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Hanna-Kaisa Lakka

Environmental Changes in Arctic Freshwaters

The Response of Indicator Species to Global Warming and Acidification in the Arctic

UNIVERSITY OF JYVÄSKYLÄ
FACULTY OF MATHEMATICS AND SCIENCE

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Editors
Jari Haimi
Department of Biological and Environmental Science, University of Jyväskylä
Päivi Vuorio
Open Science Centre, University of Jyväskylä

"The Arctic region is one of the most vulnerable systems on our planet, if and when global warming continues."
"I have said this before: if we lose the Arctic, we lose the globe."
– Sauli Niinistö, President of the Republic of Finland, The Arctic Biodiversity Congress, Rovaniemi, Finland, 9th October 2018.

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ABSTRACT

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In the Arctic region, global warming progresses quickly. Arctic freshwater indicator species were used as model organisms to study environmental change. The objective of the thesis was to evaluate the severity of warming and acidification for fauna in Arctic freshwaters. Freshwater acidification was confirmed in northern Finland. Precipitation was acidic and water pH was an alarmingly low 4.9 in small ponds. This measured low pH was also the mean precipitation pH in northern Finland. Increasing acidic precipitation together with warming are major threats to acid sensitive Arctic species especially in ponds in northern Finland, due to their low water volume and their limited buffering capacity. The new method to calculate climate risk for selected species predicts physiologically harmful temperatures in Lapland. The Arctic indicator species have not experienced these predicted high temperatures during the last 60-years. The findings highlight that the lethal effect of heat stress caused by global changes need to be studied in a species- perspective to allow predictions for Arctic populations. Behavioural patterns, such as sexual reproduction, cannibalism and colonisation can help the species to survive in the severe and fast changing Arctic. The result shows that these beneficial behavioural patterns were present in the Arctic tadpole shrimp populations in the High Arctic Svalbard. Colonisation after the Last Glacial Maximum (LGM) happened from refugia in the South-West resulting in diverse invertebrate fauna in Arctic archipelagos Svalbard, Franz Josef Land and Novaya Zemlya. Together, the results highlight populations where the possible management actions should be carried out.

Keywords: Acidification; Biogeography; Branchiopoda; Climate change; Climate risk calculation; pH.

Hanna-Kaisa Lakka, University of Jyväskylä, Department of Biological and Environmental
Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

TIIVISTELMÄ

Lakka, Hanna-Kaisa
Ympäristönmuutos arktisissa vesissä: Indikaattorilajien vaste ilmaston lämpenemiseen ja happamoitumiseen arktisella alueella
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Yhteenveto: Ympäristönmuutos arktisissa järvissä ja lammissa

Arktinen alue lämpenee kiihtyvällä vauhdilla. Arktisia makeanveden indikaattorilajeja käytettiin tässä tutkimuksessa malliorganismeina ympäristönmuutosten tutkimuksessa. Työn tavoitteena oli arvioida lämpenemisen ja happamoitumisen vaikutuksia arktisten sisävesien eliöstöön Pohjois-Suomen lammissa mitattiin hälyttävän hapanta vettä (pH 4,9), mikä johtui haitallisen happamasta sadevedestä. Sademäärän voimakas lisääntyminen yhdessä lämpenemisen kanssa on merkittävä uhka happamoitumista huonosti sietäville arktisille lajeille. Erityisen huono tilanne on lammissa johtuen niiden pienestä vesimäärästä ja rajallisesta puskurikapasiteetista. Uusi menetelmä ilmastoriskin laskemiseksi arktisille lajeille ennustaa fysiologisesti haitallisia lämpötiloja Lapissa. Arktisen alueen indikaattorilajit eivät ole kokeneet näitä ennustettuja korkeita lämpötiloja viimeisten 60 vuoden aikana. Tulokset korostavat, että maailmanlaajuisten muutosten aiheuttamaa lämpöstressin kuolleisuutta lisäävää vaikutusta on tutkittava lajien fysiologisesta näkökulmasta, jotta arktisten populaatioiden häviämisriskin ennustaminen olisi mahdollista. Seksuaalinen lisääntyminen, kannibalismi ja kolonisaatio voivat auttaa lajeja selviytymään arktisten alueiden ankarissa ja nopeasti muuttuvissa oloissa. Tulokset osoittavat, että nämä selviytymisstrategiat olivat käytössä paljakkakilpiäisten populaatioissa Huippuvuorilla. Immigraatio, eli tulomuutto, tapahtui viimeisen jääkauden jälkeen etelä-länsi suunasta Huippuvuorten, Franz Josefin maan ja Novaja Zemljan saaristossa, mikä johti monimuotoiseen selkärangatonlajistoon. Tulokset osoittavat, että toimenpiteisiin olisi ryhdyttävä ainutlaatuisten arktisen eläimistön suojelemiseksi.

Avainsanat: Biogeografia; Branchiopoda; Ilmastonmuutos; Ilmastoriskin laskenta; Happamoituminen; pH.

Hanna-Kaisa Lakka, University of Jyväskylä, Department of Biological and Environmental
Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

SAMMENDRAG (NORSK)

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Miljøforandringer i Arktiske ferskvann: Indikatorarters respons på global oppvarming og forsuring i Arktis
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I den arktiske regionen utvikler den globale oppvarmingen seg raskt. Her ble indikatorarter i ferskvann benyttet som modellorganismer for å studere miljøendringer. Formålet med undersøkelsen var å evaluere betydningen av oppvarming og forsuring for faunarn i arktisk ferskvann. Forsuring ble påvist i Nord-Finland (Lappland), og her hadde små dammer en alarmerende lav pH på 4,9. Gjennomsnittlig pH målt i nedbøren viste like lave verdier. Økende forsuring, sammen med oppvarming, er alvorlige trusler mot sensitive arktiske arter i slike lokaliteter i Nord-Finland. Dette skyldes i hovedsak at de har et lite vannvolum og en begrenset bufferkapasitet. Den nye metoden for å beregne mulige klimatiske skadevirkninger for utvalgte arter tilsier også fysiologiske skader relatert til høyere temperaturer i Lappland. De arktiske indikatorartene har ikke vært utsatt for slike forventede høye temperaturer i løpet av de siste 60 årene. Funnene viser at for arktiske arter må den dødelige effekten av varmestress forårsaket av globale klimaendringer, studeres på artsnivå. Adferdsmønstre, som seksuell reproduksjon, kannibalisme og kolonisering, kan hjelpe artene til å overleve i det ugjestmilde og raskt skiftende klimaet i disse områdene. Disse gunstige atferdsmønstrene ble også funnet hos skjoldkreps på Svalbard. Kolonisering etter siste istid skjedde fra refugier i sør-vest, og resulterte i en mangfoldig fauna av virvelløse dyr i kystnære strøk på Svalbard, Franz Josef Land og Novaya Zemlya. Resultatene viser klart hvor det bør settes inn tiltak for å bevare denne spesielle faunaen.

Nøkkelord: Biogeografi; Branchiopoda; beregning av klimatiske endringer; forsuring; klimaendringer; pH.

Hanna-Kaisa Lakka, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author´s address Hanna-Kaisa Lakka
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä, Finland
hanna-kaisa.hk.lakka@jyu.fi

Supervisors Senior Lecturer Emily Knott
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä, Finland

Professor Stephen Coulson
ArtDatabanken
Box 7007
750 07 Uppsala, Sweden

Senior Lecturer Panu Halme
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä, Finland

Reviewers Professor Milla Rautio
Département des sciences fondamentales
555, boulevard de l'Université,
Chicoutimi (Québec) G7H 2B1
Université du Québec à Chicoutimi, Canada

Professor Timo Muotka
Ecology and Genetics Research Unit
PL 8000
FI-90014 University of Oulu, Finland

Opponent Professor Leopold Füreder
Department of Ecology
Technikerstrasse 25
A-6020 Innsbruck
University of Innsbruck, Austria

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original articles, which will be referred to in the text their Roman numerals I-IV.

I Lakka, H-K. 2020. Acidification of tundra ponds and its impact on an endangered crustacean, Arctic tadpole shrimp in Finland. Manuscript.

II Lakka, H-K. 2020. Climate risk calculation; an approach for identifying a species-specific temperature risk. Submitted manuscript.

III Lakka H-K. 2015. Description of the male *Lepidurus arcticus* (Branchiopoda: Notostraca) and the potential role of cannibalism in defining male form and population sex ratio. *Journal of Crustacean Biology* 35: 319–329.

IV Coulson, S.J., Convey, P., Aakra, K., Aarvik, L., Ávila-Jiménez, M.L., Babenko, A., Biersma, E.M, Boström, S., Brittain, J.E, Carlsson, A.M, Christoffersen, K.S., De Smet, W.H., Ekrem, T., Fjellberg, A., Füreder, L. Gustafsson, D., Gwiazdowicz, D.J., Hansen, L.O., Holmstrup, M., Hullé, M., Kaczmarek, L., Kolicka, M., Kuklin, V., Lakka, H-K., Lebedeva, N., Makarova, O., Maraldo, K., Melekhina, E., Ødegaard, F., Pilskog, H.E., Simon, J.C., Sohlenius, B., Solhøy, T., Søli, G., Stur, E., Tanasevitch, A., Taskaeva, A., Velle, G. Zawierucha, K. and Zmudczyńska, K. 2014. The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef Land and Novaya Zemlya. *Soil Biology and Biochemistry* 68: 440–470.

Responsibilities of the author:

I–III First author.

IV I was responsible for the Brachiopods section and I wrote chapters related to freshwater biodiversity together with other co-authors. All co-authors made a significant contribution to planning and preparation of the paper.

ABBREVATIONS AND TERMS

Amplexus	Mating behaviour of the Arctic tadpole shrimp where often a smaller size male holds a cannibalistic female still during mating to fertilize the eggs.
SLD	Sum of lethal degrees.
Arctic	Northernmost region of the Earth, the area around the North Pole. Arctic is divided into three zones: the High, the Low Arctic and the sub-Arctic (Fig. 7).
High Arctic	Northernmost Arctic region. High Arctic region contain Arctic islands and the open tundra and the permafrost areas around glaciers and permanent snow cover areas. The shorter growing season and cooler summers than the other Arctic zones.
LGM	Last Glacial Maximum
Low Arctic	Treeless Arctic zone, between the High Arctic and the sub-Arctic regions. The July temperature is below 10 °C and does not favour tree growth.
RCP	A Representative Concentration Pathway is a greenhouse gas concentration used for climate modelling and research in the IPCC fifth assessment report. Five different greenhouse gas emission predictions (RCPs, RCP2.6, RCP4.5, RCP6, RCP8.5) gives different temperature projections for the ongoing global warming.
sub-Arctic	Area south of the Arctic. The transition zone between continuous boreal forests and treeless tundra.

PREFACE

The main purpose of this dissertation is to highlight the uniqueness and the sensitivity of the fast-changing Arctic environment and to provide concrete evidence of the environmental change using widely distributed but threatened Arctic indicator species. Effects of the global warming in freshwater systems are presented using two Red-Listed freshwater crustaceans Arctic tadpole shrimp (*Lepidurus arcticus,* Branchiopoda; Notostraca) and Arctic fairy shrimp, *Branchinecta paludosa* (Branchiopoda; Anostraca) as examples of the diverse effects of climate change in the Arctic region (Fig. 1).

Water is a key element of survival of all living organisms. Global warming is increasing the frequency and the severity of extreme water related events (Youngflesh 2018). A huge amount of water is stored in frozen soils and glaciers in the Arctic and this important water storage is melting quickly (Muhlfeld *et al.* 2011, Luoto *et al.* 2019). Indeed, the nature of water movements are changing rapidly, due to increases in precipitation and temperature, and to survive, Arctic animals have to withstand this rapid change. With help of examples of my work I show what kind of a massive changes are ongoing in Arctic habitats.

The thesis starts with an introduction giving a general overview of the environmental change in the Arctic region. It also specifically addresses the species sensitivity of environmental stressors in Arctic environment, with a focus on acidification and climate change. It ends by highlighting the importance of *cold adapted* arctic biodiversity and importance of parthenogenetic reproduction and the presence of sexual reproduction in animals experiencing the harsh but changing Arctic. Then, the introduction gives a historical overview of research on Arctic crustaceans and overview of sampling methods, recent experimental trends, and recommendations for the future research. Finally, I give recommendations for policymakers on the necessary and needed actions to protect Arctic regions and its biodiversity.

The analysis of the sensitivity of the Arctic crustaceans to environmental change is based on sampling in 66 aquatic habitats in the Arctic. Numerous individuals were collected and various abiotic measurements were done in the field, sometimes in freezing cold waters and even under the ice cover. The records and observations are based on my extensive sampling campaigns from the sub-Arctic to High Arctic regions, which were carried out with help of my supervisor, Professor Stephen Coulson, my colleagues, field assistants and my family and friends.

I hope that my overview on the sensitivity and uniqueness of Arctic freshwater ecosystems will encourage research to study Arctic freshwaters and their hidden biodiversity, increase knowledge of their importance in the changing climate, as well as strengthen the use of Arctic indicator species in the applied science, for monitoring and conservation purposes globally.

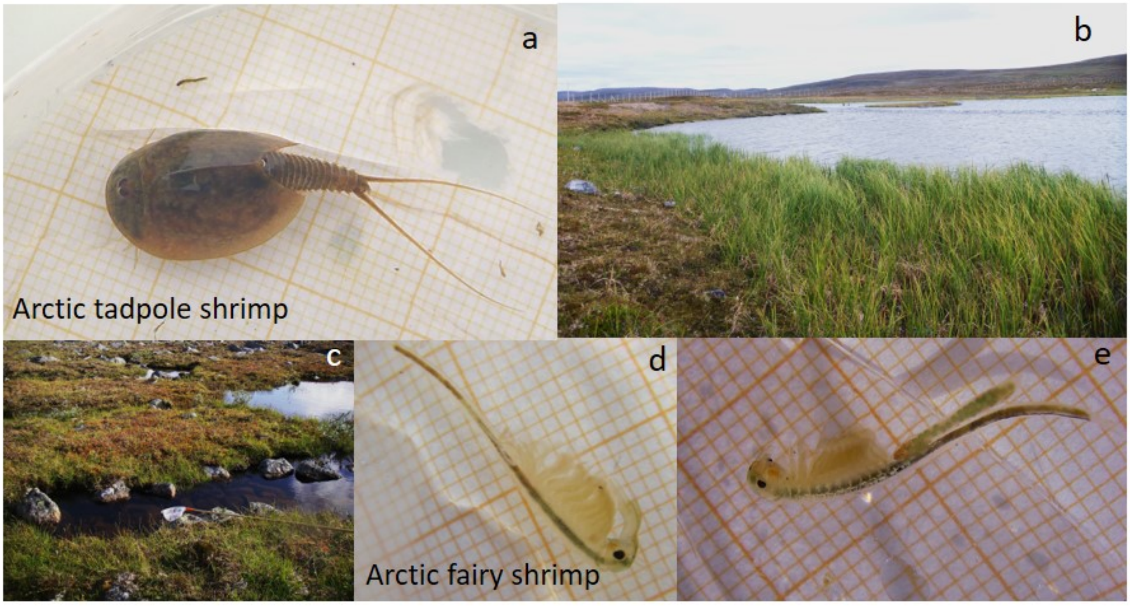


FIGURE 1 The study species and examples of crustacean habitats. Two Arctic indicator species were studied: *Lepidurus arcticus* (Arctic tadpole shrimp, a) is a freshwater crustacean inhabiting temporal and permanent waterbodies in Arctic areas (b) and *Branchinecta paludosa* (Arctic fairy shrimp, d = male and e = female) is a freshwater crustacean of fishless ponds (c). The study area in northern Finland and Svalbard contains a wide spectrum of different habitats ranging from sedge-dominated oligotrophic lakes and ponds (b), and small, rock-dominated tundra ponds and pools (c) to oligotrophic lakes on the mountaintops.

1 INTRODUCTION

1.1 Arctic environmental change and cold adapted species

The thesis topic, Arctic environmental change, is a topical issue at the moment when water movements in the Arctic areas are changing rapidly (Dyurgerov and Meier 2000) and because climate change is one of the largest issues which causes biodiversity decline on a global scale (Laske *et al.* 2019, Lento *et al.* 2019). At the same time when Arctic regions are warming faster than global averages (IPCC 2014, IPCC 2018), human activity in these sensitive areas is increasing. Global warming is projected to shift climate zones poleward (IPCC 2019). The ice-free Arctic Sea increases the shipping possibilities and the new, ice-free land enables mining in previously undisturbed Arctic areas. Indeed, the Arctic animals not only combat against climate change, but also against an ever-increasing human disturbance. Now is time to show the problems for decision-makers and also to express the new methods to investigate global change effects in the species perspective.

Two freshwater indicator species were selected to study changes in the Arctic environment, with a focus on the role of temperature and pH. The Arctic tadpole shrimp (*Lepidurus arcticus*) and the Arctic fairy shrimp (*Branchinecta paludosa*) are cold-water crustaceans in the class Branchiopoda, native to Arctic freshwaters. Their distributions are circumpolar and they have been used to for monitoring changes in the Arctic environment in northern Finland (Väinölä *et al.* 2019). No other freshwater Branchiopods are found as far north in the Northern Hemisphere (Vekhoff 1997, Lakka 2013). The Arctic tadpole shrimp is the only large sized Branchiopoda in Svalbard, found mainly in ponds located between the sea and glaciers (Lakka 2013). It is one of the rarest crustaceans in the second largest sub-Arctic lake, Lake Inarijärvi in Finland (Lakka *et al.* 2019) and its population declined in the regulated lake in the Reinheimen mountain area in Norway at the beginning of 1990's (Lakka *et al.* 2020). The Arctic fairy shrimp is the most common large branchiopod in the Barents region of Russia and the northern most known occurrence of the species is from a pool in the polar desert region of Ivanov Bay on the Novaya Zemlya Archipelago (Vekhoff 1997). In other parts of its range, such as the Nordic countries Norway, Sweden and Finland, the Arctic fairy shrimp populations are rare or declining (Lindholm *et al.* 2015, Väinölä *et al.* 2019, SLU Artdatabanken 2020). Changes in temperature form a distribution barrier to Branchiopods (Hamer and Brendonck 1997) while birds help branchiopods spread to new areas (Rogers 2014) and Arctic mountains, e.g. the Scandinavian Mountains, act as distribution corridors for these cold adapted Arctic species in mainland Europe. Indeed, Arctic tadpole shrimp and Arctic fairy shrimp presence, absence and well-being is a sign of the overall health of Arctic freshwaters ecosystems (Lakka 2013).

1.2 Theoretical framework

1.2.1 Environmental change in the Arctic freshwaters

In the Arctic, the climate change induced warming proceeds more intensely than in many other areas in the globe (IPCC 2014, IPCC 2018). In particular, aquatic species are affected by climate change through acidification (AMAP 2018), droughts (Nilsson *et al.* 2015) and reproductive difficulties (Youngflesh 2018). Global warming is changing the current species composition (Lindholm *et al.* 2015, Leopold *et al.* 2019) and the habitat use of many mobile thermally sensitive species (Trisos et al 2020). However, not all species are able to escape the heat wave or other harmful effects of climate change. The peripheral populations of thermally sensitive species, are more exposed to local extinctions due to the effects of climate change (Muhlfeld *et al.* 2011, Almodóvar *et al.* 2012). The temperature increase registered during the past years has been accompanied by rapidly decreasing ice cover (Medeiros *et al.* 2012), increasing water turbidity (Luoto *et al.* 2019), acidification (Fjellheim *et al.* 2001), water browning (Wauthy *et al.* 2018), changes in underwater light conditions, (Lindholm *et al.* 2016), new diseases of Arctic crustaceans (Lakka 2013), and increasing presence of poisonous chemicals and plastic in food webs (Gamberg 2019), finally changing the Arctic biodiversity. All these changes influence the animals' survival via the two most important physiological traits: growth and reproduction. The decline and loss of Arctic species has been reported all over the globe (Engelhard *et al.* 2014, Hyvärinen *et al.* 2019, SLU Artdatabanken 2020). Although there are many recent observations of loss of species or populations globally, a method that can show the historical and present change and explain and predict future changes is missing.

1.2.2 Adaptation to changing conditions

To survive in changing environment organisms are required to adapt constantly. Most animals have already adapted to their own specific environment and are found only within a temperature range, where they can survive and reproduce. Optimal survival is achieved by the interplay between the individual fitness and its specific environmental signals, for example temperature and light (Pasquali *et al.* 2019). This is happening at all life stages (eggs, juveniles and adults) during the lifespan of organisms. In the Arctic, the temperature is not stable and this is especially challenging for species living in aquatic environments where the light, temperature and water in liquid state control the availability of food. Organisms with a lower number of generations per unit of time are slower to adapt to forthcoming change (Fig. 2). As the impact of environmental variation and climate change affect this year's environment, those may be distinct from the impact of the next year's environment, and this might cause problems and mismatch for sensitive animals' survival on the global scale. This year's individuals are challenged to prime the new environment (e.g. temperature increase) of the offspring's environment. This is a major challenge for species that need to reach a certain size in order to reproduce and within one generation in the short Arctic summer (Fig. 2). Based on studies from Svalbard, the common life-history pattern of Arctic tadpole shrimp (*Lepidurus arcticus*) is one generation per year (Lakka 2013) and for *Daphnia,* it is two generations per year (Hessen *et al*. 2004). As a consequence, the next year's population will experience environmental conditions that their parents had not experienced before. Indeed, Arctic animals need to cope with the speed of the Arctic environmental change and to adapt to forthcoming change or even predict the coming change to survive.

Under the harsh and sometimes hostile Arctic climate conditions, asexual reproduction is common, but a changing environment could change this pattern and favour sexual reproduction. Males of some species might not be observed in Arctic freshwater populations at all (Vekhoff 1997, Scher *et al.* 2000). A good example of this is the Artic prey-predator-species-pair: the early immigrant water flea *Daphnia pulex* and the ancient Notostraca Arctic tadpole shrimp (Christoffersen 2001). Both of these freshwater crustaceans are able to reproduce parthenogenetically (Innes 1997, Wojtasik and Brylka-Wolk 2010). Populations of this species pair live in temporal and permanent ponds in the Arctic. Among twenty populations of Arctic tadpole shrimp in the High Arctic Svalbard, the majority of individuals were reproductive females (Lakka 2013).

