,c,e) variable (15% to 100%) free space, and (b,d,f) 100% free space on early post-settlement survival of *T. rosea* from (a,b) 07 to 09, (c,d) 09 to 16, and (e,f) 16 to 23 March 2010.

5.3.2 Experimental manipulation of free space

5.3.2.1 Rock temperature variability

Experimental manipulation of free space produced similar relationships between free space and rock temperature to that observed within unmanipulated quadrats with a range of adult densities (compare Fig. 5.2 and 5.7). Mean rock temperatures for each of the four treatments with variable free space differed significantly during three of the five sampling events being coolest in the 0 to 25% treatment and hottest within the unmanipulated 100% free space treatment (Fig. 5.7). For example, rock temperatures of the 0 to 25% free space treatment on the 09 March were on average 0.5°C, 2.3°C and 4.6°C cooler than the 25 to 50% and 100% manipulated treatments, and the 100% unmanipulated free space treatments, respectively. This 2.3°C difference amongst manipulated quadrats with 0 to 25% and 100% free space was considerably lower than the 4-5°C difference amongst unmanipulated quadrats with the same range of variable free space (*see* Fig. 5.2). Mean rock temperatures of manipulated quadrats with 100% free space were similar to mean rock temperatures of unmanipulated quadrats with 100% free space (Fig. 5.7).

The temperature range of treatments also varied depending on the amount of free space. For example, rock temperatures of the 0 to 25% free space treatment ranged on average by 4.1°C, and as much as 6°C, whereas rock temperatures of the manipulated 100% free space treatment ranged on average by 7.3°C, and up to 11.5°C. These differences in the range of temperatures between treatments with variable free space are most evident on 9 March (Fig. 5.7). Approximately 40% of temperature values recorded within the manipulated 100% free space treatment were greater than 27.7°C, the maximum temperature recorded within 0 to 25% treatment.

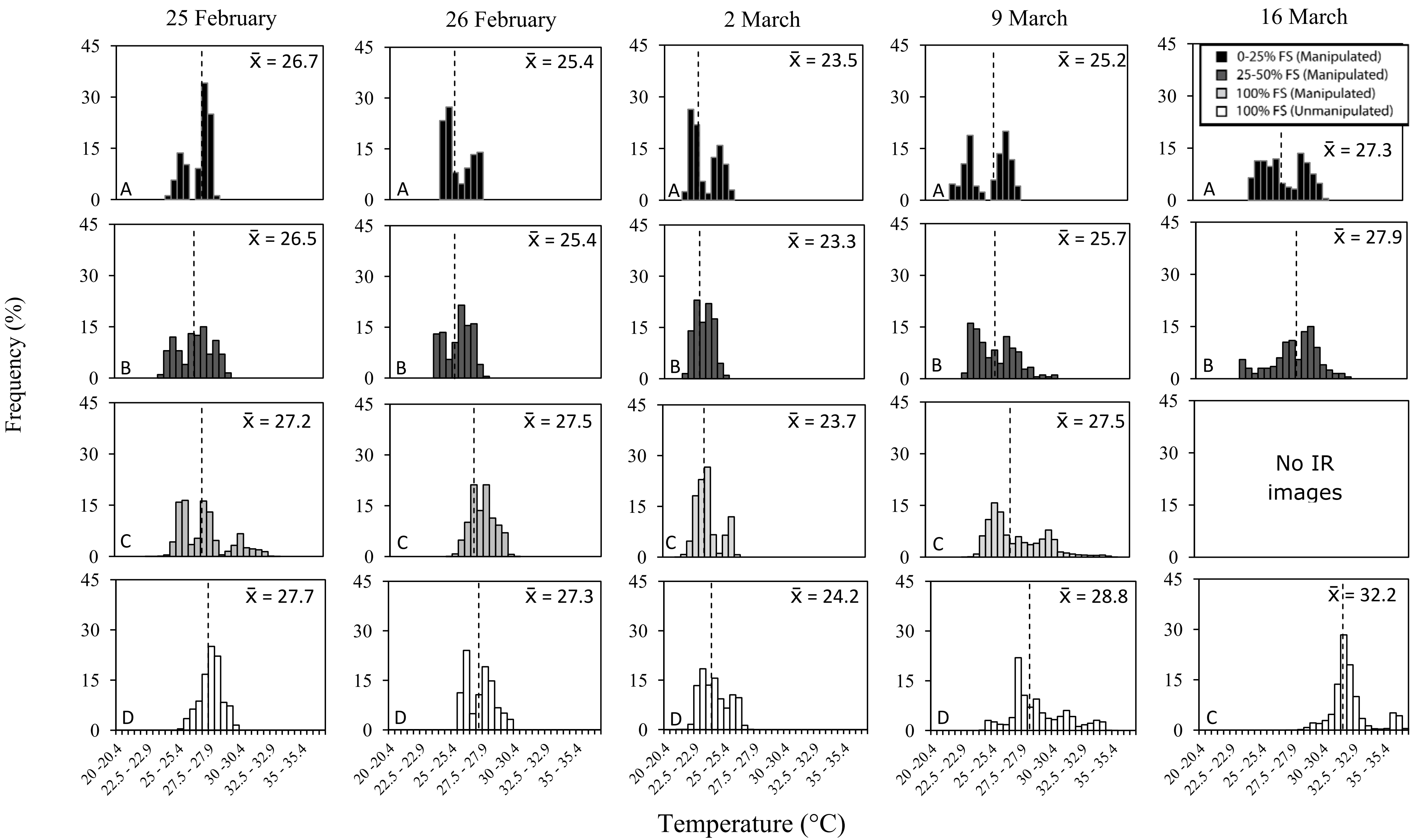

25 February
26 February
2 March
9 March
16 March
0-25% FS (Manipulated)
25-50% FS (Manipulated)
100% FS (Manipulated)
100% FS (Unmanipulated)
x̄ = 26.7
x̄ = 25.4
x̄ = 23.5
x̄ = 25.2
x̄ = 27.3
x̄ = 26.5
x̄ = 25.4
x̄ = 23.3
x̄ = 25.7
x̄ = 27.9
x̄ = 27.2
x̄ = 27.5
x̄ = 23.7
x̄ = 27.5
No IR images
x̄ = 27.7
x̄ = 27.3
x̄ = 24.2
x̄ = 28.8
x̄ = 32.2
A
B
C
D
0
15
30
45
Frequency (%)
20 -20.4
22.5 - 22.9
25 - 25.4
27.5 - 27.9
30 -30.4
32.5 - 32.9
35 - 35.4
Temperature (°C)

Figure 5.7. *(From previous page)* Rock temperature frequency distributions of the 3 experimental treatments: (i) 100% free space, (ii) 30 to 50% free space and (iii) 0 to 25% free space, plus the (iv) 100% unmanipulated free space (n=300), on 25 and 26 February and 2, 9, and 16 March 2010. Different letters denote significant differences in frequency distributions determined by two-sample Kolmogorov-Smirnov tests. Dashed vertical line indicates the median temperature of each treatment.

5.3.2.2 Early life history processes

In contrast to natural patterns, where there was greater variability of rock temperatures, I did not detect significant differences amongst the manipulated free space treatments that were consistent with differences in rock temperatures (Fig. 5.7). I found that neither rock temperature nor the amount of free space significantly influenced larval settlement within manipulated quadrats (Fig. 5.7a). This was also true for early post-settlement growth, as I detected no differences in the growth of newly settled *T. rosea* amongst treatments regardless of whether measurements were made from 9 to 16 March (Fig. 5.7b) or from 16 to 23 March (Fig. 5.7c). Early post-settlement survival did at times vary significantly among treatments, but this was not due to differences in the amount of free space or mean rock temperatures (Fig. 5.7d-f). For example, when estimates were made between 7 and 9 March early post-settlement survival was significantly greater within the unmanipulated 100% free space treatment in comparison to the manipulated treatments with 25 to 50% and 100% free space (Fig. 5.7d). Here, if rock temperature and manipulated free space were influencing early post-settlement survival, I would expect to see greater survival within the 25 to 50% free space treatment and lower survival in the 100% unmanipulated free space treatment.

