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

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Abstract

For rocky intertidal organisms, temperature is often considered the most influential factor governing early survival and growth. Nevertheless, our review of the literature revealed that few studies have manipulated temperatures in the field to test for effects on these critical early life history processes. Here, we present the results from a novel manipulation of substratum temperature using settlement plates of different colour (black, grey and white) and infrared measurements of temperature to test hypotheses that temperature influences the early survival and growth of recent settlers of the intertidal barnacle *Tesseropora rosea*. Mean surface temperatures of black and grey plates were as great as 5.8°C (on average 2.2°C) and 4.8°C (on average 1.6°C) hotter than white plates across the sampling period, respectively. Cooler, white plates had significantly greater settlement and early growth than hotter, black plates, but differences in plate temperature did not significantly influence early survival or recruitment, though patterns were consistent with thermal variability. Comparisons between grey coloured natural rock and plates indicate that grey plates thermally mimic natural rock. Nevertheless, on average, more than twice as many larvae settled on plates than on natural rock, but early post-settlement survival on natural rock was double that on plates, suggesting that this artificial surface may not adequately capture the natural variability in early life history processes. Regardless, our simple and repeatable thermal manipulation represents a useful tool for experimentally investigating the effects of temperature on recruitment processes and simulating future temperature variability associated with climate change.

Keywords

climate, rocky, stress, thermal, recruitment, manipulating, invertebrates, patterns, predict, marine, shores, changing, under

Disciplines

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

(Running head: Thermal stress on rocky shores)

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Abstract: For rocky intertidal organisms temperature is often considered the most influential factor governing early survival and growth. Nevertheless, our review of the literature revealed that few studies have manipulated temperatures in the field to test for effects on these critical early life history processes. Here we present the results from a novel manipulation of substratum temperature using settlement plates of different colour (black, grey, white) and infrared measurements of temperature to test hypotheses that temperature influences early survival and growth of recent settlers of the intertidal barnacle *Tesseropora rosea*. Mean surface temperatures of black and grey plates were as great as 5.8°C (and on average 2.2°C) and 4.8°C (and on average 1.6°C) hotter than white plates across the sampling period, respectively. Cooler, white plates had significantly greater settlement and early growth than hotter, black plates, but differences in plate temperature did not significantly influence early survival or recruitment though patterns were consistent with thermal variability. Comparisons between grey coloured natural rock and plates indicate that grey plates thermally mimic natural rock. Nevertheless, on average more than twice as many larvae settled on plates than on natural rock, but early post-settlement survival on natural rock was double that on plates, suggesting that this artificial surface may not adequately capture the natural variability in early life history processes. Regardless, our simple and repeatable thermal manipulation represents a useful tool for experimentally investigating the effects of temperature on recruitment processes and simulating future temperature variability associated with climate change.

Keywords: Climate change, early mortality, Safety Walk® tape, settlement, barnacle.

INTRODUCTION

It is not surprising that climate change research has increased rapidly over the past two decades (Harley et al. 2006) since associated increases in global temperatures are expected to alter the physiology, ecology and biogeography of organisms worldwide (Helmuth et al. 2006b). At the heart of this research is understanding 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. 2011). 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), yet few studies have measured the responses of newly settled larvae or recruits to temperature manipulations in the field (see Table 1).

In reviewing the literature we found 76 studies that have examined the effects of temperature on rocky intertidal invertebrates in the field (Table 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, such as, 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 were altered by manipulating shade (Bertness 1989, Bertness et al. 1999b), macroalgae (Bertness et al. 1999a), substratum size (Gedan et al. 2011) and substratum type (Shanks 2009) influenced the early life history processes of barnacles (Table 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 1993), 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. 2005, Broitman et al. 2008). This research has shown that differences in substratum characteristics (temperature, texture, etc.) between artificial and natural rock surfaces can influence early mortality and recruitment (e.g. Raimondi 1988, 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 hotter 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 study was to use artificial settlement plates covered with SWT of different colours to manipulate substratum 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. We achieved this by comparing settlement, early post-settlement growth, survival and recruitment of *T. rosea* on natural rock to the artificial settlement plates.

