Space-time variability in environmental thermal properties and snail thermoregulatory behaviour

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Summary

1. Behavioural adaptations of ectotherms to thermally heterogeneous environments are still overlooked in the literature despite the fact that organismal behaviour could enhance survival in the warming world. This is particularly critical in the intertidal where most ectotherms live at, or near to the upper limit of thermal tolerance.

2. This study investigated (i) the environmental factors determining the body temperatures of the intertidal gastropod *Nerita atramentosa*, (ii) the space–time variability in environmental and individual body temperatures and (iii) the potential variability in *N. atramentosa* thermoregulatory behaviours, i.e. microhabitat selection and aggregation.

3. Thermal imaging was used to assess the body temperatures of N. *atramentosa* and surrounding substrata over two seasons (autumn and summer), at two shore levels (low- vs. high-shore levels) within two habitats of different topographic complexity (rock platform and boulders) on the same rocky shore.

4. Snail body and substratum temperatures were significantly and positively correlated within each habitat at both seasons. Substratum temperature may thus be considered as a primary driver of body temperatures of organisms that attach to a substratum. Substratum temperature and other variables such as solar irradiance critically need to be integrated in climate-change models that use single climatic variables (e.g. air temperature) that are not necessarily correlated with individual body temperatures in nature.

5. The high space-time variability in both substratum and body temperatures reinforces the growing evidence that small spatial scale variations may surpass those observed at larger spatial scales.

6. *Nerita atramentosa* thermoregulatory behaviour under high thermal stress appeared to be habitat specific.

7. The small spatial scale heterogeneity in environmental and individual temperatures and in thermoregulatory behaviours has stressed the need to focus on body temperature patterns at the niche level and to integrate the organismal behaviour in climate-change models.

Key-words: behavioural adaptations, body temperature, climate change, gastropod, intertidal habitats, microhabitat, physiology, season, shore height, thermal stress

Introduction

Temperature determines a wide range of biological processes that are essential for animal life (Angilletta 2009). In particular, temperature has an effect on all physiological processes from the molecular to the organismal levels

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(Pörtner *et al.* 2006; Kingsolver 2009). Therefore, changes in temperatures affect organism fitness, performance and metabolism (Huey & Berrigan 2001; Dillon, Wang & Huey 2010), hence profoundly impact the structure, dynamic and functioning of populations and ecosystems (e.g. Morelissen & Harley 2007). However, the mean temperature and its variability have been predicted to increase in the warming climate (Planton *et al.* 2008). Nevertheless, levels of thermal tolerance and potential physiological and behavioural

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abilities of ectotherms to thermoregulate in the future climate, particularly in thermally heterogeneous environments, are still far from being understood.

The mechanistic links between the body temperatures of ectotherms, which control local (Miller, Harley & Denny 2009) and global distribution patterns (Helmuth et al. 2002), and environmental variables are not as simple as previously anticipated (Helmuth 2009). More specifically, body temperatures of both terrestrial and marine ectotherms are determined by heat fluxes towards and from an organism (Gates 1980; Harley et al. 2009) which are subject to variations generated by the interaction between climatic heat sources (heat derived from ambient conditions, i.e. coarse-scale macroclimatic data such as air and water temperatures, Helmuth 2002; Vidal et al. 2010), non-climatic heat sources at the niche level (heat originated from the sun, i.e. solar irradiance, Díaz & Cabezas-Díaz 2004; Marshall, McQuaid & Williams 2010), and biotic factors (e.g. shell morphology, Harley et al. 2009; Polo-Cavia, López & Martín 2009). Therefore, the variability in a single factor may cause unexpected heterogeneity in body temperatures and leads to counter-intuitive patterns (e.g. Helmuth et al. 2002). Body temperatures of snails have also recently been demonstrated to be primarily controlled by non-climatic heat sources at the niche level (i.e. solar irradiance) instead of climatic heat sources (i.e. air and water temperatures; Marshall, McQuaid & Williams 2010). The space-time heterogeneity in organism and environment temperatures and the related physiological and behavioural adaptations require a better understanding in order to predict future species distribution ranges.

This lack of knowledge is particularly critical in intertidal ecosystems that are thermally very heterogeneous over a range of scales, i.e. diel, tidal and seasonal variations within latitudinal and vertical clines, and microhabitats (Helmuth et al. 2006; Sinclair, Thompson & Seebacher 2006). Most intertidal invertebrates are close to the upper limit of their thermal tolerance (Somero 2002); hence, they are critically vulnerable to further changes in temperatures. Intertidal ectotherms have developed a range of physiological (Somero 2002) and behavioural adaptations (Munoz et al. 2005; Williams et al. 2005) to the natural thermal stress heterogeneity in order to maintain body temperatures within the species thermal tolerance window. Over the last decade, however, most attention has been given to the physiological responses of ectotherms and the development of new thermal sensors (e.g. biomimetic loggers, Shine & Kearney 2001; Schneider & Helmuth 2007) which have led to the establishment of new physiologically based mechanistic models, i.e. heat budget models. These models have successfully predicted individual body temperature patterns of sessile individuals such as limpets (Denny & Harley 2006) by integrating the morphology of organisms (e.g. shell shape). However, the potential buffering effect of behavioural thermoregulation of mobile ectotherms is still missing within climate change impact models (Kearney, Shine & Porter 2009).

