Are the Antarctic dipteran, *Eretmoptera murphyi*, and Arctic collembolan, *Megaphorura arctica*, vulnerable to rising temperatures?

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Abstract

Polar terrestrial invertebrates are suggested as being vulnerable to temperature change relative to lower latitude species, and hence possibly also to climate warming. Previous studies have shown Antarctic and Arctic Collembola and Acari to possess good heat tolerance and survive temperature exposures above 30°C. To test this feature further, the heat tolerance and physiological plasticity of heat stress were explored in the Arctic collembolan, *Megaphorura arctica*, from Svalbard and the Antarctic midge, *Eretmoptera murphyi*, from Signy Island. The data obtained demonstrate considerable heat tolerance in both species, with upper lethal temperatures ≥35°C (1 h exposures), and tolerance of exposure to 10 and 15°C exceeding 56 days. This tolerance is far beyond that required in their current environment. Average microhabitat temperatures in August 2011 ranged between 5.1 and 8.1°C, and rarely rose above 10°C, in Ny-Ålesund, Svalbard. Summer soil microhabitat temperatures on Signy Island have previously been shown to range between 0 and 10°C. There was also evidence to suggest that *E. murphyi* can recover from high-temperature exposure and that *M. arctica* is capable of rapid heat hardening. *M. arctica* and *E. murphyi* therefore have the physiological capacity to tolerate current environmental conditions, as well as future warming. If the features they express are characteristically more general, such polar terrestrial invertebrates will likely fare well under climate warming scenarios.

Keywords: rapid heat hardening, acclimation, thermal sensitivity, recovery, Diptera, Collembola

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Introduction

It is becoming increasingly clear that many terrestrial invertebrates resident in the Antarctic and Arctic are remarkably heat tolerant. Block *et al.* (1994), Hodkinson *et al.* (1996), Deere *et al.* (2006), Everatt *et al.* (2013), Sinclair *et al.* (2006) and Slabber *et al.* (2007) have shown survival above 30°C in a
number of polar Collembola and Acari, including ‘model’ polar species, such as Cryptopygus antarcticus, Megaphorura arctica and Alaskozetes antarcticus. In the Antarctic, typical summer microhabitat temperatures range between 0 and 10°C, whereas in the Arctic, the temperature range is slightly higher (Davey et al., 1992; Coulson et al., 1996; Hodkinson et al., 1996; Block et al., 2009). Temperatures above 30°C have been recorded, but are rare, occurring only in certain microhabitats for brief periods of minutes to hours and not consistently between years (Smith, 1988; Convey, 1996; Hodkinson et al., 1996; Everatt et al., 2013). It is generally assumed that invertebrates respond behaviourally to such temperatures, and rapidly relocate if or when they become stressful (Hayward et al., 2003). Polar Collembola and Acari therefore have ample capacity to tolerate current conditions. Annual mean temperatures have risen by over 2°C in parts of the polar regions in the last 50 years and similar, possibly more extreme, increases are predicted to occur over the next half century (Convey et al., 2009; Turner et al., 2009). Such warming is within the physiological thresholds of the resident Collembola and Acari (Block et al., 1994; Hodkinson et al., 1996; Deere et al., 2006; Sinclair et al., 2006; Slabber et al., 2007; Everatt et al., 2013).

The capacity of polar invertebrates to tolerate future warming is in line with Deutsch et al. (2008), who suggested that the sensitivity of terrestrial invertebrates to a temperature change decreases with increasing latitude (see also Addo-Bediako et al., 2000). It has even been suggested that climate warming might alleviate the stresses of living in a low-temperature environment and benefit some polar species (Convey, 2006, 2011; Bale & Hayward, 2010). This proposal is consistent with the results of some climate manipulation studies which have shown warming to increase populations of invertebrates in Antarctic communities (Convey & Wynn-Williams, 2002; Convey et al., 2002; Day et al., 2009). Convey et al. (2002) and Day et al. (2009), however, highlighted that continued water availability during warming is crucial, and some Arctic studies have shown declines or no change following artificial increases in temperature alone (Coulson et al., 1996; Webb et al., 1998). Manipulation studies should therefore be treated with care for they are complex in their effects and often inconsistent in the consequences identified, emphasizing that the changes observed are strongly influenced by the specific microhabitat characteristics and invertebrate populations investigated, as well as the seasonal timing and duration of the study (Convey et al., 2002, 2003; Bokhorst et al., 2011, 2013). Climate manipulation studies also lack an assessment of the potential impact of possible new colonists as a result of climate change.

