The terrestrial invertebrate fauna of the Svalbard archipelago in a changing world: history of research and challenges

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Abstract—The High Arctic represents a unique environment, an environment from where knowledge is limited and which is currently experiencing rapid change. The archipelago of Svalbard in the European High Arctic possesses a terrestrial and freshwater invertebrate fauna that is distinctive and diverse. However, the majority of studies concentrate on the fauna of the comparatively mild west coast. Very few investigations of the colder east coast exist. Furthermore, scientific investigations are relatively recent. Scientific records of the terrestrial invertebrate fauna begin in the mid-19th century with species inventories and community descriptions but experimental field-based studies and physiological investigations did not commence until the 1980s. Some 570 articles consider this fauna, 54% of which have appeared since 1990. There is hence a dramatic and rapid increase in our understanding, which is not only improving our comprehension of Arctic ecosystem functioning but also providing a baseline for environmental change studies. Due to a largely pristine environment, a political focus and relative ease of logistics, Svalbard is set to become a focus of such studies. This article considers the state of knowledge of the terrestrial and freshwater invertebrate fauna of Svalbard, current research, and discusses the threats to the distinctive communities.

Résumé—Le Haut-Arctique représente un environnement unique qui reste mal étudié et qui connaît actuellement des modifications rapides. L'archipel de Svalbard dans l'extrême Grand Nord européen possède des faunes d'invertébrés terrestres et aquatiques d'eau douce particulières et diversifiées. La plupart des études, cependant, s'intéressent à la faune de la côte occidentale dont le climat est relativement doux. Il existe très peu de travaux faits sur la côte orientale à climat plus froid. Ces travaux scientifiques sont aussi relativement récents. De plus, les études scientifiques de la faune invertébrée terrestre ont débuté au milieu du 19e siècle avec des inventaires d'espèces et des descriptions de communautés, mais les études expérimentales basées sur les travaux de terrain et les recherches physiologiques n'ont commencé que durant les années 1980. Il y a environ 570 articles qui traitent de cette faune, dont 54% ont paru depuis 1990. Il se produit donc un accroissement spectaculaire et rapide des connaissances qui est non seulement en train d'améliorer notre compréhension du fonctionnement des écosystèmes arctiques, mais qui fournit de plus les renseignements de base pour les études sur les changements environnementaux. À cause de son milieu en grande partie non altéré, de son intérêt politique et de la facilité relative de la logistique, Svalbard est destiné à devenir le point de convergence de telles études. Notre article traite de l'état des connaissances des faunes d'invertébrés terrestres et aquatiques d'eau douce de Svalbard, ainsi que des études courantes et il discute des menaces aux communautés particulières de l'archipel.

Introduction

The Arctic is a region experiencing rapid environmental change (Arctic Monitoring and Assessment Programme 2011a). Temperatures are rising and are projected to continue to rise, precipitation patterns will alter, sea-ice cover is in retreat, the region is a sink for pollutants originating from lower latitudes, and human activities in the High Arctic are on the increase – all of these combine to threaten the characteristic Arctic environments of the far north (Chapin *et al.* 2005). One key component of the terrestrial system that will be affected by such changes

Received 31 May 2012. Accepted 18 November 2012.

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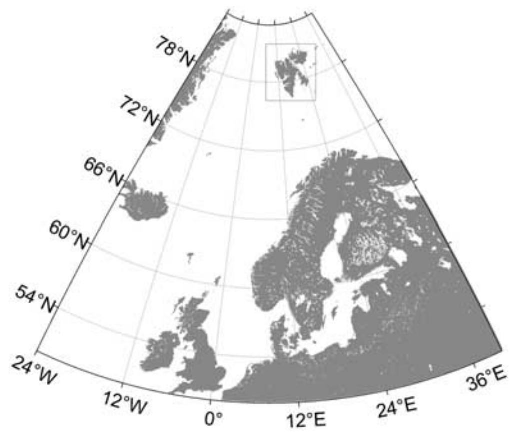
doi:10.4039/tce.2012.110

is the soil invertebrate fauna. It is clear that the invertebrate community plays a fundamental role in many ecosystem processes including nutrient cycling, energy flow, decomposition, pollination, herbivory, and parasitism (Speight *et al.* 1999; Bardgett 2005) all of which contribute to the characteristic High Arctic ecology. Moreover, the relatively simple polar (Arctic and Antarctic) ecosystems are thought to be particularly valuable for studies addressing basic questions of ecosystem function, providing examples across a wide range of levels of assemblage structure (Hodkinson *et al.* 2003; Adams *et al.* 2006). For example, biodiversity of terrestrial ecosystems may provide a robustness and stability to the characteristically large annual variation in the climate of the Arctic and, hence, also provide resilience to environmental change. Yet, the relationship between species diversity and ecosystem function often remains unclear, despite considerable debate around the importance, or otherwise, of "functional redundancy" in maintaining stability in ecosystems (Brussaard *et al.* 2007; Reich *et al.* 2012). Nonetheless, while invertebrates represent the majority of eukaryotic biodiversity, little is known about their distributions, populations, or associated trends (Mace *et al.* 2005). This is particularly true for Arctic regions. Despite this possibly inherent resilience to great natural environmental variability, these High Arctic systems may be particularly vulnerable to human disturbance (Jónsdóttir 2005), predominantly due to lengthy recovery and regeneration times. With a complex terrestrial High Arctic ecology and the intense international attention (scientific, political, and industrial), Svalbard can make an important case study for Arctic invertebrate communities.

