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The effect of acclimation temperature on thermal activity thresholds in polar terrestrial invertebrates



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ABSTRACT

In the Maritime Antarctic and High Arctic, soil microhabitat temperatures throughout the year typically range between -10 and $+5$ °C. However, on occasion, they can exceed 20 °C, and these instances are likely to increase and intensify as a result of climate warming. Remaining active under both cool and warm conditions is therefore important for polar terrestrial invertebrates if they are to forage, reproduce and maximise their fitness. In the current study, lower and upper thermal activity thresholds were investigated in the polar Collembola, *Megaphorura arctica* and *Cryptopygus antarcticus*, and the mite, *Alaskozetes antarcticus*. Specifically, the effect of acclimation on these traits was explored. Sub-zero activity was exhibited in all three species, at temperatures as low as -4.6 °C in *A. antarcticus*. At high temperatures, all three species had capacity for activity above 30 °C and were most active at 25 °C. This indicates a comparable spread of temperatures across which activity can occur to that seen in temperate and tropical species, but with the activity window shifted towards lower temperatures. In all three species following one month acclimation at -2 °C, chill coma (=the temperature at which movement and activity cease) and the critical thermal minimum (=low temperature at which coordination is no longer shown) occurred at lower temperatures than for individuals maintained at $+4$ °C (except for the CTmin of *M. arctica*). Individuals acclimated at $+9$ °C conversely showed little change in their chill coma or CTmin. A similar trend was demonstrated for the heat coma and critical thermal maximum (CTmax) of all species. Following one month at -2 °C, the heat coma and CTmax were reduced as compared with $+4$ °C reared individuals, whereas the heat coma and CTmax of individuals acclimated at $+9$ °C showed little adjustment. The data obtained suggest these invertebrates are able to take maximum advantage of the short growing season and have some capacity, in spite of limited plasticity at high temperatures, to cope with climate change.

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1. Introduction

As poikilothermic ectotherms, invertebrates have limited means of regulating their own body temperature and are instead dependent on the thermal conditions of their environment (Speight et al., 2008). It is widely acknowledged therefore that the spatial and temporal distribution and abundance of invertebrates are partly determined by the range of temperatures they can tolerate and by the range of temperatures at which they perform optimally (Gaston, 2009; Terblanche et al., 2011). Investigations into the thermal tolerance limits of invertebrates are accordingly necessary to fully understand the ecology of a species or population and to infer the impact of climate change (e.g. Deutsch et al., 2008; Everatt et al., 2013; Somero, 2005). A common limitation of many current thermal biology studies, however, is

their emphasis on organismal survival. While survival clearly underpins the fitness of a species, there are also a number of other attributes which are greatly affected by temperature (Bale, 2002). These attributes, termed sub-lethal characteristics, include courtship, reproduction, foraging/feeding and predator avoidance (Kelty and Lee, 1999; Korenko et al., 2010). When these attributes can occur is governed by the upper and lower activity thresholds of the organism, and this thermal activity 'window' demonstrates phenotypic plasticity depending on the geographic location and the thermal/physiological history of the organism being studied (Addo-Bediako et al., 2000; Bale and Hayward, 2010). Because thermal activity thresholds are affected by less extreme temperatures, more regularly encountered than those which cause mortality, the extent to which sub-lethal characteristics are affected could be of more importance than the ability to survive temperature extremes *per se*.

The limits of movement under low temperatures have been a source of fascination since the late 19th Century. Rossbach

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(1872) observed the frequency of contractions of the contractile vesicle of three protist species and noticed that, at some low temperature, contractions ceased. He termed the absence of movement 'chill coma'. By 1939, the terminology relating to chill coma encompassed four potential states; chill coma¹ – absence of activity and movement, chill coma² – final peak of activity and movement, chill coma³ – loss of coordination, and chill coma⁴ – absence of spontaneous movement, and these terms have remained in use to this day (Hazell and Bale, 2011). Within this paper, the first definition will be used, i.e. the absence of activity and movement. Cowles and Bogert (1944) applied a new term to describe chill coma³ or the loss of coordination. This term was the 'Critical Thermal minimum' (CTmin) and will be used here to define the complete loss of coordination (inability to walk or move forward). The upper thermal thresholds of activity are analogous to those of low temperature and include heat coma and the Critical Thermal maximum (CTmax) (Hazell et al., 2008).