The first studies investigating heat tolerance in polar terrestrial invertebrates concentrated on Arctic species, including three species of Collembola (M. arctica, Onychiurus groenlandicus and Hypogastrura tullbergii) and four species of mite (Camisia anomia, Dipterobates notatus, Hermannia reticulata and Ceratoppia hoeli) (Block et al., 1994; Hodkinson et al., 1996). The current study also uses M. arctica and, although it revisits this collembolan’s short- and long-term tolerance to heat, the methods used here take into account more ecologically relevant rates of warming and cooling. The ability of the collembolan to acclimate using rapid heat hardening (RHH) is also investigated for the first time. M. arctica (formerly Onychiurus arcticus) is a pale yellow collembolan found in the palaeartic regions (Fjellberg, 1994). This collembolan is common under rocks and within moss beneath bird cliffs, where it commonly aggregates in groups of 100 or more individuals (Worland, 1996). Partly because of its ability to cryoprotectively dehydrate, M. arctica is considered a ‘model’ in Arctic terrestrial invertebrate ecophysiological research (Worland et al., 1998).

Previous Antarctic studies have examined heat tolerance in Collembola and Acari (Deere et al., 2006; Sinclair et al., 2006; Slabber et al., 2007; Everatt et al., 2013), but have given little attention to Antarctic Diptera. In this study, the capacity of the midge, Eretmoptera murphyi, to respond to high temperature is investigated, including an assessment of its CTmax, and its ability to recover from heat stress. E. murphyi is native and endemic to the sub-Antarctic Island of South Georgia (55°S, 37°W). Likely as a result of plant transplant experiments in the 1960s, this midge was accidentally transferred to maritime Antarctic Signy Island (60°S, 45°W) and is now established as a non-native species there (Block et al., 1984; Convey & Block, 1996). The species has since spread to cover an area >2000 m² and is now having a significant impact on the local environment (Hughes et al., 2013). E. murphyi is closely related to the endemic Belgica antarctica of the maritime Antarctic (Allegrucci et al., 2012). While heat tolerance has received some attention in the latter species, the subject has not been explored in detail (Hayward et al., 2007; Benoit et al., 2009a).

Materials and methods

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°35’N, 11°56’E) between 14 and 24 August 2011. Summer-acclimatised larvae of E. murphyi were collected from soil and moss on Signy Island (60°S, 45°W) near to the British Antarctic Survey Signy Research Station between January and March 2012. These were subsequently transported to the University of Birmingham under refrigerated conditions and held in plastic boxes containing substratum from the site of collection at 4–5°C (0:24 L:D). The duration of travel was approximately 2 days from the Arctic and 2 months from the Antarctic. Numbers of M. arctica were limited, and as a result this species was not assessed for the effect of recovery or heat coma (‘Activity thresholds’ and ‘The effect of recovery on heat tolerance’ sections).

Microhabitat temperatures

The thermal regime experienced by M. arctica during the summer was measured at four different sheltered sites (laid on surface, but covered by rocks), two at Krykkefjellet and two at Stuphallet, between 17 and 24 August 2011. Temperature was measured at each site using a Tinytag Transit 2 Datalogger, and data were uploaded using Tinytag Explorer Software (Gemini Data Loggers, Chichester, UK). Fieldwork was not conducted on Signy Island as part of this study and microhabitat temperature data for E. murphyi are inferred from previous studies.

Upper lethal temperatures (ULTs)

The upper temperature at which a species is no longer able to survive (ULT) was determined for M. arctica and E. murphyi.
by warming individuals at 0.2°C min\(^{-1}\) from 4°C (rearing temperature) to progressively higher temperatures (30–36°C for \(M.\ arctica\) and 35–39°C for \(E.\ murphyi\)). Individuals were subsequently held at the target temperature for 1h, before being cooled back to 4°C at the same rate. Three replicates of ten individuals of each species were placed in Eppendorf tubes, inserted into glass test tubes that were then plugged with sponges, and placed inside an alcohol bath (Haake Phoenix II C50P, Fisher Scientific UK Ltd, Loughborough, UK), prior to each experimental treatment. Control groups were handled, and exposed, in the same way at 4°C. The temperature experienced by the invertebrates was measured by placing a thermocouple within an identical Eppendorf tube into one of the glass test tubes. Humidity typically remains high within this experimental setup, and is assumed not to impact survival based on previous findings (Everatt et al., 2013). At the end of experimental treatments, individuals were rapidly transferred (over ice) from the Eppendorf tubes into plastic universal tubes containing substratum, and returned to the rearing conditions (see also Everatt et al., 2013). Survival, defined by individuals moving either spontaneously or in response to gentle contact stimulus, was assessed 72h after treatment.