Svalbard

The archipelago is centred on the principle islands of Spitsbergen, Nordaustlandet, Edgeøya, and Barentsøya, lying ~700 km north of the Norwegian mainland at 78°N, 12°E (Fig. 1). The islands have a land area of 62 000 km^2, 60% of which is permanently covered by ice or snow (Hisdal 1985). Before the signing of the Treaty of Svalbard (Spitsbergen Treaty) in 1920, Svalbard was *terra nullius*, a no mans land. Increasing activity in the islands from the turn of the 20th century, primarily coal and other mineral exploration, required the legal formalisation of the archipelago. By the Treaty of Svalbard, the archipelago was assigned to Norwegian sovereignty but with certain restrictions (Arlov 2003). First and foremost is the principle of nondiscrimination and open access with regard to commercial or mining activities to signatory nations. While science is not included in the treaty nondiscrimination clause, the Norwegian state practices nondiscrimination also in the case of science.

Fig. 1. Location of the principle islands comprising the Svalbard archipelago (box) in the European High Arctic.



Science in Svalbard

Scientific activities in Svalbard commenced in the middle of the 19th century. Among the first biological investigations were those of Boheman (1865) and Holmgren (1869). But biological projects really only commenced after the turn of the century. Early pioneers included Summerhayes and Elton who together published several ground-breaking articles describing the various habitats around the islands of Spitsbergen and Nordaustlandet (Summerhayes and Elton 1923, 1928). Publications pertaining to the invertebrate fauna of the archipelago increased rapidly through the 1920s and 1930s but declined during the period 1940–1945 with the intervention of the Second World War (Fig. 2). After the restoration of peace, science activities recommenced including the development of the international research village in the former Norwegian mining settlement of Ny-Ålesund. In 1962 a gas explosion

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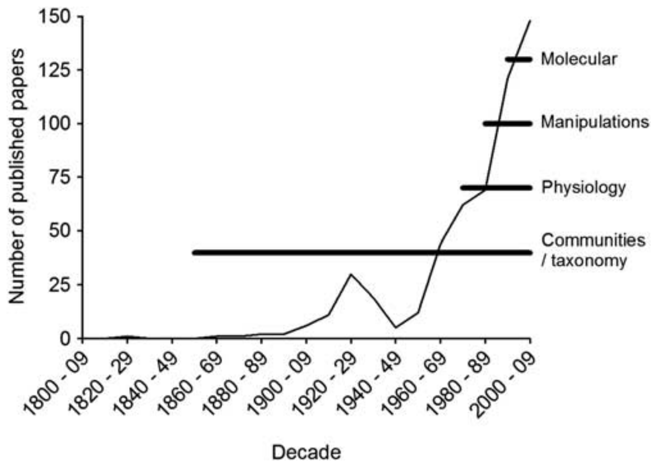
Fig. 2. Number of published articles considering the terrestrial or freshwater invertebrate fauna of Svalbard per decade. Bars indicate the range of subjects covered by publications during different periods.



in this mine resulted in the deaths of 21 miners and halted mining operations. The mine was closed the following year. In 1964, the Norwegian authorities signed an agreement with the European Space Research Organisation (ESRO) regarding the establishment of a Norwegian satellite telemetry station in Ny-Ålesund. Shortly afterwards, in 1966, Nordlysobservatoriet (Northern Light Observatory) in Tromsø set up operations in Ny-Ålesund and in 1968 the Norwegian Polar Institute established a station. The settlement attracted increased international attention and has developed into the Kongsfjord International Research Base (KIRB). At the time of writing, 13 nations have research stations located in Ny-Ålesund. The establishment of KIRB led to a rapid increase in the number of publications from 1990 in a wide range of subjects including upper atmosphere, ecotoxicology, pollutant studies, meteorology, and marine and terrestrial ecology including invertebrate studies. Collaboration by the researchers at KIRB with Svalbard Science Forum has enabled the identification of scientific priorities (Coulson *et al.* 2010).

In 1957 the Polish station in Hornsund, southern Spitsbergen, was established and is now operated year round by the Institute of Geophysics, Polish Academy of Sciences. Research at the station focusses on physical geography but there have been terrestrial invertebrate studies (Kaczmarek *et al.* 2012; Zmudczyńska *et al.* 2012). In Barentsburg there are research stations operated by several Russian institutions including the Kola Scientific Centre of Russian Academy of Sciences. While botanical projects are conducted, there appear to be few terrestrial invertebrate studies (Coulson *et al.* 2013; Coulson *et al.* in press). There are also smaller field-based projects at diverse locations around Svalbard, for example the recent establishment of Czech and Polish stations in Petuniabukta close to Isfjord, Spitsbergen.

In 1993, the University Centre in Svalbard (UNIS) located in Longyearbyen was opened. This provided new research opportunities at this High Arctic location. With an international airport in Longyearbyen, the archipelago offers perhaps unparalleled ease of access to High Arctic latitudes and comprehensive logistical support. Moreover, the current agenda within Norway is to establish the eastern regions of Svalbard as a "reference area for research" (Ministry of Justice and the Police 2009) and planning of the Svalbard Integrated Arctic Earth Observing System (SIOS) international initiative, part of the European Strategy Forum on Research Infrastructures (ESFRI) programme (European Commission 2012), is currently ongoing.

Physical environment

Svalbard is located close to the confluence of ocean currents and air masses of differing thermal characteristics (Humlum *et al.* 2007). This results in Svalbard being one of the most climatically sensitive regions in the world (Rogers *et al.* 2005).

