Overwintering of terrestrial Arctic arthropods: the fauna of Svalbard now and in the future

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Keywords
Arthropoda; Collembola; freeze avoidance; freeze tolerance; protective dehydration; Svalbard.

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doi:10.1111/j.1751-8369.2009.00141.x

Abstract

There are over 500 species of arthropods recorded from Svalbard. These animals overwinter either within the soil or on the ground surface, and have to tolerate an environment where the ground is frozen for over 9 months each year. Three cold-tolerance strategies have been described from Svalbard invertebrates: freeze avoidance, freeze tolerance and desiccation. Once in a cold-tolerant state the animals can be extremely cold tolerant in terms of both minimum exposure temperature and period of exposure. How the overwintering capabilities of these animals will be affected by climate changes during the next 100 years, as predicted by climate models, is not yet known. Four principle factors with an impact on overwintering of the terrestrial arthropod fauna are outlined here: (1) warmer winter temperatures, with an increased frequency of extreme events such as freeze–thaw cycles and surface icing; (2) changes in snow fall and snow lie; (3) pollutant load; and (4) dispersal of invertebrates to Svalbard. Finally, areas where further research is required are highlighted: including the development of controlled multi-season field experiments; effect of freeze–thaw cycles; changes in thickness and distribution of snow lie, with the subsequent effects on duration of the summer period; chill susceptibility of soil arthropods; assessing potential colonizing species and the likelihood of these species becoming established; assessing the effect of gene flow from surrounding populations; interactions between pollution and cold tolerance; anoxia stress; and the genetics of cold tolerance.

Arctic regions are characterized by extreme seasonality, including photoperiods of markedly varying lengths through the year, short cool summers and long cold winters. Such latitudes are also characterized biologically by a reduced α-diversity compared with more temperate latitudes (Chapin & Körner 1994; Strathdee & Bale 1998; Weider & Hobæk 2000; Hillebrand 2004). Several theories have been put forward to explain the reduced arthropod species richness, including limited dispersal to the Arctic during the 10 000 years since the last glacial period, and an inability to survive in Arctic regions because of the limited resources (see Strathdee & Bale 1998 for a review of these and other hypotheses). However, it seems likely that the challenge posed by the long cold Arctic winter is a central factor influencing biodiversity. Whereas birds breeding in Arctic regions often migrate to more temperate latitudes at the onset of winter, this movement is not an option available to the arthropod fauna, which must tolerate the winter environment in situ. Unlike the resident vertebrate fauna, which maintain a high body temperature, utilizing a range of metabolic and morphological adaptations, the arthropod fauna have body temperatures more or less equal to the environment, and so must withstand body temperatures well below 0°C for significant periods of the year. Nonetheless, around 140 species of terrestrial mites are recorded from Svalbard (Coulson & Refseth 2004; Coulson 2007), and 277 species of oribatid and mesostigmatid mites are known from Greenland (Makarova & Böcher 2009). Given this, it would appear that some species are well adapted to the Arctic environment, and for these species the environment is not as extreme as might first be expected. Soil arthropods play a critical role in soil biology, for example in the breakdown of dead organic matter, nutrient recycling, formation of organic soils and as predators (Bardgett 2005). Soil arthropods also influence plant growth through effects on soil processes (Bardgett 2005). It is also thought that belowground processes may regulate carbon fluxes of 10 times that of the current anthropogenic emissions (Chapin et al. 2002).

The environment of the Arctic is currently in a period of change. Both temperature and precipitation are projected to increase over the next 100 years. The average annual temperature is projected to increase by 5°C, and precipitation by 18% (Christensen et al. 2007). The greatest increase is expected to be seen during the winter. Increased temperatures will lead to an increased frequency of extreme events, freeze–thaw cycles (Henry 2008) and increased surface icing, a stressor known to have deleterious effects on the survival of overwintering arthropods on Svalbard (Coulson et al. 2000). Moreover, the Arctic is often considered a pollution sink, and levels of many pollutants are rising (AMAP 2006). There are established, but as yet unclear, links between pollutant load and arthropod cold tolerance (Holmstrup et al. 2000; Holmstrup et al. 2008). Given this, it is important to better understand the current overwintering ecology of the soil arthropod fauna, so as to be able to predict the consequences of climate change and manage the Arctic.

