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Temperature variability at the larval scale affects early survival and growth of an intertidal barnacle

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Abstract

For rocky intertidal invertebrates, the transition from pelagic larva to benthic settler represents a critical life-history stage characterised by high mortality. This mortality has been attributed to biotic factors such as predation or individual larval quality, as well as to abiotic factors such as thermal or desiccation stresses. Surprisingly little is known about how temperature varies at very fine spatial scales relevant to newly settled larvae. We used infrared (IR) imagery to determine (1) whether in situ rocky substrates during aerial exposure exhibit repeatable fine-scale (1 mm) temperature variation at the larval scale, and (2) whether the presence of adult conspecifics ameliorates effects of substratum temperature and promotes early growth and survival of settlers. We tracked the settlement and early survival of larvae to determine whether fine-scale variation in temperature influences early life history processes of the intertidal barnacle Tesseropora rosea. Larval settlement did not vary with fine-scale variation in rock temperature, but early post-settlement growth and survival were both inversely related to temperature. Furthermore, we found that rock temperatures decreased significantly with increasing proximity to adult T. rosea and that larvae that settled within 15 mm of adults survived better than those that settled within 16 to 30 mm, highlighting positive effects of gregarious settlement. This is partially explained by conspecific adults shading rock and reducing rock temperatures. We present the first use of IR technology to test for variation in rock temperature at a scale relevant to individual larvae, demonstrating that such fine-scale variation in thermal stress impacts the early-life history stages of a benthic marine invertebrate.

Keywords

affects, scale, larval, variability, temperature, barnacle, intertidal, growth, survival, early

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Temperature variability at the larval scale affects early survival and growth of an intertidal barnacle

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Abstract. For rocky intertidal invertebrates the transition from pelagic larva to benthic settler represents a critical life-history stage characterised by high mortality. This mortality has been attributed to biotic factors such as predation and individual larval quality as well as abiotic factors such as thermal and desiccation stresses. Surprisingly, however, little is known about how temperature varies at very fine spatial scales relevant to newly settled larvae. We used infrared (IR) imagery to determine (i) whether *in situ* rocky substrates during aerial exposure exhibit repeatable fine-scale (1mm) temperature variation at the larval scale, and (ii) whether the presence of adult conspecifics ameliorates effects of substratum temperature and promotes early growth and survival of settlers. We tracked the settlement and early survival of larvae to determine whether fine-scale variation in temperature influences early life history processes of the intertidal barnacle *Tesseropora rosea*. Larval settlement did not vary with fine-scale variation in rock temperature, but early post-settlement growth and survival were both inversely related to temperature. Furthermore, we 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 highlighting positive effects of gregarious settlement. This is partially explained by conspecific adults shading rock and reducing rock temperatures. This study represents the first use of IR technology to test for variation in rock temperature at a scale relevant to individual larvae, demonstrating that such fine-scale variation in thermal stress impacts the early-life history stages of a benthic marine invertebrate.

Key words: Climate change; early post-settlement mortality; infrared imagery; recruitment; settlement

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 1993, Gosselin & Qian 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 latitudinal range limits of limpets (Gilman 2006), barnacles (Herbert et al. 2007) and mussels (Jones & Wethey 2010). Still, we understand very little about temperature variability at spatial scales relevant to individual organisms or 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, Lathlean et al. 2012). 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 our 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 infrared imaging, we first demonstrate that small areas on the rocky shore remain consistently warmer or cooler relative to the surrounding substrata. We then ask whether such fine-scale variation in rock temperature affects the settlement, early growth and survival of the barnacle *Tesseropora rosea*. This barnacle is an important foundation species within mid rocky intertidal regions of south eastern Australia and plays an important role in ameliorating adjacent substrate temperatures (Lathlean et al. *in press*). Because larvae often settle in close proximity to adults, we also ask whether rock temperatures close to conspecific adults are lower and whether the shade generated by adults ameliorates thermal stress for newly settled larvae by reducing adjacent rock temperatures.

Materials and methods

Study region and species

We undertook our study at Garie Beach (34º10'38.05S, 151º03'57.77E), a temperate rocky shore within south eastern Australia, composed of grey siltstone and has an east to north easterly orientation and an overall moderate to slightly sloping (10-20°) inclination. We focussed our study on the dominant, habitat-forming barnacle *Tesseropora rosea* which is highly abundant in the mid shore area on exposed rocky shores within this region (Hidas et al. 2010, Lathlean et al. 2010). *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 approximately 13 days (Wisely and Blick 1964, Egan and 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 (Caffey 1985). The peak in January to February is generally more prominent at northern locations, and vice-versa for more southern locations (Caffey 1985). Adults typically inhabit sun-exposed emergent rock (Denley and Underwood 1979) and are geographically distributed across tropical, subtropical and temperate regions of eastern Australia (Bennett & Pope 1953, Endean et al. 1956), suggesting that *T. rosea* is tolerant of a wide range of thermal regimes.