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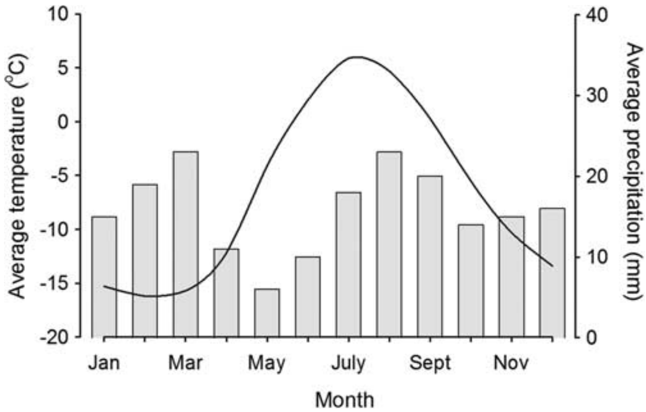
Fig. 3. Mean monthly precipitation (bars) and temperature (solid line) measured at Longyearbyen airport (Norwegian Meteorological Institute).



Low-pressure systems in the vicinity of Iceland and high-pressure systems over Greenland determine the synoptic airflow to Svalbard. In winter, this pattern is displaced further south resulting in cold air masses extending to Svalbard while in summer, warmer air from more southerly latitudes is directed to Svalbard (Hanssen-Bauer *et al.* 1990). Furthermore, considerable heat is transported north from more southerly latitudes by the West Spitsbergen Current, a branch of the North Atlantic Drift. The result is that the climate of the islands is mild for the latitude. The annual mean air temperature is −6.7 °C (Fig. 3) but four months have positive mean air temperatures, from +0.3 °C in September to 5.9 °C in July (Norwegian Meteorological Institute 2012).

Svalbard is experiencing some of the greatest changes in temperatures in the Arctic (Arctic Monitoring and Assessment Programme 2011a). Located at the southern limit of the Barents Sea winter sea ice, the winter and summer temperatures are heavily influenced by the presence or absence of this sea ice. In particular, lack of sea ice in the winter resulting in warmer winter and spring air temperatures (Rogers *et al.* 2005; Stroeve *et al.* 2012). Recent decreases in the extent of this sea ice have therefore exacerbated local increases in global mean air temperature. Warm air masses may also arrive during winter resulting in abnormally mild periods. In winter 2011–2012, temperatures were on average some 10 °C above long-term normals (Fig. 4). Precipitation was also remarkably high during this winter. Ny-Ålesund received 98 mm of rain in one 24-hour period, 28% of the average annual precipitation (Norwegian Meteorological Institute 2012). While this particular winter was unusually extreme, it demonstrates the wide variation in winter conditions that are characteristic of this region.

The settlements in Svalbard, Longyearbyen, Ny-Ålesund, and Svea (all Norwegian); Barentsburg (Russian); and Hornsund (Polish), are all located along the west coast (Fig. 5). Most of the settlements were originally established as coal mines. Hence, the west coast positions of these towns is due to a combination of the geographic location of the coal deposits and the heavier sea-ice conditions on the east coast, resulting from the southerly flowing cold East Spitsbergen Current, restricting access. Precipitation is geographically extremely variable. The west coast having the greatest precipitation, for example Barentsburg on the west coast receives a mean precipitation of 525 mm per year (Norwegian Meteorological Institute 2012) but the interior of the islands is substantially dryer. Longyearbyen, 50 km to the east of Barentsburg, recorded an average annual value of 210 mm (Fig. 3). In both cases most of the precipitation falls during winter as snow.

During the last glacial maximum (LGM), the archipelagoes of the Barents Sea were largely covered by ice (Gataullin *et al.* 2001) and were progressively exposed as the ice began to retreat ~10 000 years ago. The relatively short period

Fig. 4. Monthly precipitation and mean temperature during winter 2012 compared with long-term normals. Normals for the period 1961–1990. Svalbard airport, Longyearbyen (Norwegian Meteorological Institute). Monthly precipitation 2011–2012 = filled bars, Monthly precipitation normal = shaded bars; Mean monthly temperature 2011–2012 = solid line; Mean monthly temperature normal = broken line.

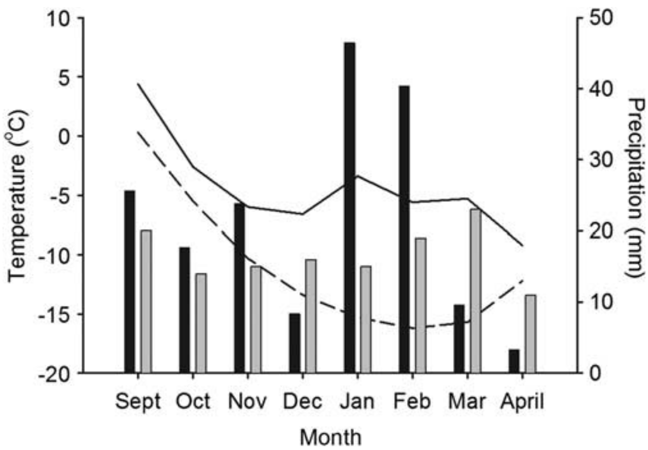


Fig. 5. Map of Svalbard with main settlements indicated.