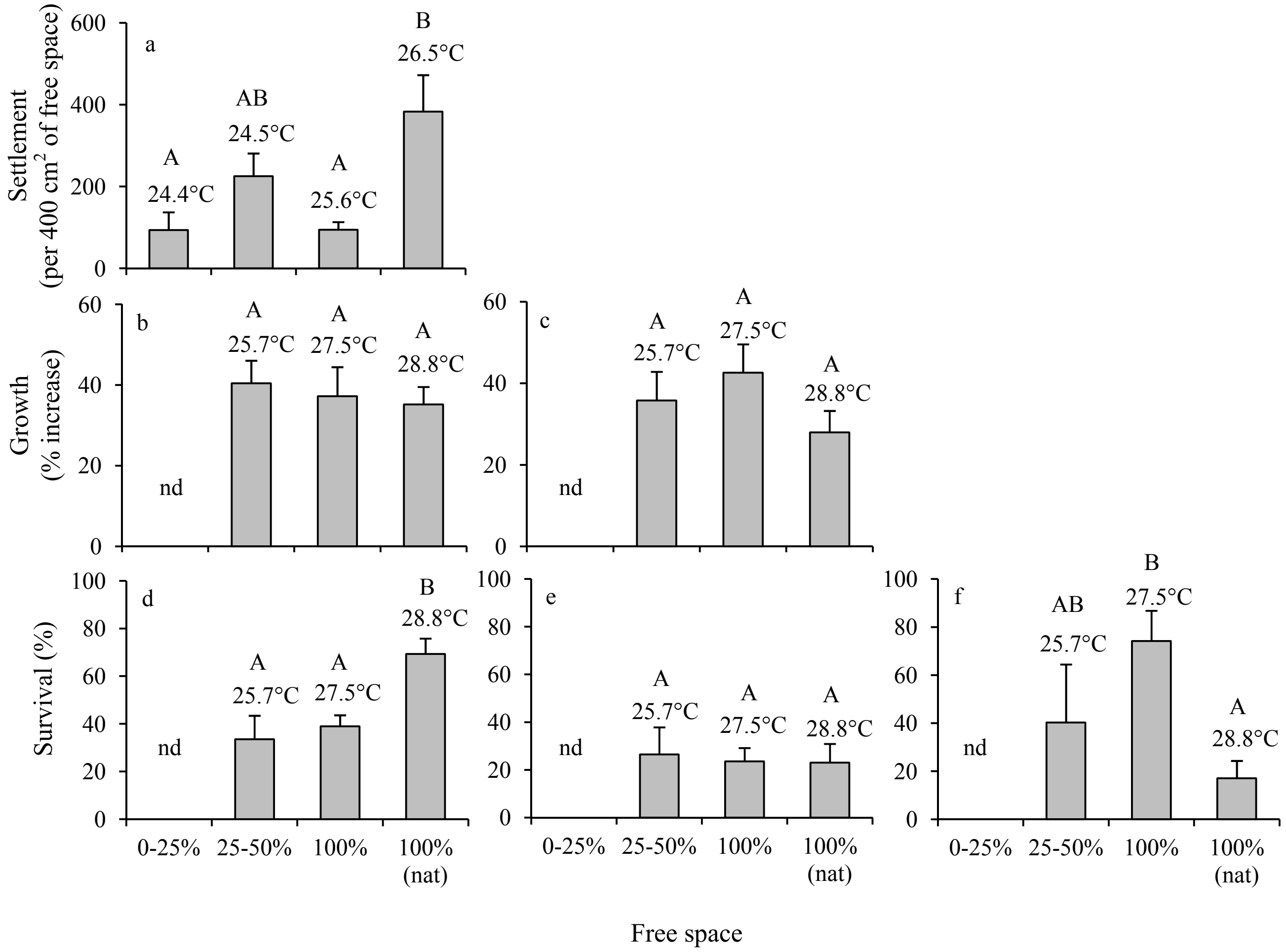


Figure 5.8. The effect of manipulated free space on *T. rosea* (a) larval settlement, (b-c) early post-settlement growth from 9 to 16 March (b), and 16 to 23 March (c), and (d-e) early post-settlement survival from 7 to 9 March (d), 9 to 16 March (e) and 16 to 23 March 2010. ND - no data because estimates of early post-settlement growth and survival could be made for 0 to 25% free space quadrats due to insufficient larval settlement.

5.4 Discussion

My use of IR photography to survey variation in rock temperatures among quadrats within the mid shore region revealed that, at the scale most relevant to a vast number of rocky shore studies, temperature varies more than has been reported in the past (Helmuth et al. 2006b) and, more importantly, that some quadrats are consistently warmer than others. This variation almost certainly reflected a range of factors including subtle variation in topography and orientation that would likely be captured within sets of experimental replicates. Indeed, these small differences may alter *T. rosea* abundance within the mid shore region since natural areas without *T. rosea* were warmer than manipulated areas without *T. rosea* that had previously been characterised by high adult densities prior to manipulation. Results also showed that the amount of free space within both natural and manipulated quadrats was a powerful determinant of quadrat temperature, which may have important implications for the many rocky intertidal experiments that manipulate cover (e.g. Connell 1961b, Denley & Underwood 1979, Fairweather 1988). Moreover, this substantial variation in temperature among quadrats significantly affected early post-settlement survival and growth of the barnacle *T. rosea*. Taken together these results indicate that the temperature variability among quadrats at the same tidal heights may be as equally useful for investigating the effects of temperature variability of intertidal organisms as the more traditional approach of comparing quadrats across intertidal heights, which can often be naturally confounded by other biological and physical factors. This high temperature variability among quadrats may also explain previously unknown causes of biological variability in a vast array of manipulative experiments (see Underwood 2000 for review of rocky intertidal experiments).

5.4.1 Rock temperature variability

Rock temperatures have been shown to significantly influence the body temperatures of intertidal barnacles (Harley & Lopez 2003) and gastropods (Chapperon & Seuront 2011) yet to the best of my knowledge the present study represents the first attempt to quantify small-scale rock temperature variability. There has also been little attempt to understand how biological communities influence rock temperature variability. Previous studies have demonstrated that temperature within the mid shore region varies between shaded and exposed areas (Bertness & Leonard 1997), vertical and horizontal surfaces (Helmuth 1998, Miller et al. 2009), north and south facing substrates (Denny et al. 2006, Harley 2008, Seabra et al. 2011) and between crevices and emergent rock (Jackson 2010). I found that within a single intertidal zone during low tide, mean rock temperatures of quadrats located only metres apart with similar substrate orientation, aspect and UV exposure vary by approximately 8°C. In comparison, air temperatures recorded by data loggers within the mid and high intertidal zone at Garie Beach during this time varied by 10.1°C (Lathlean et al. 2011). This suggests that, at least for horizontal emergent rock, temperature variability within a single microhabitat is as variable as temperature variability among several different microhabitats on wave-swept rocky shores.

Although it has previously been proposed by Bertness (1989) that increased densities of intertidal organisms positively affect early life history processes of benthic invertebrates by reducing thermal stress, the present study represents the first attempt to quantify the relationship between rock temperature and the availability of free space. As predicted by Bertness (1989), areas characterised by high percentages of free space were more thermally stressful than areas with high adult densities. This may be due to differences in fine-scale topographic features as adults not only reduce adjacent substrate temperatures by shading but may also increase interstitial humidity within small patches by reducing evaporative water loss (Kawai & Tokeshi 2004) and convective heat exchange between the substrate and higher atmospheric air temperatures (Helmuth 1998). The body temperatures of intertidal invertebrates living within different sized aggregations also display similar patterns to rock temperature variability and the amount of free space. For example, Helmuth (1998) reported that intertidal mussels living in aggregations display body temperatures 4-5°C lower than solitary individuals. Such effects may however be species-specific, because Coleman (2010) found no effect of aggregation size on the desiccation stress of the intertidal limpet *Cellana tramoserica*.

5.4.2 Measuring temperatures at small spatial scales

Quadrats have long been used as the preferred experimental unit within rocky intertidal studies (Miller & Ambrose 2000) yet recording equivalent and relevant temperature measurements at the quadrat level has proven somewhat difficult. Recent technical innovations, however, now make this possible. For example, temperature loggers with high resolution are now widely used to generate continuous temperature measurements within rocky intertidal habitats providing the most detailed information on temporal variation (see Chapter 3). Biomimetic loggers and thermocouples are also commonly used to record *in situ* body temperatures of intertidal organisms (e.g. Helmuth 1998, Harley & O'Riley 2011). Deploying multiple loggers to obtain replicate and detailed measures of spatial variation in temperature at the quadrat scale is impractical (but see Denny et al. 2011), and their current use is generally to provide information at larger spatial scales (Smale & Wernberg 2009). In contrast, IR imagery record temperatures that are representative of the spatial variation within quadrats. Consequently, the use of IR imagery represents a complimentary approach to measuring rocky intertidal temperatures and when used alongside temperature data loggers provide both detailed spatial and temporal temperature variability. Furthermore, infrared imagery measures temperature at scales relevant to recently settled larvae ($\approx 1mm^2$), and thus allows appropriate assessment of how extremely fine-scale temperature variation influences early life history processes of invertebrates (see next Chapter).

5.4.3 Early life history processes

Previous field studies concluding that early life history processes of intertidal invertebrates are particularly vulnerable to heat and desiccation stress have typically compared the survival of newly settled invertebrates amongst different microhabitats (Gosselin & Chia 1995) or experimental treatments known to differ in their thermal properties (e.g. Shanks 2009, Gedan et al. 2011). In contrast, I demonstrate that temperature variability within a single unmanipulated microhabitat (i.e. horizontal emergent rock with 100% free space) significantly influences the growth and survival of newly settled intertidal barnacles.

A significant relationship between free space and early growth and survival of *T. rosea* was not detected either within randomly chosen quadrats or the density manipulation. These findings most likely reflect the fact that while unmanipulated quadrat temperatures were determined in part by adult density they also clearly reflect other intrinsic differences between quadrats. Furthermore, density manipulation did not generate as wide a range of temperature variation as that observed for unmanipulated quadrats. For example, although they differed significantly, the average temperatures of the three manipulated groups of low, medium and high densities only varied by 2.3°C, whereas in comparison, the ten unmanipulated quadrats with 100% free space where I found significant effects of temperature on post-settlement growth and survival, varied on average by 4.7°C.