**Activity thresholds**

Activity thresholds were assessed for \(E.\ murphyi\) only, within an aluminium block arena. The temperature within the arena was regulated using an alcohol bath, and activity monitored using a digital video camera with a macro lens (see Hazell et al., 2008). Thirty larvae in groups of ten were transferred into the arena and allowed to settle before video recording (Studio Capture DT, Studio86Designs, Lutterworth, UK) and the alcohol bath programme began. The temperature of the arena was raised from 4 to 40°C at two different rates, 0.2 and 0.1°C min\(^{-1}\). The temperature at which each individual larva last moved its body was recorded.

**Long-term heat tolerance**

Five replicates of ten individuals of \(M.\ arctica\) and \(E.\ murphyi\) were transferred to either 4, 9 or 15°C for up to 210 days. Individuals were held in universal tubes with a base of moist plaster of Paris and a small amount of substratum within an incubator or temperature controlled room (9°C). The temperature inside the incubators and room was checked using a Tinytag Transit 2 Datalogger. Survival was assessed every 7 days (see also Everatt et al., 2013).

**The effect of recovery on heat tolerance**

To test the effect of recovery at cooler temperatures on heat tolerance, three replicates of ten individuals were exposed to one of three treatments: (i) 25°C for 10 days, (ii) ten 24h exposure periods at 25°C, each separated by 1h recovery at 4°C and (iii) ten 24h exposure periods at 25°C, each separated by 2h recovery at 4°C. Larvae were kept in plastic universal tubes with a base of moist plaster of Paris and substratum. Transfer from and to 25°C was followed and preceded by 1h at 15°C to avoid cold and heat shock. Survival was assessed after each day (treatment (ii)) or 24h exposure period (treatment (ii) and (iii)).

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**Rapid heat hardening**

**Determination of the discriminating temperature**

The discriminating temperature is defined as the temperature at which there is 10–20% survival (Lee et al., 1987). Three replicates of ten individuals of \(M.\ arctica\) were exposed directly (without ramping at 4°C) to progressively higher temperatures (30–36°C) for 1h, before cooling to 4°C at 0.2°C min\(^{-1}\). Invertebrate collection and handling, controls, thermocouple use, recovery and survival assessment were as described in section 'Upper lethal temperatures (ULTs)'. Preliminary trials on \(E.\ murphyi\) suggested that the midge did not show RHH (data not shown) and so RHH was only assessed in \(M.\ arctica\).

**Induction of RHH**

To test for the RHH response, three replicates of ten individuals were warmed to the discriminating temperature at three different rates, 0.5, 0.2 and 0.1°C min\(^{-1}\). As before, samples were held for 1h at the discriminating temperature and then cooled back to 4°C at 0.2°C min\(^{-1}\).

**Statistical analyses**

The Kolmogorov–Smirnov test was used to confirm whether survival and heat coma 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 either the Mann–Whitney U test or the Kruskal–Wallis test.

**Results**

**Arctic site microhabitat temperatures**

Temperatures remained above 3°C throughout the period 17–24 August 2011 (fig. 1) at both locations. At Stuphallet, temperatures averaged 6.6°C when combining data from both Tinytag sites and at Krykkefjellet, 7.8°C. Temperatures deviated considerably from these averages, rising as high as 16°C at Krykkefjellet. The first 3 days were noticeably warmer, averaging 0.8 and 1.3°C higher than over the whole period in Stuphallet and Krykkefjellet, respectively. The time at which these temperatures were recorded also coincided with the warmest period on Svalbard to date (Coulson, S.J., personal communication).

**Upper lethal temperatures**

Individuals of \(M.\ arctica\) survived up to 35°C, while larvae of \(E.\ murphyi\) survived up to 39°C (fig. 2). The difference in survival between the two species at 35°C was significant \(F_{1,4}=841.000, P<0.05\) one-way ANOVA, variances not equal). Survival in both species declined rapidly, falling by >80%, within 2–3°C as they approached the ULT.