since deglaciation, combined with the Arctic climate and continuing periglacial soil processes, have strongly influenced habitats and ecosystems. As seen across the Arctic, the environment is characteristically highly heterogeneous with, for example, dry stony ridges, periglacial features, areas of late snow-lie, heath, or wet moss all in close proximity (Jónsdóttir 2005). On a regional basis, northern ice-free areas consist largely of polar desert characterised by low precipitation and short snow-free growing seasons. Vascular plant cover is typically scarce, often <15% (Jónsdóttir 2005; Cooper 2011), and greatest along the coastal margins. While soils protected under deeper snow experience winter temperatures no lower than −10 °C (Coulson *et al.* 1995), the ridge tops, blown free of winter snow, or areas kept clear of snow by wind eddies, may track air temperatures closely and approach −40 °C on occasion. The soil surface temperature may often attain 20 °C (Coulson *et al.* 1993) due to the 24-hour midnight sun despite air temperatures rarely attaining double figures. Generally soils are thin, rarely more than a few centimetres thick, and overlie old moraine debris, patterned ground or rock but they may vary considerably in depth and form over short distances. In nutrient enriched areas, for example under bird cliffs, organic soils of over 20 cm depth may also accumulate, illustrating the impact of nutrient flow from the marine environment to the nutrient limited terrestrial habitat (Odasz 1994; Zmudczyńska *et al.* 2009). Melting snow and permafrost also provides a constant cold water source throughout the summer often resulting in wet moss areas in direct proximity to dryer polar desert vegetation. In such wet areas, the moss may develop into thick carpets, or turfs, some tens of centimetres deep, efficiently insulating

https://doi.org/10.4039/tce.2012.110 Published online by Cambridge University Press

the ground beneath against the warming effect of solar insolation (Coulson *et al.* 1993).

Running freshwaters are characterised by the dominance of glacial melt water, typically in the form of large braided river systems with high sediment loads, highly irregular flows, and low temperatures even in summer. In Svalbard, river flow may start late June to early July. Ice break-up on the lakes, however, occurs later, from mid-July until late August (Svenning and Gullestad 2002). Temporary thaw ponds, permanent shallow ponds and small lakes are numerous and because of the low water depth (usually <2 m) many of these water bodies freeze solid during winter while the shallower ones can dry out during summer.

The environment of Svalbard is hence highly heterogenous, both geographically and temporally. It is established that air temperatures globally are increasing, although precise causes are more contentious. Regions such as Svalbard are also under increasing pollutant load, both allochthonous and local, increased industrialisation, human activity, and increased threat of introduction of alien species. This article examines how these changes may affect the terrestrial and freshwater invertebrate ecology of the High Arctic, focussing on the Svalbard ecosystem.

Study of terrestrial invertebrates in Svalbard

The terrestrial invertebrate fauna of Svalbard may be among the most comprehensively catalogued for any region of the Arctic (Hodkinson in press). There are close to 600 articles in international journals considering this fauna (Fig. 2) and three checklists summarising this literature (Coulson and Refseth 2004; Coulson 2007a, 2012). The current species list for Svalbard cites some 960 species names excluding the Protoctista (Coulson 2007a, 2012) (Table 1). This list is under constant revision due to the large number of synonyms and taxonomic confusion (Ávila-Jiménez *et al.* 2011; Bayartogtokh *et al.* 2011) and new species, either to Svalbard or new to science, are constantly being described (Gwiazdowicz *et al.* 2012; Kaczmarek *et al.* 2012; Coulson *et al.* 2013). It is clear that, contrary to first appearances, Svalbard has a diverse invertebrate fauna that includes apparent endemics, for example the aphid *Acyrthosiphon svalbardicum* (Heikinheimo, 1968) (Hemiptera: Aphididae) (Heikinheimo 1968) and the mite *Amblyseius magnanalis* (Thor, 1930) (Acari: Phytoseiidae) (Thor 1930). Since until the end of the LGM Svalbard was covered with an ice sheet and no invertebrates or plants are thought to have survived the glacial maximum *in situ* (Alsos *et al.* 2007; Ávila-Jiménez *et al.* 2011), the current fauna and flora is the result of recent immigration processes, although there remains the possibility that in small refugia some plants may have persisted during this period of glaciation (Westergaard *et al.* 2011).

Table 1. Number of terrestrial and freshwater species present in Svalbard.

Group	Number of species
Rotifera	173
Nematoda	113
Acanthocephala	3
Platyhelminthes	27
Annelida	36
Tardigrada	89
Chilicerata, Acari	152
Araneae	18
Collembola	64
Insecta	252
Crustacea	33
Total	960

Source: Coulson (2012).

While a general understanding of the terrestrial and freshwater fauna is increasing fast, the great majority of the studies have been undertaken on the west coast, primarily in the Isfjord region close to Longyearbyen and from KIRB at Ny-Ålesund. Less than 10 papers consider the invertebrate fauna of the eastern regions (Coulson 2012). Those that do provide inventories of the Rotifera, Tardigrada (De Smet 1993; De Smet *et al.* 1998), and Collembola (Fjellberg 1997; Coulson *et al.* 2011). Despite the lack of knowledge of the invertebrate fauna of the eastern regions, there are indications of different communities here than those found on the west coast. Fjellberg (1997) describes 34 species of Collembola from Nordaustlandet in the far north east of Svalbard. Of these, three species have not yet been observed on the west coast. The reasons for this difference are as yet unclear but may be related to different immigration histories. The east coast being influenced by the East Svalbard Current (Skogseth *et al.* 2005) bringing driftwood from the great Russian rivers. On the west coast it is the West Spitsbergen Current that dominates, bringing warm water northwards from the Atlantic and hence potentially bearing a dissimilar fauna from the East Spitsbergen Current. An improved knowledge of the fauna of the eastern regions is urgently required.