Infrared imaging

Similarly to Lathlean et al. (2012) and Lathlean and Minchinton (*in press*) rock temperatures were measured using infrared (IR) images taken with 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 20cm × 20cm in size, from 50cm above the substratum with each laser beam producing an arc length of 1.3 milliradians (mrad) when the camera is held 1m away from the point of contact. Therefore, each IR image had a spatial resolution less than 1mm² per pixel which is the size of recently settled larvae (i.e. 0.2 to 0.3mm). Measurements at these scales allowed comparison of rock temperature variability both within and among quadrats. Importantly, measurements of rock temperature at this extremely fine (mm) scale should reflect the thermal stresses experienced by recently settled barnacles (see Lathlean et al. 2012).

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 min (FLIR, personal communication; J.A. Lathlean personal observation). 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 to 1 (Helmuth 1998, Denny & Harley 2006, Chapperon & Seuront 2011, Cox & Smith 2011). To avoid the potential effects of reflectance on estimates of rock temperature, all quadrats 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. Ambient 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). The 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.

Identifying small hot and cold spots on rocky shore

To test whether fine-scale temperature variation influences settlement, early post-settlement survival and growth of *T. rosea*, we first needed to verify that fixed points (1mm×1mm) were consistently hot or cold. Without this consistent temperature variability we would not expect to find significant effects of temperature on early life history processes at this scale. To do this we established 10 permanent 20cm×20cm sites separated by one to two metres within the mid shore region at Garie Beach on the 8 February 2010. All sites: (1) were within the mid shore region dominated by the barnacle *Tesseropora rosea* (0.8 to 1.6 m above the mean low water mark of neap tides: MLWN), (2) had at least a 400cm² 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 (although in previous years adult *T. rosea* had been present indicating the suitability of such areas as habitat – J.A. Lathlean, 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 1030am and 340pm. 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.

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 5 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, we then used those sites that consistently yielded strong relationships amongst sampling events (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.*

Early life history processes and fine-scale temperature variability

We identified and followed 585 newly settled barnacles within the three sites that produced the most consistent temperature variability and highest larval settlement (i.e. Sites 1, 2 and 8; see Table 1). We monitored the fate of each individual every 2 to 4 days from 5 February to 23 March 2010 using a high resolution digital camera (Fujifilm S9600). Settlement was greatest within these three sites between the 5 and 9 March. Therefore, we classified settlers as individuals that appeared within sites on the 5 and 9 March and recruits as settlers that were still alive on the 23 March. The small number of individuals that settled before the 5 March were ignored during analysis. 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. The position of each newly settled barnacle within each site was then overlaid onto the corresponding IR image. Because of their small size and sessile existence, the body temperatures of recently settled larvae are most likely equivalent to that of the underlying substrata (J.A. Lathlean, personal observation). Hereafter, for simplicity, we refer to these measures on the substrata as body temperatures. Therefore, body temperature of each settler was estimated using the value of the underlying pixel from the IR image. Mean body temperatures of individual settlers and recruits were calculated from IR images taken on 9 and 16 March. We then used logistic regression (χ^2) to test for significant effects of temperature variation on settlement and recruitment for each site separately. These logistic regressions used likelihood-ratios to compare (i) the distribution of mean rock temperatures (n=200 pixels per site) with mean body temperatures of settlers, and (ii) mean body temperatures of recruits with the mean body temperatures of settlers that died. To test whether fine-scale temperature influences early post-settlement growth, we measured the growth in maximal test length of 76 individuals from the 9 to 16 March and 66 different individuals (taken from the same cohort of settlers as the 76 individuals) from the 16 to 23 March. For growth estimates of the 76 individuals measured from the 9 to 16 March mean body temperatures were calculated using IR images taken on 9 and 16 March. However, for growth estimates of the 66 individuals measured from the 16 to 23 March only a single temperature value derived from IR images taken on the 16 March could be used. Maximal 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 the 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. We used Pearson correlations to examine the relationship between rock temperature and growth of settlers using IR images taken on the 9 and 16 March.