A few recent studies, although mostly terrestrial, have highlighted the importance of integrating the behaviour of mobile ectotherms (Díaz & Cabezas- Díaz 2004; Kearney, Shine & Porter 2009) that may increase the survival of mobile organism in a warming world (Huey & Tewksbury 2009). For example, locomotory abilities allow the exploitation of the ambient heterogeneity, hence the selection of thermally favourable niches (Huey et al. 2002). Because of their intrinsic complex topography, intertidal rocky shores abound with a variety of potential thermal refuges such as crevices, pits, rocks and pools that supply ectotherms with moisture and shade from solar radiations (Jackson 2010). Therefore, snails may actively select these microhabitats while travelling during the high tide to stabilize their body temperatures following emersion. Besides microhabitat selection behaviour, snails have displayed a range of thermoregulatory behaviours, e.g. mucous holdfast, raised posture and shell orientation (Garrity 1984; Munoz et al. 2005). Particularly, the formation of aggregates, commonly occurring among snails, is typically considered as a behavioural adaptation to desiccation and thermal stresses (e.g. Garrity 1984), although this is not always the case (e.g. Coleman 2010).

In this context, the present study focused on the patterns of body temperatures and the thermoregulatory behaviours of the black snail *Nerita atramentosa* (Fig. 1a,c), a species particularly abundant on south Australian intertidal rocky shores at different spatial scales during cool and hot seasons. More specifically, the main goals of this work were (i) to explore the relationship between body temperatures and substratum surface temperatures at the individual scale, to analyse the space–time variability in (ii) substratum and body temperature patterns over two seasons (autumn vs. summer) in two topographically different habitats along the same rocky shore at small spatial scales (i.e. habitat, shore and niche levels), and in (iii) the potential thermoregulatory behaviours (i.e. aggregation and selection of thermally favourable niches).

Materials and methods

STUDIED AREA AND SPECIES

This work was conducted on a moderately exposed rocky shore located in Marino Rocks, South Australia (35°02'40S–138°30'30E), characterized by the presence of an alongshore gradient of substratum topographic complexity (i.e. rock platform to boulder field). This area supports great abundances of herbivorous gastropod species such as *Bembicium* sp., and *Austrocochlea* sp. and particularly the neritacean *N. atramentosa* (Reeve 1855). Here, we focused on *N. atramentosa* (Fig. 1a,c), which has specifically been chosen as (i) it is the dominant grazer and competitor for microalgae on Australian rocky shores (Underwood & Murphy 2008) and (ii) it is particularly subject to exposure to high temperatures because of its black pigmented shell and the related high absorption of solar radiation and retention during emersion (McMahon 1990). This mobile species is able to move between microhabitats during emersion (Chapperon & Seuront, pers. obs.).

The study was undertaken at high- and low-shore levels (typically between the lower limits reached by the tidal flow at low tide in spring and neap tides, Seuront & Spilmont 2002) during low tides that



Fig. 1. Thermal images (b, d) and associated digital pictures (a, c) of *Nerita atramentosa* collected in summer on boulders, (a, b) at the high shore level within a crevice, and (c, d) at the low shore level on a flat rock. Average body temperature of snails and surrounding substratum surface within the crevice (a, b) were respectively $25\cdot27 \pm 0.19$ °C (N = 7; mean \pm standard error) and $23\cdot4 \pm 0.12$ °C. On the flat rock, snails exhibited an average body temperature of $28\cdot2 \pm 0.40$ °C (N = 2) and the surrounding substratum surface was $24\cdot81 \pm 0.09$ °C.

occurred in the morning and mid-day times (i.e. between 10 AM to 2 PM; Kuo & Sanford 2009) on four different days in both autumn 2009 (A, May 2009) and summer 2009–2010 (S, December 2009 and January 2010) on two topographically different habitats located 250 m apart. The field work started at the low tide time indicated by the Bureau of Meteorology of Australia and lasted for a minimum period of 2 h during the incoming tides. The first habitat was a rock platform (RP; 35°2′31·67″–138°30′35·37″) characterized by a flat, smooth rocky substratum with a few shallow pits and crevices at high shore level, and by the presence of pebbles and cobbles at low shore level. The second habitat was a boulder field (B; 35°2′38·04″–138°30′30·13″) mainly characterized by boulders (i.e. rock bigger than 256 mm) that provide a range of microhabitats such as pools, pits and crevices.

SNAIL DENSITY AND DISTRIBUTION PATTERNS

In each habitat and shore level, 20 quadrats $(25 \times 25 \text{ cm})$ were haphazardly placed within a 51-m² area. Digital pictures (digital camera Olympus J1 Tough-60; Olympus Imaging Corporation, Centre Valley, PA, USA) of each quadrat were taken to assess snail density and individual distribution at microscale. Individuals were classified either as being solitary or aggregated. An individual was considered aggregated when there was a direct shell contact with the shell of at least another conspecific. In addition, the microhabitat resting site of each snail was recorded. On both habitats, two microhabitats (flat rock and crevice) were defined in regards to substratum topographic complexity and exposure to solar radiations. Flat rock corresponds to a flat surface bereft of refuge to thermal stress, hence directly exposed to solar radiations. Crevice was defined as a depression wide and deep enough to fit at least one individual that may provide some protection from solar radiation, hence from thermal stress. On the rock platform, an additional microhabitat, under rock, was considered as a sheltered environment that provides entire protection from solar radiations.