The lower thermal variability within manipulated quadrats may also be because they were in naturally cooler areas on the rocky shore, hence the initially high adult densities, or because manipulated quadrats retained white basal plates (see Fig. 5.1b), which would have increased reflectance and thereby reduced substrate temperatures.

Alternatively, manipulated quadrats could have displayed lower temperatures because they remained thermally buffered by the surrounding biological community while natural quadrats were not (see Gedan et al. 2011 for example of thermal buffering). The majority of temperature manipulation experiments undertake measurements during summer when organisms are more likely exposed to greater thermal stress than recently settled *T. rosea* in the present study as measurements were taken during autumn. Indeed, the early life history processes of *T. rosea* were most affected by temperature variability amongst unmanipulated quadrats with 100% free space, where rock temperatures were typically the hottest. Consequently, density manipulations may have a greater effect on the early post-settlement growth and survival of *T. rosea* during warmer summer months when extreme temperature events are more frequent.

Through the use of infrared imagery, this chapter reveals high inter-quadrat temperature variability as well as significant temperature variation within quadrats. Therefore, the proceeding chapter investigates, firstly, whether such fine-scale temperatures are consistent through time and, secondly, whether fine-scale temperatures significantly influence early post-settlement processes. To the best of my knowledge, this represents the first time that ultra-fine scale (≈1mm) temperatures are used to assess early post-settlement life history processes of a benthic invertebrate.

CHAPTER 6: Temperature variability at the larval scale affects the early survival and growth of *Tesseropora rosea*

6.1 Introduction

For rocky intertidal invertebrates, and indeed the majority of benthic marine invertebrates, the transition from pelagic larva to benthic settler represents a critical time in their life-history, characterised by high rates of mortality (e.g. Keough & Downes 1982, Minchinton & Scheibling 1993a, Gosselin & Qian 1997, Hunt & Scheibling 1997), and typically influences the size and distribution of adult populations (e.g. Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991). Newly settled intertidal larvae need to contend with aerial exposure as the tide recedes and their small size makes them particularly vulnerable to heat and desiccation stress (Gosselin & Qian 1997). Indeed, thermal tolerance is widely considered to play a critical role in determining vertical distributions on rocky shores (Somero 2002) and range limits of limpets (Gilman 2006b), barnacles (Herbert et al. 2007) and mussels (Jones & Wethey 2010). We understand very little about temperature variability at spatial scales relevant to individual organisms, and more importantly, the response of their sensitive early life history stages.

The use of infrared imaging techniques have recently emerged as an effective method of quantifying small-scale variation in both physical and biological characteristics of rocky intertidal shores (Murphy et al. 2006, Caddy-Retalic et al. 2011, Chapperon & Seuront 2011, Cox & Smith 2011). The advantage of such infrared sensing is that temperature variability of the substrate can be assessed at fine spatial scales (~1mm) relevant to settling benthic marine invertebrates. To the best of my knowledge, this technique has yet to be used to examine the effects of temperature at the scale of recently settled larvae in the field. Such fine-scale assessment of temperature will advance our ecological understanding of how temperature influences individual level responses and, ultimately, recruitment variability.

Here, using IR imagery, I first test the hypothesis that small areas on the rocky shore remain consistently warmer or cooler relative to the surrounding substrata. I then ask whether such fine-scale variation in rock temperature affects the settlement, early growth and survival of the barnacle *Tesseropora rosea*. Since larvae preferentially settle in close proximity to adults, I also ask whether rock temperatures close to adult conspecifics are lower than substrata further from adults and whether the shade generated by adults ameliorates thermal stress for newly settled larvae by reducing adjacent rock temperatures.

6.2 Methods

6.2.1 Identifying small hot and cold spots on a rocky shore

To test whether ultra-fine scale temperature variation influences settlement, early post-settlement survival and growth of *T. rosea*, I first needed to verify that fixed points (1mm×1mm) were consistently hot or cold (N.B. without consistent temperature variability I would not expect to find significant affects of temperature on early life history processes at this scale). To do this I established 10 permanent 20cm×20cm sites within the mid shore region at Garie Beach on 8 February 2010. These sites were similar to those used in the previous chapter in that all: (1) were within the mid shore region dominated by the barnacle *Tesseropora rosea* (0.8 to 1.6m above the mean low water mark of neap tides: MLWN), (2) had at least a 400cm^2 area of flat surface without crevices, depressions or macroalgae that could retain water during low tide, (3) had horizontal to moderately sloping surfaces, and unless otherwise stated initially had no sessile invertebrates even though over previous months and years they had been characterised by high adult *T. rosea* abundance (personal observation). Stainless steel screws were drilled into diagonally opposite corners of each site to ensure accurate resampling of sites and identification of individuals. Infrared images of these sites were taken on 25 and 26 February, and 2, 9 and 16 March 2010 during low tides that fell between 10:30am and 3:40pm (for further details regarding specific IR technique see section 4.2.2). Differences in the time of sampling would have had a minimal affect on rock temperature variability because on each day the mid-intertidal zone had sufficient time (at least 3 hrs) to heat up with little variation in the incidence of sunlight. Differences between sampling events are more likely to differ due to daily variability in weather (see Appendix II).

To determine whether relative rock temperatures within sites were highly correlated over time we used IR images and the software package ThermaCAM Pro 2.9 to compare the temperatures of 49 evenly spaced fixed pixels within each site taken on the five sampling dates (i.e. one IR image per quadrat per sampling date). Areas within these sites were identified as being consistently warmer or cooler than surrounding substrata by ranking the 49 temperature values within each site and making comparisons across the five sampling events. Consistent fine-scale temperature variation would allow us to make predictions concerning the effects of fine-scale temperature variability on early life history processes. Consequently, I then used those sites that consistently yielded strong relationships (as indicated by high and significant Spearman rank correlation values) to test the effect of temperature variability at the larval scale on settlement, early post-settlement survival and growth of *T. rosea*.

6.2.2 Early life history processes and fine-scale temperature variability

Seven of 10 sites displayed consistently warmer and cooler areas at fine scales (Table 1), but only three received sufficient numbers of larvae to warrant analysis of settlement and recruitment. Newly settled barnacles were identified and followed within these three sites every two to four days from 9 February to 23 March 2010 using a high resolution digital camera (Fujifilm S9600). Settlement was greatest within these three sites between 5 and 9 March. Therefore, settlers were classified as individuals that appeared within sites on 9 March and recruits as settlers that were still alive on 23 March. Newly settled barnacles were identified by digitally mapping the location and morphology of individuals within each site and counting the number of newly metamorphosed *T. rosea,* including empty tests of individuals that had settled, metamorphosed and died, since the previous census. Logistic regression was used to test for significant effects of temperature variation on settlement and recruitment. To test whether the temperature within sites influences early post-settlement growth, I measured the growth in maximal test length of 76 individuals from 9 to 16 March and 66 different individuals (taken from the same cohort of settlers as the 76 individuals) from 16 to 23 March. Maximum test length was used instead of aperture length because it was difficult to distinguish the aperture from the test of newly metamorphosed settlers. Only individuals that settled within sites during 5 and 9 March were chosen for growth measurements. Additionally, to avoid the potentially confounding effects of crowding, individuals that were in contact with one another at any stage of the sampling period were not included for estimates of growth or survival. Pearson correlations were used to examine the relationship between rock temperature and growth of settlers using IR images taken on 9 and 16 March.

6.2.3 Proximity to adults

To test whether adult conspecifics ameliorate thermal stress for newly settled *T. rosea* at fine-spatial scales an additional 10 permanent 20cm×20cm sites were established within the mid intertidal zone on 8 February 2010. These sites were established in areas with high adult *T. rosea* densities (i.e. <25% free space) which were then experimentally manipulated to produce sites with ≈ 50% randomly distributed free space. Using IR images taken on 9 March I then measured rock temperatures for 320 random points across all these sites. This generated values for points within both shaded (n=193) and exposed (n=127) areas at varying distances from the closest adult conspecific (0 to 60mm). At the time IR images were taken (10:30am), adult *T. rosea* shaded areas up to approximately 15mm from the base of their test. Therefore, we classified shaded areas within sites as rock adjacent to the eighth (45°) of the adult barnacle facing away from direct sunlight and within 15mm of the adult test (Fig. 6.1). Conversely, unshaded or exposed areas were classified as rock within sites adjacent to the eighth of the barnacle facing directly towards the sun (Fig. 6.1). However, unlike shaded areas, unshaded areas were not restricted to 15mm from base of barnacle test. Therefore temperature measurements for unshaded points within each site were used to test the effect of proximity to closest adult conspecific on rock temperatures using Pearson correlation. Of course, the shaded side of a barnacle would be expected to shift with the movement of the sun. Consequently, the total area around the circumference of the adult test influenced by shading would be greater than the 45° within which rock temperatures were measured.

