POLISH POLAR RESEARCH
vol. 37, no. 1, pp. 105–119, 2016 doi: 10.1515/popore-2016-0003

Invertebrate communities of the High Arctic ponds in Hornsund

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Abstract: How environmental conditions influence current distributions of organisms at the local scale in sensitive High Arctic freshwaters is essential to understand in order to better comprehend the cascading consequences of the ongoing climate change. This knowledge is also important background data for paleolimnological assessments of long-term limno-ecological changes and in describing the range of environmental variability. We sampled five limnologically different freshwater sites from the Fuglebergsletta marine terrace in Hornsund, southern Svalbard, for aquatic invertebrates. Invertebrate communities were tested against non-climatic environmental drivers as limnological and catchment variables. A clear separation in the communities between the sites was observed. The largest and deepest lake was characterized by a diverse Chironomidae community but Cladocera were absent. In a pond with marine influence, crustaceans, such as Ostracoda, Amphipoda, and calanoid Copepoda were the most abundant invertebrates. Two nutrient-rich ponds were dominated by a chironomid, *Orthocladius consobrinus*, whereas the most eutrophic pond was dominated by the cladoceran *Daphnia pulex*, suggesting decreasing diversity along with the trophic status. Overall, nutrient related variables appeared to have an important influence on the invertebrate community composition and diversity, the trophic state of the sites being linked with their exposure to geese guano. Other segregating variables included water color, presence/absence of fish, abundance of aquatic vegetation and lake depth. These results suggest that since most of these variables are climate-driven at a larger scale, the impacts of the ongoing climate change will have cumulative effects on aquatic ecosystems.

Key words: Arctic, polar lakes, aquatic invertebrates, bird impact, climate change.

Introduction

The effects of the ongoing climate change are amplified in the Arctic regions, mostly due to positive feedback mechanisms related to cryospheric processes (Holland and Bitz 2003). In freshwater lakes, shortened ice-covered periods can cause an increase in primary production and community shifts due to changes in habitat availability and limnology. Furthermore, many aquatic invertebrate groups have direct response to water temperature changes (Nevalainen and Luoto 2010; Eggermont and Heiri 2012; Luoto and Nevalainen 2013). Due to present climate change, pronounced and unprecedented climate-driven regime shifts in aquatic communities have already occurred in Arctic lakes (Smol *et al.* 2005; Smol and Douglas 2007; Rühland *et al.* 2008). Arctic freshwaters are invaluable for polar biodiversity, for example, providing waters and serve as resting and feeding grounds for migratory birds (Vincent and Pienitz 1996; Latour *et al.* 2005) and as habitats for algae, plants, and invertebrates (Callaghan *et al.* 2004; Coulson *et al.* 2014). Climate warming causes many bird populations to expand, resulting in nutrient enrichment and deterioration of natural sites in the Arctic (Keatley *et al.* 2009). For example, geese can have major fecal impact on limnology of shallow Arctic coastal ponds (Côté *et al.* 2010; MacDonald *et al.* 2014).

In southern Svalbard, annual and seasonal air temperatures have increased by *ca.* 2°C since 1979 when meteorological monitoring began at the Polish Polar Station in Hornsund (Marsz and Styszyńska 2013). Concurrently, a major increase in the population sizes of barnacle geese (*Branta leucopsis*) in Svalbard has occurred (http://www.mosj.no/en/) and the hatch date of little auks (*Alle alle*) has advanced in the Hornsund area increasing their breeding success (Moe *et al.* 2009). Species distribution models for Svalbard-nesting pink-footed geese (*Anser brachyrhynchus*) suggests that climate warming may lead to a further growth in geese populations (Jensen *et al.* 2008), and therefore enhance the eutrophication of Arctic freshwaters. Lakes and ponds in Svalbard are extremely sensitive to climate changes and when combined with superimposed stressors, they have cascading effects (Birks *et al.* 2004; Guilizzoni *et al.* 2006; Luoto *et al.* 2014a; Nevalainen *et al.* 2015), such as increasing lake productivity and warming of surface waters.