SNAIL BODY TEMPERATURE AND SUBSTRATUM SURFACE TEMPERATURE

Tissue temperatures of living animals have mainly been gathered using thermocouples or thermistors (Garrity 1984; Williams et al. 2005). In this study, we used infrared thermography as a non-contact and non-invasive method of temperature measurement (Helmuth 2002; Chapperon & Seuront 2011a). Thermal imaging has recently been shown to be an accurate and reliable tool to measure the mantle tissue temperature of N. atramentosa (Caddy-Retalic 2008). A preliminary approach (Caddy-Retalic 2008) was undertaken between N. atramentosa mantle temperatures measured with a thermistor probe and N. atramentosa dorsal shell temperatures assessed with a thermal imager Fluke Ti20 (Fluke Corporation, Everett, WA, USA). A significant positive correlation (Pearson correlation coefficient, $R^2 = 0.988, P < 0.001$) was obtained between the mantle tissue temperatures and the dorsal shell temperatures (Caddy-Retalic 2008). The significant linear regression between mantle temperatures MTs and dorsal shell temperatures BTs was identified to be BT = $0.8875 \times MT + 2.7044$ (Caddy-Retalic 2008).

Here, a thermal image of each individual observed in each quadrat was obtained using a thermal imaging camera Fluke Ti20 (Fluke Corporation). The thermal sensitivity of the thermal camera is ≤ 0.2 °C at 30 °C, and the temperature measurement accuracy is 2% or 2 °C, whichever is greater. Emissivity value (ɛ) was calibrated by applying a piece of masking tape characterized by a high emissivity $(\varepsilon = 0.95)$ on 10 rocks and 10 snails. Specifically, when the temperature equilibrium was reached between tape and rock, and tape and snail, the emissivity value of the targets (i.e. rock and snail) was adjusted in order to obtain a temperature reading similar to that of the electrical tape of known emissivity. Mean emissivity values obtained for rock and body snail were respectively 0.954 ± 0.005 $(\bar{x} \pm SD; N = 10)$ and 0.946 \pm 0.009, ranged from 0.94 to 0.99 and 0.91 to 0.98, and cannot be statistically distinguished (Wilcoxon-Mann–Whitney U-test, P < 0.05). Note that these emissivity values fall into the range of emissivity values employed for substrata (i.e. 0.95-1; Campbell & Norman 1998; Helmuth 1998; Denny & Harley 2006; Finke, Bozinovic & Navarrete 2009) and intertidal invertebrates (i.e. 0.96-1; Campbell & Norman 1998; Helmuth 1998; Denny & Harley 2006; Finke, Bozinovic & Navarrete 2009; Miller, Harley & Denny 2009). Emissivity value (ɛ) was consequently assumed to be fairly identical between organism and substratum and was hence set up at 0.95. Pictures of 307 and 203 individuals were collected on the boulder field and rock platform, respectively. Each individual was photographed once. Different individuals were used in the different habitats and shore levels. Images were subsequently analysed using INSIDEIR software version 4.0.1.10 (Fluke Corporation, 2006). For each thermal picture, snail body temperature (BT) and temperature of the surrounding substratum (ST) were assessed (Fig. 1b,d).

A closed curve marker was drawn around each photographed shell in order to calculate the mean value of body (i.e. shell) temperature (BT). In addition, ST was averaged from four linear markers drawn on the substratum directly surrounding the individual shell. In particular, the distance between the linear markers and the shell was defined as approximately a quarter of the shell size measured on the picture. In addition, BTs and STs were measured during the incoming tides between 10 am and 2 pm which is the period that selects for heat tolerance (Somero 2010). It is therefore supposed that the temperatures measured corresponded to the maximal temperatures reached by both individuals and substrata, although this assumption may require further investigations. The mantle temperature MT was further calculated from the empirical relationship found between MT and BT (Caddy-Retalic 2008). Furthermore, a mantle-to-substratum temperature ratio (MST_{ratio}) was defined to examine whether or not snail mantle temperature (MT) was closely related to that of the surrounding substratum (ST). The difference between mantle temperature and surrounding substratum (MST_{diff}) was also calculated to quantify the potential difference in temperature between the snail mantle and its substratum.

The distributions of the data MT, ST, MST_{ratio} and MST_{diff} at both seasons, in both habitats, in the different microhabitats and the distributions of snail density in both habitats were not all normally distributed (Kolmogorov-Smirnov test, P < 0.05). Nonparametric tests were consequently used throughout the manuscript. Spearman's correlation coefficients were used to assess the relationship between MT and ST at both seasons and in both habitats. All pairwise comparisons of MT, ST, MST_{ratio} and MST_{diff} between habitats, seasons, microhabitats, and aggregated vs. solitary individuals were conducted with the Mann-Whitney U-test. Comparisons of MT, ST, MST_{ratio} and MST_{diff} between the three microhabitats on the rock platform were performed with the Kruskall-Wallis test and subsequent nonparametric post hoc analyses (based on the Tukey test; Zar 2010) were performed to compare the different groups of measurements. All statistical analyses were carried out using PASW STATISTICS 18 (SPSS Inc., 2009, Chicago, IL, USA).

