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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, the chill coma (= the temperature at which movement and activity cease) and 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 +10°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 +10°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.

Key words: Climate warming; supercooling point; Collembola; mite, chill coma; heat coma; CTmax; CTmin

1. Introduction

36 As poikilothermic ectotherms, invertebrates have limited means of regulating their own body temperature
37 and are instead dependent on the thermal conditions of their environment (Speight et al., 2008). It is
38 widely acknowledged therefore that the spatial and temporal distribution and abundance of invertebrates
39 are partly determined by the range of temperatures they can tolerate and by the range of temperatures at
40 which they perform optimally (Gaston, 2009; Terblanche et al., 2011). Investigations into the thermal
41 tolerance limits of invertebrates are accordingly necessary to fully understand the ecology of a species or
42 population and to infer the impact of climate change (e.g. Deutsch et al., 2008; Everatt et al., 2013;
43 Somero, 2005). A common limitation of many current thermal biology studies, however, is their emphasis
44 on organismal survival. While survival clearly underpins the fitness of a species, there are also a number
45 of other attributes which are greatly affected by temperature (Bale, 2002). These attributes, termed sub-
46 lethal characteristics, include courtship, reproduction, foraging/feeding and predator avoidance (Kelty and
47 Lee, 1999; Korenko et al., 2010). When these attributes can occur is governed by the upper and lower
48 activity thresholds of the organism, and this thermal activity 'window' demonstrates phenotypic plasticity
49 depending on the geographic location and the thermal/physiological history of the organism being studied
50 (Addo-Bediako et al., 2000; Bale and Hayward, 2010). Because thermal activity thresholds are affected
51 by less extreme temperatures, more regularly encountered than those which cause mortality, the extent to
52 which sub-lethal characteristics are affected could be of more importance than the ability to survive
53 temperature extremes *per se*.

54 The limits of movement under low temperatures have been a source of fascination since the late 19th
55 Century. Rossbach (1872) observed the frequency of contractions of the contractile vesicle of three protist
56 species and noticed that, at some low temperature, contractions ceased. He termed the absence of
57 movement 'chill coma'. By 1939, the terminology relating to chill coma encompassed four potential
58 states; chill coma¹ – absence of activity and movement, chill coma² – final peak of activity and
59 movement, chill coma³ – loss of coordination, and chill coma⁴ – absence of spontaneous movement, and
60 these terms have remained in use to this day (Hazell and Bale, 2011). Within this paper, the first
61 definition will be used, i.e. the absence of activity and movement. Cowles and Bogert (1944) applied a
62 new term to describe chill coma³ or the loss of coordination. This term was the 'Critical Thermal
63 minimum' (CTmin) and will be used here to define the complete loss of coordination (inability to walk or
64 move forward). The upper thermal thresholds of activity are analogous to those of low temperature and
65 include heat coma and the Critical Thermal maximum (CTmax) (Hazell et al., 2008).

66 The Antarctic and Arctic are characterised by long, cold winters and brief, cool summers (Avila-Jimenez
67 et al., 2010; Block et al., 2009). During the winter, air temperatures regularly fall below -10°C, and to
68 lower than -40°C, in regions of the High Arctic and maritime and continental Antarctic (Block et al.,
69 2009; Coulson et al., 1993; Strathdee and Bale, 1998; Walton, 1984). Buffered microhabitat temperatures
70 in the soil or underneath the snow are likewise sub-zero during winter, though generally these
71 temperatures do not fall much lower than -10°C (Coulson et al., 1993; Davey et al., 1992; Rinehart et al.,
72 2006; Strathdee and Bale, 1998). Water is also transformed into ice in winter and is inaccessible to living
73 organisms (Block et al., 2009). Activity is virtually impossible under these conditions. Accordingly, polar
74 terrestrial invertebrates are dormant during this period and wait until the short, four to six month, summer
75 period to resume activity (Convey, 1996). Summer air temperatures are still very cool, however, rarely
76 rising above 0°C in the continental Antarctic, 5°C in the maritime Antarctic, and slightly higher in the
77 Arctic (Davey et al., 1992; Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998). To benefit

78 from these relatively favourable conditions, these invertebrates are capable of activity at low and even
79 sub-zero temperatures. Hågvar (2010) has identified several invertebrate groups, including Collembola,
80 Mecoptera, Diptera, Plecoptera and Araneae, which are active at or below 0°C on the snow of
81 Fennoscandinavia. Block et al. (1990) and Sinclair et al. (2006) have also shown sub-zero activity in the
82 Antarctic mites *Alaskozetes antarcticus* and *Nanorchestes antarcticus*, and the Collembola *Isotoma*
83 *klovstadi*, *Cryptopygus cisantarcticus* and *Friesea grisea*, respectively.

84 Activity at high temperatures may also be important in the polar regions. Currently, buffered microhabitat
85 temperatures range up to c. 20°C in the maritime Antarctic (Convey et al., 2009; Davey et al., 1992;
86 Everatt et al., 2013), and to slightly higher temperatures in the Arctic (Coulson et al., 1993). Climate
87 warming is also rapidly affecting the polar regions. Over the last 50 years, polar amplification of global
88 climate trends has led to an average 2°C rise in air temperatures in parts of the Arctic and Antarctic, with
89 even greater increases experienced in regions such as the northern and western Antarctic Peninsula, or
90 when looked at on a seasonal basis (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009). This
91 trend is set to continue, with general circulation models predicting particularly rapid warming at polar
92 latitudes (Convey et al., 2009; Kattenberg et al., 1996). In addition, specific microhabitats, such as the
93 surfaces of rocks and bryophyte clumps, can experience maximum temperatures approaching or
94 exceeding 30°C (Convey, 1996; Everatt et al., 2013; Smith, 1988). Climate warming may increase the
95 prevalence and duration of these exposures (Bokhorst et al., 2011; Nielsen and Wall, 2013). The ability of
96 polar terrestrial invertebrates to remain active at high temperatures has only as yet been explored in three
97 continental Antarctic Collembola, and all show a remarkable capacity to remain active above 30°C
98 (Sinclair et al., 2006).

