The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef Land and Novaya Zemlya.

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Abstract

Arctic terrestrial ecosystems are generally considered to be species poor, fragile and often isolated. Nonetheless, their intricate complexity, especially that of the invertebrate component, is beginning to emerge. Attention has become focused on the Arctic both due to the importance of this rapidly changing region in the Earth System and also the inherent interest of an extreme and unique environment. The three archipelagoes considered here, Svalbard, Franz Josef Land and Novaya Zemlya, delineate the Barents Sea to the west, north and east. This is a region of convergence for Palearctic and Nearctic faunas re-colonising the Arctic following the retreat of ice after the Last Glacial Maximum (LGM). Despite the harsh Arctic environment and the short period since deglaciation, the archipelagoes of the Barents Sea are inhabited by diverse invertebrate communities. There is an obvious imbalance in our understanding of the biodiversity of each archipelago, and in our knowledge of many taxa. Research effort in Svalbard is increasing rapidly while there are still few reports, particularly in the western literature, from Franz Josef Land and Novaya Zemlya. Nevertheless, there appears to be a surprising degree of dissimilarity between the invertebrate faunas, possibly reflecting colonization history. We provide a baseline synthesis of the terrestrial and freshwater invertebrate fauna of the Barents Sea archipelagoes, highlight the taxa present, the characteristic elements of fauna and the complexity of biogeography. In doing so, we provide a background from which to assess responses to environmental change for a region under increasing international attention from scientific, industrial and political communities as well as non-governmental organizations and the general public.

Key words.

Novaja Zemlja; Frans Josef Land; Spitsbergen; Spitzbergen; biodiversity; colonization; isolation; High Arctic.

1. Introduction

Arctic terrestrial ecosystems are often considered to be species poor and fragile. The high latitude archipelagoes of the Barents Sea are also isolated due to their geographic separation from Eurasia. Nonetheless, their intricate complexity, especially that of the invertebrate component of their communities, is beginning to emerge. . The known terrestrial and freshwater invertebrate fauna of this archipelago currently contains over 1,000 named species (Coulson and Refseth, 2004; Coulson, 2007a, 2013b). Vascular plant diversity totals 74 species in Franz Josef Land (Tkach et al., 2008), 173 in Svalbard (Elven and Elvebakk, 1996) and 216 in Novaya Zemlya (Tkach et al., 2008). Bryophyta (mosses, liverworts and hornworts) form an important component of the environment in the Arctic (Turetsky et al. 2012). In Svalbard there are currently 373 accepted species (Frisvoll and Elvebakk, 1996) while lichens are more speciose, 597 species being recorded (Elvebakk and Hertel, 1996). Recent inventories of the bryophytes or lichens of Novaya Zemlya and Franz Josef Land are not available.

Investigations of poorly sampled regions within the islands along with studies of genetic diversity, including identification and quantification of cryptic speciation, are likely to lead to considerable increases in invertebrate diversity estimates (Ávila-Jiménez, 2011). The existing species inventories also suffer from taxonomic limitations, in particular relating to unidentified synonymies and misidentifications (Coulson, 2007a; Ávila-Jiménez et al., 2011; Bayartogtokh et al., 2011). Detailed knowledge of the distributions and biogeography of the majority of invertebrate species remains limited. Even in comparatively well-known regions such as western Svalbard, the publication of new species records for the archipelago is frequent, and new taxa continue to be formally described (e.g. Pilskog, 2011; Chaubet et al., 2013; Gwiazdowicz et al., 2012a, 2012b; Kaczmarek et al., 2012). Even in comparison with the uncertainties applying to Svalbard, diversity of the Russian archipelagoes of Franz Josef Land and Novaya Zemlya remains understudied, while much of the information that is available is not readily accessible in the western (English language) literature.

It is clear that the invertebrate community plays a central role in many key ecosystem processes, such as nutrient cycling, energy flow, decomposition, bioaccumulation of pollutants, herbivory, pollination and parasitism (Petersen and Luxton, 1982; Speight et al., 1999; Bardgett, 2005; Evenset et al. 2005; Ott et al., 2012). However, the relationship between species (alpha) diversity and ecosystem function often remains unclear despite considerable debate around the importance, or otherwise, of ‘functional redundancy’ in maintaining ecosystem stability (Brussaard et al., 2007). Polar (Arctic and Antarctic) ecosystems are considered to be particularly valuable for studies addressing such fundamental questions of ecosystem function, providing examples across a wide range of levels of assemblage structure (Hodkinson et al., 2003, 2004; Adams et al., 2006; Post et al., 2009). In the context of these ecosystems, the relatively high species-level biodiversity of the terrestrial and freshwater ecosystems of the High Arctic (in comparison, for instance, with those of Antarctic regions; Convey, 2007, 2013) may provide them with a robustness and stability to the characteristically large annual variation in climate and hence also provide resilience to environmental change. Nonetheless, despite this possibly inherent resilience to natural environmental variability, these High Arctic systems may be particularly vulnerable to human disturbance (Jónsdóttir, 2005) predominantly due to lengthy recovery and regeneration times.

Attention has recently become focused on the Arctic due both to the importance of this rapidly changing region in the Earth System and to the inherent interest of an extreme and unique environment. Perhaps nowhere is this more evident than in Svalbard with the establishment of the Kongsfjorden International Research Base (KIRB) at Ny-Ålesund. Nevertheless, despite close to 600 published articles concerning the invertebrate fauna of Svalbard (Coulson, 2007a, 2013a, 2013b), research has largely been fragmented and individual, with little attempt at large scale coordination. Hence there is a disparity in our knowledge between the charismatic and the less studied taxa. The recent publication of species inventories (e.g. Coulson, 2007a; Ávila-Jiménez et al., 2011) has highlighted the Svalbard archipelago as having perhaps the most complete inventory of the invertebrate fauna of any Arctic region (Hodkinson, in press). Nonetheless, an overall synthesis is lacking, either for Svalbard itself, or for the archipelagoes of the wider Barents Sea region. Now is a particularly opportune moment to provide such a synthesis, with a recent consideration of the Arctic invertebrate fauna calling for the establishment of an inventory of Arctic species as a high priority (Hodkinson, in press). Moreover, the quantity of invertebrate studies is increasing rapidly, as is the importance of Svalbard as a High Arctic research platform, including the current agenda within Norway to establish the eastern regions of Svalbard as a "reference area for research" (Ministry of Justice and the Police, 2009) and the planned Svalbard Integrated Arctic Earth Observing System (SIOS) international initiative, which forms part of the European Strategy Forum on Research Infrastructures (ESFRI) programme (European Commission, 2012). Currently, there is no overall context into which to set these international initiatives.

The three archipelagoes considered here comprise a natural geographic unit. This is a region of convergence for the Palearctic and Nearctic biota re-colonising following the ice retreat from the marginal coastline of Spitsbergen that commenced around 15,800 – 14,800 calibrated years Before Present (cal BP). Franz Josef Land began to be deglaciated around

11,200 cal BP (Landvik et al., 1995; Lubinski et al., 1999) while southern areas of Novaya Zemlya remained ice free throughout the LGM (Serebryanny et al., 1998; Velichko, 2002).

This article was catalysed by the expertise brought together for an international workshop on the Terrestrial and Freshwater Invertebrate Fauna of Svalbard held at the University Centre in Svalbard (UNIS) in 2011. We summarize the current state of knowledge of the invertebrate faunas of these archipelagoes, including biodiversity, dispersal, colonization and responses to environmental change. Of the three archipelagoes, by far the most detailed studies of the invertebrate fauna are available for Svalbard. Hence, while we focus primarily on this archipelago, we exploit the opportunity to include, wherever possible, the less well described archipelagoes of Franz Josef Land and Novaya Zemlya.

2. The archipelagoes

The three island groups ringing the Barents Sea consist of Svalbard, Franz Josef Land and Novaya Zemlya (Fig. 1). Svalbard is defined as the land area lying within the coordinates of 10° and 35°E and 74° and 81°N, and consists of four main islands, Spitsbergen, Nordaustlandet, Edgeøya and Barentsøya, along with the 'outlier' Bjørnøya (Bear Island; Fig. 2). It has a land area of approximately 63,000 km^2 of which 60% is today permanently covered by ice and snow (Hisdal, 1985). The archipelago is under Norwegian sovereignty but governed by the terms of the "Svalbard Treaty" (Treaty of Spitsbergen, 1920). Novaya Zemlya lies to the north of the Nenetsia Russian coast and is comprised of two principle islands separated by the Matochkin Shar strait, and numerous lesser islands, lying between 70° to 77°N and 51 to 69°E (Fig. 3). The main island stretches almost 900 km along a northeast axis and is up to 145 km wide (Aleksandrova, 1977) with an area of 81,280 km^2 of which 27% is currently glaciated (Zeeberg, 2002). During the Cold War Novaya Zemlya was used as a nuclear test site, with the result that for many years it has been a closed military region and thus difficult for biologists to visit (Zeeberg and Forman, 2001). Franz Josef Land lies to the north-east of Svalbard between 79°73' and 81°93'N and 37° and 65°50'E. It consists of approximately 190 largely ice-covered islands forming a total area of 12,334 km^2, 85% of which is glaciated (Aleksandrova, 1977; Zeeberg and Forman, 2001). As with Novaya Zemlya, Franz Josef Land was a closed military area for much of the Twentieth Century and access today still requires permission from the Russian authorities, including the Federal Service of National Security and Administration of Reserves and Protected Areas.

Insert Figure 1 here

The three archipelagoes all have an Arctic climate. The most northerly, Franz Josef Land, has the most extreme climate with mean July (mid-summer) temperature varying between -1.2 and +1.6ºC depending on the specific island considered (Aleksandrova, 1977). Cloudy skies occur approximately 90% of the time, reducing solar heating of the ground (Aleksandrova, 1983). Annual precipitation amounts to 300 mm, most falling as snow (Aleksandrova, 1983).

In Svalbard the annual mean air temperature recorded at the official meteorological station at the airport in Longyearbyen in the west of the archipelago (Fig. 2) is -4.6°C (mean summer temperature +5.2ºC), with 191 mm annual precipitation for the period 1981-2010 (Førland et al., 2011). Precipitation is particularly variable across this archipelago, decreasing rapidly from the west coast towards the interior. Barentsburg and Isfjord Radio, approximately 50-80 km to the west of Longyearbyen and on the coast, receive 525 and 480 mm respectively per year (Norwegian Meteorological Institute, 2013). Air temperature is also heavily influenced by the surrounding ocean and in particular the dominant local current systems. To the west, a northwards branch of the North Atlantic Drift carries relatively warm water (c. +3°C; Skogseth et al., 2005), past the archipelago. The east coast, however, is influenced by the cold water of the East Spitsbergen Current carrying polar water south at between 0.5° and -1.0°C (Skogseth et al., 2005). Hence air temperatures in the north and east of Svalbard are generally lower than in the west. Throughout the archipelago, soils may be snow-covered and frozen for at least nine months of the year (Coulson et al., 1995).

Insert Figure 2 here

The latitudinal span of Novaya Zemlya results in a considerable climatic gradient (Zeeberg and Forman, 2001). Annual mean temperature decreases from -5.4°C on the south-west coast to -10.3°C at the northern extremity. While winters (December, January) are cold, averaging around -15°C, the summers are relatively mild with July/August mean air temperature around +6°C. Annual precipitation also varies, decreasing south to north from 386 mm to 283 mm. However, as with Svalbard, the climate of Novaya Zemlya is heavily influenced by the surrounding marine environment, with advected warm North Atlantic water on the west coast while the east coast adjoins the cold Kara Sea which is ice-bound during the winter.

Insert Figure 3 here

A particular feature of the climate of the High Arctic is the extreme variation in photoperiod. For the settlement of Longyearbyen on Spitsbergen, Svalbard, the sun does not rise above the horizon between October 26 and February 16 (113 days). Conversely, during the period of the midnight sun, from April 19 until August 23 (127 days), the sun remains constantly above the horizon. However, although the sun may be permanently above the horizon from mid-April, the ground is not released from snow and ice until later in the season. For Svalbard this may be mid-June (Coulson, 2013a) and the growing season in vegetated regions, if measured from the approximate period the ground begins to clear of snow until the end of the midnight sun, may be less than 70 days. Some photosynthesis will continue to be possible longer into the autumn but the majority of higher plants shut down by mid-August. For Franz Josef Land the period of the midnight sun is approximately from April 15 until August 24 with polar night extending from October 19 until February 21. With a north-south axis the photoperiod of the islands of the Novaya Zemlya archipelago varies considerably. In the south the period of the midnight sun is only from May 21 – July 22 while in the north this period is extended, beginning around April 25 and ending August 17. The polar night is similarly shorter in the south commencing on November 22 with the sun returning on January 20 while in the north the period lasts from October 29 to February 13.

Environmental change is particularly rapid in the Arctic land areas and air temperatures are increasing more rapidly than global means, an exampe of the ‘polar amplification’ of the global process (ACIA, 2005; IPCC, 2007). The causes of this fast change are unclear but may be a consequence of general background warming, reduced sea ice cover and changes in oceanic and atmospheric circulation (Serreze et al., 2011). Annual temperatures in Svalbard over the period 1981-2010 have increased by 2.1°C over the 1961-1990 mean while winter and summer means have increased by 3.4 and 1°C respectively (Førland et al., 2011). These increases are likely to be linked with variations in atmospheric circulations, with increased frequency of southerly and south-west winds (Hanssen-Bauer and Førland 1998). Overall annual precipitation has increased marginally with a slight trend towards wetter summers and dryer winters (Førland et al., 2011) also linked to the changes in atmospheric circulation patterns (Hanssen-Bauer and Førland 1998). By the end of the current century the average winter temperatures may be up to 10°C greater than the present normal. Currently, air temperatures fall below -28°C on approximately three to four days per year. Projections suggest that winter warming by 2050 may result in air temperatures declining to only -23°C at a similar frequency (Førland et al., 2011). Similar detailed analyses for Franz Josef Land and Novaya Zemlya are not available but it is likely that these will experience similar overall general trends in temperatures and precipitation. However, current scenarios include poor sea ice representation, and recent loss of sea ice may have enhanced regional warming at the same time weakening the accuracy of these projections (Førland et al., 2011).

The history of the LGM in the Barents Sea region is complex but it is clear that Svalbard, Franz Josef Land and much of Novaya Zemlya were largely covered by a dynamic ice sheet (Gataullin et al., 2001) becoming exposed progressively as the ice began to retreat. Recent studies suggest that large areas of the Amsterdamøya plateau in the north-west of Svalbard remained ice free during the LGM (Landvik et al., 2003) providing possible glacial refugia for invertebrates, and that other regions were also periodically exposed during this period (Ingólfsson and Landvik, 2013). There is, hence, the possibility that some invertebrates survived *in situ*, but evidence is currently lacking and the predominant view remains that the present fauna is the result of recent immigration since the retreat of the ice. Similarly, it is likely that few, if any, plants survived *in situ* during the LGM (Alsos et al., 2007) although a number of recent studies, both biological and glaciological, have hinted at the possible existence of refugia (Westergaard et al., 2011), and current thinking is that flora and fauna of Svalbard is the result of recent immigration. The South Island of Novaya Zemlya remained ice-free with shrub vegetation (Serebryanny et al., 1998; Velichko, 2002).

The relatively short period 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 heterogenous with, for example, dry stony ridges, periglacial features, areas of late snow melt, heath or wet moss all in close proximity (Thomas et al., 2008). Large areas have been recently reworked by glacial action and possess continuous underlying permafrost influencing the soil hydrology. On a regional basis, northern areas consist largely of polar desert characterized by low precipitation and a short snow-free growing season. Vascular plant cover is often limited, restricted to less than 15% in both Svalbard and Franz Josef Land (Aleksandrova, 1983; Jónsdóttir, 2005; Cooper, 2011). Along the west coast of Svalbard and the southern areas of Novaya Zemlya areas of dwarf shrub tundra or heath may develop.Bare soil in all three archipelagoes often possesses a “biological crust” of cyanobacteria, bacteria, algae and lichens.

On a landscape scale the habitat is comprised of a heterogeneous mosaic (Jónsdóttir, 2005). The ridge tops, blown free of winter snow, or areas kept clear of snow by wind eddies, occasionally experience winter temperatures approaching -40°C while organic soils protected under deeper snow face temperatures no lower than -10°C and often considerably higher (Coulson et al., 1995). Melting snow and permafrost may also provide a constant cold water source throughout the summer resulting in chronically cold, wet and boggy areas in direct proximity to drier polar desert vegetation. The shallow active layer in the permafrost exaggerates this effect by hindering drainage. Soils may also vary considerably in depth and form over short distances. Generally the soils are thin, rarely more than a few centimeters thick, and overlie moraine debris, patterned ground or bedrock. In wetter areas, moss may develop into thick carpets or turfs some tens of centimeters deep, efficiently insulating the ground beneath against insolation (Coulson et al., 1993a). Under bird cliffs significant allochthonous nutrient input may occur. Under little auk (*Alle alle*) colonies, circa 60 tonnes dry matter guano per km^2 may be deposited each season (Stempniewicz et al. 2006). In such nutrient enriched areas, organic soils of over 10 cm depth may also accumulate illustrating the impact of nutrient flow from the marine environment to the often nutrient limited terrestrial habitat (Odasz, 1994). These ornithogenic soils and their associated vegetation (Odasz, 1994; Zmudczyńska et al., 2009, Zwolicki et al., 2013) form a characteristic element of the High Arctic environment (Jónsdóttir, 2005; Zmudczyńska et al., 2012) and one that may be especially vulnerable to the introduction of non-native species (Coulson et al., 2013a).