Results

SPACE-TIME DYNAMIC OF NERITA ATRAMENTOSA DENSITY AND DISTRIBUTION PATTERNS

Boulder field

The density of individuals was significantly higher in summer $(Z = -4.212, P < 0.001; 64 \text{ ind m}^{-2})$ than in autumn (48 ind m⁻²). The proportion of individuals in crevices was higher at the high shore level in both seasons (Fig. 2a). Instead, individuals rested more often on flat rocks at low shore levels (Fig. 2a). Overall, 58% and 29% of the total number of individuals were aggregated in summer and in autumn, respectively. Aggregation behaviour was more frequent at the high shore level in summer (Fig. 2a). In addition, *N. atramentosa* was found to aggregate more frequently within crevices than on flat rocks (Fig. 2a).

Rock platform

No significant difference in density (Z = -1.121, P = 0.262) was observed between the two seasons. Overall, *N. atramen*-



Fig. 2. *Nerita atramentosa* microhabitat occupation and aggregation frequency in both seasons and shore levels on boulder field (top) and rock platform (bottom). A-LS, autumn low shore; A-HS, autumn high shore; S-LS, summer low shore; S-HS, summer high shore. The white, grey and black bars respectively correspond to flat rock, crevice and under rock microhabitats. The numbers at the bottom of each bar indicate the proportion of aggregation observed within each microhabitat. The italic numbers at the top of each bar represent the total number of individuals observed within each microhabitat.

tosa was mainly observed on flat rocks (46%) rather than in crevices (35%) or under rocks (19%) over the two seasons. In autumn at low shore level, 96% of individuals were on flat rocks (Fig. 2b). In summer, however, organisms were mainly under rocks (Fig. 2b), particularly at low shore level (Fig. 2b; 63%). Most individuals were solitary in both seasons and at both shore levels (Fig. 2b) with the exception of the high shore level in autumn where 55% of individuals were aggregated. Moreover, individuals were found to be more aggregated within crevices and under rocks in both seasons (Fig. 2b).

SPACE-TIME DYNAMICS OF ENVIRONMENT AND SNAIL BODY THERMAL PROPERTIES

Significant positive linear relationships were found between MT and ST in both habitats and seasons (Fig. 3a,b). More specifically, in autumn, MT, ST, MST_{ratio} and MST_{diff} were



Fig. 3. *Nerita atramentosa* individual mantle temperatures (MT) and substratum temperatures (ST) and air temperature (AT; only on c and d) on the boulder field (a, c) and the rock platform (b, d) in both seasons. (a, b) autumn and summer temperature values are respectively represented by white and grey circles (N = 510). The black line represents the first bissectrix, i.e. MT = ST. To improve the clarity of the graph, a value (47.93, 54.34) recorded in summer on the boulder field was removed. Positive and significant correlations were found between MT and ST in both habitats and at both seasons (autumn: $\rho_{\rm B} = 0.967$, P < 0.001, n = 91; $\rho_{\rm RP} = 0.954$, P < 0.001, n = 142; summer: $\rho_{\rm B} = 0.827$, P < 0.001, n = 216; $\rho_{\rm RP} = 0.883$, P < 0.001, n = 61). (c, d) Mean values of MT (black bars) and ST (grey bar) observed in both season and shore levels. A-HS: autumn high shore level, A-LS: autumn low shore level, S-HS: summer high shore level, S-LS. Errors bars are standard errors. Mean ATs were calculated from the data collected in Port Stanvac (i.e. closest meteorological station from Marino Rocks, *ca.* 10 km apart) during the studied low tides (source: Bureau of Meteorology of Australia). *** < 0.001 (Mann–Whitney *U*-test).

significantly higher on the rock platform than on boulders ($Z_{\text{MT}} = -12.183$, $Z_{\text{ST}} = -11.432$, $Z_{\text{MST}_{\text{ratio}}} = -11.915$, $Z_{\text{MST}_{\text{diff}}} = -12.028$, P < 0.001; Table 1, Fig. 3a,b). In summer, no significant differences in MT, ST, MST_{ratio} and MST_{diff} were found between the two habitats ($Z_{\text{MT}} = -0.005$, P = 0.996; $Z_{\text{ST}} = -1.619$, P = 0.105; $Z_{\text{MST}_{\text{ratio}}} = -1.866$, P = 0.062; $Z_{\text{MST}_{\text{diff}}} = -1.607$, P = 0.108; Table 1, Fig. 3a,b).