99 The vast majority of polar terrestrial invertebrates express seasonal and shorter term thermal tolerance
100 strategies to enable survival of shifts in temperature (Cannon and Block, 1988; Worland and Convey,
101 2001; Denlinger and Lee, 2010). However, the ability of polar terrestrial invertebrates to acclimate or
102 acclimatise their thermal activity thresholds is less well known. Only two polar species, the aphid, *Myzus*
103 *polaris*, and the collembolan, *Isotoma klovstadi*, have been demonstrated to have this ability, with a
104 depression in the CTmin of individuals reared at, or taken from, lower temperatures (Hazell et al., 2010;
105 Sinclair et al., 2006). In the current study, the lower and upper thermal activity thresholds are
106 characterised in three common polar invertebrates widely regarded as ‘model’ species in their respective
107 ecosystems: *Cryptopygus antarcticus* (Block et al., 2009; Tilbrook, 1967) and *Alaskozetes antarcticus*
108 (Block and Convey, 1995; Burn, 1986) from the maritime Antarctic, and *Megaphorura arctica* (Fjellberg,
109 1994) from the High Arctic. In particular, how the thermal activity thresholds of these species respond to
110 acclimation is explored.

111 **2. Materials and methods**

112 *2.1. Invertebrate collection and storage conditions*

113 Summer acclimatised individuals of *M. arctica* were collected from moss-covered slopes at Krykkefjellet
114 and Stuphallet, near Ny-Ålesund, Spitsbergen, Svalbard (78°55’N, 11°56’E) in August 2011. Summer
115 acclimatised individuals of *C. antarcticus* and *A. antarcticus* were collected from moss and algae, and the
116 underside of rocks, on Lagoon Island (67°35’S, 68°16’W) and Léonie Island (67°36’S, 68°21’W), near to

117 Rothera Research Station, Adelaide Island (western Antarctic Peninsula, maritime Antarctic), between
118 January and March 2012.

119 Samples of *C. antarcticus* and *A. antarcticus* were held at +4°C (24:0 L:D) in plastic bags or boxes
120 containing substratum from the sites at which they were found whilst at Rothera Research Station and
121 were used shortly after collection in experiments 2.3, 2.4 and 2.6. These individuals were designated as
122 the “summer acclimatised” group. Following each respective field season, samples of *M. arctica*, and *C.*
123 *antarcticus* and *A. antarcticus*, were transported to the University of Birmingham under refrigerated
124 conditions and then held in plastic boxes containing substratum from the site of collection at +4°C (0:24
125 L:D). The duration of travel was ~ 2 d from the Arctic and ~ 2 months from the Antarctic. Each species
126 was split into two additional acclimatory groups (-2 and +10°C, 0: 24 L:D), representing early spring/late
127 autumn microhabitat temperature and upper summer microhabitat temperature, respectively. Samples
128 were held for at least two weeks at +10°C, and for at least one month at -2°C prior to experimentation.
129 The age of individuals used for experimentation was not uniform, as it was not possible to breed same age
130 populations of the polar invertebrates in a laboratory setting. Difficulties in obtaining active individuals of
131 *M. arctica* from acclimation at -2°C meant that individuals used in observations of locomotion (section
132 2.5) were instead taken from a one month acclimation at 0°C.

133 2.2. *Experimental conditions*

134 Activity thresholds were assessed within an aluminium block arena. The temperature within the arena was
135 regulated using an alcohol bath (Haake Phoenix II C50P, Thermo Electron Corporation), and activity
136 monitored using a digital video camera with a macro lens (see Hazell et al., 2008). Thirty individuals
137 were transferred into the arena in groups of 10 (initially set to +4°C), and were allowed to settle before
138 video recording (Studio Capture DT, Studio86Designs, Lutterworth, UK) and the alcohol bath
139 programme began. This procedure was performed for each species and for each acclimation treatment.

140 2.3. *CTmin and chill coma*

141 The temperature of the arena was reduced from +4 to -10°C at 0.2°C min⁻¹. Although a rate of change
142 more closely in line with that experienced by the study species would have been preferable, a rate of
143 0.2°C min⁻¹ was chosen due to time constraints. The temperatures at which each individual last walked
144 (CTmin) and last moved its body, legs and/or antennae (chill coma) were subsequently recorded.

145 2.4. *CTmax and heat coma*

146 The temperature of the arena was raised from +4 to +40°C at 0.2°C min⁻¹. The temperatures at which each
147 individual last walked (CTmax) and last moved its body, legs and/or antennae (heat coma) were recorded.

148 2.5. *Locomotion analysis*

149 The arena and video equipment, as described in 2.2, was used to record the total distance travelled by
150 individuals within a 5 min observation period at temperatures representative of either current
151 spring/winter conditions, or current and future (predicted) summer microhabitat conditions.
152 Spring/winter conditions: +4, 0, -4 and -8°C; summer conditions: 10, 15, 20, 25, 30 and 35°C. Groups of
153 5 individuals were held in the arena for each recording, and cooled or warmed from 4°C at a rate of 0.2°C

154 min⁻¹. For each acclimation group, the same 10 individuals were used for the +4, 0, -4 and -8°C
155 exposures, and a second set of 10 individuals were used for 10, 15, 20, 25, 30 and 35°C. Thus, in the
156 spring/winter temperature exposures, individuals were observed at +4°C for 5 minutes, then ramped to
157 0°C and observed for 5 minutes, then ramped to -4°C and so on. This technique more accurately reflects
158 the gradual change in microhabitat conditions within terrestrial habitats than would be represented by
159 direct transfer to each temperature. The distance travelled within each 5 min holding period was measured
160 using Studio Measure (Studio86Designs, Lutterworth, UK). Inactive periods were not screened out so as
161 to take account of both the propensity and ability of each species to move at each temperature.