The physical and chemical properties of Arctic inland waters vary greatly including glacier-fed rivers, snow-melt streams, cold oligotrophic lakes and shallow temporary or permanent ponds. Running freshwaters are characterised by a dominance of glacial meltwater inputs, typically in large braided river systems with high sediment loads, highly irregular flows (even cessation after the main period of snow melt), and very low temperatures even in summer. However, in coastal, glacier-free areas, there are snowmelt and spring-fed streams, as well as lake outflows (Füreder and Brittain, 2006), where conditions can be more favourable, although even here many snowmelt streams dry up in summer. There are also warm springs in two areas in the western part of Spitsbergen that have been the subject of chemical and microbiological studies (Hammer et al., 2005; Jamtveit et al., 2006; Lauritzen and Bottrell, 1994). In Svalbard, river flow may initiate in late June to early July. Ice break-up however occurs later, from mid-July until late-August (Svenning and Gullestad, 2002). The lakes and ponds in the archipelagoes of the Barents Sea are typically found in coastal, lowland areas as in most other Arctic regions (Bøyum and Kjensmo, 1978; Pienitz et al., 2008; Rautio et al., 2011). Temporary thaw ponds, permanent shallow ponds and small lakes are numerous and, because of the low water depth (usually less than 2 m) or small catchments, these water bodies tend to freeze solid during winter while shallower ones can dry out completely during summer.

Shallow ponds are often hotspots of biodiversity and production for micro-organisms, plants and animals in most Arctic regions (Smol and Douglas, 2007), although containing no fish populations. Nutrient input from grazing geese may be significant (Van Geest et al., 2007). Larger and deeper lakes are also present, although are not as numerous as, for example, in West Greenland and Alaska. Lakes with a water depth of more than 3 m are more stable, not freezing solid or drying out, and can host a permanent fish population. However, the environmental conditions for organisms in High Arctic lakes are different from other northern climatic zones as the ice-free period is very short (typically 1-2 months), water temperatures and nutrient concentrations are constantly low and the intensity of ultraviolet radiation is often high compared to more temperate regions. Furthermore, there are physical barriers restricting colonisation such as ice caps or remoteness. As a consequence, the biodiversity of freshwater organisms in still waters in Svalbard and other isolated islands is expected to be low even compared to other High Arctic regions such as West Greenland and Alaska (Gíslason, 2005; Samchyshyna et al., 2008). Arctic rivers, ponds and lakes have a biocomplexity that resembles that of temperate regions, including phototropic biota (algae and macrophytes), invertebrates (insects, crustaceans and rotifers) and fish, although with much fewer taxa and thus with a simpler food web structure than temperate lakes (Christoffersen et al., 2008).

Set against this environmental background, we here provide a synthesis of the known invertebrate fauna of the terrestrial and limnic environments of the three archipelagoes enclosing the Barents Sea, as a baseline for future ecological studies. Examination of complex ecological linkages is beyond the scope of this review. Nonetheless, we attempt to set each taxonomic group in context and discuss the biodiversity of the islands. In particular, we address the history of research and knowledge development, highlighting gaps in our understanding (which varies considerably between the archipelagoes).

3. The invertebrate fauna.

3.1 Rotifera

Studies on the rotifer fauna of Svalbard commenced in the second half of the Nineteenth Century, when von Goes (1862) reported two bdelloid '*Callidina*' species and Ehrenberg (1874) reported *Callidina* (now *Pleuretra*) *alpium* (Ehrenberg, 1853) from moss collected in Spitsbergen. Further early records of the rotifer fauna of terrestrial mosses from Spitsbergen, mainly bdelloids, were provided by Bryce (1897, 1922), Murray (1908) and Summerhayes and Elton (1923). Early planktonic rotifer reports were restricted to monogononts, mostly from Spitsbergen (Richard, 1898; Olofsson, 1918). In the second half of the Twentieth Century, studies focused on monogononts from the plankton and/or periphyton of Barentsøya (Pejler, 1974; De Smet, 1993), Bjørnøya (De Smet, 1988), Edgeøya (De Smet et al., 1988), Hopen (De Smet, 1990), Nordaustlandet (Thomasson, 1958) and Spitsbergen (Thomasson, 1961; Amrén 1964a, b, c; Vestby, 1983; De Smet et al., 1987; Kubíček and Terek, 1991; Jørgensen and Eie, 1993; De Smet, 1995; Janiec, 1996; Janiec and Salwicka, 1996). Amrén (1964a, b) carried out long-term population studies of *Keratella quadrata* (Müller, 1786) and *Polyarthra dolichoptera* (Idelson, 1925) in ponds on Spitsbergen, finding temporal morphological variation in *K. quadrata* and thereby demonstrating that the phenomenon was not limited to low altitudes and latitudes as was previously thought. Interest in bdelloids has recently been revived by Kaya et al. (2010) studying representatives from terrestrial mosses from different localities in Svalbard. Limited physiological studies are available, excepting Opaliński and Klekowski (1989, 1992), who measured oxygen consumption in *Macrotrachela musculosa* (Milne, 1886) and *Trichotria truncata* (Whitelegge, 1889) obtained from Spitsbergen tundra. These studies demonstrated relative temperature independence in the range of 2-6°C for *M. musculosa*, suggesting metabolic cold adaptation. Limited older literature, and no recent studies, are available for Novaya Zemlya (Murray, 1908; Idelson, 1925; Økland, 1928; Gorbunow, 1929; Retowski, 1935) and Franz Josef Land (Murray, 1908; Retowski, 1935).

3.1.1.Bdelloidea.

Of the two major divisions of Rotifera, the Bdelloidea have been largely neglected because of difficulties with identification. Their diversity is underestimated since most studies use animals recovered from rehydrated moss samples, precluding recovery of species lacking, or with poor, capacity to form dormant anhydrobiotic stages. Moreover, as is likely to be the case in many groups, recent molecular biological studies have demonstrated that cryptic diversity is high in bdelloids (Fontaneto et al., 2007).

A total of 68 formally identified bdelloid morphospecies have been recorded from the Barents Sea archipelagoes, with around 15% of the current global diversity of Bdelloidea (460 morphospecies distributed over 20 genera; Segers, 2008) being present in Svalbard. These include the majority (85%) of the bdelloids known from the Arctic region (De Smet unpubl.). Virtually all the species reported from these archipelagoes are widespread or cosmopolitan, with *Pleuretra hystrix* Bartos, 1950 being the only Arctic-Alpine endemic. However, the discovery of more endemics may be expected as generalists exhibit the highest cryptic diversity (Fontaneto et al., 2009). Data for Svalbard are only available from the islands of Edgeøya, Prins Karls Forland and Spitsbergen. The known Svalbard fauna comprises 67 morphospecies. Only three and two morphospecies, respectively, have been reported from Franz Josef Land and Novaya Zemlya. All morphospecies recorded in the Barents Sea archipelagoes occur in limno-terrestrial habitats (mosses, lichens) with 15 also reported from freshwater habitats (permanently submerged vegetation, cryoconite).

3.1.2. Monogononta.

In this group, older reports are biased in favour of the loricates, a group that includes species with a rigid body wall that fix well and are amenable to microscopic study. Species with a soft integument, the illoricates, contract on fixation and become unrecognizable. Furthermore, re-examination of historical samples (Olofsson, 1918), has shown that loricate diversity per sample was on average 2-4 times higher than in the original publication (De Smet unpubl.). Interpretation of older data may also be compromised due to taxonomic inconsistencies. For example, several monogononts show large phenotypic plasticity, while some taxa originally considered to exhibit wide morphological variation are now recognized to consist of several species. Given these reservations it is impossible to differentiate, for instance, the currently recognised species *Keratella hiemalis* Carlin, 1943, *K. quadrata* and *K. testudo* (Ehrenberg, 1832) in earlier reports of '*Anuraea* (*Keratella*) *aculeata*' and its forms in the absence of preserved material. Many monogononts have, again, been shown also to be complexes of cryptic species (e.g. Suatoni et al., 2006).

To date, 163 limno-terrestrial and aquatic monogonont morphospecies have been reported from the Barents Sea archipelagoes, with 134 species from Svalbard, 20 from Franz Josef

Land and 71 from Novaya Zemlya. Unequal sampling effort across the different islands and habitats within the archipelagoes clearly hampers comparison of their rotifer biodiversity. The global diversity of non-marine Monogononta totals approximately 1,500 species (Segers, 2008), of which 11% occur in the Barents Sea archipelagoes. In the Arctic region as a whole 327 species are known (De Smet unpubl.) of which 50% have been reported from these archipelagoes. Only 16 species occur occasionally in aerophytic moss, with the most frequently found being *Encentrum incisum* Wulfert, 1936, *Lecane arcuata* (Bryce, 1891) and *Lepadella patella* (Müller, 1786). As with the bdelloids, the majority of the monogonont species are cosmopolitan or widespread, although a small proportion show more restricted distributions: the Arctic endemic *Notholca latistyla* (Olofsson, 1918) occurs in all three archipelagoes; *Trichocerca longistyla* (Olofsson, 1918), described from Spitsbergen, is also known from Novaya Zemlya and Swedish Lapland; *Encentrum boreale* Harring and Myers, 1928, *E. dieteri* (De Smet, 1995), *E. murrayi* Bryce, 1922 are currently thought to be endemic to Spitsbergen, and the sub-species *Synchaeta lakowitziana arctica* De Smet, 1988 is restricted to Bjørnøya.

3.2 Gastrotricha

The phylum Gastrotricha is a group of aquatic microinvertebrates. They are a common and important component of the benthic, epibenthic and epiphytic communities in all types of freshwater, brackish water and marine habitats (Balsamo et al., 2008; Todaro and Hummon, 2012; Todaro et al., 2012). The Gastrotricha are, as a group, considered cosmopolitan (Balsamo et al. 2008).

Arctic Gastrotricha are extremely poorly known. No comprehensive studies have been conducted on the Svalbard archipelago. Scourfield (1897) and De Smet et al. (1987) recorded the genus *Chaetonotus* from Spitsbergen and De Smet (1993) noted that Gastrotricha compose 1 - 18% of the invertebrate taxa obtained from submerged moss samples from Barentsøya. The taxon has never been studied on Franz Joseph Land or Novaya Zemlya.

In the light of our poor knowledge of Gastrotricha from the Barents Sea region, future studies are likely to find many more species in habitats such as cryoconite holes, raised bogs, water bodies, moist soil, fjords and marine interstitial zones (Valdecasas et al., 2006; Todaro and Hummon, 2012).

3.3. Helminthofauna

3.3.1. Free-living terrestrial and freshwater Nematoda.

Despite widespread recognition of the almost ubiquitous presence of nematodes in soil faunas globally and their particular importance in soils of some Antarctic ecosystems where most other invertebrates are poorly or not represented (Freckman and Virginia, 1997; Adams et al., 2006; Maslen and Convey, 2006), this group has received limited attention in the archipelagoes of the Barents Sea and there are no records from Franz Josef Land. The first record of terrestrial nematodes from Svalbard is that of Aurivillius (1883a) who described the new species *Aphelenchus nivalis* (Aurivillius, 1884) found in algae on the snow. Menzel (1920) recorded four species, *A. nivalis*, *Dorylaimus* sp., *Acrobeloides bütschlii* Gadea, 1954 and *Plectus cirratus* Bastian, 1865. To date, the only extensive collection of terrestrial nematodes in Svalbard (specifically from Spitsbergen) was carried out by H. van Rossen in 1965. These samples contained about 75 taxa of which 15 were described as new species (Loof, 1971). Samples collected in the area around Ny-Ålesund by G. Rudbäck in 1985 were examined in part by Boström (1987, 1988, 1989) resulting in the description of one new species but otherwise mainly corroborating the findings of Loof (1971). Although a few other records are available (for example Klekowski and Opaliński, 1986; Janiec, 1996), the majority of information available on the terrestrial nematode fauna of Svalbard remains that provided by Loof (1971). Checklists of terrestrial and freshwater nematode species found in Svalbard include 95 taxa (Coulson and Refseth, 2004).

The first recorded collections of terrestrial nematodes from Novaya Zemlya are those of L. Stapfer in 1907 (Steiner, 1916), which included 27 species from 13 genera. More recently, Gagarin (1997a, b, c, 1999, 2000) has described many new species from these islands. In total Gagarin (2001) lists 63 species of terrestrial and freshwater nematodes for the archipelago, although 18 of the species recorded by Steiner (1916) are not included among them. There are 24 species in common between Svalbard and Novaya Zemlya, all taxa which are more or less cosmopolitan.

Free-living terrestrial and freshwater nematodes have been largely omitted from soil ecology studies conducted in Svalbard and hence almost nothing is known concerning their abundance, biomass or ecological or functional importance. In 1994, B. Sohlenius collected samples in Adventdalen and Gluudneset (Kongsfjorden) confirming the presence of high diversities and population densities. The mean population density was 78 nematodes g^{-1} soil dry mass in Adventdalen and 119 g^{-1} dry mass at Gluudneset (B. Sohlenius unpublished data), values similar to reports from other Arctic areas. Between 24 and 27 taxa of nematodes were identified. At both sites, the genera *Eudorylaimus*, *Plectus* and *Teratocephalus* were found in all samples examined and were amongst the most abundant taxa. In most samples, Adenophorea bacterial feeders and dorylaims were most abundant. Only very few representatives of obligate plant parasitic nematodes were found. The fauna found thus closely resembles that of other cold areas both in the Arctic (Kuzmin, 1976; Procter, 1977; Sohlenius et al., 1997; Ruess et al., 1999a) and in the sub- and maritime Antarctic (Andrássy, 1998; Convey and Wynn-Williams, 2002; Maslen and Convey, 2006).

3.3.2. Animal parasitic taxa.

The most detailed investigations of parasitic nematodes in Svalbard are from terrestrial mammals, where five species have been identified. Studies have focussed on the parasitic nematodes of the Svalbard reindeer (*Rangifer tarandus plathyrynchus*), and are reviewed by Halvorsen and Bye (1999). The abomasal nematode community consists of three polymorphic species of the order Strongylida, where two dimorphic and one trimorphic species have been identified with major and minor morphotypes. Additionally, *Nematodirus* eggs have also been found in faecal samples. The major morphs, *O. gruhneri* Skrjabin, 1929 and *M. marshalli* (Ransom, 1907), represent 95% of the parasite population in adult reindeer of both sexes. *Ostertagia gruehneri* is host specific to reindeer whilst *M. marshalli* has a wide host and geographical distribution, infecting both bovid and cervid species. It is typically a parasite of cold deserts (Halvorsen, 1986; Halvorsen and Bye, 1999; Irvine et al., 2000). The adult *O. gruehneri* load can reach up to 8,000 worms per adult reindeer, while that of *M. marshalli* can exceed 15,000 (Irvine et al., 2001). These nematodes have a direct life cycle in which transmission of the infective stage to the host occurs during grazing. Experimental work has implicated the parasite as a significant factor in regulating population dynamics of Svalbard reindeer through negative effects on fecundity (Irvine et al., 2000; Albon et al., 2002; Stien et al., 2002). As is common for most gut nematodes, *O. gruehneri* is transmitted in the summer when conditions are favourable for survival and development of the free-living stages in the terrestrial environment. Faecal egg densities in the summer vary between 124 – 241 eggs per gram fresh weight (van der Wal et al., 2000) but no eggs are produced during the winter period (Irvine et al. 2001). Providing a surprising contrast, therefore, *M. marshalli* is transmitted from October to April, which is also when peak egg output occurs at around 8 eggs per gram faecal material (Irvine et al., 2000; 2001, Carlsson et al., 2012, 2013).