Boulder field

In autumn, mantle and surrounding substratum temperatures were significantly higher at low shore level than at high shore level ($Z_{\rm MT} = -6.849$, $Z_{\rm ST} = -7.663$, P < 0.001; Fig. 3c). However, no significant differences in MST_{ratio} and MST_{diff} were found between shore levels ($Z_{\rm MST_{ratio}} = -0.846$, P = 0.398; $Z_{\rm MST_{diff}} = -0.830$, P = 0.407). In summer, MT,

Table 1. Mean (standard deviation), minimum and maximum values in MT (mantle temperature), ST (substratum temperature), MST_{ratio} (body-to-substratum temperature ratio) and MST_{diff} (difference of temperature between the mantle of individuals and the surrounding substratum) on RP (rock platform) and B (boulders) in A (autumn) and S (summer)

		MT (°C)	ST (°C)	MST _{ratio}	MST _{diff} (°C)
RP-A $(N = 142)$	Mean (SE)	22.13 (0.44)	19.64 (0.29)	1.12 (0.01)	2.49 (0.18)
	Min	15.84	15.44	0.89	-1.81
	Max	36.19	32.34	1.44	9.31
B-A $(N = 91)$	Mean (SE)	15.48 (0.13)	15.46 (0.13)	1.00 (0.93)	0.01(0.04)
	Min	11.44	11.42	0.93	-1.08
	Max	18.74	18.24	1.06	1.14
RP-S $(N = 61)$	Mean (SE)	29.30 (0.43)	26.15 (0.32)	1.12 (0.01)	3.15 (0.22)
	Min	24.33	22.43	1.01	0.40
	Max	37.55	34.29	1.26	7.05
B-S ($N = 216$)	Mean (SE)	29.55 (0.32)	25.71 (0.22)	1.15 (0.01)	3.84 (0.17)
	Min	21.30	19.40	0.79	-5.98
	Max	54.34	47.93	1.36	8.88

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MST_{ratio} and MST_{diff} were significantly greater at low shore level than at high shore level ($Z_{MT} = -4.409$, $Z_{MST_{ratio}} = -8.413$, $Z_{MST_{diff}} = -7.626$, P < 0.001; Table 1, Fig. 3c). ST, however, was not significantly different between shore levels ($Z_{ST} = -0.453$, P = 0.651).

Rock platform

In autumn, MT, ST, MST_{ratio} and MST_{diff} were significantly greater at low shore level than at high shore level $(Z_{\rm MT} = -6.665, Z_{\rm ST} = -6.808, Z_{\rm MST_{ratio}} = -5.086, Z_{\rm MST_{diff}} = -5.606, P < 0.001; Table 1, Fig. 3d). In summer, MT, ST, MST_{ratio} and MST_{diff} were significantly higher at high shore level than at low shore level <math>(Z_{\rm MT} = -5.031, Z_{\rm ST} = -4.332, Z_{\rm MST_{ratio}} = -3.170, Z_{\rm MST_{diff}} = -3.363, P < 0.001; Table 1, Fig. 3d).$

MICROHABITAT OCCUPATION AND THERMAL PROPERTIES

Boulder field

All results are summarized in Table 2. In autumn, MT, ST, MST_{ratio} and MST_{diff} were significantly higher on flat rocks than in crevices (Fig. 4a). At high shore level, no significant

Table 2. Mann–Whitney *U*-test to investigate the variation in MT, ST, MST_{ratio} and MST_{diff} between the two microhabitats, i.e. crevice (C) and flat rock (FR) on the boulder field in autumn (A) and summer (S) in total (all), and specifically at the low and high shore levels (LSL and HSL, respectively). Results of the tests are indicated in the last column

Boulders		Ζ	Р	
A				
All	MT	-2.72	0.007	FR > C
	ST	-2.85	0.004	
	MST _{ratio}	-2.94	0.003	
	MST _{diff}	-2.92	0.003	
LSL	MT	-1.43	0.154	NS
	ST	-0.92	0.358	
	MST _{ratio}	-3.30	< 0.001	FR > C
	MST _{diff}	-3.36	< 0.001	
HSL	MT	0.46	0.470	NS
	ST	0.58	0.581	
	MST _{ratio}	0.51	0.524	
	MST _{diff}	0.55	0.562	
S				
All	MT	-1.03	0.303	NS
	ST	-3.09	0.002	FR < C
	MST _{ratio}	-5.95	< 0.001	FR > C
	MST _{diff}	-5.14	< 0.001	
LSL	MT	0.59	0.600	NS
	ST	0.59	0.600	
	MST _{ratio}	0.16	0.162	
	MST _{diff}	0.28	0.286	
HSL	MT	-3.33	< 0.001	FR < C
	ST	-4.21	< 0.001	
	MST _{ratio}	-0.55	0.585	NS
	MST _{diff}	-0.12	0.864	

NS, non-significant.

difference in MT, ST, MST_{ratio} and MST_{diff} was observed between microhabitats. At low shore level, MST_{ratio} and MST_{diff} were significantly greater on flat rocks than in crevices. MT and ST did not significantly differ between microhabitats. In summer, ST was significantly cooler on flat rocks than within crevices (Fig. 4c). However, MT did not significantly differ between microhabitats (Fig. 4c). MST_{ratio} and MST_{diff} values were significantly greater on flat rocks than within crevices. At high shore level, MT and ST were significantly warmer in crevices than on flat rocks. MST_{ratio} and MST_{diff} were not significantly different between microhabitats. At low shore level, no significant difference was found in MT, ST, MST_{ratio} and MST_{diff} between microhabitats.