162 2.6. Supercooling points (SCPs)

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

172 2.7. Statistical analysis

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

177 3. Results

178 3.1. CTmin and chill coma

179 3.1.1. Interspecific comparisons

180 The point at which each species (+4°C acclimation) no longer showed coordination (CTmin) and lost
181 mobility entirely (chill coma) both typically occurred at temperatures below 0°C (Fig. 1). The chill coma
182 temperature was lower than -3.8°C in all species, and was lowest in *A. antarcticus* (-4.6°C). The CTmin
183 occurred at similarly low temperatures in the two collembolan species (*C. antarcticus*: -3.5°C, *M. arctica*:
184 -4°C), but was significantly higher in the mite (-0.6°C, $P < 0.05$ Kruskal-Wallis test).

185 3.1.2. Effect of acclimation

186 Following 1 month at -2°C, all species showed significantly lower chill coma values ($P < 0.05$ Kruskal-
187 Wallis test [*C. antarcticus* and *M. arctica*], $P < 0.05$ Tukey’s multiple range test [*A. antarcticus*]), and
188 generally lower or equivalent CTmin values, than individuals maintained at +4°C (Fig. 1). Individuals of
189 *A. antarcticus* (-2°C acclimation) also exhibited significantly lower CTmin and chill coma values in

190 comparison with summer acclimatised individuals ($P < 0.05$ Tukey's multiple range test). There were no
191 significant differences in the CT_{min} and chill coma values between species acclimated at +10°C and
192 those at +4°C, except for *M. arctica* in which the CT_{min} was significantly higher in the +10°C acclimated
193 group ($P < 0.05$ Kruskal-Wallis test).

194 3.2. CT_{max} and heat coma

195 3.2.1. Interspecific comparisons

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

200 3.2.2. Effect of acclimation

201 A one month acclimation at -2°C significantly reduced CT_{max} and heat coma temperatures compared to
202 individuals maintained at +4°C in all species (Fig. 2, $P < 0.05$ Kruskal-Wallis test). A two week
203 acclimation at +10°C also led to lower (or unchanged – *C. antarcticus*) CT_{max} and heat coma
204 temperatures, though this was only significant for the heat coma temperature of *A. antarcticus* ($P < 0.05$
205 Kruskal-Wallis test). Summer acclimatised individuals of *C. antarcticus* exhibited significantly lower
206 CT_{max} and heat coma temperatures than individuals acclimated at either -2°C or +4°C, while summer
207 acclimatised individuals of *A. antarcticus* only showed significantly lower CT_{max} and heat coma
208 temperatures than individuals maintained at +4°C.

209 3.3. Locomotion analysis

210 3.3.1. Interspecific comparisons

211 Across all temperatures between -4 and 20°C, both collembolan species were significantly more active
212 and travelled a greater distance than the mite ($P < 0.05$ Kruskal-Wallis test, 4°C acclimation, Fig. 3). In
213 all species previously acclimated at +4°C, movement increased with temperature up to 25°C (except at
214 10°C in *M. arctica*), before decreasing again at temperatures $\geq 30^\circ\text{C}$.

215 3.3.2. Effect of acclimation

216 Following an acclimation period at -2°C (0°C for *M. arctica*), there was no significant difference in
217 locomotion at temperatures $\leq 0^\circ\text{C}$, except for *M. arctica*, in which movement was significantly greater at
218 -4°C ($P < 0.05$ Tukey's multiple range test, variances not equal) (Fig. 3). At 15 and 20°C, movement was
219 most rapid in *C. antarcticus* acclimated at -2°C, as compared with the two other acclimation groups. The
220 movement of *M. arctica*, acclimated at 0°C, was also more rapid at 20°C. Individuals of both collembolan
221 species given an acclimation period at +10°C exhibited considerably slower movement at temperatures
222 above +4°C than individuals maintained at +4°C. In contrast, movement was greater across all
223 temperatures between 0 and 25°C in +10°C acclimated individuals of *A. antarcticus*.

224 3.4. SCPs

225 3.4.1. Interspecific comparisons

226 There were no significant differences in the SCPs of the three species when maintained at +4°C (Table 1,
227 $P < 0.05$ Kruskal-Wallis test). *Alaskozetes antarcticus* was the only species to show a bimodal
228 distribution.

229 3.4.2. Effect of acclimation

230 In all three species, the SCPs of individuals acclimated at -2°C for one month, and summer acclimatised
231 individuals of *C. antarcticus* and *A. antarcticus*, were significantly lower than those of individuals
232 maintained at +4°C ($P < 0.05$ Kruskal-Wallis test). Conversely, the SCP of individuals after a +10°C
233 acclimation period was not significantly different to those maintained at +4°C ($P > 0.05$ Kruskal-Wallis
234 test). Summer acclimatised individuals of *C. antarcticus* also had significantly lower SCPs than
235 individuals acclimated at -2°C ($P < 0.05$ Kruskal-Wallis test).