Next, I measured the distance between settlers and their nearest adult conspecific for 346 individuals that settled within these sites between 5 and 7 March. These settlers were chosen irrespective of whether or not that were shaded at the time measurements were taken. I then followed the fate of these 346 settlers until 23 March and used a one-tailed logistic regression to test whether individuals within 15mm of adults had greater recruitment success. Lastly, to test whether proximity to adults influences early post-settlement growth, I measured the maximum test length of 51 individuals on 9 and 16

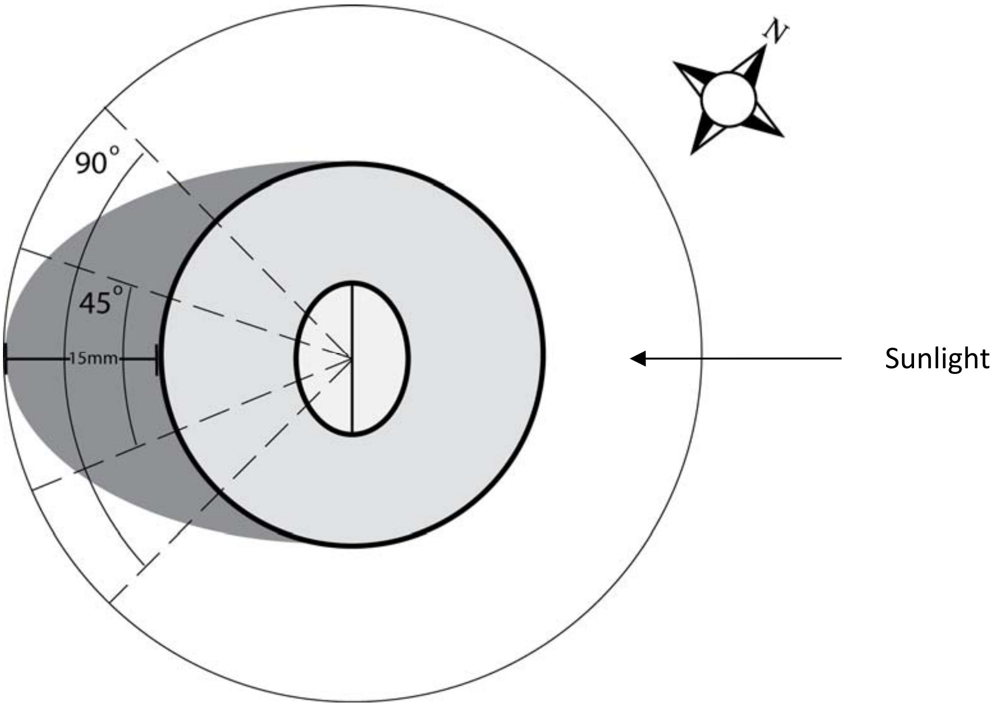


Figure 6.1. Schematic diagram illustrating shaded and unshaded areas adjacent to an adult barnacle during a morning low tide in the southern hemisphere. Shaded temperature measurements sampled from IR images were taken of rock adjacent to the eighth (45°) of the adult barnacle facing directly away from the main direction of the sun and within 15mm of the adult test.

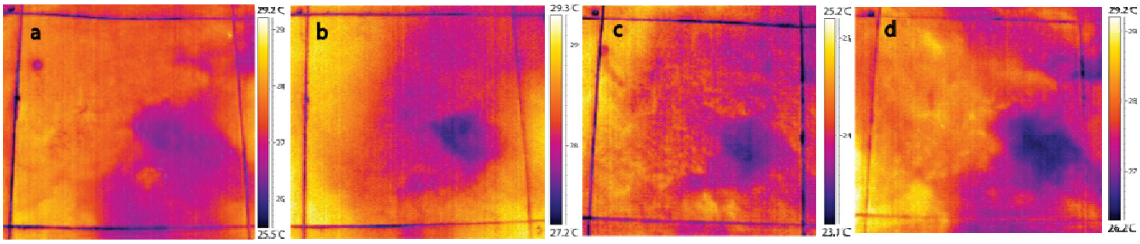


Figure 6.2. Infrared images of a single site (20cm×20cm) on 25 and 26 February (a – b) and 2 and 9 March 2010 (c – d). Warmer areas are represented by yellow and orange colours while cooler temperatures are represented by blue, pink and purple colours.

March and calculated growth as the percentage increase in shell length by 16 and 23 March, respectively. These individuals were chosen because (i) they settled within sites between 5 and 9 March, (ii) they were not in contact with other individuals at any stage of the sampling period, and (iii) they varied in their proximity to adult conspecifics. Linear regressions were used to compare the growth of individuals with proximity to closest adult conspecifics.

6.3 Results

6.3.1 Consistent fine-scale temperature variation

Individual larvae only centimetres apart experienced considerably different temperatures since IR images revealed that rock temperatures within sites varied by as much as 5°C and that this temperature variability was consistent through time (Table 1). Areas within all sites produced consistent temperature variation for at least three sampling events, while three sites displayed temperatures that were consistent across all five sampling events (see Fig. 6.1 for an illustration of this consistent temperature variability). Furthermore, 66 of 96 (68.8%) correlations between the temperatures of fixed points within sites over the five sampling events returned significant positive relationships (Table 6.1). Temperature variability within sites captured by IR images taken on 2 March were the most representative measures of temperature variability within sites for the entire sampling period because 31 of 39 (79.5%) of correlations involving temperatures taken on the 2 March produced significant and positive relationships (Table 6.1).

6.3.2 Early life history processes and fine-scale temperature variability

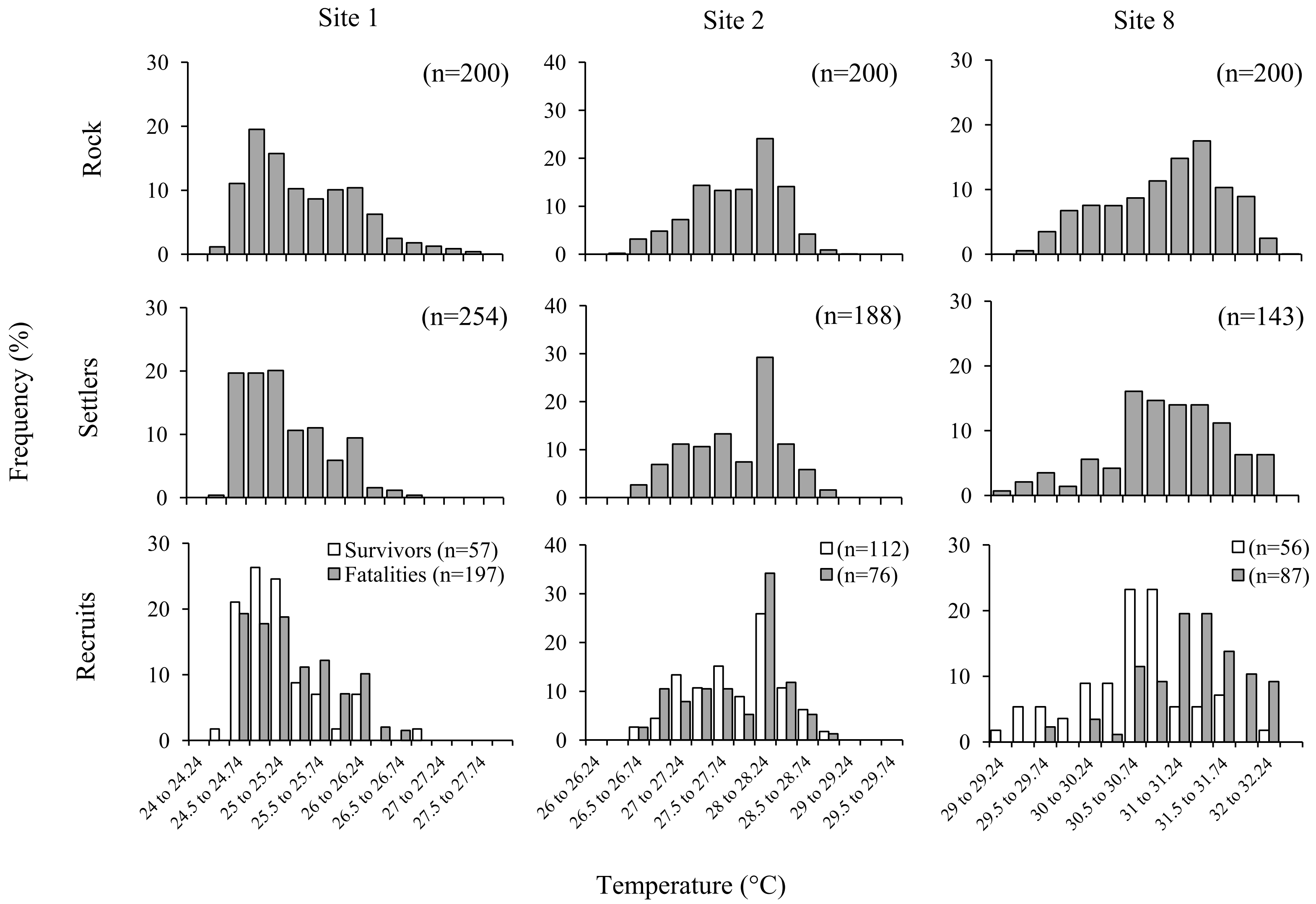
Significant but spatially variable effects of ultra-fine scale temperature variation were detected using each of the three measures of early life-history performance. In total, I identified and followed the fate of 585 newly settled *T. rosea* larvae within sites 1, 2 and 8. For sites 2 and 8, larval settlement did not vary between hot or cold areas at the 1mm scale (χ^2= 0.28, d.f.=1 p=0.60 and χ^2=1.14, d.f.=1, p<0.29, respectively) (Fig. 6.2). In contrast, cooler areas within site 1 had a greater number of settlers compared to warmer areas (χ^2=18.59, d.f.=1, p<0.0001).