Rock platform

All results are summarized in Table 3. In autumn, MT, ST, MST_{ratio} and MST_{diff} were significantly greater on flat rocks than under rocks than in crevices (Fig. 4b). At the high shore level, MT, ST, MST_{ratio} and MST_{diff} were significantly higher on flat rocks and under rocks than within crevices. No significant differences in MT, ST, MST_{ratio} and MST_{diff} were found between flat rocks and under rocks. At low shore level, N. atramentosa was only found on flat rocks with the exception of one observation under rock. In summer, MT, ST and MST_{diff} were significantly warmer in crevices and on flat rocks than under rocks. No significant difference in MT, ST and MST_{diff} was found between crevices and flat rocks. MST_{ratio} was warmer on flat rocks than under rocks. No significant difference in MST_{ratio} was found between crevices and under rocks, and flat rocks. At the high shore level, MT and ST did not significantly differ between microhabitats. MST_{ratio} and MST_{diff} were significantly higher on flat rocks than under rocks. At the opposite, at low shore level, MT and ST were significantly warmer on flat rocks than under rocks. MT within crevices was not significantly different from MT measured in the two others microhabitats. Similarly, ST in crevices was not significantly different from ST on flat rocks but was significantly higher than ST under rocks. $\ensuremath{\mathsf{MST}_{\mathsf{ratio}}}$ and $\ensuremath{\mathsf{MST}_{\mathsf{diff}}}$ were not significantly different between microhabitats.

AGGREGATION BEHAVIOUR AND THERMAL PROPERTIES

Boulder field

All results are summarized in Table 4. In autumn, no significant difference was found in MT, ST, MST_{ratio} and MST_{diff} between aggregated and solitary individuals. Similar results were found at high shore level. At low shore level, aggregated individuals were warmer and rested on warmer substrata when compared with solitary individuals. MST_{ratio} and MST_{diff} did not significantly differ between aggregated and solitary snails. At the opposite, in summer, aggregated individuals displayed significant cooler MT and were observed on cooler substrata when compared with solitary individuals. MST_{ratio} and MST_{diff} were significantly lower among aggre-

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Rock platform		d.f.	χ^2	Р	Post hoc		
А							
All	MT	2	31.74	< 0.001	FR > UR > C		
	ST	2	26.57				
	MST _{ratio}	2	23.65				
	MST _{diff}	2	25.94				
HSL	MT	2	41.07	< 0.001	FR = UR > C		
	ST	2	33.58				
	MST _{ratio}	2	31.15				
	MST _{diff}	2	34.30				
S							
All	MT	2	19.89	< 0.001	C = FR > UR		
	ST	2	12.98	0.002			
	MST _{ratio}	2	12.96	0.002	FR > UR = C		
	MST _{diff}	2	17.43	< 0.001	C = FR > UR		
HSL	MT	2	3.78	0.151	NS		
	ST	2	4.04	0.133			
	MST _{ratio}	2	6.29	0.043	FR > UR = C		
	MST _{diff}	2	6.43	0.040			
LSL	MT	2	7.71	0.021	FR > UR; FR = C; UR = C		
	ST	2	10.824	0.004	FR = C > UR		
	MST _{ratio}	2	0.020	0.966	NS		
	MST _{diff}	2	0.682	0.711			

Fig. 4. *Nerita atramentosa* individual mantle temperatures (MT) vs. substratum temperatures (ST) on the boulder field (a, c; N = 307) and the rock platform (b, d; N = 203) in autumn (a, b) and summer (c, d) in different microhabitats (white: flat rock, grey: crevice, black: under rocks). The black lines represent the first bissectrix, i.e. MT = ST. To improve the clarity of the graph, a value (47.93, 54.34) recorded in summer on the boulder field was removed.

Table 3. Kruskall–Wallis test and subsequent multiple comparisons (*post hoc* based on the Tukey test) to investigate the variation in MT, ST, MST_{ratio} and MST_{diff} between the three microhabitats, i.e. crevice (C), flat rock (FR) and under rock (UR) on the rock platform in autumn (Au) and summer (Su) in total (all), and specifically at the low and high shore levels (LSL and HSL, respectively). Results of the tests are indicated in the last column

NS, non-significant.

gated individuals. At high shore level, MT, ST, MST_{ratio} and MST_{diff} were significantly greater for solitary individuals. At low shore level, MT, ST, MST_{ratio} and MST_{diff} did not significantly differ between aggregated than solitary individuals.