Environmental change challenges facing the current invertebrate communities

Temperature

Air temperatures in Svalbard are rising and are expected to continue to do so (Arctic Climate Impact Assessment 2004). The greatest rise will be during the winter period (Arctic Monitoring and Assessment Programme 2011a). For many of the invertebrates such temperature increase will have little effect. Snow cover insulates the ground surface and reduces both the minimum temperatures experienced by overwintering invertebrates and also the number, extent and rapidity, of short-term fluctuations (Coulson *et al.* 1995) but in areas where snow is thin, or accumulates late in the year, soil temperatures may track air temperatures closely. Some invertebrates overwinter in areas with only shallow snow cover. This strategy exposes these species to the potentially low air temperatures but it does provide the animal with the maximum summer period. With no snow pack to melt, the animals can become active early in the spring (Strathdee and Bale 1995; Ávila-Jiménez and Coulson 2011a). For such species, a rise in average winter air temperature will be experienced due to current environmental change, but this may not pose a significant challenge since average temperatures will remain below 0 °C. However, elevated winter air temperatures may affect overwintering soil animals in two ways. First, elevated winter air temperatures will increase the rate at which snow evaporates reducing the thickness and hence decreasing the insulating capacity of the snow. Second, there will be an increase in the number of rain-on-snow (ROS) events. Warm air masses arriving at Svalbard already periodically bring such events. Projections of how the snow pack and ROS events will change are few but the likelihood is that for large areas of the Arctic ROS events will increase in both frequency and area affected (Rennert *et al.* 2009). Such events result in the formation of ice lenses either within the snow or on the ground surface. These events may have significant ecological consequences. Coulson *et al.* (2000) demonstrated a reduction in survival of Oribatidae mites and Collembola following manipulation of winter ice thickness. The experimental ice layer reduced the densities of these two groups by up to 50%, mites being more resistant than the Collembola. Moreover, there was an interaction between the thickness and the duration of the ice layer. The cause of mortality is unclear since the animals were already encased in ice within the frozen ground and that it has been shown that many of the same species can survive extended ice encasement at below −20 °C (Coulson and Birkemoe 2000). An increased frequency of icing events may therefore be expected to have deleterious consequences for the overwintering soil fauna. This may also include the nematode gut parasites of the Svalbard reindeer. *Marshallagia marshalli* (Ransom, 1907) (Nematoda: Trichostrongylidae) is deposited as eggs in the faeces of the reindeer during winter, often on the winter grazing areas on the tops of the wind-blown ridges where snow cover is thin. The parasite reinfects the host when the infective third instar the following winter (Carlsson *et al.* 2012). Changes in ice lense occurrence and form may have effects on the parasite survival but may also effect movement and grazing patterns of the host resulting in changes in infection rates.

Freeze–thaw cycles are expected to increase in frequency in many Arctic regions (Arctic Climate Impact Assessment 2004). Such cycles have attracted attention in the sub-Arctic (Sjursen *et al.* 2005; Konestabo *et al.* 2007; Bokhorst *et al.* 2012) but the situation in the High Arctic may be somewhat different. During the spring, thaw the snow pack and upper soil layers typically gradually warm until they become isothermal and close to 0 °C. The whole pack then melts rapidly. Since this does not occur until well after the beginning of the midnight sun, once the ground becomes free of snow it immediately warms considerably due to the potential 24-hour insolation (Fig. 6; Coulson *et al.* 1995, Fig. 2). Hence, there are fewer diurnal freeze–thaw cycles than in alpine environments. Experimentally creating such events at sub-Arctic Abisko, Sweden, has revealed complicated responses of the soil fauna to freeze–thaw cycles. Konestabo *et al.* (2007) found no

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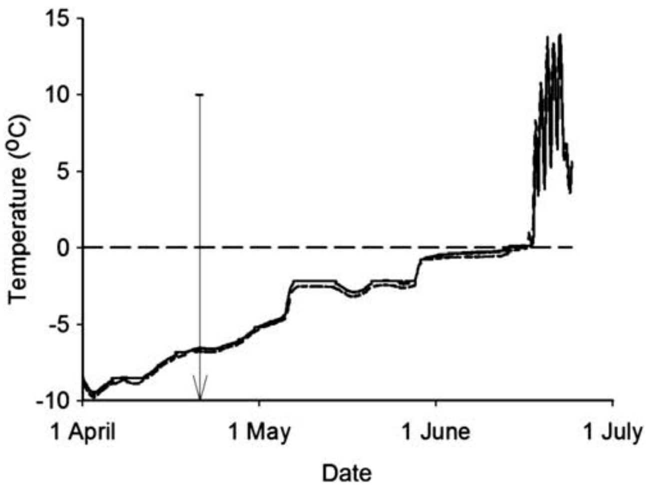
Fig. 6. Soil temperatures at 5 mm depth between April and July 2011 recorded by two TGP-4020 Tinytag dataloggers (Gemini, Chichester, West Sussex, United Kingdom) in *Dryas octopetala* vegetation in Adventdalen, Svalbard (78°12′N, 15°49′E). Vertical arrow indicates the start of the period of midnight sun (19 April).



mortality effect on the oribatid mites or Collembola, while (Bokhorst *et al.* 2012) concluded that survival depended more on life form and species trait than taxa *per se*. With the presence of permafrost in Svalbard, such freeze–thaw events are not expected to penetrate deep into the organic soil layers but the invertebrate fauna inhabiting the upper layers of the organic soil may be subjected to additional temperature stresses during future winters with consequences for community composition.