The Antarctic and Arctic are characterised by long, cold winters and brief, cool summers (Avila-Jimenez et al., 2010; Block et al., 2009). During the winter, air temperatures regularly fall below -10°C , and to lower than -40°C , in regions of the High Arctic and maritime and continental Antarctic (Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998; Walton, 1984). Buffered microhabitat temperatures in the soil or underneath the snow are likewise sub-zero during winter, though generally these temperatures do not fall much lower than -10°C (Coulson et al., 1993; Davey et al., 1992; Rinehart et al., 2006; Strathdee and Bale, 1998). Water is also transformed into ice in winter and is inaccessible to living organisms (Block et al., 2009). Activity is virtually impossible under these conditions. Accordingly, polar terrestrial invertebrates are dormant during this period and wait until the short, four to six month, summer period to resume activity (Convey, 1996). Summer air temperatures are still very cool, however, rarely rising above 0°C in the continental Antarctic, 5°C in the maritime Antarctic, and slightly higher in the Arctic (Davey et al., 1992; Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998). To benefit from these relatively favourable conditions, these invertebrates are capable of activity at low and even sub-zero temperatures. Hågvar (2010) has identified several invertebrate groups, including Collembola, Mecoptera, Diptera, Plecoptera and Araneae, which are active at or below 0°C on the snow of Fennoscandinavia. Block et al. (1990) and Sinclair et al. (2006) have also shown sub-zero activity in the Antarctic mites *Alaskozetes antarcticus* and *Nanorchestes antarcticus*, and the Collembola *Isotoma klovstadi*, *Cryptopygus cisantarcticus* and *Friezea grisea*, respectively.

Activity at high temperatures may also be important in the polar regions. Currently, buffered microhabitat temperatures range up to c. 20°C in the maritime Antarctic (Convey et al., 2009; Davey et al., 1992; Everatt et al., 2013), and to slightly higher temperatures in the Arctic (Coulson et al., 1993). Climate warming is also rapidly affecting the polar regions. Over the last 50 years, polar amplification of global climate trends has led to an average 2°C rise in air temperatures in parts of the Arctic and Antarctic, with even greater increases experienced in regions such as the northern and western Antarctic Peninsula, or when looked at on a seasonal basis (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009). This trend is set to continue, with general circulation models predicting particularly rapid warming at polar latitudes (Convey et al., 2009; Kattenberg et al., 1996). In addition, specific microhabitats, such as the surfaces of rocks and bryophyte clumps, can experience maximum temperatures approaching or exceeding 30°C (Convey, 1996; Everatt et al., 2013; Smith, 1988). Climate warming may increase the prevalence and duration of these exposures (Bokhorst et al., 2011; Nielsen and Wall, 2013). The ability of polar terrestrial invertebrates to remain active at high temperatures has only as yet been explored in three continental Antarctic Collembola, and all

show a remarkable capacity to remain active above 30°C (Sinclair et al., 2006).

The vast majority of polar terrestrial invertebrates express seasonal and shorter term thermal tolerance strategies to enable survival of shifts in temperature (Cannon and Block, 1988; Worland and Convey, 2001; Denlinger and Lee, 2010). However, the ability of polar terrestrial invertebrates to acclimate or acclimatise their thermal activity thresholds is less well known. Only two polar species, the aphid, *Myzus polaris*, and the collembolan, *Isotoma klovstadi*, have been demonstrated to have this ability, with a depression in the CTmin of individuals reared at, or taken from, lower temperatures (Hazell et al., 2010; Sinclair et al., 2006). In the current study, the lower and upper thermal activity thresholds are characterised in three common polar invertebrates widely regarded as 'model' species in their respective ecosystems: *Cryptopygus antarcticus* (Block et al., 2009; Tilbrook, 1967) and *Alaskozetes antarcticus* (Block and Convey, 1995; Burn, 1986) from the maritime Antarctic, and *Megaphorura arctica* (Fjellberg, 1994) from the High Arctic. In particular, how the thermal activity thresholds of these species respond to acclimation is explored.

2. Materials and methods

2.1. Invertebrate collection and storage conditions

Summer acclimatised individuals of *M. arctica* were collected from moss-covered slopes at Krykkefjellet and Stuphallet, near Ny-Ålesund, Spitsbergen, Svalbard ($78^{\circ}55'\text{N}$, $11^{\circ}56'\text{E}$) in August 2011. Summer acclimatised individuals of *C. antarcticus* and *A. antarcticus* were collected from moss and algae, and the underside of rocks, on Lagoon Island ($67^{\circ}35'\text{S}$, $68^{\circ}16'\text{W}$) and Léonie Island ($67^{\circ}36'\text{S}$, $68^{\circ}21'\text{W}$), near to Rothera Research Station, Adelaide Island (western Antarctic Peninsula, maritime Antarctic), between January and March 2012.

Samples of *C. antarcticus* and *A. antarcticus* were held at $+4^{\circ}\text{C}$ (24:0 L:D) in plastic bags or boxes containing substratum from the sites at which they were found whilst at Rothera Research Station and were used shortly after collection in experiments 2.3, 2.4 and 2.6. These individuals were designated as the "summer acclimatised" group. Following each respective field season, samples of *M. arctica*, and *C. antarcticus* and *A. antarcticus*, were transported to the University of Birmingham under refrigerated conditions and then held in plastic boxes containing substratum from the site of collection at $+4^{\circ}\text{C}$ (0:24 L:D). The duration of travel was ~ 2 d from the Arctic and ~ 2 months from the Antarctic. Each species was split into two additional acclimatory groups (-2 and $+9^{\circ}\text{C}$, 0: 24 L:D), representing early spring/late autumn microhabitat temperature and upper summer microhabitat temperature, respectively. Samples were held for at least two weeks at $+9^{\circ}\text{C}$, and for at least one month at -2°C prior to experimentation. The age of individuals used for experimentation was not uniform, as it was not possible to breed same age populations of the polar invertebrates in a laboratory setting. Difficulties in obtaining active individuals of *M. arctica* from acclimation at -2°C meant that individuals used in observations of locomotion (Section 2.5) were instead taken from a one month acclimation at 0°C .