There are many reviews of invertebrate overwintering strategies (Cannon & Block 1988; Bale 1993; Strathdee & Bale 1998; Voituron et al. 2002; Sinclair, Addo-Bediako et al. 2003; Sinclair, Vernon et al. 2003; Turnock & Fields 2005). However, these studies have generally focused on invertebrates dwelling in a wide variety of habitats, from alpine to Arctic and Antarctic, and are either primarily concerned with the physiology of the animals or try to bring an evolutionary perspective to the development of cold tolerance. Comprehensive studies of winter ecophysiology of Arctic invertebrates, integrating Arctic climate change scenarios and forecasting the consequences of these on overwintering strategies and success, are limited (Dollery et al. 2006), or focused on the ecophysiological response to seasonal climate variations (Hawes et al. 2006). Here, we review the state of knowledge concerning the overwintering of the arthropod fauna of Svalbard, beginning by discussing the current arthropod fauna, characterizing the winter conditions experienced by this fauna, now and in the future, and the overwintering ecophysiological strategies used to minimize the stresses of winter. We further highlight that information about the responses of the arthropod fauna to changes forecast by climate models is lacking (Henry 2008), and suggest future areas of winter ecological research.

Arthropods in Svalbard

The Svalbard archipelago lies in the Norwegian High Arctic, at approximately 76.5–80.0° N, 10–21° E, 700 km north of mainland Norway (Fig. 1), with a land area of 61 200 km^2. Over 60% of the land area is permanently covered by snow and ice (Hisdal 1998), and the arthropod fauna is therefore largely restricted to the coastal margin, especially the milder west coast. The recognized arthropod fauna of Svalbard currently consists of over 500 species, but this list is incomplete and new species are being recorded even from the relatively well-known areas around the fjords Isfjorden and Kongsfjorden (Coulson 2007; Ávila-Jiménez et al. 2008). The composition of the fauna is typical for Arctic regions, being similar to Greenland, for example, but with lower species diversity (Jensen & Christensen 2003). There are also notable gaps in the Svalbard fauna. For example, Tipulidae are not recorded from Svalbard but are from Greenland (Jensen & Christensen 2003). As is often observed in the Arctic, the species diversity of Coleoptera is much reduced, whereas that of the Diptera is increased, with respect to global averages (Vernon et al. 1998; Chernov & Makarova 2008). On a world basis Coleoptera and Diptera comprise 38 and 12% of insect species diversity, respectively (Grimaldi & Engel 2005). However, in Svalbard, as in other Arctic regions, the positions are reversed, with Coleoptera and Diptera represented by 8.8 and 56.6% of the total species of Insecta (Coulson 2007). The decline in Coleoptera abundance has been explained by excessive investment in metabolically expensive cuticles at low temperatures (Vernon et al. 1998), but the exact causes remain unclear.

Although the invertebrate fauna of many regions of Antarctica has proved to be ancient (Marshall et al. 1996; Stevens et al. 2006; Stevens et al. 2007; Convey et al. 2008), it is likely that Svalbard and Greenland have been colonized within the last 10 000 years following the retreat of the ice (Böcher 1997; Coulson 2007). How often invertebrates disperse to the Arctic has not been measured in detail, but accidental dispersal of some Lepidoptera to Svalbard has been observed (Laarsonen 1985; Coulson et al. 2002), and studies of phoresy by oribatid mites on seabirds suggests that this mode of dispersal might be a common phenomenon in the Arctic (Lebedeva & Krivolutsky 2003; Lebedeva et al. 2006), especially with species migrating from Europe in the spring. Although the majority of species are Holarctic in distribution, endemic species do occur, for example the two resident aphids, *Acyrthosiphon svalbardicum* (Heikinheimo, 1968) and *Sitobion calvulus* Ossiannilsson, 1958, or the mesostigmatid mite *Zercon forsslundi* Sellnick, 1958.