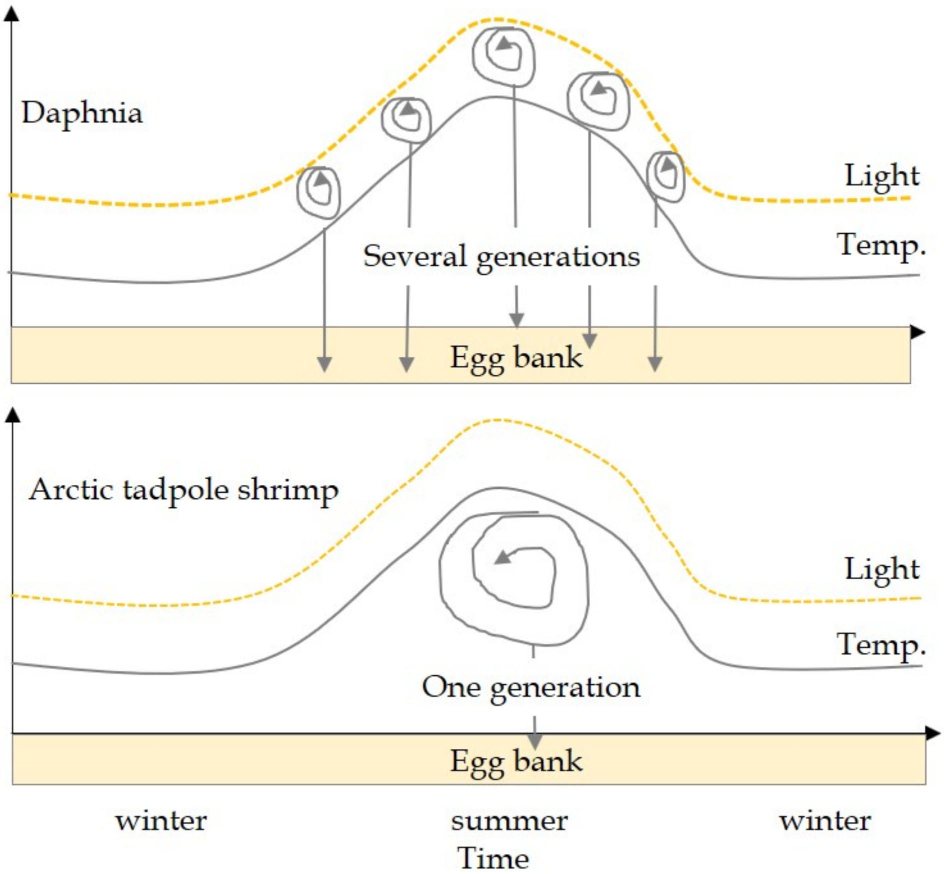


FIGURE 2 Arctic freshwater crustaceans have different kinds of strategies for survival in an extreme and rapidly changing Arctic environment. *Daphnia* water fleas may have several generations per year. Arctic tadpole shrimp (*Lepidurus arcticus*) has one generation per year.

The Arctic species might have also other kinds of strategies for survival. All behavioural patterns which increase survival are beneficial. For example, the flexibility of feeding behaviour may support better growth and reproductive success (McMeans *et al.* 2016, Wootton 2017). The large body size of Arctic tadpole shrimp is closely related to their better reproductive efficiency (Lakka 2013), and the presence of Arctic tadpole shrimp increases the size of fish (Lakka *et al.* 2020). Although omnivorous feeding behaviour supports fitness in the Arctic, Arctic tadpole shrimp populations require favourable environmental conditions at the right time to survive (Fig. 2). This is also true for many other Arctic animals that reproduce only once a year or less frequently in harsh Arctic conditions.

1.3 Contextual background

1.3.1 Acidification (Paper I)

In the Northern hemisphere, spring snow melt can cause short-term acidification in small lakes (Borgstrøm and Hendrey 1976). An earlier study has concluded that the pH of snow in Finnish Lapland is low 5.5–5.7 (Forsström *et al.* 2007). Small ponds might be even more exposed to acidification than lakes due to their small size and volume, especially in areas where precipitation is a major source of incoming water. Acidic waters are lethal for some Arctic crustaceans e.g. Arctic tadpole shrimp and *Gammarus lacustris* (Borgstrøm and Hendrey 1976), but information of water pH are scattered from the Arctic region. Amount of precipitation can be different in the High Arctic and the sub-Arctic regions (Fig. 3). The joint effect of the sub-Arctic climate, 1) the warmer temperature and 2) more and possibly acidic precipitation than in the High Arctic might be an invisible and silent killer for the sensitive Arctic organisms in many sub-Arctic areas. In theory, the acid sensitive species may survive better in larger lakes, the lake refuges, where the lake buffering capacity is better than in small lakes or ponds in the sub-Arctic region.

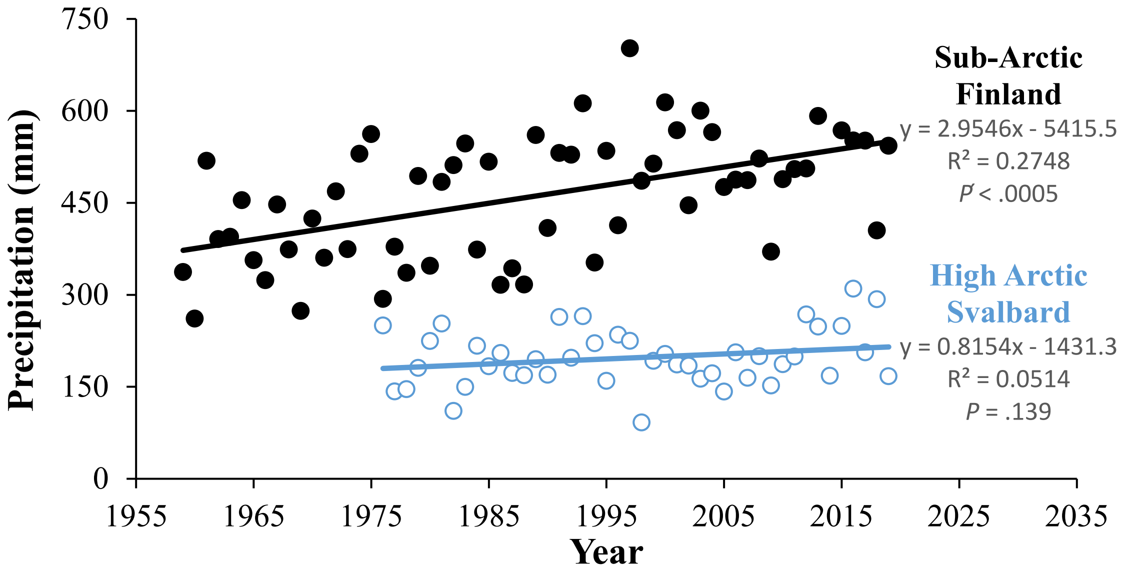


FIGURE 3 The precipitation increase is significant in sub-Arctic Finland (●) but not in the High Arctic Svalbard (○). Populations of the same Arctic species are exposed to the Arctic environmental change in different ways and rates in their distribution areas. Precipitation of Sub-Arctic Finland during the period 1959–2019 measured by the Finnish Meteorological Institute at the Kilpisjärvi meteorological station. Precipitation of High Arctic Svalbard during the period 1976–2019 measured by the Norwegian Meteorological Institute at the Svalbard Airport meteorological station.

Arctic freshwaters support the Arctic biodiversity, because they are important drinking water sources for many animals. Northern Finland has many endangered Arctic species e.g. Arctic fox (*Vulpes lagopus*) and purple sandpiper (*Calidris maritima*). These two species breed and feed close to the Arctic tadpole shrimp (*Lepidurus arcticus*) ponds in the High Arctic Svalbard (Lakka 2013). *L. arcticus* itself is the IUCN categories listed as a vulnerable species in Sweden (SLU Artdatabanken 2020) and as an endangered species in Finland (Väinölä *et al.* 2019). The populations living in the southern edge of the distribution area are especially interesting because the expected Arctic environmental changes should happen first in these habitats. However, it was unclear, what key variable explains the low numbers of Arctic tadpole shrimp populations in Finland. Previous *L. arcticus* observations from Finland were rather old and the habitats were very dissimilar, a 2.5-hectare small pond (in 1955) versus two lakes: Lake Somasjärvi (1.81 km^2, in 2012, 2013 and 2019) and the second biggest Sub-Arctic lake, Lake Inarijärvi (1 084 km^2, in 1977 and 2018). Therefore, more research is needed on the baseline state of crustacean populations and water chemistry in Arctic lakes and ponds.

1.3.2 Climate risk calculation (Paper II)

Climate change progresses in the Arctic faster than in other areas of the globe (IPCC 2014) and the suitable cool areas for Arctic animals are moving toward the poles (IPCC 2019). These changes are also happening in different ways and rates in different parts of the Arctic (Fig. 3 and 4). The species' responses to warming are also not uniform, but depend on the physiological limits of the organisms. Hence, a new way to investigate and predict the environmental change based on species specific responses is needed. Thermal exposure needs to be examined from many perspectives and the sum of the risk factors constitutes an actual or predicted climatic risk to the animals.

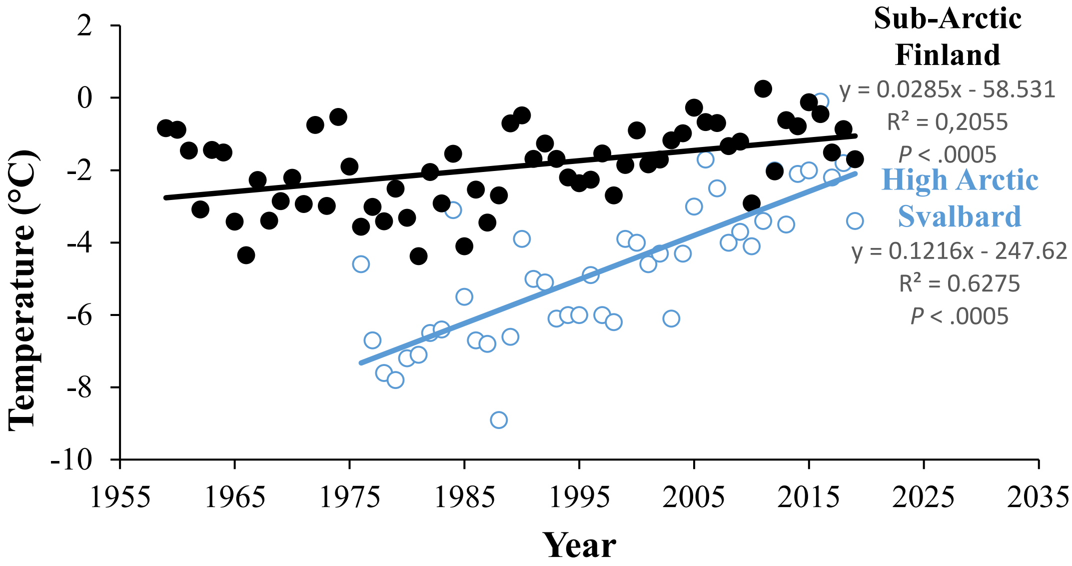


FIGURE 4 The air temperature increase is significant in sub-Arctic Finland (●) and in the High Arctic Svalbard (○). Populations of the same Arctic species are exposed to environmental warming at different rates in their distribution areas. Mean temperature during the period 1959–2019 measured by the Finnish Meteorological Institute at the Kilpisjärvi meteorological stations. Mean temperature of High Arctic Svalbard during the period 1976–2019 measured by the Norwegian Meteorological Institute at the Svalbard Airport meteorological station.

1.3.3 Physical characteristics of organism (Paper III)

Body size affects functional properties (Burton *et al.* 2020) and behaviour (Niiranen *et al.* 2019) of individuals. How well and at what rate the individual reaches the optimal body size depends on the environment in which it is present. Environmental change is affecting animals' vital rates e.g. growth and reproduction (Betini *et al.* 2020). Due to the changing climate's effect on growth, the appearance of organisms might not reflect physical descriptions based on individuals exposed to different climatic conditions. It is crucial to follow a verified scientific method for animals' measurements under the fast-changing environment. If such a method is not available or it is incorrect, the introduction of a new best practice to carry out the measurements is needed. This was the case in article III, when the detailed morphological measurements were needed to describe the rare Arctic tadpole shrimp males for science and compere the animal's morphology living in remote populations in the High Arctic. Verified measurements are irreplaceable ecological tools, also because such measurements give the opportunity to study historical samples in museum collections as well as remains from lake sediments, and compare them to more recent samples.

Notostraca (tadpole shrimp) has been present at least from the Carboniferous era (Korhola and Rautio 2001). The study species, the Arctic tadpole shrimp, is a living fossil, with million years old remains found from lake sediments (Zinovyev *et al.* 2019, Neretina *et al.* 2020) and more recent remains from fish stomachs (Qvenild and Hesthagen 2019). These unique Arctic animals can be found stored for museum collections (Finstad *et al.* 2019) and the living specimens of Arctic tadpole shrimps are still swimming in lakes and ponds in the 21st century.

1.3.4 Biodiversity of the Arctic archipelagos (Paper IV)

We are losing species at an exceptional rate because of climate change (Hyvärinen *et al.* 2019, SLU Artdatabanken 2020). Moreover, rapid climate change causes concern because many areas of the Arctic are still unexplored and we do not know the state of biodiversity. Some of the dominant large branchiopods found in the High Arctic lakes and ponds are also present across the Arctic. The broad biogeographical distributions are expected to be obtained via passive dispersal (Arnold 1966), and migratory birds are expected to play an important role in this respect (Dodson and Egger 1980). Indeed, the movements of Arctic species connect the different types of Arctic freshwater habitats if the conditions are suitable in receiving habitats. Fishless habitats enable the vital occurrence of Arctic tadpole shrimp (*Lepidurus arcticus*) in Greenland and Svalbard (Jeppesen *et al.* 2001, Lakka 2013), while in a lake with a multiple fish species Arctic tadpole shrimp is rare even within its own distribution boundary in northern Finland (Lakka 2019). Translocation and stocking of fish in Arctic inland waters is a serious threat to the large branchiopods, because it can negatively affect their survival and recruitment.

There is a growing need to understand ecosystems as a whole especially in light of climate changes. We cannot separate the abiotic and the biotic information in the Arctic or other regions. Nevertheless, to provide reliable species-specific information we need expert know-how, the real person who can identify the species or run the DNA analyses. Despite this identification problem, the written information describing historical records of biodiversity can be scattered. Biodiversity information may be found in many scientific journals, databases, books written in several languages, specimens in museum collections and worst of all, the information can be tacit, so that only one person or group have that knowledge. The most topical research needs on Arctic biology and terrestrial ecosystems are summarised in AMAP / EU-PolarNet 2020 report. The globe is facing biodiversity loss simultaneously with climate change, but lacks biodiversity information for monitoringing and estimating the extinction risk of Arctic species, and especially to conduct necessary mitigation actions. Paper (IV) provides taxonomic information to advance understanding about biodiversity in the fast-changing Arctic archipelagos.

1.4 Research aims and scope

The main aim of the thesis was to study how acidification and climate warming influence the survival, habitat quality and potential fitness of endangered Arctic tadpole shrimp in Arctic lakes and ponds (Fig. 5).

The main study hypotheses were:

1. Freshwater acidification, acid rain and long-term climatic impacts restrict the occurrence of Arctic tadpole shrimp in small ponds and lakes in the Scandinavian mountains (I).
2. Filtered meteorological data can enable species-specific extinction estimates. The climate is a risk for the selected Arctic species in a certain time and space (II)
3. Tadpole shrimp morphological measurements can be used to identify rare males, and cannibalism by females might explain sexual dimorphism, which can lead to biased female/male ratios (III).
4. Similarities and dissimilarities of biodiversity in the Arctic archipelagos reveal the colonisation routes of terrestrial and freshwater invertebrates to the three Arctic archipelagos, Svalbard, Novaya Zemlya and Franz Josef Land, in the Barents Sea region (IV).

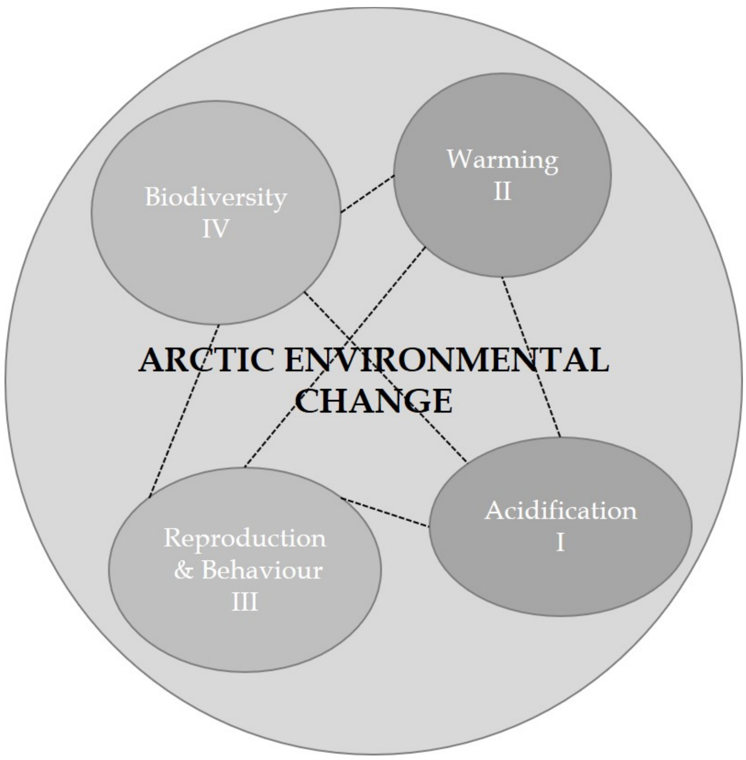


FIGURE 5 Schematic illustration of the thesis topics and their interactions.

This thesis aims to integrate field data, laboratory experiments, historical records and climate data into species-specific ecological knowledge of environmental change in the Arctic, as well as to develop new methods to detect and predict ongoing change. Study focuses on the Barents region's freshwater ecosystems, from the High Arctic Svalbard to the sub-Arctic Finland. My thesis is focused on understanding population- and species -level changes in a changing Arctic, using the IUCN threatened freshwater crustaceans Arctic tadpole shrimp (*Lepidurus arcticus,* Branchiopoda, Notostraca) and Arctic fairy shrimp, (*Branchinecta paludosa* (Branchiopoda, Anostraca) as examples that experience the harmful effects of warming and acidification. I have particular focus on the impacts of acidification and climate change effects on Arctic populations, and how these massive environmental changes are potentially changing the species reproduction and survival. This area of study has implications for better understanding how the Arctic species are responding to climate change, and also introduce the method to point out the species and the populations that may be more vulnerable to extinction in the near future. The aim of this thesis is not only to show the problems, but also to give recommendations on how to solve or mitigate the enormous climatic problem that the Arctic nature is facing today.

1.5 Policy background

This work's driving force was to provide scientific information for policymakers about the ongoing environmental change in the Arctic. Much time and effort has been spent in the Arctic investigating changes in on-going natural phenomena, in confirming these observations in laboratory experiments and with real climate data, or *vice versa*. The data behind this thesis has been collected from freshwater sources – from the glacier fed ponds in the High Arctic Svalbard to the large sub-Arctic lakes in the open tundra in Finland. In doing so, wider knowledge of problems related to the arctic environment change were reached. This work underlines environmental problems, but also gives tools to study ongoing environmental change. The purpose of the presented new tool *Climate risk calculation* is to give new way to investigate climate change effects for selected species on the spatial and the temporal scale.

2 METHODS

2.1 Study areas and surveys

This thesis' geographic scope covered three study areas in the Arctic. Northwest Svalbard (II and III) and northern Finland (I and II), and the literature review was focused on the biodiversity of the Barents Sea archipelagos, Svalbard, Franz Josef Land and Novaya Zemlya (IV) (Fig. 6 and 7).

Forty-three study ponds and lakes are situated in the sub-Arctic region of northern Finland (69° N, 20°–21°W) and 23 in the High Arctic of northwest Svalbard (78°–79° N, 11°–16° W). The lakes and ponds were sampled in 2010 in Svalbard and

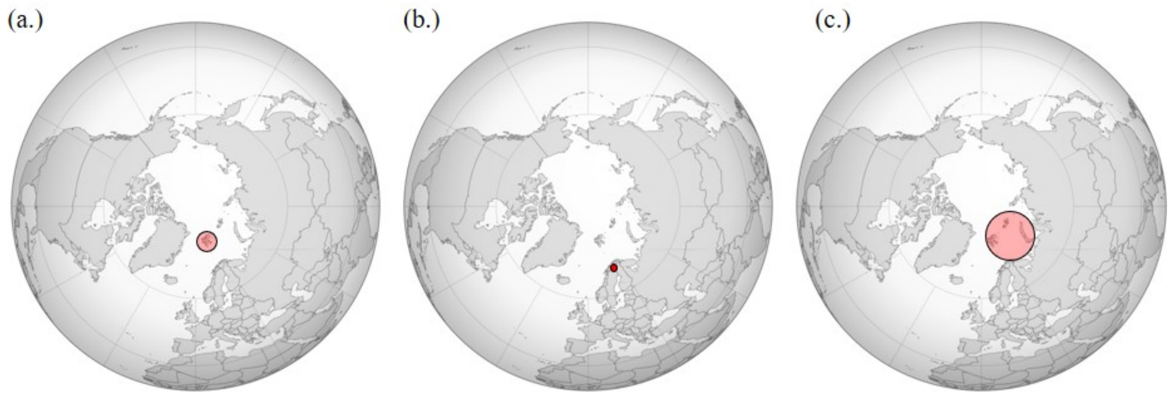


FIGURE 6 The geographic scope of the thesis: a. Svalbard, b. northern Finland and c. Archipelagos of the Barents Sea.

2012–2019 in Finland. More detailed description of the High Arctic sampling sites can be found in Lakka 2013 and the Sub-Arctic sampling sites are described in the acidification study (I).

Two Arctic surveys were carried out. The target of the surveys was to study abiotic and biotic elements of Arctic pools, ponds and lakes. First survey was High Arctic survey in Northwest Svalbard from July to September in 2010 (I, III, IV). This

FIGURE 7 Circumpolar map indicating the locations of three Arctic zones, High Arctic, Low Arctic and Sub-Arctic.

field campaign was conducted in 23 ponds or small lakes in the Longyeabyen, Kapp Linné, Pyramiden, Kilneset, Polheim, and Ny-Ålesund area on the western and northern part of Spitsbergen, Svalbard, Norway. The second survey in Sub-Arctic region was carried out over several years. These Sub-Arctic surveys were done during the autumns (August – October) in 2012, 2016, 2017 and 2019 in northern Finland (I and II). Field campaigns were conducted in 43 ponds or small lakes in Pitsusjärvi-, Mallajärvi-, Urtasvaara-, Somasjärvi- and Bossovárri area in the northern part of Finland. Surveys included water chemistry information and presence absence information for Arctic tadpole shrimp, (*Lepidurus arcticus* Branchiopoda; Notostraca) from all study systems.

Thesis taxonomic scope focused on two threatened Arctic freshwater species Arctic tadpole shrimp, *Lepidurus arcticus* (Branchiopoda; Notostraca, Pallas, 1793, I-IV) and Arctic fairy shrimp, *Branchinecta paludosa* (Branchiopoda; Anostraca, O.F. Müller, 1788, II). The Arctic tadpole shrimp was used as a model organism to study the Arctic environmental change. The Arctic tadpole shrimp shows life history traits, namely cannibalism and rare sexual reproduction, both of which are tightly related to fitness and survival in the severe Arctic environment.

2.2 Research approach

2.2.1 Data compilation

The thesis is largely based on the recent studies on ecology of the Arctic tadpole shrimp ecology (Lakka 2013). All of the studies started with an open research question that was not answered in the existing literature. The first step was to perform a literature review and collect climate data from databases. The second step was to plan the field surveys or/and the laboratory experiments. The third step was to write and submit the project application. The fourth step was collect the data or put in to practice the laboratory experiments and do all morphological measurements and finally the fifth step was to analyse the data and finally, to read more and, write and submit the manuscripts to suitable scientific journals.

In this thesis, the environmental data was combined with field observations and measurements. Data from abiotic environmental variables (air temperature, water temperature, precipitation pH, water pH, were collected from databases. Amount of precipitation and precipitation pH was one dataset, the water pH and temperature from lake Kilpisjärvi was a second dataset, and the air temperatures was the third dataset that were used in this study. For the acidification manuscript (I), a lot of fieldwork was needed to collect the information at the right time from the ponds and lakes in order to observe in nature what the precipitation measurements were showing about acidification.