The project Quantifying climate variability since Late-glacial in Southern Svalbard (QUAL) aims to increase the general understanding of Arctic paleoenvironments and the impacts of climatic changes (natural and human-induced). In this study, the objective is to provide background knowledge of local environmental factors that influence freshwater ecosystems. At the regional scale, the spatial distribution of northern invertebrate communities, especially those of Chironomidae and Cladocera, are dictated by dispersal and climate conditions (Heiri *et al.* 2011; Nevalainen *et al.* 2013; Luoto *et al.* 2014b). However, there is little knowledge of the local non-climatic environmental factors that influence invertebrate communities, although these factors may change with time and their long-term relationships with direct climate variables can also fluctuate (Shala *et al.* 2014; Rantala *et al.* 2015a, b). Therefore, in order to increase our understanding of the contemporary drivers of the invertebrate communities at the study region, we measured the physical characteristics and investigated the invertebrate communities of five freshwater sites. We look for catchment and limnological drivers for modern community composition so that in the future we can more reliably use the "modern analogs" of regional calibration models when reconstructing past environmental conditions from fossil invertebrate assemblages in sediment cores. In particular, we investigate the influence of water depth, color, pH, and several other limnological variables that may have importance on faunal distribution (Brooks and Birks 2004; Zawisza and Szeroczyńska 2011).

Material and methods

Study sites. — The five study sites (called here as Revvatnet, Brackish pond, Station pond, Fugledammen, and Coastal pond) are located in the periglacial area of the Hornsund fjord, southern Svalbard, within 4 km range from each other, between 77°00'–77°02'N and 15°36'E–15°53'E (Fig. 1), and under the same prevailing climate conditions. The average present day summer air temperature (June–August) in the area is 4.4°C and the average annual precipitation is < 400 mm (Marsz and Styszyńska 2013). The biologically active vegetation period lasts only for *ca.* 8 weeks. The catchments lie on the tundra area of the Fuglebergsletta post-glacial marine terrace between the Hornsund Bay and the mountain summit of Fugleberget (Fig. 1). The terrain between the bay and the mountain consists of outwash plains and undulating ground moraine with some marginal and lateral ridges and with abundant solifluction tongues and talus cones on sides of higher hills. The Hansbreen Glacier borders the eastern margin of Fuglebergsletta, however, no glacial meltwaters enter the studied basins with the exception of Revvatnet, which is influenced by the Werenskioldbreen Glacier in its northern side. The most common bird species on Fuglebergsletta is the barnacle goose (*Branta*

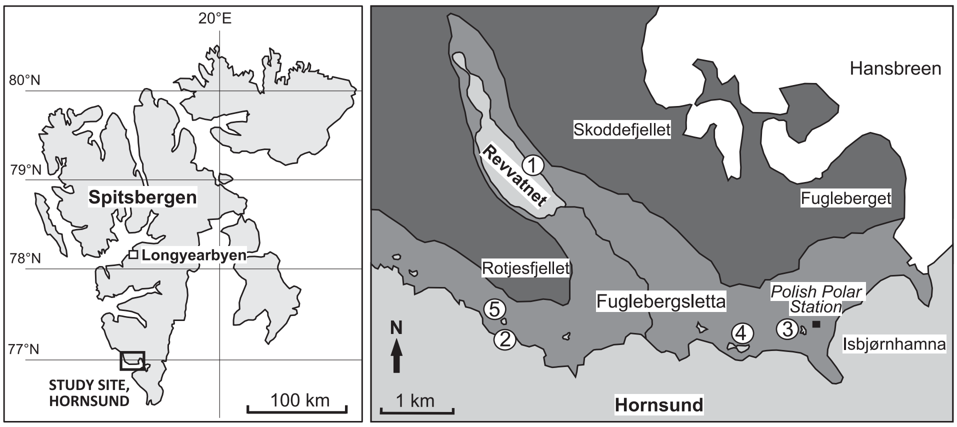


Fig. 1. Study area and sites in southern Spitsbergen, Svalbard. The lake and the ponds are located in the Fuglebergsletta marine terrace between the Hornsund Fjord (south) and mountain summits (north). The Hansbreen Glacier borders the eastern side of the terrace. Study sites: 1, Revvatnet; 2, Brackish pond; 3, Station pond; 4, Fugledammen and 5, Coastal pond.

Table 1

Limnological measurements of the study sites including maximum water depth, color of water, dissolved oxygen (DO), pH, specific conductivity, and total dissolved solids (TDS). The water properties were measured at the end of July 2013 from the epilimnion.