Proximity to adults

To test whether conspecific adults ameliorate thermal stress for newly settled *T. rosea* at fine-spatial scales we established an additional 10 permanent 20cm×20cm sites separated by one to two metres within the mid intertidal zone on the 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 the 9 March we 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 conspecific adult (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. 2). Conversely, unshaded or exposed areas were classified as rock within sites adjacent to the eighth of the barnacle facing directly towards the sun (Fig. 2). However, unlike shaded areas, unshaded areas were not restricted to 15mm from base of barnacle test. We therefore used temperature measurements for unshaded points within each site 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, we measured the distance between settlers and their nearest adult conspecific for 346 individuals that settled within these sites during the 5 to 7 March. These settlers were chosen irrespective of whether they were shaded at the time measurements were taken. We then followed the fate of these 346 settlers until 23 March and used a one-tailed logistic regression to test whether individuals closer to adults had greater recruitment success. Lastly, to test whether proximity to adults influences early post-settlement growth, we measured the maximum test length of 51 individuals on 9 and 16 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. We used linear regression to examine the relationship between growth of individuals and proximity to closest adult conspecific.

Results

Consistent fine-scale temperature variation

Based on the number of significant positive correlations, eight of 10 sites displayed consistently warm and cool areas at fine-scales. For example, 66 of 96 (68.8%) correlations between the temperatures of fixed points within sites over the 5 sampling events returned significant positive relationships (Table 1). Areas within all sites produced correlated temperature variation for at least three sampling events, while four sites displayed temperatures that were correlated across all five sampling events (see Fig. 1 for an illustration of this consistent temperature variability). IR images revealed that rock temperatures within sites (measured at the mm scale) varied by as much as 5°C and that this temperature variability was consistent through time (Table 1) (see Figure 4 in Lathlean et al. 2012 for additional temporal and spatial analysis of IR images). Consequently, our results indicate that individual larvae only centimetres apart consistently experienced substantially different temperatures.

Early life history processes and fine-scale temperature variability

We detected significant but spatially variable effects of fine-scale temperature variation using each of our three measures of early life-history performance. In total, we identified and followed the fate of 585 newly settled *T. rosea* larvae within sites 1, 2 and 8 (the three sites with the highest number of settlers and most consistent fine-scale temperature variability) (See Appendix I for temperature frequency plots of all eight sites that produced consistent fine-scale temperature variability). For sites 2 and 8, larval settlement did not vary between warmer or cooler 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. 3). In contrast, cooler areas within site 1 had greater numbers of settlers compared to warmer areas (χ^2=18.59, d.f.=1, p<0.001).

The response of recruitment to variation in temperature varied among sites but recruitment was generally greater 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 settlers surviving to the 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. 3). In contrast, for the 188 individuals that settled in site 2 survival to the 23 March was not dependent on temperature (χ^2=0.07, d.f.=1, p=0.795).

Early post-settlement growth during the first week after settlement was inversely related to temperature (r=0.24, p<0.001, n=76) but not during the second week (r<0.01, p=0.314, n=66) (Fig. 4). During the first week individuals that experienced temperatures less than 30°C grew to an average size of 1.50mm in basal length while individuals that experienced temperatures higher than 30°C grew to approximately 1.17mm in basal length (i.e. a 22% reduction in growth).

Proximity to adults

Rock temperature varied strongly with proximity to adults and this variation was at least partially explained by the shade generated by adults. Within unshaded areas rock temperature was inversely correlated with distance to the nearest adult (r=0.127, p<0.001, n=193) (Fig. 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. We 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 (χ^2=3.19, d.f.=1, p=0.041) (Fig. 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. 5c).

Discussion

While a considerable number of studies claim that temperature significantly influences early life history processes (see Gosselin & Qian 1997, Hunt & Scheibling 1997 for reviews), this study, to the best of our knowledge, represents the first time that fine-scale temperature variability has been shown to influence the early growth and survival of a benthic marine invertebrate. Our results reveal that small-scale variability in rock temperature occurs on even finer scales than is usually reported (Helmuth et al. 2006) with areas only centimetres apart differing by up to 5°C. Such fine-scale rock temperature variability could be caused by minute topographic variability which can only be detected through the use of high-resolution IR imagery (Lathlean et al. 2012, Lathlean and Minchinton *in press*). Our results support an increasing number of studies that 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. We found consistent temporal variation in rock temperatures within sites at the same tidal height, suggesting that at the larval scale, small areas (1mm^2) on a rocky shore can be identified as being consistently warmer or cooler than the surrounding substrata. Furthermore we show that these 'hot' and 'cold' spots (which are consistently warmer and cooler than the surrounding substrata) influence both the early post-settlement growth and survival of recently settled larvae, two processes important for structuring the adult population (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991) (see Fig. 2 in Lathlean et al. 2012 for a detailed description of local-scale temporal variability at Garie Beach during the current sampling period) . Interestingly, Underwood and Chapman (1996) found that *T. rosea* abundance was most variable at small spatial scales (centimetres to metres) in comparison to variation in abundance across sites separated by hundreds of metres and kilometres. Our results suggest that this small-scale variation in the abundance of *T. rosea* may be the result of fine-scale rock temperature variability, which could co-vary with a number of other factors including fine-scale topographic variation.