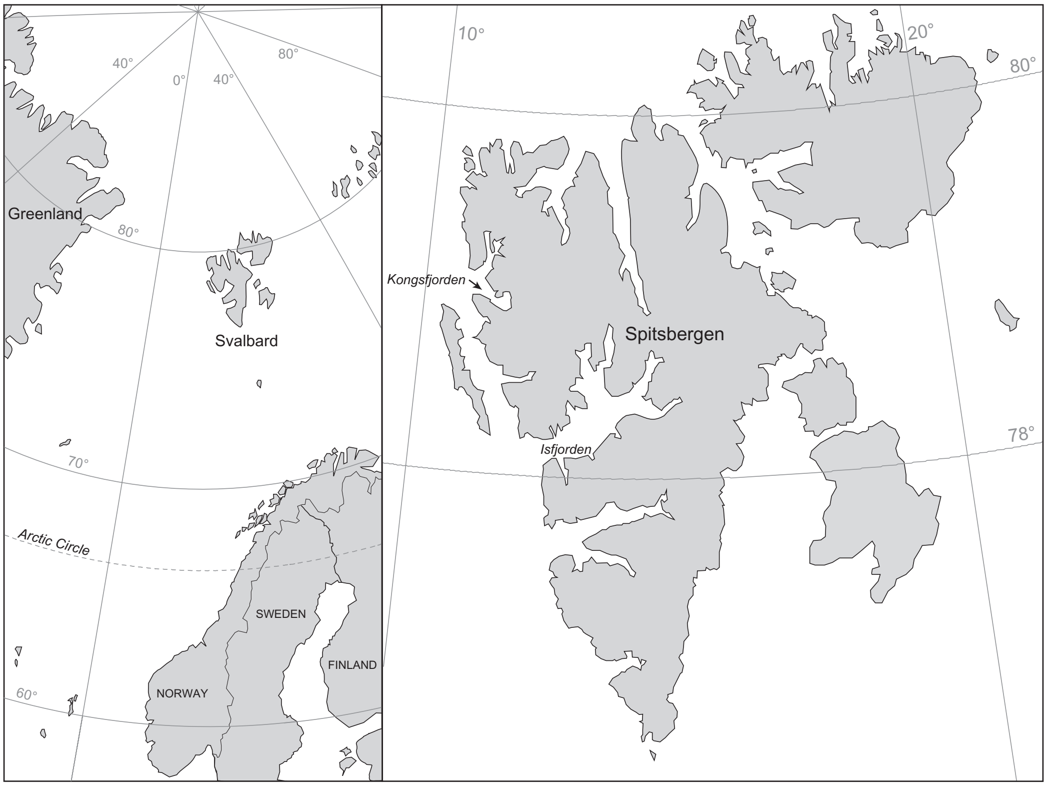

Fig. 1 Location of Svalbard.

Many Arctic terrestrial invertebrates are either true soil dwellers or spend part of their life cycles in the soil. For example, sawfly larvae pupate in the soil, and some species of chironomids pass their larval and pupal stages in the soil. Nonetheless, Arctic soil ecosystems are dominated by Collembola and Acari, as well as Enchytraeidae (Nurminen 1965, 1966), and these can be found in large densities. For example Collembola densities vary between 10 000 and 268 000 individuals m^{-2}, whereas the mites are commonly present at densities of between 4000 and 247 000 individuals m^{-2} (Bengtson et al. 1974; Coulson et al. 1996 and references therein). Collembola communities are often dominated by one species (Babenko 2000), and therefore impacts on key species can have a highly significant effect on the ecosystem.

Climate in the soil

As has been pointed out previously (Hodkinson et al. 1998), climatic averages have little consequence to living organisms: the animals experience the full range of the environment. It is also important to appreciate that the overwintering environment of the arthropods is markedly different from that recorded by standard meteorological stations, which often record temperatures at 2 m above the ground (Coulson et al. 1995). The difference between such measurements and the actual surface temperature can often be 10–20°C, and in extreme cases even more. During summer the surface layers of dry soils in Svalbard can, on occasion, attain 30°C (Coulson et al. 1993). Close to the soil surface (in the first few millimetres) the only heat exchange between the soil and the air is through conduction, with hardly any vertical heat exchange. The temperature therefore decreases exponentially with height above the surface during summer. A few centimetres above the surface, heat exchange through convection occurs, and the air temperature here is closer to the normal air temperature measured at 2 m. In the soil, the temperature often decreases considerably with depth during summer, and summertime diurnal variations can be seen down to a maximum of approximately 1 m (Arya 2001). In winter, the air temperature is instead likely to increase with height above the surface, and the surface is much colder than the air temperature measured at 2 m. If the soil surface is snow-covered, the snow will provide an insulating layer protecting it from the coldest temperatures. But, if the soil surface is snow-free, large amounts of heat will leave the surface, causing it to cool rapidly. The temperature in the soil will then increase rapidly with