236 4. Discussion

237 4.1. Activity at low temperatures

238 Temperate and tropical invertebrates, such as the peach-potato aphid, *Myzus persicae*, the predatory
239 mirid, *Nesidiocoris tenuis*, and the brown planthopper, *Nilaparvata lugens*, lose the ability to coordinate
240 movement (CTmin) at temperatures above 0°C, and more usually above +3°C (Chidwanyika and
241 Terblanche, 2011; Clusella-Trullas et al., 2010; Hazell et al., 2010; Hughes et al., 2010; Nyamukondiwa
242 and Terblanche, 2010; Piyaphongkul personal communication). These CTmin values are not compatible
243 with polar summer microhabitat temperatures, which regularly fall below 0°C and average less than +3°C
244 in the maritime and continental Antarctic, and only a little more in the High Arctic (Davey et al., 1992;
245 Block et al., 2009; Coulson et al., 1993; Strathdee and Bale, 1998). It is not surprising, therefore, that
246 polar terrestrial invertebrates have lower thermal thresholds than their temperate and tropical
247 counterparts, and have been observed performing activity at temperatures as low as -13.3°C (Sinclair et
248 al., 2006), including attempts to fly at -4°C (Hågvar, 2010). Other examples of sub-zero activity are found
249 in high altitude environments and include Himalayan *Diamesa* sp., which has been observed walking at -
250 16°C (MacMillan and Sinclair, 2011). In the current study, the CTmin and chill coma of the two
251 Collembola, *M. arctica* and *C. antarcticus*, and the mite, *A. antarcticus*, were below -0.6 and -3.8°C,
252 respectively. Locomotion analysis also showed that the invertebrates walked in a coordinated manner at
253 +4 and 0°C, and that they were capable of movement at -4°C, but at a reduced speed (Figs. 3, 4, 5).

254 In the two collembolan species, the CTmin of individuals maintained at +4°C was low, averaging
255 between -3.5 and -4°C. Conversely, the CTmin of the mite only averaged -0.6°C, even though its chill
256 coma was similar to both Collembola (Fig. 1). Observation revealed that the mites tended to aggregate or
257 stop moving early in the cooling regime and moved little thereafter. *Alaskozetes antarcticus* is well
258 known to aggregate in the field, and has been observed aggregating in numbers of tens, hundreds and
259 even many thousands of individuals (Richard et al., 1994; Strong, 1967; Tilbrook, 1973). Block and
260 Convey (1995) and other authors suggest that, due to the reduced surface area to volume ratio of the
261 aggregation, this behaviour may buffer the mite against low temperatures and reduce water loss. The
262 reason that mites may aggregate so early on during the cooling regime at temperatures near to 0°C, rather

263 than attempting to select for more “optimal” thermal conditions, may be a consequence of their relatively
264 restricted mobility. Unlike Collembola, which are more capable of moving rapidly to habitats in their
265 preferred temperature range (Figs. 3, 4, 5), restricted mobility leaves non-acclimated mites susceptible to
266 a sudden cold exposure. Hence, it may be better for mites to select sub-lethal low temperatures and
267 acclimate. Hayward et al. (2003) have demonstrated such a preference for low temperatures in *A.*
268 *antarcticus* using a thermal gradient. The high CT_{min} value of the mite may therefore be a product of
269 “choice” rather than an inability to coordinate movement.

270 4.2. Activity at high temperatures

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

286 4.3. Thermal activity windows

287 While the polar terrestrial invertebrates of this study showed little sensitivity to a temperature rise, their
288 thermal range of activity is similar to that of temperate and tropical species. The activity of *M. arctica*
289 ranged from -4 (CT_{min}) to 31.7°C (CT_{max}), a thermal activity window of 35.7°C. Likewise, *C.*
290 *antarcticus* and *A. antarcticus* showed activity windows of 33.6°C and 34.7°C, respectively. These
291 windows of activity are comparable to the temperate aphid, *Myzus persicae*, in which the CT_{min} was
292 between 4 and 9.4°C, and the CT_{max} between 39.6 and 40.7°C, but are shifted towards lower
293 temperatures (Alford et al., 2012). Other temperate species such as the predatory mirid, *Nesidiocoris*
294 *tenuis*, the mite, *Tetranychus urticae*, and moth, *Cydia pomonella*, and tropical species such as the seed
295 harvester ant, *Messor capensis*, show somewhat broader thermal activity windows of around 40°C or
296 more (Chidwanyika and Terblanche, 2011; Clusella-Trullas et al., 2010; Hughes et al., 2010).
297 Invertebrates native to locations slightly further north in the sub-Antarctic, such as the spiders, *Myro*
298 *kerguelenensis* and *Prinerigone vegans*, also show thermal activity windows above 40°C (Jumbam et al.,
299 2008).

300 4.4. The effect of low temperature acclimation on thermal activity thresholds

301 The role of acclimation on thermal activity thresholds has only been explored infrequently. Most studies
302 have been carried out on the fruit fly, *Drosophila*, and have shown a clear relationship between the
303 acclimation temperature and the CTmin (Hori and Kimura, 1998; Hoffman et al., 2005; Kelty and Lee,
304 2001; Mellanby, 1939; Rako and Hoffman, 2006). Gibert and Huey (2001) showed that the CTmin of
305 several *Drosophila* species decreased by 1°C for every 4°C drop in development temperature. This result
306 is in line with the Beneficial Acclimation Hypothesis (BAH), which suggests that the performance of
307 individuals is improved at temperatures close to those which they have previously experienced (Leroi et
308 al., 1994). Frazier et al. (2005) provided further evidence supporting the BAH in *D. melanogaster* by
309 demonstrating greater flight performance at cool temperatures in individuals acclimated at 15 rather than
310 28°C. More recent work in other invertebrates, including the cricket, *Acheta domesticus*, the moth, *C.*
311 *pomonella*, and the spiders, *M. kerguelenensis* and *P. vegans*, also support the BAH with respect to low
312 temperature activity (Chidwanyika and Terblanche, 2011; Jumbam et al., 2008; Lachenicht et al., 2010).
313 There are exceptions, however, such as in the ant, *M. capensis*, in which individuals acclimated at an
314 intermediate temperature performed best under the coolest conditions tested, this instead supporting the
315 Optimal Acclimation Hypothesis (OAH = individuals acclimated at an intermediate temperature will
316 perform better at all temperatures) (Clusella-Trullas et al., 2010; Huey and Berrigan, 1996). The
317 acclimatory ability of the three polar species examined here was in agreement with the former hypothesis,
318 BAH. A period of one month at -2°C lowered chill coma onset significantly in all three species, and
319 lowered the CTmin in the two Antarctic invertebrates, compared with individuals maintained at +4°C
320 (Fig. 1). Further evidence of beneficial acclimation was seen for the CTmax and heat coma, with both
321 showing a considerable downward shift following time at -2°C, as well as following summer
322 acclimatisation (averaging approximately +1°C) in the two Antarctic species (Fig. 2). While these
323 findings are consistent with the reports in *Drosophila* and other aforementioned species, they contrast
324 with those of Young (1979), who reported that the chill coma temperature of *A. antarcticus* was
325 unaffected by acclimation.