2.2. Experimental conditions

Activity thresholds were assessed within an aluminium block arena. The temperature within the arena was regulated using an alcohol bath (Haake Phoenix II C50P, Thermo Electron Corporation), and activity monitored using a digital video camera with a macro lens (see Hazell et al., 2008). Thirty individuals were transferred into the arena in groups of 10 (initially set to $+4^{\circ}\text{C}$), and

were allowed to settle before video recording (Studio Capture DT, Studio86Designs, Lutterworth, UK) and the alcohol bath programme began. This procedure was performed for each species and for each acclimation treatment.

2.3. CTmin and chill coma

The temperature of the arena was reduced from +4 to -10°C at $0.2^{\circ}\text{C min}^{-1}$. Although a rate of change more closely in line with that experienced by the study species would have been preferable, a rate of $0.2^{\circ}\text{C min}^{-1}$ was chosen due to time constraints. The temperatures at which each individual last walked or moved forward (CTmin) and last moved its body, legs and/or antennae (chill coma) were subsequently recorded.

2.4. CTmax and heat coma

The temperature of the arena was raised from +4 to $+40^{\circ}\text{C}$ at $0.2^{\circ}\text{C min}^{-1}$. The temperatures at which each individual last walked or moved forward (CTmax) and last moved its body, legs and/or antennae (heat coma) were recorded.

2.5. Locomotion analysis

The arena and video equipment, as described in Section 2.2, was used to record the total distance travelled by individuals within a 5 min observation period at temperatures representative of either current spring/winter conditions, or current and future (predicted) summer microhabitat conditions. Spring/winter conditions: +4, 0, -4 and -8°C ; summer conditions: 10, 15, 20, 25, 30 and 35°C . Groups of 5 individuals were held in the arena for each recording, and cooled or warmed from 4°C at a rate of $0.2^{\circ}\text{C min}^{-1}$. For each acclimation group, the same 10 individuals were used for the +4, 0, -4 and -8°C exposures, and a second set of 10 individuals were used for 10, 15, 20, 25, 30 and 35°C . Thus, in the spring/winter temperature exposures, individuals were observed at $+4^{\circ}\text{C}$ for 5 min, then ramped to 0°C and observed for 5 min, then ramped to -4°C and so on. This technique more accurately reflects the gradual change in microhabitat conditions within terrestrial habitats than would be represented by direct transfer to each temperature. The distance travelled within each 5 min holding period was measured using Studio Measure (Studio86Designs, Lutterworth, UK). Inactive periods were not screened out so as to take account of both the propensity and ability of each species to move at each temperature.

2.6. Supercooling points (SCPs)

The supercooling points (SCP = freezing point of body fluids) of each acclimation group were determined by cooling 32 (24 in summer acclimatised group) individuals of each species from +4 to -30°C at $0.5^{\circ}\text{C min}^{-1}$. Each individual was placed in contact with a thermocouple (one individual per thermocouple, except in the "summer acclimatised" groups in which there were three individuals per thermocouple). This was housed within an Eppendorf tube, itself in a glass test tube plugged with sponge, inside an alcohol bath. The SCP was defined as the temperature at the onset of the freezing exotherm and was recorded using Picolog Recorder Software (Pico Technology Limited, UK) (cf. Hawes et al., 2006). The SCP is known to be the lower limit of survival, and equivalent to the lower lethal temperature, in the three species studied (Canon and Block, 1988; Worland et al., 1998).

2.7. Statistical analysis

The Kolmogorov–Smirnov test was used to determine whether activity threshold and SCP data were normally distributed. Normally distributed data were analysed using analysis of variance (ANOVA) and Tukey's multiple range test, and non-normally distributed data were analysed using the Kruskal–Wallis test.

3. Results

3.1. CTmin and chill coma

3.1.1. Interspecific comparisons

The point at which each species ($+4^{\circ}\text{C}$ acclimation) no longer showed coordination (CTmin) and lost mobility entirely (chill coma) both typically occurred at temperatures below 0°C (Fig. 1). The chill coma temperature was lower than -3.8°C in all species, and was lowest in *A. antarcticus* (-4.6°C). The CTmin occurred at similarly low temperatures in the two collembolan species (*C. antarcticus*: -3.5°C , *M. arctica*: -4°C), but was significantly higher in the mite (-0.6°C , $P < 0.05$ Kruskal–Wallis test).

