Freshwater diversity in Svalbard; providing baseline data for ecosystems in change

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Abstract

The high Arctic is in a rapid transition due to climate change, and both direct effects due to warming and an extended growing season, as well as an indirect effect caused by increased bird activity and density (notably geese), strongly affect ponds and lakes. Our study presents the hitherto most comprehensive data on invertebrate freshwater diversity at Svalbard and had three main purposes: to provide a current "baseline" of community composition, to compare current species distribution and occurrence with older data to identify changes that have already occurred, and finally to identify how diversity and community composition are related to the age of localities. To address these aims we conducted a survey of freshwater invertebrates in 75 ponds and lakes at Svalbard in August 2014 and 2015. We provide a full report of the species inventory for zooplankton, benthos and meiofauna. We also provide data for species that have likely colonized the sites over the past decades. Finally, our study also clearly demonstrates a diversity gradient related to ecosystem age and/or parameters confounded with age (e.g. productivity), which may hint at the rate of colonization over the time span from the oldest to the youngest localities.

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Introduction

Few places on the planet have witnessed a more dramatic climate change than the high Arctic, and this is expected to continue for the foreseeable future (IPCC 2013). The loss of sea ice, together with increasing air and water temperatures, has also caused major changes on terrestrial habitats such as of the Svalbard archipelago in the North Atlantic (Bhatt et al. 2010). Climatic recordings on the west-coast of the archipelago show a steady increase of approximately 2° C in air temperature over the past 30 years (Holm et al. 2012), with some truly extreme temperature records over the past few years. Extended growing seasons, the retreat of glaciers, thawing of permafrost, changes in hydrology and "greening" by increased vegetation cover are prominent effects in the Arctic (IPCC 2013; Xu et al. 2013). Also, numerous small water-bodies, ponds and many arctic lakes are impacted by direct warming, permafrost melt and increased fluxes of organic carbon and nutrients from the surrounding landscape (Quinlan et al. 2005; Smol et al. 2005; Smol and Douglas 2007; Rautio et al. 2011; Luoto et al. 2015). Also, faunal changes, notably birds, may serve a dual role by fertilizing and/or serving as vector for species migrations (van Geest et al. 2007; Hessen et al. 2017).

Research on the impacts of climate change in the Arctic has become a priority issue, and there is currently a wide range of studies on climate, environment and ecosystem issues. Extensive terrestrial monitoring programs have been conducted (e.g. Ims et al. 2014), and there are both regional and national monitoring programs of pollution covering high-arctic territories in Svalbard. Extensive efforts on research and data collection have been carried out on abiotic systems (atmosphere, meteorology, glaciers) and ecosystems (terrestrial and marine systems). There has been less effort devoted to freshwater ecosystems in the high Arctic, despite their strong vulnerability to climate change and other stressors (Smol et al. 2005; Smol and Douglas 2007; Christoffersen et al. 2008). Being closed entities ("aquatic islands") with simple ecosystems, they also offer ideal monitoring units. The need for more efforts towards responses in freshwater ecosystems has also recently prompted the establishment of a Freshwater Expert Monitoring Group (Culp et al. 2012). To separate faunal changes from random variability, there is a strong demand not only for time series and monitoring but also for proper baseline data.

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Most of the freshwater sites in Svalbard are young, and many of them are temporary. The glacial history of Svalbard has been disputed, but the distribution of glaciers since 1936/1972 and until recent time has been mapped (Kônig et al. 2013). It means that freshwaters younger than 80 years can be roughly dated. The history of older lakes, often situated closer to the coastline, is more uncertain, but mapping of the freshwater fauna along a gradient from the edge of the glacier and to the coastline will likely reflect the colonization history.