	Revvatnet	Brackish pond	Station pond	Fugledammen	Coastal pond
Coordinates	77°02'N, 15°38'E	77°00'N, 15°37'E	77°00'N, 15°53'E	77°00'N, 15°50'E	77°00'N, 15°36'E
Max. depth [m]	26	0.5	2	2	3
Water color	0	0	5	0	35
DO (mg l^{-1})	9.1	7.7	8.4	7.9	7
pH	7.6	7.2	7.4	7.3	6.6
Conductivity (µg l^{-1})	30	730	130	120	140
TDS (µg l^{-1})	10	2300	60	50	60

leucopsis), and little auk (*Alle alle*) colonies are present on the mountain slopes. A recent expansion of bird colonies along the coast has been observed (Wojczulanis-Jakubas *et al.* 2008; Zmudczyńska *et al.* 2009).

Based on visual observations made at the end of July 2013, Revvatnet and Brackish pond appeared to have nutrient-poor lake state. Revvatnet, the only site with fish, Arctic char (*Salvelinus alpinus*) present, is a relatively large and deep open-basin with unfertile rocky shores and having a glacial water inlet in its northern side and an outlet in its southern side. Continuous water mixing is observed in Revvatnet during the summer, while it ceases during the winter when the lake freeze (Nowiński and Wiśniewska-Wojtasik 2006). All the other sites are small and shallow ponds and freeze to their bottom during winter. Brackish pond is located in the coastal shoreline just in the margin of the reach of marine tidal waves. During the sampling a single specimen of *Fucus* sp. was found in the rocky pond suggesting intertidal activity. The other ponds represent strictly freshwater habitats. Station pond, Fugledammen, and Coastal pond had an unpleasant sulfurous odor, and the shorelines were covered by algal masses giving a general appearance of murky eutrophic sites. Aquatic macrophytes and moss fringes occupied the edges of these lakes and the immediate catchments were completely covered by bird guano, mostly that of geese. In general, Fuglebergsletta and the slopes of Fugleberget have relatively thick moss layer due to fertilizing effects of birds. Based on field observations, Coastal pond was the most bird-impacted, followed by Fugledammen. Also Station pond, located next to the Polish Polar Station in Hornsund, was in visually poor status. Limnological measurements from the end of July 2013 are tabulated in Table 1.

Sampling and invertebrate analysis. — Plankton net sampling of invertebrates was performed as a single collection in the five study sites during the short open-water season at the end of June 2013. The samples were taken with a 100-µm plankton net sampling approximately the same volume in each lake from selected locations close to shoreline to obtain animals from different habitats, *e.g.* from open water, aquatic vegetation, soft sediment, and barren surfaces. In the field, the sampled material was stored in ethanol. The samples were placed in a cold room for later preparation. All invertebrates were counted from the disposable samples and identified under a stereomicroscope using a Petri dish or a Bogorov counting chamber. For closer identification some specimens were transferred to a cuvette and an inverted microscope was used. A series of identification keys and guides were used (*e.g.* Wiederholm 1983; Røen 1995). Limnological measurements were performed using Hanna Instruments © portable pH/EC/TDS/temperature, water color, and dissolved oxygen meters from the epilimnetic wate.