METHODS

Study region and species

Our study 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 (0-20°) inclination. *In situ* measurements recorded by TidbiT® v2 Temp data loggers (Onset Stowaway logger, model UTBI-001, accuracy ±0.2°C) every 10 min show that mid-intertidal air temperatures at Garie Beach (including both day- and night-time temperatures) 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). 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 5 years (Hidas et al. 2010, Lathlean et al. 2010). We 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).

Manipulation of substratum temperatures

After preliminary investigations, we 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. 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. 1d).

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.* The fourth treatment allowed comparisons between natural rock and artificial surfaces. One advantage of using plates with SWT to manipulate substratum temperature is that all substrata have identical surface textures. Differences in colour among artificial surfaces would not be expected to influence processes after barnacle settlement, other than by influencing substratum temperatures. Indeed, 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. There are, however, minor chemical differences between black SWT, which is made of polyurethane 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 the unavailability of all three coloured SWT of identical textures. Therefore, to minimise any differences in chemical properties of differently coloured plates and SWT, we thoroughly cleaned plates using freshwater and allowed them to soak for 24 hrs before applying SWT. Once SWT was applied we further conditioned plates in the field for 3-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).

Fifteen plates (five per treatment) were allocated haphazardly and screwed onto horizontal to slightly sloping 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. Sites were constrained to be horizontal to slightly sloping emergent rock with at least 400cm^2 area of flat surface without crevices or depressions that could retain water during low tide. We monitored plates daily while they were being conditioned in the field, and no barnacles were observed to have settled on plates or rock during this conditioning period. Therefore, we did not need to remove any settlers before the start of the experiment.

Measuring substratum temperatures using infrared imaging

To measure rock and plate temperatures, infrared (IR) images were taken using a digital IR camera (FLIR S65 ThermaCAM) 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.

The thermal resolution of the IR camera is 0.08°C at 30°C, and by recalibrating the camera approximately every 2 minutes the accuracy of IR measurements were ±0.2°C (see below). Emissivity (ε) 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 (Denny and Harley 2006; Chapperon and Seuront 2011; Cox and Smith 2011). Emissivity values of polyurethane and polyethylene products (i.e. black and clear SWT, respectively) generally vary between 0.95 and 0.97

depending on ambient conditions (J.A. Lathlean, personal observation). Altering emissivity values between 0.95 and 0.97 typically produced a 0.6°C difference in plate temperatures (unpublished data). Therefore, differences due to emissivity values woud not have significantly influences our results. 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 we 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.

Early life history processes

To test the effect of temperature and artificial surfaces on the early life history processes of *T. rosea*, we estimated settlement, early post-settlement growth, survival and recruitment 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 the 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 we 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.

Data analysis

We used two-way ANOVA 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 differences in temperatures and early life history processes among treatments. We also wanted to test separately for differences among the three artificial surfaces (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. We confirmed that the data were normally distributed and showed equal variance using the Shapiro-Wilks' test for normality and Cochran's test, respectively, and therefore data were not transformed.

RESULTS

Manipulation of substratum temperatures

Substratum temperatures were significantly different among the four substratum types, but differences varied depending on the date temperature measurements were taken (interaction of substratum type × 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. Moreover, black plates were significantly hotter than all other treatments, and grey plates and rock were significantly hotter than white plates (SNK tests). Consequently, the thermal properties of natural rock were most similar to those of grey plates (Fig. 2).

When substratum temperatures were analysed separately for each day, we detected significant differences among treatments for 11 of the 16 sampling dates, with hotter dates showing greater differences among substrata than cooler dates (Fig. 2, SNK tests). In general, black and grey plates and rock were consistently hotter 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. 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. 2). Interestingly, the surface temperatures of grey natural rock were most similar to those of grey plates.