Fortunately, there exist some old recordings of the Svalbard freshwater fauna (Brehm 1917, Thor 1930), and the most extensive study dates more than 100 years back to a survey in 1910 (Olofsson 1918). These data, focusing on rotifers and crustaceans, were gathered in the Isfjorden and Van Mijenfjorden area, possessing numerous ponds and a few lakes. Since Olofsson's seminal survey there have only been some scattered studies on crustaceans (e.g., Halvorsen and Gullestad 1976, Jørgensen and Eie 1993 Husman et al. 1978, Kubicek and Terek 1991). Some studies have also specifically addressed the clonal diversity of the widespread and dominant cladoceran *Daphnia* (Weider and Hobaek 1994) as well as the impact of birds on species and clonal composition (van Geest et al. 2007; Alfsnes et al. 2016). For other compartments of the freshwater fauna, there is even more scarce information, and some groups are hardly recorded, at least not in any systematic manner. Among the insects, there is a strong dominance of Diptera, which is the most species-rich freshwater group in Svalbard, being 122 species at Svalbard and Bear Island (Coulson and Refseth 2004; Coulson 2014). This group is better adapted to the cold and harsh climate in the artic than any other order of insects (Coulson and Refseth 2004).

To fill some of the knowledge gaps of freshwater invertebrates at Svalbard and establish, at least regionally, a kind of "baseline" survey for later studies, zooplankton, meiobenthos and macrobenthos were sampled in a number of localities in August 2014 and 2015. While this only covers the central, western part of the Svalbard Archipelago, this is the area with the highest temperatures owing to the oceanic currents, the highest productivity and diversity, and the region most impacted by both humans and the increased goose populations. It is also the area for which there is some previous data on the freshwater fauna, and thus we believe this should provide a good representation of

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current freshwater fauna as well as already observed changes at the community or species level since earlier studies (i.e. Olofsson 1918).

The aim of this study was to provide a full report of the species inventory for zooplankton, benthos and meiofauna in the sampled waterbodies. We also provide data for species that have apparently colonized the sites over the past decades. Finally, we related diversity and community composition to the age of the ecosystem and (or key parameters that co-vary to age), which may hint at the rate of colonization over the time span from the oldest to the youngest.

Material and Methods

Altogether 75 localities were sampled in Svalbard in 2014 and 2015. In the period 18–24 August 2014, sampling was conducted in different parts of Isfjorden: Longyearbyen (2 localities), the gradient Aldegondabreen-Grønfjorden (16), Randvika (12), Barentsburg (2), Ymerbukta (4), Pyramiden (6), Kapp Napier (6) and Diabasodden (2) (Fig. 1). In 2015 (17 – 19 August) 15 localities in Ny-Ålesund area (including six localities along the gradient from the sea and to the glacier Midtre Lovènbreen) and 10 localities along the gradient from Grønfjorden to the glacier Vestre Grønfjordbreen were sampled. These localities also covered the areas sampled in 1910 (Olofsson 1918).

Since the age of the locality was assumed relevant, we made sure that localities along the gradient from the edge of glaciers and to the seashore were represented wherever possible. We focused on the most species-rich groups, Crustacea and Diptera, which was identified to the species level, while the taxonomic resolution for other groups was in cases restricted to higher levels. The composition of the invertebrate communities should presumably be related to important environmental variables such as age, temperature, size, longitude and latitude, elevation, water chemistry and the presence of fish. We also compared our invertebrate inventories with previous (yet more incomplete) studies to document changes that have occurred already and relate diversity to key drivers to possibly predict future changes.

The waterbodies were categorized into four classes according to their size and approximate average depth. The categories were based on an already existing concept presented by CAFF (Conservation of Arctic Flora and Fauna) Freshwater Expert

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Monitoring Group for Pan-Arctic Monitoring program and from other literature sources (Culp et al. 2012; Rautio et al. 2011). The localities ranged from 4 m to 166 m above sea; surface area varied from puddles less than 2 m^2 to 460 ha and depths of 0.25 to 37 m. Lake Linnè was the largest and deepest lake. For the analysis we categorized the sites in four classes according to their size; 1 (puddle): ≤ 0.01 ha, 2 (small pond): 0.01–0.1 ha, 3 (large pond): 0.1–1.0 ha, 4: (lake) > 1.0 ha, and three classes according to their average depths (1: ≤ 0.25 m, 2: 0.25–1 m, 3: > 1 m). With a few exceptions, all ponds were shallow and less than 1 m deep. Depth estimates for the lakes are, however, somewhat rough since they for logistic reasons had to be performed without the use of a boat. Examples of these categories are provided in Fig. 2.

