

RESEARCH NOTE

Standing in the sun: infrared thermography reveals distinct thermal regulatory behaviours in two tropical high-shore littorinid snails

Laurent Seuront¹ and Terence P. T. Ng²

¹CNRS, Univ. Lille, Univ. Littoral Côte d'Opale, UMR LOG 8187, LOG, Laboratoire d'Océanologie et de Géosciences, 62930, Wimereux, France; and
²The Swire Institute of Marine Science and School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong SAR, China

Correspondence: L. Seuront; e-mail: laurent.seuront@cnrs.fr

The understanding of how climate warming may affect the ecological and geographical distributions of intertidal ectotherms requires insight into how their body temperatures vary in relation to environmental temperature (Angilletta, 2009; Helmuth *et al.*, 2010). This issue is particularly relevant in high-shore environments, in which species experience extreme thermal stress regimes during the periods of aerial exposure (McMahon, 1990; Marshall, McQuaid & Williams, 2010a; Marshall, Qadirulisyam Bin Mustafa & Williams, 2010b). In fact, high-shore intertidal species are considered more vulnerable to climate warming than low-shore or subtidal species, because they are typically living closer to their thermal tolerance physiological limits in the tropics (see Somero, 2012 for a review). While physiological responses may be relatively limited in mitigating heat stress, behavioural responses may, however, be critical to buffer thermal stress as shown in ectotherms that use a wide range of thermal environments (Kearney, Shine & Porter, 2009).

Thermal regulatory behaviours are critical on rocky shores due to the latter's high degree of topographic complexity, hence the related variety of thermal microhabitats (Chappon & Seuront, 2011a; Lathlean, Ayre & Minchinton, 2012) and considerable temporal and spatial fluctuations in environmental temperature (Denny *et al.*, 2011; Gedan *et al.*, 2011; Lathlean, Ayre & Minchinton, 2014). The behaviours include selection of thermally more benign microhabitats (Chappon & Seuront, 2011a; Iacarella & Helmuth, 2011), formation of aggregations (Chappon & Seuront, 2012), shell orientation relative to the sun (Muñoz *et al.*, 2005) and shell-posturing behaviour (Marshall *et al.*, 2010a, b).

High shore littorinid snails exhibit shell-posturing behaviour during low tide, i.e. individuals retract their foot into their shell, close their operculum and glue themselves to the substratum with a mucus holdfast that allows them to lift their body off the substratum (McMahon, 1990; Lang, Britton & Metz, 1998). This behaviour is considered as an adaptive strategy that minimizes conductive transfer from the substratum to the shell by reducing the amount of the shell in contact with the substratum, while maximizing the shell surface exposed to air currents, hence allowing increased heat transfer from the shell through convective cooling (Miller & Denny, 2011; Marshall & Chua, 2012). More specifically, improved cooling is achieved through shell-standing (Lim, 2008; Miller & Denny, 2011; Marshall &

Chua, 2012) and shell-stacking (Marshall *et al.*, 2010b), two related behaviours whereby a snail is respectively attached to the substratum with its aperture facing perpendicularly to the surface (as opposed to downwards) and climbs onto other snails to form a stack or 'tower' (Marshall *et al.*, 2010b).

Both shell standing and towering behaviours have previously been shown to be effective strategies to mitigate thermal stress in *Echinolittorina malaccana* (Marshall *et al.*, 2010b; Marshall & Chua, 2012). These studies were, however, based on the use of biomimetic snail models with thermocouples inserted in them. Such models allow continuous long-term measurements, avoid spurious physiological and behavioural consequences of inserting thermocouples into small organisms and show reasonable correlations between body temperature of model snails and live snails, including for littorinids (Iacarella & Helmuth, 2011; Marshall *et al.*, 2010a; Miller & Denny, 2011). Their generality is, however, intrinsically limited by the number of snails that can be simultaneously studied, e.g. a tower of three *E. malaccana* shells (Marshall *et al.*, 2010b), and four *E. malaccana* shells glued on a flat rock surface in standing and non-standing position either under direct sunlight or in the shade (Marshall & Chua, 2012). Further, this approach does not allow simultaneous measurement of snail and substratum temperature at spatial scales compatible with the considerable thermal heterogeneity observed on intertidal rocky shores (Denny *et al.*, 2011; Lathlean *et al.*, 2014). This is not the case, however, with infrared thermography (IRT) that allows—in a relatively limited amount of time and with limited logistics compared with traditional thermal methods—non-invasive simultaneous measurements of both the body temperature of multiple snails and the thermal properties of their substratum at scales compatible with the behavioural biology and ecology of individual organisms (see Lathlean & Seuront, 2014, for a review).