Nematodes of the genus *Trichinella* are common throughout the world, with the species *Trichinella nativa* Britov and Boev, 1972 being the most common in the Arctic with the polar bear (*Ursus maritimus*) as the main reservoir. A recent sero-prevalance survey found a higher prevalence of this parasite in the Svalbard region (78%) than in the Barents Sea (east of longitude 30˚E) (51%) (Asbakk et al., 2010). Ascaridoid nematodes, likely to be predominantly *Toxascaris leonine* (Linstow, 1902), have been found at a prevalence of 33% in the Arctic fox (*Vulpes lagopus*) (Stien et al., 2010). This is a common parasite of Arctic foxes and has a direct life cycle although it may also use rodents as a paratenic host. Other parasite species found in Arctic foxes from Spitsbergen include cestodes (*Echinococcus multilocularis* Leuckart, 1863*, Taenia crassiceps* (Zeder 1800), *T. polycantha* (Leucart, 1856)*, T. krabbei* Moniez 1879 and *Diphyllobothrium* sp.) and Ancanthocephala (Stien et al., 2010). The taeniid tapeworm *E. multilocularis* is sylvatic, with foxes comprising the definitive host and the vole *Microtus levis* (initially described as *Microtus rossiaemeridionalis*) the secondary host. The vole-transmitted cestodes, *E. multilocularis*, *T. crassiceps* and *T. polycantha*, decrease in prevalence in the fox population with increasing distance from the intermediate host population (Stien et al., 2010) which is extremely restricted in Svalbard and centered on the abandoned coal mine at Grumont, Isfjord (Henttonen et al., 2001). The local conditions here enable the survival of the vole, but it is thought unlikely to be able to expand its range (Fuglei et al., 2008). *Echinococcus* *multilocularis* is known from Novaya Zemlya (Davidson et al., 2012) but is unlikely to be present in Franz Josef Land due to the lack of intermediate host.

Helminth parasites of the Svalbard reindeer include *Moniezia benedina* Moniez, 1872 and *Taenia ovis krabbei* (Moniez, 1879) Verster, 1969 (Bye, 1985). *Moniezia benedina* is present in around 43% of Svalbard reindeer, a similar level of infection as observed in Greenland (Bye, 1985). *Moniezia benedina* forms a link with the soil microarthropod fauna as oribatid mites comprise the intermediate host. *Taenia ovis krabbei* appears to have large population cycles, with infection rates between 1981 and 1982 decreasing from 61% to 29% (Bye, 1985).

The fauna of parasitic nematodes identified in the seabirds of the Barents Sea archipelagoes consists of predominantly widespread species (Kuklin and Kuklina, 2005). For some (*Anisakis* sp. and *Hysterothylacium aduncum* (Rudolphi, 1802)) birds are not primary hosts but the nematodes may enter together with ingested fish. The first records of parasitic helminths from seabirds in the Barents Sea region were obtained from material collected off the western coast of Svalbard during the Swedish Zoological Expedition of 1900 (Odhner, 1905; Zschokke, 1903). Since then, there have been few studies of the avian helminthofauna of Svalbard (Kuklin et al., 2004; Kuklin and Kuklina, 2005). Markov (1941) published on the helminthofauna of Novaya Zemlya (from Bezymyannaya Bay, on the South Island) (Fig. 3) while Kuklin surveyed the helminth fauna of seabirds from Archangelskaya Bay (North Island) (Kuklin 2000, 2001). In 1926, Skryabin published an examination of the helminthological collections of the Sedov expeditions to the North Pole (1912-1914) and it is likely that the majority of this material was collected from Franz Josef Land. More recent studies were performed in Franz Josef Land in 1990-93 (Galaktionov and Marasaev, 1992; Galaktionov, 1996).

Throughout the archipelagoes of the Barents Sea, parasitilogical studies exist from 11 species of seabirds (Markov, 1941; Galaktionov, 1996; Kuklin, 2001; Kuklin et al., 2004). From these, 47 species of parasitic worm species comprising 10 trematodes, 23 cestodes, 10 nematodes and four acanthocephalans have been identified. A characteristic feature of the helminthofauna of seabirds in Arctic regions, noted for North Island of Novaya Zemlya and in Franz Josef Land (Galaktionov, 1996; Kuklin, 2001), is the extremely low species diversity of the trematode fauna. This is likely due to the lack of intermediate hosts, predominantly littoral molluscs, in Arctic ecosystems (Dunton, 1992) and the extreme climatic conditions preventing completion of the life cycle; primarily by restricting free-swimming larval stages (Baer, 1962; Galaktionov and Bustness, 1999).

Typical of the cestodes from seabirds in the northern archipelagoes is their broad range of host species. For example, *Microsomacanthus diorchis (*Fuhrmann, 1913) (otherwise specific for anatides) and *Arctotaenia tetrabothrioides* (Loenberg, 1890) (previously found only in waders) are recorded parasitizing glaucous gulls (*Larus hyperboreus*) on Spitsbergen and *Microsomacanthus ductilus* (Linton, 1927) (a widespread parasite of gulls) is found in common eiders (*Somateria mollissima*) and Brünnich's guillemots (*Uria lomvia*) in Franz Josef Land (Galaktionov, 1996; Kuklin et al., 2004). This ability is likely to enhance their persistence at the northern boundary of their distribution

3.4. Oligochaeta

Enchytraeids are engaged both directly and indirectly in decomposition processes and nutrient mineralization in the soil (Williams and Griffiths, 1989). Records of Enchytraeidae from

Svalbard are to date limited to Spitsbergen, and other regions of Svalbard are poorly investigated. Early records from Svalbard include those of Michaelsen (1900), Ude (1902) and Stephenson (1922, 1924, 1925). During the 1990s several locations were intensively sampled for enchytraeids (Adventdalen, Bjørndalen, Grumant and Ny-Ålesund), recording 13 species of which two (*Mesenchytraeus argentatus* Nurminen, 1973, *Bryodrilus parvus* Nurminen, 1970) were new to Spitsbergen (Birkemoe and Dozsa-Farkas, 1994; Sømme and Birkemoe, 1997; Birkemoe et al., 2000). In total, 42 species of Enchytraeidae from nine genera have been recorded from Spitsbergen (Nurminen, 1965; Birkemoe and Dozsa-Farkas, 1994; Sømme and Birkemoe, 1997; Birkemoe et al., 2000; Coulson et al., 2013a). Even with the limited sampling available, their diversity in Spitsbergen is high compared to other High Arctic locations, for example north-eastern Greenland and the Arctic archipelagoes of Canada where only 12 and 18 species have so far have been reported, respectively (Christensen and Dozsa-Farkas, 2006; Sørensen et al., 2006). All the recorded genera in Spitsbergen are Holarctic, but the common and widely distributed genus *Achaeta* has so far not been recorded in Svalbard or at any other High Arctic location. It is also noteworthy that *Cognettia sphagnetorum* (Vejdovsky, 1878) has only been recorded once from a single location on Spitsbergen despite this species being abundant in cold and wet environments such as heathland, tundra and boreal forest throughout the sub-Arctic (Nurminen, 1966, 1967; Maraldo and Holmstrup, 2010). In general, members of the enchytraeid fauna of Spitsbergen are also found in northern Europe, and it has been suggested that the entire Oligochaeta fauna is of recent origin (Nurminen, 1965; Christensen and Dozsa-Farkas, 2006). No data are available from Franz Josef Land and Novaya Zemlya.

Nurminen (1965) reported the observation of a single damaged and undeterminable lumbricid on Spitsbergen, while Coulson et al. (2013a,b) recently recorded two species, *Dendrodrilus* *rubidus* (Savigny, 1826) and *Dendrobaena hortensis* (Michaelsen, 1890), in anthropogenic soils below the abandoned cowsheds in Barentsburg. These latter species appear to have been introduced to Svalbard with imported soils for the greenhouse or fodder and have not been recorded beyond the unusual manure-augmented soils in the town. Lumbricidae have also been observed in Novaya Zemlya where *Dendrobaena octaedra* (Savigny, 1826) is recorded (Stöp-Bowitz, 1969).

3.5. Tardigrada

The Tardigrada is a relatively small group of micrometazoans that contains more than 1,000 described species (Degma et al., 2013). Tardigrades are known from almost all ecosystems, from polar and high altitude regions to the tropics on land, and to the abyssal depths in the sea. Terrestrial species are most often encountered in mosses, lichens and liverworts but they can be found also in leaf litter and soil. Freshwater and marine species can be found in sediment, on aquatic plants and sometimes in the pelagic zone. A particular feature of tardigrades is their high tolerance to unfavorable environmental conditions, including desiccation, freezing and radiation stresses, in some cases being able to tolerate exposure to levels of these stresses (such as being submerged in liquid nitrogen, liquid helium or the vacuum of space) that lie well beyond the extreme values ever naturally experienced. They have the ability to enter different types of anabiotic states (anabiosis) in response to these stressors, but they can also survive some extremes in an active state (Wełnicz et al., 2011).

Although terrestrial and freshwater Tardigrada have been studied in Arctic regions since the early Twentieth Century only fragmentary and mostly faunistic data are available. The most frequently studied Arctic regions are the Svalbard archipelago and Greenland, but some studies have also addressed Arctic regions of Canada, Jan Mayen, Franz Josef Land and

Novaya Zemlya (McInnes, 1994), and Alaska (Johansson et al., 2013). Around 200 terrestrial and freshwater tardigrade species have been recorded from Arctic regions (Pugh and McInnes, 1998)

The first record of terrestrial tardigrades in Svalbard is that of Scourfield (1897) describing the new species *Testechniscus spitsbergensis* (Scourfield, 1897), while Richard (1898) reported the first freshwater tardigrade from Spitsbergen, *Dactylobiotus macronyx* (Dujardin, 1851). Increasingly intensive studies were conducted during the Twentieth Century. Early papers of Murray (1907) and Richters (1903, 1904, 1911), were followed by studies from a number of authors (Marcus, 1928; Węglarska, 1965; Binda et al., 1980; Pilato et al., 1982; Dastych, 1983, 1985; Klekowski and Opaliński, 1986, 1989; Pilato and Binda, 1987; De Smet et al., 1987, 1988; Van Rompu and De Smet, 1988, 1991, 1994; De Smet and Van Rompu 1994; Maucci, 1996; Pugh and McInnes, 1998; Łagisz, 1999; Tumanov, 2006; Smykla et al., 2011; Kaczmarek et al., 2012; Zawierucha et al. in press). Most of these studies were limited to reports and descriptions of new species, and only Węglarska (1965), Dastych (1985), Maucci (1996); Pugh and McInnes (1998) and Kaczmarek et al. (2012) undertook more comprehensive studies, including discussion of ecology, origin of the Arctic Tardigrada, and remarks on taxonomy and zoogeography. The majority of studies have concentrated on the largest island in the archipelago, Spitsbergen, and only De Smet et al. (1988) and Van Rompu and De Smet (1988, 1991, 1994) studied freshwater tardigrades on other islands in the archipelago, including Barentsøya, Bjørnøya, Edgeøya and Hopen. Across all these studies, 89 Tardigrade taxa have been reported, although some older reports have not been verified based on modern taxonomy (Kaczmarek et al., 2012). Among the species known from this region, 17 were described as new to science and four are currently considered endemic. It is clear that Svalbard has been studied very selectively and a comprehensive study of the entire archipelago is still required.

The tardigrades of Franz Josef Land have been reported only by Murray (1907) and Richters (1911). Murray (1907) reported 21 taxa (19 species and two *varietas*) of which, based on modern taxonomy, 17 species are currently valid. Richters (1911) reported a total of seven taxa (six currently valid species). Therefore, in total, only 19 species are currently known from Franz Josef Land.

Older studies of the tardigrades of Novaya Zemlya are again limited to Murray (1907) and Richters (1911), who reported a total of eight species. Biserov (1996, 1998) published the first modern studies of Tardigrada from Novaya Zemlya, reporting 42 species. Biserov (1999) then reviewed the available knowledge of Novaya Zemlya tardigrades. Based on all published papers, 81 taxa (68 valid species) are currently known from this archipelago, including one marine taxon, eight marked as "*cf.*", "gr." or "aff." (uncertain identification) species and four taxa identified only to the genus level.

3.6. Chelicerata

3.6.1. Acari

3.6.1.1. Mesostigmata

The first records of mesostigmatid mites from Svalbard are those of Trouessart (1895), who reported *Uroseius acuminatus* (C.L. Koch, 1847) and *Laelaps* sp. In early publications classifying the natural communities of Svalbard, Summerhayes and Elton (1923, 1928) recorded *Haemogamasus ambulans* Thorell, 1872. Thor (1930) described two genera (*Arctoseius, Vitzthumia*) and four species new to science from Svalbard. Unfortunately, the type material has not survived (Winston, 1999) and the original photographic documentation included in the study is inadequate for verification and revision of these species. The status of the type species of the genus *Arctoseius*, *A. laterincisus* Thor, 1930, is therefore unclear as this species has not been observed since its initial description, although nine other species of *Arctoseius* are now known from the archipelago (Ávila-Jiménez et al., 2011). Lindquist and Makarova (2011) considered that, although the genus *Arctoseius* was established on a presumed monotypy, the type series could include specimens of two (or several) morphologically similar species.

More recent studies have included further descriptions of new species or redescription (Hirschmann, 1966; Petrova and Makarova, 1991; Gwiazdowicz and Rakowski, 2009; Gwiazdowicz et al. 2011a, b; Lindquist and Makarova, 2011), faunistic records (Makarova, 1999, 2000a, 2000c, 2011, 2012; Gwiazdowicz and Gulvik, 2008; Gwiazdowicz et al., 2009, 2012a, 2012b; Coulson et al., 2011), and the ecology of the group, especially in soil communities (Byzova et. al., 1995; Gwiazdowicz and Coulson, 2011), the specific parasitic complex associated with the introduced vole, *Microtus levis* (Krumpàl et al., 1991) and phoretic associations with Diptera (Gwiazdowicz and Coulson, 2010).

Twenty-nine species of mesostigmatid mites are currently known from Svalbard, with two apparently restricted to Bjørnøya (Summerhayes and Elton, 1923, 1928; Ávila-Jiménez et al., 2011, Gwiazdowicz et al., 2012a, 2012b; Makarova, 2013; Coulson et al., 2013b). This diversity is comparable with that of other High Arctic sites such as Ellesmere Island and northern Taymyr (Makarova, in press). The majority of these species are characteristic of polar areas, but many (44%) also have European or Holarctic temperate, boreal or polyzonal distributions. Four vertebrate parasitic species are present, usually associated with bird nests or small mammals (Krumpàl et al., 1991), and one ectoparasite of birds (Gwiazdowicz et al., 2012a). Phoresy is also known, for example *Thinoseius spinosus* (Willmann, 1939). This species, usually found on the Holarctic seashore and dispersing on various species of Diptera (Makarova and Böcher, 2009), has been found on the calliphorid fly *Protophormia terraenovae* (Robineau-Desvoidy, 1830) (Gwiazdowicz and Coulson, 2010).

Along the western coasts of the Svalbard archipelago, which experience a milder climate, a relatively high mesostigmatid diversity is present but, in constrast, in polar desert landscapes only five gamasid species were recorded by Ávila-Jiménez et al. (2011). Population densities on this milder coast of Spitsbergen vary widely between habitats, from 20 to 4,200 individuals m^{-2}, with the maximum density recorded being found in mossy vegetation near a colony of little auks (*Alle alle*) (Seniczak and Plichta, 1978; Byzova, et al., 1995). High density (1,000-1,840 individuals m^{-2}) and species diversity have also been observed at other locations with rich vegetation cover (Byzova et al., 1995; Ávila-Jiménez et al., 2011). Poorly vegetated areas such as saline meadows generally contain fewer species and lower densities (Gwiazdowicz and Coulson, 2011).

There are no detailed investigations of gamasid mites in the Novaya Zemlya archipelago. The first information, based on material of large-scale Arctic expeditions, was published in the late Nineteenth and early Twentieth Centuries (L. Koch, 1879; Trägårdh, 1904, 1928) and cited only five species. A further nine species were identified during the revision of High Arctic *Arctoseius* species from the collections of V.I. Bulavintsev (Makarova, 2000b, 2000c; Lindquist and Makarova, 2011). Thirteen additional species have been found in samples collected by G.V. Khakhin and S.V. Goryachkin. The total number of species of Mesostigmata from Novaya Zemlya now numbers 27, similar number to the diversity on

Svalbard (Ávila-Jiménez et al., 2011). Considering the long latitudinal gradient, providing a range of environmental conditions, and the current lack of acarological studies, this number is likely to increase. Eleven species of gamasid are common to both Novaya Zemlya and Svalbard (Makarova, 2009). Unlike Svalbard, the South Island of the Novaya Zemlya archipelago was mainly free of ice during the LGM (Velichko, 2002), retaining shrub vegetation (Serebryanny et al., 1998). This, as well as subsequent immigration, may explain the presence of bumble bees, lemmings and their associated gamasid mite fauna (members of genera *Laelaps, Parasitellus, Melichares*), in Novaya Zemlya. With the exception *of L. hilaris,* associated with the introduced vole in the derelict mining town of Grumant (Krumpàl et al. 1991), these genera are absent in Svalbard (Ávila-Jiménez et al., 2011). In both archipelagoes a third of the gamasid species belong to the genus *Arctoseius*, most of which (61-74%) have Arctic or alpine ranges.

Six species of gamasid mites are recorded from Franz Josef Land (Bulavintsev and Babenko, 1983; Makarova, 1999, 2000c, 2013), five of which belong to the genus *Arctoseius* and one to *Zercon* (*Z. michaeli* Halaškova, 1977).