2.2.2 Arctic tadpole shrimp sampling and samplers

Sampling in the Arctic has to be well-planned because most lakes are remote and it may not be possible to return to the lakes to collect sampling devices or repeat the sampling. The sampling time was also limited, sampling had to be done within two hours in a lake or a pond, and sometimes, work had to be stopped earlier than was planned because of safety issues. To ensure enough specimens for morphological or laboratory analysis, several field methods were used to collect *L. arcticus.*

The used samplers can be divided to three types 1) a density sampler, 2) a trap that was based on the predator olfaction capacity (the sense of smell) and 3) an active sampler (Fig. 8). Windy or rainy weather that breaks the water surface makes *L. arcticus* sampling difficult when using an active sampler. Calm weather, which is often in the early morning and in the evenings, was the best time to collect *L. arcticis* samples.

In situ density sampling was the first sampling procedure in the lake, because the place intended for *L. arcticus* sampling needed to be in its natural state. Five undisturbed sediment core samples were investigated in each lake littoral zone using a customised sediment core sampler (Fig. 8b.) to determine Arctic tadpole shrimp density. First, the sediment core sampler was pushed gently into the sediment. Then the sampling depth was measured using a measuring stick inside the sampler. If the water was clear inside the sampler, *L. arcticus* could be counted and specimens were collected using a hand-held net. If the water in the sampler was mixed with the sediment, the sediment paddle was pushed carefully to the gap in the sampler and the sediment cores were investigated when the water was drained out and *L. arcticus* individuals were easy to pick up from the top of the sediment. This method was also tested for density estimates of planktonic juvenile stages of *L. arcticus,* but even though the sediment cores were studied in the laboratory and under a microscope, no *L. arcticus* juveniles were found. This described method is suitable for benthic invertebrates, but not for planktonic organisms, such as *L. arcticus* juveniles. A plankton net is the best method for catching planktonic juveniles.

Collected specimens were placed in 250 ml containers filled with pond water alive or in 80 % ethanol, depending on the experimental setup. Live animals were kept dark and cold in pond water during the transport to the laboratory. Holding the container with *L. arcticus* specimens in warm hands raises the water temperature and may kill the crustaceans.

Samples of Arctic tadpole shrimps *Lepidurus arcticus* (n ≥ 30) were studied morphologically from each location and were used in behaviour experiments (III).

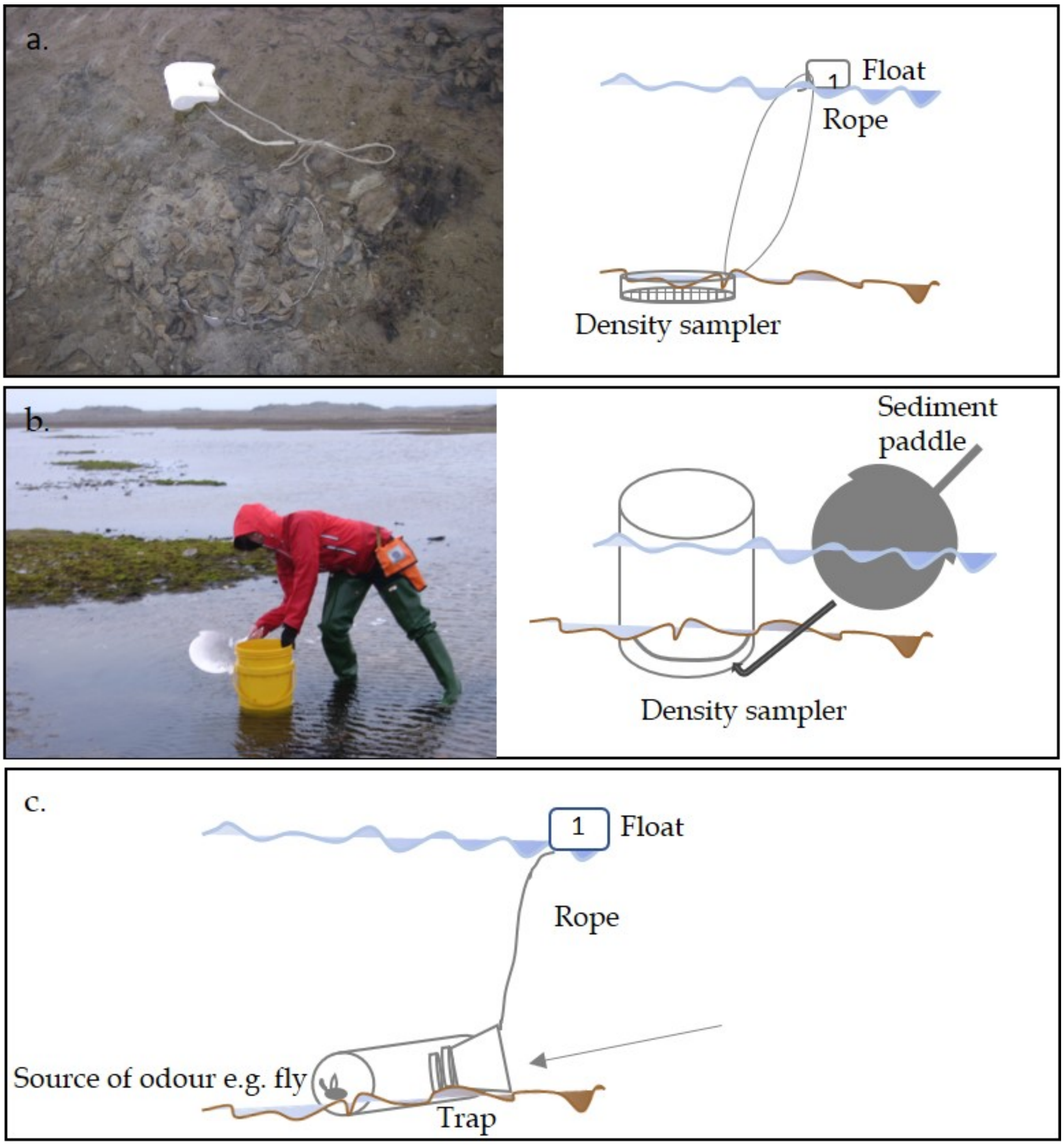


FIGURE 8 Arctic tadpole shrimp (*Lepidurus arcticus*) were collected using different kinds of field methods. a.) a passive density sample, and b,) an active density sampler were used in Svalbard and a trap c.) that was based on the predator's olfaction capacity was used in northern Finland. Also, more traditional sampling methods were used, e.g. a hand net and a kick net.

3 RESULTS AND DISCUSSION

3.1 Summary of the articles: aims, methods and result

3.1.1 Acidification (I)

My previous study showed that the High Arctic ponds located close to human activity e.g. coal mines or dog yards can be more acidic than pristine ponds in the High Arctic (Lakka 2013). The direct anthropogenic disturbance seems to be an important acidification driver in the High Arctic Svalbard, but what the acidification situation is in Sub-Arctic Finland was not clear. Because it is known that acidification causes mortality for sensitive crustaceans (Borgstrøm and Hendrey 1976) and it is linked to global warming (AMAP 2018) the acidification-crustacea project ColdShrimp was started 2012 to investigate this important topic. Remote areas in Finland, indeed, contain unique aquatic environments and often their hidden biodiversity is unstudied because their sampling can be expensive, impracticable or difficult to carry out. In this study, the selected study area was extensive and the sampling needed years to cover enough area to get the needed information for Arctic tadpole shrimp distribution and the possible acidification in freshwaters in the Sub-Arctic northern Finland. Sampling campaigns were carried out during biologically important times in late autumn, when the mature crustaceans are easy to observe and when they produce resting eggs for the coming summers.

This work combined three types of information: the water pH measurements from lakes and ponds, precipitation pH and the presence-absence observations of Arctic tadpole shrimp. Four sampling campaigns covered 43 ponds and lakes in six areas. Three to six pH measurements were done per lake in the field and three to nine pH measurements were done in the laboratory to confirm the field measurements. To get correct values, all pH meters were calibrated before and during the field trips. The precipitation pH data at Pallas Matorova station was used for the period 2000–2018, monitored by the Finnish

Meteorological Institute. The presence-absence of the Arctic tadpole shrimp (*Lepidurus arctius*) was investigated for each lake or pond in two hours. Two persons were looking for *L. arcticus* using a hand net or a kick net and sampling so that the study area covered the littoral zone around the lake or pond.

The results point out that climatic impacts restrict the occurrence of Arctic tadpole shrimp in small ponds and lakes in the Scandinavian mountains. Freshwater acidification, acid rain and long-term climatic impacts have negative impact of acid sensitive species survival in the northern Finland (Table 1).

3.1.2 Climate risk calculation (II)

This aim of this work was studying climate change from the animals' perspective. How populations respond to the climate warming and how harmful is the warming was studied considering the animals' physiological perspective and also taking into account the spatial and the temporal scale.

Temperature data from animals' known distribution areas were combined to the temperature range where they survive. Special focus was given to the nature of temperature variation, a) the length of harmful temperature stress, b) how many days the temperature stress was experienced, c) sum of lethal degrees out of the animal's tolerated temperatures and d) maximum heat stress. These were calculated from available climate data and further predictions were estimated using IPCC 2014 projections RCPs, RCP2.6, RCP4.5, RCP6.0 and RCP8.5. The five projections predict the climate warming in different intensity from a 0.3°C–0.7 °C temperature increase to a 2.6°C–4.8°C increase. Two threatened freshwater species were used as examples for the climate risk calculation method.

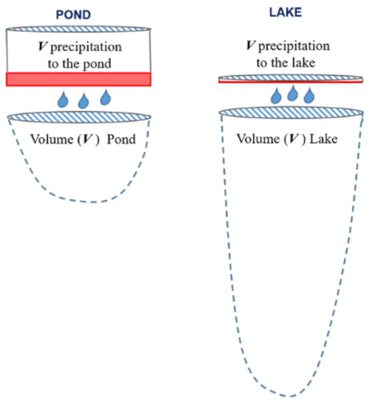
The combination of animal physiology and temporal and spatial aspect is crucial to take account when predicting animal survival rates in the warming climate.

3.1.3 Physical characteristics of organism (III)

To understand how Arctic animals respond to the changing environment, it is necessary to study what are the life history elements that might be important for the animal's survival in Arctic environment, especially considering that important life history events can only take place during a short period of time and under severe climate conditions. What kind of hidden behaviours or reproduction styles might be beneficial for the optimal fitness of the Arctic animals?

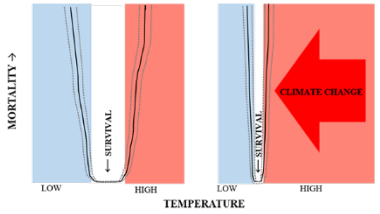
Arctic tadpole shrimp morphology was studied to identify the presence of males and the morphological differences between the genders. Biological studies have been focused on importance of females with great success (Wathne *et al.* 2020), but males are understudied for many taxa. Nevertheless, males are important for species evolution and genetic biodiversity offered by males might be one of the key elements to enable survival in the fast-changing Arctic environment.

TABLE 1 Summary table from contents of the doctoral thesis.

Paper	Objective	Method	Illustration	Main finding / conclusion
I Acidification of tundra ponds and its impact on an endangered crustacean, Arctic tadpole shrimp in Finland	The objective of this study was to study if acidification and long-term climatic impacts could restrict the occurrence of Arctic tadpole shrimp in small ponds and lakes in the Scandinavian mountains.	Freshwater acidification was studied in situ water pH measurement in the ponds and lakes and as well as analysing perspiration pH.		1. Water pH in ponds can drop down to pH 4.9, which is the mean precipitation pH in northern Finland. 2. 74 % of the precipitation can be considered as acid rain (pH < 5) and 98% of precipitation is too acid for the Arctic tadpole shrimp in northern Finland. 3. Acidic precipitation together with climate warming (increasing temperature and precipitation) may severely impact the survival of cold adapted or/and acid sensitive species living in ponds and pools in the Scandinavian mountains

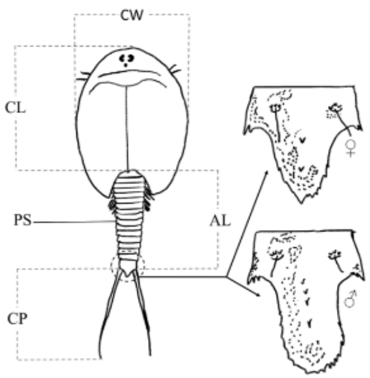
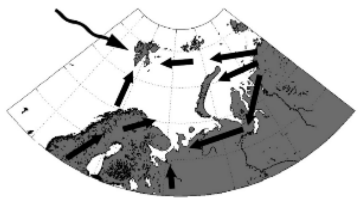
continues

TABLE 1 continues

Paper	Objective	Method	Illustration	Main finding / conclusion
II Climate risk calculation; an approach for identifying a species-specific temperature risk	Climate change could affect the shape of temperature-mortality relationships. The presented new method provides a way to estimate and detect the species-specific extinction risk in a selected time and place.	I introduce an approach to filter temperature datasets to determine climate change species-specific risks. Arctic indicator species were used as examples. • The new method examines 1.) the exposure time, 2.) the intervals, 3.) the degree sum 4.) and the maximum expedient heat stress in species perspective in the selected distribution area. • Species -specific data was fitted to five IPCC 2014 climate		• Global warming needs to be studied from a species perspective. The temperature stress is multidimensional and species-specific. • The increasing temperatures cause heat stress and reduce sensitive animals' survival. Presented predictions describe the nature of warming, and provide insight into a species-specific vulnerabilities under different climate scenarios. • Climate change may pose an increased heat stress to Arctic crustaceans, due to their low thermal tolerance. This can impact negatively to performance in terms of growth and reproduction, but also potentially increase the risk of mortality and ultimately leads to the loss of populations.

continues

TABLE 1 continues

Paper	Objective	Method	Illustration	Main finding / conclusion
III Description of the male *Lepidurus arcticus* (Branchiopoda: Notostraca) and the potential role of cannibalism in defining male form and population sex ratio	The sexual dimorphism of Arctic tadpole shrimp (*L. arcticus*) was not known, partly because males are extremally rare and are not necessarily needed for reproduction. The study objective was to find out if males (sexual reproduction) will be needed when the climate change progress fast in the Arctic. • I investigate the presence of rare males and cannibalistic behaviour in the High Arctic populations.	• Sex and morphological measurements for 783 Arctic tadpole shrimp individuals from 19 ponds and six areas in the western and northern parts of Spitsbergen, in Svalbard, Norway were investigated. • Two laboratory experiments about the cannibalistic behaviour of Arctic tadpole shrimp was carried out.		• Rare males were smaller and had more compact and robust bodies than females. • Arctic tadpole shrimp is capable to cannibalism, which can be vital behaviour characteristic to survive in the fluid and severe Arctic environment. • Presence of males enable genetic variation, and a better disease resistance and adaptation to the changes in the warming Arctic
IV The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef Land and Novaya Zemlya	The objective of this study was to find out how well do we know Barents Sea terrestrial and freshwater invertebrate biodiversity and they colonisation routs in three Arctic archipelagoes.	The method of this synthesis article was to perform a literature survey to create baseline about the terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea; Svalbard, Franz Josef Land and Novaya Zemlya.	 Colonisation routes the Arctic archipelagoes in the Barents Sea. Modified from Coulson *et al*. 2014.	• The archipelagos of the Barents Sea are inhabited by a diverse community of invertebrates. • The colonisation routes and physical isolation appears to explain the Arctic biodiversity in Svalbard, Franz Josef Land and Novaya Zemlya. • Clear South-West colonisation but natural colonisation (birds, wind and current) largely undocumented and increasing threat of biological invasion driven by the warming and the increasing human activity in the Arctic.

The second objective was to study the Arctic tadpole shrimp female's capability to behave in a cannibalistic way. In the nutrient poor Arctic waters, the omnivorous, but sometimes carnivorous feeding style is common (Grigor *et al.* 2015). How common the cannibalistic behaviour is among Arctic tadpole shrimp populations was not known. The cannibalistic behaviour of crustacean may increase individual fitness, because the other conspecifics are large-sized and energy-rich prey (Lien 1978) and thus, enable to the cannibalistic individual to grow faster. In fact, the large-sized individuals can produce more offspring than smaller individuals (Lakka 2013).

The result from high Arctic, revealed that females dominate the populations, but also males were found. Presence of males gives a strong signal for the presence of sexual reproduction in the high Arctic. Cannibalistic behaviour of females was common.

The differences in the appearance between the genders may be explained by the different fitness benefits of the sexes. Males were smaller, but the limbs were thicker than in females. The small-sized males have to find mating partners and avoid the bird predators, but be able to hold cannibalistic females still during copulation and also escape after the encounter with a female.

3.1.4 Biodiversity of the Arctic archipelagos (VI)

Arctic crustacean communities are currently undergoing rapid changes due to the environmental drivers (Lindholm *et al.* 2015). In addition, some crustaceans are among the most successful invasive invertebrates (Altermatt *et al.* 2019).

Colonisation history of Arctic archipelagos after the last ice age maximum may give a hint for forthcoming Arctic migration and possible routes for invasive species. This synthesis article objective was to give a baseline of the Arctic archipelagos' biodiversity in terrestrial and freshwater habitats. The result of the synthesis of invertebrate biodiversity from the Barents Sea region archipelagos shows that the colonisation history may explain the current taxa of Arctic archipelagos. The south-west colonisation route was supported by similarities among taxa. However, Svalbard's taxa are more well-known due to recent research efforts, and the other two archipelagos, Frans Josef Land and Novaya Zemlya, are less studied in the western literature.

Crustaceans are an excellent candidate group for biodiversity monitoring in the Arctic, not only due to their sensitivity to the ongoing environmental change (I and II) but also because they support the survival of many Arctic animals in fast changing Arctic region (Fig. 9). The survival of Arctic animals and peoples depend on the availability and quality of freshwater. When this essential element, water, as a habitat and a source of drinking water starts to disappear and change to be more hostile to living beings, we see changes in the Arctic biodiversity. Arctic freshwater ponds and lakes are essential for life in the Arctic – they protect Arctic biodiversity and enable the survival in otherwise harsh climate conditions. Arctic freshwaters should be seen as biodiversity stepping stones that are used to find water, food and shelter. They can be physically nonconnected water bodies located in different Arctic areas, but, Arctic animals connect these habitats.

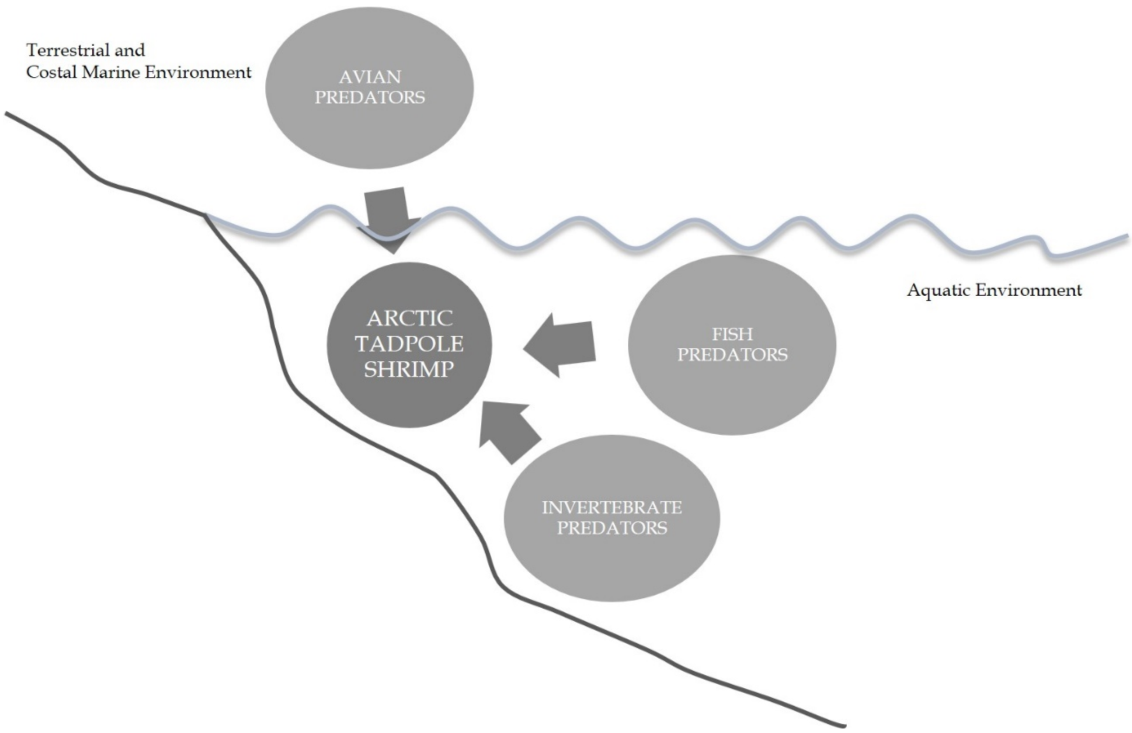


FIGURE 9 Arctic tadpole shrimp (*Lepidurus arcticus*) are essential prey for many Arctic animals such as birds (*Sterna paradisaea*, *Calidris alpine* and *Calidris maritima*), fish (*Salmo trutta* and *Salvelinus alpinus*) and aquatic beetles (*Dytisticus lapponicus and Colymbetes dolabratus*) in the Arctic. The freshwater Crustacea maintain Arctic biodiversity and connect Arctic environments. The collapsing of crustacean populations is the first warning sign of change in the Arctic environment.

4 CONCLUSIONS

4.1 Climate conditions

The results of this thesis give strong evidence that environmental change should be studied from a species' perspective (II) to get the most accurate predictions of where populations are under a high extinction risk and where possible management actions should be carried out. Ocean acidification in the Barents Sea is influenced by the freshwater input from the Arctic (AMAP 2018), and the results of the thesis strongly suggest that Finnish Lapland is one source of the acidic Arctic water (I). Northern countries should pay more attention to this acidification progress in the freshwater and start management programs to mitigate the lethal effect of acidic waters.

The climate of northern Finland is characterized by increasing temperatures and precipitation (Fig. 3 and 4). Warmer temperatures and increased acid precipitation, may explain the freshwater acidification in the High Arctic Svalbard (Betts-Piper *et al.* 2004, Lakka 2013) and it most likely explains the acidification in ponds in northern Finland (I). Global warming is progressing rapidly in the Arctic region (IPCC 2014, IPCC 2018) which has a strong impact on freshwater lakes and ponds. The shortening winters combined with a high depth of snow, pose a major challenge to aquatic organisms because the timing of the water movement is changing in the spring; e.g. shortening lakes' ice cover, changing the start of spring runoff, causing floods and altering small water systems through drying. The combination of low water level and the acidic precipitation in hot summers it is an especially hazardous combination for the Arctic freshwater species survival (I).

In the species perspective, climate warming contains different types of ecophysiological stresses. These sometimes-lethal temperature effects include the temporal variation of heat stress, the quantitative level of heat stress, the physical effectiveness of heat stress and the maximum experienced heat stress. The presented climate calculation method combines all these possible harmful temperature effects and create a realized and a projected climate risk matrix (II).