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

331 The maximisation of activity and adaptation to the low temperature environment was also seen in relation
332 to the SCP. When the body fluids of an invertebrate are frozen, the invertebrate is no longer considered
333 capable of movement and the SCP is seen as the absolute limit of mobility. In many temperate and
334 tropical species, the lower lethal thresholds, and thus also the CTmin and chill coma, are well above the
335 SCP (Bale, 2002). However, in the current study, prior to acclimation, the chill coma temperature of all
336 three species, and the CTmin of the two Collembola, were within 2-3°C of the SCP (Fig 1; Table 1).
337 Likewise, the continental Antarctic collembolan, *Isotoma klovstadi*, was observed to be capable of
338 walking at all temperatures down to its SCP, with an average chill coma onset temperature of -11.9 to -
339 13.3°C over the summer season (Sinclair et al., 2006). These organisms are consequently able to search
340 for more preferable habitats as the temperature falls, and possibly perform beneficial activities, such as
341 foraging, very near to their SCP.

342 4.5. The effect of high temperature acclimation on thermal activity thresholds

343 Climate warming has resulted in a significant rise in polar temperatures, and will undoubtedly lead to
344 future increases (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009). An advantage may
345 therefore be gained by being able to acclimate to higher temperatures. However, the species examined
346 here showed no acclimation ability allowing an increase in their upper activity thresholds following a two
347 week period at 10°C, and even showed a decline in both their CT_{max} and heat coma (Fig. 2). Everatt et
348 al. (2013) and Slabber et al. (2007) also found that acclimation to higher temperatures (10 and 15°C,
349 respectively) either resulted in no change in, or impaired, survival at temperatures above 30°C in both
350 Collembola and Acari. Further, a number of studies have shown little plasticity in upper thermal tolerance
351 traits in non-polar species, including in the cricket, *A. domesticus*, the fruit fly, *D. melanogaster*, dung
352 beetles, and the tsetse fly, *Glossina pallidipes* (Gaston and Chown, 1999; Goto et al., 2000; Hoffman et
353 al., 2005; Lachenicht et al., 2010; Terblanche et al., 2007). There is now a general consensus that thermal
354 tolerance shows less phenotypic plasticity at higher temperatures than at lower temperatures in
355 invertebrates, and that this may be due to each involving a distinct suite of physiological and molecular
356 mechanisms (Bowler and Terblanche, 2008). Even though the polar species of this study show a limited
357 ability to acclimate their upper thermal thresholds to higher temperatures, the upper thermal tolerance
358 they already possess (see section 4.2.) gives these invertebrates sufficient capacity to cope with future
359 climate warming.

360 Intriguingly, a subtle difference may exist between the locomotion speeds of the mite and the Collembola.
361 In *A. antarcticus*, movement was greater between 0 and 25°C in individuals which had received a 2 week
362 acclimation at 10°C, as compared to individuals reared at 4°C. Whereas in the Collembola, movement
363 was impaired between 0 and 20°C by the same acclimation treatment. *Alaskozetes antarcticus* is already
364 known to have a greater capacity to survive higher temperatures than the Collembola (Everatt et al.,
365 2013). It is therefore plausible that *A. antarcticus* is able to benefit physiologically from a period at 10°C,
366 while the Collembola may find the temperature damaging.

367 It should be noted that, while no acclimation response was exhibited for the CT_{max} and heat coma
368 following two weeks at 10°C, acclimation did occur in both -2 and +4°C reared individuals, with all
369 species showing significantly higher CT_{max} and heat coma temperatures under +4 vs -2°C treatments
370 (Fig. 2). The ability to acclimate in response to these two temperature regimes perhaps illustrates the
371 process of natural acclimatisation between winter and summer conditions. However, as the upper
372 thresholds of activity in -2°C acclimated individuals are already above the highest summer temperatures
373 they experience, the observed change may simply reflect the acclimation of their lower activity
374 thresholds, which are lowered following one month at -2°C (Fig. 1). This further supports the consensus
375 highlighted above, that greater plasticity is shown at lower temperatures but not at higher temperatures.
376 Physiological changes that improve activity at low temperatures, such as increased membrane fluidity and
377 subsequent improvement in the function of neurotransmitters, ATPases and ion channels (MacMillan and
378 Sinclair, 2011), are likely to be to the detriment of higher temperature activity.

379 **5. Conclusion**

380 The current study has expanded on previous studies to show that the polar mite, *A. antarcticus*, and
381 Collembola, *C. antarcticus* and *M. arctica*, are capable of sub-zero activity. These invertebrates also show

382 plasticity in their CT_{min} and chill coma temperature following acclimation at lower temperatures, as well
 383 as being capable of activity at temperatures close to their SCPs. By depressing their lower thermal activity
 384 thresholds as temperature falls, these invertebrates are able to maximise the short growing season. At
 385 higher temperatures, these species are able to remain active above 30°C, a temperature far higher than is
 386 experienced in their Antarctic or Arctic habitats. This indicates polar terrestrial invertebrates have a
 387 thermal activity window comparable to that of temperate and tropical insects and, in spite of their limited
 388 physiological plasticity at higher temperatures, have thermal scope to tolerate future rises in temperature
 389 under climate change.

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 395 Science for Planet Earth' and SCAR 'Evolution and Biodiversity in Antarctica' research programmes.