We used IRT to investigate and compare the potential consequences of standing and towering behaviours on the body temperature of two tropical rocky-shore snails, *Echinolittorina malaccana* (Philippi, 1847) and *E. radiata* (Souleyet, 1852) (Caenogastropoda: Littorinidae). These two species were chosen as they co-occur in the high-shore zone of Hong Kong where they experience extreme heating, with rock temperature often exceeding 50 °C in summer (Williams, 1994). Field observations were conducted during both Hong Kong's cold, dry winter (4 December 2014) and its hot, wet summer (5–6 August 2014;

Kaehler & Williams, 1997) during daytime low tides (i.e. below 1.4 m above CD) when snails were consistently dry and inactive on a semiexposed shore (Lobster Bay, Cape D'Aguiar, Hong Kong). The section of the shore we investigated was a flat rocky platform characterized by a paucity of topographic features such as rock pools, cracks and crevices. The abundance and behaviour of *E. malaccana* and *E. radiata* were assessed from 15 haphazardly placed 25 × 25 cm quadrats. All quadrats were placed in the high-intertidal zone, on dry rocks directly exposed to sun, and thermal measurements conducted between 10.00 and 14.00. This procedure ensured the absence of any behavioural difference driven by rock humidity and time of day (see Muñoz *et al.*, 2005). Further, no significant differences were observed in the thermal properties of the quadrats (Kruskal-Wallis test, $P > 0.05$), with substratum temperatures consistently ranging between 40.5 and 55 °C. The observed postural behaviours included 'non-standing' (shell glued to the substratum with its aperture facing the substratum horizontally), 'standing' (shell glued to the surface with its aperture facing perpendicularly to the surface, and the major shell axis laying vertically) and 'towering' (a snail was attached to the substratum with its aperture facing the substratum either horizontally or vertically and up to three other snails were glued vertically on top of each other to form a stack). 'Aggregation' describes an individual in direct shell contact with the shell of at least one other conspecific (Chapperon & Seuront, 2011a, b). Substratum and snail body temperatures (T_s and T_b , respectively) were measured with thermal imaging cameras, a Testo 875-1iSR (Testo AG, Germany) in winter and a Fluke Ti25 (Fluke Corporation, USA) in summer. The thermal performances of cameras are very similar (sensitivities at 30 °C are <0.05 °C (Testo) and ≤ 0.09 °C (Fluke) and do not vary significantly with temperature (L. Seuront, unpublished data), and accuracy for both is 2% or 2 °C, whichever is greater). Preliminary measurements of various surface temperatures did not exhibit any significant differences in the temperature returned by both cameras. Shell temperature (assessed through IRT) was used as a proxy for snail body temperature (assessed with type K thermocouples inserted into the mantle) as preliminary laboratory trials found no significant differences ($P > 0.05$) in *E. malaccana* and *E. radiata* between shell temperature and mantle temperature, respectively, in the range 25–45 °C. Thermal images were subsequently analysed using IRSOFT v. 3.1 (Testo AG, Germany) and SmartView v. 3.2.639.0 (Fluke Corporation, USA). This is consistent with previous work conducted on *Littoraria scabra* (Chapperon & Seuront, 2011a) and *Nerita atramentosa* (Caddy-Retalic, Benkendorff & Fairweather, 2011; Chapperon & Seuront, 2011b). The difference, ΔT , between T_b and T_s quantified the difference in temperature between the snail body and its substratum. The ratio $R_T = T_b/T_s$ was used as a standardized measure of the difference between substratum and snail body temperatures. Because the variables T_b , T_s , ΔT and R_T were non-normally distributed (Kolmogorov-Smirnov test, $P < 0.05$), nonparametric statistics were used throughout. All pairwise comparisons between species, site and season were conducted using the Wilcoxon-Mann-Whitney U -test. Multiple comparisons between postural behaviours were conducted using the Kruskal-Wallis test, and a subsequent multiple comparison procedure based on the Tukey test was used to identify distinct groups of measurements (Zar, 1999). No significant differences in size were found between species, sites and season ($P > 0.05$); *E. malaccana* ranged between 4.2 and 11.9 mm in shell length ($N = 232$) and *E. radiata* between 4.5 and 11.8 mm ($N = 226$).