This study demonstrated the possible vulnerabilities of the Arctic shrimps to ongoing environmental change in the Arctic (I, II). It is clear that Arctic tadpole shrimp (*L. arcticus*) is an important link of nutrient transport between freshwater, terrestrial and costal marine habitats (Fig. 9). It is a nutrition-rich food item (Lien 1978), which, when present in the area, is connected to large-sized fishes (Lakka *et al.* 2020) and the nesting areas of crustacean-eating birds (Quakenbush *et al.* 2004, Lakka 2013). Indeed, the possible collapse of this important indicator species may have far-reaching consequences.

The conservation value of a given species is not typically determined only based on its characteristics, but also based on the ecosystem services it provides. For example, crustaceans act as an enabler for fast-growing fish stock and the vibrant bird population. The large-sized fishes are a wanted catch and food, while the bird populations offer recreation value and are important spreader of crustacean eggs (Rogers 2014) and plant seeds (Côrtes and Uriarte 2013). An apparent issue is that when the Arctic indicator species and populations are viable, they support the survival of many other Arctic species.

4.2 Knowledge gaps and future research priorities

This thesis provides novel insight into the environmental change of freshwater lakes and ponds in Sub-Arctic and high Arctic regions. However, some field work methods could have been developed further to provide a better answer to the research questions if more time, labour resources and technology had been available in the field. These sensitive and valuable Arctic systems need to be studied widely in the different Arctic zones from the High Arctic to the Sub-Arctic region to understand if the current water chemistry is a threat for Arctic aquatic life. As shown in figures 3 and 4, the climate change happens at different rates and the most critical climate variable can be different in the different areas in the Arctic region.

Human-induced biological invasions occur around the world and contribute to the loss of biodiversity (Meltofte, 2013). An increasing number of human-introduced species are becoming established in the fresh water systems, and are putting indigenous species under pressure (Gederaas *et al.* 2012, Niemivuo-Lahti 2012). Many disruptive invasive species are found in the Arctic and they will probably be able to spread to new areas in the changing environment (Sandvik *et al.* 2020). This thesis points out the effects of environmental change on Arctic biodiversity (I, II, IV) and advantages of the flexibility of reproductive systems and food intake, as well as how colonisation can increase survival in the changing Arctic (III and IV).

Currently, the main gaps of information are related to the freshwater species distributions and the ecophysiology. Long-term monitoring projects are needed to provide 1) the presence - absence information for the species and 2) the abiotic information from fast-changing freshwater habitats. Due to demanding sampling conditions and remote locations in the Arctic, many important freshwater habitats get less attention than they deserve. Also, long lasting laboratory experiments are needed to study the Arctic animals' different life stages. This is because, firstly, Arctic animals face a climate that they have not experienced in nearby decades, and secondly, the information of the physiological responses are scattered or not-available. Short laboratory experiments are easier to carry out, but long-term experiments provide crucial information of both chronic and acute effects. In the future, research should focus on these more demanding research settings in the field and laboratory but not forgot the importance of basic research.

The Arctic tadpole shrimp is an important indicator species for climate change in the Arctic (Lakka 2013). It lives in diverse Arctic habitats, is a generalist feeder (Christoffersen 2001) and important prey for many fishes and birds. The goal of nature conservation is that all existing species are preserved (Fig. 9). Monitoring and protecting each and every species is a major challenge of the 21st century, but at least indicator species, such as the Arctic tadpole shrimp and the Arctic fairy shrimp should attract more of the scientific, government and public attention. Acidification is by no means a new environmental problem, but its frequency has grown remarkably over the past year (AMAP 2018). We should take strong action to address acidification and climate change in the Arctic. These anthropogenic environmental changes will be a growing problem as the climate change is making parts of the Arctic unsuitable for Arctic animals. Due to global warming, extreme weather conditions will increase in the future (Smale *et al.* 2019). Mining (Silva 2011, Lakka 2013) and burning of non-renewable fossil fuels may increase acidification in the Arctic freshwater. Governments need to address these issues before it is too late. Significant cuts in the greenhouse gas emissions would be a relatively quick way of contributing this goal (Montzka *et al*. 2011). It is also crucially important to continue the monitoring program and strive for preservation of the Arctic biodiversity, especially in small waterbodies. Limiting and removing the harmful effect of acidification and warming is the way to save to the sensitive Arctic fauna.

4.3 Implications for policy

The thesis revealed that aquatic ecosystems of the Arctic face several challenges with regard to species diversity. The Arctic will likely confront an even warmer environment, and together with drought and freshwater acidification, many of the Arctic freshwater populations will not escape certain death in the near future (I and II). Arctic biodiversity will change and we will see more negative changes in the growth and reproduction of Arctic species.

The escalating environmental change in the Arctic region is a defining topical environmental issue of our lifetime. Precipitation is constantly acidic in northern Finland (I). The combination of hot and dry summers is very harmful in small ponds. When acidic precipitation is coming after a dry period when water level is low, the acidic precipitation effect for biota is the strongest (I). This kind of acid precipitation kills aquatic animals (Fellheim *et al.* 2001). This progress has to change, and soon. Paper (I) sends an important message about the need for monitoring water pH and other key environmental variables in Arctic ponds and lakes. One approach used to mitigate the effects of surface water acidification is the treatment of calcium carbonate ($CaCO_3$). However, chemical approaches should always be used with care. The rapid rate of re-acidification could occur after calcium treatment because of the shallow depth and short retention time of Arctic ponds. Calcium particles can also affect the respiration of eggs if the treatment is ill-timed.

Our children are living the warmest climate the globe has experienced in the past millennium (Jones *et al.* 2001) and they are inheriting an increasingly warming globe. Public economy based on black carbon is socially irresponsible, and politics without action is no longer enough. My research and that of several other scientists all over the globe have same message: Reduce the carbon emissions and save the globe = save your children and grandchildren. Activities involved in extracting and using fossil fuels, are including many of the world's largest polluters. Because of use of fossil fuels will continue and because these pollutants accumulate in the Arctic region (Evenset *et al.* 2005) the Arctic nature is and will be in the grip of an emergency. To slow down and mitigate the ongoing loss of the biodiversity and habitats which related to warming and acidification in the Arctic, the world needs firm and lasting decisions and fast actions. Already two of the true Arctic branchiopods (Anostraca and Notostraca) distributed in the circumpolar region are classified as threatened in northern Finland. The best solutions to save arctic freshwater biodiversity are to reduce the use of fossil fuels and improve our management strategies for freshwater ecosystems.

To mitigate the negative effects of the climate change, acidification and loss of Arctic species in freshwaters in the Arctic region, consideration of the following by both scientists and managers should continue:

1.) Reducing of harmful effects of temperature in Arctic aquatic habitats;
   - Cold water has to be available also in the lower parts of Arctic catchments. Cold temperatures (water, snow, ice and permafrost) act as a physiological and /or physical barrier for more temperate species.
   - Shading habitats are important to cool water habitats e.g. in the forests in the polar region, so clear-cuttings in nearby inland water shorelines and rivers should be avoided.
   - Man-made structures that e.g. increase connectivity (Koksvik *et al.* 2009), change water flow, decrease depth in watercourses or heat up surface waters (Normyle and Pittock 2020), including fishways, dams, mountain pumped-storages and turbine tunnels in hydropower systems, may facilitate migration and establishment of new invasive species in Arctic and alpine freshwater habitats.

2.) Monitoring and preventing invasive species migration to the Arctic;
- A special focus on the distribution of the Arctic tadpole shrimp's (*Lepidurus arcticus*) fish predators would be useful. More collaboration between fish and crustacean researchers is needed.
- Catch reporting should be a part of the monitoring control of recreational fishing in the Arctic.
- Fishless lakes and ponds are important habitats in the Arctic (Lakka 2013). The presence of fish does not necessarily increase the ecological value of Arctic waters.
- Stocking and relocation of fish should be restricted in *L. arcticus* lakes and instead focus on enabling natural reproduction.

3.) Monitoring of the harmful effects of acidification in Arctic aquatic habitats;
- Long-term monitoring of pH and temperature in ponds and lakes are needed in the whole circumpolar region.
- Mining practises could have a harmful effect of Arctic tadpole shrimp survival (Lakka 2013) through the lowering of incoming water pH to 2.44–3.88 (Silva *et al.* 2011).
- It would be advisable to study the possibilities, ecological impacts and cost of lime treatment in inland waters.

4.) Monitoring methods that do not require the killing the endangered animals should be preferred, (Figure 8).
- Stomach content analyses for ≥ 25 cm fish is recommended to confirm the presence of Arctic tadpole shrimp (*Lepidurus arcticus*) in lakes with fish (Järvinen *et al.* 2014, Qvenild *et al.* 2018, Lakka *et al.* 2019, Lakka *et al.* 2020). The test fishing and traditional stomach content analyses or sampling fish gut content using gastric lavage (stomach flushing) of live fish should be performed from August to October, when *L. arcticus* has reached an adult size and are easy to identify.
- In the largest lake containing Arctic tadpole shrimp in Finland, Lake Inarijärvi (Lakka *et al.* 2019), the whitefish monitoring program of Natural Resources Institute Finland (Luke) should include stomach content analyses in their annual methods.

5.) and, increasing cross-border collaboration
- Regionally coordinated management of protected areas is needed in the circumpolar Arctic region.
- Sufficient funding to support research, long term monitoring and education are needed in the Arctic region.

Special thanks to my supervisors Senior Lecturer Emily Knott, Senior Lecturer Panu Halme and Professor Stephen Coulson. Thank you, Professor Stephen Coulson, for introducing the Arctic tadpole shrimp to me. I never forget the day in Kapp Linnè where you held this fascinating creature on your hand. Thank you for your guidance and for the breathtaking moments at Svalbard over the years.

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To build the theoretical framework of the climate risk calculation manuscript (II) was a several years' project even though the doctoral thesis itself was finalized in a year. Many important and clever people were helping me along the way. Their contribution has been significant in the development of the new method. I would like to thank my colleagues and co-workers for inspiring conversations and collaboration, as well as all editors and reviewers whose valuable work improved my thinking. Warm thanks for that essential help.

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It was complicated to combine the work and family life, be a mother to my five-year-old daughter Saana and be a partner to Antti who also did research at home like almost everyone now. It was hard to find time to write during the day time when Saana you wanted to play with me. Saana, you are a great research assistant and your analytical thinking is exceptional. But I had to do this properly, in the Finnish way, *"Mutta voimallinen tahto vie miehen läpi harmaan kiven" – Aleksis Kivi, the national author of Finland, Seven Brothers 1870,* with the help of a sauna, of course.

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YHTEENVETO (RÈSUMÈ IN FINNISH)

Ympäristönmuutos arktisissa järvissä ja lammissa

Pohjoisen pallonpuoliskon arktiset ja subarktiset järvet ja lammet ovat tärkeitä elinympäristöjä monelle arktiselle lajille ja pohjoisten alueiden asukkaille. Järvistä saadaan juomavettä sekä ravintoa, niin ihmisille kuin eläimillekin. Arktisten vesistöjen rantavyöhykkeet toimivat laidunalueina mm. hanhille, poroille ja huippuvuorenpeuralle. Ne ovat myös tärkeinä pesimäalueina monille arktisille linnuille, jotka käyttävät ravintonaan kylmiin vesiin sopeutuneita ravinnerikkaita äyriäisiä. Runsas eläimistö vesistöjen läheisyydessä taas houkuttelee ympäristöön naaleja ja suurempiakin petoja kuten jääkarhuja. Arktiset vesistöt ylläpitävät pohjoisten alueiden ainutlaatuista luonnon monimuotoisuutta ja ovat monien lajien selviytymisen kannalta erittäin tärkeitä.

Huippuvuorilla vesistöt sijaitsevat jäätiköiden ja meren väliin jäävällä maavyöhykkeellä, jossa ne saavat suuren osan vedestään jäätikköjen ja lumen sulamisvesistä. Huippuvuorilla järvien ja lampien pohjat voivat olla jäässä myös kesällä ja siellä sataa vähemmän kuin Suomen Lapissa. Paljakan vesistöt Suomen luoteis-Lapissa sijaitsevat Suomen korkeimpien tuntureiden juurella ja alueella niin sademäärät kuin lämpötilatkin ovat nousseet merkittävästi. Arktiset ja subarktiset järvet ja lammet ovat merkittäviä tutkimuskohteita ilmastonmuutoksen seurannassa, koska muutokset näissä vesissä vaikuttavat suurelle alueelle aina tunturin huipun lammesta mereen asti. Arktiset lammet ja järvet valuma-alueineen ovat tärkeitä monien eläinlajien lisääntymis- ja elinalueita, ja monet näistä kylmiin olosuhteisiin sopeutuneista lajeista ovat uhanalaisia. Ympäristönmuutos arktisilla alueilla on nopeaa ja huomaamatonta, varsinkin järvien ja lampien pinnan alla, jossa muutos tapahtuu ihmiseltä huomaamatta. Näin ollen arktisten vesieliöiden populaatioita häviää ilmaston muuttuessa ilman, että lajien esiintyminen alueella tunnetaan tai että tilannetta seurattaisiin. Tässä väitöskirjassa tutkin, miten elottomat ympäristötekijät, kuten sadeveden- ja järvien happamuus (pH) ja lämpötila vaikuttavat aktisten indikaattorilajien selviytymiseen ilmaston muuttuessa. Työssä käytettiin kahta makeanveden indikaattorilajia pohjoisen ilmastonmuutoksen mallilajeina. Aineistoa kerättiin yhteensä 66:sta Huippuvuorilla ja Pohjois-Suomessa sijaitsevasta järvestä ja lammesta, jotka vaihtelivat niin ilmasto-olojen, pinta alan (4.5 m^2–1 084 km^2) kuin arktisen sijainnin suhteen. Vesistöjen happamoitumista tutkittiin mittaamalla järvien ja lampien veden pH:ta sekä tutkimalla sadeveden happamuutta Pohjois-Suomessa. Ilmaston lämpenemisen aiheuttamaa elinympäristöjen muuttumista tutkin arktisten lajien fysiologisten sietorajojen näkökulmasta. Kaikilla lajeilla on optimilämpötila-alue, joka on niille suotuisa kasvun ja lisääntymisen kannalta. Tätä lajien fysiologista tietoa käytettiin lajien selviytymisen mittarina, jota voidaan hyödyntää populaatioiden eloonjäämisen ennustamisessa, ilmaston muuttuessa eri nopeudella, eri alueilla, nyt ja tulevaisuudessa. Meneillään olevan ympäristönmuutoksen hidastaminen ja sen haitallisten vaikutuksien lievittäminen vaatii työkaluja, joilla jo koettuja ympäristönmuutoksia voidaan tutkia jopa miljoonien vuosien takaa. Tähän tarpeeseen vastattiin tutkimalla koiraiden ja naaraiden välisiä eroja arktisten vesien indikaattorilajilla, jonka jäänteet säilyvät järvien sedimentissä hyvin.

Paljakkakilpiäinen on kylmiin vesiin sopeutunut arktinen äyriäinen, joka on luokiteltu kansainvälisten kriteerien (International Union for Conservation of Nature, IUCN) mukaan erittäin uhanalaiseksi lajiksi Suomessa. Laji esiintyy kylmissä ja niukkaravinteisissa subarktisissa järvissä ja arktisissa lammissa pohjoisella pallonpuoliskolla. Kaikkiruokaisena ja nopeakasvuisena lajina se on merkittävä ravintokohde monelle arktisen alueen kala- ja lintulajille. Se on isokokoinen ja ravinteikas saalis sekä tehokas peto, joka saalistaa myös omia lajitovereitaan. Tämä arktisissa vesissä elävä äyriäinen on myös elävä fossiili, jonka rakenne on pysynyt muuttumattoman miljoonia vuosia.

Väitöskirjan ensimmäisen osatyön (I) tavoitteena oli selvittää, onko happamoituminen uhka arktisille äyriäisille sekä muille herkille akvaattisille lajeille Pohjois-Suomessa. Tulokset osoittivat, että sadevesi on hapanta Pohjois-Suomessa. Vuosina 2010–2018 sadeveden pH:n keskiarvo oli 4.9 eli sadevedestä 98 % oli niin hapanta, että se voi aiheuttaa kuolleisuutta ja fysiologisia ongelmia paljakkakilpiäisen selviytymiselle ja useille muille herkille lajeille Lapin vesistöissä. Tulokset osoittivat, että subarktisissa lammissa veden happamuus voi vaihdella vuosien välillä huomattavasti. Vertailtaessa Mallan luonnonsuojelualeen läheisyydessä sijaitsevien kalkkialueen lampien veden happamuutta vuosien 2016 ja 2019 välillä havaittiin, että emäksisten lampien vesien pH oli laskenut pH = 8,4:stä aina pH = 6,7:ään. Lammet, jotka eivät sijaitse happamuutta puskuroivilla alueilla voivat olla erittäin happamia (pH 4,9), jolloin vesi on monelle lajille haitallisen, jopa kuolettavan hapanta. Sadannan on ennustettu lisääntyvän Suomen Lapissa. Happamien sateiden määrän lisääntyminen muodostaa yhdessä ilmaston lämpenemisen kanssa vakavan uhan arktisten lajien selviytymiselle. Tulokset osoittavat, että varsinkin lammissa, joiden tilavuus on pieni, puskurikyky on heikko, ja ne lammet, jotka saavat merkittävän osan sadannasta suoraan lammen pinnalle ovat hyvin alttiita happamoitumiselle. Happamoitumista pidetään vanhana ja jo ratkaistuna ympäristöongelmana, mitä näin se ei valitettavasti tämän tutkimusten perusteella Suomen subarktisella alueella ole. Tutkimusalueella ei ole pistekuormitusta, joten happosade saa alkunsa Suomen Lapin ulkopuolelta. Happamoitumisen aiheuttamat muutokset Lapin vesistöjen tilassa voivatkin aiheuttaa merkittäviä muutoksia herkässä pohjoisen alueen lajistossa, jos mm. happamoittavaa kivihiilen polttoa suositaan uusiutuvien energiamuotojen sijasta.

Jokainen elävä organismi esiintyy sille tyypillisissä lämpötiloissa. Jos ilmasto muuttuu niin, että elinympäristön lämpötila ei vastaa eläimen sietorajoja, lajin populaatio häviää. Väitöskirjani toisessa osatutkimuksessa selvitin ilmastonmuutoksen haitallisuutta lajeille ja osoitin arktisten indikaattorilajien avulla miten lämpenevä ilmasto aiheuttaa lämpötilastressiä, joka tulee johtamaan populaatioiden häviämiseen. Uudessa menetelmässä yhdistettiin eläimen fysiologinen lämpötilan sietoalue meteorologiseen lämpötila-aineistoon sekä käytettiin ilmastoskenaarioita lajispesifisen lämpötila-altistuksen haitallisuden ennustamiseksi. Ilmaston lämpenemisen aiheuttamaa stressiä eläimille pitää tarkastella lajien fysiologian näkökulmasta. Tutkimuksessa osoitettiin, että ilmastonmuutoksen aiheuttama populaatioihin kohdistuva lajispesifinen häviämisriski pitää laskea lajille ja niiden populaatioille erikseen, koska lämpötilastressin voimakkuus vaihtelee lajin levinneisyysalueen sisällä. Tutkimuksessa käytettiin ilmastonmuutoksen mallilajeina kahta arktisten alueiden indikaattorilajia eli paljakkakilpiäistä ja pohjanlehtijalkaista, jotka ovat myös uhanalaisia Suomessa. Tutkimus osoitti, että jos ilmastonmuutos Suomessa jatkuu ennusteiden mukaisesti, tulee se aiheuttamaan molemmilla lajeilla häviämisriskin. Esitettyä uutta mallia voidaan käyttää ilmastonmuutoksen aiheuttaman lajikohtaisen häviämisriskin ennustamiseen lajien koko levinneisyysalueella sekä niiden alueiden paikantamiseen, joissa häviämisriski on suurin.

Ympäristön muuttuessa lisääntyminen on yksi lajien keino sopeutua paremmin valitseviin oloihin. Väitöskirjan kolmannessa osatyössä (III) tutkin, onko Huippuvuorten paljakkakilpiäispopulaatiossa ollenkaan koiraita, ja jos niitä on, niin miten ne voi tunnistaa. Lisäksi tutkin miten yleistä naaraiden kannibalistinen käyttäytyminen on. Tutkimuslaji on elävä fossiili, jonka rakenne on säilynyt muuttumattomana miljoonia vuosia, mutta lajin koiraiden rakennetta ei ollut tarkemmin kuvattu, koska ne ovat hyvin harvinaisia. Tarvetta koiraiden tarkemmalle tutkimukselle oli, koska lajin jäänteet säilyvät hyvin järvien sedimentissä ja niitä voidaan käyttää paleoekologissa tutkimuksissa. Lisäksi lämpötilan on osoitettu vaikuttavan sukupuolen määräytymiseen vesieläimillä ja näin myös koiraat tulisi pystyä tunnistamaan. Tulosteni mukaan koiraat olivat pienempiä kuin naarat, mutta niiden raajat olivat rakenteeltaan paksummat. Koiraiden ruumista suojaava selkäkilpi sekä uintiin käytettävät takaruumiin päättävä kilpi (telson) ja sukaset olivat lyhyemmät kuin naaraalla. Kohtaamiset lajikumppanien kanssa voivat johtaa kannibalismiin, jota havaittiin sekä luonnossa että laboratoriossa. Koiraiden pieni koko voi vähentää saaliiksi joutumisen riskiä, kun saalistajana on näköaistinsa avulla saalistava lintu. Koiras voi hyötyä vahvoista jaloistaan naaraiden etsinnässä ja pitäessään naaraan paikoillaan parittelun aikana. Naaraan suurempi selkäkilpi antaa naaraille ja niiden munille suojaa saalistajilta. Nämä tulokset osoittivat, että koiraita esiintyy harvalukuisena osassa Huippuvuorten populaatioita. Naaraiden kannibalistinen käytös mahdollistaa nopean kasvun vähäravinteisissa arktisissa vesissä, joissa koiraita ei välttämättä tarvita lisääntymiseen.

Arktisen alueen luonnon monimuotoisuus muodostuu suurelta osin selkärangattomista eläimistä. Väitöskirjan neljännen osatyön (IV) tarkoitus oli selvittää, minkälainen on selkärangatonlajiston monimuotoisuus Barentsinmeren saariston alueella. Tarkasteltava Barentsinmeren tutkimusalue sisälsi kolme arktista aluetta: Huippuvuoret, Frans Joosefin maan ja Novaja Zemljan. Tutkimustulokset osoittivat, että Barentsinmeren saaristossa on monimuotoinen selkärangatonlajisto siitä huolimatta, että alueella vallitsee ankarat arktiset ympäristöolosuhteet ja saaret ovat vapautuneet mannerjäätikön alta hiljattain. Erilaiset kolonisaatiohistoriat selittävät todennäköisesti näiden arktisten tutkimussaarten lajistojen erilaisuuden. Eroja havaittiin erityisesti Huippuvuorten ja Novaja Zemljan välillä, mikä voi olla seurausta idästä tai lännestä saapuvista lajeista sekä alueellisista eroista jäätiköiden muodostumis- ja sulamisprosesseissa. Vuorenhuiput, jotka eivät olleet mannerjäätiköiden peitossa viime jääkaudella, saattoivat toimia äyriäisten turvapaikkoina kylmimpinä aikoina. Artikkelin tarkoitus oli myös osoittaa arktisen lajiston monitoroinnin merkitys. Monet arktiset alueet ovat tutkittu vain kerran eikä vertailukelpoisia näytteenottoja ole tehty Barentsinmeren saaristossa. Tämä on tärkeä huomioida arktisten alueiden biodiversiteetin tutkimuksen suunnittelussa niin, että resursseja kohdennetaan erityisesti pitkäaikaisseurantoihin sekä lajiston suojelutoimiin. Luonnon monimuotoisuuteen vaikuttavat ympäristötekijättekijät, kuten lämpötila ja veden määrä ja laatu ohjaavat voimakkaasti arktisten ekosysteemien toimintaa. Nopeasti etenevä ilmastonmuutos altistaa arktiset eliöyhteisöt oloille, jotka eivät ole niille optimaalisia ja aiheuttaa lajien taantumista ja jopa häviämistä. Erityisen tarkasti pitää seurata populaatioita, jotka esiintyvät levinneisyysalueensa rajoilla. Lajien päälevinneisyysalueeseen kohdistuvat pitkäaikaisseurannat ovat myös tärkeitä, koska esimerkiksi voimakas äyriäispopulaatioiden tiheyksien pieneneminen vaikuttaa muiden lajien selviytymiseen, ei pelkästään arktisella alueella, vaan myös todennäköisesti äyriäisiä käyttävien lintujen muuttoreittien varrella. On tärkeä ymmärtää, että muutosta ei voida havaita, mikäli arktisten alueiden biodiversiteettiä ei ole tutkittu.