The past coverage of glaciers on Svalbard is shown in the digital atlas of "Glaciers on Svalbard" published by the Norwegian Polar Institute (http://svalbardkartet.npolar.no/html5/index.html?viewer=svalbardkartet). The basis for the atlas is three sets of maps showing the distribution of the glaciers created in the period 1936–72, in 1990 and later in the period 2001–2010. Based on the atlas we grouped the localities into four age classes; 1) 2001/2010 to the present (1 locality), 2) 1990–2001/2010 (3 localities), 3) 1936/1972–1990 (19 localities) and 4) < 1936–1972 (52 localities). The age of the oldest localities may cover a wider span (i.e Velle et al. 2011), but in the absence of proper dating we have pooled them into one category that has been without a permanent ice-cover for an extended period.

pH was > 7.0 in all waterbodies with a mean of 8.5, and a max of 9.5 (small pond, Diabasodden). The lowest pH, 7,3, was recorded in a small pond in Ymerbukta. Most sites had high conductivity (mean 413, max 1750 $\mu S\ cm^{-1}$). pH, conductivity and temperature were measured by applying Hanna Instruments waterproof tester (HI98129 and HI98130).

Five ponds/lakes had a fish population. The occurrence of fish (only Arctic charr, *Salvelinus alpinus*) was categorized as present or absent based on existing knowledge (K. S. Christoffersen and M. Svenning, unpublished data); thus no attempts were made to assess the density or biomass of fish.

Zooplankton, macrobenthos and meiobenthos, were sampled from all localities as follows:

Zooplankton was sampled from four habitats: the open water, the littoral zone, the near-sediment layer and the upper sediment layer. In all cases, samples were performed with a 100 mm diameter, 50-µm mesh zooplankton net. For larger sites, a floating device was used to bring the net near the center, and care was taken to sample both from the open waters and the near-bottom and littoral habitats. In very shallow ponds, samples were taken by dragging the net horizontally in the water by walking. When this method was not possible due to the small size or the presence of stones, water was collected in a bucket and then filtered for animals. In the littoral zone, samples were taken with a small net having a long handle. The samples were preserved with 96 % ethanol. In general, the entire sample was washed and prepared to have a total volume of 100 ml, and thereafter counted to get the relative species distribution (see below). In samples with high densities subsamples were examined until at least 200 organisms were counted for each group. For identification and taxonomy see Novichkova et al. (2014).

Meibenthos was sampled using a plastic tube that was inserted into the uppermost 3–4 cm of the sediment layer. From each site, 2–3 samples were taken randomly, all representing different meiobenthic habitat substrates if possible, and then pooled. Each sample covered an area of 3 cm^2. The samples were preserved with 96 % ethanol and filtered (50-µm mesh) before identification following Dussart and Defaye (1983), Bartsch (2006) and Alekseev and Tsalolikhin (2010).

Macrobenthos samples were taken from the shore to a depth of ca 1.5 m (or max depth in the more shallow sites). We used a hemispherical scraper (diameter 16 cm, area 0.02 m^2, mesh size 0.5 mm) and 5–10 samples (depending on the density of organisms) were merged into one sample. Mud and coarse gravel were eliminated before the sample was preserved with 96 % ethanol. Identification was performed according to Wiederholm (1983), Timm (2009) and Makarchenko (2001).

Neither of these samplings allowed for a precise quantitative judgment; hence we applied four “dominance classes” on an ordinal scale to reflect the dominance of species based on frequencies in the individual sample (0: absent, 1: <1%, 2: 1–10%, 3: >10%) (Walseng et al. 2006). The relationship between taxa richness and the environmental variables longitude, latitude, elevation, depth, area, age, presence of fish, pH, conductivity and water temperature was analyzed by univariate multiple linear regression. Due to the high number of possible interactions between environmental variables, interactions were not included in the analysis. Taxa richness was checked for normality and homogeneity of variances. A backward selection procedure was used to exclude predictors from the model ($P > 0.1$). Elevation and conductivity were log-transformed. For pair-wise comparisons of means of taxa richness in the different age classes, t-tests with Bonferroni correction was applied. Hence, the observed significance level is adjusted for multiple comparisons. The youngest age class only contained one water body. Therefore, the pairwise comparisons were only conducted between age classes 2, 3 and 4.