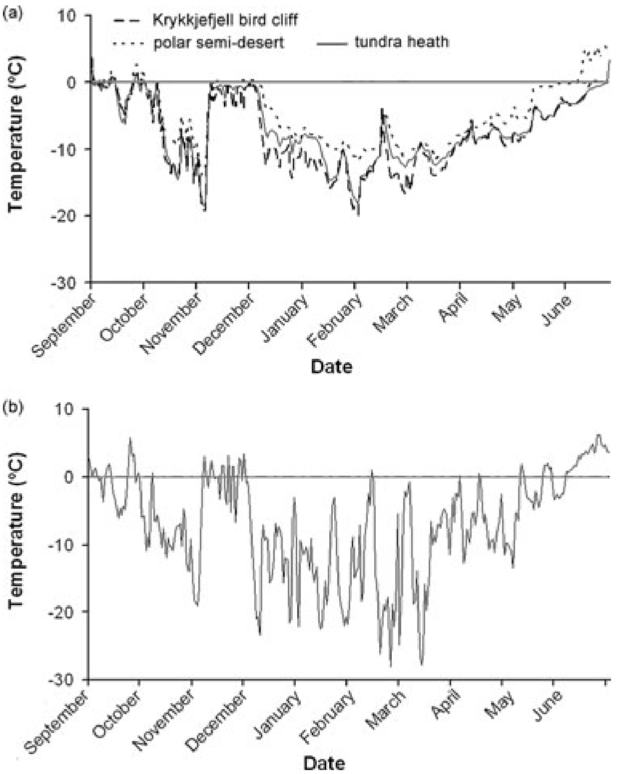

Fig. 2 (a) Soil temperatures at 3 cm depth and (b) screen air temperatures in Kongsfjorden, Svalbard, during winter 1993/94 (after Coulson et al. 1995). A 0°C reference line is shown on both panels.

depth, but even if the air temperature increases above 0°C, the ground will still stay frozen because of the large amount of heat required to melt the ice. The surface layer of the ground typically begins to freeze in mid-September, and will remain frozen until the spring thaw the following year, often commencing in mid-June (Fig. 2). The ground is therefore frozen for approximately 10 months each year. Soil temperatures in the upper layer track air temperature fluctuations until the onset of accumulation of snow in January (Fig. 2). Hereafter, the soil temperatures are buffered against rapid swings in air temperature, and are typically between −5 and −10°C until snow melt in June.

Annual precipitation in Svalbard is low: for example, 190 mm at Svalbard Airport (Longyearbyen) and 355 mm at Ny-Ålesund. However, strong winter winds redistribute fallen snow, creating extremely heterogenous snow-layer depths that vary from several metres in hollows and in the lee of ridges to a few centimetres on the tops of windswept ridges and in wind scoops. Occasional periods of air temperature above 0°C result in meltwater percolating through the snow pack and refreezing at the ground surface. The resultant surface ice layer can vary in thickness from millimetres to many centimetres, reaching values of up to 15 cm thickness (Coulson et al. 2000), with potentially severe consequences on Arctic ecosystems (Kohler & Aanes 2004), including soil arthropods (Coulson et al. 2000).

Overwintering strategies

The physiological strategies by which overwintering arthropods survive extended exposure to low temperatures can be broadly divided into three classes: freeze avoidance, freeze tolerance (*sensu* Bale 1993) and the more recently described desiccation (Holmstrup et al. 2002). Once fully cold-hardened, these animals may be extremely cold tolerant, surviving 4 years at below −20°C (Coulson & Birkemoe 2000). Other studies have demonstrated the survival of *Heleomyza borealis* (Boheman, 1865) larvae (Diptera, Heleomyzidae) after exposure to −60°C (Worland et al. 2000). However, success in the Arctic is more than just overwintering survival, and species have also adopted strategies that enable survival in short cool summers: for example, the highly modified life cycle of the endemic aphid *Acyrthosiphon svalbardicum* (Strathdee et al. 1993), or the free-running life cycles requiring several years to complete, as in the oribatid mite *Ameronothrus lineatus* (Thorell, 1871) (Søvik & Leinaas 2003). Here, we illustrate the three strategies with examples of invertebrates overwintering in Svalbard: a collembolan, an endemic aphid and a dipteran. Each species employs a different strategy, and overwinters in a different life stage (Table 1).