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III

DESCRIPTION OF THE MALE *LEPIDURUS ARCTICUS* (BRANCHIOPODA: NOTOSTRACA) AND THE POTENTIAL ROLE OF CANNIBALISM IN DEFINING MALE FORM AND POPULATION SEX RATIO

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DESCRIPTION OF THE MALE *LEPIDURUS ARCTICUS* (BRANCHIOPODA: NOTOSTRACA) AND THE POTENTIAL ROLE OF CANNIBALISM IN DEFINING MALE FORM AND POPULATION SEX RATIO

Hanna-Kaisa Lakka *

Department of Environmental Sciences, University of Helsinki, Niemenkatu 73, 15140 Lahti, Finland

ABSTRACT

Sexual dimorphism in the Arctic tadpole shrimp, *Lepidurus arcticus* (Pallas, 1793), was examined. Selective forces shape sexes differently. Males fitness increases by successful mate searching, whereas females increase reproductive potential by attaining large sizes. Sexual dimorphism was examined in 331 *L. arcticus* from Svalbard, Norway. Males were significantly smaller than females and had significantly smaller carapaces, telsons and cercopods. *Lepidurus arcticus* is an omnivorous, sometimes cannibalistic, predator. Cannibalism potential effects on sexual dimorphism were studied in the field and laboratory. Cannibalism frequency did not differ significantly between populations. Females dominated in all populations. Male *L. arcticus* searching for females are at greater risk due to increased chance of encounters with predators and cannibalistic females. Male small body size is advantageous against visually hunting predators, while more robust limbs help males search for females effectively and amplex them. In contrast, the significantly larger female carapace protects her and her eggs from predators.

KEY WORDS: body shape, carapace, reproductive anatomy, sexual size dimorphism, size cost and benefits, telson

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INTRODUCTION

Lepidurus arcticus (Pallas, 1793) is important ecologically as a predator and serving as prey for many breeding birds and economically important fish species (Borgstrøm et al., 1985; Jeppesen et al., 2001; Lakka, 2013; Järvinen et al., 2014). This species has specific environmental requirements; in particular clean, cold, alkaline freshwaters (Arnold, 1966; Fjellheim et al., 2001; Lakka, 2013). These requirements make this species ideal as an indicator of environmental change.

Lepidurus arcticus ranges across the Arctic region, including: Svalbard, Bear Island, Iceland, Greenland, Norway, Sweden, Finland, Russia, Alaska, and Canada (Blomkvist, 1995; Scher et al., 2000; Rogers, 2001; Hessen et al., 2004; Lakka, 2013; Järvinen et al., 2014); it has a fairly widespread distribution throughout the Svalbard Archipelago in the European High Arctic (Coulson, 2000). However, there are no previous records of the males of *L. arcticus* in Svalbard (Summerhayes and Elton, 1923; Halvorsen and Gullestad, 1976; Wojtasik and Brylka-Wolk, 2010). The males are rare (Longhurst, 1955), and only a few published papers provide information on males. Bushnell and Byron (1979) reported one such male on Baffin Island in the Canadian Arctic. Sayenko and Minakawa (1999) found four males in Kuril Island in the North Asia. Beton and Hebert (1988) reported 3.4% average proportion of males in four ponds in the Melville Peninsula in the Northwest Territories. However, in most cases, males have not been observed in Svalbard, East Greenland, Iceland, Finland, or the Barents Region of Russia (Koli, 1957; Arnold, 1966; Vekhoff, 1997; Scher et al., 2000; Wojtasik and Brylka-Wolk, 2010; Järvinen et al., 2014). The most recent genetic study shows that *L. arcticus* is capable of parthenogenesis and sexual reproduction (Wojtasik and Brylka-Wolk, 2010). The main morphological differences between males and females is that males lack brood pouches on the eleventh thoracopod pair. This specialized eleventh thoracopod pair appears when females reach a carapace length of 4-7 mm (Sømme, 1934; Arnold, 1966). Hence, the males resemble young females of the same length. Sars (1896) hypothesised that this similarity between sexes is the main reason why males have been so rarely reported. Bushnell and Byron (1979) noted that detailed morphological examinations of *L. arcticus* are difficult. These results suggest that there is a need for further detailed information about the rare males of this key environmental indicator species. Beaton and Hebert (1988) mentioned that further study is needed to establish geographical patterns in *L. arcticus*-sex ratios if such exist. Thus, the primary purpose of this paper is to provide and compare male and female morphology from Spitsbergen populations of *L. arcticus*.

The second purpose is to study the factors driving any potential sexual dimorphism in *L. arcticus*. Females are larger than males in many species of insects, spiders, fish, and some crustaceans such as *L. arcticus*. Females of many taxa are sedentary and sparsely distributed, thus males need to search for them. This is also the case in *L. arcticus*. Behavioural differences lead to radically different selection

* E-mail: hanna-kaisa.lakka@helsinki.fi

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pressures on the sexes. Vollrath and Parker (1992) argued that dwarf size in male spiders is associated with a difference in adult mortality between the sexes, where males suffer from a much higher predation risk during mate search than sedentary females. *Lepidurus arcticus* have both fish and bird predators (Summerhayes and Elton, 1923; Sømme, 1934; Borgstrøm et al., 1985; Jeppesen et al., 2001; Lakka, 2013; Järvinen et al., 2014), but intraspecific predation or cannibalism prevalence is not clear. Mouthpart structure and the first throacopod pair indicate that *L. arcticus* lives principally by preying on other crustaceans (Sars, 1896). Arnold (1966) reported that dead and injured *L. arcticus* individuals were rapidly eaten when 20-30 animals were kept in the same tank during an experiment. In the same study Arnold (1966) mentioned that when animals met in a tank, they rapidly moved away from each other. Similar evasive behaviour has been reported on the giant predatory fairy shrimp *Branchinecta raptor* (Rogers et al., 2006). Because cannibalism may explain the sedentary and retreating behaviour of *L. arcticus* females, cannibalism prevalence was studied.

Little is known concerning sexual dimorphism, sex ratios and cannibalism in *L. arcticus*. I investigated the sexual differences in Svalbard *L. arcticus* and examined potential factors that could cause these differences. This study focused on two main hypotheses: 1) external morphology measurements can be used to identify rare males; 2) cannibalism by females might explain sexual dimorphism, which can lead to biased female/male ratios.

Materials and Methods

Morphological Analyses

A total 21 males and 768 females of *L. arcticus* were collected from 19 ponds in six areas in the western and northern parts of Spitsbergen, in Svalbard, Norway (Fig. 1). The specific collections came from Mosselhavøya, Reindyrflya, Ny-Ålesund, Pyramiden, Longyearbyen, and Kapp Linné areas (78°-80°N, 10°-17°W). The sampling period was between 7 July and 6 September. The length of growing season and the water temperature data are given in Table 1. A more detailed description of the sampling sites can

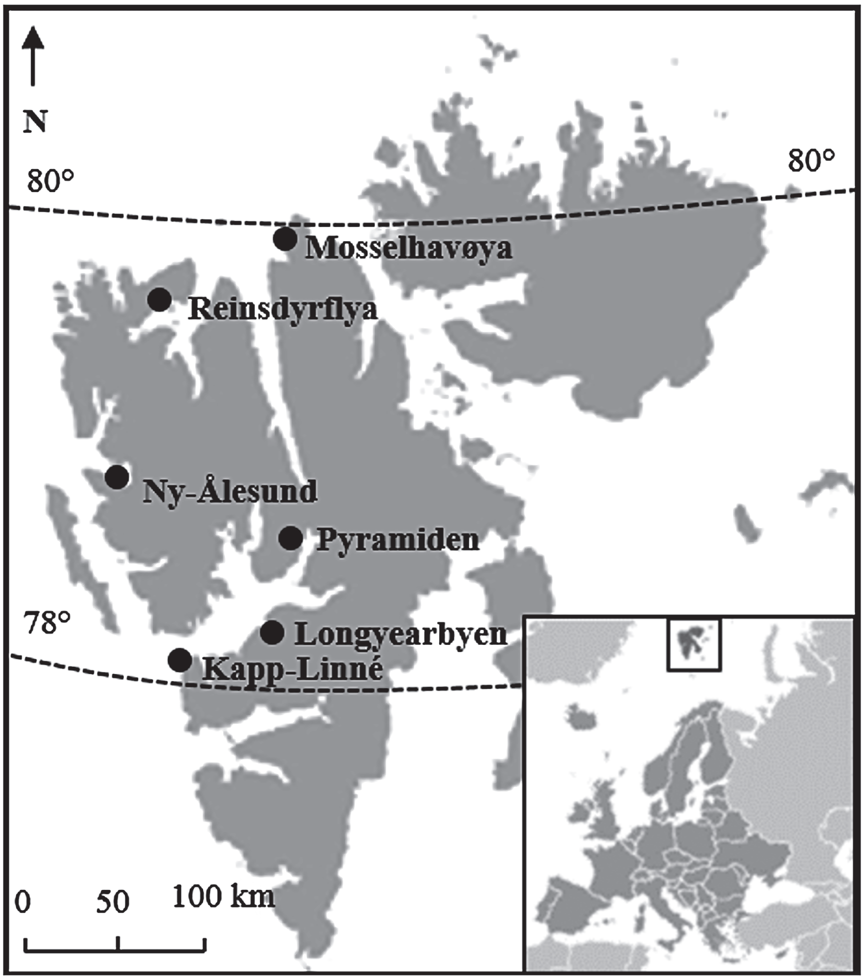

Fig. 1. Map of the study area.

Table 1. Length of the growing season and water temperatures in Svalbard based on the mapping of Karlsen et al. (2013), Karlsen et al. (2014) (*) and Lakka (2013) (●). N/A = value not available.

Area	Pond	Sampling date	Length of the growing season (months)*	Water temperature (°C)●
Mosselhavøya	Polheim	3 August	N/A	5.1
Reinsdyrflya	Kilneset	4 August	>2	2.3
Ny-Ålesund	Solvatnet	6 August	>2	1.8
Ny-Ålesund	Solvatnet	31 August	>2	4.1
Ny-Ålesund	Tvillingvatnet	2 August	>2	4.5
Ny-Ålesund	Tvillingvatnet	7 August	>2	0.8
Ny-Ålesund	Storvatnet	8 August	>2	3.1
Ny-Ålesund	Storvatnet	1 September	>2	4.5
Ny-Ålesund	Trehyrdingen 1	8 August	>2	N/A
Ny-Ålesund	Trehyrdingen 1	1 September	>2	3.3
Ny-Ålesund	Trehyrdingen 2	1 September	>2	3.7
Ny-Ålesund	Kolhamna	9 August	>2	4.2
Ny-Ålesund	Brandallaguna	9 August	>2	N/A
Ny-Ålesund	Brandallaguna	1 September	>2	3.1
Pyramiden	Pond 5	16 July	2	3.1
Longyearbyen	Longyearyen	7 July	2	1
Longyearbyen	Dammyra	31 July	2	4.2
Longyearbyen	Adventalen 2	18 August	2	4.1
Longyearbyen	Adventalen 3	23 August	2	N/A
Longyearbyen	Nybyen	6 September	2	4.2
Kapp Linné	Pond 1	12 July	2	4.2
Kapp Linné	Pond 2	12 July	2	4.9
Kapp Linné	Pond 3	12 July	2	2.1
Kapp Linné	Pond 4	11 July	2	0.5

be found in Lakka (2013). *Lepidurus arcticus* were commonly found in shallow, soft bottom, fishless, lakes, and ponds.

The sampling was done with a tablespoon and a 500 μm mesh hand net. Most animals were sampled from shallow (<0.3 m deep) littoral zone with a tablespoon to avoid harming the animals. Only in two ponds (Solvatnet and Brandallaguna) were the animals living in deeper parts (0.3-1 m) of the ponds and then a hand net was used. The animals were preserved in 80% ethanol, later examined under a stereomicroscope at 6× magnification, and measured to the nearest 0.1 mm. After preservation there were no changes in the body dimensions, e.g., shrinking of soft body parts. *Lepidurus arcticus* can shrink up to 15% in total length when animals are placed in ethanol (Järvinen et al., 2014). Shrinkage takes place in the body segments, not in the carapace, last segment of the abdomen (the telson), or cercopods. The following parameters were measured (Fig. 2): length and width of carapace (CL and CW), total body length (^{tot}L), abdomen length (AL) from carapace to the end of telson constriction, length of intact cercopods (CP), length of telson (T), and number of posterior segments not covered by the carapace (PS). The ratios of CL/T, CL/AL, CL/CW, CL/CP, CW/T, AL/T, CP/T, ^{tot}L/CL, ^{tot}L/CW, ^{tot}L/T, ^{tot}L/AL, ^{tot}L/CP and T/one body segment size were calculated from each individual. The carapace area was also calculated and the number of eggs was counted. The size of one body segment was calculated using the formula (AL-(T/3))/PS and carapace area was calculated using the formula ((CL/2) × (CW/2)) × 2. The formula that was used to estimate the surface area of carapace does not give an exact carapace area but is a broad estimate of how widely the carapace covers the animal body (Fig. 2). To study the external morphology of *L. arcticus*, 21 males and 310 of the females belonging to the same size class were selected. These animals were 4.5-23.6 mm in total length (^{tot}L) and 2.7-7.8 mm in carapace length (CL). Sexual differences were visible in small animals from Svalbard. The end of the juvenile stage (the size when the animal started carrying eggs) occurred at the carapace length of ⩾4 mm in Svalbard (Lakka, 2013) and sexual characteristics (brood pouches and shape of supra-anal plate) were visible in small animals. Animals of uncertain sex were not used in the analysis.

To evaluate the reliability of sexually dimorphic characters, the morphological measurements and comparisons were done in groups: one including only small animals (CL = 2.7-4.2 mm, 12 males and 57 females), one including animals of all size classes from one population (i.e., CL = 4.7-11.7 mm, five males and 28 females, 18 without eggs, from Brandallaguna pond). The first instance was used to determine if the observed morphological differences were already present in small animals. The second instance was used to determine if morphological differences between males and females remained the same in a single population. Thus, the animals in the second analysis were in the same size range as the animals in the main morphological analysis.

Cannibalism Experiment

Specimens of *L. arcticus* were collected from Kapp Linné area on the western coast of Spitsbergen (78°04′N, 13°42′E), Svalbard, Norway. A total of 705 individuals were collected on 13-14 July 2010. In the laboratory, the animals were put into 250 ml containers filled with water from the collection site, each container having five animals. Small sized animals stayed at or near the water surface while the medium and large sized animals stayed at the bottom. Because of these behavioural differences, only animals of the similar size were used in the final experiment. Animals, all immature females with visible brood pouches but without eggs, were kept in a temperature controlled laboratory (air temperature 10-11°C) for two to three days, with constant day light mimicking the summer time midnight sun typical in the High Arctic regions. During the experiment, all water was changed every day before animals were fed with 3 ml of concentrated phytoplankton and zooplankton mixture. Animals were counted daily. Animal behaviour was noted every 24 hours. Animals were acclimated to the laboratory temperature for 24 hours. Before the actual experiment was started, all animals were fed with 1 ml of concentrated phytoplankton and zooplankton mixture.

The first experiment lasted for 48 hours. A total of 81 test containers with five animals in each (total = 405) were collected from four populations and used in the final experiment. All animals were immature females with their mean carapace length of 4.8 mm (SD 1.33) and a mean total length of 11 mm (SD 3.17).

The second experiment lasted for 72 hours with a total of 300 animals in 60 test containers. All were immature females with a mean carapace length of 4.9 mm (SD 1.07) and a mean total length of 11.4 (SD 2.37) mm.

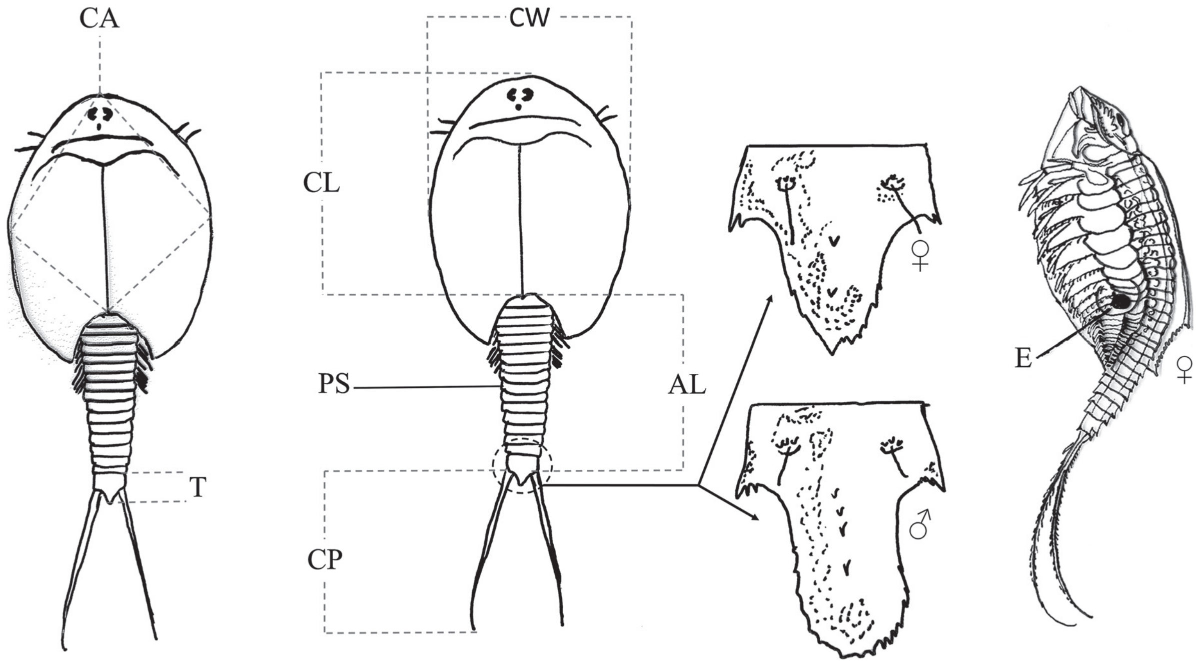

Fig. 2. *Lepidurus arcticus*. Examined morphological parameters, differences in supra-anal plates between females and males, and place of females' specialised 11th pair of legs (E). Last segment of abdomen (the telson) has a media extension, the supra-anal plate, between the two long cercopods. CA = area of carapace, T = length of telson, CW = carapace width, CL = carapace length, AL = length of abdomen from carapace to the end of telson constriction, CP = length of intact cercopod and PS = number of posterior segments not covered by the carapace.

Statistical Analyses

The statistical analyses were conducted with IBM SPSS Statistics 22 software. All variables were tested for normality. Differences in morphological variables were tested using Student's t-test or the Mann-Whitney U-test, if the homoscedasticity assumption for the parametric t-test was not met. Differences in cannibalistic behaviour between populations were tested using the Kruskal-Wallis test.

Results

Male Morphology

Males had stronger and more robust legs than females and had supra-anal plates broadly rounded (Figs. 2 and 3). Males were significantly smaller and had smaller telsons, body segments, and shorter cercopods than females (see Table A1 in the Appendix in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x; Table 2, Fig. 4). The number of posterior segments not covered by the carapace was 8-19 in males and 5-20 in females (mean for both sexes was 13).

Males had more compact and robust bodies than females. Males had more rounded carapaces than females shown by the significantly smaller CL/CW ratio, carapace width and length, and carapace area covering a significantly smaller amount of the body in males than in females (see Table A1 in the Appendix in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x; Table 2). Morphological differences were seen in the body part ratios. Males had significantly lower CP/T and ^{tot}L/CW ratios and significantly higher ^{tot}L/CP and CL/CP ratios than females (see Table A1 in the Appendix in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x; Table 2).

Morphological differences were evident in small males and females (CL = 2.7-4.2 mm). Males were significantly smaller and had shorter cercopods than females (see Tables A1 and A2 in the Appendix in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x). Small males and females showed similar morphological differences in body part ratios as the larger ones except that small males had also significantly lower ^{tot}L/CL ratios than females.

When all animals from the Brandallaguna-population were analysed (CL = 4.7-11.7 mm), only three significant differences were found between males and females. Males and females showed similar morphological differences in ^{tot}L/CP and CL/CP ratios as the Spitsbergen analysis except that males had also significantly higher CP/T ratios than females (see Tables A1 and A3 in the Appendix in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x).