In winter, *E. malaccana* and *E. radiata* were both found on substrata ranging from 17 to 19 °C (Fig. 1). Both species were observed occurring higher on the shore as compared with summer during low tide and aggregating in crevices (Table 1) at densities ranging between 0 and 260 m⁻². No postural

behaviour was ever observed in either *E. malaccana* or *E. radiata*. Body temperatures T_b were significantly positively correlated (Pearson's r , $P < 0.01$) with substratum temperature T_s in both species. T_b were not significantly different ($P > 0.05$) from T_s for both species. This resulted in ΔT and R_T that were, respectively, not significantly different from 0 and 1 for both *E. malaccana* and *E. radiata* ($P > 0.05$). These results differ from previous winter observations conducted on *Nerita atramentosa* on South Australian rocky shores (Chapperon & Seuront, 2012). First, *N. atramentosa* was consistently significantly warmer than its substratum for both solitary (1.21 ± 0.01 °C) and aggregated (1.41 ± 0.02 °C) individuals. This suggests that in contrast to *N. atramentosa*, *E. malaccana* and *E. radiata* may not benefit from direct solar heating in winter, as suggested for *E. malaccana* with biometric models (Marshall & Chua, 2012). Second, our results show that aggregated *E. malaccana* and *E. radiata* exhibit similar thermal properties whether they were solitary or aggregated. This suggests that aggregation does not provide any thermal benefit to *E. malaccana* and *E. radiata* in winter. This contrasts with previous observations showing that aggregated individuals of *N. atramentosa* were significantly warmer than their surrounding substratum, with the thermal difference ΔT being *c.* 2 °C greater for aggregated than solitary individuals (Chapperon & Seuront, 2012).

In summer, both *E. malaccana* and *E. radiata* were found on surfaces with temperatures, respectively, in the range 40.5 to 54.5 °C, and 42.3 to 52.0 °C (Fig. 1; Table 1) and at densities ranging between 0 and 320 m⁻² for *E. malaccana* and 0 and 224 m⁻² for *E. radiata*. *Echinolittorina malaccana* was not observed in aggregation and this rarely occurred in *E. radiata* (Table 1). Note that dense aggregations of both species were, however, not uncommon during low tide in summer (Stafford, Davies & Williams, 2007), which suggests temporal variations in the behaviour. The observed behavioural properties were not equally likely (χ^2 tests, $P < 0.01$). Specifically, non-standing, standing and towering snails represented 29.5, 24.1 and 46.4% of postural behaviours in *E. malaccana*, and 20.4, 31.5 and 38.1% in *E. radiata* (Table 1). No significant correlation was found between snail

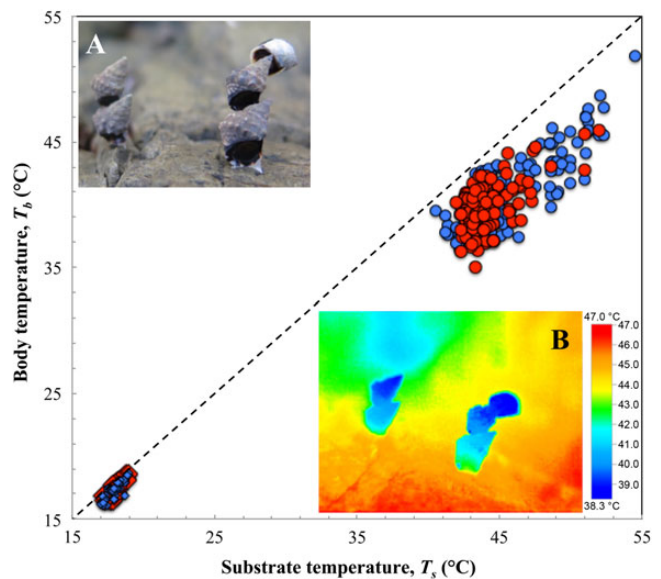


Figure 1. Body temperature T_b of *Echinolittorina malaccana* (red) and *E. radiata* (blue) as a function of their substratum surface temperature T_s in winter (diamonds) and summer (circles). The dashed line is the first bisectrix, $T_b = T_s$. The insets show a digital image (A) and the corresponding thermal image (B) of a monospecific tower of *E. malaccana* (left) and a heterospecific tower made of two *E. malaccana* and one *E. radiata* at the top (right).

density and any of the observed behavioural properties for both species ($P > 0.05$). This suggests that tower formation is not related to any density-dependent effect.