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574 **Figure legends**

575 **Fig. 1.** CTmin (A) and chill coma (B) of *C. antarcticus*, *A. antarcticus* and *M. arctica*, following
576 acclimation at 4, 10 and -2°C, and individuals acclimated to the Antarctic summer (*C. antarcticus* and
577 *A. antarcticus* only). Means \pm S.E.M. are presented for 30 individuals. Asterisks indicate a treatment
578 significantly different from 4°C acclimated individuals for each species at $P < 0.05$ (Kruskal-Wallis test;
579 Tukey's multiple range test).

580 **Fig. 2.** CTmax (A) and heat coma (B) of *C. antarcticus*, *A. antarcticus* and *M. arctica*, following
581 acclimation at 4, 10 and -2°C, and individuals acclimated to the Antarctic summer (*C. antarcticus* and
582 *A. antarcticus* only). Means \pm S.E.M. are presented for 30 individuals. Asterisks indicate a treatment
583 significantly different from 4°C acclimated individuals for each species at $P < 0.05$ (Kruskal-Wallis test).

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

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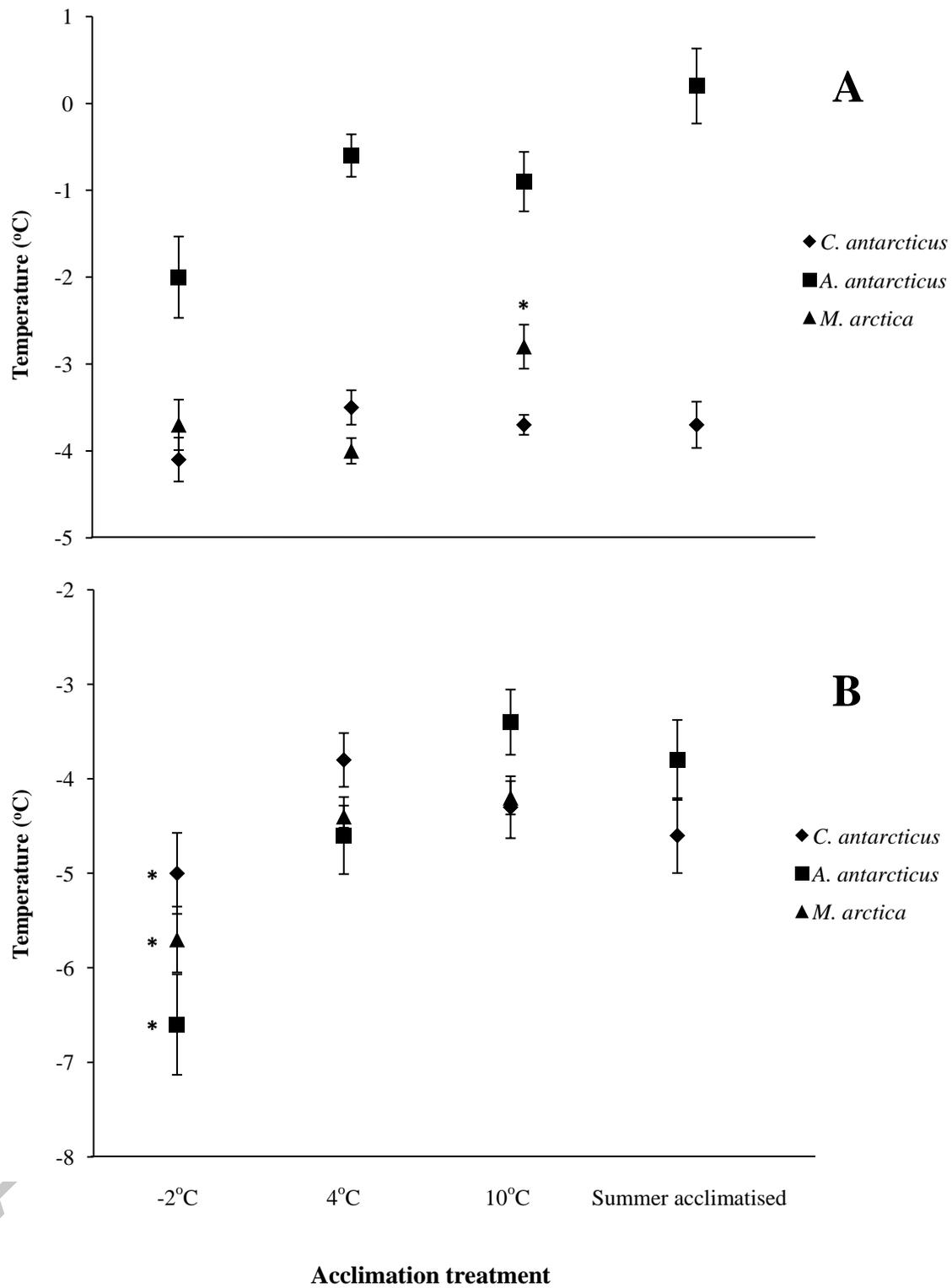