**Heat coma**

The point at which \(E.\ murphyi\) larvae no longer showed signs of movement (heat coma) occurred above 31°C under two different rates of warming, 0.1 (31.4±0.14°C) and 0.2°C min\(^{-1}\) (32.3±0.18°C). The heat coma temperature was significantly higher under faster warming \(F_{1,52}=18.523, P<0.05\) one-way ANOVA.
Long-term heat tolerance

Survival of both species was greatest at 4°C (fig. 3). *M. arctica* tolerated 9°C for 91 days, while survival of *E. murphyi* was still above 75% following 56 days, when the experiment finished. Both species tolerated a 15°C exposure for at least 56 days (fig. 3), at which point survival was greater in *E. murphyi* (32%) than in *M. arctica* (13%). Survival of *E. murphyi* larvae at all temperatures was not significantly different after 35 days (P>0.05 Tukey’s multiple range test, variances not equal in some cases). However, survival after 56 days was significantly lower for larvae exposed to 15°C compared to 4 or 9°C (P<0.05 Tukey’s multiple range test). Survival of *E. murphyi* at 9 or 4°C did not differ significantly for any of the durations tested (P>0.05 Tukey’s multiple range test).

Effect of recovery on heat tolerance

Constant exposure to 25°C was lethal after 8 days, but survival increased with the introduction of daily recovery periods of 1 or 2h at 4°C (fig. 4). This was significant overall (F2=9.064, P<0.05 two-way ANOVA), but the interaction between time and recovery was not significant (F14=1.849, P>0.05 two-way ANOVA). Survival following a daily 2h recovery period at 4°C was greater than survival without recovery over the course of the entire experiment (days 2–8), though the difference in survival was only significant after 6 days (P<0.05 Tukey’s multiple range test). A 1h recovery period also gave greater survival for days 3–5 and day 8, but none of these differences were significant when analysed individually.

Rapid heat hardening

Determination of the discriminating temperature

The discriminating temperature was determined to be 34.5°C for *M. arctica* (17% survival, fig. 5).

RHH induction

Mean survival was significantly higher following warming at a rate of 0.1°C min⁻¹ (73%), compared with survival after direct transfer (17%) to the discriminating temperature (P<0.05 Tukey’s multiple range test, variances not equal, fig. 6). Survival was also raised following warming at a rate of 0.2 and 0.5°C min⁻¹, but this was not significant (P>0.05 Tukey’s multiple range test, variances not equal).

Discussion

As poikilothermic ectotherms, invertebrate body temperatures are determined by, and vary with, the external environment (Speight et al., 2008). Invertebrates are therefore susceptible to injuries, and impaired development and reproduction, resulting from exposure to temperature alterations, such as those that may result from climate change (Bale & Hayward, 2010). Changes in temperatures due to climate warming are already known to affect invertebrate population
dynamics and distribution (Parmesan, 1996; Walther et al., 2002). For example, climate warming has led to the occurrence of extreme heat events, which have resulted in the mass mortality of tropical species, such as corals (Walther et al., 2002). Tropical species are particularly vulnerable to temperature change as the upper temperatures they are able to tolerate lie very close to the upper temperatures experienced in their environment (Somero, 2010). Indeed, in some cases, tropical species live at temperatures which exceed their physiological optima (Somero, 2010). The current study considers whether polar species are also vulnerable to climate warming, by examining the heat tolerance and activity thresholds of the dipteran, E. murphyi, from the Antarctic, and further examining the heat tolerance capacity of the Arctic collembolan, M. arctica.