3.1.2. Effect of acclimation

Following 1 month at -2°C , all species showed significantly lower chill coma values ($P < 0.05$ Kruskal–Wallis test [*C. antarcticus* and *M. arctica*], $P < 0.05$ Tukey's multiple range test [*A. antarcticus*]), and generally lower or equivalent CTmin values, than indi-

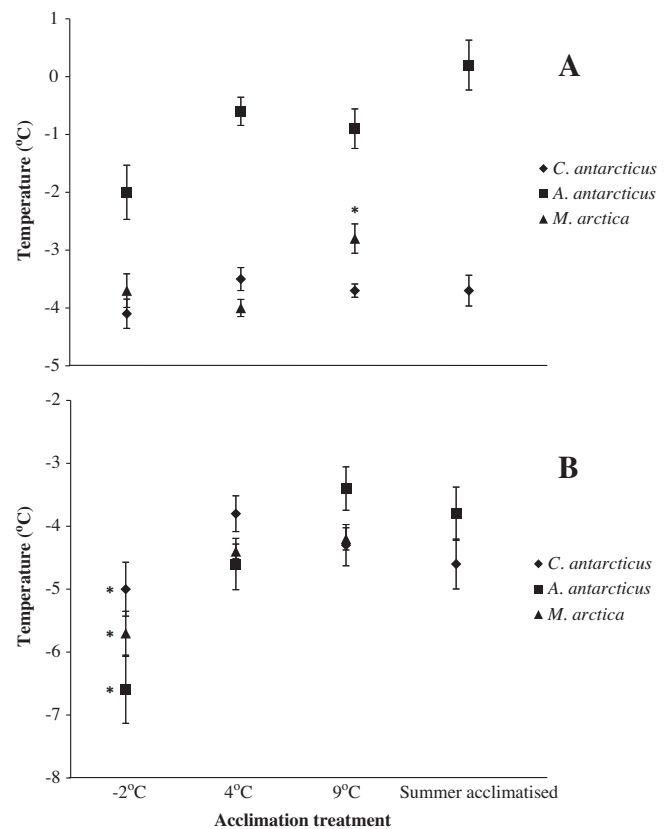


Fig. 1. CTmin (A) and chill coma (B) of *C. antarcticus*, *A. antarcticus* and *M. arctica*, following acclimation at 4, 9 and -2°C , and individuals acclimatised to the Antarctic summer (*C. antarcticus* and *A. antarcticus* only). Means \pm S.E.M. are presented for approximately 30 individuals. Asterisks indicate a treatment significantly different from 4°C acclimated individuals for each species at $P < 0.05$ (Kruskal–Wallis test; Tukey's multiple range test).

viduals maintained at +4 °C (Fig. 1). Individuals of *A. antarcticus* (−2 °C acclimation) also exhibited significantly lower CTmin and chill coma values in comparison with summer acclimatised individuals ($P < 0.05$ Tukey's multiple range test). There were no significant differences in the CTmin and chill coma values between species acclimated at +9 °C and those at +4 °C, except for *M. arctica* in which the CTmin was significantly higher in the +9 °C acclimated group ($P < 0.05$ Kruskal–Wallis test).

3.2. CTmax and heat coma

3.2.1. Interspecific comparisons

In all species maintained at +4 °C, both CTmax and heat coma temperatures were typically above 30 °C (Fig. 2). Both CTmax and heat coma values were significantly different between species and were progressively greater from *C. antarcticus* (30.1 and 31.8 °C), through *M. arctica* (31.7 and 34.6 °C), to *A. antarcticus* (34.1 and 36.9 °C) ($P < 0.05$ Tukey's multiple range test, variances not equal).

3.2.2. Effect of acclimation

A one month acclimation at −2 °C significantly reduced CTmax and heat coma temperatures compared to individuals maintained at +4 °C in all species (Fig. 2, $P < 0.05$ Kruskal–Wallis test). A two week acclimation at +9 °C also led to lower (or unchanged – *C. ant-*