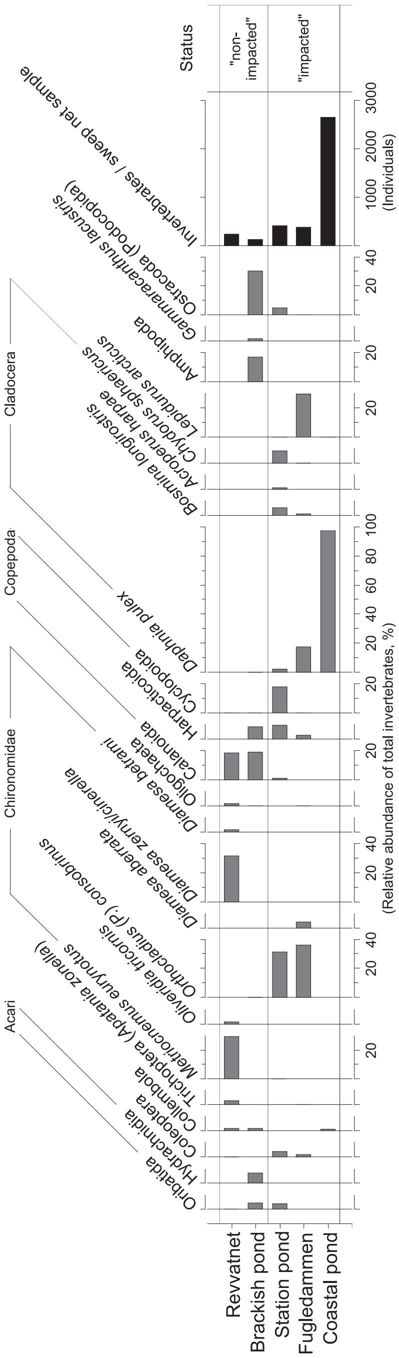
Statistical analyses. — Detrended correspondence analysis (DCA) was used as an ordination method to illustrate invertebrate community variance between the study sites. The DCA was run with supplementary variables, detrending by segments, and relative species data log transformed using CANOCO 5 (Šmilauer and Lepš 2014). Similarity percentage analysis (SIMPER) using Bray-Curtis similarity/dissimilarity measure was done on relative taxon abundances to indicate the divergence between the sites (Clarke 1993). The Bray-Curtis similarity measure is implicit to SIMPER, which was run with PAST 3.01 (Hammer *et al.* 2001).

Results

The most abundant taxa in Revvatnet included the chironomids *Diamesa zernyi/cinerella*-gr. (32.3%) and *Metriocnemus eurynotus* (29.9%) together with calanoid copepods (18.9%) (Fig. 2). In Brackish pond, ostracods (Podocopida) (31.2%), calanoids (19.6%), and amphipods (17.4%) were the most abundant taxa. Hydrachnidia (8.0%) were present only in Brackish pond. The chironomid *Orthocladius (Pogonocladius) consobrinus* was the most common taxon in Station pond (32.2%) and Fugledammen (36.6%). In addition, cyclopoid copepods (18.2%) were abundant in Station pond and the tadpole shrimp *Lepidurus arcticus* (29.9%) in Fugledammen. Coastal pond was dominated by the cladoceran *Daphnia pulex* (97.7%).

Among the chironomids, greatest diversity was found in Revvatnet, while Brackish pond, Station pond, and Fugledammen were dominated by one or two taxa, all including *O. consobrinus* (Fig. 3). Calanoids were the most abundant copepods in Revvatnet and Brackish pond, whereas cyclopoids were dominant in Station pond and harpacticoids in Fugledammen. Among cladocerans, Brackish pond, Fugledammen, and Coastal pond were dominated by *D. pulex* and *Chydorus sphaericus* was most abundant in Station pond. Chironomids and copepods were absent in Coastal pond and cladocerans in Revvatnet.

The largest number of invertebrate individuals was found from Coastal pond (2660) and the lowest from Brackish pond (138) (Fig. 2). Gradient length of the first DCA axis was 3.24 SD and length of the second axis was 2.49 SD, whereas the



eigenvalues were 0.662 and 0.289, respectively. The first DCA axis explained 38.97% and the second 16.98% of the total variance. The first primary DCA axis was characterized mostly by nutrient-related variables, such as lake trophic state, presence of aquatic vegetation, and geese impact (Fig. 4), whereas the secondary axis included variables such as color of water and pH. Revvatnet was situated at negative end of the trophic gradient (DCA axis 1), Brackish pond at the middle, and Station pond and Fugledammen were closely clustered at the high end of the trophic gradient. Coastal pond had high both DCA axis 1 and 2 scores. According to the DCA, all the sites had their own associated invertebrate taxa. Based on the SIMPER analysis, most of the sites had completely differing invertebrate faunal composition (Table 2). The closest resemblance between communities was between Station pond and Fugledammen (53.8% difference), whereas the largest divergence was between Revvatnet and Coastal pond (98.5%).