By removing adult conspecifics we were 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 we 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 our data imply that adults are unlikely to be randomly distributed with respect to temperature since we have shown that recruitment rates are higher in consistently cooler areas. Future studies could tease apart the effects of adult shading and consistently cooler areas by manipulating adult densities (similar to present study) and arranging moulds of adult barnacles in areas that don't support high adult densities.

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). Our results provide evidence that even at fine spatial scales increased temperatures reduce early post-settlement growth and 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. It also supports the findings of Chan and Williams (2003) who found that heat stress was the major limiting factor influencing the survival of two tropical intertidal barnacle species *Tetraclita japonica* and *Tetraclita squamosa.* In contrast, laboratory and field experiments carried out by Findlay et al. (2010) showed that temperature had no effect 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. Connell 1985, Roughgarden et al. 1985, Minchinton & Scheibling 1991), and large-scale temperature variability affects settlement and recruitment (Lagos et al. 2005), future research should focus on the relative importance of large-scale versus 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). The task of predicting future thermal consequences on intertidal taxa are further complicated since any two species occupying the same habitat may experience different levels of thermal stress (Broitman et al. 2009) and their responses may differ depending on the strength of particular biological interactions (Kordas et al. 2011). Recent studies have also suggested that small spatial scale heterogeneity in rock temperatures may increase the survival of invertebrates in the warming climate (Chapperon & Seuront 2011; Denny et al. 2011).

Strikingly, we 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 temperatures 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.

We did not find consistent effects of rock temperature variability on larval settlement since only one of three sites displayed greater settlement within small areas that experience lower temperatures during aerial exposure. This is not surprising since larvae arrive during high tide when substrate temperatures are less variable and are unlikely to reflect the temperature variability that occurs during low tide. 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). Therefore, we may expect larvae to settle in response to bacterial communities grown under particular thermal regimes.

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. 1999). For filter feeders such as barnacles aggregated settlement will also increase rates of intraspecific competition for food and space (Connell 1985). Our results 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. We 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, our results may reflect a greater proportion of competent larvae with greater energy reserves settling and surviving within close proximity to adults which may be their preferred habitat (Jarrett and Pechenik 1997, Thiyagarajan et al. 2003). Adults may also influence rates of larval settlement through consumption (Navarrete & Wieters 2000), settlement cues (Raimondi 1988), altering the availability of suitable substrate (Minchinton & Scheibling 1993) and water flow (Wright & Boxshall 1999). Consequently, adult conspecifics may indirectly affect the early life history processes of benthic marine invertebrates in multiple ways other than reducing thermal stress. This may explain why temperature in the present study had no effect on early post-settlement growth when adult conspecifics were present, but did when they were absent.

The results of our 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 along the southeast coast of Australia (Pitt et al. 2010; Wernberg et al. 2011). Our results provide an important link between rock temperature variability and the response of individual invertebrates during a critical stage in their life history. Such a focus on the small-scale variability in rock temperature and the early life stages of invertebrates is rare since most climate change studies focus on adults. Yet for benthic marine invertebrates it is these processes influencing the early life stages that are most likely to have the greatest impact on their ability to respond to further climate change. The increasing attention to climate change research has also 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, we expect future research to become increasing concerned with incorporating temperature measurements at various large and small spatial scales.

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Table 1. Summary of Spearman rank correlation values (r) between the mean rock temperatures of 49 fixed points within sites across the 5 sampling events. Bold font indicates significant positive relationship with p-value <0.05 (n= 49 pixels). Settlers/ Recruits refer to the number of *T. rosea* that settled within site from the 5 to 9 March and the number of these individuals that were recounted as recruits on the 23 March 2010. Shaded sites are those that did not produce consistent fine-scale temperature variability. Individuals within sites 1, 2 and 8 were used to estimate early life history processes.

	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)

Figure Legends

Figure 1. Infrared images of a single site (20cm × 20cm) on the 25 and 26 February (a – b) and the 2 and 9 March 2010 (c – d). Images are displayed in greyscale with darker colours representing cooler temperatures.