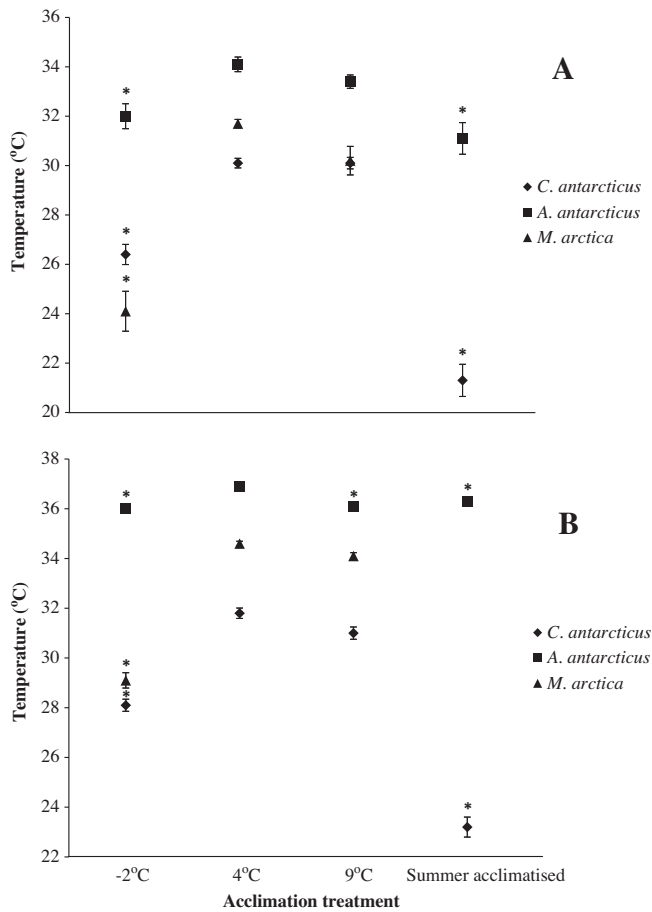


Fig. 2. CTmax (A) and heat coma (B) of *C. antarcticus*, *A. antarcticus* and *M. arctica*, following acclimation at 4, 9 and −2 °C, and individuals acclimatised to the Antarctic summer (*C. antarcticus* and *A. antarcticus* only). Means \pm S.E.M. are presented for approximately 30 individuals. Asterisks indicate a treatment significantly different from 4 °C acclimated individuals for each species at $P < 0.05$ (Kruskal–Wallis test).

arctica) CTmax and heat coma temperatures, though this was only significant for the heat coma temperature of *A. antarcticus* ($P < 0.05$ Kruskal–Wallis test). Summer acclimatised individuals of *C. antarcticus* exhibited significantly lower CTmax and heat coma temperatures than individuals acclimated at either −2 °C or +4 °C, while summer acclimatised individuals of *A. antarcticus* only showed significantly lower CTmax and heat coma temperatures than individuals maintained at +4 °C.

3.3. Locomotion analysis

3.3.1. Interspecific comparisons

Across all temperatures between −4 and 20 °C, both collembolan species were significantly more active and travelled a greater distance than the mite ($P < 0.05$ Kruskal–Wallis test, 4 °C acclimation, Fig. 3). In all species previously acclimated at +4 °C, movement increased with temperature up to 25 °C (except at 9 °C in *M. arctica*), before decreasing again at temperatures ≥ 30 °C.

3.3.2. Effect of acclimation

Following an acclimation period at −2 °C (0 °C for *M. arctica*), there was no significant difference in locomotion at temperatures

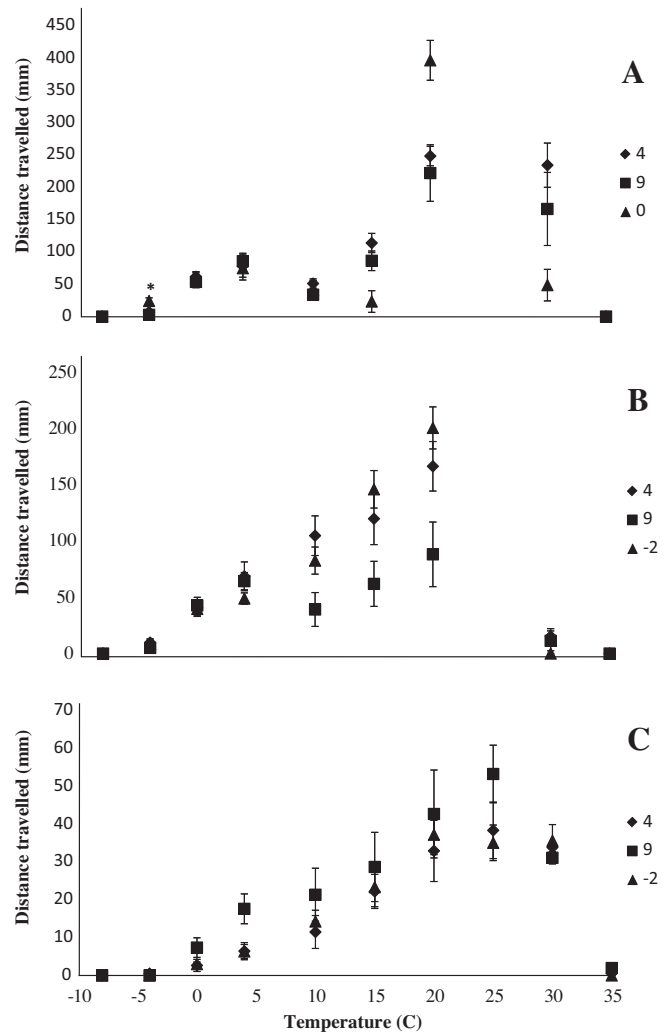


Fig. 3. Locomotion analysis (distance travelled in 5 min) of *M. arctica* (A), *C. antarcticus* (B) and *A. antarcticus* (C), following acclimation at 4, 9, and −2 °C (0 °C for *M. arctica*). Means \pm S.E.M. are presented for approximately 10 individuals. Asterisks indicate a treatment significantly different from 4 °C acclimated individuals for each species at $P < 0.05$ (Kruskal–Wallis test; Tukey's multiple range test). Movement speeds at 25 °C were not analysed for *M. arctica* and *C. antarcticus*.

≤ 0 °C, except for *M. arctica*, in which movement was significantly greater at -4 °C ($P < 0.05$ Tukey's multiple range test, variances not equal) (Fig. 3). At 15 and 20 °C, movement was most rapid in *C. antarcticus* acclimated at -2 °C, as compared with the two other acclimation groups. The movement of *M. arctica*, acclimated at 0 °C, was also more rapid at 20 °C. Individuals of both collembolan species given an acclimation period at $+9$ °C exhibited considerably slower movement at temperatures above $+4$ °C than individuals maintained at $+4$ °C. In contrast, movement was greater across all temperatures between 0 and 25 °C in $+9$ °C acclimated individuals of *A. antarcticus*.