Early life history processes

From the 24 March to 2 April, settlement of barnacle larvae varied significantly amongst substrata and was greatest on white and grey settlement plates and least on natural rock ($F_{3,17}$=3.75, p=0.036) (Fig. 3a). Larval settlement on white plates varied significantly from 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. 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. 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. 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. 3b). Surprisingly, our thermal manipulation did not have a significant effect on early post-settlement survival of settlers on artificial surfaces of different colour (Fig. 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. 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. 3c). Here, individuals that settled on cooler, white plates were 15% larger than those on hotter, black plates (Fig. 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. 3d). Although not statistically significantly, white plates had almost twice the number of recruits compared to grey plates (Fig. 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 substratums produce similar estimates of recruitment in comparison to rock.

DISCUSSION

Our 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 we manipulated average substratum temperatures 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, we 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.

Manipulating rocky intertidal temperatures

Apart from the present study, to our knowledge 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 substratum 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). Our 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, our manipulation of the thermal environment may also be potentially confounded because plates and SWT differed in colour and could thus be chemically different (see Discussion below).

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 different coloured plates 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 substratum temperatures influenced larval settlement directly since larvae arrive during high tide when substratum 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). Similarly, 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*. Whether or not thermal variability indirectly influences larvae settlement by altering biofilm communities has yet to be empirically tested, but could be an important indirect effect of changing temperature conditions.

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 indirectly settle in response to colour, not temperature or biofilm, as the intensity of light associated with different colours can be a particularly strong 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 suggests 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. We believe this to be unlikely because we 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 our artificial plates covered in SWT in comparison to the natural substrata supports Menge et al. (2010) who demonstrated 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 or some other factor (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, and indeed any artificial surface, to estimate early life history processes.

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, we found no effect of our thermal manipulation (i.e. different coloured plates) on early post-settlement survival of *T. rosea* even though white plates were up to 5.8°C cooler than black plates. In contrast, numerous studies have shown thermal stress to significantly influence the early post-settlement survival and recruitment of intertidal barnacles. For example, Bertness (1989), Bertness et al. (1999a. b) and Gedan et al. (2011) have collectively shown that the survival of recently metamorphosed *Semibalanus balanoides* is greater (i) within cooler low intertidal regions relative to hotter high intertidal regions, (ii) on boulders compared to smaller (and hotter) cobbles, and (iii) under experimental shade plots and higher macroalgae canopy cover. 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. We also report unusually high (≈76%) 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. Our 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 we found no difference in early post-settlement survival among our three differently coloured plates. Perhaps early post-settlement survival among plates may have varied under a different set of thermal conditions, such as during extreme heat events. Apart from thermal stress, bulldozing by the abundant limpet *Cellana tramoserica* might also be a source of early mortality for intertidal barnacles in the study region (Jeffery 2003), but this explanation is unlikely because these limpets were rarely observed on plates. Furthermore, for each of the three daily cohorts early post-settlement survival varied consistently among our four substratum types. Early post-settlement growth and survival has been shown to vary among daily cohorts of newly settled barnacle larvae due to differences in larval quality (Jarrett and Pechenik 1997, Pineda et al. 2006) and, consequently, it is likely that larvae among daily cohorts in our relatively short-term study were of similar quality.

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, we 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 hotter grey and black plates. In contrast, laboratory experiments carried out by Findlay et al. (2010a, b) show that temperature has no affect on the early post-settlement growth of the intertidal barnacles *Semibalanus balanoides* and *Elminius modestus,* while field studies on intertidal mussels have found increased temperatures to either increase (Blanchette et al. 2007) or decrease adult growth (Petes et al. 2007). Our 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.