The observed towers included two to five layers of snails. In the vast majority of cases (93.2%), only one snail was found per layer. Layers made of two or three snails also occurred however, in 4.7% and 2.1% of observed towers, respectively. These snails were consistently found on the second layer of towers. Towers were either monospecific or heterospecific. Heterospecific towers (Fig. 1) occurred occasionally, representing 3.4% of the observed towers. The size of snails consistently decreased from the bottom to the top of a tower in 96.2 and 97.6% of the towers observed in *E. malaccana* and *E. radiata*, respectively, and in 100% of the heterospecific towers. Towers of two snails were by far the most abundant (Table 1).

Substratum temperatures T_s significantly differ between *E. malaccana* behavioural groups ($P < 0.05$; Table 1). Specifically, in *E. malaccana* non-standing, standing snails and snail towers including less than three snails were found on surfaces with not significantly different temperatures T_s ($P > 0.05$). These substrata were significantly cooler ($P < 0.05$) than substrata holding towers of three to five individuals. These towers were found on significantly increasingly hot surfaces ($P < 0.05$). Noticeably, T_s did not significantly differ between solitary (either non-standing or standing) *E. radiata*, and *E. radiata* in towers of up to four individuals (Table 1). In turn, towers of five snails and both non-

standing and standing snails in aggregates were found on significantly warmer surfaces ($P < 0.05$). As observed in winter, T_b were significantly positively correlated ($P < 0.01$) with T_s for both species. However, T_b were significantly cooler than T_s for both species ($P < 0.05$), with the difference ΔT ranging on average between 2.6 and 10.3 °C for *E. malaccana*, and between 2.7 and 7.8 °C for *E. radiata*, depending on snail postural behaviour (Table 2). Similarly, R_T was between 0.94 and 0.80 in *E. malaccana* and 0.94 and 0.83 in *E. radiata* (Table 2). The temperature difference ΔT and temperature ratio R_T , respectively, significantly decreased and increased from non-standing to standing snails, and with the elevation of a snail in a tower (Table 2). No correlation was found between snail size and any of the thermal properties investigated here, irrespective of the elevation of a snail in a tower ($P > 0.05$). These observations show that the behaviourally-induced cooling effect consistently increases with the vertical distance to the substratum, irrespective of snail size. The reported changes in postural behaviour are hence likely to reduce convective heat gain from the substratum, while improving convective cooling, and stress the thermal advantages of both standing and towering behaviours (Marshall *et al.*, 2010b; Marshall & Chua, 2012).

The temperature differences ΔT reported here are much larger than those estimated from aestivating *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* (respectively, 0.10 ± 0.61 and 0.71 ± 0.98 °C for non-standing and standing individuals; Lim,

Table 1. Absolute and relative frequency of occurrence of different behaviours (solitary, towering and aggregated) and postures (non-standing *vs* standing) in *Echinolittorina malaccana* and *E. radiata* in winter and summer, and the corresponding substratum temperature T_s (°C).