3.4. SCPs

3.4.1. Interspecific comparisons

There were no significant differences in the SCPs of the three species when maintained at $+4$ °C (Table 1, $P < 0.05$ Kruskal–Wallis test). *Alaskozetes antarcticus* was the only species to show a bimodal distribution.

3.4.2. Effect of acclimation

In all three species, the SCPs of individuals acclimated at -2 °C for one month, and summer acclimated individuals of *C. antarcticus* and *A. antarcticus*, were significantly lower than those of individuals maintained at $+4$ °C ($P < 0.05$ Kruskal–Wallis test). Conversely, the SCP of individuals after a $+9$ °C acclimation period was not significantly different to those maintained at $+4$ °C ($P > 0.05$ Kruskal–Wallis test). Summer acclimated individuals of *C. antarcticus* also had significantly lower SCPs than individuals acclimated at -2 °C ($P < 0.05$ Kruskal–Wallis test).

4. Discussion

4.1. Activity at low temperatures

Temperate and tropical invertebrates, such as the peach-potato aphid, *Myzus persicae*, the predatory mirid, *Nesidiocoris tenuis*, and the brown planthopper, *Nilaparvata lugens*, lose the ability to coordinate movement (CTmin) at temperatures above 0 °C, and more usually above $+3$ °C (Chidwanyika and Terblanche, 2011; Clusella-Trullas et al., 2010; Hazell et al., 2010; Hughes et al., 2010; Nyamukondiwa and Terblanche, 2010; Piyaphongkul personal communication). These CTmin values are not compatible with polar summer microhabitat temperatures, which regularly fall below 0 °C and average less than $+3$ °C in the maritime and continental Antarctic, and only a little more in the High Arctic (Davey et al., 1992; Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998). It is not surprising, therefore, that polar terrestrial invertebrates have lower thermal thresholds than their temperate and tropical counterparts, and have been observed performing activity at temperatures as low as -13.3 °C (Sinclair et al., 2006), including attempts to fly at -4 °C (Hågvar, 2010). Other examples of sub-zero activity are found in high altitude environments and include Himalayan *Diamesa* sp., which has been observed walking at -16 °C (MacMillan and Sinclair, 2010). In the current study, the

CTmin and chill coma of the two Collembola, *M. arctica* and *C. antarcticus*, and the mite, *A. antarcticus*, were below -0.6 and -3.8 °C, respectively. Locomotion analysis also showed that the invertebrates walked in a coordinated manner at $+4$ and 0 °C, and that they were capable of movement at -4 °C, but at a reduced speed (Figs. 3–5).

In the two collembolan species, the CTmin of individuals maintained at $+4$ °C was low, averaging between -3.5 and -4 °C. Conversely, the CTmin of the mite only averaged -0.6 °C, even though its chill coma was similar to both Collembola (Fig. 1). Observation revealed that the mites tended to aggregate or stop moving early in the cooling regime and moved little thereafter. *Alaskozetes antarcticus* is well known to aggregate in the field, and has been observed aggregating in numbers of tens, hundreds and even many thousands of individuals (Richard et al., 1994; Strong, 1967; Tilbrook, 1973). Block and Convey (1995) and other authors suggest that, due to the reduced surface area to volume ratio of the aggregation, this behaviour may buffer the mite against low temperatures and reduce water loss. The reason that mites may aggregate so early on during the cooling regime at temperatures near to 0 °C, rather than attempting to select for more “optimal” thermal conditions, may be a consequence of their relatively restricted mobility. Unlike Collembola, which are more capable of moving rapidly to habitats in their preferred temperature range (Figs. 3–5), restricted mobility leaves non-acclimated mites susceptible to a sudden cold exposure. Hence, it may be better for mites to select sub-lethal low temperatures and acclimate. Hayward et al. (2003) have demonstrated such a preference for low temperatures in *A. antarcticus* using a thermal gradient. The high CTmin value of the mite may therefore be a product of “choice” rather than an inability to coordinate movement.

4.2. Activity at high temperatures

Deutsch et al. (2008) suggested that, with increasing distance away from the equator, the thermal sensitivity of terrestrial invertebrates to a temperature rise decreases. Many studies, including that of Piyaphongkul et al. (2012), have shown tropical insects to have upper lethal temperatures (ULTs) very close to the highest temperatures they experience in their natural habitat, while Everatt et al. (2013), Deere et al. (2006), Sinclair et al. (2006) and Slabber et al. (2007) have shown the converse in polar Collembola and mites. The current study also supports the suggestion of Deutsch et al. (2008), and shows the CTmax of three polar species to be above 30 °C, and even as high as 34.1 °C in *A. antarcticus* (Fig. 2). In addition, each species exhibited their fastest movement at 25 °C (data not shown for Collembola), a temperature rarely experienced in the High Arctic or maritime Antarctic habitats typical for these species. While some polar microhabitats may already briefly exceed 30 °C (Everatt et al., 2013; Smith, 1988), these instances are rare and of very restricted physical extent. Even if such extremes become more frequent as a result of climate warming, it is unlikely that an individual invertebrate would be present in such a location, and even if so, it could quickly move to a more suitable microhabitat. Based on predicted microhabitat temperature increases of around 5 °C over the next 50–100 years (Convey et al., 2009; Turn-