The relationships between environmental variables and the invertebrate community from the respective localities were analyzed using unconstrained and constrained ordination techniques. Detrended correspondence analysis (DCA, Hill and Gauch 1980) showed that the first DCA axis spanned a gradient length of 2,9 SD units for the invertebrate community. Due to the relatively long gradient length, we applied the constrained ordination technique canonical correspondence analysis (CCA) in the analysis of the impact of environmental variables on the invertebrate community (cf. Økland 1990). The statistical significance of the relationship between the species or taxa and the set of environmental variables was examined by testing the significance of the canonical axes together with a Monte-Carlo permutation test. The development of a "minimal adequate model" was done by forward selection of environmental variables with a Monte Carlo test (499 permutations). Only variables that made significant independent contributions to the variation in species abundance ($\alpha = 0.05$ level) were included in the model. The dominance scores of the different taxa were used as input data in the CCA- analysis. The following parameters were included in the RDA: longitude, latitude, elevation, depth, area, age, presence of fish, pH, conductivity and water temperature. Elevation and conductivity were transformed ($\log_{10}(X + 1)$). The multivariate regressions were conducted in SPSS Statistics 24 (IBM). The ordination analysis was conducted with the software CANOCO 5.0 (ter Braak and Šmilauer 2012).

Results

The most prevalent taxa were the nematodes found in 74 of the 75 localities, while Ostracods and tardigrads were found in 51 and 45 localities, respectively (Fig. 3). Altogether 53 taxa were found of which 37 were identified to a species level (Appendix 1). The number of taxa in one location varied between 2 and 14 (mean 8.8). The most taxon-rich locality was Lake Solvatn, a nutrient-rich and bird-affected shallow locality close to Ny-Ålesund.

The two most taxon-rich invertebrate groups were crustaceans and chironomids, both constituting 22 and 21 taxa, respectively. Crustaceans were found in both zooplankton and meiobenthos samples and were represented by four groups; Cladocera (8 taxa), Cyclopoida (4 taxa), Calanoida (2 taxa) and Harpactoida (6 taxa) (Appendix 1). On average 4.3 species of crustaceans were found per locality (from zero to 8 species). The most common cladoceran, *Daphnia cf. pulex*, was found in 39 localities and was often the dominating species. The most common harpactoid, *Maraenobiotus brucei*, was found in nearly half of the localities (34). Another common crustacean was *Lepidurus arcticus*, a cold water, primarily benthic notostracan, which was recorded in 27 localities.

Chironomids was the most numerous group in macrobenthos samples, and the number of taxa varied between zero and 6 with a mean of 2.6. The most common species were *Paratanytarsus austriacus* (30 localities), *Psectrocladius barbimanus* (28 localities) and *Cricotopus (s. str.) tibialis* (24 localities).

Estimated age of localities co-varied with other key properties such as temperature (Tab. 1), implying that age could be confounded by these or other parameters. The positive correlation between age, class and temperature reflected the altitudinal gradient or decreasing glacial impact with increasing distance from the glacier. Conductivity was negatively correlated to elevation, likely reflecting increasing marine impact in water bodies at a lower elevation closer to the sea.

The model for taxon richness was statistically significant (F1, 73) = 22.838, p = 0.000, R^2 = 0.238 %, n = 75) and included significant effects of water body age (Tab. 2).