The response of recruitment to variation in temperature varied among sites but recruitment was generally higher in cooler spots. For the 254 and 143 individuals that settled in sites 1 and 8, respectively, increased rock temperatures significantly reduced the chance of setters surviving to 23 March (χ^2= 4.46, d.f.=1 p=0.03 and χ^2=35.92, d.f.=1, p<0.0001, respectively) (Fig. 6.2). Whereas for the 188 individuals that settled in site two survival to 23 March was not dependent on temperature (χ^2=0.07, d.f.=1, p=0.795).

Most strikingly, early post-settlement growth during the first week after settlement was inversely related to temperature (r^2=0.24, p<0.001, n=76) but not during the second week (r^2<0.01, p=0.314, n=66) (Fig. 6.4). During the first week, individuals that experienced temperatures less than 30°C grew to an average size of 1.5mm in basal length, while individuals that experienced temperatures higher than 30°C generally grew to approximately 1.17mm in basal length (i.e. a 22% reduction in growth).

Table 6.1. Summary of outcomes for the Spearman rank correlation (r) between the mean rock temperatures of 49 fixed points within sites for the five separate sampling events. Bold font indicates significant positive relationships with p-value <0.05 (n=49 pixels). *indicates that a significant negative relation was found. Settlers/ Recruits refer to the number of *T. rosea* that settled within site from 5 to 9 March 2010 and the number of these individuals that were recounted as recruits on 23 March 2010.

	25 Feb	**26 Feb**	**2 March**	**9 March**	**(Settlers/ Recruits)**
Site 1					
26 Feb	**0.54**				
2 March	**0.08**	**0.26**			
9 March	**0.66**	**0.46**	0.03		
16 March	0.03	<0.01	0.01	0.07	(254/ 57)
Site 2					
26 Feb	**0.50**				
2 March	**0.26**	**0.45**			
9 March	**0.66**	**0.36**	**0.31**		
16 March	0.05	**0.29**	**0.12**	<0.01	(188/ 112)
Site 3					
26 Feb	0.03				
2 March	0.06	**0.27**			
9 March	0.02	0.12*	0.14*		
16 March	**0.15**	**0.27**	**0.54**	0.12*	(284/ 20)
Site 4					
26 Feb	**0.37**				
2 March	**0.26**	**0.27**			
9 March	**0.35**	**0.58**	**0.23**		
16 March	<0.01	<0.01	<0.01	<0.01	(68/ 0)
Site 5					
26 Feb	**0.32**				
2 March	**0.33**	**0.80**			
9 March	**0.26**	**0.46**	**0.28**		
16 March	**0.42**	**0.85**	**0.78**	**0.51**	(60/ 0)
Site 6					
26 Feb	Na				
2 March	Na	**0.46**			
9 March	Na	**0.74**	**0.41**		
16 March	Na	**0.67**	**0.59**	**0.54**	(119/ 0)
Site 7					
26 Feb	**0.30**				
2 March	**0.23**	**0.75**			
9 March	**0.12**	**0.33**	**0.60**		
16 March	**0.23**	**0.82**	**0.82**	**0.45**	(121/ 1)
Site 8					
26 Feb	**0.22**				
2 March	**0.55**	**0.09**			
9 March	**0.56**	0.05	**0.71**		
16 March	**0.17**	**0.17**	**0.09**	0.05	(143/ 56)
Site 9					
26 Feb	0.04				
2 March	**0.44**	0.01			
9 March	**0.23**	0.01	**0.32**		
16 March	**0.52**	<0.01	**0.57**	**0.37**	(76/ 5)
Site 10					
26 Feb	**0.72**				
2 March	**0.57**	**0.52**			
9 March	<0.01	<0.01	<0.01		
16 March	<0.01	<0.01	0.06	0.03	(173/ 8)


Site 1
Site 2
Site 8
Rock
Settlers
Recruits
Frequency (%)
(n=200)
(n=200)
(n=200)
(n=254)
(n=188)
(n=143)
□Survivors (n=57)
■Fatalities (n=197)
□(n=112)
■(n=76)
□(n=56)
■(n=87)
0
10
20
30
40
24 to 24.24
24.5 to 24.74
25 to 25.24
25.5 to 25.74
26 to 26.24
26.5 to 26.74
27 to 27.24
27.5 to 27.74
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27.5 to 27.74
28 to 28.24
28.5 to 28.74
29 to 29.24
29.5 to 29.74
29 to 29.24
29.5 to 29.74
30 to 30.24
30.5 to 30.74
31 to 31.24
31.5 to 31.74
32 to 32.24
Temperature (°C)

Figure 6.3. (*from previous page*) Temperature frequency distributions of rock substrate, settlers and recruits within three sites with 100% naturally available free space. Settlers are individuals that settled within sites from 5 to 9 March 2010, while recruits are settlers that survived to 23 March 2010. Fatalities represent the temperature of individuals that did not survive to 23 March 2010 (*n* is either the number of rock temperature measurements, settlers or recruits).

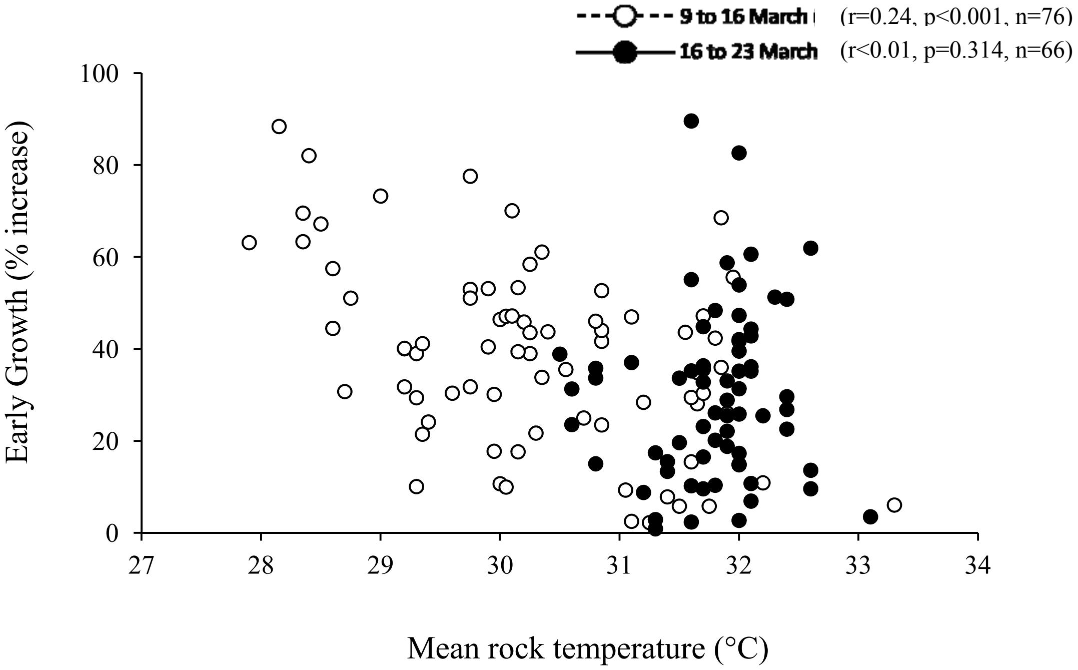

Figure 6.4. The influence of mean rock temperature on the early post-settlement growth (percentage increase from initial maximum test length) of recently settled individual *T. rosea* from 9 to 16 March (white circles) and 16 to 23 March 2010 (black circles).

6.3.3 Proximity to adults

It was found that rock temperature varied strongly with proximity to adults and that this variation was at least partially explained by the shade generated by adults. Within unshaded areas rock temperature displayed a significant inverse correlation with distance from the nearest adult ($r^2=0.127$, $p<0.0001$, $n=193$) (Fig. 6.5a). Points within 15mm of adults were on average 0.62°C cooler on shaded verses unshaded sides of adults ($t=7.00$, d.f.=252, $p=0.008$) revealing that the shade generated by adults lowers rock temperatures. Importantly it was found that the survival of settlers significantly increased the closer they were to adults, regardless of whether they were shaded by adults or exposed to the sun at the time measurements were taken ($\chi^2=3.19$, d.f.=1, $p=0.04$) (Fig. 6.5b). In contrast, proximity to closest adult had no effect on early post-settlement growth, irrespective of whether estimates were made during the first or second week after settlement ($r^2<0.01$, $n=48$, $p=0.635$, and $r^2<0.01$, $n=51$, $p=0.62$, respectively) (Fig. 6.5c).