	Season	Solitary		Towering				Aggregated	
		Non-standing	Standing	T ₂	T ₃	T ₄	T ₅	Non-standing	Standing
<i>E. malaccana</i>									
N (%)	Winter	10 (22.2%)	–	–	–	–	–	35 (77.8%)	–
	Summer	33 (29.5%)	27 (24.1%)	40 (35.7%)	4 (3.6%)	5 (4.5%)	3 (2.7%)	–	–
T_s	Winter	18.0 ± 1.1 ^a	–	–	–	–	–	18.0 ± 0.5 ^a	–
	Summer	45.5 ± 1.2 ^a	44.35 ± 0.9 ^a	45.3 ± 1.1 ^a	48.5 ± 1.1 ^b	49.2 ± 1.0 ^c	52.7 ± 1.3 ^d	–	–
<i>E. radiata</i>									
N (%)	Winter	9 (17.3%)	–	–	–	–	–	43 (82.7%)	–
	Summer	22 (20.4%)	34 (31.5%)	26 (24.1%)	7 (6.5%)	6 (5.6%)	2 (1.9%)	7 (6.5%)	4 (3.7%)
T_s	Winter	17.9 ± 0.5 ^a	–	–	–	–	–	17.3 ± 0.6 ^a	–
	Summer	43.8 ± 1.5 ^a	43.9 ± 1.2 ^a	44.3 ± 0.9 ^a	44.5 ± 1.1 ^a	44.1 ± 1.0 ^a	47.0 ± 0.7 ^b	44.2 ± 0.7 ^a	43.5 ± 0.8 ^a

The symbols T_i indicate the number of snail layers found in a tower, where $i = 2$ to 5. Note that in the vast majority of observed cases (93.2%) only one snail was found per layer; in 4.7% and 2.1% of the observed towers, we found two and three snails on the second layer (i.e. T₂). The ± errors are 95% confidence intervals. The letters a–d identify statistically distinct groups of measurements.

Table 2. Thermal properties of *Echinolittorina malaccana* and *E. radiata* in summer for different behaviours (solitary, towering and aggregated) and postures (non-standing *vs* standing).

	Solitary		Towering				Aggregated			
	Non-standing	Standing	T _{bns}	T _{bs}	T ₁	T ₂	T ₃	T ₄	Non-standing	Standing
<i>E. malaccana</i>										
T_b	41.0 ± 1.7	39.6 ± 1.0	39.7 ± 0.7	40.3 ± 2.1	38.7 ± 1.7	39.4 ± 1.5	37.5 ± 0.6	38.2 ± 0.4	–	–
DT	2.6 ± 1.2	4.1 ± 1.3	2.81 ± 1.0	4.05 ± 1.3	5.8 ± 1.6	6.9 ± 1.0	7.9 ± 1.7	10.3 ± 1.1	–	–
R_T	0.94 ± 0.02	0.91 ± 0.03	0.94 ± 0.02	0.91 ± 0.03	0.87 ± 0.03	0.88 ± 0.02	0.86 ± 0.03	0.80 ± 0.02	–	–
<i>E. radiata</i>										
T_b	42.8 ± 2.5	40.2 ± 1.7	41.3 ± 0.9	41.7 ± 3.1	39.5 ± 2.5	42.6 ± 3.8	42.2 ± 3.1	42.4 ± 3.0	40.3 ± 0.9	39.4 ± 1.1
DT	2.7 ± 1.0	4.3 ± 1.3	4.6 ± 0.8	4.2 ± 1.4	5.7 ± 1.4	5.7 ± 1.5	6.5 ± 0.7	7.8 ± 1.2	3.9 ± 0.6	4.1 ± 1.1
R_T	0.94 ± 0.02	0.90 ± 0.03	0.90 ± 0.02	0.91 ± 0.03	0.87 ± 0.03	0.88 ± 0.03	0.85 ± 0.02	0.83 ± 0.02	0.91 ± 0.01	0.91 ± 0.03

T_{bns} and T_{bs} : non-standing and standing snails found at the bottom of a tower; T₁, T₂, T₃ and T₄: standing snails found on 1st, 2nd, 3rd and 4th levels of a tower, respectively. The ± errors are 95% confidence intervals.