Table 1

SCP of *C. antarcticus*, *A. antarcticus* and *M. arctica*, following acclimation at 4, 9 and -2 °C, and individuals acclimated to the Antarctic summer (*C. antarcticus* and *A. antarcticus* only). Means \pm S.E.M. are presented for approximately 32 individuals (24 for summer acclimated individuals). Asterisks indicate a treatment significantly different from 4 °C acclimated individuals for each species at $P < 0.05$ (Kruskal–Wallis test).

Species	4 °C	9 °C	-2 °C	Summer acclimated
<i>C. antarcticus</i>	-6.31 ± 0.2	-7.71 ± 0.8	$-8.9 \pm 0.7^*$	$-14.9 \pm 1.4^*$
<i>A. antarcticus</i>	-7.42 ± 0.9	-7.8 ± 0.7	$-15.9 \pm 1.8^*$	$-11.9 \pm 1.6^*$
<i>M. arctica</i>	-6.13 ± 0.1	-5.9 ± 0.2	$-8.1 \pm 0.3^*$	

er et al., 2009), the heat tolerance of these polar invertebrates certainly suggests scope for them to endure future warming.

4.3. Thermal activity windows

While the polar terrestrial invertebrates of this study showed little sensitivity to a temperature rise, their thermal range of activity is similar to that of temperate and tropical species. The activity of *M. arctica* ranged from -4 (CTmin) to 31.7 °C (CTmax), a thermal activity window of 35.7 °C. Likewise, *C. antarcticus* and *A. antarcticus* showed activity windows of 33.6 °C and 34.7 °C, respectively. These windows of activity are comparable to the temperate aphid, *Myzus persicae*, in which the CTmin was between 4 and 9.4 °C, and the CTmax between 39.6 and 40.7 °C, but are shifted towards lower temperatures (Alford et al., 2012). Other temperate species such as the predatory mirid, *Nesidiocoris tenuis*, the mite, *Tetranychus urticae*, and moth, *Cydia pomonella*, and tropical species such as the seed harvester ant, *Messor capensis*, show somewhat broader thermal activity windows of around 40 °C or more (Chidwanyika and Terblanche, 2011; Clusella-Trullas et al., 2010; Hughes et al., 2010). Invertebrates native to locations slightly further north in the sub-Antarctic, such as the spiders, *Myro kerguelensis* and *Prienerigone vegans*, also show thermal activity windows above 40 °C (Jumbam et al., 2008).

4.4. The effect of low temperature acclimation on thermal activity thresholds

The role of acclimation on thermal activity thresholds has only been explored infrequently. Most studies have been carried out on the fruit fly, *Drosophila*, and have shown a clear relationship between the acclimation temperature and the CTmin (Hori and Kimura, 1998; Hoffman et al., 2005; Kelty and Lee, 2001; Mellanby, 1939; Rako and Hoffman, 2006). Gibert and Huey (2001) showed that the CTmin of several *Drosophila* species decreased by 1 °C for every 4 °C drop in development temperature. This result is in line with the Beneficial Acclimation Hypothesis (BAH), which suggests that the performance of individuals is improved at temperatures close to those which they have previously experienced (Leroi et al., 1994). Frazier et al. (2008) provided further evidence supporting the BAH in *D. melanogaster* by demonstrating greater flight performance at cool temperatures in individuals acclimated at 15 rather than 28 °C. More recent work in other invertebrates, including the cricket, *Acheta domesticus*, the moth, *C. pomonella*, and the spiders, *M. kerguelensis* and *P. vegans*, also support the BAH with respect to low temperature activity (Chidwanyika and Terblanche, 2011; Jumbam et al., 2008; Lachenicht et al., 2010). There are exceptions, however, such as in the ant, *M. capensis*, in which individuals acclimated at an intermediate temperature performed best under the coolest conditions tested, this instead supporting the Optimal Acclimation Hypothesis (OAH = individuals acclimated at an intermediate temperature will perform better at all temperatures) (Clusella-Trullas et al., 2010; Huey and Berrigan, 1996). The acclimatory ability of the three polar species examined here was in agreement with the former hypothesis, BAH. A period of one month at -2 °C lowered chill coma onset significantly in all three species, and lowered the CTmin in the two Antarctic invertebrates, compared with individuals maintained at $+4$ °C (Fig. 1). Further evidence of beneficial acclimation was seen for the CTmax and heat coma, with both showing a considerable downward shift following time at -2 °C, as well as following summer acclimatisation (averaging approximately $+1$ °C) in the two Antarctic species (Fig. 2). While these findings are consistent with the reports in *Drosophila* and other aforementioned species, they contrast with those of Young (1979), who reported that the chill coma temperature of *A. antarcticus* was unaffected by acclimation.