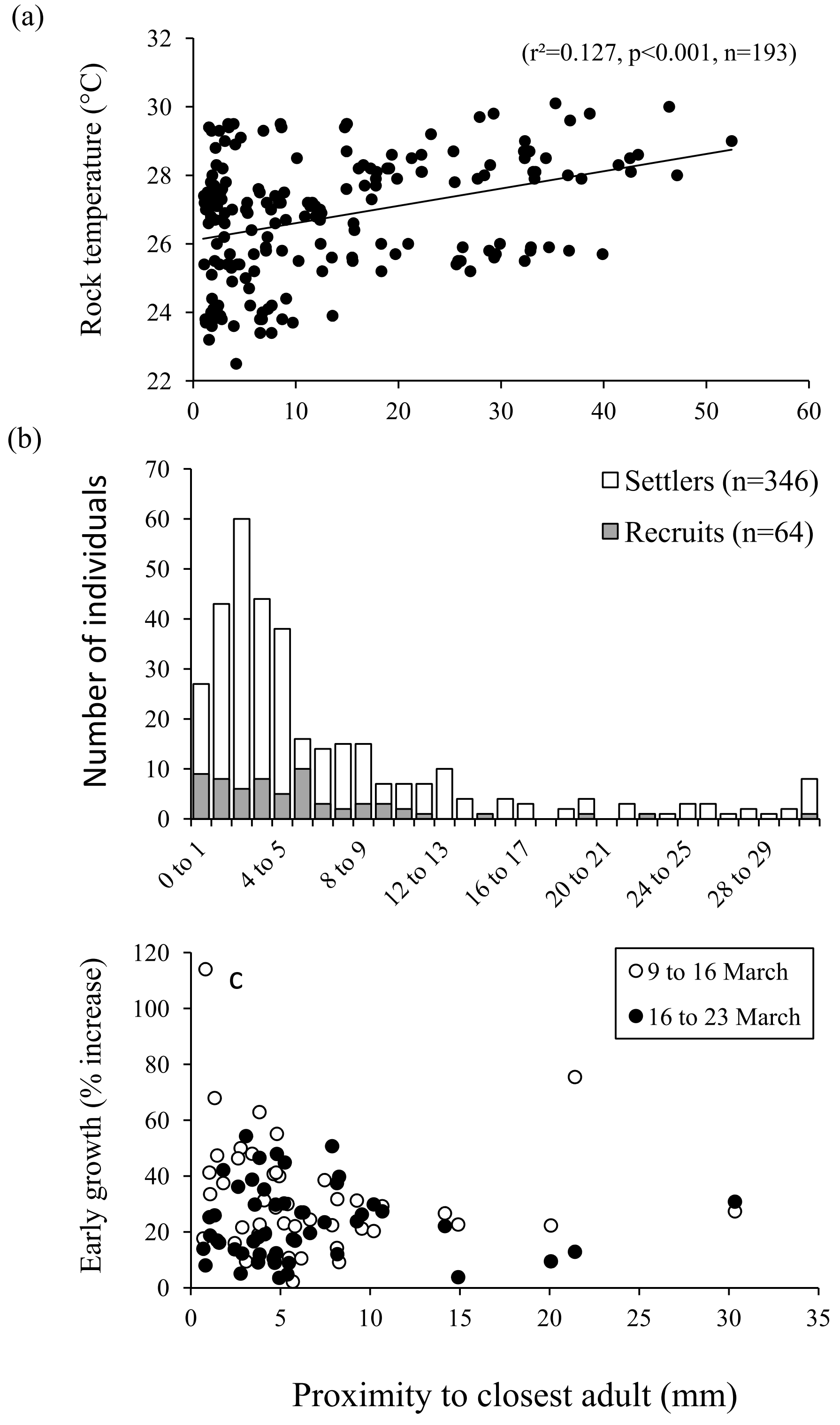

Figure 6.5. The influence of proximity (mm) to closest adult conspecific on (a) rock temperatures (includes only exposed areas), (b) settlement and recruitment (includes both exposed and shaded individuals), and (c) early post-settlement growth (includes both exposed and shaded individuals).

6.4 Discussion

The results of this chapter reveal that small-scale variability in rock temperature occurs on even finer scales than is usually reported (Helmuth et al. 2006b) with areas only centimetres apart differing by up to 5°C. This supports an increasing number of studies which have demonstrated considerable rocky intertidal temperature variability across small spatial scales (Jackson 2010, Denny et al. 2011, Meager et al. 2011). For example, Denny et al. (2011) deployed 221 temperature data loggers along a 336m transect within the mid shore region and found temperatures to differ by as much as 25°C. Surprisingly, I found consistent temporal variation in rock temperatures within sites, suggesting that at the larval scale, small areas (1mm^2) on a rocky shore can be identified as being consistently hot or cold. Furthermore, it was shown that, at least within three of 10 sites these hot and cold spots significantly influence both the early post-settlement growth and survival of recently settled larvae, key processes structuring the adult population (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991). By removing adult conspecifics I was also able to show that those larvae settling within 15mm of adults experience lower temperatures and survive better than those that settle further away. Shading provides at least partial explanation for this effect. It seems likely that in using a threshold distance of 15mm I may have underestimated the effect of shading due to variation in the size of adults. Additionally, we might also expect the presence of adults to modify temperature through effects such as evaporative cooling (Kawai & Tokeshi 2004) and results imply that adults are unlikely to be randomly distributed with respect to temperature since recruitment rates were higher in consistently cool areas. Whilst a considerable number of studies claim that temperature significantly influences early life history processes (see Gosselin & Qian 1997 for review), this is the first time that fine-scale temperature variability relevant to individual settlers has been shown to be related to the early life history stages of a benthic marine invertebrate.

6.4.1 Early life history processes and fine-scale temperature variability

Newly settled intertidal invertebrates are believed to be particularly vulnerable to heat and desiccation stress (e.g. Gosselin & Qian 1996). Results from this chapter provide evidence that even at ultra-fine spatial scales increased temperatures reduce early post-settlement survival. This supports previous work undertaken at larger spatial scales by Shanks (2009) who found that early post-settlement survival of the intertidal barnacle *Balanus glandula* was lower on warmer settlement plates covered in safety walk tape than cooler ceramic tiles. In contrast, laboratory and field experiments carried out by Findlay et al. (2010a) show that temperature has no affect on the early post-settlement survival and growth of the intertidal barnacles *Semibalanus balanoides* and *Elminius modestus*. Such discrepancies are not uncommon, suggesting certain species are more thermally tolerant than others, and further highlights the importance of measuring temperature variability at the larval scale.

Since early post-settlement survival and rates of recruitment are strong determinants of adult population size and structure (e.g. Minchinton & Scheibling 1991), and large-scale temperature variability affects settlement and recruitment (Lagos et al. 2005b), future research should focus on the relative importance of large-scale verses small-scale temperature variability on recruitment processes. Indeed, if fine-scale temperature variability is equivalent to or greater than latitudinal variation in temperature, predicting how organisms will respond to the increasing frequency of extreme temperature events associated with climate change may be equally as challenging for a single population as it is for multiple populations spread across large geographic regions (Denny et al. 2011). Furthermore, due to their small size and sessile existence, the body temperatures of recently settled larvae are largely determined by the underlying substrate. Yet rock temperature variability has been largely ignored as a potential source of early mortality for rocky intertidal invertebrates (but see Gedan et al. 2011), with most studies measuring air and body temperatures of adults (Helmuth et al. 2006b). Recent studies have also suggested that small spatial scale variability in rock temperatures may increase the survival of invertebrates in the warming climate (Chapperon & Seuront 2011; Denny et al. 2011).

Strikingly, I found that rates of early post-settlement growth at the scale of the individual were negatively associated with increasing substrate temperature during the first week after settlement. Although sublethal, the effect of increased temperature on early post-settlement growth might be expected to prolong the time it takes for juveniles to either reach reproductive maturity or a particular size whereby they are no longer as vulnerable to environmental stress or predation. For example, the ability of an intertidal invertebrate to withstand extreme air temperatures is largely related to its ability to regulate heat shock proteins (Somero 2002) and, consequently, juveniles or newly metamorphosed individuals may experience reduced growth rates or survival at high temperatures due to an inability to produce heat shock proteins in sufficient quantities.

Similarly to Chapter Five, rock temperature variability did not consistently effect larval settlement since only one of three sites displayed greater settlement within small areas that experienced lower temperatures during aerial exposure. Previous studies have demonstrated, however, that settling larvae can distinguish between biofilms that have developed under different environmental conditions (Qian et al. 2003, Hung et al. 2005). For example, settlement of the barnacle *Balanus amphitrite* varies depending on whether biofilms are established within the high, mid or low intertidal region (Qian et al. 2003), while settlement of the polychaete *Hydroides elegans* is lower on biofilms exposed to high ultraviolet radiation (UVR) (Hung et al. 2005).

6.4.2 Proximity to adults

Many authors have observed that sessile invertebrates settle preferentially in close proximity to adults or experience reduced mortality when recruit densities are high due to neighbours buffering thermal stress (Bertness et al. 1999a). For filter feeders such as barnacles aggregated settlement will also increase rates of intraspecific competition for food and space (Connell 1985). Results from this chapter show that bare substrata immediately adjacent to adult barnacles are significantly cooler than equivalent areas just a few centimetres further away from adults and that this is partially the result of adults shading nearby rock. It was also found that individuals that settled closer to adults were more likely to survive than those that settled further away because these areas closer to adults are less thermally stressful. This supports the findings of Kawai & Tokeshi (2004) who show that on a moderately exposed rocky shore in southern Japan, shading effects of the goose barnacle *Capitulum mitella* ameliorates heat stress for the mussel *Septifer virgatus* by lowering body temperatures and increasing interstitial humidity within patches. Alternatively, adults may influence rates of larval settlement and early post-settlement survival through consumption (Navarrete & Wieters 2000), settlement cues (Raimondi 1988b), altering the availability of suitable substrate (Minchinton & Scheibling 1993a) and water flow (Wright & Boxshall 1999). Consequently, adult conspecifics may indirectly affect the early life history processes of benthic marine invertebrates in multiple ways in addition to reducing thermal stress.