Testing the effects of climate change on rocky intertidal shores

Using settlement plates of different colour but similar texture may provide a useful tool for experimentally investigating how increasing temperatures associated with climate change will affect intertidal populations and communities. For example, field experiments that manipulate temperature are particularly useful for addressing the role of extreme temperature events on future populations because they directly elevate body temperatures to reflect future scenarios and don’t require long-term monitoring or particularly extreme weather to simulate future temperatures (Smale and Wernberg 2012). Alternatively, range limits are expected to shift towards the poles in response to increasing temperatures (Helmuth et al. 2006b) and large-scale transplant experiments are often used to help understand the factors which limit a species distribution (e.g. Gilman 2006a). However, transplanted individuals may survive or grow differently to resident individuals due to local adaptations or physical conditions other than temperature. For transplant experiments involving rocky intertidal invertebrates, different coloured plates could be used to tease apart the effects of geographic region and temperature or simulate future temperature variability. Our thermal manipulation could also be used to examine other ecological processes in the field including predator-prey interactions and changes in whole species assemblages, both of which are expected to change in response to increasing temperatures (Sanford 1999, Harley 2011).

Conclusion

It is clear from the literature (Table 1), and from the results of this experiment, that our empirical understanding of how temperature influences the early life history stages of benthic marine invertebrates has been largely influenced by laboratory studies and limited by our ability to (i) measure *in situ* temperatures at scales relevant to settlers and recruits, and (ii) manipulate temperature in the field. Previous work by the current authors attempts to address the first of these two issues by measuring ultra-fine scale (1mm^2) temperature variability and relating this thermal variability to the fate of individual settlers. Results indicate that even at such fine spatial scales thermal variability significantly influences early post-settlement processes (J.A. Lathlean unpublished data). The present paper, however, presents a possible solution to the latter of the two limitations. Our results also indicate that certain early life history processes of intertidal barnacles may be more susceptible to thermal stress than others. Nonetheless, our review of the literature highlights the need for future experimental field work to investigate the effect of temperature on early life history processes of benthic marine invertebrates. We propose that the thermal manipulation techniques developed in this study could be used to help fill this gap in the literature.

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Table 1. Summary of methods used to measure temperature and its effects on rocky intertidal organisms in the field. We excluded laboratory and modelling studies without a field component, and studies that did not directly measure biological responses to temperature variability.*Safety-Walk Tape (SWT)

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

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

No		Biomimetic data logger	Mussels	Natural rock	Adult	Thermal stress	Washington, USA	Helmuth 1998
No		Thermocouple	Mussels	Natural rock	Adult	Thermal stress	Washington, USA	Helmuth 1999
No		Biomimetic data logger	Mussels	Natural rock	Adult	Thermal stress	Pacific Coast, USA	Helmuth et al. 2006

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

No		Biomimetic data logger	Sea star	Natural rock	Adult	Thermal stress	British Columbia, Canada	Szathmary et al 2009
No		Data logger (SST only)	Barnacles	Plate: plexiglas with SWT*	Juvenile	Settlement	Central Chile	Tapia & Navarrete 2010
No		Satellite SST	Numerous	Natural rock	Juvenile-adult	Range shift	Portugal-France	Wethey et al. 2011