Freeze avoidance (susceptibility)

Freeze-avoiding species are defined as those that would die should their body water (extracellular water) begin to freeze. This class of invertebrates depresses their freezing temperature, the supercooling point (SCP), and when fully winter cold-hardened often possess SCPs below −20°C (Turnock & Fields 2005). The majority produce cryoprotectants, usually low molecular weight sugars and sugar alcohols such as glycerol and trehalose, to reduce the SCP and stabilize the supercooled state. Others also produce antifreeze proteins (thermal hysteresis proteins) that stabilize the supercooled state by non-colligative means, binding to incipient ice crystals and preventing further growth (Barrett 2001).

The endemic Svalbard aphid *Acyrthosiphon svalbardicum* overwinters as an egg, and the life cycle is finely tuned to the short Svalbard summer to ensure the presence of sexual morphs in late summer and the production of eggs before winter (Strathdee et al. 1993). These eggs are extremely cold tolerant, with a mean SCP of between −36.2 and −38.2°C, dependent on acclimation temperature (Strathdee, Howling et al. 1995). The need for such

Table 1 Overwintering strategies shown by three terrestrial invertebrates in Svalbard.

Species	Overwintering strategy	Overwintering stage	Mean SCP* of overwintering stage	Habitat	General distribution
Acyrthosiphon svalbardicum (Hemiptera)	Freeze avoidance	Egg	–36.2/–38.2°C	*Dryas octopetala* patches on exposed ridges	Endemic
Heleomyza borealis (Diptera)	Freeze tolerance	Larva	ca. –7°C	Ornithogenic debris under bird cliffs	Palaearctic
Megaphorura arctica (Collembola)	Protective dehydration	Adult and juvenile	Dependent on acclimation temperature. Down to –27°C	Widespread. Common beneath bird cliffs	Northern Palaearctic

* SCP, supercooling point.

high levels of cold tolerance becomes apparent when the overwintering site is considered. The eggs are attached to the leaves of *Dryas octopetala* L. along ridgelines or at the top of slopes (Strathdee & Bale 1995), where there is only a thin insulating snow lie because winds sweep the areas clear. This results in the eggs being exposed to the low air temperatures close to the ground during the polar winter, when temperatures can on occasion fall below −30°C. However, the advantage of inhabiting areas with limited snow accumulation is that they are also among the first areas to clear of snow the following spring, and hence have the longest duration of summer (Strathdee & Bale 1995).

Freeze tolerance

Freeze-tolerant species survive the freezing of extracellular body water, and often synthesize specialist ice-nucleating proteins in their haemolymphs to ensure freezing is initiated here. For most freeze-tolerant species intracellular freezing is lethal, and freezing is restricted to extracellular water, with the only known exceptions of the Antarctic nematode *Panagrolaimus davidi* Timm, 1971, which has been demonstrated to survive intracellular freezing (Wharton & Ferns 1995; Strathdee & Bale 1998). Freeze tolerance has evolved several times in different insect orders, probably in response to different environmental challenges (Sinclair, Addo-Bekiako et al. 2003). Many freeze-tolerant species have a relatively high SCP of around −7°C (Turnock & Fields 2005). Once ice formation has been triggered in the haemolymph, water is drawn out of the cells in response to the increasing osmolality of the haemolymph, resulting from the growing ice crystal removing liquid water. This desiccates the cells, in turn increasing their solute concentration, and so depressing the freezing temperature of the intracellular matrix and inhibiting freezing. Overwintering in this semi-frozen state has several advantages: the risk of lethal intracellular freezing is reduced, the metabolic rate is decreased and body fluids are conserved (compare with the desiccation strategy).

The heleomyzid dipteran *Heleomyza borealis* overwinters as a final-stage larva, and is common in the ornithogenic debris under bird colonies on Svalbard, especially in black-legged kittiwake (*Rissa tridactyla*) colonies. Here, winter soil temperatures typically average −10°C (Fig. 2; Coulson et al. 1995), but may decline significantly further on occasion because the overwintering habitat is under the wind scoop at the base of the cliffs, and is not often covered by an insulating snow layer. When temperatures rise in the following spring the animal pupates and the adults emerge a few weeks later. The overwintering larvae are freeze tolerant, with an SCP of –7°C (Worland et al. 2000). However, Morton-Firth et al. (1996) observed that the SCPs clustered around two groups, one at –2.3°C and one centered at −9.7°C, and suggested that this could result from the upper group freezing as a result of gut content nucleators, whereas the lower group had ceased feeding but had not yet synthesized the efficient ice nucleators often observed in freeze-tolerant insects (Turnock & Fields 2005). Little is known about the cryoprotectants of *H. borealis*, but Worland et al. (2000) observed that after acclimation at −2°C, fructose levels rose rapidly from 6.1 $\mu g\ mg^{-1}$ to 17 $\mu g\ mg^{-1}$. Once in this frozen state the animal is extremely cold tolerant: 80% of the larvae survived exposure to −60°C (survival recorded 120 days after exposure) (Worland et al. 2000). At −60°C, 81% of the body water is frozen, with the remaining water being osmotically inactive. The cause of low temperature mortality is unknown, but is possibly related to membrane damage as a result of cell shrinkage (Morton-Firth et al. 1996). However, this species is not limited to High Arctic latitudes. The animal is also found in the UK, but the overwintering strategy here is as yet unknown. Few freeze-tolerant species are known from the UK (Hart & Bale 1997).