Figure 1

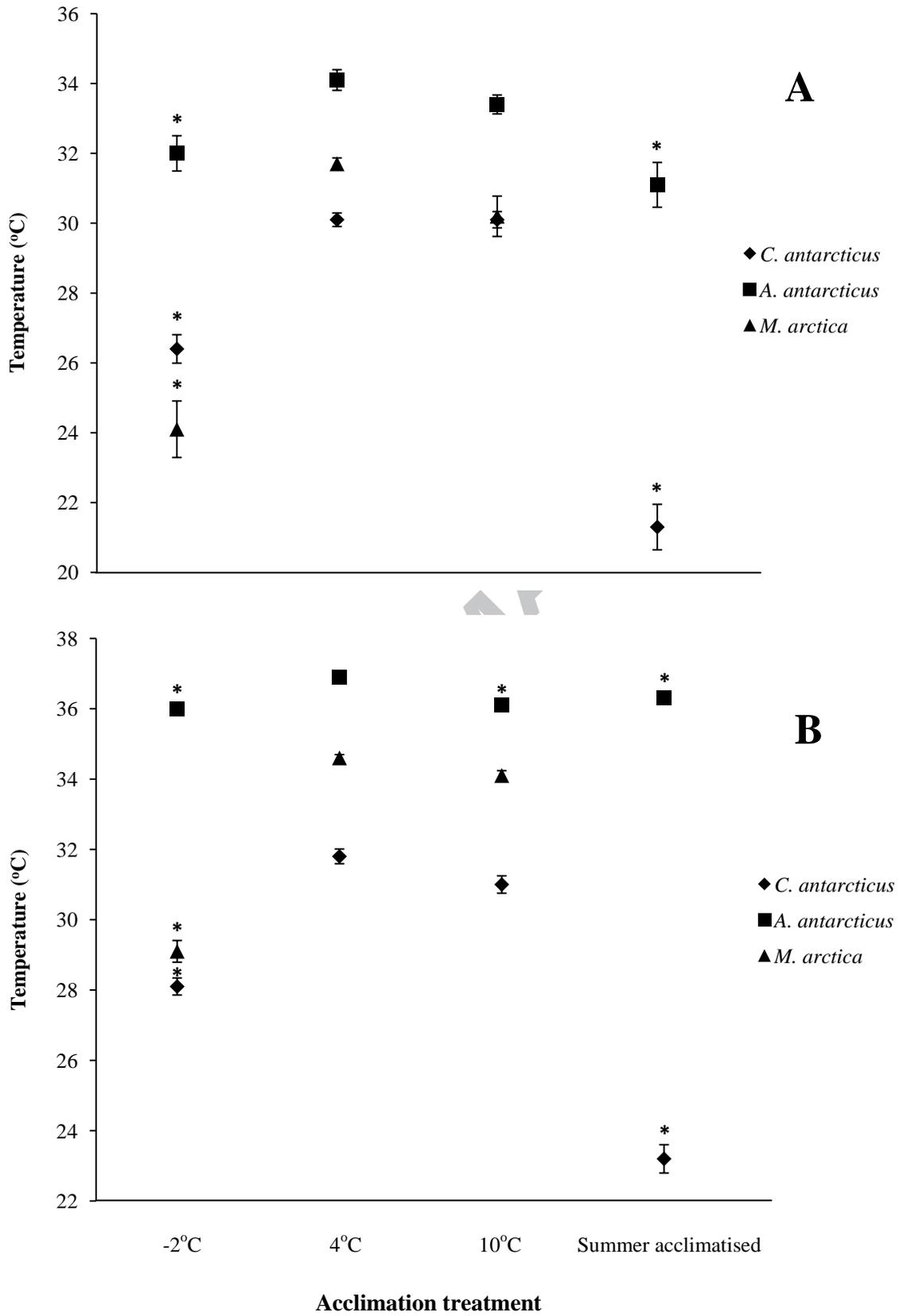


Figure 2

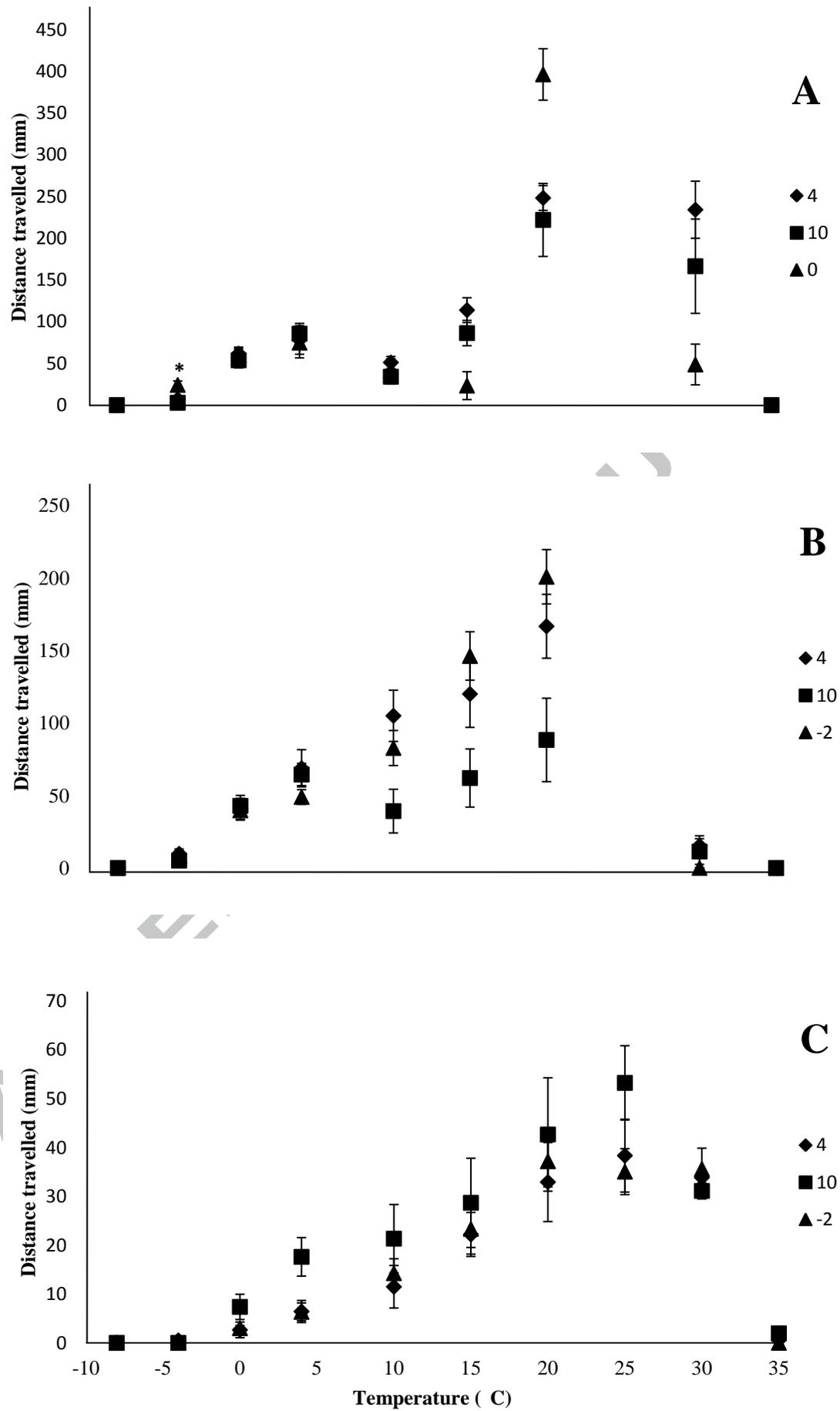


Figure 3

612 **Table legend**

613 **Table 1.** SCP of *C. antarcticus*, *A. antarcticus* and *M. arctica*, following acclimation at 4, 10 and -2°C,
614 and individuals acclimatised to the Antarctic summer (*C. antarcticus* and *A. antarcticus* only). Means ±
615 S.E.M. are presented for 32 individuals (24 for summer acclimatised individuals). Asterisks indicate a
616 treatment significantly different from 4°C acclimated individuals for each species at $P < 0.05$ (Kruskal-
617 Wallis test).

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Species	4°C	10°C	-2°C	Summer acclimatised
<i>C. antarcticus</i>	-6.31 ± 0.2	-7.71 ± 0.8	-8.9 ± 0.7 *	-14.9 ± 1.4 *
<i>A. antarcticus</i>	-7.42 ± 0.9	-7.8 ± 0.7	-15.9 ± 1.8 *	-11.9 ± 1.6 *