Summer air temperatures are predicted to rise only slightly (Arctic Climate Impact Assessment 2004). Given the great current inter-annual variation, it is not clear that changes in summer air temperatures will have any immediate influence on the invertebrate fauna. Nonetheless, a gradually elevated mean temperature may have slight, but cumulative, effects. Many polar invertebrates may be preadapted to warmer summers. The respiratory Q_{10} of the collembolan *Megaphorura arctica* (Tullberg, 1876) (Collembola: Onychiuridae) is between 5.8 and 7.0, which has been interpreted as providing the ability to respond rapidly to small thermal increments in the surroundings (Block *et al.* 1994). It is also important to appreciate that summer air temperatures may be significantly lower than temperatures experienced by many invertebrates at the soil surface. Soil surface temperatures may be raised considerably above air temperature by heating from solar insolation (Coulson *et al.* 1993) while basking insects taking advantage of floral solar furnaces (Kevan 1975) may be several degrees warmer than air temperatures. Hence, a rise of average air temperature of 1 °C may increase the summer air temperature day degree sum by a considerable percentage, yet have only a negligible influence on the invertebrate fauna at ground level. Conversely, increased cloud cover, resulting in lowered insolation, may result in lower soil temperatures despite small increases in average air temperatures. The importance of understanding the microhabitat conditions cannot be overemphasised.

Few studies have investigated the effect of warming soils on the invertebrate communities in Svalbard (Coulson *et al.* 1993; Webb *et al.* 1998; Dollery *et al.* 2006). In grassland, Briones *et al.* (2008) observed that warming soil had little effect on soil respiration. Some groups, Oligochaeta and Prostigmata (Acari) mites, decreased in densities while Enchytraeidae (Oligochaeta) moved to deeper soil regions. In Svalbard, with generally thin organic soils, moving deeper may not be an option. How the soil ecosystem will respond to temperature change is hence difficult to project. Using open top chambers (OTC), Dollery *et al.* (2006) investigated the above-ground invertebrate community in Endalen close to Longyearbyen. They observed

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similar effects on the Collembola and oribatid mite fauna to that measured previously in tundra heath vegetation at Ny-Ålesund (Coulson *et al.* 1993). However, they also detected trophic level-specific effects of the warming. After two years of warming, the densities of aphids and Symphyta larvae were greater in controls than in the warmed OTCs. They explained this by suggesting that the rapid increase in population densities of the herbivores in the OTCs after the first summer of warming attracted large numbers of predators that reduced the herbivore densities in summer two. It is not clear how to fully interpret these results since it is likely that the highly mobile predators may have moved into the OTCs in response to the high prey densities after the first treatment summer. Complimentary field and laboratory studies on the aphid *A. svalbardicum*, which feeds on *Dryas octopetala* Linnaeus (Rosaceae), suggested that aphid population densities would increase rapidly with a longer summer, warmer summers, or a combination of both (Strathdee *et al.* 1993). This was based on the more frequent reproduction of the additional viviparous generation under such climate scenarios. However, subsequent field investigations have failed to detect this extra generation despite the occurrence of several summers with the predicted appropriate thermal sums (Hullé *et al.* 2008). It is nonetheless clear that considerable changes in the *D. octopetala* invertebrate communities may be expected.

Precipitation

Precipitation is projected to increase (Arctic Monitoring and Assessment Programme 2011a). The majority of this will fall as additional snow during the winter. Errors in the projections of precipitation are considered to be greater than for changes in temperature since precipitation is to some extent dependent on the accuracy of temperature projections (Arctic Monitoring and Assessment Programme 2011a). Snow lying on the ground in Svalbard has usually been redistributed and modified by the wind (Jaedicke *et al.* 2000). Wind speeds may have an average velocity of over 5 m/second and with the open landscape and lack of tall vegetation, many areas may be blown free of snow the entire winter, while in lee sides, hollows, valleys, and behind obstructions, the snow may accumulate to a depth of several metres (Eckerstorfer and Christiansen 2011).

While snowfall may increase, it is not clear whether this will result in deeper snow or whether this extra snow will be blown in the sea. If the additional snow does accumulate then there will be an interaction with elevated winter temperatures. Higher temperatures will increase the rate of evaporation of snow reducing the resultant accumulation. Similarly, extreme ROS events, such as that seen in January/February 2012 (Fig. 4), can result in the melting and removal of the snow pack and lead to an extremely thin snow layer the remaining winter. This may potentially have consequences for the overwintering soil fauna. Where snow is thinner mean winter soil temperatures may actually decrease (Isard *et al.* 2007) due to lack of insulation despite increases in average air temperature. During periods when warm air masses are directed over Svalbard, such as in winter 2011–2012 (Fig. 4) the soil fauna may experience repeated freeze–thaw cycles.

If there is an overall accumulation of snow due to elevated winter precipitation then this will have consequences for the duration of the subsequent summer experienced by the invertebrate fauna. Deep snow takes longer to thaw, and thus to release the ground, than shallow snow layers. Activity of Arctic invertebrates is more related to the timing of snow clearance than average air temperatures (Høye and Forchhammer 2008). The effect of deep snow reducing the summer period to below a critical minimum required to complete the life cycle seems to be a factor limiting the local distribution of the endemic aphid *A. svalbardicum* (Strathdee *et al.* 1993; Ávila-Jiménez and Coulson 2011a). No time series data on the date of snow clearance in Svalbard appears in the literature. Date of the onset of snow melt may be a proxy but fails to take into account depth of snow and the effect that this has on the duration of the melt period. While extremely geographically variable throughout the Svalbard archipelago, the current evidence is that the date of the summer melt onset is generally becoming earlier rather than later (Rotschky *et al.* 2011). On a pan-Arctic scale no current trend is detectible (Wang *et al.* 2011), but time series are short.