3.6.1.2. Ixodida

The bird tick *Ixodes uriae* (White, 1852) is common on seabirds breeding on Bjørnøya but has only recently begun to be observed in large numbers in colonies on Spitsbergen (Coulson et al., 2009). It is unclear why the tick populations in the northern regions of Svalbard are becoming more apparent but a recent study has implicated warmer winters (Descamps, 2013). *Ixodes uriae* is very widely distributed, circumpolar and bipolar, but recorded only from marine birds and their breeding sites. The species is reported from 52 bird species, the main hosts being auks, tube-nosed sea birds, cormorants, seagulls and penguins. In the north

Atlantic, ticks are most common on guillemots (*Uria aalge, U. lomvia*), black guillemot (*Cepphus grylle*), razorbill (*Alca torda*), puffin (*Fratercula arctica*) and herring gull (*Larus argentatus*) (Mehl and Traavik, 1983).

3.6.1.3. Oribatida

The Oribatida is a suborder of the Sarcoptiformes (Krantz and Walter, 2009). They are often the dominant arthropod group in soil-litter systems, including those of the High Arctic and maritime Antarctic (Block & Convey, 1995; Norton and Behan-Pelletier, 2009). Early records of oribatids from Svalbard date back to Thorell (1871), who described four species new to science of which three, *Diapterobates notatus* (as *Oribata notata*), *Ameronothrus lineatus* (as *Eremaeus lineatus*) and *Hermannia reticulata* are common throughout the archipelago. Thorell also described *Camisia borealis* from the islands, a species which is thought today to be within the variability of *Camisia horrida* (Hermann 1804) (Seniczak et al., 2006). Following on from Thorell, various reports discussing Oribatidae from Svalbard appeared (for example Trouessart, 1895; Trägårdh, 1904; Hull, 1922; Summerhayes and Elton, 1923, 1928; Thor, 1930, 1934; Hammer, 1946). Additional reports during the past 50 years (for example Forsslund, 1957, 1964; Block, 1966; Karppinen, 1967; Niedbała, 1971; Solhøy, 1976; Seniczak and Plichta, 1978; Byzova et al., 1995) have resulted in a current inventory of 81 species of oribatid mites belonging to 17 superfamilies and 25 families from Svalbard (Bayartogtokh et al., 2011). However, these authors did not include several known representatives of the genera *Brachychthonius*, *Spatiodamaeus, Achipteria* (mentioned in Lebedeva et al., 2006); *Gymnodamaeus* and *Microtritia* (in Seniczak and Plichta, 1978) or *Berniniella* sp. (in Coulson, 2007a). With inclusion of these taxa the checklist of oribatid mites of Svalbard includes 87 species from 17 superfamilies and 27 families. However, taxonomic confusion remains a significant problem with the current inventory. For example, the genus *Camisia* requires revision based on modern taxonomic methodologies (Bayartogtokh et al., 2011). For others, the species status is currently being debated, for example Bayartogtokh et al. (2011) regards *Moritzoppia neerlandica* (Oudemans, 1900) and *Oppia translamellata* Willmann, 1923 as the same species (*neerlandica*) while Weigmann (2006) regards them as separate species. Such confusion is mirrored in other species and genera of oribatid mites. Often the specimens originally described or identified no longer exist. A new inventory based on fresh material lodged in appropriate museums is urgently required.

The density of oribatid mites in the Arctic tundra of Svalbard is quite high, often between 9,168 to 81,400 individuals m^{-2} (Seniczak and Plichta, 1978; Byzova et al., 1995), comparable with values recorded in the northern tundra of the European part of Russia (Melekhina and Zinovjeva, 2012). These values are also comparable with studies in the maritime Antarctic, where oribatid mites are one of the dominant groups of the terrestrial invertebrate fauna (e.g. Block and Convey, 1995; Convey and Smith, 1997).

Recent work on the oribatids of Svalbard has focused on ornithogenic substrates (Lebedeva and Krivolutsky, 2003; Lebedeva et al., 2006, Pilskog, 2011) and has implicated phoresy with migrating birds as a possible dispersal pathway for soil mites from the mainland to remote Arctic islands and archipelagos (Lebedeva and Lebedev, 2008).

Oribatid mite research commenced in the Russian Arctic in the late Nineteenth to early Twentieth Centuries. The first information concerning the oribatid mites of Novaya Zemlya were published by L. Koch (1879) who identified and described mites that Nordenskiöld collected during the Swedish Arctic expedition of 1875. L. Koch named seven species of oribatid mites for Novaya Zemlya. He described three species new to science, *Ceratoppia sphaerica* (L. Koch, 1879) (as *Oppia sphaerica*), *Oromurcia lucens* (L. Koch, 1879) (as *Oribata lucens*) and *Platynothrus punctatus* (C. L. Koch, 1839), (as *Nothrus punctatus*). Furthermore, he described as new to science the species *Oribata crassipes.* Later Trägårdh (1904) identified this species as the variable species *Notaspis exilis* Nicolet 1855, now transferred to the genus *Zygoribatula.* L. Koch also recorded *Ameronothrus lineatus* (Thorell, 1871) (as *Eremaeus lineatus*), *Camisia borealis* (Trägårdh, 1902), *Nothrus borealis* (Thorell, 1871) and *Diapterobates notatus* (Thorell, 1871) (as *Oribata notata*) from Novaya Zemlya. Further information on the oribatid mites of Novaya Zemlya appeared in Trägårdh (1901, 1904, 1928). Based on museum collections of Nordenskiöld's samples, Trägårdh (1904) noted nine species from Novaya Zemlya. However, three of these (*Ameronothrus nigrofemoratus* L. Koch, 1879*, Hermannia reticulata* Thorell, 1871 and *Hermannia scabra* L. Koch, 1879) Nordenskiöld were collected from the island of Vaigach which is not formally part of the Novaya Zemlya archipelago (Kox, 1879). Intensive studies of soil oribatid mites on the islands and archipelagoes of the Russian sector of the Arctic were carried out during 1989-2003. Krivolutsky and Kalyakin (1993) found 23 species of oribatid mites in Novaya Zemlya. Krivolutsky et al. (2003) presented a summary checklist of oribatid mites from the Russian Arctic reporting 58 taxa of oribatid mites, of which 52 were identified to species and six identified to genus from 27 families in Novaya Zemlya. Currently, 64 oribatid mite taxa, of which 58 are identified to species, representing 28 families are known from Novaya Zemlya.

Less is known for Franz Josef Land than from Svalbard or Novaya Zemlya. In his monograph Trägårdh (1904) recorded two species of oribatid mite from Franz Josef Land: *D. notatus* and *Oribata fischeri* Michael (the current taxonomic status of the latter is unclear).

Krivolutsky and Kalyakin (1993) recorded one species of oribatid mite (*Fuscozetes sellnicki* Hammer, 1952) from Franz Josef Land. The 15 taxa now known include nine identified to species and six identified to genus level representing 13 families of oribatid mites (Krivolutsky et al., 2003). Further investigations in Novaya Zemlya and Franz Josef Land will undoubtedly increase the species inventories of these archipelagos.

In the three archipelagos the greatest number of species belong to the families Brachychthoniidae, Camisiidae, Oppiidae, Suctobelbidae and Ceratozetidae, as is also seen in the mite communities of the European mainland tundra of the Arctic (Melekhina, 2011). Thirty nine species of oribatid mites are common to both Svalbard and Novaya Zemlya (representing 48% of the 81 species of Svalbard and 67% of the 58 species of Novaya Zemlya). The oribatid mite fauna of Svalbard shows only a low similarity to the fauna of the continental tundra. Of the 81 species of oribatid mites in Svalbard, only 36 (44%) were found in the tundra of the Kola Peninsula, although caution must be applied in interpreting these figures given the taxonomic challenges described earlier in this section. Most of the oribatid mites in the three archipelagoes are Holarctic and cosmopolitan in distribution. Only a few are restricted to the Arctic, for example *Ceratozetes spitsbergensis* (Thor, 1934), *Svalbardia paludicola* (Thor, 1930), *Autogneta kaisilai, Oribatella arctica* (Thor, 1930), *Ceratoppia sphaerica* (Koch, 1879), *Iugoribates gracilis* (Sellnick, 1944) and *Trichoribates setiger* (Trägårdh, 1910) from Svalbard, while only two species found in Novaya Zemlya are truly Arctic, *S. paludicola* and *O. arctica*.

3.6.1.4. Trombidiformes

3.6.2. Araneae

Spiders are major invertebrate predators in virtually all terrestrial ecosystems on Earth (with the exception of Antarctica) (Oedekoven and Joern, 2000; Platnick, 2012). They have filled a large spectrum of niches and recent research suggests they may have an important control function on their prey populations. Spiders possess good dispersal abilities and are amongst the first colonisers of new ground revealed by retreating glaciers in Svalbard (Hodkinson et al., 2001). In common with other groups of animals and plants, their diversity generally decreases with latitude and tropical faunas are by far the most diverse. However, one important family, the Linyphiidae (dwarf spiders and sheet-weavers) second only to the jumping spiders (Salticidae) in terms of species numbers (Platnick, 2012), reaches its highest species diversity in the northern region of the Northern Hemisphere (van Helsdingen, 1984) and attains dominant levels furthest north. The Linyphiidae is also the only family of Araneae represented in the sub-Antarctic islands (Pugh, 1994).

The spider fauna of the Svalbard archipelago is comparatively well known. Holm (1958) provided a review of earlier literature and reported a total of 15 species. Since then only two further species have been reported, *Oreoentides vaginatus* (Thorell, 1872) from the warm spring area in Bockfjorden (Tambs-Lyche, 1967) and *Thanatus formicinus* (Clerck, 1757) from Ny-Ålesund (Aakra and Hauge, 2003). Of this total of 17 species, three are clearly introduced to Svalbard (see Holm, 1958; Aakra and Hauge, 2003) - *Hahnia helveola* Simon, 1875, *Tapinocyba insecta* (L. Koch, 1869) and *T. formicinus*. The 14 naturally occurring species are all Arctic-alpine in distribution and all, except one, belong to the Linyphiidae. The exception, *Micaria constricta* (Emerton, 1882) (previously listed as *M. eltonii* Jackson, 1922, for example by Aakra and Hauge, 2003), belongs to the ground spider family Gnaphosidae. It is so far only known from a few localities around Billefjorden in Spitsbergen. Given the total area of Svalbard, the spider fauna is impoverished, probably a result of both environmental severity and geographic isolation. Most spiders are widely distributed across the archipelago but some have only been found in one or a few localities. Other than *M. constricta*, geographically restricted species include *O. vaginatus*, *Collinsia thulensis* (Jackson, 1924) and *Walckenaeria karpinskii* (O. P. Cambridge, 1873). The most common and widely distributed species, *Collinsia spetsbergensis* (Thorell, 1872), *Erigone arctica palaearctica* Braendegaard, 1934, *E. psychrophila* Thorell, 1872, *Hilaria glacialis* (Thorell, 1871) and *Mughiphantes sobrius* (Thorell, 1872), are recorded from all, or most of, the major islands.

The majority of spider species known from Svalbard are also found in northern Fennoscandia and neighboring parts of Russia, but there are three exceptions, *Collinsia thulensis* (Jackson, 1934), *Hilaira glacialis* (Thorell, 1871) and *Mughiphantes sobrius* (Thorell, 1872). These are High Arctic species also known from Alaska, Canada and Greenland (*C. thulensis*) and Russia (*H. glacialis* and *M. sobrius*), but not currently from Fennoscandia (see Platnick, 2012). The native species are all found below rocks and in the sparse vegetation cover. One, *O. vaginatus,* may be restricted to warm spring habitats where a more diverse flora and fauna can be found. Although known native diversity in this group is unlikely to increase significantly, there are areas of Svalbard that are insufficiently studied and which may yield new species. As with work on many groups, most investigations have concentrated on the main island, Spitsbergen (see Hauge and Sømme, 1997), and any future studies targeting spider diversity should be focussed on the remaining islands and, in particular, their easternmost parts including Kong Karls Land, Svenskøya and Hopen.

The spider fauna of Novaya Zemlya is also well-studied, comprising 20 species of linyphiids, only eight of which are in common with Svalbard. These shared species are all widespread Arctic species (*Agyneta nigripes, Collinsia holmgreni, C. spetsbergensis, Erigone arctica palearctica, E. psychrophila, E. tirolensis, Hilaira glacilalis* and *M. sobrius*) (see Tanasevitch, 2012), and are likely to be excellent aerial dispersers. The spider fauna of Novaya Zemlya includes some species near their western limit in Europe and that do not occur on Svalbard, including *Erigone remota, Collinisa borea, C. proletaria, Hybauchenidium aquilonare, Masikia indistincta, Oreoneta leviceps, Praestigia groenlandica* and *Semljicola arcticus* (see Nentwig et al., 2012). This fauna is clearly strongly influenced by that of the adjacent continental mainland.

In clear contrast with both Svalbard and Novaya Zemlya, only two species of spider have been recorded from Franz Josef Land (Tanasevitch, 2012). These species, *C. spetsbergens*is and *E. psychrophila*, are, as previously mentioned, common and widespread species in the region.

3.7 Hexapoda

3.7.1 Collembola

The first comprehensive collections of Collembola from the European Arctic were those of the Swedish Nordenskiöld expeditions along the north coast of Russia during 1875-1880. The pioneering work of Tullberg (1876) reported 15 species from Novaya Zemlya and five from Svalbard. Prior to that, Boheman (1865) was the first to record a collembolan from Svalbard, "*Podura hyperborea*", a taxon which has subsequently proved impossible to determine under current taxonomy. Schött (1899) reported four species from Franz Josef Land. Other major works from this initial phase of Arctic exploration include those of Schäffer (1895, 1900), Skorikow (1900) and Lubbock (1898). In the period 1900-1960 the faunistics and biogeography of the Arctic archipelagoes were further elaborated, in particular in the Atlantic sector of the Arctic (Brown, 1936; Carpenter, 1900, 1927; Carpenter and Phillips, 1922; Schött, 1923; Zschokke, 1926; Thor, 1930; Linnaniemi, 1935a, b). Stach (1962) and Valpas (1967) provided good overviews of the Svalbard springtail fauna and Fjellberg (1994) provided the first illustrated identification key to the Collembola species from the Norwegian Arctic islands. A recent inventory of the Svalbard fauna was published by Coulson and Refseth (2004), while Babenko and Fjellberg (2006) provided an extensively referenced catalogue of the Collembola of the whole circumpolar Arctic. From 1960 onwards the focus of research shifted to understanding the ecological functions of soil invertebrates in the Arctic and the physical and genetic mechanisms underlying distributional patterns (Ávila-Jiménez, 2011).

A critical review of published and unpublished species lists from Svalbard results in 68 recognized species including a few probably introduced species. Corresponding numbers from Novaya Zemlya and Franz Josef Land are 53 and 14. Franz Josef Land clearly has a depauperate fauna consisting of mainly circumpolar species. Two of these, *Hypogastrura trybomi* (Schött, 1893) and *Vertagopus brevicaudus* (Carpenter, 1900) are not present in Svalbard although they are known from both the Russian and Canadian sectors of the Arctic. The springtail fauna of Novaya Zemlya has clear affinities to the rich fauna of the northern parts of the Russian mainland. Almost 60% of the species from Novaya Zemlya (33 of the 53 species) are not recorded from Svalbard. These include a large proportion of boreal species which also are not known from Fennoscandia. Similarly, more than 70% of the Svalbard fauna (49 of its 68 species) are not recorded from Novaya Zemlya, illustrating the strong North Atlantic influence on the Svalbard springtail fauna. The proportion of true Arctic (i.e.

not recorded from the Fennoscandian mainland) species in Svalbard is low, only 14 of 68 species (21%). Most of these are more or less circumpolar in distribution, although there is a small but significant group with an eastern Palearctic affinity which appears to show a distribution restricted to the eastern part of Svalbard.

The long history of human presence in Svalbard may have resulted in introduction and subsequent dispersal of new Collembola species. Some of these may have become naturalized to such a degree that their dispersal history is no longer evident. Others may still be present only in their original locations. Recently, five species new to Svalbard were identified in imported soils in the Russian settlement in Barentsburg (Coulson et al., 2013a). One of these, *Deuteraphorura variablis* (Stach, 1964), is not present in Fennoscandia but is well known as a species associated with human settlements in mainland Europe. This species is also common in several natural northern communities of the European part of Russia, the Karelian coast of the White Sea (Pomorski and Skarzynski, 1995), flood-lands in northern taiga of the Komi Republic (Taskaeva, 2009) and coastal tundra of the same region (Taskaeva and Nakul, 2010) Pomorski and Skarzynski (2001) reported the species as being particularly common in ornithogenic soils of the Karelian coast of the White Sea. Now that it has achieved a foothold on Svalbard, it may have the potential of becoming established as an invasive species in nutrient-enriched soils near seabird colonies. The widespread boreal species *Vertagopus pseudocinereus* Fjellberg, 1975 was originally reported from under bark on imported timber at Ny-Ålesund (Fjellberg, 1975) but is unlikely to become naturalised in Svalbard and has not been recorded since.