<i>M. arctica</i>	-6.13 ± 0.1	-5.9 ± 0.2	-8.1 ± 0.3 *	

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643 Table 1

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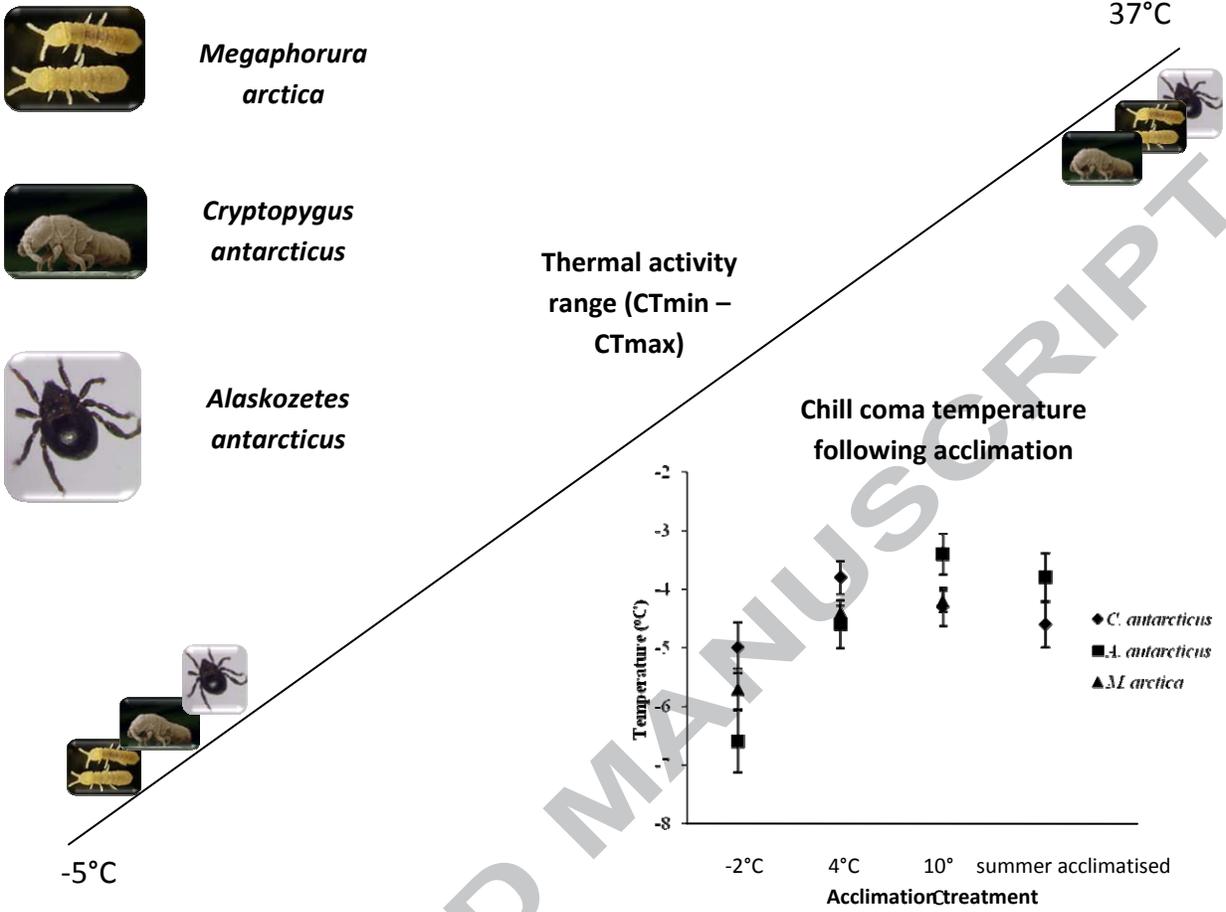
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656 Highlights

657 - Microhabitat temperatures in the polar regions frequently fall below 0°C, but can also exceed 20°C.

658 - The thermal activity thresholds of three polar terrestrial invertebrates were investigated.

659 - The activity of these invertebrates was shown to range from below 0°C to above 30°C.

660 - Depression of their lower thermal activity thresholds was also shown following acclimation.

661 - The results suggest these invertebrates are able to maximise the growing season.

662