An ability to depress their lower thermal thresholds of movement and hence remain active at lower temperatures would be of great benefit to polar terrestrial invertebrates. Currently, polar summers can last for as little as 1–3 months of the year (Convey, 1996). By acclimatising their thresholds of activity to lower temperatures, polar terrestrial invertebrates would be better able to forage and reproduce during the spring and autumn, as well as during cooler periods in summer.

The maximisation of activity and adaptation to the low temperature environment was also seen in relation to the SCP. When the body fluids of an invertebrate are frozen, the invertebrate is no longer considered capable of movement and the SCP is seen as the absolute limit of mobility. In many temperate and tropical species, the lower lethal thresholds, and thus also the CTmin and chill coma, are well above the SCP (Bale, 2002). However, in the current study, prior to acclimation, the chill coma temperature of all three species, and the CTmin of the two Collembola, were within 2–3 °C of the SCP (Fig 1; Table 1). Likewise, the continental Antarctic collembolan, *Isotoma klovstadi*, was observed to be capable of walking at all temperatures down to its SCP, with an average chill coma onset temperature of -11.9 to -13.3 °C over the summer season (Sinclair et al., 2006). These organisms are consequently able to search for more preferable habitats as the temperature falls, and possibly perform beneficial activities, such as foraging, very near to their SCP.

4.5. The effect of high temperature acclimation on thermal activity thresholds

Climate warming has resulted in a significant rise in polar temperatures, and will undoubtedly lead to future increases (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009). An advantage may therefore be gained by being able to acclimate to higher temperatures. However, the species examined here showed no acclimation ability allowing an increase in their upper activity thresholds following a two week period at 9 °C, and even showed a decline in both their CTmax and heat coma (Fig. 2). Everatt et al. (2013) and Slabber et al. (2007) also found that acclimation to higher temperatures (9 and 15 °C, respectively) either resulted in no change in, or impaired, survival at temperatures above 30 °C in both Collembola and Acari. Further, a number of studies have shown little plasticity in upper thermal tolerance traits in non-polar species, including in the cricket, *A. domesticus*, the fruit fly, *D. melanogaster*, dung beetles, and the tsetse fly, *Glossina pallidipes* (Gaston and Chown, 1999; Goto et al., 2000; Hoffman et al., 2005; Lachenicht et al., 2010; Terblanche et al., 2011). There is now a general consensus that thermal tolerance shows less phenotypic plasticity at higher temperatures than at lower temperatures in invertebrates, and that this may be due to each involving a distinct suite of physiological and molecular mechanisms (Bowler and Terblanche, 2008). Even though the polar species of this study show a limited ability to acclimate their upper thermal thresholds to higher temperatures, the upper thermal tolerance they already possess (see Section 4.2.) gives these invertebrates sufficient capacity to cope with future climate warming.

Intriguingly, a subtle difference may exist between the locomotion speeds of the mite and the Collembola. In *A. antarcticus*, movement was greater between 0 and 25 °C in individuals which had received a 2 week acclimation at 9 °C, as compared to individuals reared at 4 °C. Whereas in the Collembola, movement was impaired between 0 and 20 °C by the same acclimation treatment. *Alaskozetes antarcticus* is already known to have a greater capacity to survive higher temperatures than the Collembola (Everatt et al., 2013). It is therefore plausible that *A. antarcticus* is able to benefit physiologically from a period at 9 °C, while the Collembola may find the temperature damaging.

It should be noted that, while no acclimation response was exhibited for the CT_{max} and heat coma following two weeks at 9 °C, acclimation did occur in both –2 and +4 °C reared individuals, with all species showing significantly higher CT_{max} and heat coma temperatures under +4 vs –2 °C treatments (Fig. 2). The ability to acclimate in response to these two temperature regimes perhaps illustrates the process of natural acclimatisation between winter and summer conditions. However, as the upper thresholds of activity in –2 °C acclimated individuals are already above the highest summer temperatures they experience, the observed change may simply reflect the acclimation of their lower activity thresholds, which are lowered following one month at –2 °C (Fig. 1). This further supports the consensus highlighted above, that greater plasticity is shown at lower temperatures but not at higher temperatures. Physiological changes that improve activity at low temperatures, such as increased membrane fluidity and subsequent improvement in the function of neurotransmitters, ATPases and ion channels (MacMillan and Sinclair, 2010), are likely to be to the detriment of higher temperature activity.

5. Conclusion

The current study has expanded on previous studies to show that the polar mite, *A. antarcticus*, and Collembola, *C. antarcticus* and *M. arctica*, are capable of sub-zero activity. These invertebrates also show plasticity in their CT_{min} and chill coma temperature following acclimation at lower temperatures, as well as being capable of activity at temperatures close to their SCPs. By depressing their lower thermal activity thresholds as temperature falls, these invertebrates are able to maximise the short growing season. At higher temperatures, these species are able to remain active above 30 °C, a temperature far higher than is experienced in their Antarctic or Arctic habitats. This indicates polar terrestrial invertebrates have a thermal activity window comparable to that of temperate and tropical insects and, in spite of their limited physiological plasticity at higher temperatures, have thermal scope to tolerate future rises in temperature under climate change.

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