**Basal tolerance**

Both study species demonstrated considerable heat tolerance and showed survival above 34°C for a period of 1h (Fig. 2.). The heat coma temperature of E. murphyi was also very high, averaging above 31°C following warming at 0.1 or 0.2°C min⁻¹. Correspondingly, Everatt et al. (2013) demonstrated survival up to 37°C in the collembolan, C. antarcticus and survival up to 40°C in the mite, A. antarcticus, with similar results also being demonstrated in other Antarctic species (Deere et al., 2006; Sinclair et al., 2006; Slabber et al., 2007). Block et al. (1994) and Hodkinson et al. (1996) likewise demonstrated high-temperature survival in Arctic Acari and Collembola, including in M. arctica. The survival of M. arctica in this study was almost identical to that found by both Block et al. (1994) and Hodkinson et al. (1996), with all three studies showing virtually 100% survival after a 1h exposure at 30°C and an ULT of 35°C. Extending the exposure time to 3h shifted survival downwards, but still gave survivorship above 30°C (Block et al., 1994; Hodkinson et al., 1996). These temperatures are considerably higher than the temperatures experienced throughout the year in both the Antarctic and Arctic, including in summer and short duration extreme maxima. Temperature
conditions varied across small spatial scales at both the Stuphallet and Krykkefjellet sites (fig. 1), and microhabitat buffering would further protect terrestrial invertebrates from temperature extremes. *M. arctica* and *E. murphyi* therefore have considerable capacity to tolerate current summer conditions, including conditions that are unusually warm. These species also have the capacity to tolerate the much higher temperatures that will likely occur as a result of climate warming (Arctic Council, 2005; Convey et al., 2009; Turner et al., 2009), further consolidating the hypothesis set out by Deutsch et al. (2008).

In addition to the well characterised cellular damage inflicted during acute exposure to temperature extremes, injury can also occur following long-term exposure to more moderate temperatures (e.g. Czajka & Lee, 1990). To assess this, in the current study, both *M. arctica* and *E. murphyi* were exposed to 9 and 15°C for several weeks. Although mortality occurred at these temperatures, both species survived well for the first 4 weeks, particularly at 9°C (fig. 3). The collembolan survived until 91 days at 9°C and 56 days at 15°C and, while the experiment was only carried out over 56 days for *E. murphyi*, mean survival at 9°C was still above 70%. Hodkinson et al. (1996) showed similarly good survival in *M. arctica* at 10°C, with the collembolan surviving up to 196 days, with less than 50% mortality after 140 days, in that instance. Some individuals were also able to survive up to 68 days at 25°C. Such tolerance is notable when compared with their Arctic microhabitat temperatures where, for only a few periods of no more than 24h, did temperatures exceed 9°C, and at only one point did they exceed 15°C (fig. 1). Likewise, maximum temperatures 3 cm below the soil surface recorded between 1991 and 1993 did not exceed 14°C (Hodkinson et al., 1996). Temperatures above 9°C are even more unusual on Signy Island or more generally in the maritime Antarctic (Davey et al., 1992; Bokhorst et al., 2008).

**Physiological plasticity**

Polar terrestrial invertebrates are exposed to a highly variable climate. At the extreme, temperatures can vary seasonally by up to 100°C and daily by as much as 50°C (Convey, 1996). Even in buffered microhabitats, there can be considerable variation. Terrestrial invertebrates will therefore not be exposed to either constant low or high temperatures, and will also be exposed to milder transitional temperatures, giving them an opportunity to recover from thermal injuries. It has already been shown in a number of invertebrates, including the firebug, *Pyrrhocoris apterus* (Koštál et al., 2007), the beetle, *Alphitobius diaperinus* (Renault et al., 2004; Koštál et al., 2007; Colinet, 2011; Lalouette et al., 2011), the parasitic wasp, *Aphidius colemani* (Colinet et al., 2007) and the flesh fly, *Sarcophaga crassipalpis* (Dolto et al., 2010), that pulses at warmer temperatures allow recovery from chilling injury. However, few studies have looked at analogous recovery from higher temperatures. In the current study, larvae of *E. murphyi*

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**Fig. 4.** Survival (%) of *E. murphyi* at 25°C over a period of 9 days. Larvae were either given no recovery period, 1h at 4°C after each 24h period or 2h at 4°C after each 24h period. Means±SEM are presented for three replicates of ten individuals. Asterisks indicate a recovery treatment significantly different from the constant treatment at P<0.05 (Tukey’s multiple range test).

**Fig. 5.** Survival (%) of *M. arctica* following direct exposure (without ramping) to progressively higher temperatures (30–35°C) for 1h. Means±SEM are presented for three replicates of ten individuals. Survival was assessed 72h after treatment. Means with the same letter are not significantly different at P<0.05 (Tukey’s multiple range test).