Figure 2. 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 3. Frequency distribution of rock temperatures, and larval settlement and recruitment corresponding to different rock temperatures of 3 sites with 100% naturally available free space. Settlers are individuals that settled within sites from the 5 to 9 March, while recruits are settlers that survived to the 23 March 2010. Fatalities represent the temperature of individuals that did not survive to the 23 March (n is either the number of rock temperature measurements, settlers or recruits).

Figure 4. The influence of mean body temperature on the early post-settlement growth (percentage increase from initial maximum test length) of recently settled individual *T. rosea* from the 9 to 16 March (white circles) and the 16 to 23 March (black circles). Body temperatures for individuals that were measured between the16 to 23 March only represent values derived from IR images taken on 16 March.

Figure 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).

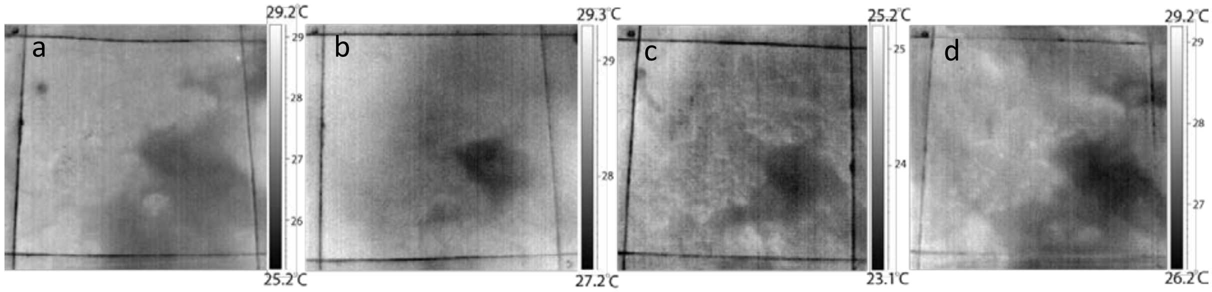


Figure 1.