Discussion

The invertebrate taxa found from the five study sites are rather typical for lakes and ponds in the region (Janiec 1996; Coulson 2007; Zawisza and Szeroczyńska 2011; Coulson *et al.* 2014). Revvatnet, which was the only deep basin, had unique faunal composition with only some resemblance to Brackish pond. The chironomid fauna was diverse in Revvatnet (Fig. 3), *Diamesa zernyi/cinerella* and *Metriocnemus eurynotus* being the most abundant taxa (Fig. 2). *Diamesa* are usually found in turbulent water (Brooks *et al.* 2007),

Fig. 2. Relative abundance of invertebrates in the study sites. Only taxa with abundance of >1% in any of the sites are illustrated. Revvatnet and Brakish pond appeared visually in non-impacted state, whereas Station pond, Fugledammen, and Coastal pond were bird-impacted and in poor limnological state.

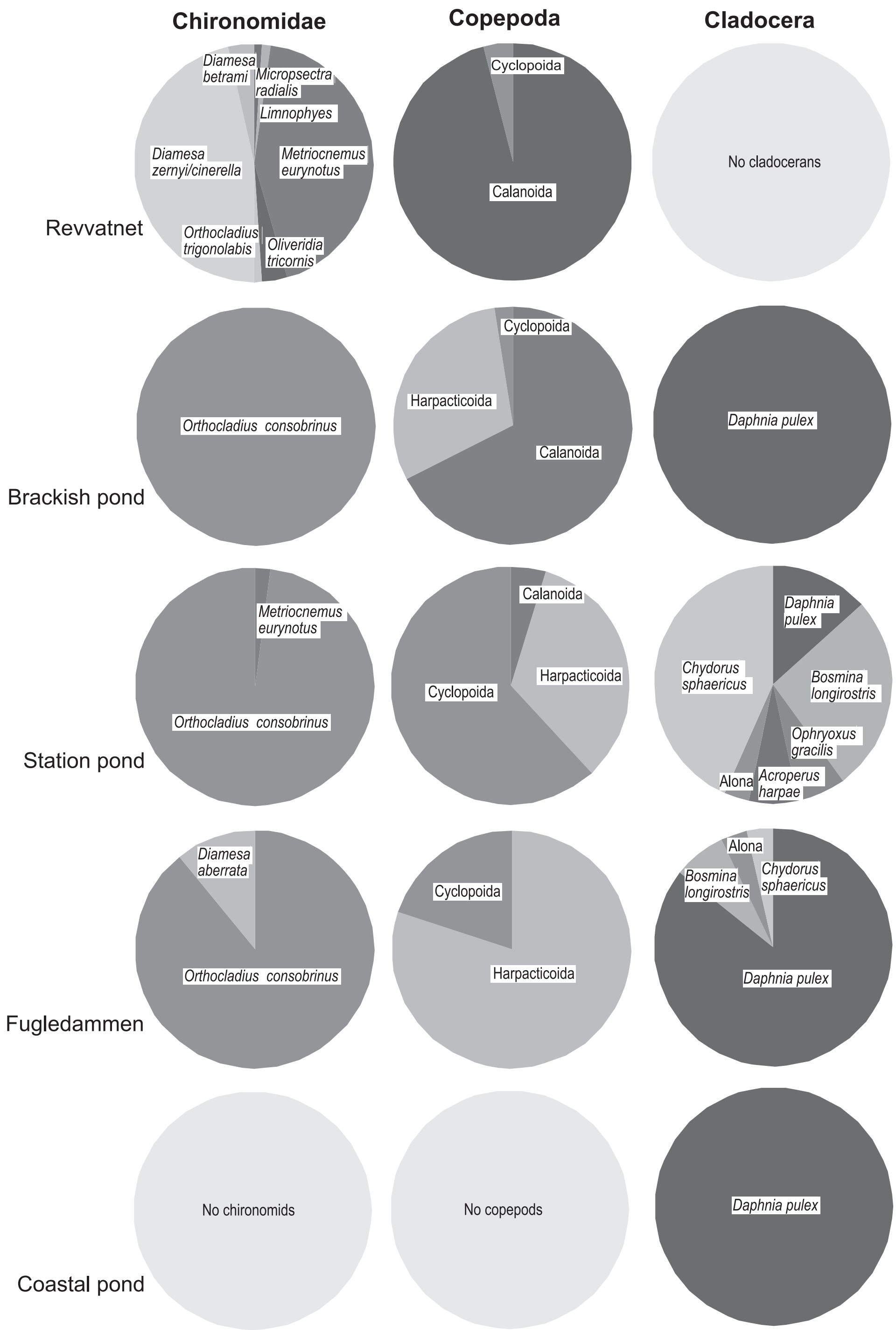


Fig. 3. Site-specific relative abundance of Chironomidae, Copepoda, and Cladocera taxa.