2008); these species do not form towers, however, even at substratum temperatures that are suggested to trigger towering behaviour in *E. malaccana* and *E. radiata* (Lim, 2008; L. Seuront, unpublished data). Further, the R_T values reported in the present work are consistently smaller than previous estimates obtained under similar conditions of heat stress from *Littoraria scabra* in a Fijian mangrove (R_T in the range 0.99–1.01; Chapperon & Seuront, 2011a) and *Nerita atramentosa* on South Australian rocky shores (R_T in the range 1.00–1.15; Chapperon & Seuront, 2011b; Chapperon, Le Bris & Seuront, 2013); these species do not exhibit any postural behaviour, but instead select thermally favourable microhabitats (Chapperon & Seuront, 2011a, b; Chapperon *et al.*, 2013). To our knowledge, the only attempt to link substratum temperature and postural behaviour mechanistically in an intertidal gastropod showed that *E. malaccana* standing behaviour was triggered by the presence of a temperature gradient in the boundary layer air above the solar-heated rock surface, but was not observed when snails were heated in the absence of this gradient (Marshall & Chua, 2012). While this is at best speculative, the measured very hot substratum temperature and the absence of wind during our observations were compatible with the presence of a thermal gradient in the boundary layer air. Such a gradient would typically favour larger snails (Marshall & Chua, 2010b), though no significant differences in size were found between non-standing and standing solitary snails ($P > 0.05$). In turn, since heat transfer is inversely proportional to size in both stagnant and moving air (see, e.g. Denny, 1993), small individuals would theoretically benefit from a higher position in a tower. This observation is consistent with the fact that all observed towers were formed of snails of decreasing size from bottom to top. Furthermore, even if towering behaviour has been suggested to be rather incidental (Marshall *et al.*, 2010b) and to result from trail-following at benign temperatures (Marshall & Chua, 2012), the frequency of the observed postural behaviours, their links to substratum temperature and their clear effects on snail body temperature are all in favour of an adaptive behaviour driven by selection.

This work uniquely used infrared thermography—a still relatively novel method in molluscan research (see Lathlean & Seuront, 2014)—to reveal unexpected differences in the behavioural ecology and thermal biology of two species of snails co-occurring in a topographically simple though thermally extreme environment, which may suggest niche differentiation. Our results also show that *E. malaccana* and *E. radiata* are very well adapted to heat stress among littorinids in particular, and intertidal gastropod in general. There is a need to identify the spectrum of behavioural strategies available to various species (e.g. posturing, aggregation and habitat selection) to reach a better understanding of how high-shore gastropods may face climate variability in an era of global change.

We thank the Agriculture, Fisheries and Conservation Department of the Hong Kong SAR Government for the permission to work at the Cape D'Aguiar Marine Reserve (Permit No.: (107) in AF GR MPA 01/5/2 Pt.15). The Testo thermal camera was funded by the Small Project Fund (Grant No.: 201309176082) from The University of Hong Kong. L. Seuront was financially supported by a Bonus Qualité Recherche (BQR) International from the University of Lille 1 – Sciences and Technologies (France). Prof. Mark Davies and two anonymous referees are acknowledged for their constructive comments and suggestions on a previous version of this work. Prof. Davies is acknowledged for his contribution in improving the language of the manuscript.