The pair-wise comparison revealed that mean taxa richness in age class 2 was significantly lower than that of age class 4 (Fig. 4, t-test with Bonferroni correction, difference between means = 4.891, p = 0.003). The first two CCA axes in the ordination of the invertebrate community had eigenvalues of 0.1925 and 0.1053, respectively, and explained 10.8 % of the variation in the species' composition and 47.0 % of the variation in the species-environment relationship (Table 3; Fig. 5). There was a significant relationship between the set of environmental variables and species' composition (i.e. all canonical axes, pseudo-F =1.9, p = 0.002). The "minimal adequate model" resulting from the forward selection included the explanatory variable water body age (pseudo-F = 3.5, p = 0.002), temperature (pseudo-F = 2.2, p = 0.006), conductivity (pseudo-F = 2.1, p = 0.002), longitude (pseudo-F = 2.1, p = 0.002) and latitude (pseudo-F = 2.1, p = 0.002). The intra-set correlations of environmental variables with the CCA axes (Tab. 3) and the CCA biplot (Fig. 5) showed that the invertebrate community in the water bodies was distributed mainly along a gradient of age and temperature on CCA axis 1. CCA axis 2 was mainly correlated with conductivity (Tab. 1, Fig. 5).

Many invertebrate taxa, such as chironomids. sp., *E. raboti*, *D. pulex*, *M. hirsuticornis* and *L. arcticus* were associated with low axis 1 scores (Fig. 5), i.e. the "oldest" sites with the highest temperatures. Other taxa such as *Oliveridia tricornis* and *Diamesa gr. arctica* were associated with higher axis 1 scores, i.e. lower age class and temperature. Tardigrada and Nematoda were the "pioneer groups" and the only taxa in age class 1, but they also occurred in the older localities. Examples of taxa associated with low axis 2 scores, that is high conductivity, are *Tahidius discipes* and *Metriocnemis gr. fuscipes*, while *Micropsectra sp., M. radialis* and *Apatania zonella* are examples of species associated with high axis 2 scores, i.e. low conductivity.

As age – or distance from sea or glacier, respectively – was the most important of the environmental variables, we have sorted the occurrence of the different taxa according to the water body age classes (Appendix 1). It appears that Nematoda and Tardigrada are the earliest colonizers of the water bodies, as they are the only invertebrates recorded in age class 1. In the slightly older water bodies, in age-class 2, one cyclopoid, five chironomids and one annelid appear. The number of taxa in age classes 3 and 4 was 38 and 47, respectively.

Discussion

Drivers: Among the variables used in our analysis, age appeared to be the most important driver of the observed invertebrate diversity found in 75 freshwater localities situated in the central/western parts of Svalbard. However, CCA (Fig. 5) explained a low fraction of the total variance, and only 10.8 % of the variation was explained by the first two axes. This could partly be owing to the limited number of variables included, but it could also be a result of more stochastic events. The interpretation of age and temperature should be judged with caution since other potentially important parameters such as nutrients (phosphorus and nitrogen), as well as phytoplankton biomass, were not included. Sites at lower altitudes not only have a higher age and higher temperature, which is a minimum factor at high latitudes, they are also often surrounded by vegetation, promoting dissolved organic matter that could shield off UV-radiation in these otherwise clear ponds (cf. Hessen et al. 1996). They attract grazing birds that could serve a dual role by fertilizing the ponds as well as being vectors of invertebrates, promoting species and clonal richness (van Geest et al. 2007; Alfsnes et al. 2016). Disentangling age from these covariates is not straightforward, and likely several of these factors may contribute to the observed community composition and diversity. Clearly a faster colonization would be expected for flying insects compared with other groups, but still age will likely play a major role simply due to the available time-span for colonization.

No doubt predation could also affect richness and community composition. With regard to fish, Arctic charr (*S. alpinus*) is the only species present at Svalbard, and then only in 5 of the surveyed localities. These are also generally larger and deeper than fishless sites, again opening for confounding effects, but we found no statistical effect on fish (as a presence-absence nominal category) in our study.

Thus, it is hard to arrive at strong predictors of species distribution and community composition, but some intriguing patterns, notably related to age, could be detected. The main aim was, however, to provide a "baseline", at least regionally, for key freshwater taxa, and below we thus discuss the species and communities in more detail.