Table 2

Faunal dissimilarity between the sites based on similarities percentage (SIMPER) analysis.

	Brackish pond	Station pond	Fugledammen	Coastal pond
Revvatnet	77.4%	95.6%	96.9%	98.5%
Brackish pond		76.5%	93.4%	97.8%
Station pond			53.8%	96.4%
Fugledammen				81.3%

which in the present case is explained by the northern inlet and the open nature of the basin (Fig. 1). Plumes of suspended sediment were clearly observed in over- and interflow in Revvatnet during the melt water season in July 2013. *Metriocnemus* are often semi-terrestrial (Cranston and Judd 1987) but their abundance can increase in seabird affected Arctic lakes (Michelutti *et al.* 2011; Stewart *et al.* 2013) suggesting a catchment influence in Revvatnet. In addition, springtails (Collembola), which had their maximum abundance in Revvatnet, may attain high population densities beneath bird cliffs in Hornsund (Byzova *et al.* 1995; Zmudczyńska *et al.* 2012). The little auks are nesting on the hills of Rotjesfjellet and Skoddefjellet in the immediate catchment of Revvatnet (Fig. 1). The little auks fertilize the tundra with their excrement by transporting nutrients from the marine feeding areas to terrestrial nesting ground (Zmudczyńska *et al.* 2012). However, the limnological impact of these seabirds has thus far remained relatively small, since the lake is currently oligotrophic. This is at least partly because Revvatnet is an open basin receiving a large amount of cold melt water from the mountain area in north, and hence its residence time is short, enabling the transport of nutrients efficiently back to the marine realm. Cladocerans were completely absent from Revvatnet (Fig. 2) that supports the low planktonic productivity in the lake. Revvatnet is also the only study site with fish present that can explain the absence of particular cladoceran species, since zooplankton communities benefit from the absence of fish following reduced predation pressure (Jeppesen *et al.* 2001). The only crustaceans in Revvatnet were calanoid copepods, which probably can better succeed in lakes with low algal productivity and predation pressure by the Arctic char. Calanoids also prefer colder lakes than the other copepods (Rautio *et al.* 2011) that may be explained by the fact that as a larger and deeper basin receiving cold water from the glacier, water temperature in Revvatnet remains cold through the summer. Although temperature data from the study sites is not available, it is common that shallow ponds are warmer than large lakes in the Arctic (Schindler and Smol 2006). This is emphasized in the current data set, since Revvatnet, the only large lake, has input of cold meltwater from the glacier. This has a potential effect on the timing and phenology of the fauna. Therefore, the sampling, on a single date, may provide a slightly biased picture of the fauna in each pond.

Brackish pond is limnologically the most dissimilar from the other sites due to the increased salinity (Table 1). In its faunal composition, it has some similarity