Rock platform

All results are summarized in Table 4. In autumn, aggregated individuals exhibited significantly cooler MT and occupied significantly cooler substrata than solitary individuals. MST_{ratio} and MST_{diff} were significantly greater for solitary than aggregated individuals. At high shore level, mantles of aggregated snails were significantly cooler than those of solitary snails. No significant differences in ST, MST_{ratio} and MST_{diff} were observed between aggregated and solitary individuals. At low shore level, all individuals were solitary. In summer, no significant differences in MT, ST, MST_{ratio} and MST_{diff} were found between aggregated

Table 4. Mann–WhitneyU-testtoinvestigate the variation in MT, ST, MST_{ratio} and MST_{diff} between aggregated and solitaryindividuals at both seasons and in bothhabitats, in total (all), and specifically at thelow and high shore levels (LSL and HSL,respectively). All individuals were solitary atthe low shore level on the rock platform inautumn. Results of the tests are indicated inthe last column

	Boulders			Rock platform			
	Ζ	Р		Ζ	Р		
Au							
All	MT	-0.728	0.466	NS	-4.052	0.001	A < S
	ST	-1.392	0.164		-3.781	0.001	
	MST _{ratio}	-1.550	0.121		-2.969	0.003	
	MST _{diff}	-1.507	0.132		-3.211	0.001	
HSL	MT	-1.019	0.308	NS	-2.068	0.039	A < S
	ST	-1.161	0.246		-1.569	0.117	NS
	MST _{ratio}	-0.659	0.510		-1.205	0.228	
	MST _{diff}	-0.659	0.510		1.331	0.183	
LSL	MT	-2.654	0.008	A > S			
	ST	-2.700	0.007				
	MST _{ratio}	0.572	0.567	NS			
	MST _{diff}	-0.572	0.567				
Su	um						
All	MT	-4.533	0.001	A < S	-0.056	0.955	NS
	ST	2.889	0.004		-0.702	0.483	
	MST _{ratio}	-4.290	0.001		-1.565	0.118	
	MST _{diff}	-4.553	0.001		-1.468	0.142	
HSL	MT	-4.319	0.001	A < S	-0.452	0.651	NS
	ST	-3.656	0.001		-1.684	0.092	
	MST _{ratio}	-3.638	0.001		-1.937	0.053	
	MST _{diff}	-4.025	0.001		-1.679	0.093	
LSL	MT	0	1	NS	0.225	0.822	NS
	ST	-0.426	0.670		-0.644	0.520	
	MST _{ratio}	-0.426	0.670		-0.435	0.664	
	MST _{diff}	-0.213	0.831		0.306	0.760	

NS, non-significant.

and solitary individuals. Similar results were found at both shore levels.

Discussion

SUBSTRATUM TEMPERATURE AS A PRIMARY DETERMINANT OF NERITA ATRAMENTOSA MANTLE TEMPERATURE

Substratum temperature appears to be the primary factor that determines N. atramentosa body temperature as demonstrated in others organisms that attach the substratum (e.g. barnacles, snails; Bertness 1989; Chapperon & Seuront 2011a). N. atramentosa mantle temperature was significantly and positively correlated with that of the surrounding substratum at each season and in both habitats. This temperature correlation may result from the high thermal conductance between mantle and substratum in organisms that exhibit a direct foot contact to the substratum (Wethey 2002). This also emphasizes the need to integrate in climatechange studies organismal adaptations to heat sources such as substratum that contribute more importantly to the determinism of body temperature patterns than air or water temperatures (Marshall, McQuaid & Williams 2010; Fig. 3c,d). These adaptations seem critical as they are likely to increase the thermal tolerance of organisms in the warming climate (Chapperon & Seuront 2011a; Marshall, McQuaid & Williams 2010).

Nerita atramentosa mantle temperature did not perfectly match that of the surrounding substratum (as expressed by MST_{ratio} and MST_{diff} ; see Table 1), as previously observed in others mollusc species (Williams & Morritt 1995). This deviation between snail mantle and substratum temperatures likely resulted from the interaction between a range of abiotic factors such as air temperature (Helmuth 1998) and solar exposure (Schneider & Helmuth 2007) and biotic factors (e.g. body size, Helmuth 1998).

MOSAICS OF SUBSTRATUM AND BODY TEMPERATURE PATTERNS AT DIFFERENT SPATIAL SCALES

Nerita atramentosa experienced a heterogeneous thermal stress conveyed by substratum temperature that was highly variable between two habitats of different topographic complexity (a rock platform and a boulder field), especially in autumn (i.e. 4·18 °C of mean temperature difference) and reached extreme temperatures in summer (e.g. up to 47·93 °C). The variability in thermal properties between the two habitats could be related to the difference in the topographic complexity of the substratum to which an individual is attached (Bertness 1989). For instance, the lower substratum temperatures observed on the boulder field in autumn can be related to the potential greater buffering effect of large boulders to extreme temperatures than cobbles, present on the rock platform (Bertness 1989). Besides the environmental temperature variability between habitats, *N. atramentosa*

also faced a thermal stress that was variable within a habitat, i.e. at the two different shore levels.

The observed differences in thermal stress between shore heights did not always follow the intuitive pattern that high shore is the most stressful intertidal location owing to prolonged emersion and the related high mortality rate (Bertness et al. 1999). The seasonal variability in thermal stress observed on the rock platform between shore levels may be explained by the intensity of solar radiations received by organisms and the substratum (i.e. more intense in summer), the duration of sun exposure related to the emersion time (i.e. prolonged immersion at low shore level) and the water temperature during preceding high tide (Wethey 2002). On the boulder field, the temperature deviation between snails and substrata between shore levels may be related to differences in the physiological adaptations of individuals to thermal stress, i.e. high shore snails have likely developed greater physiological adaptations than low shore individuals as they inhabit a more thermally stressful environment (McMahon 1990; Somero 2002). This last hypothesis was however far beyond the scope of this study and thus requires further investigations.