Community and species responses: Nematodes and tardigrades were the only taxa represented in the newly established waterbody in front of the glacier in Grønfjorden. Both groups include extremely tolerant forms and have successfully adapted to nearly all ecosystems. Free-living nematodes are a major component of both pelagic and meiofaunal communities (Majdi and Traunspurger 2015) and 95 species have been reported from Spitzbergen inhabiting mosses, soil and water (Coulson 2014). Even from debris-covered glaciers, several species have been reported (Azzoni et al. 2015).

Likewise, tardigrades constitute a permanent and ubiquitous faunal component of polar regions (Zawierucha et al. 2016) and have also been recorded in supraglacial ecosystems like small puddles at glaciers (De Smet and van Rompu 1994, Hodson et al. 2008). Due to their size and robustness, this group can easily spread to nearby locations by wind and birds. This group has a high tolerance to harsh conditions, such as dehydration, freezing and radiation, and can survive either in anabiosis or an active state where morphological, physiological and molecular adaptations may occur (Wełnicz et al. 2011). According to Pugh and McInnes (1998), arctic tardigrades was probably derived from wind-blown Nearctic propagules that colonized the region during the Holocene.

Chironomids are better adapted to the arctic environment than any other insect group and are hence an important contributor to arctic diversity (Coulson et al. 2014). As other winged insects they are capable of dispersal and rapid colonization. In age-class 2 localities (covered with ice until 1990), we recorded five species, among others *Oliveridia tricornis*, which was associated with low temperature (CCA- ordination, Fig. 5). It has a rather low-temperature optimum and is characteristic of ultra-oligotrophic lakes (Coffman et al. 1986; Luoto et al. 2015). According to Brooks and Birks (2004), *Oliveridia* sp was the only repentant of chironomdes found in a glacier-fed lake (Lake Birgervatnet) on the West coast of Spitzbergen. We recorded the species in a very clean pond formed from a river not far from the Aldegondabreen glacier.

Other early colonizers or pioneer species were the cyclopoid copepod *Cyclops abyssorum* and a representative for the phylum Annelida (Lumbricillus sp.), both represented in age-class 2. *C. abyssorum* was the most common copepod in our study, found in nearly half of the localities. Its preference for cold sites is confirmed by its presence on the mainland Norway, where it is most abundant in alpine lakes (situated > 1000 m above sea) and it is also among the most common copepods in the Alps (Jersabek 2001).

Localities formed in the period 1932–1990 or prior to this contained most taxa among the surveyed sites, and the diversity differed only marginally between these categories, suggesting quite a fast colonization. The localities are, however, closely situated, and repeated transmission of species by birds is likely. For the cladocera, which has asexual formation and resting stages tolerant to freezing and desiccation, wind is also a likely spreading mechanism (Bennike 1999, Incagnone et al. 2015), which is especially effective for small distances in-between sites. Finally, humans may also serve as vectors related to transportation, tourism and scientific fieldwork (Waterkeyn et al. 2010; Incagnone et al. 2015).

Conductivity was an important driver along axis 2, most probably due to high marine impact because of the close distance to the sea. The harpacticoid *Tahidius discipes* and the annelid *Marionina* sp. were both strongly associated with high conductivity. *T. discipes* is a brackish water species (Song et al. 2009), while *Marionina* sp, among others, includes two species (*M macgrathi* and *M. ulstrupae*) that live on wave-exposed rocky shores (Healy 2007). Micro sp., *Micropsectra radiali* and the trichoptera *Apatania zonella* were, in contrast, strongly associated with low conductivity. The latter is associated with the outlet from lakes (Lods-Crozet et al. 2007).

The diversity assessed in this study cover taxa down to species level. A closer examination of taxa that may cover species-complexes like *Daphnia* cf. pulex (Vergilino et al. 2011) and *Chydorus sphaericus* (Belyaeva & Taylor, 2009) could have revealed a somewhat higher diversity but would have required molecular analysis. This also holds for clonal diversity, which may clearly add another level of variance to species diversity for the cladocerans, which often are obligate asexual at these high latitudes. *Daphnia* encompasses a species complex with high clonal diversity (Sarnelle and Wilson 2004). Alfsnes et al. (2016) recorded the highest species and clonal diversity of *Daphnia* in nutrient-rich and bird-impacted localities at Svalbard and concluded, based on comparisons with data from the same localities in 1992, that increased species and clonal changes could likely be attributed to climate change and increased bird impacts.