Collembola may attain very high population densities. In Svalbard densities of almost 600,000 individuals m^{-2} have been reported in enriched moss tundra beneath bird cliffs

(Bengtson et al., 1974; Byzova et al., 1995) while in ornithogenic substrates in Novaya Zemlya, Babenko and Bulavintsev (1993) observed densities of 1,200,000 individuals m^{-2}. With the absence of large detritivores such as earthworms and terrestrial isopods the Collembola may assume a major role in primary decomposition and mineralization of plant material, though their precise contribution is yet to be quantified. The abundance and easy accessibility of surface-active species are exploited by feeding birds such as the purple sandpiper (Bengtson et al., 1975; Leinaas and Ambrose, 1992, 1999).

The very obvious patchiness of habitats and the sharp environmental gradients have been the focus for several studies regarding population dynamics and structure (Birkemoe and Leinaas, 2001; Hertzberg et al., 2000; Coulson et al., 2003a; Ims et al., 2004). Similar characteristics are seen in Antarctic terrestrial habitats (Usher and Booth 1984, 1986), although Antarctic and even sub-Antarctic collembolan assemblages are much simpler than those of the Arctic with typically only 1-3 species being encountered regularly in any given habitat (e.g. Usher and Booth, 1984; Richard et al., 1994; Greenslade, 1995; Convey and Smith, 1997). Cold adaptation and survival under the harsh environmental stresses has also attracted considerable research (Coulson and Birkemoe, 2000; Coulson et al., 2000; Hodkinson and Bird, 2004). In particular, the initial studies of Holmstrup and Sømme (1998) and Worland et al. (1998) on dehydration and cold hardiness in *Megaphorura arctica* (Tullberg, 1876) (previously *Onychiurus arcticus*) shed light on the important and previously undescribed survival mechanism of cryoprotective dehydration in Arctic invertebrates (Sørensen and Holmstrup 2011).

3.7.2 Insecta

3.7.2.1 Phthiraptera

The Phthiraptera (lice) are obligate ectoparasites of birds and mammals. Since they lack a free dispersal stage the Phthiraptera known from any given area are strongly correlated with the available hosts (Clay, 1976; Price et al., 2003). The history of phthirapteran studies on Svalbard is patchy, beginning with Boheman (1865), Giebel (1874), Mjöberg (1910), Waterston (1922a) and Timmermann (1957), who identified a total of 11 species. The first thorough survey of the Phthiraptera of Svalbard was performed by Hackman and Nyholm (1968) who included 44 species (all from birds). However, many of these were limited to Bjørnøya, were identified to genus level only, or the samples and identifications consisted only of nymphs. Kaisila (1973a) added one species of mammal louse. Mehl et al. (1982) reviewed the species list of avian lice of Svalbard, omitting 19 of Hackman and Nyholm's (1968) records as unidentified or uncertain and adding 11 new records. The number of phthirapteran species recognized from Svalbard currently stands at 37 including two only recorded from Bjørnøya and two subspecies. To this can be added four species recorded by Hackman and Nyholm (1968) that were not determined to species level but which are known from adult individuals that could potentially be reliably determined.

Three suborders of Phthiraptera have been recorded from Svalbard from 22 species of bird and two species of mammal (Kaisila, 1973a; Mehl et al., 1982). The most speciose suborder is the Ischnocera (27 species, two only found on Bjørnøya), while the Amblycera (eight species) and the Anoplura (two species) are less represented. This reflects both the global diversity in each group (Price et al., 2003), and the fact that ischnoceran lice are typically more common on birds than are the amblycerans (e.g. Eveleigh and Threlfall, 1976; Hunter and Colwell, 1994).

The Ischnocera of Svalbard have all been obtained from birds, with most (18 of 27 species) from shorebirds (Charadriiformes). The two most speciose genera on Svalbard are *Saemundssonia* (10 species and two subspecies) and *Quadraceps* (six species), both primarily parasites of shorebirds. Other Ischnoceran genera include *Lunaceps*, *Lagopoecus*, *Perineus* and *Anaticola*.

As with the Ischnocera, the majority of the Amblycera recorded on Svalbard have been obtained from shorebirds (five of eight species). While the genus *Austromenopon* has been recorded from five shorebird species on Svalbard, the quill-boring (Waterston, 1922a) shorebird louse genus *Actornithophilus* has been recorded so far only as nymphs (Hackman and Nyholm, 1968) and the species was omitted from Mehl et al.'s (1982) list. Two amblyceran species have been recorded from the Arctic fulmar (*Fulmarus glacialis*) and one from two species of geese; barnacle (*Branta leucopsis*) and pink-footed (*Anser brachyrhynchus*) (Waterston 1922a).

Quill-boring lice, such as *Actornithophilus* and *Holomenopon*, have been implicated in feather loss or "wet-feather" disorder in hosts which may subsequently die from pneumonia (Humphreys, 1975; Taylor, 1981). Hosts infested with these lice may be more likely to die before the parasite can transfer to a new host individual and these louse genera may therefore be missing or rare in the High Arctic. However, more thorough sampling of potential hosts of *Actornithophilus* (shorebirds) and *Holomenopon* (ducks and geese) is required to confirm this.

No Phthiraptera have been recorded from Franz Josef Land. A total of seven have been reported from Novaya Zemlya (Ferris, 1923; Markov, 1937) but there are no recent published records. Of these, one is from the Amblycera and the remainder from the Ischnocera. Four of these species have also been recorded from Svalbard.

3.7.2.2. Ephemeroptera, Tricoptera and Plecoptera

No Plecoptera are known from Svalbard or Franz Josef Land. Three species were recorded from Novaya Zemlya by Morten (1923): *Capnia vidua* (Aubert, 1950), *C. zaicevi* (Klapalek, 1914) and *Nemoura arctica* Esben-Petersen, 1910. There is only one dubious record of a mayfly (Ephemeroptera) from Svalbard (Jørgensen and Eie, 1993; Coulson and Refseth, 2004; Coulson, 2007a), but *Acentrella lapponica* Bengtsson, 1912 has been recorded from Novaya Zemyla (Ulmer, 1925). The circumpolar trichopteran, *Apatania zonella* Zetterstedt, 1840 occurs sporadically throughout the western parts of the Svalbard archipelago, as well as on Bjørnøya (Bertram and Lack, 1938) and Novaya Zemlya (Ulmer, 1925). Although mainly found in lakes, *A. zonella* also occurs in and around lake outflows.

3.7.2.3. Hemiptera

Virtually all records of Hemiptera species from the archipelagoes of the Barents Sea are restricted to Svalbard and are exclusively of aphids (Hemiptera: Aphididae). A single published aphid record exists for the South Island (Fig. 3) of the Novaya Zemlya archipelago (*Aphis* (s.l.) sp.) (Økland, 1928). The earliest reports of Svalbard aphids are from Parry's North Pole Expedition (Parry, 1828). However, these reports were of aphid specimens found on pack ice or floating trees and were probably transported by wind, ships or sea currents from distant sources (Elton, 1925a). The first inventory of the aphid fauna from Svalbard (Heikinheimo, 1968) was based on previous published works (Ossiannilsson, 1958) or collections and described "seven or eight species". Two of these were reported as endemic, *Acyrthosiphon calvulus* (Ossiannilsson, 1958) (later revised to *Sitobion calvulum* (Eastop and

Blackman, 2005)) and *Acyrthosiphon svalbardicum* Heikinheimo, 1968, one as Arctic (*Pemphigus groenlandicus* (Rübsamer, 1898)), one as boreal (*Cinara abieticola* (Cholodkovsky, 1899)) and four not identified to species level.

In their catalogue of the terrestrial and marine fauna of Svalbard, Coulson and Refseth (2004) listed two resident aphid species (*A. calvulus* and *A. svalbardicum* (formerly listed as *A. svalbardicus* by Heikinheimo (1968)), and five migrant aphid species (*Aphis borealis* (Curtis, 1828), *Aphis* sp., *Cavariella salicis* (Monell, 1879), *Cinara abieticola* (Cholodkovsky, 1899) and *Pemphigus groenlandicus* Rübsaamen, 1898). Finally, Coulson (unpublished data) has located a third resident species in Krossfjord whose identity has not yet been formally confirmed but most likely corresponds to *P. groenlandicus*, a species reported from Iceland, Greenland and the Canadian Arctic (Hille Ris Lambers, 1960; Richards, 1963). Thus, there is clear evidence that at least three aphid species are currently resident on Svalbard: *A. svalbardicum* which appears to feed exclusively on *Dryas octopetala* (Strathdee et al., 1993), *S. calvulum* which feeds primarily on *Salix polaris* but also on *Pedicularis hirsuta* (Gillespie et al., 2007) and *Pemphigus* sp. which apparently feeds on roots of *Poa* spp. in Svalbard. Hille Ris Lambers (1952) reports this species feeding on the roots of various Gramineae in Greenland. Other earlier aphid records are unlikely to be resident in Svalbard as they have not been subsequently observed and their host plants generally do not occur. *Sitobion calvulum* is restricted to only few sites on the west coast of Spitsbergen, namely Adventdalen and Colesdalen (Gillespie et al., 2007) and Grøndalen. *Acyrthosiphon svalbardicum* is more common along the west coast of Spitsbergen but its spatial distribution is very patchy at the local scale (Strathdee and Bale, 1995; Ávila-Jiménez and Coulson, 2011b), its occurrence perhaps being partially determined by winter snow depth modulating the length of the summer growing season (Strathdee et al., 1993; Ávila-Jiménez and Coulson, 2011b).

Pemphigus sp. feeds on roots and is unlikely to be observed without targeted specialist surveys, and therefore its distribution is likely to be currently underestimated.

Ecological studies on Svalbard aphids commenced in the early 1990s (Strathdee et al., 1993; Gillespie et al., 2007; Hullé et al., 2008; Simon et al., 2008; Ávila-Jiménez and Coulson, 2011b) and have focused on the two resident aphid species, *A. svalbardicum* and *S. calvulum*. These studies have highlighted peculiar traits and life histories thought to result from adaptations and constraints exerted by the harsh conditions of the High Arctic (Table 1). Both species have an extremely reduced life cycle compared to their temperate counterparts. *Sitobion calvulum* displays a two-generation life cycle with a first generation of asexual females hatching from cold-resistant eggs in early June and a second generation of sexual forms that mate and lay eggs before the arrival of frost in early August. *Acyrthosiphon svalbardicum* has a similar life cycle but, in some instances, may produce an extra intermediate generation although there are uncertainties whether this is achieved in the field (Strathdee et al., 1993; Hullé et al., 2008). When *A. svalbardicum* displays this three-generation life cycle, the first generation hatching from the overwintering egg produces a mixture of asexual and sexual morphs with the former then generating a third generation exclusively composed of sexual individuals. In field environmental manipulation experiments, the inclusion of the extra generation leads to an order of magnitude increase in the numbers of overwintering eggs (Strathdee et al., 1993, 1995). Although the cascade effects of this potential change in primary consumer population density have not been researched there are indications that predator and parasitoid densities may increase (Dollery et al., 2006). In the sexual generations of the two species, the sex ratio is biased towards females as a result of local mate competition (Strathdee et al., 1993; Gillespie et al., 2007). Both species also have reduced dispersal capabilities. *Sitobion calvulum* has no known winged form and its populations occur as small, isolated colonies (Gillespie et al., 2007). Populations of *A. svalbardicum* are also patchily distributed (Strathdee and Bale, 1995) and winged individuals were unknown until the discovery of one alate on Storholmen island (Kongsfjord) (Hodkinson et al., 2002) and several additional specimens in other areas around Ny-Ålesund (Simon et al., 2008). Whether this apparently recent appearance of small numbers of winged morphs in *A. svalbardicum* results from the recent warming of Svalbard, from other factors that may operate locally and only in certain years, or indeed simply from researchers not previously encountering them, is unclear (Hodkinson et al., 2002; Simon et al., 2008).

Insert Table 1 here

Very little is known of the biology of natural enemies of Svalbard aphids. Two newly described parasitoid wasps (Hymenoptera: Braconidae) exploit Svalbard aphids as hosts (Chaubet et al., 2013). *Diaeretellus svalbardicum* Chaubert, 2012 parasitizes exclusively the aphid *A. svalbardicum* and displays a unique case of wing polymorphism with macropterous and micropterous forms in both genders. By contrast, *Aphidius leclanti* Chaubert, 2012 can utilize both aphid species as host. Parasitism rates in field-collected aphids are extremely variable between individuals and collection sites, although can reach up to 50% (Outreman et al., unpublished).

3.7.2.4. Coleoptera

The first report of Coleoptera from Svalbard was of a dead specimen of *Philonthus* collected from under seaweed on a beach by the Swedish polar expedition in 1868 (Holmgren, 1869). In the light of current knowledge of the beetle fauna this specimen is of uncertain origin, although likely originating from ship ballast (Strand, 1942). In 1882, the first living beetle was reported from Billefjord (Beetlefjord) by Nathorst (1884). Although the material was not collected a new sample was taken in 1898 and *Atheta graminicola* (Gravenhorst, 1806) *Boreophila (Atheta) subplana* (J. Sahlberg, 1880), and *Isochnus flagellum* (Erichson, 1902) were recorded (Sahlberg, 1901). A review of the Coleoptera from Svalbard was published by Strand (1942), and subsequent additional reports of new species for the archipelago were provided by Strand (1969), Kangas (1967, 1973), Bengtson et al. (1975) and Fjellberg (1983), as well as further information being included in several reviews (Sømme, 1979; Klemetsen et al., 1985; Coulson and Refseth, 2004; Coulson, 2007a).

A total of 19 species of Coleoptera are currently known from Svalbard, including six only recorded from Bjørnøya. However, only 14 of these species have been confirmed to be native to the archipelago. Just *B. subplana*, *A. graminicola* and *I. flagellum* are commonly recorded, whilst most species are found only occasionally. Most of the species have a wide distribution throughout Arctic regions and none are restricted to Svalbard. Two species, *Coccinella septempunctata* L., 1758 and *Oryzaephilus mercator* (Fauvel, 1889), have only been found inside buildings and are considered to be introduced and, if resident rather than transient, then synanthropic. *Atomaria lewisi* Reitter, 1877 has certainly colonized in recent times and is mainly associated with synanthropic habitats (Ødegaard and Tømmerås, 2000). The single specimen of *Gonioctena* (*Phytodecta*) sp. collected by the Oxford Expedition in 1924 is lost and it is not now possible to confirm its identity although, based on general biogeography, this is most probably *G. arctica* (*affinis*) (Strand, 1942). Only one species of weevil, *I. flagellum* is recorded from Spitsbergen, with the report of *I. foliorum* (*saliceti*) (Coulson and Refseth, 2004) referring to the same species (see Strand, 1942).

In recent times, there have been only two studies that have attempted to search for Coleoptera in Franz Josef Land (Bulavintsev and Babenko, 1983; Bulavintsev, 1999) and, as yet, none have been found. Only a few expeditions have collected Coleoptera from Novaya Zemlya. The Nordenskiöld expedition in 1875 reported nine species (Mäklin, 1881). In 1879 the area was further investigated (Markham, 1881) and in 1897 the Russian entomologist Georgii G. Jacobson spent a summer there. Both expeditions provided new additions to the beetle fauna (Jacobson, 1898; Sahlberg, 1897). By 1910, 16 beetle species were known from Novaya Zemlya, of which *Upis ceramboides* (L. 1758) and *Pediacus fuscus* (Erichson, 1845) are considered to be introduced. Poppius (1910) added *Hyporoprus acutangulus* (published as *H. sumakowi* Popp.). A major contribution was made by the Norwegian expedition to Novaya Zemlya in 1921, where F. Økland and R. Tveten collected some 300 specimens of beetles which were identified by T. Münster (Münster, 1925). There have been no recent collections or reports of beetles from Novaya Zemlya, excepting Yunakov and Korotyaev's (2007) addition of *Phyllobius pomaceus* (leg. K. Baer) to the species identified from the Russian expedition in 1827.

A number of taxonomic advances have been made since these older collections and publications. Both *Boreophilia frigida* and *B. sibirica* are recorded from Novaya Zemlya in Mäklin (1881) and Münster (1925), but these species are now synonymised (Löbl and Smetana 2004). The record of *Olophrum boreale* (Paykull, 1792) from Novaya Zemlya (Münster, 1935) is likely to be incorrect. Both Münster (1925) and Poppius (1910) mention the specimen from the island of Vaigatsh published by Mäklin (1881), which may have led to confusion. Moreover, Vaigatsh is not politically part of Novaya Zemlya. Finally, according to Poppius (1910) and Münster (1925), *Tachinus apterus* (*T. arcticus*) is found in Novaya Zemlya. *Tachinus arcticus* Motsch, 1860 is now regarded as separate species from *T. apterus*

(Ullrich and Campbell, 1974). According to the current distribution of the two species (Ullrich and Campbell, 1974), it is undoubtedly *T. arcticus* occurring in Novaya Zemlya. In total, and incorporating updated taxonomy, there are 31 species of beetle known from Novaya Zemlya, 27 of which are considered native. Most have a wide distribution in Arctic areas (Münster, 1925), but three are currently reported only from Novaya Zemlya, *Phyllodrepa polaris* (J. Sahlberg, 1897), *Atheta holtedahli* (Münster, 1925) and *Oxypoda oeklandi* (Münster, 1925) (Löbl and Smetana, 2004). Novaya Zemlya has only one species of coleopteran in common with Svalbard, *O. boreale*.