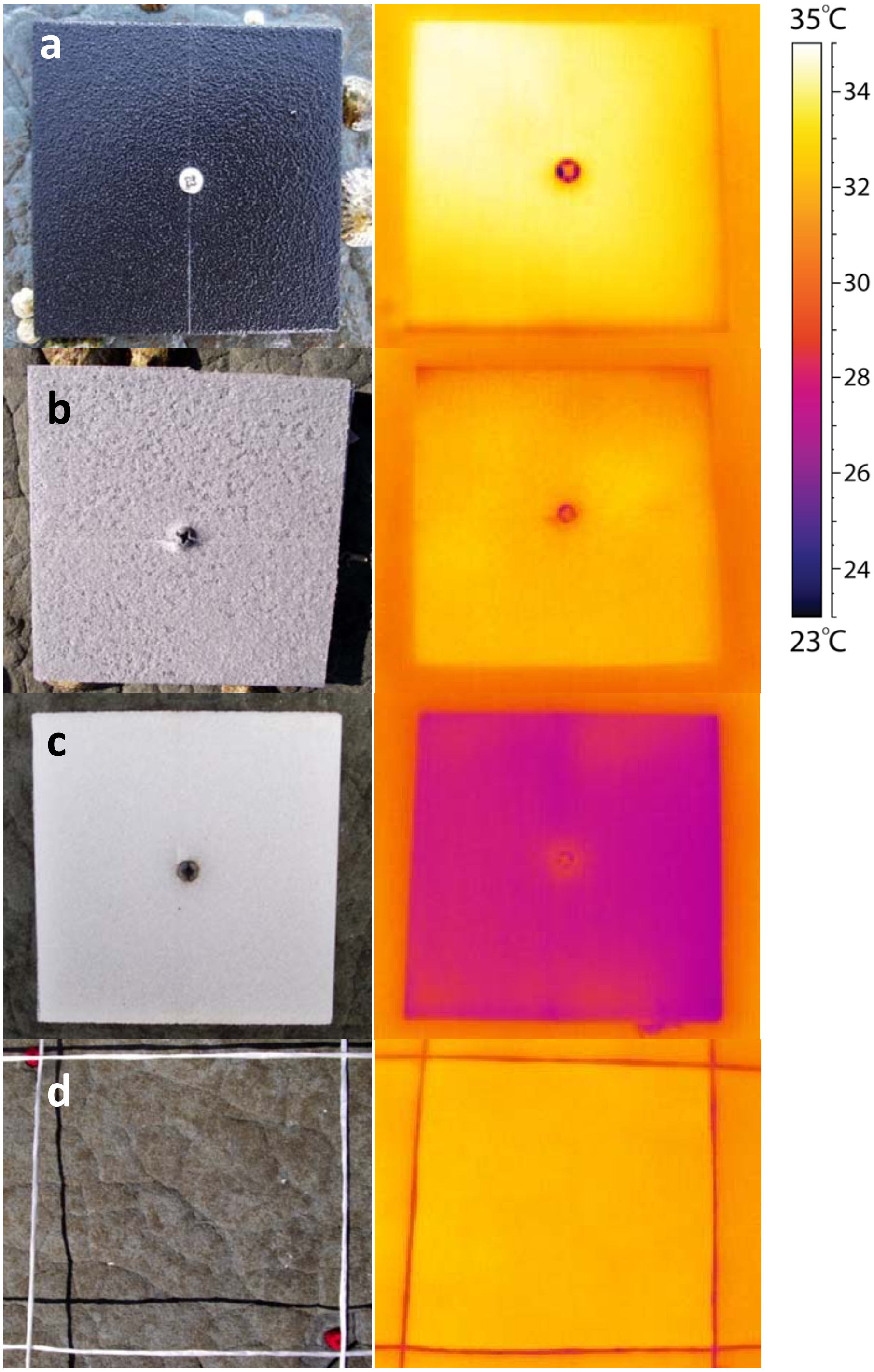

Figure 1. Photographs and infrared images of (a) black, (b) grey, and (c) white settlement plates and (d) natural rock. Infrared images were taken between 11:00am and 12:00pm (low tide: 11:45am) on 16 March 2011 when ambient air temperatures were on average 31.7°C.