The results of this study have broad ranging implications for attempts to predict the effect of changing temperatures associated with climate change on species distributions. Indeed, poleward range retractions and expansions have already been documented for several intertidal species (Pitt et al. 2010). These results provide an important link between temperature variability and the response of individual invertebrates during a critical stage in their life history. In contrast, the increasing attention to climate change research has indirectly caused an overrepresentation of large-scale (10's metres to kilometres) temperature studies within the literature (Denny et al. 2011). This study presents evidence that small-scale temperature variability may be just as variable as large-scale temperature variability and, consequently, future research should become increasing concerned with incorporating temperature measurements at various large and small spatial scales.

CHAPTER 7: General Discussion

As recent research is beginning to discover (e.g. Chapperon & Seuront 2011, Denny et al. 2011), and as I have demonstrated, temperature variability on rocky shores differs significantly across fine spatial scales, which in turn directly influences the growth and survival of invertebrates. I show that this fine-scale temperature variability is particularly important during critical early life history stages of the habitat-forming intertidal barnacle *T. rosea* (Chapters 4 to 6). Until now, such fine-scale temperature variability has previously gone undetected because weather stations and satellites, the most common devices used for measuring rocky intertidal temperatures, do not adequately capture the temperature variability that exists between sites separated by 10s of centimetres.

For populations of *T. rosea* along the southeast coast of Australia I found no evidence to support the hypothesis that a latitudinal decline in SST, originally detected by satellites and later confirmed by *in situ* data loggers, is associated with large-scale variability in early life history processes (Chapter 2). Therefore, at least with respect to *T. rosea*, local processes that influence small-scale temperature variability may be vital for explaining larger scale patterns of recruitment and adult population structure. I also predict that fine-scale manipulative experiments, such as those developed in this study (see Chapter 4 and 5), will become increasingly important in translating the effects of small-scale temperature variability on local populations and communities to larger scale biogeographic processes. Although the effectiveness of these thermal manipulation techniques may be largely limited to rocky intertidal shores, hopefully they will inspire innovative thermal manipulations in other study systems and habitats. For example, techniques have recently been developed that electrically heat settlement plates within subtidal habitats (Smale et al. 2011). Technological improvements will obviously play a critical role in facilitating future thermal manipulation experiments in the marine environment.

7.1 Potential processes limiting the southern range limit of **T. rosea**

The lack of latitudinal trends in the production, settlement and recruitment of *T. rosea* larvae suggests that populations in the middle and edge of the range receive similar levels of larval supply and recruitment success. This contrasts with expectations that larval supply would decline as *T. rosea* approached its southern range limit due to a combination of reduced larval production, caused by lower seawater temperatures (Barber & Blake 1983, Brey 1995, Amaro et al. 2005, Vilchis et al. 2005), and increasingly unreliable larval transport by the East Australian Current from north to south (Ridgway 2007). Indeed, there is no evidence indicating that recruitment limitation, either through limited larval supply, settlement or increased early mortality, is influencing local populations at the southern range limit of *T. rosea* (see also Hidas et al. 2010). This study, however, was conducted over a relatively short period (two years) and geographic patterns of adult abundances might reflect environmental cycles with longer periodicity. For example, infrequent extreme temperature events could have long lasting impacts on rocky intertidal populations and the sampling period may have been too brief to document such effects (Denny et al. 2009, Mislan et al. 2009, Wethey et al. 2011b). Unfortunately, long term studies that monitor several early life history processes across large spatial scales are uncommon. Results presented in the second chapter of this thesis represent, to the best of my knowledge, one of only a few studies (*c.f.* Gilman 2006a, b) that investigate biogeographic variability in early life history processes towards a species range limit.

The southern range limit of *T. rosea* may be set by a biogeographic barrier to dispersal since the range limit coincides with the northern extent of Ninety-mile Beach, approximately 250km of unsuitable habitat (Hidas et al. 2007, Ayre et al. 2009). This dispersal barrier may also explain why several other rocky intertidal taxa have southern range limits just north of Ninety-mile Beach (Knox 1963, O'Hara & Poore 2000, Hidas et al. 2007). If penetration of the East Australian Current (EAC) continues to strengthen with climate change we might expect 'sudden' range expansions of several rocky intertidal invertebrates, including *T. rosea*, as dispersing larvae reach suitable rocky substrata south of Ninety-mile Beach. The detection of small ephemeral populations of *T. rosea* within southern Victoria, however, suggests that dispersal of *T. rosea* to these habitats are not always limited. Therefore, unfavourable environmental conditions within southern Victoria may be equally responsible for limiting *T. rosea* populations to the northern extent of Ninety-mile Beach (Ayre et al. 2009). A dispersal barrier is thought to have previously limited the northern distribution of the marine neogastropod *Kelletia kelleti* in California, USA, before increased seawater temperatures allowed larvae to disperse further north (Zacherl et al. 2003). Within south eastern Australia, strengthening of the EAC would not only extend the dispersal abilities of *T. rosea* larvae further south but it would also increase average sea surface temperatures (Ridgway 2007). This in turn may enhance the survival of juveniles to reproductive maturity. It is therefore not unreasonable to predict that within coming populations of *T. rosea* may become persistent around Wilsons Promontory (i.e. the most south-eastern point of mainland Australia) and eastern Tasmania. However, based on the low densities of present day populations near *T. rosea's* current southern range limit, any near future *T. rosea* populations in southern Victoria and eastern Tasmania are unlikely to be as abundant as populations in northern and central New South Wales.

7.2 Linking broad-scale temperature variability with organism physiology

A number of studies, within a variety of habitats, have begun to recognise the limitations of remotely sensed temperature measurements in characterising habitat-level temperature variability (e.g. Helmuth 2009, Smale & Wernberg 2009, Graae et al. 2012). Similar to the outcomes of this thesis, these studies also show that weather stations significantly underestimate the number of extreme temperature events. This is somewhat alarming since extreme temperature events not only significantly affect biological processes but are also expected to become more frequent with climate change (Easterling et al. 2000, Denny et al. 2009, Wethey et al. 2011b). To date, my characterisation of regional rocky intertidal temperature variability represents the only study that describes the temporal and spatial temperature variability of rocky shores for this region. I have also demonstrated for the first time that rocky intertidal air and water temperatures decrease with increasing latitude along the southeast coast of Australia. This is important because we might predict southern range limits of intertidal invertebrates within this region to be limited by a latitudinal temperature gradient (see discussion above). Unfortunately, these local-scale temperature measurements do not necessarily reflect the body temperatures of *T. rosea* or other common intertidal invertebrates within this region (see Fitzhenry et al. 2004, Broitman et al. 2009, Helmuth 2009). For example, due to differences in morphology, behaviour and surface properties between species, two organisms subjected to the same habitat-level temperature variability may display significantly different body temperatures (Broitman et al. 2009). Thus, *in situ* data logger measurements used in the present study provide a coarse estimate of temperature variation.

Along the east and west coasts of the United States, studies monitoring the body temperatures of numerous intertidal taxa have been underway for over a decade (e.g.

Helmuth 1998, Harley & Helmuth 2003, Denny & Harley 2006, Schneider 2008, Szathmary et al. 2009). These studies have produced numerous models capable of accurately estimating body temperatures of mussels (Helmuth 1998, Gilman et al. 2006, Wethey et al. 2011a), barnacles (Wethey 2002), limpets (Miller et al. 2009) and predatory seastars (Szathmary et al. 2009). In contrast, there is relatively little research describing and identifying sources of body temperature variability of rocky intertidal organisms within temperate Australia (but see Cole 2010, Coleman 2010, Caddy-Retalic et al. 2011, Chapperon & Seuront 2011). Consequently, there is great potential for future research to establish long-term environmental monitoring programs within south eastern Australia where temperatures are expected to have an increasing effect on rocky intertidal organisms.

7.3 Temperature, early life histories and climate change

While most studies to date have successfully measured the body temperatures of adult intertidal invertebrates (e.g. Helmuth 1998, Broitman et al. 2009, Szathmary et al. 2009), infrared imaging techniques developed in the present study represent the first attempt to quantify the body temperatures of an intertidal invertebrate during their vulnerable early life history stages. This is particularly important because early life history processes significantly contribute to structuring the size and distribution of the resulting adult population (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Caley et al. 1996, Menge 2000). Therefore, thermal stresses that affect intertidal invertebrate settlers and recruits may disproportionately influence population and community structure. Indeed, my results indicate that even at ultra-fine spatial scales, temperature significantly influences the early life history processes of *T. rosea*. Further research is required to understand how these fine-scale patterns in early life history processes influence rocky intertidal populations and communities and how such fine-scale temperature variability will be modified with future climate change.