3.7.2.5. Diptera

Diptera are better adapted to the cold and harsh climate in the Arctic than any other order of insects and comprise an important part of the insect fauna both with regard to species number (for example Coulson and Refseth, 2004) and biomass (for example Bengtson et al., 1974). Nevertheless, our knowledge of Diptera diversity in the Barents Sea archipelagoes is still insufficient, in particular for the most remote and inaccessible islands such as the Nordaustlandet (Svalbard), Franz Josef Land and Novaya Zemlya.

Within the Barents Sea archipelagoes, the best known and well documented dipteran fauna is that of Svalbard (including Bjørnøya) (Coulson and Refseth, 2004; Coulson, 2007a), including a total of 122 species. Of these, the Chironomidae comprise more than 66 recognised species and at least four undescribed taxa (Sæther and Spies, 2012; Ekrem and Stur, unpublished data). Taxonomic confusions endure, for example *Orthocladius mixtus* (Holmgren, 1869), originally described from Svalbard but currently regarded as *nomen dubium*.

Seventeen fly species are known from Bjørnøya, excluding the Chironomidae, which probably are represented by up to 40 species (Ekrem and Stur, unpublished data; Sømme 1979). Among the non-chironomids, four have not been reported from elsewhere in Svalbard including the simuliid *Prosimulium ursinum* (Edwards, 1935) (Edwards, 1935). A similar situation exists for the Chironomidae, where certain species are restricted to one or two smaller areas in the Svalbard archipelago. A noteworthy example is *Micropsectra logani* Johannsen, 1928 which is widely distributed in the northern Holarctic and also numerous on Bjørnøya. It is, however, not recorded from the other islands of Svalbard.

The first records of Diptera from Novaya Zemlya are those of Holmgren (1883) collected during Nordenskiöld's expedition. In total, 81 species were recorded, including many new species. Further species were added by the Norwegian Novaya Zemlya Expedition in 1921 (Alexander, 1922; Lenz and Thienemann, 1922; Sack, 1923; Kieffer, 1922, 1923). Since then only scattered records have been published. The most recent list contains 147 species (and subspecies) (Fauna Europaea, 2011), but this is far from complete as several species already reported by Holmgren (1883) are missing (e.g. *Tanytarsus gracilentus* Holmgren, 1883) and additional chironomid taxa have been added (Makarchenko et al., 1998). About 49% of the Diptera species (73 spp.) recorded from Novaya Zemlya are chironomids (Makarchenko et al., 1998, Sæther and Spies, 2012). Due to the region's proximity to the Eurasian continent and its geographic extent, the dipteran fauna of Novaya Zemlya is likely to be the most diverse among the archipelagoes. Nine families recorded here have not been reported from Svalbard, among them 3 families in the superfamily Tipuloidea (Limonidae, Pediciidae, and Tipulidae). The two archipelagoes have only about 30 species of Diptera in common. This disparity probably does reflect true differences, but may in part also be underlain by different taxonomic traditions between Russian and European dipterists, highlighting the need for taxonomic revision and collaboration.

The Dipteran fauna of Franz Josef Land is very poorly known. Uspenskiy et al. (1987), based on a Russian expedition in 1980-81, mentions five species of Diptera belonging to the Chironomidae and Mycetophilidae (of which the latter probably refers to Sciaridae). Four species are listed in Fauna Europaea (2011), *Hydrobaenus conformis* (Holmgren, 1869), *Ditaeniella grisescens* (Meigen, 1830), *Myennis octopunctata* (Coqubert, 1798) and *Seioptera vibrans* (L. 1758), of which the latter two are most unlikely to inhabit the islands.

3.7.2.6. Siphonaptera

Two species of flea (Siphonaptera) are present in Svalbard, *Ceratophyllus vagabundus vagabundus* Boheman, 1866 and *Mioctenopsylla arctica arctica* Rothschild, 1922 (Coulson and Refseth, 2004), both belonging to the Ceratophyllidae. The first record of *C. v. vagabundus* was in 1864 (Boheman, 1865) and the species was later observed in pink-footed geese nests by Dampf (1911). Other studies concerning the fleas of Svalbard include Thor (1930), Cyprich and Krumpàl (1991), Mehl (1992), Coulson et al. (2009) and Pilskog (2011). Only one species of Siphonaptera is recorded from Novaya Zemlya, *M. a. arctica.* This species was first described from Novaya Zemlya (Rothschild, 1922) and later recorded in Svalbard in 1965 in a room in Longyearbyen where black-legged kittiwakes had been skinned (Kaisila, 1973a). There appear to be no reports of Siphonaptera from Franz Josef Land.

Ceratophyllus v. vagabundus has a northern Holarctic distribution and is common on members of the bird families Anatidae and Laridae and their predators (Brinck-Lindroth and

Smit, 2007). In Svalbard it is recorded as an ectoparasite of the common eider duck (*Somateria mollissima*), barnacle goose (*Branta leucopsis*), pink-foot goose (*Anser brachyrhynchus*) and glaucous gull (*Larus hyperboreus*) (Dampf, 1911; Pilskog, 2011) and has also been recorded in nests of snow bunting (*Plectrophenax nivalis*) (Pilskog, 2011). As *C. v. vagabundus* is a generalist that uses hosts belonging to different families of birds (Tripet et al., 2002; Brinck-Lindroth and Smit, 2007) further studies are likely to increase the list of host species present in Svalbard. The second species, *M. a. arctica*, is also known from northern Norway (including Jan Mayen), Iceland and Alaska (Mehl, 1992; Brinck-Lindroth and Smit, 2007). This species currently has two subspecies, *M. a. arctica* and *M. a. hadweni* Ewing, 1927. However, although only *M. a. arctica* is recorded as present in Svalbard, it is possible that the sub-specific division is not valid (R.E. Lewis pers. comm.). *Mioctenopsylla a. arctica* is a host-specific flea only present on black-legged kittiwakes (*Rissa tridactyla*) in Svalbard and, with the exception of Coulson et al. (2009), all records have been obtained from black-legged kittiwake plumage and nests (Kaisila, 1973a; Cyprich and Krumpàl, 1991; Mehl, 1992; Pilskog, 2011) or in the immediate vicinity of their colonies (Hågvar, 1971). The finding of adult *M. a. arctica* in nests of common eider duck and glaucous gull in Kongsfjorden in Svalbard by Coulson et al. (2009) was probably a misidentification, as this species was not found by Pilskog (2011) in a more thorough investigation of the common eider duck nests in the same area. The effect the fleas have on the host birds is unknown, but high flea infestations generally reduce breeding success in some species of bird including geese breeding in the Arctic such as Ross's, *Chen rossii*, and lesser snow geese, *Chen caerulescens caerulescens* (Harriman and Alisauskas, 2010).

Bird fleas spend most of their lives in the nests of their host where they feed on adult birds and chicks (Lewis and Stone, 2001). High densities of adult fleas and juvenile stages can be present in bird nests in Svalbard (Cyprich and Krumpàl, 1991; Mehl, 1992; Pilskog, 2011), often being the numerically dominant arthropods in the nests of common eider duck, barnacle goose, black-legged kittiwake and glaucous gull breeding in the Kongsfjord area (Pilskog, 2011). Although the bird fleas are known to bite humans (Mehl, 1992; B. Moe pers.comm.), no fleas have been reported from mammals in Svalbard.

3.7.2.7. Lepidoptera

Twenty-three species of Lepidoptera have been recorded from Svalbard and Novaya Zemlya, seven of which (30%) are considered to be vagrants and not resident in the archipelagoes. No Lepidoptera have been recorded from Franz Josef Land. Kaisila (1973b) summarized the Lepidoptera from Svalbard reporting six species, four of which were considered to be resident. With recent additions (Sendstad et al., 1976; Laasonen 1985; Coulson, 2007a) the total observed in Svalbard, including accidental migrants, has risen to 10 species, but with no increase in the number of resident species. The resident species total now is considered to be three; *Plutella polaris* Zeller, 1880 (Bengtsson and Johansson, 2011) (Plutellidae), *Matilella fusca* (Haworth, 1811) (Pyralidae) (Coulson et al., 2003b) and *Apamea exulis* (Lefèbvre, 1836) (Noctuidae) (Rebel, 1925; Alendal et al., 1980; Hodkinson, 2004). Kaisila (1973b) also considered *Plutella xylostella* (L., 1758) as resident. However, while this cosmopolitan and migratory species often disperses in great numbers, and has been recorded on several occasions in the Arctic (and likewise in the Southern Hemisphere (Convey, 2005)), it is unlikely that it can overwinter in the archipelago. The closely related *P. polaris* is a distinct species so far only known from Svalbard (Bengtsson and Johansson, 2011). It is unclear why this species has not been observed since it was first recorded, but the type material of *P. polaris* is held in the Natural History Museum, London, and was studied by Baraniak (2007) who drew wings and male genitalia, the distinct features of which currently support the specific status of *P. polaris*. Ideally, molecular studies would be required to confirm the relationship between these two species.*Apamea exulis* has been recorded from Svalbard under three different species names, *A. exulis, A. maillardi* and *A. zeta*, and this has caused some confusion. According to current taxonomy, *A. maillardi* and *A. zeta* are both species from mountainous regions in southern and central Europe and do not occur at more northern latitudes (Zilli et al., 2009). *Matilella fusca,* often reported as *Pyla fusca* in the Svalbard literature, was recorded from Svalbard in 1974 (Aagaard et al., 1975) and 2002 (Coulson et al., 2003b). The old record of *Pempelia dilutella* (Denis and Schiffermüller, 1775) (Elton, 1925b) probably also refers to *M. fusca*. The latter species is clearly able to maintain populations in Arctic environments as it is also present in Greenland, Labrador and Alaska (Kaisila, 1973b). *Matilella fusca* is a polyphagous species, with *Salix polaris* and *S. reticulata* being indicated as possible food plants in Svalbard (Coulson et al., 2003b).

Lepidoptera recorded from the Swedish Nordenskiöld expedition to Novaya Zemlya were published by Aurivillius (1883b) and those of the Norwegian expedition in 1921 by Rebel (1923). Of the 15 species recorded from Novaya Zemlya only one species, *P. xylostella*, is considered an immigrant resulting in a resident total of 14. Moreover, *P. xylostella* is the only lepidopteran species that Novaya Zemlya and Svalbard have in common and is also the only species of Lepidoptera recorded from Bjørnøya (Lack, 1933; Sømme, 1979) but is again unlikely to be resident (although, note the caveat mentioned above with reference to the separation of this species from *P. polaris*). The lepidopteran fauna of Novaya Zemlya is composed mainly of species with broad circumpolar Arctic distributions. However, the record of *Argyroploce mengelana* (Fernald, 1894) (Tortricidae) in Novaya Zemlya is the only observation of this species so far from the Eurasian continent. This species is otherwise known from Greenland, Canada (North West Territory, Yukon), and Alaska (Jalava and

Miller, 1998), and *Glacies coracina* (Esper, 1796) (Geometridae) is known only from the Palearctic, and is distributed from Fennoscandia to Japan (Skou, 1984).

3.7.2.8. Hymenoptera

The Hymenoptera is one of the most speciose orders of insects. The majority of species are parasitoids, attacking a wide variety of insects and other invertebrates. Where there are possible hosts present there are usually hymenopterans and they may occur even in the harshest climate. Nonetheless, it is notable that no species are associated with the two resident Diptera or microarthropods of the Antarctic Peninsula and that very few species are known from the sub-Antarctic islands, both of which have climates less extreme than those of the Barents Sea archipelagoes (Greenslade, 2006; Gressitt, 1970; Convey, 2013).

A total of 39 species of Hymenoptera are currently recorded from Svalbard (Waterston, 1922b; Yu et al., 2005; Coulson and Refseth, 2004; Coulson, 2007a; Jong, 2011). The majority are parasitoids belonging to the families Ichneumonidae (22 species) and Braconidae (five species) in the suborder Apocrita. In addition, the Symphyta is represented by seven species of Tenthredinidae.

Braconids are known to parasitise the two Svalbard endemic aphid species. No hymenopterans have yet been reported from Franz Josef Land, although since some vascular plants (e.g. *Salix polaris*) and associated insects are present (Hanssen and Lid, 1932; Jong, 2011) it is plausible that they may occur.

Novaya Zemlya has only 40 species of hymenopteran recorded, probably reflecting low collecting activity given the archipelago’s sizeable land area and the close proximity to the continental mainland. The Swedish Nordenskjöld expedition (Holmgren, 1883) and the Norwegian Novaya Zemlya expedition (Friese, 1923) were of great importance in investigating the hymenopteran fauna of this archipelago. Most of the recorded species again belong to the families Ichneumonidae (20 species) and Braconidae (four species). Overall, there are few hymenopteran species shared between Svalbard and Novaya Zemlya, which may support different underlying immigration patterns. Three species of bumblebee are also present (Holmgren, 1883; Friese, 1923), a family not resident in Svalbard. The honey bee, *Apis mellifera* L., 1758 has been reported from all three archipelagoes (Jong, 2011) as an accidental migrant. Records of two species of *Camponotus* (Formicidae) in Novaya Zemlya are unconfirmed.

3.8 Freshwater ecosystems

3.8.1. Ecosystem function in lakes and ponds

Investigations of freshwater invertebrates on the major islands of the Barents Sea date back more than a hundred years to pioneers such as Bryce (1897), Scourfield (1897) and Olofsson (1918). Summerhayes and Elton (1923) visited Bjørnøya and Spitsbergen in 1921 and sampled ponds and lakes while Økland (1928) reported on species distribution from a Norwegian expedition to Novaya Zemlya in 1921. More recent investigations in Svalbard have typically been carried out in areas close to established research stations on Spitsbergen in Isfjorden (Colesdalen and Kapp Linné), Kongsfjorden (Ny-Ålesund and Brøggerhalvøya), Hornsund and Mosselbukta (Halvorsen and Gullestad, 1976; Husmann et al., 1978; Jørgensen and Eie, 1993; Janiec, 1996), and Bjørnøya (Koch and Meijering, 1985). The branchiopod fauna of Novaya Zemlya is summarized by Vekhoff (1997). Information on the freshwater crustacean fauna of the Franz Joseph land archipelago is exceedingly scarce and primarily based on a single report from Scott (1899). Apart from this area there is a fairly good understanding of the biodiversity of some organisms (crustaceans and fish); however, knowledge of microscopic groups such as protozoans is less developed (e.g. Opravilova, 1989; Beyens and Chardez, 1995; De Jonckheere, 2006). Comparison of different Arctic regions based on crustacean species richness (Gíslason, 2005, Samchyshyna et al., 2008) indicates that glaciation history has played an important role in determining community diversity.

The list of Rotifera (section 3.1) and crustacean species recorded from the Barents Sea archipelagoes is diverse. All of these are currently thought to be circumpolar and the communities do not differ greatly from sub-Arctic regions in Europe, Russia or North America (Ghilarov, 1967; Samchyshyna et al., 2008). The zooplankton species distribution resembles that of Greenland and Alaska, with dominance by cladoceran over copepod species. Several calanoid copepod species (e.g. *Eurytemora raboti* Richard, 1897 and *Limnocalanus marcus* G.O. Sars, 1863) are widely distributed in the lakes of Novaya Zemlya and Svalbard (Olofsson, 1918; Halvorsen and Gullestad, 1976; Vekhoff, 1997).

The large branchiopods living in the Barents Sea region occupy the most extreme aquatic environments in Arctic regions (Vekhoff 1997). Vekhoff (1997) lists four species of Anostraca (*Polyartemia forcipata* (S. Fischer), *Artemiopsis bungei plovmornini* (Jaschnov, 1925), *Branchinecta paludosa* (Gajl, 1933), and *Branchinectella media* (Schmankewitsch, 1873)) and two species of Spinicaudata, *Caenestheria propinqua* (Sars, 1901) and *C. sahlbergi* (Simon, 1886), in addition to *Lepidurus arcticus* (Pallas, 1793) (Branchiopoda, Notostraca) at Novaya Zemlya. It is notable that the northern-most known occurrence of *B. paludosa* is at Ivanov Bay (77^{o}N) in the Novaya Zemlya archipelago (Fig. 3, Vekhoff, 1997).