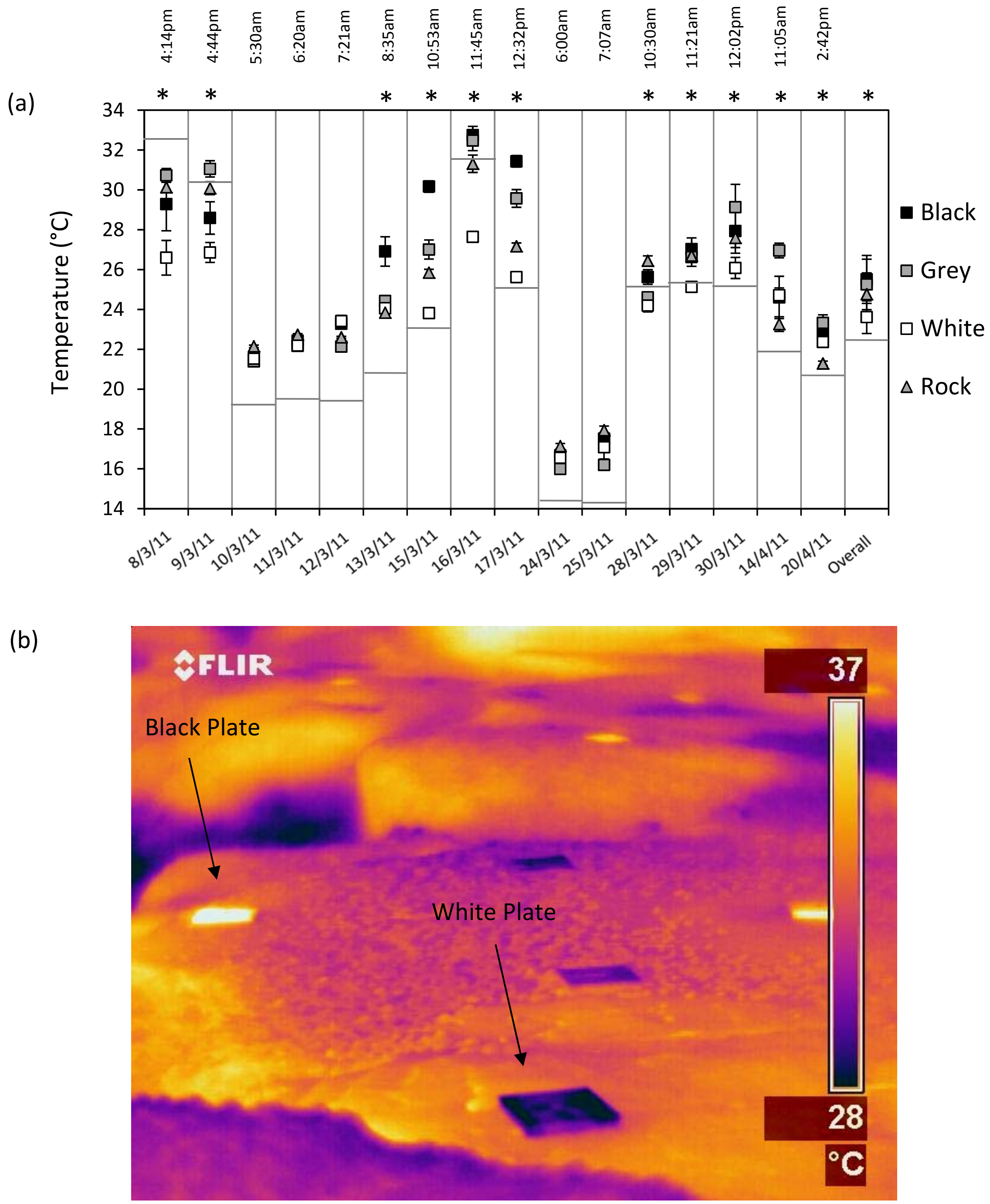

Figure 2. (a) Mean (±SE) temperature of black, grey and white settlement plates and natural rock measured from infrared images taken at low tide between 8 March and 20 April 2011. Horizontal lines indicate the mean air temperatures recorded by *in situ* data loggers during the time of sampling. Timing 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 among treatments; (b) IR image of plates in the field on 16 March 2011.