Given that insects such as microlepidoptera are known to be regular accidental migrants to Svalbard (Laarsonen 1985; Coulson et al. 2002), it seems not unreasonable that Diptera such as *H. borealis* may also arrive not infrequently. Indeed, the species has been shown to be a fast disperser, being one of the first insect species colonizing the volcanic island of Surtsey, Iceland (Ólafsson 1978). Hence, there is the possibility of regular genetic input from a more southerly population, with potential effects on the overwintering strategy of the resident Svalbard population.

Desiccation

The third strategy, desiccation, was first observed in overwintering earthworm cocoons (Holmstrup & Westh 1994), and was later demonstrated in Collembola (Worland 1996; Worland et al. 1998; Holmstrup et al. 2002). The strategy relies on the high permeability of the collembolan cuticle, mostly in euedaphic species (Worland & Block 1986; Block et al. 1990; Kærsgaard et al. 2004), and the fact that they overwinter in pores in the frozen soil. Nonetheless, in principle some mites can also lose water through stigmata, and other "openings" and sutures (Evans 1992). At high subzero temperatures the animal remains unfrozen by virtue of its solute concentration after the soil has begun to freeze. As the vapour pressure of liquid water is greater than ice there will be a net movement of water vapour from the animal to the surrounding ice, and the animal will desiccate until the vapour pressure of the body fluids equals that of the atmosphere within the soil pore. The SCP of the desiccated tissues thus decreases, and the collembolan will not freeze (Holmstrup et al. 2002; Worland & Block 2003). In principle, this strategy is akin to freeze tolerance, except that with freeze tolerance the frozen water remains in the animal, whereas in desiccation the water freezes outside the body. As the soil warms up during spring the relative humidity of the air surrounding the collembolan increases, and the animal rehydrates and eventually regains activity.

Megaphorura arctica (*Onychiurus arcticus* Tullberg, 1876) is a large collembolan that is common beneath bird cliffs, where it can be collected in large numbers using a pooter under stones. Its general distribution is northern Palaearctic, although there are records from as far south as the UK (Pitkin 1979). In Svalbard the ground beneath the bird cliffs is frozen between September and June, and for much of the period is at −10°C (Fig. 2; Coulson et al. 1995). Initial studies determined a summer SCP of around −6.1°C, and that the species is freeze avoiding (Worland 1996). The cuticle of *M. arcticus* is freely permeable to water vapour (Worland 1996), and desiccation in a dry atmosphere is rapid and lethal, with the animal losing >60% of their body water in less than 1 hour (Hodkinson et al. 1994). However the paradox of a freeze-avoiding invertebrate with a high SCP was resolved by studies on the rate of desiccation. Desiccated slowly in the presence of ice, the animals can survive extended periods at subzero temperatures (Holmstrup et al. 2002). Molecular mechanisms underlying desiccation tolerance are often complex, and are not yet completely understood. In cooled, desiccated *M. arctica*, the expression of genes involved in trehalose and glycogen (cryoprotectants) synthesis pathways has been observed, as well as various aquaporins involved in the movement of water to the outside of the cell, genes related to antioxidant activity and late embryogenesis abundant (LEA) proteins (Clark et al. 2007). Although trehalose has been shown to act as a cryoprotectant (Kandror et al. 2002), LEA proteins appear to be common protective molecules in drought-resistant organisms (Solomon et al. 2000; Tunnacliffe et al. 2005; Chakrabortee et al. 2007), preventing molecular aggregation (Chakrabortee et al. 2007), but also acting as antioxidants, molecular shields and membrane stabilizers, among other potential functions (Tunnacliffe & Wise 2007). Recently it has been shown that levels of LEA proteins increase with desiccation in *M. arctica*, as does the stress protein heat shock protein 70 (HSP70) in the Collembola *Orchesella cincta* (L.) and *Folsomia candida* (Willem, 1902) (Bahrndorff et al. 2009). Heat shock proteins have not been studied in *M. arctica*; nonetheless, heat shock proteins are suspected to play a role in conferring protection to a cold shock following non-lethal dehydration in the collembolan *F. candida* (Bayley et al. 2001), and are known to play a role in the overwintering survival of other invertebrate species (Rinehart et al. 2007; Clark & Worland 2008).