Lepidurus arcticus frequently occupies shallow freshwater lakes and ponds with no fish population (Jeppesen et al., 2001) but may exceptionally co-occur with fish in some deep lakes, in shallow cold lakes or in lakes with refugia from fish at the southern-most edges of its distribution range in sub-Arctic regions of mainland Norway and in Iceland (Primicerio and Klemetsen, 1999; Woods, 2011). *Lepidurus arcticus* has been recorded in multiple sites on Spitsbergen, Bjørnøya, Novaya Zemlya and Franz Josef Land (Olofsson, 1918; Janiec, 1996; Vekhoff, 1997 (and references therein); Hessen et al., 2004). The crustacean can utilize different habitats in sub-Arctic and Arctic regions including shallow near-shore habitats in Svalbard (Lakka, 2013) and deeper regions of lakes on mainland Norway (Sømme, 1934). Food web studies in Bjørnøya have shown that environmental contaminants can enter the Arctic aquatic food web and that *L. arcticus,* chironomids and Arctic charr can contain elevated levels of both PCBs and DDT (Evenset et al. 2005). *Lepidurus arcticus* is sensitive to various environmental disturbances and therefore can be used as an indicator species of ongoing environmental change in the Arctic and sub-Arctic (Lakka, 2013).

Bottom-dwelling macroinvertebrate species belonging to Nematoda, Oligochaeta, Ostracoda, Hydracarina, Chironomidae, and Trichoptera have been reported in several studies (Summerhayes and Elton, 1923; Jørgensen and Eie, 1993; Janiec, 1996) but there is no detailed information on the biology of the groups. The chironomid diversity is substantial (Styczynski and Rakusa-Susczzewski, 1963; Hirvenoja, 1967; Section 3.7.2.5).

Five species of cestode are known to parasitize the Arctic char (*Salvelinius alpinus*) in Svalbard. Two of these, *Eubothrium salvelini* (Schrank, 1790) and *Proteocephalus exiguous* (Swiderski and Subilia, 1978), utilize Arctic char as their final host, whereas *Diphyllobothrium ditremum* (Creplin, 1825) employs various fish-eating birds as the definite host which, in Svalbard, is likely to be the red-throated diver (*Gavia stellate*) (Hammar, 2000). Additional groups known to parasitize Arctic char in Svalbard include one species of nematode (*Philonema oncorhynchi* Kuitunen-Ekbaum, 1933) and a copepod (*Salmoncola edwardsii* Olsson 1869, Siphonostomatoida) (Kennedy, 1978; Sobecka and Piasecki, 1993).

Studies of food web structure in lakes and ponds are limited, but a number of recent experimental studies have focused on nutrient addition to lakes and ponds by geese (van Geest et al., 2007), the role of dissolved organic carbon for microbial communities (Hessen et al., 2004), the implications of UV radiation on plankton growth (van Donk et al., 2001) and the dynamics of microbial communities (Ellis-Evans et al., 2001; Laybourn-Parry and Marshall, 2003). Such studies are important in order to understand the complexity of Arctic aquatic ecosystems and to be able to predict effects of human activities and environmental change (Prowse et al., 2006). Furthermore, van der Wal and Hessen (2009) have highlighted important analogies between aquatic and terrestrial food webs in the High Arctic, as a result of harsh conditions leading to grazer dominated food web dynamics.

3.8.2 Ecosystem function in streams and rivers

Biodiversity in running waters in Svalbard is low, as is probably also the case in Franz Josef Land, although there is little information on the latter. Freshwater biodiversity is however, higher in Novaya Zemlya due to its proximity to the mainland and its more southerly location. Colonisation by freshwater invertebrate fauna is limited by the isolation of the archipelagoes (Gíslason, 2005). In addition, the short summer season and the cessation of flow in most river systems during the long winter render environmental conditions unsuitable for many taxa.

There have been few ecological studies of Svalbard streams and rivers compared to terrestrial or even lake systems, and almost none from Novaya Zemlya or Franz Josef Land. Studies of hydrological and chemical processes, especially in glacier-fed systems are, however, more common (e.g. Gokhman, 1988; Hagen and Lefauconnier, 1995; Bogen and Bønsnes, 2003; Killingtveit et al., 2003; Krawczyk and Pettersson, 2007; McKnight et al., 2008). The significance of microbial activity for nutrient processes in glacial meltwater has also been highlighted from Svalbard studies (Hodson et al., 2008) and there have been studies of freshwater algae and cyanobacteria in the vicinity of Ny-Ålesund (Kim et al., 2011).

Freshwater invertebrate species records derive from both early expeditions and more recent collecting trips (e.g. Morten, 1923; Ulmer, 1925; Bertram and Lack, 1938), or from studies of the aerial insect fauna (Hodkinson et al., 1996; Coulson et al., 2003b). These records are frequently based on collections of adults, mainly chironomids, making it difficult to assign them to the larval environment - terrestrial, wetlands, lakes or streams. The invertebrate fauna of streams and rivers is dominated by chironomids, especially Diamesinae, although Nematoda, Enchytraeidae and Tardigrada have also been recorded from freshwater habitats in Svalbard (Styczynski and Rakusa-Susczzewski, 1963; Hirvenoja, 1967; Janiec, 1996; Coulson and Refseth, 2004). Planktonic and benthic crustaceans can also be found drifting downstream of lakes (Maiolini et al., 2006).

In recent years there has been an increasing focus towards understanding the influence of hydrological processes on stream fauna (ecohydrology). Studies of the influence of water source on benthic stream communities have been undertaken on Svalbard (Brittain and Milner, 2001), demonstrating the importance of channel stability and water temperature in structuring benthic invertebrate communities (Castella et al., 2001; Lods-Crozet et al., 2001;

Milner et al., 2001). . These studies have focused on two contrasting rivers in Svalbard in the vicinity of Ny-Ålesund, Bayelva and Londonelva. These rivers have been monitored for discharge, sediment transport and water temperature for over 20 years (Bogen and Bønsnes, 2003; Brittain et al., 2009). Bayelva is a glacier-fed river, whereas Londonelva is fed by rain and snowmelt. This difference in water source gives rise to distinct differences in their chironomid faunas, with higher densities in Londonelva, a greater proportion of Orthocladiinae and different species of *Diamesa* (Diamesinae) (Lods-Crozet et al., 2007). Chironomidae (especially the genus *Diamesa*) dominate in the glacial system, whereas in the non-glacial systemtheir relative abundance decreases, and the subfamily Orthocladiinae as well as other taxa including Oligochaeta, Copepoda, Acari, Collembola and Tardigrada become more frequent (Füreder and Brittain, 2006). At species level, most of those occurring in these systems are in common with those of nearby sub-Arctic areas such as the coastal regions of the Barents Sea, or to more temperate areas. Subsequent studies in a wider range of streams (Füreder and Brittain, 2006) have shown that species number, abundance and food web complexity follow a gradient with regard to catchment characteristics such extent of ice cover and the extent of nutrient input from bird cliffs or upstream lakes.

Invertebrate drift is generally a widespread and important phenomenon in running waters, and this is again the case on Svalbard. Studies during the Arctic summer in a stream near Ny-Ålesund (Maiolini et al., 2006; Marziali et al., 2009) showed that drift rates can be high and that there are distinct diurnal patterns, even in continuous daylight, which are controlled by environmental variables such as water temperature and discharge rate. Drift rates were enhanced by artificial shading of the stream, indicating a strong behavioural component. Invertebrate drift from streams and glacial outlet rivers contributes a significant source of food for seabirds and waders (Mehlum, 1984). It is clear that freshwaters on Svalbard are an important link for nutrients and biota between terrestrial, estuarine and marine ecosystems.

4. Adaptation to conditions – ecophysiology and life histories

The climates of all three archipelagoes are characterized by low precipitation, subzero temperatures for most of the year, and only a short summer season allowing the growth and reproduction of invertebrates. The low winter air temperatures (monthly means of -10 to -15°C for at least 6 months, and much lower extreme minima) combined with permafrost and shallow depth of snow pose a significant challenge to the invertebrates, because thermally buffered microhabitats are often not available above or in the soil (Coulson et al., 1995). Clearly, the species occurring in these archipelagoes have appropriate ecophysiological and more general life history adaptations to their harsh conditions, and these have formed a focus of polar invertebrate research generally and that in Svalbard specifically.

Two primary cold tolerance strategies are widely used by Arctic invertebrates. Freeze-tolerant animals have the capacity to survive ice formation in extracellular body fluid compartments whereas freeze-avoiding species possess physiological mechanisms that promote extensive supercooling of body fluids throughout the winter (for reviews of, and an introduction to, the biology of extreme environments and the wider cold tolerance literature see Zachariassen, 1985; Sømme, 1999; Wharton, 2002; Thomas et al., 2008; Ávila-Jiménez et al., 2010; Denlinger and Lee, 2010; Bell, 2012). These two main strategies for survival of extreme conditions ensure that body water is more or less conserved during winter, either trapped as ice (in freeze-tolerant species) or because typical freeze-avoiding species often have a relatively impermeable cuticle that limits evaporative water loss.

Many soil and freshwater invertebrates such as tardigrades, nematodes, enchytraeids, prostigmatid mites and Collembola are often of small size (<5 mm length) and have little resistance to evaporative water loss through their cuticle (Harrisson et al., 1991; Convey et al., 2003). At the same time, groups such as nematodes, annelids and tardigrades, which are active within the surface layer of water on soil particles and in moss / peat are also susceptible to inoculative spreading of ice to body fluids when the soil or sediment water that they are in contact with freezes, meaning that freeze-avoidance by supercooling is not possible (e.g. Wharton, 1986, 2002; Convey and Worland, 2000). Thus, such invertebrates have only two options: survive freezing of body fluids or avoid freezing by other means than supercooling (Pedersen and Holmstrup, 2003). Encasement in air spaces in frozen soil or sediment may lead to desiccation of small species with low resistance to water loss, as water inevitably transfers from the liquid state within the animal's body to the ice crystals surrounding it (Scholander et al., 1953; Danks, 1971; Holmstrup and Westh, 1994). A few invertebrates have taken advantage of this process, developing a third strategy, termed cryoprotective dehydration, driven by differences in water vapour pressure between the unfrozen body fluids and surrounding ice (Salt, 1963; Worland et al., 1998; Holmstrup et al., 2002; Sørensen and Holmstrup, 2011).

Many Arctic invertebrates, due to the short growing season, show extended development, and often Arctic populations have life cycles of two or more years whereas the same or closely related species in temperate regions have annual life cycles or more than one generation each year (Danks, 1992; Strathdee and Bale, 1998). Thus, Collembola, enchytraeids and Acari from Svalbard may have two-year life cycles or longer (Birkemoe and Sømme, 1998; Birkemoe and Leinaas, 1999; Birkemoe et al., 2000; Søvik, 2004). These life cycles may become closely adapted to, and synchronised with, the local environmental conditions. For example, chironomids may have sufficient life cycle flexibility to permit one or two periods of adult emergence each summer, probably depending on temperature conditions (Hodkinson et al., 1996). One striking example is the Svalbard endemic aphid, *A. svalbardicum* (see Section 3.7.2.3) which has a highly modified programmed life cycle (Strathdee et al., 1993, 1995; Table 1).

5. Paleocommunities - trends of the past

Svalbard was covered by extensive glaciers during the LGM (c. 30,000–18,000 calibrated years BP (cal BP) (Landvik et al., 1998). At approximately 14,800 cal BP ocean warming commenced at the continental margin off western Svalbard and the western Barents Sea (Hald et al., 1996). The ice sheet started to recede from the marginal coastline of Spitsbergen around 15,800 – 14,800 cal BP (13,000 – 12,500 ^{14}C years BP), whereas the central fjord region became ice-free around 11,500-10,800 cal BP (Lehman and Forman, 1992; Mangerud et al., 1992). Towards the south, Bjørnøya was deglaciated at around 11,500 cal BP (Wohlfarth et al., 1995) and towards the east, Edgeøya, Barentsøya and Franz Josef Land were fully deglaciated at around 11,200 cal BP (Landvik et al., 1995; Lubinski et al., 1999). The early Holocene summer temperatures of Spitsbergen were about 2°C warmer than today (Birks, 1991) causing local cirque glaciers to retreat or disappear in western Svalbard (Svendsen and Mangerud, 1997). These glaciers re-appeared from about 4,000-3,000 cal BP during the mid-Holocene cooling and generally advanced towards the Little Ice Age. The environmental conditions have been close to those prevailing today during the last 2,500-2,000 years with the coldest period occurring during the Little Ice Age (Birks, 1991; Velle et al., 2011). For much of the Holocene, temperatures on Franz Josef Land were 4 to 1°C warmer than today with retracted glaciers and snowfields (Lubinski et al., 1999; Forman et al., 2000). Reindeer (*Rangifer tarandus*) have been absent in historical time in Franz Josef Land, but antlers dated to 6,400 – 1,300 cal BP suggest a viable population has existed previously and was possibly driven to extinction during a distinct glacial advance around 1,000 cal. BP (Forman et al., 2000).

Some areas of the archipelagoes of the Barents Sea were ice free during parts of the last glaciation, including nunataks above 300 meters altitude in northwest Svalbard (Landvik et al., 2003), low lying areas along the west coast of Spitsbergen and Prins Karls Forland down at sea level (Andersson et al., 2000; Ingólfsson and Landvik, 2013), and substantial parts of Novaya Zemlya (Mangerud et al., 2008). Nunataks have been proposed to act as refugia for some crustaceans with the ability to survive as relicts due to their hardy resting eggs (Samchyshyna et al., 2008). However, most biota could not survive on nunataks (Brochmann et al., 2003; Schneeweiss and Schönswetter, 2011) due to the prevailing polar desert conditions in the ice free areas (Andersson et al., 2000). These harsh conditions and the general observation that a relatively limited number of species currently occur on nunataks is consistent with the *tabula rasa* hypothesis; that is, that few if any plants or animals survived in Svalbard during the LGM and that the communities observed today are the result of recent immigration after the retreat of the ice. However, local microclimatic and microhabitat conditions vary widely on small spatial scales, as do species distributions, and survival in small but particularly benign ice-free refugia at either low or higher altitudes cannot automatically be discounted (Landvik et al., 2003; Paus et al., 2006; Skrede et al., 2006;

Westergaard et al., 2011). Notwithstanding this, the general contempory view is that post-glacial colonization has been the major process populating the area. Furthermore, species richness is often found to be lower in areas that are known to have been covered by ice sheets during the last glaciation, suggesting that dispersal limitation has been a key factor structuring many contemporary communities in the Arctic (Samchyshyna et al., 2008; Strecker et al., 2008; Ávila-Jiménez and Coulson, 2011a).

Relatively few Late Quaternary and Holocene palaeozoological studies have been performed in freshwater or terrestrial environments in Svalbard and to our knowledge such studies are lacking in Franz Josef Land and Novaya Zemlya. The oldest terrestrial sub-fossils from Svalbard are recorded from Visdalen (Edgeøya) and dated to 14,700 ± 500 cal BP (Bennike and Hedenas, 1995), suggesting very early post-glacial colonization or perhaps the presence of glacial refugia (rapidity of colonisation being consistent with local refugia, cf. Convey et al., 2008). The assemblage includes *L. arcticus*, *Candona* sp. (Crustacea, Podocopida) and a questionable Lepidoptera. Several other taxa are recorded from Visdalen during the early Holocene, including Oribatida, Chironomidae, a questionable Ichneumonidae, *Olophrum boreale*, *Daphnia pulex* and *Erigone* sp. (Bennike and Hedenas, 1995). The presence of *Lepidurus*, *Daphnia* and *Candona* suggests that mesotrophic ponds existed in the area. The staphylinid beetle *Olophritm boreale* has also been recorded from Early Holocene lake sediments on Bjørnøya (Wohlfarth et al., 1995) together with the beetles *Agabus bipustulatus* and *Eucnecosum tenue*. The only Trichoptera in the palaeoecological record, noted as Limnephilidae indet, was also found in the Early Holocene sediments of Bjørnøya, as well as *Lepidurus* sp. and an unidentified Hymenoptera (Wohlfarth et al., 1995). In addition to the abovementioned studies, rotifer resting eggs and testate amoeba have been retrieved from sediments in Kongressvatn (Grønfjord) on Spitsbergen and Rosenbergdalen on Edgeøya, respectively (Beyens and Chardez, 1987; Guilizzoni et al., 2006).

Remains of Chironomidae and Cladocera have received the greatest attention in palaeozoological studies from Svalbard. Unidentified chironomids have been recorded from Bjørnøya (Wohlfarth et al., 1995) and Edgeøya (Bennike and Hedenas, 1995), while studies from Nordaustlandet (Luoto et al., 2011) and from five lakes on Spitsbergen (Brooks and Birks, 2004; Fadnes, 2010; Velle et al., 2011) included detailed identifications and environmental interpretations based on the chironomid assemblages. These records typically include about 10 taxa and show large among-site differences in species assemblages. Most likely, some sites experienced nutrient enrichment from bird guano or proximity to the sea, whereas others were influenced by glacial meltwater. In a survey of chironomid sub-fossils retrieved from the upper 1 cm of sediment (representing about 25 years) from 23 western Svalbard lakes, 18 taxa were found. The abundance and distribution of these taxa were primarily influenced by pH, nutrient concentrations, water temperature and water depth (Brooks and Birks, 2004).