Substratum temperatures were highly variable at the niche level. For instance, the maximum substratum temperature range observed on the boulder field at high shore level in summer (i.e. 28.54 °C) is consistent with the existence of mosaic patterns of thermal properties at the niche level in intertidal areas (Helmuth *et al.* 2006). Similarly, thermal microhabitat mosaics have been observed in terrestrial habitats such as mountain terrains of complex topography (Scherrer & Körner 2010). In addition, substratum temperature difference at the niche level was far greater than that observed between the two habitats (i.e. 4.18 °C in autumn and 0.44 °C in summer). This is consistent with recent studies suggesting that microhabitat variations in thermal properties may surpass large-scale variations in both marine and terrestrial environments (Jost & Helmuth 2007; Scherrer & Körner 2010).

VARIABILITY IN THERMOREGULATORY BEHAVIOUR: A GAP IN CLIMATE CHANGE STUDIES

Motile ectotherms such as reptiles, insects and invertebrates are not passively subject to environmental conditions (Kearney & Porter 2009). Indeed, they can exploit the environment thermal heterogeneity to seek favourable microclimatic conditions in order to avert low or high environmental temperatures (Kearney, Shine & Porter 2009). For instance, lacertid lizards and wood turtles move back and forth between sunlit and sun-shade patches to bask or avoid the sun (e.g. Díaz & Cabezas- Díaz 2004; Dubois et al. 2009). In the intertidal, microhabitats such as crevices are commonly assumed to provide shelter from thermal and desiccation stresses (Jackson 2010). This study, however, stresses the space-time variability (i.e. season, habitat and shore height) in the potential role (e.g. thermal haven) played by different microhabitats on body temperature patterns. For instance, in autumn in both habitats, crevices were the cooler microhabitats, hence the most efficient in reducing the temperature deviation between individuals and substrata. On the other hand, in summer in both habitats, crevices (and flat rocks on the rock platform) constituted the most thermally stressful microhabitat. This result highlights that microhabitats usually considered as shelters (i.e. crevices) in the literature do not always follow this intuitive pattern but rather vary from it in both space and time.

On the rock platform in summer, the higher frequency of individuals and lower MT, ST, MST_{ratio} and MST_{diff} values observed under rocks suggest that individuals actively selected this microhabitat. The bottoms of rocks likely created a local microclimate and thermally stable conditions that protected individuals from summer thermal conditions as shown for the limpet *Cellana tramoserica* (Sinclair, Thompson & Seebacher 2006). Similarly, the limpet *Cellana grata* took refuge in the cooler microhabitats available on the rocky shore (e.g. vertical surfaces non-exposed to full heat of the sun, Williams & Morritt 1995). This result demonstrates that *N. atramentosa* was able to behaviourally thermoregulate through the selection of thermally advantageous microhabitats (i.e. under rocks) available within the mosaics of substratum temperatures.

On the other hand, microhabitat occupation did not play a role in N. atramentosa thermoregulation on the boulder field in summer. Individuals occupied more frequently crevices that were thermally more stressful than flat rocks. The high frequency of crevice occupation may thus result from the potential benefits of this microhabitat in terms of desiccation (Jones & Boulding 1999) or feeding (Underwood & Murphy 2008). In contrast to the rock platform, aggregated individuals at the high shore level maintained cooler mantle temperatures and smaller temperature deviations with the substratum than solitary individuals. Aggregation in N. atramentosa may hence be considered as a thermoregulatory behaviour. Aggregation behaviour has previously been demonstrated to be variable in space and time (Chapman 1995). N. atramentosa aggregates found at other time or location could therefore be related to the diverse benefits of grouping evocated in the literature, such as reduction of predation risk (Coleman 2010) and resource exploitation (Lauzon-Guay & Scheibling 2009). Aggregation may also result from conspecific trail following behaviour (Chapperon & Seuront 2011a) or may be simply caused by the tendency of N. atramentosa to group in depressions, as shown in other gastropod species (Stafford & Davies 2004).

Conclusion

Substratum temperature appeared to be the main determinant of *N. atramentosa* mantle temperature. Variables such as substratum heat (at least for species with large areas of contact with the substratum) and solar irradiance critically need to be integrated in climate-change models to improve our predictions of future body temperature patterns. The present study demonstrated space-time variability in substratum and snail thermal properties. Mosaics of substratum temperatures at the niche level were characterized by a range of temperatures greater than that observed between habitats separated by 250 m. *N. atramentosa* has developed a thermoregulatory behaviour specific to each habitat. The behavioural flexibility in *N. atramentosa* (Chapperon & Seuront 2011b, this study) may be particularly advantageous in the warming climate and may increase the survival of organisms locally. In particular, the behavioural ability to explore environment thermal heterogeneity implies that individuals are likely to find a refuge under new environmental conditions. The behaviour of ectotherms challenges the predicted shifts in species distribution patterns and hence critically needs to be integrated in climatechange models.

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