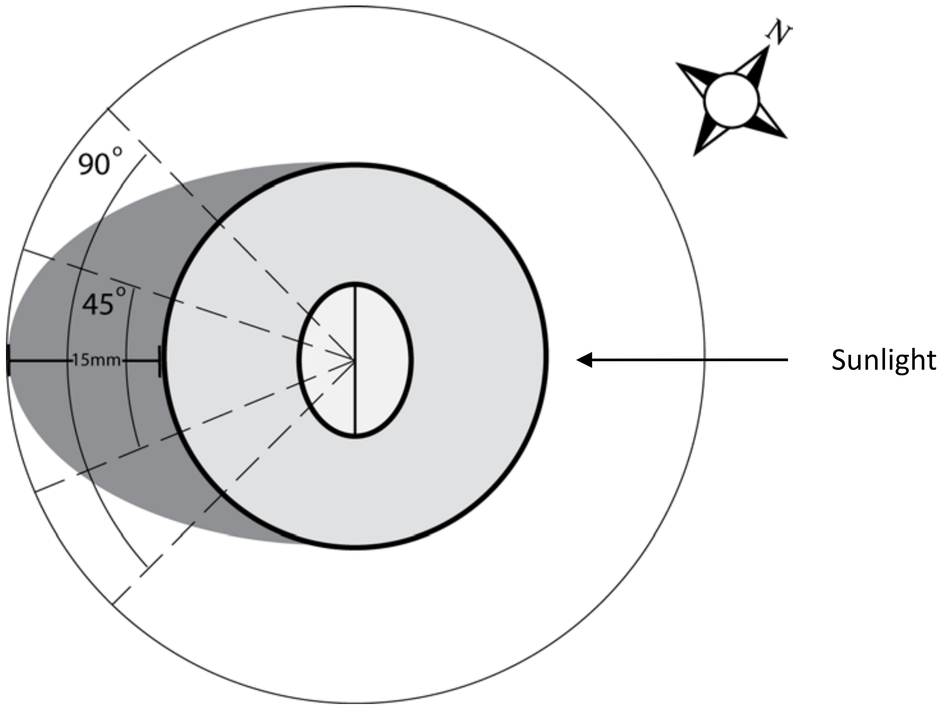
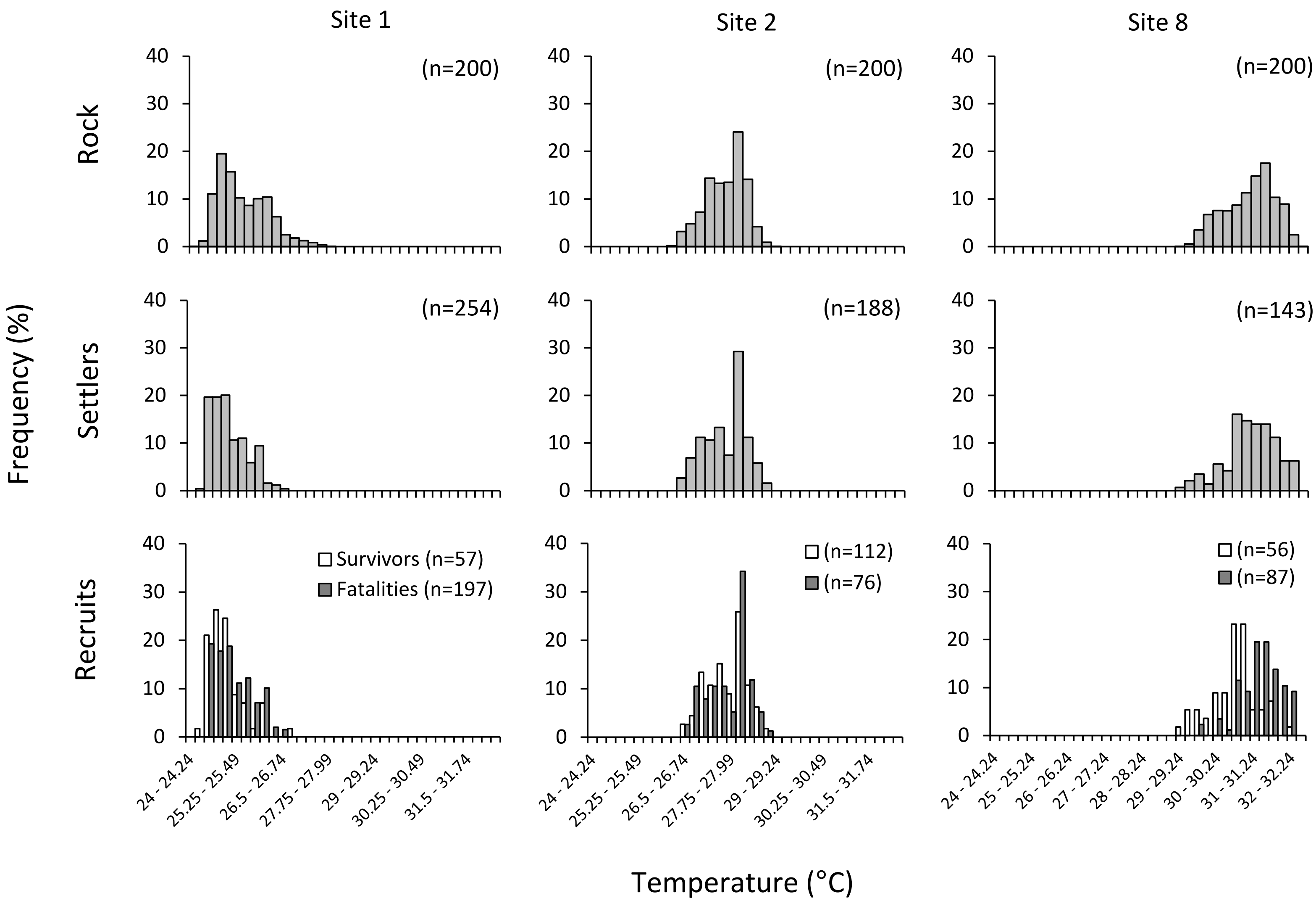


Figure 2.



Site 1
Site 2
Site 8
Frequency (%)
Rock
Settlers
Recruits
(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)
40
30
20
10
0
24 - 24.24
25.25 - 25.49
26.5 - 26.74
27.75 - 27.99
29 - 29.24
30.25 - 30.49
31.5 - 31.74
25 - 25.24
26 - 26.24
27 - 27.24
28 - 28.24
30 - 30.24
31 - 31.24
32 - 32.24
Temperature (°C)