It is not generally thought that vascular plants in Svalbard are moisture limited. The main

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limiting factors governing species distributions may often be nutrient availability and geological characteristics influencing soil type (Jónsdóttir 2005). Nonetheless, summer precipitation may have an effect on the invertebrate fauna, for example drought susceptible Collembola. Results from a cloche manipulation experiment (Coulson *et al.* 1993) suggested that Collembola populations decrease when soils desiccate, probably due to the inability to reduce evaporation through their permeable cuticle (Harrisson *et al.* 1991; Hertzberg and Leinaas 1998). No such population reduction was seen for the oribatid mites with largely impermeable integuments (Webb *et al.* 1998). Hence, it is possible that Collembola densities in certain areas will decrease as a result of increased temperature and effects on soil moisture while oribatid mite populations may benefit by reduced resource competition with the Collembola. Enchytraeidae are also considered to be susceptible to drying soils and less able to adapt to dryer climates (Maraldo and Holmstrup 2009). However, elevated soil temperatures are highly dependent on insolation and an increase in cloudy days, or increased summer precipitation, may counter this and reduce soil desiccation. The effect of these changes in soil invertebrate community structure, and processes such as nutrient flow, are difficult to predict.

The short summers constrain the annual cycle of invertebrates in Arctic regions (Høye and Forchhammer 2008). Changes in the date of the spring melt will have consequences, for example, on the timing of the emergence of Diptera. In warm summers, there may be two peaks of emerging Chironomidae (Diptera) in Svalbard while in cooler years only one (Coulson *et al.* 1996). This will have implications for breeding success of insectivorous birds such as snow buntings (*Plectrophenax nivalis nivalis* (Linnaeus, 1758); Aves: Calcariidae). Changes in phenologies may disrupt synchronies between host and herbivore/parasitoid. The aphid *A. svalbardicum* clearly prefers to feed on flowering shoots (Ávila-Jiménez and Coulson 2011a), probably due to the availability of high-nutrient phloem sap. Changes in development rate with elevated temperatures may result in a lack of synchrony between host and herbivore with difficult to predict outcomes for both host and herbivore.

Other climate-related changes may be even more subtle. Wolf spiders in Greenland are showing a gender size dimorphism response to climate change with mean female body size increasing greater than male (Høye and Hammel 2010) with implications for egg batch size and possible sexual cannibalism. They suggest that such effects on the top predator in the system may have feedbacks on the system as a whole.

Allochthonous pollutants

There is considerable attention on the deposition of pollutants in Arctic regions (Arctic Monitoring and Assessment Programme 2010, 2011a, 2011b), but little research has been undertaken on the relationship between pollutants and the invertebrate fauna. There is reduced bioaccumulation/biomagnification of persistent organic pollutants in the terrestrial food chain due to the lack of lipid as a major component of body mass as is common in the marine system. However, it is possible that heavy metal pollution challenges the soil animals. Mercury may affect cold tolerance and hence the ability of the soil fauna to tolerate the long winter (Holmstrup *et al.* 2000, 2008; Sjursen and Holmstrup 2004). Moreover, it is becoming appreciated that stressors often act synergistically (Holmstrup *et al.* 2000; Bindesbol *et al.*, 2009). Nonetheless, animals may be able to adapt to such pollutants. Earthworms have been demonstrated to acquire a genetic tolerance to some metals (Fisker *et al.* 2011). To date the research undertaken has concentrated on laboratory studies so the response in the natural environment, especially in the Arctic, is unclear.

Tourism, industrialisation, and science

Tourism, and in particular, cruise ship traffic has increased. In 1996, 52 landing sites were visited by cruise ship tourists and by 2010 this had increased to 144 (Evenset and Christensen 2011). This activity has negative local impacts, especially on the vulnerable vegetation due to trampling (Hagen *et al.* 2012).

Of concern is the potential for increased human traffic to introduce alien invertebrate species to the archipelago. The resident invertebrate fauna of Svalbard consists of a community of species with largely Holarctic or Palaearctic distributions. Environmental change may open opportunities for new species to colonise the Arctic. However, such colonisation events are often stochastic and hence

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difficult to predict. Even when suitable habitats become available it does not follow that invertebrates will be able to disperse to these regions and exploit the new opportunities (Van der Putten *et al.* 2010). Within mainland Arctic Europe it is clear that invertebrate communities are reacting to environmental change by changing species composition, for example among the insect pollinators (Franzen and Ocklinger 2012). For isolated islands, immigration may often depend on rare long-distance dispersal events followed by short-distance local population expansion (D'Andrea *et al.* 2009). A recent biogeographical analysis of Collembola species in the Arctic concluded that the current distribution patterns are the result of dispersal from refugia since the end of the LGM rather than the constraints of local physical environments (Ávila-Jiménez and Coulson 2011b). Hence, the establishment of new species and community response to climate change may be slow. Recently, the role of migrating birds has been implicated in creating soil invertebrate biodiversity in the Arctic (Lebedeva and Lebedev 2008). This would provide a potentially rapid mechanism by which alien invertebrate species may disperse, and potentially establish, in Svalbard.

Human introduction of alien species has caused large changes in ecosystems in many polar regions, for example the sub-Antarctic islands (Scheffrahn *et al.* 2009; Greenslade and Convey 2012). In a recent review, Hughes and Convey (2010) considered invasions by non-indigenous species to be among the greatest threats to biodiversity. But there are few examples of accidental introduction of invertebrates into the terrestrial ecosystem of the Arctic, although a number of introductions into the Arctic terrestrial system are believed to have occurred in Arctic Canada, Iceland, and the Faroes (Solhøy 1981; Forbes 1995; Rundgren 2007; Majka and Klimaszewski 2008). Aphids (Hemiptera: Aphididae) are also recognised to have been introduced to Arctic regions following human introduction of host plants (Stekolshchikov and Buga 2009) but there are few current records of humans introducing invertebrates to the natural environment at High Arctic latitudes, for example, Svalbard (Coulson *et al.* 2013). The lack of recently introduced invertebrate species into the High Arctic may also be due to relatively great, on geological timescales. Species connectivity via dispersal to mainland populations enabling natural movement and colonisation processes to dominate.