REFERENCES

- ANGILLETTA, M.J. 2009. *Thermal adaptation: a theoretical and empirical synthesis*. Oxford University Press, Oxford.
- CADDY-RETALIC, S., BENKENDORFF, K. & FAIRWEATHER, P.G. 2011. Visualizing hotspots: Applying thermal imaging to monitor internal temperatures in intertidal gastropods. *Molluscan Research*, **31**: 106–113.
- CHAPPERON, C., LE BRIS, C. & SEURONT, L. 2013. Thermally-mediated body temperature, water content and aggregation behaviour in the intertidal gastropod *Nerita atramentosa*. *Ecological Research*, doi:10.1007/s11284-013-1030-4.
- CHAPPERON, C. & SEURONT, L. 2011a. Behavioral thermoregulation in a tropical gastropod: links to climate change scenarios. *Global Change Biology*, **17**: 1740–1749.
- CHAPPERON, C. & SEURONT, L. 2011b. Space-time variability in environmental thermal properties and snail thermoregulatory behaviour. *Functional Ecology*, **25**: 1040–1050.
- CHAPPERON, C. & SEURONT, L. 2012. Keeping warm in the cold: on the thermal benefits of aggregation behaviour in an intertidal ectotherm. *Journal of Thermal Biology*, **37**: 640–647.
- DENNY, M.W. 1993. *Air and water: the biology and physics of Life's media*. Princeton University Press, Princeton.
- DENNY, M.W., DOWD, W.W., BILIR, L. & MACH, K.J. 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. *Journal of Experimental Marine Biology and Ecology*, **400**: 175–190.
- GEDAN, K.B., BERNHARDT, J., BERTNESS, M.D. & LESLIE, H.M. 2011. Substrate size mediates thermal stress in the rocky intertidal. *Ecology*, **92**: 576–582.
- HELMUTH, B., BROITMAN, B.R., YAMANE, L., GILMAN, S.E., MACH, K., MISLAN, K.A.S. & DENNY, M.W. 2010. Organismal climatology: analysing environmental variability at scales relevant to physiological stress. *Journal of Experimental Biology*, **213**: 995–1003.
- IACARELLA, J.C. & HELMUTH, B. 2011. Experiencing the salt marsh environment through the foot of *Littoraria irrorata*: behavioral responses to thermal and desiccation stresses. *Journal of Experimental Biology*, **409**: 143–153.
- KAEHLER, S. & WILLIAMS, G.A. 1997. Do factors influencing recruitment ultimately determine the distribution and abundance of encrusting algae on seasonal tropical shores? *Marine Ecology Progress Series*, **156**: 87–96.
- KEARNEY, M., SHINE, R. & PORTER, W.P. 2009. The potential for behavioural thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences of the USA*, **106**: 3835–3840.
- LANG, R.C., BRITTON, J.C. & METZ, T. 1998. What to do when there is nothing to do: the ecology of Jamaican intertidal Littorinidae (Gastropoda: Prosobranchia) in repose. *Hydrobiologia*, **378**: 161–185.
- LATHLEAN, J., AYRE, D.J. & MINCHINTON, T.E. 2014. Estimating latitudinal variability in extreme heat stress on rocky intertidal shores. *Journal of Biogeography*, **41**: 1478–1491.
- LATHLEAN, J. & SEURONT, L. 2014. Infrared thermography in marine ecology: methods, previous applications and future challenges. *Marine Ecology Progress Series*, **514**: 263–277.
- LATHLEAN, J.A., AYRE, D.J. & MINCHINTON, T.E. 2012. Using infrared imagery to test for quadrat-level temperature variation and effects on the early life history of a rocky shore barnacle. *Limnology and Oceanography*, **57**: 1279–1291.
- LIM, S.S. 2008. Body posturing in *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* (Mollusca: Gastropoda: Littorinidae): a behavioural response to reduce heat stress. *Memoirs of the Queensland Museum*, **54**: 339–347.
- MARSHALL, D.J. & CHUA, T. 2012. Boundary layer convective heating and thermoregulatory behaviour during aerial exposure in the rocky eulittoral fringe snail *Echinolittorina malaccana*. *Journal of Experimental Marine Biology and Ecology*, **430**: 25–31.
- MARSHALL, D.J., McQUAID, C.D. & WILLIAMS, G.A. 2010a. Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biology Letters*, doi:10.1098/rsbl.2010.0233.
- MARSHALL, D.J., QADIRULISYAM BIN MUSTAFA, S.A. & WILLIAMS, G.A. 2010b. Cooling towers of marine snails: is higher better? *Scientia Bruneiana*, **11**: 47–52.

RESEARCH NOTE

- McMAHON, R.F. 1990. Thermal tolerance, evaporative water loss, air-water oxygen consumption and zonation of intertidal prosobranchs: a new synthesis. *Hydrobiologia*, **193**: 241–260.
- MILLER, L.P. & DENNY, M.W. 2011. Importance of behaviour and morphological traits for controlling body temperature in littorinid snails. *Biological Bulletin*, **220**: 209–223.
- MUÑOZ, J.L.P., FINKE, G.R., CAMUS, P.A. & BOZINOVIC, F. 2005. Thermoregulatory behaviour, heat gain and thermal tolerance in the periwinkle *Echinolittorina peruwiana* in central Chile. *Comparative Biochemistry and Physiology, Part A*, **142**: 92–98.
- SOMERO, G.N. 2012. The physiology of global change: linking patterns to mechanisms. *Annual Review of Marine Science*, **4**: 39–61.
- STAFFORD, R., DAVIES, M.S. & WILLIAMS, G.A. 2007. Computer simulations of high shore littorinids predict small-scale spatial and temporal distribution patterns on rocky shores. *Marine Ecology Progress Series*, **342**: 151–161.
- WILLIAMS, G.A. 1994. The relationship between shade and molluscan grazing in structuring communities on a moderately-exposed tropical rocky shore. *Journal of Experimental Marine Biology and Ecology*, **178**: 79–95.
- ZAR, J.R. 1999. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River.