Figure 3

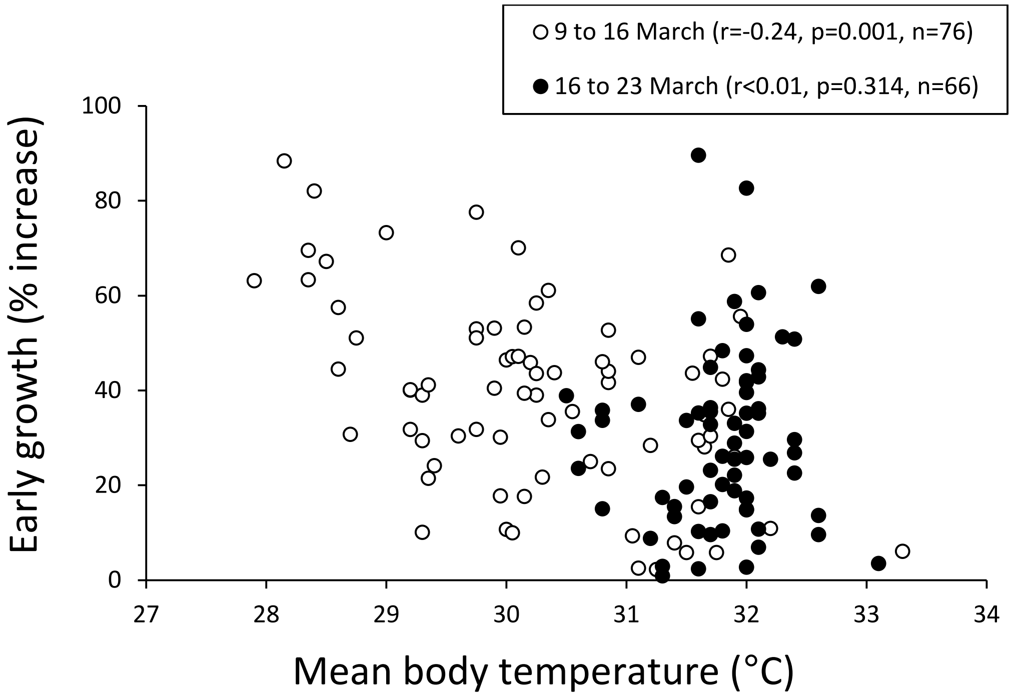
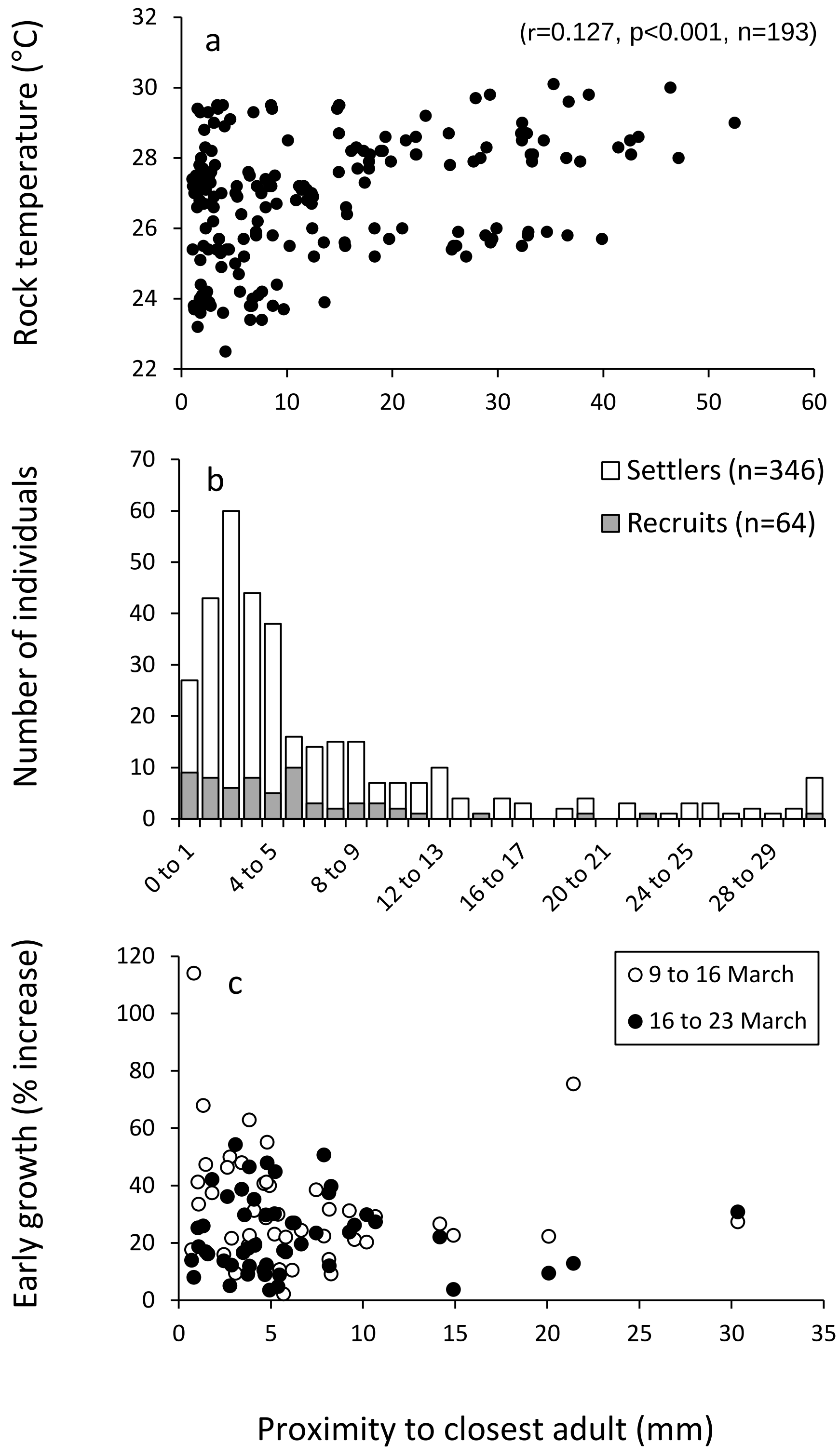