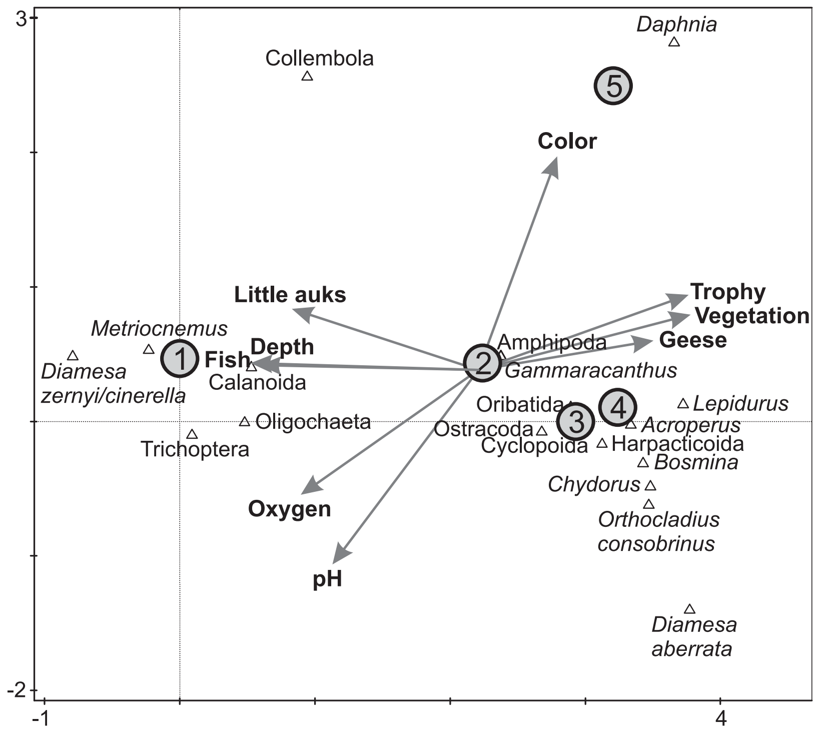


Fig. 4. Detrended correspondence analysis (DCA) of invertebrates and study sites, together with most important supplementary environmental variables. The first DCA axis explains 39% and the second 17% of the total variance. Study sites: 1, Revvatnet; 2, Brackish pond; 3, Station pond; 4, Fugledammen and 5, Coastal pond.

with Revvatnet through the success of calanoids but also with Station pond through the presence of harpacticoid copepods, oribatid mites, and ostracods (Fig. 2). However, the pond includes distinct brackish taxa, which are absent from the freshwater sites, such as amphipods, including *Gammaracanthus lacustris*. Chironomids were absent from Brackish pond, except for a single occurrence of *Orthocladius (P.) consobrinus*, reflecting the lack of soft substrate as the pond had rocky shores and only a very small sediment accumulation area in its central parts. Also *Lepidurus arcticus* and cladocerans were missing, with only a single specimen of *Daphnia*, indicating their lack of mechanisms to buffer the adverse effects of salinity (Bezirci *et al.* 2012) and suggesting that amphipods, copepods, and ostracods have occupied the planktonic niche in the brackish site. However, since the sampling was done by a plankton net, it may partly fail to describe species living in the substrate. For example, only a small proportion of *Lepidurus* individuals are found above the substrate during a single sampling effort that can lead to underestimation of the taxon in the present study.

Compared to Revvatnet and Brackish pond, Station pond and Fugledammen are more productive systems. Of all the studied sites, Station pond and Fugledammen are the most alike (Table 2). A common feature of these two geese-impacted ponds is that *O. consobrinus* is the most abundant invertebrate taxon (Fig. 2) dominating the chironomid community (Fig. 3). Lacustrine chironomids in Svalbard are primarily influenced by pH, nutrients, water temperature, and water depth, and moreover a distinctive chironomid fauna typical of lakes with high bird impact and productivity can be distinguished (Brooks and Birks 2004). Fitting well with the present findings, previous studies have shown that *O. consobrinus* tends to increase following bird-driven eutrophication in Svalbard (Brooks and Birks 2004; Luoto *et al.* 2014a; Kivilä, unpublished results). Station pond was the only study site where all the three copepod groups (Calanoida, Harpacticoida, and Cyclopoida) were present (Fig. 2). Moreover, the cladoceran diversity, including planktonic and littoral species, was the highest (Fig. 3) suggesting food and habitat availability for both open-water (algae for grazing) and shallow areas (littoral vegetation). Also the limnological measurements suggest that the surface water is relatively well oxygenated in Station pond enabling a diverse aquatic fauna to flourish. However, in Fugledammen, which is a more eutrophic and heavily impacted pond, the crustacean fauna was dominated planktonic by *Daphnia pulex* and the tadpole shrimp *Lepidurus arcticus* (Figs 2 and 3). This indicates the oxygen deficient and turbid nature of Fugledammen that was also demonstrated in a recent paleolimnological study (Luoto *et al.* 2015). This previous long-term study indicated that initially the pond had clear water, vegetation-associated littoral community with fish present, and allochthonous productivity. During the 20th century, the pond became nutrient-rich, fish disappeared, and the invertebrate community became dominated by planktonic *D. pulex*, by *L. arcticus,* and eutrophy- indicating *O. consobrinus*. Apparently, the pond changed from benthic production to planktonic production, as it turned into a self-supporting nutrient system where algal productivity enhances the increased external nutrient load from expanding geese population suppressing the benthic system. All these changes occurred concurrently with climate warming (Luoto *et al.* 2015). The paleolimnological findings of the most recent development of Fugledammen are confirmed by the present results of contemporary fauna and observations of the modern limnological state, suggesting that combining modern ecology and paleolimnology is a promising approach to unravel limnoecological dynamics of the area.