Previous studies have also highlighted the importance of habitat heterogeneity in combating the effects of climate change on local populations (Denny et al. 2011, Gedan et al. 2011, Meager et al. 2011). In the present study, high within-site temperature variability suggests that extreme temperature events are likely to have a mosaic effect on local populations (Chapters 5 and 6). For instance, extreme temperature events are expected to increase the number of localised extinctions of populations. Nevertheless, small-scale temperature variability will allow some species to simply occupy less thermally stressful areas on the shore rather than becoming locally extinct. Of course, invertebrates with a mobile adult stage are more capable of using such an adaptation. The multifactorial nature of small-scale temperature variability on rocky intertidal shores may limit our ability to predict how large-scale temperature variability will affect species distributions (Helmuth et al. 2006a). Furthermore, species responses to increasing thermal stress may be largely idiosyncratic as some species will adapt to further increases in temperature better than others (Somero 2010).

The results of this study have other broad ranging implications for understanding how rocky intertidal invertebrates will respond to increasing temperatures and extreme events associated with climate change. Range limits are expected to shift towards the poles in response to increasing temperatures (Helmuth et al. 2006b). Large-scale transplant experiments are often used to help understand the factors that limit a species distribution (e.g. Gilman 2006b). However, a major confounding factor of these large-scale transplants is that, due to localised adaptations to temperature, transplanted individuals may survive or grow differently to resident individuals. Consequently, for transplants involving rocky intertidal invertebrates, the simple thermal manipulation technique developed in Chapter 4, involving different coloured settlement plates, could be used to tease apart the effects of geographic region and temperature. Furthermore, thermal manipulations may be particularly useful for simulating the effects of future temperature variability or extreme temperature events on intertidal communities. This is because they directly elevate body temperatures to reflect future scenarios and do not require long-term monitoring or particularly extreme weather to simulate extreme events.

My results also highlight the importance of incorporating temperature variability caused by differences in the biotic community into climate change models and predictions. Indeed, variable free space along the southeast coast of Australia (see Figure 1.2) may cause rock temperatures within southern regions to be equally or more thermally stressful than northern regions. The fact that such local variability can override large-scale processes is becoming increasingly obvious (see Helmuth *et al.* 2006a). My results add to the increasing debate over the appropriate scales of measure needed to understand processes that influence recruitment population structure and range shifts of species in a warming climate.

7.4 Future directions

Since increasing temperatures will effect intertidal organisms either directly through physiological performance or indirectly by altering biotic interactions, future research should focus on (i) characterising the basic thermal biology of various intertidal invertebrates (i.e. thermal limits, optima, *in situ* body temperatures etc.), (ii) relating these to local, regional and large-scale distributions, and (iii) investigating how increasing temperatures will change algae-herbivore and prey-predator relationships. *Tesseropora rosea* may again serve as a useful model species for investigating the effects of temperature on interspecific interactions as it is the primary competitor of the intertidal barnacle *Catomerus polymerus* (Denley & Underwood 1979), it provides suitable habitat for the limpet *Patelloida latistrigata* (potentially due to thermal amelioration) (Creese 1982) and is the preferred prey item of the predatory whelk *Morula marginalba* (Fairweather 1984).

To understand how rocky intertidal communities will respond to climate change we first need to understand how changing temperatures will influence the supply and survival of new recruits. To my knowledge, there are currently no long-term large-scale rocky intertidal recruitment studies being undertaken within south eastern Australia. In comparison, large-scale studies within the United States and Chile have been documenting patterns of larval settlement and recruitment of rocky intertidal invertebrates for decades. Such studies significantly contribute to our current understanding of how environmental variability influences early life history processes (Broitman et al. 2005a, Lagos et al. 2005b, Blanchette & Gaines 2007, Broitman et al. 2008a, 2008b, Navarrete et al. 2008, Menge et al. 2009, 2011). Therefore, future research should investigate the effects of large-scale and biogeographic temperature variability within south eastern Australia on rates of larval settlement and recruitment of intertidal invertebrates. Such information is necessary if we are to accurately model and predict the threat of climate change on these intertidal communities.

In summary, numerous factors need to be considered when assessing the effect of temperature on the early life history processes of intertidal invertebrates, including biotic factors and consistent small-scale temperature variability. The results of my thesis show that for a single species, the effects of temperature not only vary during different life history stages, but also, across different spatial scales. These findings contribute to the growing body of work that highlights the importance of small-scale temperature variability in influencing the biogeographic and physiological responses of rocky intertidal communities in the face of climate change.

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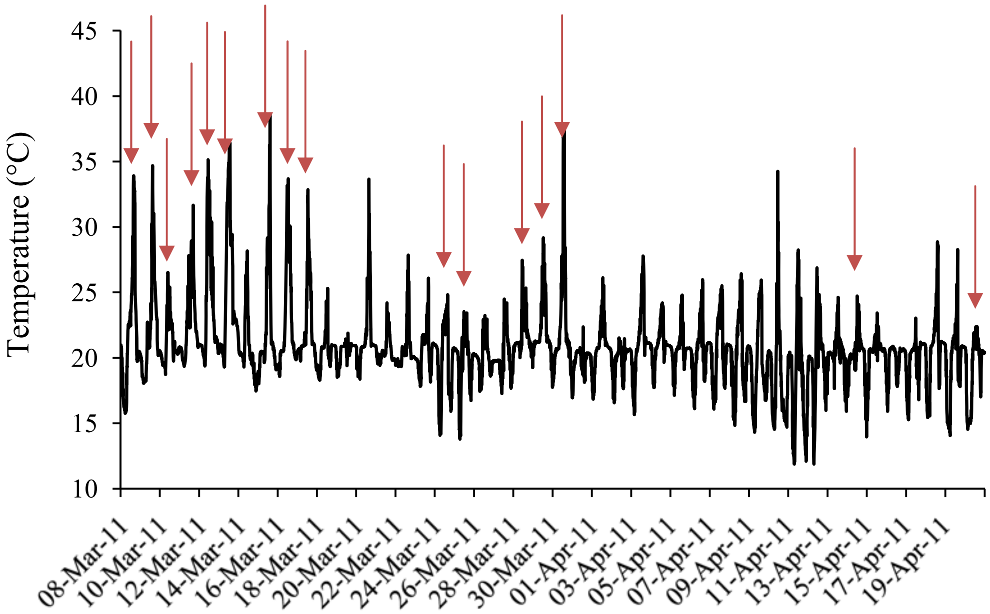
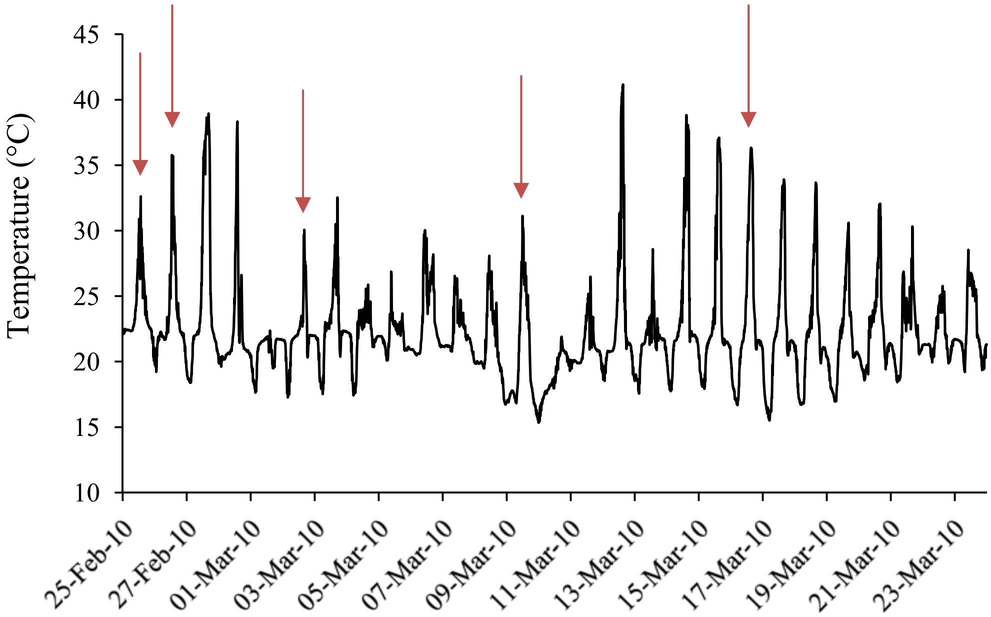
Appendices



Appendix I. Continuous intertidal temperature variability recorded by an *in situ* temperature data logger (TidbiT® v2 Onset Stowaway logger, model UTBI-001, accuracy ±0.2°C) within the mid-shore region at Garie Beach from 8 March 2010 to 20 April 2011 (sampling period used in chapters 4). Red arrows indicate the 16 sampling events when IR images where taken.



Appendix II. Continuous intertidal temperature variability recorded by two *in situ* temperature data loggers (TidbiT® v2 Onset Stowaway logger, model UTBI-001, accuracy ±0.2°C) within the mid-shore region at Garie Beach from 25 February 2010 to 23 March 2010 (sampling periods used in chapters 5 and 6). Red arrows indicate the five sampling events when IR images where taken.