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**Fig. 6.** Survival (%) of *M. arctica*, following exposure to the discriminating temperature (34.5°C) for 1h, after being warmed to the discriminating temperature at one of three rates (0.5, 0.2 or 0.1°C min⁻¹). Survival following these three rates is shown in comparison to direct transfer, which is denoted as 34.5. Means±SEM are presented for three replicates of ten individuals. Survival was assessed 72h after treatment. Means with the same letter are not significantly different at P<0.05 (Tukey’s multiple range test).
exhibited improved survival following daily recovery of 1h, but particularly following 2h, at 4°C (fig. 4). Greater survival with increasing duration of recovery has also been demonstrated in A. diaperinus (Colinet et al., 2011). The lethal time (LT₉₀) of the beetle increased significantly from a 0.5 to 4h recovery period. We speculate that longer recovery times than used in the current study would further enhance survival of E. murphyi larvae. Recovery from, and repair of, chilling injury has been shown to involve ion gradient homeostasis (Koštál et al., 2007), induction of antioxidants (Lalouette et al., 2011) and the up-regulation of key proteins (Colinet et al., 2007). Analogous responses during recovery from high-temperature injury may also occur. The up-regulation of heat shock proteins (HSPs), for example, is a common response to stressful conditions and is known as the ‘heat shock response’ because of its role in repair of heat shock injuries (Clark & Worland, 2008). HSPs help refold and stabilise proteins and other macromolecules during stress (Clark & Worland, 2008), and may also be involved with the recovery of microfilament dynamics (Tammaro et al., 1999) and the regulation of apoptosis (Yi et al., 2007).

A further means by which terrestrial invertebrates show physiological plasticity to high temperatures is through acclimation. However, the benefits of long-term acclimation (weeks to months) have so far been shown to be slight in polar terrestrial invertebrates. Following long-term acclimation, the widespread collembolan, C. antarcticus and mite, A. antarcticus, were shown to either exhibit no improvement in their survival or reduced survival, at high temperatures (Slabber et al., 2007; Everatt et al., 2013). Acclimation to higher temperatures can also occur over shorter timescales in the form of RHH, which is defined as the rapid induction of heat tolerance over minutes to hours (Benoit et al., 2009b). Unlike rapid cold hardening, which has now been demonstrated in an increasing number of species (e.g. Kelty & Lee, 1997; Powell & Bale, 2004; Lee et al., 2006; Owen et al., 2013) including E. murphyi (Everatt et al., 2012), RHH has been little explored. In polar terrestrial invertebrates, there is evidence for the effect only in C. antarcticus and A. antarcticus (Everatt et al., 2013). The current study also showed an RHH response in M. arctica (fig. 6). Following a warming rate of 0.1°C min⁻¹, survival of M. arctica at 34.5°C was increased by 56%, compared with survival after a direct transfer to the same temperature. However, survival was not raised at 34.5°C following a rate of 0.2 or 0.5°C min⁻¹. Greater survival at a rate of 0.1°C min⁻¹ can be explained by an increased time being available for protection-inducing temperatures has also been shown to improve survival or reduced survival, at high temperatures (Slabber et al., 2007; Day et al., 2009). However, rising temperatures are also expected to reduce snow cover and thaw ice earlier in the season, in turn resulting in the earlier evaporation of meltwater during the summer, which may instead leave invertebrates susceptible to desiccation (Callaghan et al., 1992; Walther et al., 2002; Ávila-Jiménez et al., 2010). Under this scenario, polar terrestrial invertebrates have been shown to fare less well. Block et al. (1994) and Hodkinson et al. (1996) demonstrated the heat tolerance of collembola, including M. arctica, to be reduced when desiccated, as compared to those which were hydrated, while Couson et al. (1996), Convey et al. (2002) and Day et al. (2009) showed decreasing numbers of Collembola under field conditions. Even so, because the heat tolerance of polar terrestrial invertebrates far exceeds buffered microhabitat temperatures, as shown in the current study, and because their heat tolerance still remains high under desiccation (Block et al., 1994; Hodkinson et al., 1996), we speculate that changes associated with climate warming will result in a positive change to the invertebrate fauna.

The probability of alien species establishment is also predicted to increase with climate warming. As temperatures rise, areas which were previously too stressful for invading organisms are beginning to open up (Frenot et al., 2005; Chwedorzewska, 2009). Increasing human activity, as a result of scientific research and, more recently, tourism is also aiding the transfer of alien species by allowing them to bypass geographical and environmental barriers, particularly in the Antarctic (Frenot et al., 2005; Chown et al., 2012). Events in the sub-Antarctic provide a glimpse into what might happen, with native flora and invertebrate fauna of many islands suffering in the presence of invasive alien species (Frenot et al., 2005; Chwedorzewska, 2009).