When females with eggs were removed, so that the size range of the tested animals (CL = 4.7-7.3 mm) were same as the Spitsbergen and small animal analyses (CL = 2.7-7.8 mm), three significant differences were found between males and females. Males and females showed similar morphological differences in ^{tot}L/CP and CL/CP ratios as in the Spitsbergen-analysis except that males also had a significantly longer abdomen length

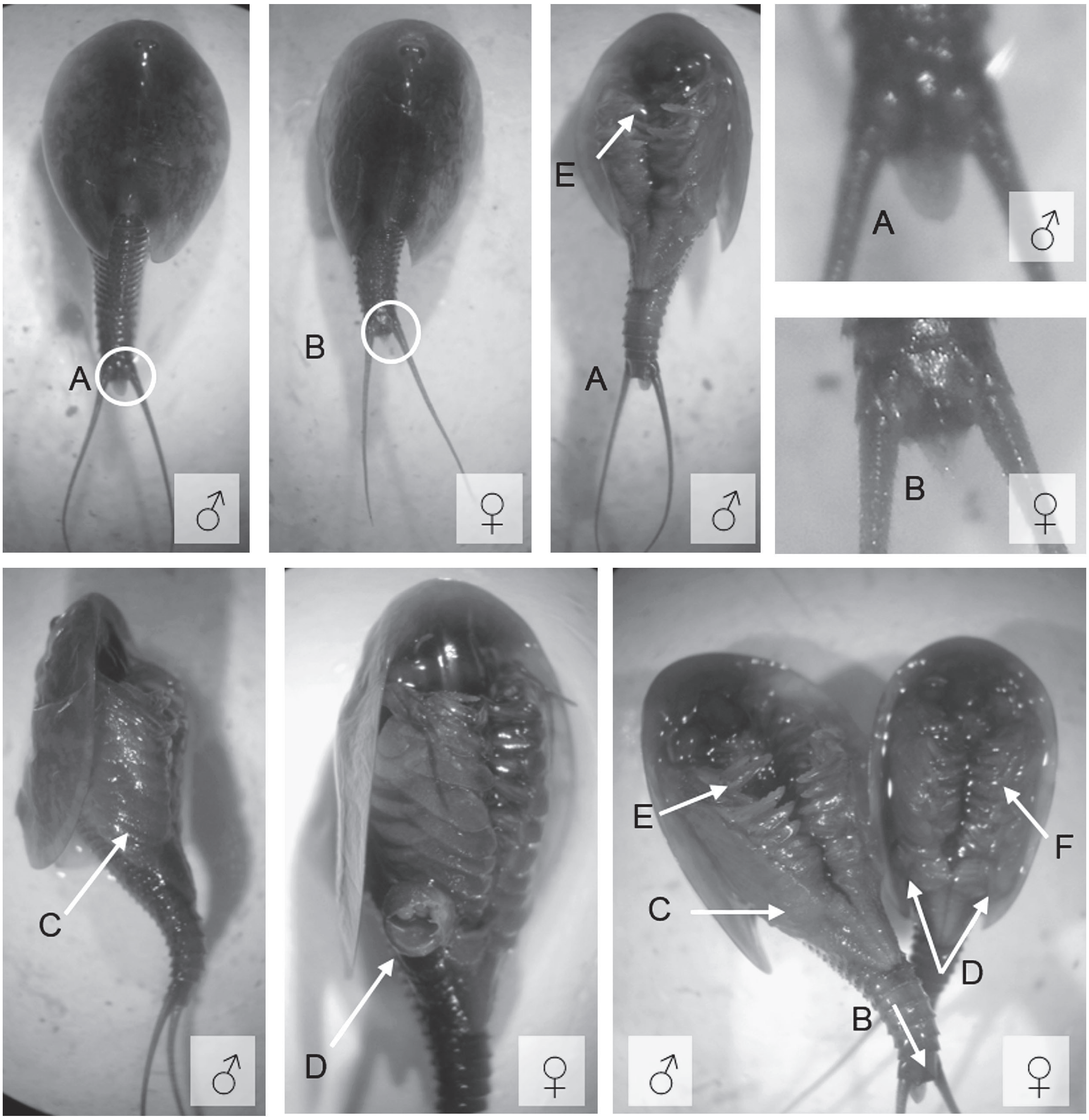

Fig. 3. *Lepidurus arcticus*. The main differences between males and females. A, males have a blunt and shovel-shaped; B, females have a small and sharp supra-anal plate; C, in the male, the structure of 11th pair of legs is the same as in the leg pairs immediately preceding and following it; D, the females have the specialized 11th pair of legs; E, males have stronger and more robust legs; F, females legs less robust.

than females (see Table A1 and A4 in the Appendix in the online version of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x).

The sex ratios in each of the 19 ponds at Svalbard where males were observed showed a strong female bias. The mean male/female ratio was 1/16 in the seven ponds where males were found (Table 3). However, the sex ratio varied widely, from 1/5.6 to 1/38 between the populations. A total of 21 males were found in seven ponds: from six ponds located on the western coast and from one pond on the northern coast of Spitsbergen (Table 3). Males were found between 11 July and 28 August. The majority of the males were found in mid July and in early August.

Lepidurus arcticus is clearly capable of cannibalism, as it was common in both experiments. There were no significant differences in cannibalism between the four tested populations (Kruskal-Wallis test: $p = 0.10$). Cannibalism was ob-

Table 2. *Lepidurus arcticus*. Morphological measurements (mean, minimum, maximum and standard deviation, SD) of males ($n = 21$) and females ($n = 310$) collected from Svalbard. The animals were 4.5-23.6 mm in total length and 2.7-7.8 mm in carapace length. The symbols ♂ and ♀ indicate which sex has the higher value. *Statistically significant difference ($p < 0.05$).

	Male				Female			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Total length (^{tot}L)	10.79*	5.00*	23.44*	4.71*	♀ 13.98*	4.46*	23.75*	4.01*
Carapace length (CL)	4.67*	2.66*	7.81*	1.71*	♀ 5.83*	2.00*	7.85*	1.40*
Carapace width (CW)	4.41*	2.31*	7.34*	1.50*	♀ 5.19*	1.85*	7.69*	1.15*
Carapace area	11.47*	3.32*	28.69*	7.70*	♀ 15.12*	1.85*	29.30*	6.578
Length of abdomen (AL)	1.89	0.78	6.88	1.46	♀ 3.13	0.92	7.038	1.45
Length of telson (T)	0.71*	0.46*	1.41*	0.30*	♀ 0.86*	0.31*	1.56	0.25*
Length of cercopod (CP)	2.71*	1.56*	8.75*	1.88*	♀ 5.02*	1.54*	9.38*	1.68*
1 segment size	0.18*	0.06*	0.34*	0.08*	♀ 0.22*	0.708	0.45*	0.07*
T/1 segment	♂ 4.37	1.93	8.25	1.41	4.12	1.73	8.08	0.90
CL/CW	♂ 1.06*	0.86*	1.27*	0.11*	1.12*	0.79*	1.55*	0.13*
CL/AL	2.12	1.07	3.40	0.74	♀ 2.18	0.78	6.17	0.92
CL/CP	♂ 1.43*	0.86*	2.18*	0.37*	1.22*	0.65*	2.63*	0.26*
CL/T	6.77	5.17	9.00	1.05	♀ 6.94	4.11	10.33	0.97
CW/T	♂ 6.45	4.75	9.00	1.21	6.12	4.14	9.67	0.97
AL/T	3.58	1.67	6.00	1.24	♀ 3.64	1.20	9.00	1.20
CP/T	4.97*	3.33*	6.67*	1.18*	♀ 5.85*	3.33*	6.67*	1.18*
$^{tot}L/CL$	2.28	1.78	3.10	0.34	♀ 2.39	1.76	3.73	0.32
$^{tot}L/CW$	2.41*	1.89*	3.20*	0.37*	♀ 2.68*	1.76*	3.75*	0.38*
$^{tot}L/T$	15.33	10.67	20.67	2.55	♀ 16.21	11.25	22.75	2.03
$^{tot}L/CP$	♂ 3.16*	2.52*	4.59*	0.51*	2.81*	2.15*	4.93*	0.39*
$^{tot}L/AL$	4.63	3.20	6.86	1.18	♀ 4.98	2.42	12.33	1.63

served in 85% of the test containers during the two day experiment (Fig. 5). In the three day experiment, cannibalism was observed in 85% of the test containers after the first 48 hours and in all the containers after the third day (Fig. 6). In the containers where cannibalism was observed at the beginning of the experiment, 1-3 individuals of *L. arcticus* were consumed per day (on average 1.1 animals in the first, 1.2 animals in the second and 1.1 animals on the third day). When observing the behaviour of all animals, the predation rate remained stable in the first two days but rose slightly on the third day. The mean predation rate of pond 1 population was 0.52 animals per day in the first day, 0.58 animals per day in the second day and 0.72 animals per day in the third day.

Discussion

This study confirms that males of *L. arcticus* are present at least in four areas around Svalbard and morphological measurements can be used to separate males from females. A total of 12 significant differences were observed between males and females of *L. arcticus* (Table 2 and Fig. 4).

The males have a significantly smaller carapace length, width, area and CL/CW ratio, which is useful as the hard carapace does not shrink in ethanol. Sømme (1934) reported a similar trend in carapace lengths of large *L. arcticus* as was observed in smaller animals in this study. On Bear Island, the average carapace lengths were 9.36 mm in males and 10.67 mm in females (Sømme, 1934), whereas in Svalbard they were 4.67 mm in males and 5.83 mm in females. Carapace length can be considered a reliable way to distinguish males from females in all size groups.

The increased mobility of males is supported by their significantly smaller carapace area and carapace length/width ratio. The round carapace enables males to move more freely and effectively than females. The male small carapace leaves room for the strong thoracopods and makes the males of agile and fast swimmer. Lakka (2013) demonstrated that these males use their powerful legs to amplex females. Amplexus in *Lepidurus* was first described by Sramek-Husek et al. (1962), described in the related spinicaudatan clam shrimp by Somorowska (1956), detailed for laevicaudatan clam shrimp by Sigvardt and Olesen (2014), and reviewed for anostracans by Rogers (2002). The males of *L. arcticus* could benefit from their greater swimming agility, especially if the females start to behave aggressively before or after the copulation.

In the Brandallaguna-population, the mean abdomen length was significantly higher in males (2.9 mm) than in females (2.3 mm). The longer abdomen of males might provide added strength for swimming and for making circular movements in the water column when *L. arcticus* hunt for *Daphnia* (Lakka, 2013). Nevertheless, in the whole population analysis, males did not have longer abdomens than females. In fact, body segment size was significantly smaller in males than in females in the whole population analysis. However, the possibility of morphological plasticity within the populations must be taken into account, because *L. arcticus* have two different haplotypes and they can co-occur in the same lake (Hessen et al., 2004). The smaller animals showed similar significant differences between males and females in a whole population analysis. The carapace length, the telson length and the total length were significantly smaller in males than females and these parameters are recommended to be used in separating small animals.

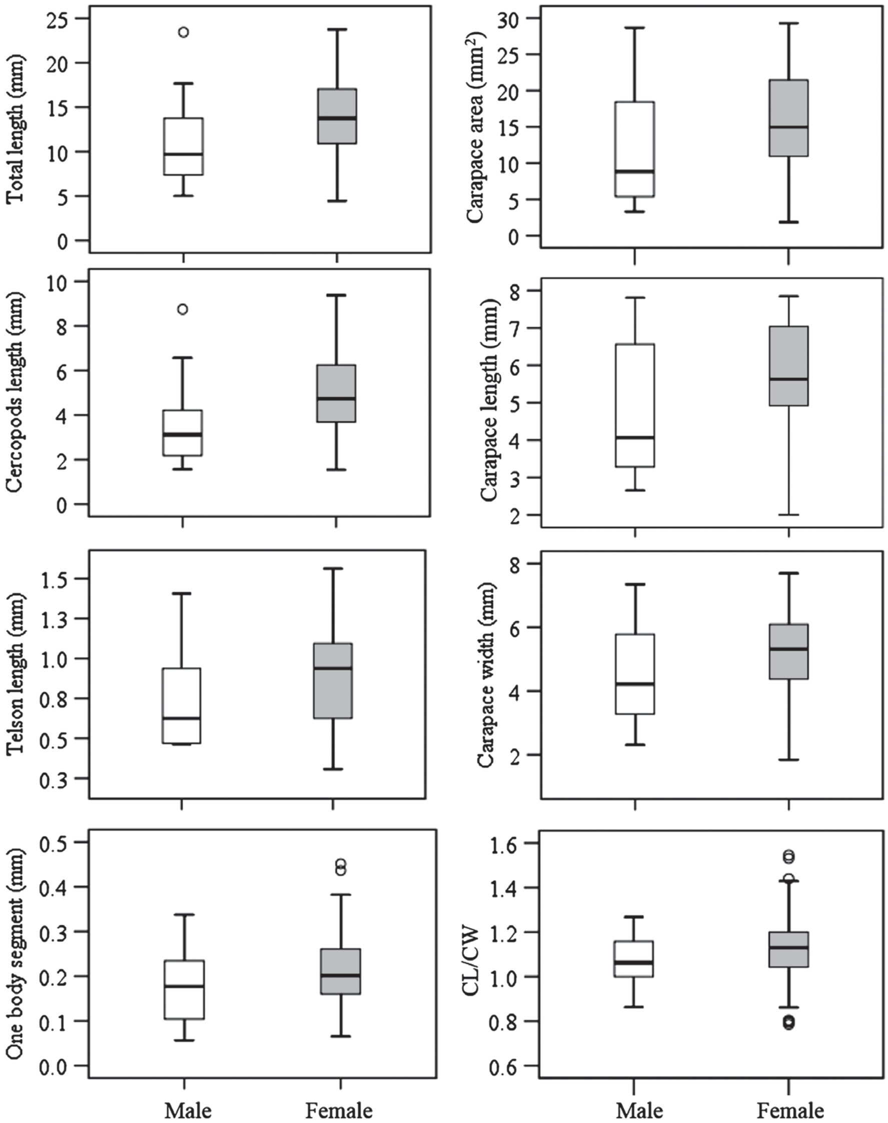

Fig. 4. *Lepidurus arcticus*. Box plots showing morphological differences between males ($n = 21$) and females ($n = 310$). Circles (○) indicate animals with exceptional morphology.

The supra-anal plate shape and telson size varied between males and females. The observations by Sømme (1934) of the broadly rounded supra-anal plate typical for the males seems to be true. The depictions of male supra-anal plate structure presented here (Figs. 2 and 3) are very similar to the previous drawings by Sømme (1934) and Longhurst (1955). In the Svalbard material, the telsons were significantly smaller in males than in females. However, in an earlier study by Sømme (1934), males had longer supra-anal plates than females in late autumn on Bear Island. The supra-anal plate length is approximately 2/3 of the telson length. It should be noted that most populations on Bear Island belong to a different haplotype than populations on Svalbard. Hessen et al. (2004) found that telsons were significantly smaller in the Svalbard-haplotype than in Bear Island-haplotype. Thus, it is important to know to which haplotype of *L. arcticus* one has before conducting morphological comparisons.

Sars (1896) showed that males are considerably smaller than females, and the same observation was made in this study. However, according to Sømme (1934) the males were larger in body size than females in late autumn in Bear Island. The males were 0.30 mm bigger in body size than females in Bear Island (Sømme, 1934) and the males were 3.19 mm smaller than females in Svalbard. Organisms can generally reach larger body sizes when the growing season is longer (Roff, 1992). Bear Island is located at 74°N, whereas in this study the northernmost sampling place was at 79°N.

Table 3. *Lepidurus arcticus*. Occurrence of males and females in 19 ponds sampled around Svalbard between July and September 2010.

Area	Pond	Date	Males	Females	Total
Kapp Linné	Pond 1	12 July 2010	2	40	42
Kapp Linné	Pond 2	12 July 2010	2	41	43
Kapp Linné	Pond 3	12 July 2010	5	29	34
Kapp Linné	Pond 4	11 July 2010	2	29	31
Reinsdyrflya	Kilneset	4 August 2010	4	35	39
Ny-Ålesund	Brandallaguuna	9 August 2010	5	28	33
Longyearbyen	Longyearbyen	28 August 2010	1	38	39
Pyramiden	Pond 5	16 July 2010	0	1	1
Longyearbyen	Dammyra	31 July 2010	0	12	12
Mosselhavøya	Polheim	3 August 2010	0	38	38
Ny-Ålesund	Solvatnet	6 August 2010	0	33	33
Ny-Ålesund	Tvillingvatnet	7 August 2010	0	33	33
Ny-Ålesund	Storvatnet	8 August 2010	0	33	33
Ny-Ålesund	Trehyrding 1	8 August 2010	0	32	32
Ny-Ålesund	Kolhamna	9 August 2010	0	43	43
Longyearbyen	Advent. 2	18 August 2010	0	33	33
Longyearbyen	Advent. 3	23 August 2010	0	36	36
Ny-Ålesund	Trehyrdingen 1	30 August 2010	0	28	28
Ny-Ålesund	Solvatnet	31 August 2010	0	32	32
Ny-Ålesund	Storvatnet	1 September 2010	0	42	42
Ny-Ålesund	Trehyrdingen 2	1 September 2010	0	37	37
Ny-Ålesund	Brandallaguna	1 September 2010	0	29	29
Ny-Ålesund	Tvillingvatnet	2 September 2010	0	35	35
Longyearbyen	Nybyen	6 September 2010	0	31	31

The length of growing season can vary notably between localities in Svalbard (Table 1). Consequently, the length of growing season can partly explain the observed differences in male sizes between Bear Island and Svalbard. There could be differences in hatching time between males and females, but this has not been explored, but it is unlikely because the growing season is short in Svalbard (Karlsen et al., 2013, 2014). It is also possible that the reported differences in total lengths and telson sizes between different haplotypes make the use of these parameters unreliable. However, the same haplotype (A1) that was found in Svalbard also occurs in Russia, in mainland Norway and at least in one population in Bear Island (Hessen et al., 2004). Because of the high genetic diversity of *L. arcticus* (Hessen et al., 2004) and obvious differences between haplotypes, more genetic analyses are needed to complement and explain the results of morphological studies.

It has been proven that fixation fluids can affect the size of soft tissues. Järvinen et al. (2014) demonstrated that fixation in ethanol causes shrinkage of the abdomen length by 15%. This is due to the fact that the animals contract their segments tightly together in ethanol. Sømme (1934)

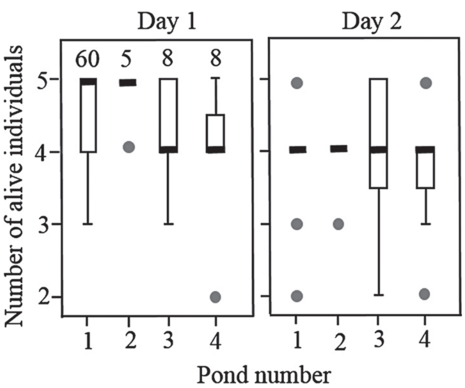

Fig. 5. Cannibalism of *Lepidurus arcticus* in 48 hour experiment. Total 405 *L. arcticus* individuals, 5 individuals per container and total 81 containers. In box plots, lines indicate medians, boxes show upper and lower quartiles and whiskers stand for the observed minimum and maximum values, with outliers shown by grey circles and number indicate number of containers.

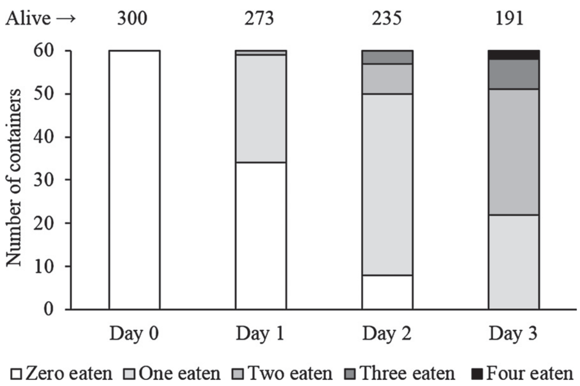

Fig. 6. The commonness of cannibalism of *Lepidurus arcticus* in an experiment where five animals were placed in a 250 ml container for three days and fed with 3 ml of concentrated phytoplankton and zooplankton mixture once per day. The total numbers of alive *L. arcticus* individuals are shown above each bar. The bar colours indicate what has happened in the 60 containers during the experiment.

assumed that the great variation in total lengths has been caused by different fixation fluids; formalin and alcohol. Thus, it would be important to use the same fixation fluid and compare the results to other studies where the same fixation method has been used. In recent studies with *L. arcticus*, researchers have mainly used ethanol (Hessen et al., 2004; Lakka, 2013; Järvinen et al., 2014) or measured live animals (Christoffersen, 2001).

The cercopod length was significantly smaller in males than in females. A broken cercopod can encumber swimming and hamper the return of the tadpole shrimp from the water surface back to the water column (Lakka, 2013). The body shape and structure support the active behaviour of males. The shorter cercopods of males might facilitate swimming longer distances, whereas the longer cercopods of females help in disengaging from the water surface tension.

The evidence reported here suggests that the carapace length is the most relevant taxonomic measurement for distinguishing males and females across the species' distribution region. However, it is recommended that in future studies the telson size, the cercopod length, the carapace width and the total length should be measured. All these morphological parameters were significantly smaller in males than in females in Svalbard-populations. The present morphological results give new knowledge that can be used in studies of old museum samples or in paleolimnological studies, both of which could use *L. arcticus* remains to evaluate the historical reproduction ecology of this Arctic keystone species.

Large body size and strength in males may be less advantageous when they are rare in a population, because then they do not have to fight with other males or protect eggs. Small males may also be better in escaping or avoiding cannibalism. Cannibalism might be a major force in structuring the populations of *L. arcticus*. Sexual cannibalism has been observed to be common in aggressive and hungry females, and it can increase hatching success (Berning et al., 2012). In the spider *Agelenopsis pensylvanica* (Koch, 1843), the egg case mass and the number of offspring is positively correlated in cannibalistic but not in noncannibalistic females (Berning et al., 2012). The cannibalistic behaviour could produce a fitness benefit for the cannibalistic females of *L. arcticus* in nutrient poor waters where the growing season is short. Cannibalism might represent one of the most extreme forms of sexual conflicts and thus could explain the low number of males in populations.

Lepidurus arcticus have three bird predators in Svalbard (Lakka, 2013): purple sandpiper, *Calidris maritima*; dunlin, *Calidris alpina*; and arctic tern, *Sterna paradisaea*. Purple sandpiper's eggs hatch in the beginning of July, and dunlins and artic terns hatch in the end of July (Kovacs and Lydersen, 2006a, b). It is probable that active notostracan males are more vulnerable to predation than sedentary and sparsely distributed females. Abonyi (1926) reported that the broader, flat, short, and rounded shell, and the smaller size of the males of *Triops cancriformis* (Bosc, 1801) than of females are probably due to the general mobility of the males. The males of *L. arcticus* have similar characteristics as *T. cancriformis*. The male anatomy supports a more active behaviour, but is not clear what causes the absence of males in late autumn. It might be possible that cannibalistic females or/and elevated predation pressure may cause the small number or absence of males in autumn. Sexual cannibalism may in a short term lower the initial male ratio in the population. However, this phenomenon has not been proven because in this study, cannibalism by males was not explored and cannibalism was only studied between females.

The females of *L. arcticus* were significantly larger than males in Svalbard. It has been shown that large individuals (>12.5 mm) are more effective in preying upon *Daphnia* sp. than the smaller ones (Christoffersen, 2001). The benefits of large body size are not only limited to more efficient foraging capacity, but also the number of eggs increases with increasing size (Lakka, 2013). Thus, natural selection might favour the larger body size of females than males. The females' large carapace can probably offer better protection against bird predators than the males' small carapace. Failed bird attacks can cause holes and cracks on the carapace (Lakka, 2013). Birds have been proven to be one of the dispersal vectors for large branchiopods (Brochet et al., 2010; Rogers, 2014). Consequently, females benefit from their larger body size in two ways: both foraging efficiency and reproductive capacity rise. Also the females' large carapaces give better protection against the predators' attacks.

Differences in male and female behavioural patterns can explain the low 1/16 male/female ratio. The active males may be more vulnerable to predation than stationary females. The observed cannibalistic behaviour of females might increase the mortality rate of already rare males. It might be possible that the whole population size is reduced through cannibalism on females in dense populations.

One remarkable result was the occurrence of the males of *L. arcticus* very far North (79°N, 13°W) and the presence of males in the study sites at the beginning of July or August. However, males have not been observed later in autumn in Svalbard (Table 3). Males comprised a mean of 9.4% of the whole population in Svalbard. Males were more common in Svalbard populations than previously reported in the Canadian Melville Peninsula (3.4%, Beaton and Hebert, 1988), and Baffin Island (0.9%; Bushnell and Byron, 1979) and the Russian Kuril Archipelago (7.1%; Sayenko and Minakawa, 1999). The low number of males in the present and previous surveys may be due to males being significantly smaller in body size than females. The 23% smaller male body size in early and middle summer may protect them against visually hunting predators as well as against a scientist trying to capture them using different kinds of nets, a large beaker or a tablespoon. Nevertheless, males have the potential to grow larger than females (Sømme, 1934). The males in Bear Island collected by Sømme (1934) were bigger than females and thus easier to detect. Despite this, males have not been observed in September in Svalbard. Sømme (1934) suggested that bathymetric distribution of two sexes may explain why males are so rarely found: females occupied shallow water, whereas males stayed in deeper waters if they were present. This hypothesis by Sømme (1934) may be correct if the small males can avoid cannibalistic predation by immature females. However, more studies are needed to show bathymetric distribution and the male ability to avoid cannibalistic females.