9 to 16 March (r=-0.24, p=0.001, n=76)
16 to 23 March (r<0.01, p=0.314, n=66)
Early growth (% increase)
100
80
60
40
20
0
27
28
29
30
31
32
33
34
Mean body temperature (°C)

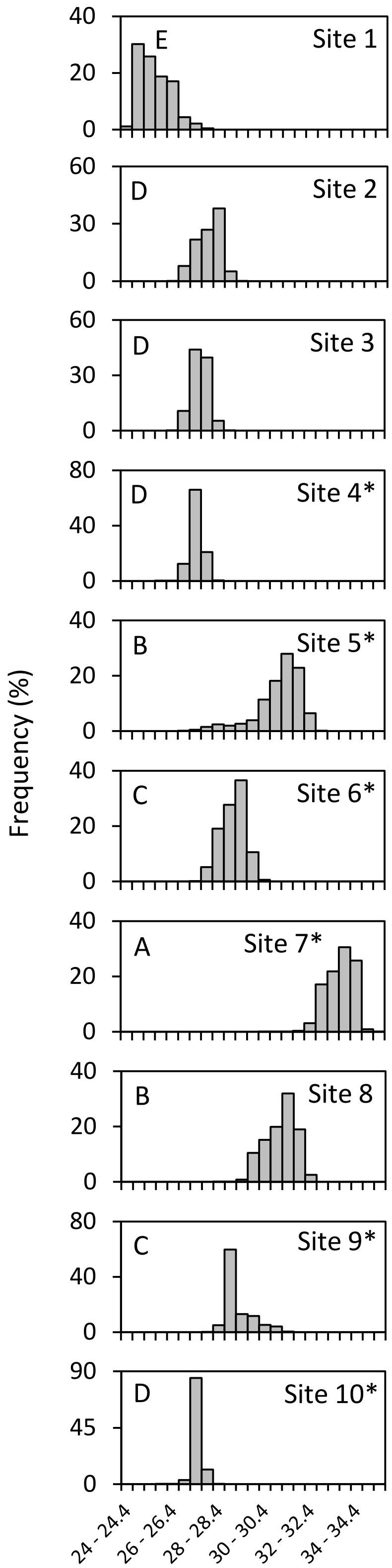
Figure 4



Rock temperature (°C)
a
(r=0.127, p<0.001, n=193)
32
30
28
26
24
22
0
10
20
30
40
50
60
Number of individuals
b
Settlers (n=346)
Recruits (n=64)
70
60
50
40
30
20
10
0
0 to 1
4 to 5
8 to 9
12 to 13
16 to 17
20 to 21
24 to 25
28 to 29
Early growth (% increase)
c
9 to 16 March
16 to 23 March
120
100
80
60
40
20
0
0
5
10
15
20
25
30
35
Proximity to closest adult (mm)

Figure 5

Appendix



Mean rock temperature (°C)

Appendix I**.** Mean rock temperature frequency distributions (%) taken from IR images recorded on the 9 and 16 March of the ten 20 x 20cm permanent quadrats (sites) used throughout this study. Individuals that settled in sites 1, 2 and 8 were used to assess the effect of small-scale temperature variability on settlement, growth and recruitment. Sites marked with an asterisks (*) indicate those sites which had less than 10 individual recruits (see Table 1). Plots not connected by a similar letter denote sites that displayed significantly different rock temperatures following a SNK post hoc analysis.