In the last 100 years, human activity in Svalbard has increased dramatically. In 2012, there were ~2500 permanent residents in the settlements (primarily Longyearbyen and Barentsburg) and tourist visitors have increased from 20 000 per annum in 2000 to almost 40 000 in 2010 (Sysselmannen 2012). There is an increasing risk of human-introduced species arriving and becoming established. Approximately 60 species of alien vascular plants have been recorded in the settlements of Svalbard and 28–37 are believed to have been firmly established but do not seem to be spreading far beyond the point of establishment (Elven and Elvebakk 1996; Liška and Soldán 2004; Alsos *et al.* 2012). Several species of synanthropic invertebrate such as the merchant beetle, *Oryzaephilus mercator* (Fauvel, 1889) (Coleoptera: Silvanidae) (Coulson 2007b), appear to be established in human dwellings. Additionally, there are the ectoparasites and intestinal parasites of the introduced sibling vole (*Microtus levis* Miller, 1908; Mammalia: Cricetidae) restricted to the derelict mining town of Grumant, Isfjord (Krumpàl *et al.* 1991; Henttonen *et al.*, 2001). Recently, Coulson *et al.* (2013) surveyed the soils beneath the abandoned greenhouses and cowsheds in Barentsburg and identified 46 invertebrate species, 11 of which (24%) were new records for Svalbard and none of which are considered High Arctic species. They concluded that these species had been brought into Svalbard with the imported soils for the greenhouse and that the rich manured soils created a unique environment enabling persistence. Few of the new species identified were considered potentially invasive but it was noted that two species of Collembola could potentially establish in the rich ornithogenic soils beneath the sea bird colonies. These Collembola had demonstrated an invasive habit in Iceland and it was thought that the bird cliff communities, highly characteristic of the Svalbard terrestrial ecosystem (Jónsdóttir 2005), may be vulnerable. However, while the potential for accidental introduction remains, there seem to be few exotic invertebrates in the archipelago.

In addition to import with machinery or industry (Hughes *et al.* 2010), species may hitchhike with travellers themselves. Ware *et al.* (2011)

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found a great number of alien seeds on the shoes of travellers passing through Svalbard airport, an average of 3.9 seeds per traveller. Twenty-six percent of these seeds germinated under simulated Svalbard conditions indicating at least the possibility of potential establishment. Similar studies for the invertebrate fauna are in progress.

Apart from the danger of new invasive species becoming established there is the less conspicuous, and potentially insidious, effect of additional genetic input. New individuals of a species already known from Svalbard may introduce additional genetic material and/or cryptic species (Schäffer *et al.* 2010). Hidden genetic diversity may be significant (Emerson *et al.* 2011) and constitute a major component of biodiversity but there are, as yet, few studies on this topic (Mace *et al.* 2005). The consequences of such introduction of new genetic material in a period of rapid environmental change are unclear.

Industry in Svalbard (primarily mining activities) has decreased and is currently restricted to Longyearbyen, Svea, and Barentsburg. Detailed impact assessments are required for proposed industrial activity to limit environmental harm, for example the expansion of the coal mine at Svea into Lunckefjell (Hagen *et al.* 2010). Potential oil reserves have not been identified on land in Svalbard, although there is activity in the Barents Sea. However, exploitation of these reserves is costly, logistically complicated, and in many cases is not likely to commence in the near future (Potts and Hoel 2011).

The impact of human activities, such as local pollution or cruise ship landings, may be locally intense but is not widespread. The introduction of new regulations, such as the ban on ships using heavy fuel oil in the nature reserves and national parks in Svalbard (Evenset and Christensen 2011) and the management plan for the eastern regions of the archipelago, are designed to increase the level of environmental protection for this region of the Arctic and will reduce deleterious impacts on the soil fauna.

The number of science publications has increased (Fig. 2). However, the archipelago is governed by the Svalbard Environmental Act (2001) and 65% of the land area is protected as either national park or nature reserve. All projects that have an impact on the environment must be registered with the Research in Svalbard database (Svalbard Science Forum) and obtain permission from the office of the Governor of Svalbard (Sysselmannen). Hence, while the number of scientific projects is increasing dramatically, and is set to increase further if the SIOS project is fully funded, there are checks in place to limit the environmental impact of these activities.

Conclusions

In summary, the ecology of Svalbard has attracted increasing attention during the last 100 years. Knowledge of the invertebrate fauna and its role in the ecosystem is rapidly increasing. However, the archipelago is going through a period of rapid environmental change including both climate and industrialisation. The effect of any, or all, of these changes is species specific. Yet alterations in the ecology of one species will have implications for the rest of the ecosystem through interspecific and trophic level interactions (Walter 2010). It is not the aim of this article to review all the effects of climate change. However, it is clear that the effects of a changing environment on the invertebrate fauna of Svalbard are hard to project. The invertebrate fauna of Svalbard is among the best known for any Arctic region (Hodkinson in press). Even so, there are many unknowns and uncertainties that still need investigation.

Acknowledgements

The author thanks Malin Daase for the preparation of Fig. 1 and two anonymous reviewers for valuable contributions that improved the manuscript.

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