In addition to *O. consobrinus*, *D. pulex* has been shown to increase along with intensified bird influence in Svalbard (Luoto *et al.* 2014a). *Daphnia* is also sensitive to fish predation pressure (Jeppesen *et al.* 2001; Manca and Armiraglio 2002; Nevalainen *et al.* 2014), together with *L. arcticus*, and vulnerable to the presence of fish in its habitats (Jeppesen *et al.* 2001). Though *L. arcticus* can feed on *D. pulex*, they have also been shown to coexist in High Arctic lakes when fish are absent (Christoffersen 2001; Jeppesen *et al.* 2001), such as in Fugledammen. Fish (Arctic char) are absent from ponds that freeze solid during winter (Brackish pond, Station pond, Fugledammen, and Coastal pond) and present in deeper lakes, such as Revvatnet.

According to the SIMPER analysis, the largest divergence in invertebrate community composition was between the "clean" sites (Revvatnet and Brackish pond) and Coastal pond (Table 2) suggesting that the trophic gradient has an important role. In addition to a few springtails (Collembola), which are common in the vegetated terrain of the bird-impacted tundra (Byzova *et al.* 1995), Coastal pond was dominated by a mass occurrence of *D. pulex* as the abundance of individuals in the plankton net sample was in average tenfold greater compared to the other sites (Fig. 2). Together with lower oxygen levels and reduced light penetration (Table 1), the completely planktonic invertebrate community suggests that Coastal pond, which was assessed as the most bird-impacted site, is indeed nutrient-enriched. Thus, the dominance of *D. pulex* suggests that a nutrient enrichment threshold related to increased planktonic primary production has been crossed, since *Daphnia* is dependent on planktonic food (Bertilsson *et al.* 2003). Also another planktonic cladoceran, *Bosmina longirostris*, which was present in the other impacted ponds (Fig. 2) but absent in Coastal pond, benefits from nutrient enrichment (Luoto *et al.* 2013; Nevalainen and Luoto 2013). The reason why *B. longirostris* is missing from Coastal pond is most likely related to planktonic food web competition with *D. pulex* as these taxa share a similar ecological niche. The alternate and exclusive success between *Daphnia* and *Bosmina* is typical for the relatively simple aquatic food webs in Svalbard (Guilizzoni *et al.* 2006; Luoto *et al.* 2011).

Conclusions

The studied lacustrine basins in Fuglebergsletta were ecologically fundamentally different and environmental factors related to productivity were the main drivers of the invertebrate communities and diversity. The oligotrophic lake Revvatnet was characterized by a diverse benthic chironomid fauna and the brackish site by saline inhabitants: calanoids, amphipods and ostracods. In the impacted lakes, a common feature was the abundance of the chironomid *Orthocladius consobrinus* and presence of the cladoceran *Bosmina longirostris*. The most impacted pond was dominated by the planktonic grazer *Daphnia pulex*. Besides bird-impact, water color, presence of fish, abundance of aquatic vegetation, and lake depth had influence on the invertebrate communities. Apparently, the influence of barnacle geese was greater than that of little auks.

Our results provide important information on the present conditions at the Hornsund Fjord area that is invaluable in selecting suitable sedimentary sites and studying of the long-term paleoecological and paleoclimatological sediment sequences in the future. Combining paleolimnology and modern ecology can provide a fruitful basis for predicting future changes in this extremely sensitive part of the High Arctic.

Acknowledgements. — This paper is a contribution to the QUAL-project funded by the Academy of Finland (A.E.K. Ojala, grant# 259343). We thank Marek Zajączkowski for the help and express our gratitude to the crew of the Polish Polar Station in Hornsund for friendly atmosphere and logistical support during the research. We are grateful to Stephen Coulson and an anonymous referee for valuable comments on the manuscript.

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Received 11 May 2015
Accepted 12 December 2015