Future climate scenarios

Although the variation among climate models remains high, there is a consensus that the Arctic will become warmer during this century. The estimated temperature changes range from an increase of 4.3 to 11.4°C in winter, and from 1.2 to 5.3°C in summer (Christensen et al. 2007). At the same time, precipitation is expected to increase by 10–30%, with the largest increase occurring in winter. This will result in a thicker snow layer in winter, but as the temperature increases, the period when the soil is covered by snow is expected to decrease on average because of an earlier spring melt, and because of greater evaporation. There is also an indication of an increased frequency of positive air temperature events during the winter. This will increase the number of freeze–thaw cycles in winter, which will affect the soil temperature close to the surface, where an insulating layer of snow is lacking. In summer, soil moisture will initially increase (Mehl et al. 2007) because of thawing permafrost, but if the thawing depth becomes significant, a reduction in moisture is most likely to occur, as a result of the increased temperature and consequent evaporation from the surface.

Effects of the predicted future climate on invertebrate fauna

Climate change scenarios predict large-scale changes to winter conditions in Arctic regions (Christensen et al. 2007). Here, we highlight how these changes might be expected to impact the arthropod fauna.

Warming winter with increased frequency of extreme events

The effect of increased frequency of freeze–thaw events is unclear. Sulkava & Huhta (2003) found a marked decline in the arthropod fauna densities with increasing freeze–thaw cycles. Sjursen et al. (2005) found no effect except for a slight increase in the abundance of Acaridida, but Konestabo et al. (2007) observed large increases in many groups with increasing numbers of freeze–thaw events. In all these studies the freeze–thaw cycles were in late autumn or early spring, during periods when the soil fauna might expect such events given natural climate variability. Unusual freeze–thaw events mid-winter may prove more of a challenge. Other authors have also observed a variety of results, and it is safe to say the picture is as yet unresolved. An increased frequency of freeze–thaw events will also increase the occurrence and thickness of any surface ice layer. Perhaps not unexpectedly, an increased thickness in this surface ice layer has been shown to have an impact on Arctic ecosystems, e.g., being detrimental to the overwintering survival of reindeer in Svalbard because these animals continue to feed throughout the winter (Aanes et al. 2000). This ice layer also appears to act as a stressor to arthropods already frozen in the soil matrix, with mortality of Collembola overwintering in frozen soil under a 25-cm ice layer exceeding 54% compared with non-iced controls (Coulson et al. 2000). Oribatid mites were less susceptible and showed no significant effect of the surface ice layer.

Snow fall and lie

Increased snowfall will insulate the soil. However, it is important to appreciate that at high-latitude regions such as Svalbard the snow often arrives well after the ground has frozen, unlike the situation at more southerly latitudes (Leinaas 1981; Coulson et al. 1995). Snow cover depends on the interaction between precipitation and wind strength and direction and evaporation. This is especially the case in Svalbard, where precipitation is low and where the winds are often strong. Increased snow depth will insulate the soil, reduce temperature extremes and provide a more constant winter environment (Fig. 2). Nonetheless, Isard et al. (2007) demonstrated decreasing winter soil temperatures during the past 50 years in northern central USA, despite slightly warmer winters. They hypothesized that this was the result of thinner snow lie conditions because of reduced winter precipitation. However, because of increased evaporation rates the date of snow clearance may be earlier than present, and will result in a longer snow-free summer period (Christensen et al. 2007; Mehl et al. 2007). For some species the timing of snowmelt controls the local distribution, for example, the endemic aphid *Acyrthosiphon svalbardicum*, which is only present in areas with minimal winter snow lie and hence a long summer (Strathdee, Bale et al. 1995). Strathdee, Bale et al. (1995) predicted that under such conditions there would be a rapid population increase and expansion of the range of *A. svalbardicum*. However, the complexity of the system was demonstrated by Dollery et al. (2006), who observed the predicted population increase of *A. svalbadicum* after 1 year of experimental summer warming, but after 2 years of warming the predator populations also increased, and aphid populations were no longer significantly different from controls.