Conclusion

As with the polar Collembola and Acari that have been studied to date, the Antarctic midge, E. murphyi, possesses considerable heat tolerance that equips it to survive current and predicted future environmental conditions. This species and the Arctic collembolan, M. arctica, also demonstrate physiological plasticity with respect to recovery from high temperature, and RHH, respectively. Polar terrestrial invertebrates may therefore be protected from the harmful consequences of a temperature rise that may result from climate change, at least at a physiological level (Addo-Bediako et al., 2000; Deutsch et al., 2008). However, to identify likely consequences at the community level, it is imperative that this is also balanced with other factors, including changes in water availability and competition from alien species, and that the sub-lethal characteristics of invertebrates, including development and reproduction, are also considered.

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Water availability and alien species in an era of climate warming

Although the direct impacts of high temperature are important, climate warming in the polar regions is also associated with changes in water availability and a heightened threat of alien species establishment. As climate warming intensifies, precipitation is predicted to increase at mid-high latitudes (Walther et al., 2002; Ávila-Jiménez et al., 2010). Under conditions of increased water availability, Antarctic invertebrates have been shown to thrive under warming, with increases in both Collembola and mite numbers (Convey et al., 2002; Schulte et al., 2008; Day et al., 2009). However, rising temperatures are also expected to reduce snow cover and thaw ice earlier in the season, in turn resulting in the earlier evaporation of meltwater during the summer, which may instead leave invertebrates susceptible to desiccation (Callaghan et al., 1992; Walther et al., 2002; Ávila-Jiménez et al., 2010). Under this scenario, polar terrestrial invertebrates have been shown to fare less well. Block et al. (1994) and Hodkinson et al. (1996) demonstrated the heat tolerance of collembola, including M. arctica, to be reduced when desiccated, as compared to those which were hydrated, while Couson et al. (1996), Convey et al. (2002) and Day et al. (2009) showed decreasing numbers of Collembola under field conditions. Even so, because the heat tolerance of polar terrestrial invertebrates far exceeds buffered microhabitat temperatures, as shown in the current study, and because their heat tolerance still remains high under desiccation (Block et al., 1994; Hodkinson et al., 1996), we speculate that changes associated with climate warming will result in a positive change to the invertebrate fauna.

The probability of alien species establishment is also predicted to increase with climate warming. As temperatures rise, areas which were previously too stressful for invading organisms are beginning to open up (Frenot et al., 2005; Chwedorzewska, 2009). Increasing human activity, as a result of scientific research and, more recently, tourism is also aiding the transfer of alien species by allowing them to bypass geographical and environmental barriers, particularly in the Antarctic (Frenot et al., 2005; Chown et al., 2012). Events in the sub-Antarctic provide a glimpse into what might happen, with native flora and invertebrate fauna of many islands suffering in the presence of invasive alien species (Frenot et al., 2005; Chwedorzewska, 2009).

Conclusion

As with the polar Collembola and Acari that have been studied to date, the Antarctic midge, E. murphyi, possesses considerable heat tolerance that equips it to survive current and predicted future environmental conditions. This species and the Arctic collembolan, M. arctica, also demonstrate physiological plasticity with respect to recovery from high temperature, and RHH, respectively. Polar terrestrial invertebrates may therefore be protected from the harmful consequences of a temperature rise that may result from climate change, at least at a physiological level (Addo-Bediako et al., 2000; Deutsch et al., 2008). However, to identify likely consequences at the community level, it is imperative that this is also balanced with other factors, including changes in water availability and competition from alien species, and that the sub-lethal characteristics of invertebrates, including development and reproduction, are also considered.

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References


Polar terrestrial invertebrates vulnerable to rising temperatures?

Marine and terrestrial invertebrates are likely to be greatly affected by climate change, with polar regions being particularly vulnerable. Climate change is expected to increase temperatures in these regions, leading to shifts in species distributions and changes in community composition. Rising temperatures may also affect the growth, development, and survival of these invertebrates, potentially leading to population declines and the introduction of new species.

Incorporating projections of future climate conditions and understanding the biological responses of polar invertebrates is crucial for developing effective conservation strategies. Further research is needed to identify the specific impacts of climate change on polar invertebrates and to develop strategies to mitigate these impacts.