Cladocera sub-fossils have been retrieved from lake sediments in Kongressvatn and in the Hornsund area of Spitsbergen (Guilizzoni et al., 2006; Zawisza and Szeroczyńska, 2011), in Visdalen on Edgeøya (Bennike and Hedenas, 1995), and in Lake Einstaken on Nordaustlandet (Luoto et al., 2011; Nevalainen et al., 2012). The sub-fossil Cladocera assemblages often have a low diversity compared to contemporary assemblages, although this may be the result of physical and chemical processes influencing the preservation of the remains in sediments, such as bottom water freezing during winter (Sywula et al., 1994; Zawisza and Szeroczyńska, 2011).

6. Invertebrate immigration, dispersal and biogeography in the archipelagoes of the Barents Sea.

Molecular studies have hinted at plant refugia in Svalbard during the LGM (Westergaard et al., 2011). This, however, awaits confirmation and, as mentioned above, it is currently generally assumed that no invertebrates survived this period *in situ*. Hence, the contemporary invertebrate fauna is currently thought to be primarily the result of recent immigration and colonization processes. Pugh and McInnes (1998) suggested that the biogeography of Tardigrada in the Arctic can be explained by colonization from a Nearctic source following the retreat of the ice. Similarly, the community structure of Collembola throughout the Arctic appears to be the result of colonization from numerous source populations outside of the Arctic with subsequent dispersal within the Arctic (Ávila-Jiménez and Coulson 2011a; Fig. 4). Arctic plant communities are considered to have been selected for species with high dispersability by the repeated cycle of glaciation in the Arctic (Alsos et al., 2007). Parts of the South Island, Novaya Zemlya, were certainly ice-free, with shrub vegetation surviving throughout the last glaciation (Serebryanny et al., 1998; Velichko, 2002; Mangerud et al., 2008), providing source populations for the colonization of other islands in the archipelago as the ice retreated.

With the existence of widespread plant refugia on Novaya Zemlya, and the putative presence of plant refugia and /or deglaciated areas on Svalbard, it is highly likely that invertebrate faunas also existed in these refugia. Studies from Antarctica have demonstrated that, even in the most climatically extreme and isolated ice-free areas, there is a viable, if limited, terrestrial fauna (Convey, 2013). But, although a glacial refugium has been proposed for certain freshwater species such as the *Daphnia pulex* complex in the Canadian High Arctic archipelago (Weider and Hobæk, 2000), no evidence of *in situ* faunal survival has yet been described for Svalbard or Franz Josef Land. Increasingly, molecular and bioinformatic analytical techniques devoted to defining biogeographic and phylogeographic patterns are being applied to studies in the polar regions. These approaches permit more accurate definition of the timing of divergence events, both between species and between populations within species, potentially allowing detailed descriptions of dispersal and colonization patterns (Allegrucci et al., 2006; Stevens, 2006; Stevens et al., 2006, 2007; McGaughran et al., 2010; Mortimer et al., 2011). Their application has led to a paradigm shift in the interpretation of the antiquity of the contemporary Antarctic terrestrial biota (Convey and Stevens, 2007; Convey et al., 2008, 2009; Vyverman et al., 2010). However, as yet these approaches have not been applied to the study of Arctic terrestrial invertebrates, and have so far generally focused on floral biogeography (Abbott and Brochmann, 2003; Brochmann et al., 2003; Alsos et al., 2007; Ávila-Jiménez, 2011).

Insert Figure 4 here

Several dispersal vectors have been suggested for invertebrate species colonizing the polar regions. Airborne dispersal by active flight may account for many winged species. Chernov and Makarova (2008) consider the Coleoptera fauna of Svalbard to consist of flighted migratory species. Passive dispersal with air currents (anemochory) may be also responsible for many of the species or taxa seen in the islands, for example Tardigrada, Aphididae, Syrphidae, Tipulidae and Lepidoptera (Elton, 1925a, 1934; Kaisila, 1973b; Pugh and McInnes, 1998; Coulson et al., 2002b). Similarly, passive dispersal by ocean currents (hydrochory), either floating on the ocean surface or rafting with floating debris of terrestrial or marine origin, such as tree trunks, seaweed rafts, or human rubbish may account for the arrival of others (Coulson et al., 2002a). Further species may hitch with migratory birds or mammals (zoochory). Lebedeva and Lebedev (2008) speculated on the possible role of birds in transporting soil microarthropods to the Arctic, although clear confirmation of the occurrence of this process is lacking. Non-parasitic mites have also been described as phoretic on larger invertebrate species such as Diptera (Coulson, 2009; Gwiazdowicz and Coulson, 2010). Transport assisted by human processes (anthropochory) may be an increasingly common immigration route. This is especially the case with plants, where around 100 vascular plant species are now known to have been introduced to Svalbard *via* human activity compared to the natural flora of 164 species (Alsos et al., 2013). The effect of human-mediated dispersal on invertebrate immigration patterns has not been quantified in the High Arctic, although it is recognised as a factor far outweighing natural dispersal events in the Antarctic (Frenot et al., 2005) where it has also been highlighted as a major threat to biodiversity (Hughes and Convey, 2010, 2012; Chown et al., 2012a 2012b; Greenslade and Convey 2012). In the anthropogenic soils of the mining town of Barentsburg (Svalbard), 11 of the 46 identified invertebrate species (24%) were non-native (Coulson et al., 2013a, 2013b). Svalbard may be particularly vulnerable to anthropogenic introduction of alien species due to the high volume of visitors arriving both by ship and aeroplane (Ware et al., 2011). In contrast, access to Franz Josef Land and Novaya Zemlya is currently more restricted, albeit after a long history of military usage with, presumably, little or no attention to biosecurity issues.

A range of synanthropic species have also been described from the Svalbard archipelago in human settlements (Coulson, 2007b) which are, in the main, unlikely to establish in the natural environment due to the Arctic conditions. However, as is characteristic of human introductions elsewhere, and in particular in the Antarctic (Frenot et al., 2005: Greenslade et al., 2012), a proportion of such species are likely to be able to survive in the natural environment and subsequently become invasive. Furthermore, the majority of invertebrate fauna are cryptic and require specialist expertise for recognition and the probability of successful remedial extermination once establishment has occurred is likely to be low (see Hughes and Convey, 2012 for discussion of these issues in a parallel Antarctic context).

Most terrestrial invertebrate biogeographic studies carried out to date in Arctic areas are based on community assemblages and have examined groups such as Collembola (Hågvar, 2010; Ávila-Jiménez and Coulson, 2011a; Fig. 4), Tardigrada (Pugh and McInnes, 1998), or Rotifera (Gíslason, 2005). For many groups meaningful comparisons of the invertebrate communities between the archipelagoes are not possible due primarily to lack of sampling effort and taxonomic confusion. However, for some groups it is feasible to make an overall assessment of similarities (Table 2). Within data limitations it is notable that, for many groups, the species diversities of Svalbard and Novaya Zemlya are numerically similar, but that they have few or very few species in common, indicating limited connectivity between the archipelagoes.

Insert Table 2 here

7. Environmental change

The archipelagoes of the Barents Sea lie in the High Arctic region that is expected to be particularly sensitive to oceanographic and climatic changes, and a strong indicator of their biological consequences (ACIA, 2005: Chapin III et al., 2005: Convey et al., 2012). Svalbard, and even Novaya Zemlya, are subject to warm North Atlantic influences from the west, and cold Arctic Ocean influences from the east, as well as lying at the boundary of the region experiencing large-scale changes in winter and multi-year Arctic sea ice extent (Serreze et al., 2007). All three archipelagoes lie at the high latitudes subject to the 'polar amplification' of general global climate trends, although Svalbard is the only location of the three archipelagoes considered here to have a detailed publically accessible long term meteorological record by which to confirm recent warming trends (Førland et al., 2011). Increasingly sophisticated general circulation models continue to predict considerable further warming over the next century in the high latitude polar regions (IPCC 2007). Temperature warming is accompanied by a suite of other changes of biological relevance, including in the form and amount of precipitation, cloudiness, humidity and insolation, and the timing and frequency of freeze-thaw events. Finally, although the Arctic does not normally experience the organized formation of a seasonal ozone hole, as is seen in the Antarctic through accumulation of anthropogenic atmospheric pollutants and catalytic destruction of stratospheric ozone in the austral spring, intermittent and significant depletion does occur spatially at Arctic latitudes throughout the Arctic summer, with a number of potential biological impacts identified (e.g. Rozema, 1999).

The general biological responses to environmental change in the Arctic have received considerable attention (e.g. for review see Callaghan et al., 2004a, 2004b; Chapin III et al., 2005; AMAP, 2011). However, studies on the impacts of climate change on soil animal communities in High Arctic environments are limited. Although environmental manipulation methodologies have been applied widely in the context of ITEX studies to a range of Arctic vegetation habitats, generally these studies have focussed on vegetation responses and have not addressed, or included, the soil or other elements of the invertebrate fauna. Studies of soil nematode communities at Abisko, Sweden, have indicated that, while population densities are increased, biodiversity is generally affected negatively and distinct changes in trophic structure are caused by environmental perturbations (Ruess et al., 1999a). This seems to be an indirect effect of changes in vegetation cover, plant species composition, litter quality and below-ground input by plants, which in turn will have a major impact on nutrient turnover through microorganisms and soil fauna (Ruess et al., 1999b; Sohlenius and Boström, 1999; Simmons et al., 2009). Similar initial responses to manipulations have also been reported in Antarctic studies, which also identified that caution needs to be used in separating initial and sometimes drastic artefactual changes in population density and diversity from those that appear to become established after longer periods of manipulation have permitted the impacted communities to stabilise (Convey and Wynn-Williams, 2002).

Webb et al. (1998), in a three year open-topped chamber manipulation at Ny-Ålesund, found very little change in soil oribatid mite community composition, although noting possible subtle changes in species relative abundances. These authors concluded that the soil microhabitat would be more buffered from short-term changes in temperature than would be the case for invertebrates of the overlying vegetation. This difference is perhaps illustrated by the striking findings of Strathdee et al. (1993), who reported an order of magnitude increase in overwintering aphid eggs within versus outside chamber-manipulated vegetation, indicating a possible step change in the population dynamics of this species under realistic warming scenarios. However, as noted above, a similar response has not been observed in recent studies of natural aphid populations in areas that are thought to have warmed already by a similar amount in recent decades.

In general terms, the two most important environmental variables subject to change in Arctic (and Antarctic) terrestrial ecosystems of relevance to the invertebrate fauna are those relating to temperature and the availability of liquid water. While water may provide the primary limiting factor to the temporal activity of invertebrates in these ecosystems, temperature provides the energy required to fuel biological processes. In many instances, where climate change leads to relaxation of the constraints provided by either or both of these variables, the invertebrate biota are likely to benefit, with expectation of increased production, biomass, population size, community complexity, and colonisation (Convey, 2011; Nielsen et al., 2011; Nielsen and Wall, 2013). However, in terms of biodiversity, these positive impacts of climate change may then be outweighed by other impacts of human activities, in particular the establishment of invasive non-indigenous species.

More broadly, anthropogenic climate change poses a serious threat to freshwater ecosystems in Barents Sea region. Widely reported reductions in sea ice have been mirrored in freshwater systems. For example, an extended ice free period has resulted higher water temperatures and lower water levels in Kongresvatnet in Svalbard (Holm et al., 2011). Elevated snow fall may increase the opacity of translucent block-ice delaying the start of primary production in the spring (Svenning et al., 2007). Recently, lakes on granitic bed rock appear to have become more acid, perhaps due to increased acid precipitation, a spring influx of low pH water during the melt and the low buffering capacity of granitic rocks (Betts-Piper et al., 2004).

It is important to recognize that increased temperature due to global warming may induce a multitude of changes in detail in the High Arctic environment, in addition to the broad generalizations described above. Included amongst these are increased snow depth, earlier snow melt and more frequent freeze-thaw cycles in winter (Christensen et al., 2007; AMAP, 2011; Wilson et al., 2013). In particular, the presence of a solid ice cover directly on the soil surface may seriously affect the Collembola and presumably other communities (Coulson et al., 2000). Changes in local faunal composition are likely to occur under current warming scenarios, but over the short to medium term (years to decades) the Svalbard environment probably has sufficient buffer capacity to offer suitable habitats for even the most cold-adapted species. In terms of biodiversity conservation, special attention should be given to monitoring the status of species which are absent from Arctic continental mainland landmasses, as these may be the first to be pushed towards extinction.

8. Conclusions and future research priorities

The archipelagoes of the Barents Sea are inhabited by diverse communities of invertebrates, despite the short period since deglaciation and the clear environmental challenges. There is an obvious imbalance in our understanding of the biodiversity of the three archipelagoes. Research in Svalbard is increasing rapidly while there are still few reports, particularly in the western literature, from Franz Josef Land and Novaya Zemlya. Our knowledge of the faunas of all three archipelagoes is relatively recent, the majority of records commencing in the early Twentieth Century.

In attempting to describe or compare the invertebrate fauna of the archipelagoes of the Barents Sea it is immediately clear from the consideration of all taxa here that great problems exist that challenge our understanding of the region. First, there is the lack of comprehensive sampling campaigns. Many locations have only been sampled on one occasion, sampling locations were often selected primarily due to logistical considerations, sampling was carried out by non-specialists, and often a limited range of taxa were focused on driven by the skills and interests of the particular taxonomists / ecologists associated with the sampling programme. There is a strong need for repeated sampling campaigns designed to capture seasonal and interannual variation in the Barents Sea region. For Novaya Zemlya and Franz Josef Land there has been the added problem of access to a closed military region. Hence, we often have a very prejudiced knowledge biased towards locations with relative ease of access and to particular taxa. The second hurdle to surmount is the taxonomic confusion existing in the historic literature and the current ongoing debates within particular taxa. Several invertebrate taxa present in the Arctic may belong to species groups with an intricate taxonomy and which are challenging to identify. There are multiple instances of misidentifications and synonyms in the literature. Of the 88 Tardigrade taxa currently recognised in the literature from Svalbard many originate from older reports and identifications have not been verified based on modern taxonomy (Kaczmarek et al., 2012). Another example is given by the 87 species of oribatid mite reported from Svalbard, many of which have not recently been observed and where synonyms and misidentifications may be suspected. This situation exists with most, if not all, the taxa discussed in this article. To complicate the situation further, material from earlier sampling may no longer exist, either being lost or, as in the case of much of Thor’s material (including type specimens), deliberately destroyed (Winston, 1999). Hence, re-examination using modern taxonomic principles is no longer possible and a new inventory based on fresh material lodged in appropriate museums and collections is urgently required. Furthermore, forthcoming studies should employ molecular methods such as DNA-barcoding, which have yielded promising results in recent studies of Chironomidae (Stur and Ekrem, 2011). Molecular data may prove to be valuable in the identification of dispersal routes and timescales for the invertebrate fauna of the Barents Sea archipelagoes. Based on morphological studies, efforts should also be made in preparing good and well-illustrated identification keys accessible to non-specialists so as to increase the taxonomic value of upcoming ecological studies and enable future monitoring programs in the Arctic.

For both the terrestrial and freshwater systems there is clearly a need to assess biodiversity in areas away from the main settlements, and in specific habitats such as warm springs, naturally nutrient-rich locations and more extreme habitats. Better understanding of food webs, life history strategies and the interactions between freshwater, terrestrial and marine ecosystems in different regions of the Arctic is also required. Work is underway to develop a monitoring network for freshwater biodiversity in the Arctic under the auspices of the Arctic Council (Culp et al., 2011), including locations on Svalbard, and the same is required in the terrestrial environment.

Current knowledge indicates that there are relatively few species endemic either to individual archipelagoes or to the region as a whole. This most likely reflects either the young age of the communities or relatively high linkage to mainland populations, both issues that may be resolved by the application of molecular methodologies. Observed endemism levels may also be more apparent than real, and reflect the limited sampling effort in other Arctic regions. Aspects of the dissimilarity of the invertebrate faunas of the different archipelagoes are striking. In particular, it might have been expected that Novaya Zemlya and Svalbard would show greater similarity or overlap in diversity than this study has found (Table 2). Clarification of the relative importance of eastern and western sources of colonizing diversity over time and in relation with regional glacial processes for both archipelagoes is clearly required.

This extensive synthesis of Barents Sea archipelago invertebrate biodiversity provides both a benchmark for the region and the foundation for future research in several key areas. In summary, we highlight the need for:

- explicit phylogeographical studies across the entire region (and more widely in the High Arctic),
- resolution of taxonomic confusion and the development of combined molecular and morphological approaches,
- strengthening of the linkages across biological and physical disciplines (e.g. glaciology, geomorphology, geology) in order to more clearly identify potentially ice-free areas,
- integration with oceanography and climatology in the context of understanding the role currents play in the occurrence and frequency of transfer events,
- linkage with regional climate change studies, to provide baselines for the documentation of, and studies of, colonizing species (including those associated with anthropogenic influence) and their impacts,
- integration of biodiversity studies across groups to give better description of ecosystem structure and function, especially in the context of large-scale carbon and nitrogen cycles, linkages between terrestrial and marine environments, and linkages between terrestrial and freshwater environments at catchment scale

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