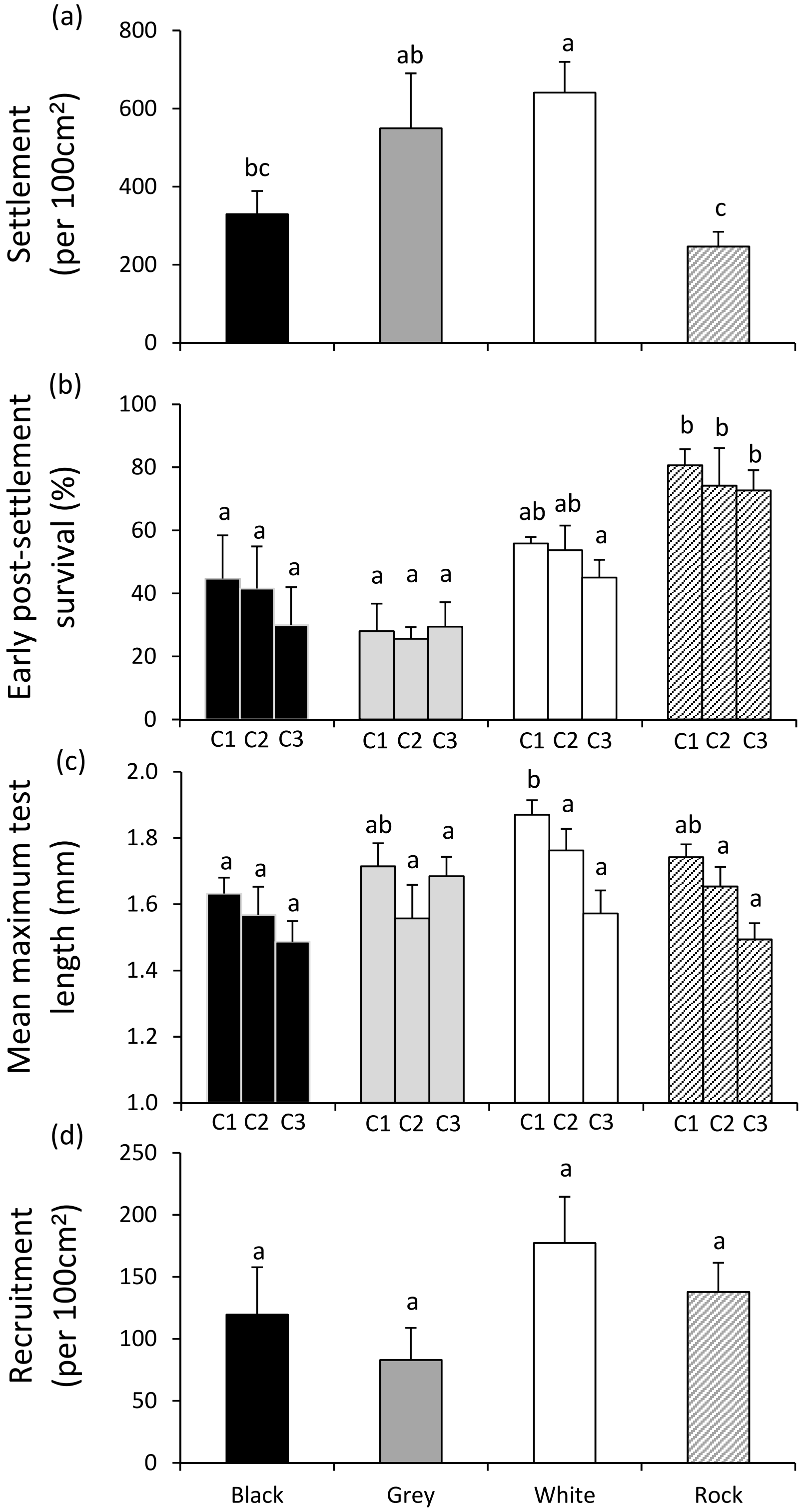

Figure 3. Mean (±SE) (a) settlement of *T. rosea* from 24 March to 2 April (n=5), (b) percentage of daily cohorts that settled on 28 (C1), 29 (C2) and 31 (C3) March surviving to 14 April (n=5), (c) final maximum test length of daily cohorts that settled on 28 (C1), 29 (C2) and 31 (C3) March on 14 April (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).