Populations of *L. arcticus* lacking males are commonly observed, but based on the genetic studies by Wojtasik and Brylka-Wolk (2010) in Svalbard, males seem to participate in reproduction. The authors did not observe males, but hypothesised that low numbers of males are present, or males do not occur every year. Previous studies by Sømme (1934) suggest that the first eggs are probably produced parthenogenetically, whereas the later eggs may be sexually produced. However, males were only found in late autumn (2 September) on Bear Island, whereas in this study the males were found earlier, between 12 July and 28 August. The new results suggest that in *L. arcticus*, sexual reproduction might be possible in the early and middle part of the season. Sexually reproducing populations probably have a wider niche than asexual populations. The rapid climate variations in the High Arctic, including increasing temperatures in surface waters and air temperatures in Svalbard (Holm et al., 2011), could favour sexual reproduction of populations. Even small changes in relatively stable High Arctic environment may favour sexual reproduction of *L. arcticus*.

More data is required before any final conclusions can be drawn concerning the geographical distribution of sex ratios in *L. arctius*. Wojtasik and Brylka-Wolk (2010) stated that male reproduction participation is probable in southern Svalbard, as is also supported by this study. The broad occurrence of males indicates that sexual reproduction is the normal mode of reproduction in High Arctic ponds in Svalbard.

The predation rates on *Daphnia* have been shown to be size dependent: significantly higher predation efficiency was observed in larger animals than in smaller individuals (Christoffersen, 2001). Nevertheless, aggressive behaviour is not always size dependent, because a smaller *L. arcticus* can attack a larger conspecific (Lakka, 2013). Similar results were reported by Berning et al. (2012). The observations of cannibalistic behaviour in nature indicate that *L. arcticus* can supplement their diet by preying on other conspecifics. This aggressive predation enables *L. arcticus* to grow continuously throughout the short growing season of the Arctic.

It should be noted that the selected study setting did not give any escape possibilities for the prey and the amount of food provided may have been insufficient. Straszynski (1992) used 1-2 ml of particulate organic matter from a pond to feed one *L. arcticus*. Starvation could change the normal behaviour. The animals' density in the 250 ml test container did not correspond to the natural density of *L. arcticus* in Kapp Linne region, which varied between 2-18 individuals per square meter (Lakka, 2013). The test setting was probably stressful for females; *Lepidurus arcticus* need at least 0.06 m^2 living space without conspecifics (Lakka, 2013). Arnold (1966) showed that evasive behaviour to avoid cannibalistic conspecifics was common in the laboratory, as was observed in this study. The frequency of cannibalism could partly explain the sedentary behaviour of *L. arcticus*. Spatial segregation between predator and prey is probably the most important factor allowing coexistence (Christoffersen, 2001). Secondly, the lack of available food in nature may also explain the sedentary behaviour. Arctic ponds are ultraoligotrophic in Svalbard (Lakka, 2013). In nutrient poor waters, where a limited amount of food is available, an optimal foraging strategy would be to feed on as many food items as possible (Christoffersen, 2001). The generalist *L. arcticus* has evidently adapted to feed on different types of food (Sars, 1896; Sømme, 1934; Arnold, 1966; Einarsson, 1979; Miller, 1980; Christoffersen, 2001) and may supplement its diet with conspecifics.

Lepidurus arcticus is an indicator species of environmental change (Lakka, 2013). New studies are important for conservation across its range. *Lepidurus arcticus* is a Red List species; it is under threat due to immigration of beetles such as *Dytiscus* sp. (Järvinen et al., 2014) and the minnow *Phoxinus phoxinus* (Borgstrøm et al., 1985), extensive fish stocking (Tammie et al., 1999; Hessen et al., 2004), acidification (Fjellheim et al., 2001; Lakka, 2013), and climate change (Hessen et al., 2004; Lakka, 2013).

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APPENDIX

Table A1. Statistical comparisons of *Lepidurus arcticus* body proportions between males and females. The animals used in the tests were analysed in four groups. The first group contained all measured animals ($n = 331$). The animals were 4.5-23.6 mm in total length and 2.7-7.8 mm in carapace length. The second croup, case study one, contained 69 small animals (CL = $2.7 - 4.2$ mm). The third group, case study two 1/2, contained animals from only one population ($n = 30$). The fourth group, case study two 2/2, contained the same animals as the case study two 1/2, but females with eggs were excluded, leaving a total of 23 animals to be studied. *Statistically significant difference ($p < 0.05$).

Unit (mm or mm^2*)	All animals (♀ = 310, ♂ = 21)	Case study one: small animals (♀ = 57, ♂ = 12)	Case study two 1/2: one population (♀ = 25, ♂ = 5)	Case study two 2/2: one population (♀ = 18, ♂ = 5)
Total length (^{tot}L)	$U = 1833$, $p = 0.001$*	$t = -2.786$, $p = 0.007$*	$t = -1.026$, $p = 0.313$	$t = 0.779$, $p = 0.445$
Carapace length (CL)	$U = 1888$, $p = 0.001$*	$t = -2.062$, $p = 0.043$*	$t = -0.698$, $p = 0.491$	$t = 1.415$, $p = 0.172$
Carapace width (CW)	$U = 2225$, $p = 0.014$*	$t = -1.154$, $p = 0.253$	$t = -0.979$, $p = 0.335$	$t = 0.856$, $p = 0.402$
Carapace area*	$U = 2028$, $p = 0.003$*	$t = -1.594$, $p = 0.116$	$t = -0.899$, $p = 0.032$*	$t = 1.450$, $p = 0.162$
Length of abdomen (AL)	$U = 2448$, $p = 0.057$	$t = -1781$, $p = 0.078$	$t = 0.280$, $p = 0.782$	$t = 2.107$, $p = 0.047$*
Length of telson (T)	$U = 2102$, $p = 0.005$*	$U = 257$, $p = 0.158$	$t = -0.934$, $p = 0.357$	$U = 35$, $p = 0.431$
Length of cercopod (CP)	$U = 1629$, $p = 0.000$*	$t = -2.938$, $p = 0.005$*	$t = -1.932$, $p = 0.064$	$t = -1.598$, $p = 0.126$
1 segment size	$U = 2363$, $p = 0.0358$	$t = -0.910$, $p = 0.366$	$t = -0.844$, $p = 0.405$	$t = 0.468$, $p = 0.645$
T/1 segment	$U = 2922$, $p = 0.436$	$t = 1.415$, $p = 0.006$*	$t = -0.348$, $p = 0.730$	$t = -0.178$, $p = 0.860$
CL/CW	$U = 2315$, $p = 0.029$*	$t = -0.585$, $p = 0.560$	$t = 0.192$, $p = 0.849$	$t = 0.784$, $p = 0.287$
CL/AL	$U = 3234$, $p = 0.961$	$t = 1.536$, $p = 0.129$	$t = -1.157$, $p = 0.286$	$t = -1.371$, $p = 0.185$
CL/CP	$U = 2033$, $p = 0.004$*	$t = 2.680$, $p = 0.009$*	$t = 3.414$, $p = 0.002$*	$t = 2.838$, $p = 0.010$*
CL/T	$U = 2876$, $p = 0.374$	$U = 298$, $p = 0.493$	$t = 0.415$, $p = 0.681$	$t = 0.391$, $p = 0.758$
CW/T	$U = 2994$, $p = 0.542$	$t = -0.002$, $p = 0.998$	$t = 0.089$, $p = 0.929$	$t = -0.265$, $p = 0.794$
AL/T	$U = 3195$, $p = 0.888$	$t = -1.253$, $p = 0.214$	$t = 1.287$, $p = 0.208$	$t = 1.368$, $p = 0.186$
CP/T	$U = 1920$, $p = 0.001$*	$t = 0.002$, $p = 0.214$	$t = -2.097$, $p = 0.045$*	$t = -1.581$, $p = 0.130$
^{tot}L/CL	$t = -1.540$, $p = 0.125$	$t = -2.237$, $p = 0.029$*	$t = -1.137$, $p = 0.264$	$t = -0.761$, $p = 0.455$
^{tot}L/CW	$t = -3.141$, $p = 0.002$*	$U = 180$, $p = 0.009$*	$t = -0.622$, $p = 0.539$	$t = 0.156$, $p = 0.878$
^{tot}L/T	$U = 2491$, $p = 0.072$	$t = -1.728$, $p = 0.086$	$t = -0.217$, $p = 0.830$	$t = -0.014$, $p = 0.989$
^{tot}L/CP	$U = 2034$, $p = 0.004$*	$t = 1.914$, $p = 0.060$	$t = 4.284$, $p = 0.000$*	$t = 3.760$, $p = 0.044$*
^{tot}L/AB	$U = 2943$, $p = 0.465$	$t = -0.970$, $p = 0.333$	$t = -1.924$, $p = 0.064$	$t = -1.908$, $p = 0.070$

Table A2. Case study one: Sexual differences in small animals. Morphological measurements (mean, minimum, maximum and standard deviation, SD) for small *Lepidurus arcticus* males ($n = 12$) and females (57). The animals were 2.7-4.2 mm in carapace length. The symbols ♂ and ♀ indicate which sex has the higher value. *Statistically significant difference ($p < 0.05$).

Unit (mm or mm^2*)	Male				Female			
	Mean	Min	Mean	Min	Mean	Min	Mean	Min
Total length (^{tot}L)	7.51*	5.00*	10.78*	1.64*	♀ 8.74*	4.46*	10.94*	0.32*
Carapace length (CL)	3.38*	2.66*	4.22*	0.49*	♀ 3.69*	2.00*	4.22*	0.47*
Carapace width (CW)	3.29	2.31	4.53	0.71	♀ 3.49	1.85	4.53	0.52
Carapace area	5.70	3.32	8.90	2.03	♀ 6.52	1.85	9.56	1.52
Length of abdomen (AL)	1.71	0.78	3.13	0.73	♀ 2.06	0.92	3.54	0.59
Length of telson (T)	0.49	0.46	0.63	0.06	♀ 0.53	0.31	0.78	0.10
Length of cercopod (CP)	2.42*	1.56*	3.75*	0.69*	♀ 2.99*	1.54*	4.22*	0.60*
1 segment size	0.12	0.06	0.24	0.05	♀ 0.13	0.07	0.19	0.03
T/1 segment	♂ 4.62*	1.93*	8.25*	1.74*	4.13*	2.67*	7.20*	0.92*
CL/CW	1.04	0.86	1.27	0.11	♀ 1.07	0.79	1.42	0.12
CL/AL	♂ 2.25	1.25	3.40	0.79	1.93	1.09	4.17	0.62
CL/CP	♂ 1.46*	1.04*	1.90*	0.26*	1.27*	0.96*	2.09*	0.22*
CL/T	6.87	5.67	9.00	1.06	♀ 7.03	5.25	9.50	1.06
CW/T	6.68	5.00	9.00	1.33	♀ 6.68	4.75	9.67	1.15
AL/T	3.48	1.67	6.00	1.39	♀ 3.90	1.75	6.33	0.98
CP/T	4.88*	3.33*	6.67*	1.16*	♀ 5.70*	2.75*	8.33*	1.14*
^{tot}L/CL	2.21	1.88	2.76	0.26	♀ 2.37	1.76	2.37	0.22
^{tot}L/CW	2.30*	1.89*	3.20*	0.33*	♀ 2.52*	1.76*	3.16*	0.30*
^{tot}L/T	15.24	10.67	20.67	2.94	♀ 16.65	11.25	22.33	2.48
^{tot}L/CP	♂ 3.18	2.55	3.65	0.38	2.97	2.41	4.09	0.33
^{tot}L/AL	♂ 4.81	3.20	6.86	1.34	4.46	3.04	7.57	1.02

Table A3. Case study two 1/2: Sexual differences within a population. Morphological measurements (mean, minimum, maximum and standard deviation, SD) of *Lepidurus arcticus* males ($n = 5$) and females ($n = 28$) collected from Brandallaguna pond. The animals were 9.2-24.5 mm in total length and 4.7-11.7 mm in carapace length. The symbols ♂ and ♀ indicate which sex has the higher value. Statistically significant difference ($p < 0.05$).

Unit (mm or mm^{2}*)	Male				Female			
	Mean	Min	Max	SD	Mean	Min	Max	SD
Total length (^{tot}L)	13.84	10.94	17.66	2.50	♀ 16.05	9.22	24.53	4.66
Carapace length (CL)	6.47	4.84	7.34	0.97	♀ 7.07	4.69	11.72	1.85
Carapace width (CW)	5.63	4.53	6.09	0.64	♀ 6.18	4.22	9.06	1.23
Carapace area*	18.43	10.97	22.38	4.39	♀ 22.85	10.55	53.10	10.73
Length of abdomen (AL)	♂ 2.94*	2.19*	4.06*	0.85*	2.81*	1.25*	4.84*	0.93*
Length of telson (T)	0.91	0.63	1.09	0.17	♀ 1.03	0.47	1.56	0.27
Length of cercopod (CP)	4.44	3.28	6.25	1.11	♀ 6.45	3.91	11.72	2.25
1 segment size	0.23	0.16	0.27	0.04	♀ 0.26	0.16	0.44	0.07
T/1 segment	3.96	3.50	4.77	0.49	♀ 4.12	1.62	6.43	1.01
CL/CW	♂ 1.15	1.07	1.22	0.07	1.14	0.89	1.30	0.13
CL/AL	2.31	1.81	3.21	0.58	♀ 2.64	1.68	4.00	0.59
CL/CP	♂ 1.51*	1.18*	2.14*	0.38*	1.13*	0.77*	2.14*	0.27*
CL/T	♂ 7.22	5.17	11.67	0.75	6.99	5.17	11.67	1.16
CW/T	♂ 6.30	5.57	7.25	0.63	6.24	4.50	11.67	1.35
AL/T	♂ 3.29	2.33	4.33	0.88	2.79	1.33	4.67	0.78
CP/T	5.01	3.50	6.67	1.38	♀ 6.34	4.86	10.00	1.28
^{tot}L/CL	2.15	1.78	2.40	0.23	♀ 2.26	1.80	2.67	0.21
^{tot}L/CW	2.46	2.16	2.90	0.29	♀ 2.57	1.84	3.44	0.40
^{tot}L/T	15.51	12.57	18.83	2.57	♀ 15.82	11.67	26.33	2.94
^{tot}L/CP	♂ 3.18*	2.80*	3.81*	0.43*	2.57*	2.07*	3.08*	0.26*
^{tot}L/AL	4.85	4.00	5.71	0.68	♀ 5.93	3.93	8.78	1.21

Table A4. Case study two 2/2: Sexual differences within a population. Morphological measurements (mean, minimum, maximum and standard deviation, SD) of *Lepidurus arcticus* males ($n = 5$) and immature females ($n = 18$) collected from Brandalaguna pond. The animals were 9.2-17.7 mm in total length and 4.7-7.3 mm in carapace length. The symbols ♂ and ♀ indicate which sex has the higher value. *Statistically significant difference ($p < 0.05$).

Unit (mm or mm^{2}*)	Male				Female			
	Mean	Min	Mean	Min	Mean	Min	Mean	Min
Total length (^{tot}L)	♂ 13.84	10.94	17.66	2.50	13.05	9.22	15.94	1.89
Carapace length (CL)	♂ 6.47	4.84	7.34	0.97	5.89	4.69	7.34	0.76
Carapace width (CW)	♂ 5.63	4.53	6.09	0.64	5.39	4.22	6.25	0.51
Carapace area*	♂ 18.43	10.97	22.38	4.39	15.97	10.55	22.95	3.06
Length of abdomen (AL)	♂ 2.94*	2.19*	4.06*	0.85*	2.56*	1.25*	3.13*	0.58*
Length of telson (T)	♂ 0.91	0.63	1.09	0.17	0.86	0.47	1.09	0.14
Length of cercopod (CP)	4.44	3.28	6.25	1.11	♀ 5.07	3.91	6.41	0.67
1 segment size	♂ 0.23	0.16	0.27	0.04	0.22	0.16	0.29	0.04
T/1 segment	3.96	3.50	4.77	0.49	♀ 4.04	1.62	6.00	1.04
CL/CW	♂ 1.15	1.07	1.22	0.07	1.10	0.89	1.30	0.12
CL/AL	2.31	1.81	3.21	0.58	♀ 2.75	2.00	4.00	0.65
CL/CP	♂ 1.51*	1.18*	2.14*	0.38*	1.18*	1.00*	1.60*	0.17*
CL/T	♂ 7.22	5.17	11.67	0.75	7.02	5.17	11.67	1.35
CW/T	6.30	5.57	7.25	0.63	♀ 6.49	4.50	11.67	1.57
AL/T	♂ 3.29	2.33	4.33	0.88	2.70	1.33	4.67	0.83
CP/T	5.01	3.50	6.67	1.38	♀ 6.01	4.86	10.00	1.21
^{tot}L/CL	2.15	1.78	2.40	0.23	♀ 2.21	1.84	2.49	0.16
^{tot}L/CW	♂ 2.46	2.16	2.90	0.29	2.43	1.84	3.09	0.35
^{tot}L/T	15.51	12.57	18.83	2.57	♀ 15.53	11.67	26.33	3.24
^{tot}L/CP	♂ 3.18*	2.80*	3.81*	0.43*	2.63*	2.29*	3.08*	0.24*
^{tot}L/AB	4.85	4.00	5.71	0.68	♀ 6.06	3.93	8.78	1.35

IV

THE TERRESTRIAL AND FRESHWATER INVERTEBRATE BIODIVERSITY OF THE ARCHIPELAGOES OF THE BARENTS SEA; SVALBARD, FRANZ JOSEF LAND AND NOVAYA ZEMLYA

by

Stephen James Coulson, Peter Convey, Kjetil Aakra, Leif L. Aarvik, María Luisa Ávila-Jiménez, Anatoly Babenko, Elisabeth Machteld Biersma, Sven Bostrom, John E. Brittain, Anja Morven Carlsson, Kirsten S. Christoffersen, Willem H. de Smet, Torbjørn Ekrem, Arne Fjellberg, Leopold Füreder, Daniel Roland Gustafsson, Dariusz J. Gwiazdowicz, Lars Ove Hansen, Martin Holmstrup, Maurice Hullé, Łukasz Kaczmarek, Małgorzata Kolicka, Vadim V. Kuklin., Hanna-Kaisa Lakka, Natalia Lebedeva, Olga L. Makarova, Kristine Maraldo, Elena N. Melekhina, Frode Ødegaard, Hanne Eik Pilskog, Jean Christophe Simon, Björn Sohlenius, Torstein Solhøy, Geir E.E. Søli, Elisabeth Stur, Andrei V. Tanasevitch, Anastasia A. Taskaeva, Gaute Velle, Krzysztof Zawierucha and Katarzyna Zmudczyńska-Skarbek.
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Review paper

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

S.J. Coulson [a,*], P. Convey [b], K. Aakra [c], L. Aarvik [d], M.L. Ávila-Jiménez [a], A. Babenko [e], E.M. Biersma [b], S. Boström [f], J.E. Brittain [d], A.M. Carlsson [a,g], K. Christoffersen [h], W.H. De Smet [i], T. Ekrem [j], A. Fjellberg [k], L. Füreder [l], D. Gustafsson [m], D.J. Gwiazdowicz [n], L.O. Hansen [d], M. Holmstrup [o], M. Hullé [p], Ł. Kaczmarek [q], M. Kolicka [q], V. Kuklin [r], H.-K. Lakka [s], N. Lebedeva [t], O. Makarova [e], K. Maraldo [u], E. Melekhina [v], F. Ødegaard [w], H.E. Pilskog [a,x], J.C. Simon [p], B. Sohlenius [f], T. Solhøy [y], G. Søli [d], E. Stur [j], A. Tanasevitch [z], A. Taskaeva [v], G. Velle [aa], K. Zawierucha [q], K. Zmudczyńska-Skarbek [ab]

[a] Department of Arctic Biology, University Centre in Svalbard, P.O. Box 156, 9171 Longyearbyen, Svalbard, Norway
[b] British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK
[c] Midt-Troms Museum, Pb. 1080, Meieriveien 11, 9050 Storsteinnes, Norway
[d] University of Oslo, Natural History Museum, Department of Zoology, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway
[e] Institute of Ecology and Evolution, Russian Academy of Sciences, Leninski pr., 33, Moscow 119071, Russia
[f] Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden
[g] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK
[h] Freshwater Biological Laboratory & Polar Science Center, University of Copenhagen, Universitetsparken 4, DK-2100 Copenhagen Ø, Denmark
[i] University of Antwerp, Campus Drei Eiken, ECOBE Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium
[j] Department of Natural History, NTNU University Museum, NO-7491 Trondheim, Norway
[k] Mageroveien 168, 3145 Tjøme, Norway
[l] Faculty for Biology, Technikerstraße 15, Universität Innsbruck, Innrain, 52, A-6020 Innsbruck, Austria
[m] Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112, USA
[n] Poznan University of Life Sciences, Department of Forest Protection, Wojska Polskiego 71, 60-625 Poznań, Poland
[o] Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark
[p] UMR 1349 INRA/Agrocampus, Ouest/Université Rennes, 1, Institut de Génétique, Environnement et Protection des Plantes (IGEPP), Domaine de la Motte, 35653 Le Rheu Cedex, France
[q] Department of Animal Taxonomy and Ecology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland
[r] Murmansk Marine Biological Institute, Russian Academy of Sciences, Vladimirskaya St. 17, 183010 Murmansk, Russia
[s] Department of Environmental Sciences, University of Helsinki, Niemenkatu 73, 15140 Lahti, Finland
[t] Southern Scientific Centre, Russian Academy of Sciences and Azov Branch Kola Scientific Centre, Russian Academy of Sciences, Chekhova 41, Rostov-on-Don 344006, Russia
[u] Aarhus University, Department of Agroecology, Blichers Allé, DK-8230 Tjele, Denmark
[v] Institute of Biology of Komi Scientific Centre of the Ural Branch of the Russian Academy of Sciences, Kommunisticheskaja, 28, Syktyvkar, Russia
[w] Norwegian Institute for Nature Research, P.O. Box 5685 Sluppen, NO-7485 Trondheim, Norway
[x] Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Aas, Norway
[y] EECRG, Institute for Biology, Universitety of Bergen, P.O. Box 7820, N-5020 Bergen, Norway
[z] Centre for Forest Ecology and Production, Russian Academy of Sciences, Profsoyuznaya Str., 84/32, Moscow 117997, Russia
[aa] Uni Environment, Uni Research, Thormøhlensgate 49b, 5006 Bergen, Norway
[ab] Department of Vertebrate Ecology and Zoology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland

* Corresponding author. Tel.: +47 79 02 33 34.
E-mail addresses: Steve.coulson@unis.no, sjcoulson1@gmail.com (S.J. Coulson), pcon@bas.ac.uk (P. Convey), kjetil.aakra@mtmu.no (K. Aakra), leif.aarvik@nhm.uio.no (L. Aarvik), mlavilaj@gmail.com (M.L. Ávila-Jiménez), lsdc@mail.ru (A. Babenko), elisebiersma@gmail.com (E.M. Biersma), Sven.Bostrom@nrm.se (S. Boström), j.e.brittain@nhm.uio.no (J.E. Brittain), anjamorven@gmail.com (A.M. Carlsson), kchristoffersen@bio.ku.dk (K. Christoffersen), willem.desmet@ua.ac.be (W.H. De Smet), torbjorn.ekrem@ntnu.no (T. Ekrem), arnecoll@gmail.com (A. Fjellberg), Leopold.Fuereder@uibk.ac.at (L. Füreder), kotatsu.no.leo@gmail.com (D. Gustafsson), dagwiazd@au.poznan.pl (D.J. Gwiazdowicz), l.o.hansen@nhm.uio.no (L.O. Hansen), mho@dmu.dk (M. Holmstrup), maurice.hulle@rennes.inra.fr (M. Hullé), kaczmar@amu.edu.pl (Ł. Kaczmarek), malgorzata.kolicka@gmail.com (M. Kolicka), VV_Kuklin@mail.ru (V. Kuklin), hanna-kaisa.lakka@helsinki.fi (H.-K. Lakka), bird_happy@mail.ru (N. Lebedeva), ol_makarova@mail.ru (O. Makarova), kmaraldo@hotmail.com (K. Maraldo), melekhina@ib.komisc.ru (E. Melekhina), frode.odegaard@nina.no (F. Ødegaard), hanne.pilskog@umb.no (H.E. Pilskog), Jean-Christophe.Simon@rennes.inra.fr (J.C. Simon), bjorn.sohlenius@nrm.se (B. Sohlenius), geir.soli@nhm.uio.no (G. Søli), Elisabeth.Stur@ntnu.no (E. Stur), tanasevitch@gmail.com (A. Tanasevitch), taskaeva@ib.komisc.ru (A. Taskaeva), gaute.velle@uni.no (G. Velle), k.p.zawierucha@gmail.com (K. Zawierucha), biozmud@ug.ed.pl (K. Zmudczyńska-Skarbek).