Interaction between cold tolerance and pollutants

Stress tolerance is known to be affected by environmental contaminants, for example, the effect of pollutants on drought tolerance in Collembola (Højer et al. 2001). There are also indications that such pollutants can also reduce cold tolerance (Holmstrup et al. 2000, 2008; Sjursen & Holmstrup 2004), and that the interactions between climate stress and pollutant may be synergistic (Holmstrup et al. 2000). With Arctic regions acting as a pollutant sink (AMAP 2006) it is likely that Arctic arthropods will encounter increasing pollutant loads. The effect of this on their winter ecology is not known. A further complication is that any pollutant effect may be dependent on interspecific relationships (Cortet et al. 2006) and so will vary between soils and communities.

Immigration of animals to Svalbard

Immigration is often thought of in terms of new invasive species. However, gene flow from mainland populations must be regarded as a key factor for species survival in a changing environment. It is likely that most of the invertebrate groups, if not all, colonized Svalbard within the last 10 000 years (Coulson 2007), and that for some groups of plants and animals connectivity to more southerly populations is relatively high (Coulson et al.

2002; Alsos et al. 2007). Accidental dispersal to Svalbard has been recorded in several species of Lepidoptera (Laarsonen 1985; Coulson et al. 2002), and it seems reasonable to suppose that such dispersal occurs in other groups as well. Hence, there is a potential input of genetic material from populations already inhabiting warming conditions, and this may expedite the adaptation of the Svalbard arthropod fauna to the warmer conditions forecasted by climate modellers, at least among some groups of arthropod.

Future research

Current interactions between climate change, overwintering strategies and invertebrate performance in High Arctic regions are unknown and difficult to elucidate, primarily because of too many undescribed variables, such as predation pressure or genetic input from other populations. Future winter ecology studies based on complementary laboratory and field studies of experiments should address the following themes.

- Winter mortality of key/common species and stages within species in common plant communities, especially gradients of soil moisture, snow thickness, organic soil depth and nutrient status (under bird cliffs), including the Upper Limit Cold Injury Zone of Turnock & Fields (2005).
- The effect of increasing freeze–thaw cycles, from both the stresses of such a temperature change on invertebrate survival and from the effect of the increased thickness of the surface ice layer, and associated potential anoxia stress.
- Changes in thickness and distribution of snow lie and subsequent effects on the duration of the summer period.
- Assessing future potential colonizing species, and the likelihood of these species becoming established.
- Assessing the gene flow from surrounding populations, and the effects this may have on overwintering survival.
- Interaction between pollution and cold tolerance.
- Diapause induction and termination.
- Molecular biology of cold tolerance, in particular the genetics of cold tolerance, gene control, and the role and upregulation of stress proteins.

Conclusions

Much of the study of arthropod winter ecology in polar areas has, until recently, concentrated on determining cold tolerance primarily from laboratory studies. As such, there is a good understanding of the main classes of cold tolerance and the physiological basis to these. Nonetheless, there are relatively few field studies of the overwintering ecology of High Arctic arthropods, and this is an area that needs additional research. During the past 20 years there have been an increasing number of field manipulation experiments investigating the response of the soil arthropod fauna to environmental disturbance. However, it is becoming increasingly apparent that there is still a lack of knowledge of long-term cold tolerance, including chill susceptibility, effects of freeze–thaw cycles, effects of changes in snow lie and effects of the increasing pollutant load in Arctic regions. Alterations in the vegetation associated with climate change will also influence the below-ground processes. As all these factors are linked by numerous feedback loops, modelling changes in arthropod winter ecology cannot be undertaken without considering the system as a whole. Moreover, the possible input of genes involved in overwintering from populations in more southerly latitudes has not been considered. It is becoming increasingly evident that the concept of a simple redistribution of southerly species northwards with climate change is simplistic in the extreme for Arctic regions.

There is hence an urgent need for integrated field studies of arthropod winter ecology, with complementary laboratory studies to take the theme of arthropod winter ecology further.

Acknowledgements

We thank the two anonymous reviewers for useful comments and suggestions on the manuscript.

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