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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 for the Earth 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 recolonising the Arctic following the retreat of the 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. But there is an obvious imbalance in our knowledge of many taxa 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 their 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.

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 the Svalbard archipelago currently contains over 1000 named species (Coulson and Refseth, 2004; Coulson, 2007a, 2013b).

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) and 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., 2012b). Just as with the uncertainties applying to Svalbard, the 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, 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 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) have highlighted the Svalbard archipelago as having perhaps the most complete inventory of the invertebrate fauna of any Arctic region (Hodkinson, 2013). 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, 2013). 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) 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.

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) and comprise a natural geographic unit. This is a region of convergence for the Palearctic and Nearctic biota re-colonising following the retreat of the ice. Svalbard is defined as the land area lying within the coordinates of 10° and 35°E and 74° and 81°N, and consists of five main islands, Spitsbergen, Nordaustlandet, Edgeøya and Barentsøya, and 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° and 77°N and 51° to 69°E (Fig. 3). The main islands stretch almost 900 km along a north–east 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

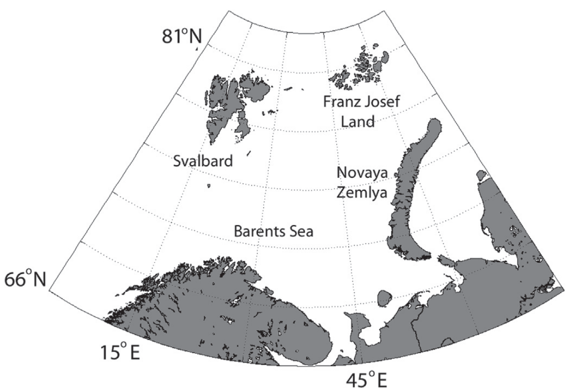

Fig. 1. The location of the three archipelagoes surrounding the Barents Sea: Svalbard, Franz Josef Land and Novaya Zemlya.

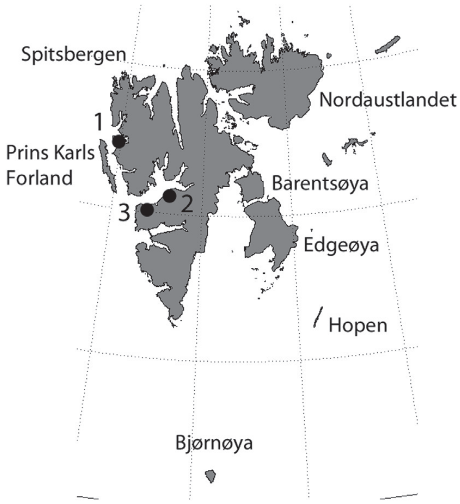

Fig. 2. The Svalbard archipelago with the locations discussed in the text indicated: 1 Ny-Ålesund; 2 Longyearbyen; 3 Barentsburg.

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.

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 +1.6 °C 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 +5.2 °C), 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 west 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 (> +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 nine months of the year (Coulson et al., 1995).

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

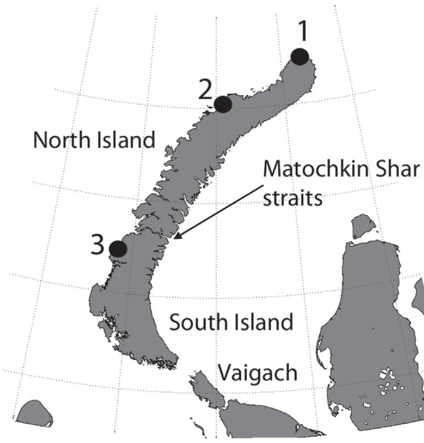

Fig. 3. Novaya Zemlya with locations discussed in the text indicated: 1 Ivanov Bay; 2 Archangelskaya Bay; 3 Bezymiannaya Bay.

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.

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 vascular plants may start to senesce from late July to mid-August (Cooper et al., 2011). 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 example 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 Last Glacial Maximum (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; Ingólfsson and Landvik, 2013) becoming exposed progressively as the ice began to retreat. At approximately 14,800 cal yr 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 yr BP (13,000–12,500 ^{14}C yr BP), whereas the central fjord region became ice-free around 11,500–10,800 cal yr BP (Lehman and Forman, 1992; Mangerud et al., 1992). Towards the south, Bjørnøya was deglaciated at around 11,500 cal yr BP (Wohlfarth et al., 1995) and towards the east, Edgeøya, Barentsøya and Franz Josef Land were fully deglaciated at around 11,200 cal yr 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 reappeared from about 4000–3000 cal yr 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 2500–2000 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 1–4 °C warmer than today with retracted glaciers and snowfields (Lubinski et al., 1999; Forman et al., 2000). Reindeer (*Rangifer tarandus* L., 1758) have been absent in historical time in Franz Josef Land, but antlers dated to 6400–1300 cal yr BP suggest a viable population has existed previously and was possibly driven to extinction during a distinct glacial advance around 1000 cal yr BP (Forman et al., 2000).

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 the LGM *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 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 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). 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. 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 below −30 °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 centimetres thick, and overlie moraine debris, patterned ground or bedrock. In wetter areas, moss may develop into thick carpets or turfs some tens of centimetres 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 in Svalbard, 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 snow-melt 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 1–3 months) (Svenning et al., 2007; Vincent et al., 2008), 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 (Svalbard) (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).

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 invertebrate 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 holes).

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* (Müller, 1786) and *Keratella 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 1500 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, *Encentrum dieteri* (De Smet, 1995), *Encentrum 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 (freshwater and marine) 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) and, as a group, considered cosmopolitan (Balsamo et al., 2008).

Arctic Gastrotricha are extremely poorly known. No comprehensive studies have been conducted in the Svalbard archipelago. Scourfield (1897) but 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, 1883) found in algae on the snow. Menzel (1920) recorded four species, *A. nivalis*, *Dorylaimus* sp., *Acrobeloides bütschlii* (de Man, 1884) Thorne, 1925 and *Plectus cirratus* Bastian, 1865. To date, the only extensive collection of terrestrial nematodes in Svalbard (specifically from Spitsbergen) was carried out by 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 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 (e.g., 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 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 per gram soil dry mass in Adventdalen and 119 nematodes per gram dry mass at Gluudneset (B. Sohlenius unpublished data), values are 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 (Loof, 1975; 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 (*R. tarandus platyrhynchus* Vrolik, 1829) 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, *Ostertagia gruhneri* Skrjabin, 1929 and *Marshallagia marshalli* (Ransom, 1907), represent 95% of the parasite population in adult reindeer of both sexes. *O. 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 8000 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. Larvae hatching from the deposited eggs develop into T3 infective stages and infect the next host the following season (Carlsson et al., 2012, 2013). 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. Faecal egg densities in the summer vary between 124 and 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). Surprisingly, *M. marshalli* is transmitted during the cold period 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* Phipps, 1774) 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), *Taenia polycantha* (Leucart, 1856), *Taenia 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). *E. 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). *M. benedina* is present in around 43% of Svalbard reindeer, a similar level of infection as observed in Greenland (Bye, 1985). *M. 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* Gunnerus, 1767) on Spitsbergen and *Microsomacanthus ductilus* (Linton, 1927) (a widespread parasite of gulls) is found in common eiders (*Somateria mollissima* (L. 1758)) and Brünnich's guillemots (*Uria lomvia* (L. 1758)) 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

Enchytraeid worms 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 on Spitsbergen 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 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 1167 described species (Degma et al., 2013; Vicente and Bertolani, 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 unfavourable 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) (according to Kaczmarek et al. (2008, 2012a) the taxonomic position of this species is uncertain). 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; Bernardová and Košnar, 2012; Kaczmarek et al., 2012b; Zawierucha et al., 2013). 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. (2012b) 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 (Fig. 2). Across all these studies, 92 tardigrade taxa have been reported although some older reports have not been verified based on modern taxonomy (e.g., Bertolani and Rebecchi, 1993; Claxton, 1998; Michalczyk and Kaczmarek, 2006; Fontoura and Pilato, 2007; Bertolani et al., 2011; Kaczmarek et al., 2011, 2012b; Michalczyk et al., 2012a,b). 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) published the first modern studies of Tardigrada from Novaya Zemlya, reporting 42 species. Biserov (1999) then reviewed the available knowledge of Novaya Zemlya tardigrades and also described three new species. 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; 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, *M. levis* (Krumpàl et al., 1991) and phoretic associations with Diptera (Gwiazdowicz and Coulson, 2010a).

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, 2013b; Coulson et al., 2013b). This diversity is comparable with that of other High Arctic sites such as Ellesmere Island and northern Taymyr (Makarova, 2013a). 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, 2010a).

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 4200 individuals m^{-2}, with the maximum density recorded being found in mossy vegetation near a colony of little auks (*A. alle*) (Seniczak and Plichta, 1978; Byzova et al., 1995). High density (1000–1840 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 (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; 2013b). 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, 2013b), 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 sea birds 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) since the tick overwinters in rock crevices at the nesting sites of its host. *I. 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, sea gulls and penguins. In the north Atlantic, ticks are most common on guillemots (*Uria aalge* (Pontoppidan, 1763), *U. lomvia*), black guillemot (*Cepphus grille* (L., 1758)), razorbill (*Alca torda* (L. 1758)), puffin (*Fratercula arctica* (L. 1758)) and herring gull (*Larus argentatus* Pontoppidan, 1763) (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 and 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 Oribatida from Svalbard appeared (e.g. Trouessart, 1895; Trägårdh, 1904; Hull, 1922; Summerhayes and Elton, 1923, 1928; Thor, 1930, 1934; Hammer, 1946). Additional reports during the past 50 years (e.g. 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 9168 and 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 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 *A. lineatus* (Thorell, 1871) (as *E. lineatus*), *C. borealis* (Thorell, 1871) (as *Nothrus borealis* (Thorell, 1871)) and *D. notatus* (Thorell, 1871) (as *O. notata*) from Novaya Zemlya. Further information on the oribatid mite 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; *H. reticulata* Thorell, 1871 and *Hermannia scabra* L. (Koch, 1879) Nordenskiöld were collected from the island of Vaigach (Fig. 3) which is not formally part of the Novaya Zemlya archipelago (Koch, 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 mites 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 listed from Svalbard by Bayartogtokh et al. (2011), only 36 (44%) were found in the tundra of the Kola Peninsula (Karppinen and Krivolutsky, 1982), 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* (Karppinen, 1967), *Oribatella arctica* (Thor, 1930), *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. Other taxa of Acari. Coulson and Refseth (2004) present 32 species names of Trombidiformes (Actinedida) from Svalbard. However, there are no recent published studies of this fauna and the concerns about taxonomic uncertainty expressed for the Oribatida must also be considered here. No information is available from Franz Josef Land and Novaya Zemlya concerning other taxa of Acari.

3.6.2. Araneae

Spiders are major invertebrate predators in virtually all terrestrial ecosystems (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 neighbouring parts of Russia, but there are three exceptions, *C. thulensis*, *Hilaira glacialis* (Thorell, 1871) and *M. 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* (Simon, 1884), *Collinsia holmgreni* (Thorell, 1871), *C. spetsbergensis, E. arctica palearctica, E. psychrophila, E. tirolensis, H. 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* L. Koch, 1869, *Collinsia borea* (L. Koch, 1979), *C. proletaria* (L. Koch, 1879), *Hybauchenidium aquilonare* (Koch, 1879), *Masikia indistincta* (Kulczynski, 1908), *Oreoneta leviceps* (Koch, 1879), *Praestigia groenlandica* Holm, 1967, 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. spetsbergensis* 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*) has 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* (L., 1761)) and one from two species of geese; barnacle (*Branta leucopsis* (Bechstein, 1803)) and pinkfoot (*Anser brachyrhynchus* Baillon, 1834) (Waterston, 1922a).

Holomenopon and the quill-boring *Actornithophilus* 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, Trichoptera and Plecoptera. No Plecoptera are known from Svalbard or Franz Josef Land, although three species of Plecoptera were recorded from Novaya Zemlya by Morten (1923): *Capnia vidua* (Klapálek, 1904), *C. zaicevi* (Klapálek, 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 (formerly listed as *A. svalbardicus* by 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*, and five migrant aphid species (*Aphis borealis* (Curtis, 1828), *Aphis* sp., *Cavariella salicis* (Monell, 1879), *C. abieticola* (Cholodkovsky, 1899) and *P. 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* L. (Strathdee et al., 1993), *S. calvulum* which feeds primarily on *Salix polaris* Wahlenb. but also on *Pedicularis hirsuta* L. (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. *S. calvulum* is restricted to only few sites on the west coast of Spitsbergen, namely Adventdalen and Colesdalen (Gillespie et al., 2007) and Grøndalen. *A. 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); 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. *S. 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. *A. 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. *S. 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 (in Kongsfjord close to Ny-Ålesund; Fig. 2) (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).

Table 1
Comparison of fauna and life histories of aphids in Svalbard with those of their temperate counterparts.

Svalbard aphid fauna	Temperate aphid fauna
2 (3) generations a year	12-20 generations per year
Apterae; none, or rare, winged forms	Massive production of winged forms (alates)
Cues for wing production unknown	Winged forms induced by crowding
Highly host-specialized species	Larger host spectrum
Obligate holocyclic lifecycle.	Facultative holocyclic life cycle.
Sexual forms produced when 24 h photoperiod	Sexual forms often induced by shortening day length
Biased sex ratios induced by local mate competition	Even sex ratios with rare exceptions

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* Chaubet and Tomanvić, 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* Tomanvić and Chaubet, 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's 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 collection 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. The majority 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 *Hydroporus acutangulus* (published as *H. sumakowi* Popp.). A major contribution was made by the Norwegian expedition to Novaya Zemlya in 1921 (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. 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. But, Vaigatsh is not geographically part of Novaya Zemlya (Fig. 3). Finally, according to Poppius (1910) and Münster (1925), *Tachinus apterus* (*Tachinus arcticus*) is found in Novaya Zemlya. *T. 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. Both *Boreostiba frigida* (J. Sahlberg, 1880) and *B. sibirica* (Mäklin, 1880) are recorded from Novaya Zemlya in Mäklin (1881) and Münster (1925). These two species where erroneously synonymised by Löbl and Smetana (2004), but Brundin (1940) showed that these are closely related good species.

In total, and incorporating updated taxonomy, there are 32 species of beetles known from Novaya Zemlya, 28 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*. But, as previously mentioned, the record *O. boreale* from Novaya Zemlya is probably incorrect.

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 (e.g. Coulson and Refseth, 2004) and biomass (e.g. 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 of which at least four are undescribed (Sæther and Spies, 2012; Ekrem and Stur, unpublised 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 (Kaisila, 1973a; Coulson et al., 2009; Pilskog, 2011). 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 (*S. mollissima*), barnacle goose (*B. leucopsis*), pink-foot goose (*A. brachyrhynchus*) and glaucous gull (*L. hyperboreus*) (Dampf, 1911; Pilskog, 2011) and has also been recorded in nests of snow bunting (*Plectrophenax nivalis* (L., 1758)) (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. *Mioctenopsylla a. arctica* is a host-specific flea only present on black-legged kittiwakes (*Rissa tridactyla* (L., 1758)) 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 may generally reduce breeding success in some species of bird including geese breeding in the Arctic such as Ross's, *Chen rossii* (Cassin, 1861) and lesser snow geese, *Chen caerulescens caerulescens* (L., 1758) (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, Svalbard (Pilskog, 2011). Although the bird fleas are known to bite humans (Mehl, 1992) 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), *Pyla 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 currently support the specific status of *P. polaris*. Ideally, molecular studies would be required to confirm the relationship between these two species. *A. 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). *P. fusca* 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 refers to *P. 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). *P. fusca* is a polyphagous species; *S. polaris* and *S. reticulata* (L.) are 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.

Novaya Zemlya has 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. No hymenopterans have yet been reported from Franz Josef Land, although since some vascular plants (e.g. *S. polaris*) and associated insects are present (Hanssen and Lid, 1932; Jong, 2011) it is plausible that they may occur.

3.8. *Freshwater ecosystems*

In polar regions freshwater ecosystems are intimately linked with their catchments. Perhaps here more than anywhere else there is a gradation, or grey area, between truly terrestrial and truly limnetic ecosystems. The underlying permafrost results in considerable surface flow during the spring melt (Pienitz et al., 2008) enhancing linkages and resulting in substantial nutrient input to freshwater systems from the surrounding terrestrial terrain (Van Geest et al., 2007; Rautio et al., 2011) and freshwater habitats are traditionally considered along with the terrestrial in polar regions.

3.8.1. *Biodiversity and ecosystem function in ponds and lakes*

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 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; *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°N) in the Novaya Zemlya archipelago (Fig. 3, Vekhoff, 1997). *L. 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). *L. 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). *L. arcticus* seems 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-Suszczewski, 1963; Hirvenoja, 1967; Section 3.7.2.5).

Five species of cestode are known to parasitize the Arctic char (*Salvelinius alpinus* (L., 1758)) 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* (Pontoppidan, 1763)) (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 mediated 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.

Despite their wide distribution, 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; Killingtveit et al., 2003; Krawczyk and Pettersson, 2007). 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-Suszczewski, 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 in Svalbard over the last 10–15 years (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). In general Chironomidae (especially the genus *Diamesa*) dominate in glacial systems whereas in non-glacial systems their 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). However, most species are similar to the nearby sub-Arctic areas as the coastal regions of the Barents Sea or more temperate areas. 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 glacier cover and the extent of nutrient input from bird cliffs or upstream lakes. Furthermore, a recent study of geothermal streams on Iceland (Woodward et al., 2010) demonstrated that water temperature is a key parameter among the factors directly affecting community structure and trophic interactions.

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 (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 (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

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 subfossils from Svalbard are recorded from Visdalen (Edgeøya) and dated to 14,700 ± 500 cal yr 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, *O. boreale*, *Daphnia pulex* (L., 1758) 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 *O. boreale* has also been recorded from Early Holocene lake sediments on Bjørnøya (Wohlfarth et al., 1995) together with the beetles *Agabus bipustulatus* (L., 1767) and *Eucnecosum tenue* (LeConte, 1863). 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 melt-water. 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 areas 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

Some areas of the archipelagoes of the Barents Sea were ice free during parts of the last glaciation, including nunataks above 300 m 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. For example, molecular studies have indicated that plant diversity in the Arctic is the result of glaciation cycles combined with subsequent dispersal barriers (Eidesen et al., 2013). 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). 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 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) and 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 (Fig. 3), were 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 in Novaya Zemlya, and the putative presence of plant refugia and/or deglaciated areas in 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 *D. 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 (Weider et al., 1999; Marková et al., 2013). 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).

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, 2010b). 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.

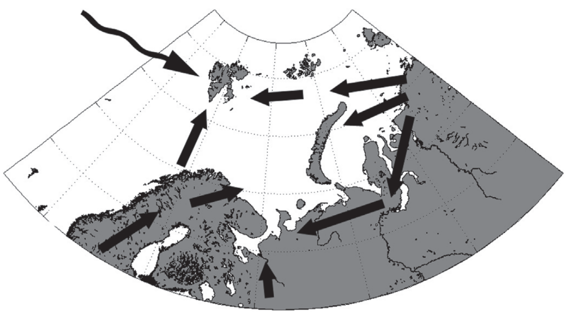

Fig. 4. Dispersal routes suggested to and within the Arctic archipelagoes in the Barents Sea. Solid arrows indicate dispersal directions for Collembola species (modified from Ávila-Jiménez and Coulson, 2011a). Undulating arrow indicates a link with the Nearctic region suggested for the Tardigrada (Pugh and McInnes, 1998).

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

Table 2
Similarities between the invertebrate faunas of the archipelagoes. Figures indicate: total number of species in common (total number of species in first archipelago; total number of species in second archipelago). Only species considered resident are included. Dashes indicate comparisons not possible, usually as no species of the group concerned have been recorded from Franz Josef Land.

Group		Novaya Zemlya to Svalbard	Franz Josef Land to Svalbard	Franz Josef Land to Novaya Zemlya
Rotifera	Bdelloidea	1 (2:67)	3 (3:67)	0 (0:2)
	Monogononta	45 (71:134)	16 (20:134)	15 (20:71)
Gastrotricha		0 (0:1)	–	–
Nematoda	Freeliving	24 (81:95)	–	–
Annelida	Lumbricidae	0 (1:2)	–	–
Tardigrada		40 (68:92)	17 (19:92)	12 (19:68)
Acari	Mesostigmata	11 (27:29)	3 (6:29)	4 (6:27)
	Oribatida	39 (64:87)	5 (15:87)	8 (15:64)
Araneae		8 (20:14)	2 (2:14)	2 (2:20)
Collembola		20 (53:68)	12 (14:68)	8 (14:53)
Insecta	Phthiraptera	4 (7:37)	–	–
	Hemiptera	0 (1:3)	–	–
	Coleoptera	1 (28:14)	–	–
	Diptera	29 (150:122)	1 (4:122)	0 (4:150)
	Chironomidae	19 (73:66)	1 (1:66)	0 (1:73)
	Other Diptera	10 (77:56)	0 (3:56)	0 (3:77)
	Siphonaptera	1 (1:2)	–	–
	Lepidoptera	0 (14:3)	–	–
Crustacea	Cladocera	5 (8:17)	–	–
	Copepoda	1 (16:6)	–	–
	Anostraca	0 (4 : 0)	–	–
	Ostracoda	0 (5:2)	–	–
	Notostraca	1 (1:1)	–	–
	Malacostraca	0 (3:1)	–	–

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, 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 in higher water temperatures and lower water levels in Kongressvatnet 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 and sampling frequently 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., 2012b). 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) 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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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.10.006.

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