The strong increase in temperatures and extended growing season over the past few decades in the high Arctic (Holm *et al.* 2012; Xu et al. 2013) will undoubtedly affect freshwater ecosystems with respect to productivity, community composition and the establishment of new species. For example, five copepods and two cladocerans new to Svalbard were recorded during our samplings: *Diacyclops abyssicola*, *Epactophanes richardi*, *Geeopsis incisipes, Nitokra spinipes, Diaptomus* sp., *Alona werestchagini* and *Polyphemus pediculus* (details in Dimante-Deimantovica et al. in prep). *Epactophanes richardi* was the most common of the newcomers found in 15 localities, often in high number. The others were all found in less than four localities, but then commonly in high number. It should be noted, however, that since previous studies to our knowledge did not search specifically for harpacticoid species, "new to Svalbard" may not, in this case, imply that they have become established over the past 100 years.

Among cladocerans, a recent and prominent trend is a widespread establishment of *Bosmina longispina*. This is by far the most common species in mainland lakes in Norway (Hessen and Walseng 2006) but has previously not been positively identified at Svalbard. We cannot exclude the possibility that it has been mistaken for *B. longirostris* for which there exists a couple of observations (Zawisza and Szeroczynska 2011; Luoto 2015). Neither of these species was recognized by Olofsson (1918), and since *B. longispina* is now occurring in some of the sites he visited as well as 15 of the localities that were sampled during our campaign in 2014/15, it very likely has benefited from the elevated temperatures and extended growing season. None of the previously recorded species has disappeared; hence the total species richness will potentially continue to increase over the coming years.

In some of the fishless ponds, truly planktonic species were only found in a near-bottom layer. It appears that these species have rather abandoned the pelagic zone due to the heavy pressure of the *Daphnia* population. Some of the recorded species were rare and found in one or only a few localities, while others were common and could either be widespread or the occurrence could vary geographically as for example the cladoceran *Macrothrix hirsuticornis* and the copepod *Eurytemora raboti*. These species were most common in the northern part of the study area, i.e. Billefjorden and Ny-Ålesund. Here, they occurred in >50% of the localities, while the corresponding figure for Grønfjorden further south was <20%.

Generally, all macrobenthic communities in Svalbard have a simple and very similar taxonomical structure, with dominance of chironomids larvae (Brooks and Birks 2004, Lods-Crozet et al. 2007). Except for *M. insignilobus* which was for the first time reported from Svalbard in 2011 (Velle et al. 2011), most taxa seem to be rather common.

To evaluate possible recent changes in abundance and frequency, we compared our data on chironomids with data from a study in 23 lakes situated in western Svalbard sampled in 1993 (Brooks and Birks 2004). The species were here presented as abundance/frequency from the upper 1 cm of the sediment. The two most frequent/abundant taxa of his study, *Micropsectra radialis* and *Orthocladius* sp, were less common in our study. On the other hand, *Paratanytarsus austriacus* had become much more abundant and found in 30 localities in our study. Whether this reflects weather, climate or stochastic events remains an open question.

While not a true "baseline" study in the sense of an inventory prior to anthropogenic effects, our study presents the hitherto most comprehensive data on invertebrate freshwater diversity at Svalbard, and in areas where there are most biotic activity, ponds and likely highest diversity. It may thus serve as a reference for future changes but also demonstrate that climate change, both directly and indirectly, notably via increased geese density and activity (Hessen et al. 2017), affect the species composition and diversity of these high Arctic ecosystems. Finally, our study also clearly demonstrates a diversity gradient related to ecosystem age or parameters related to age (like productivity), which may hint at the rate of colonization over the time span from the oldest to the youngest localities.

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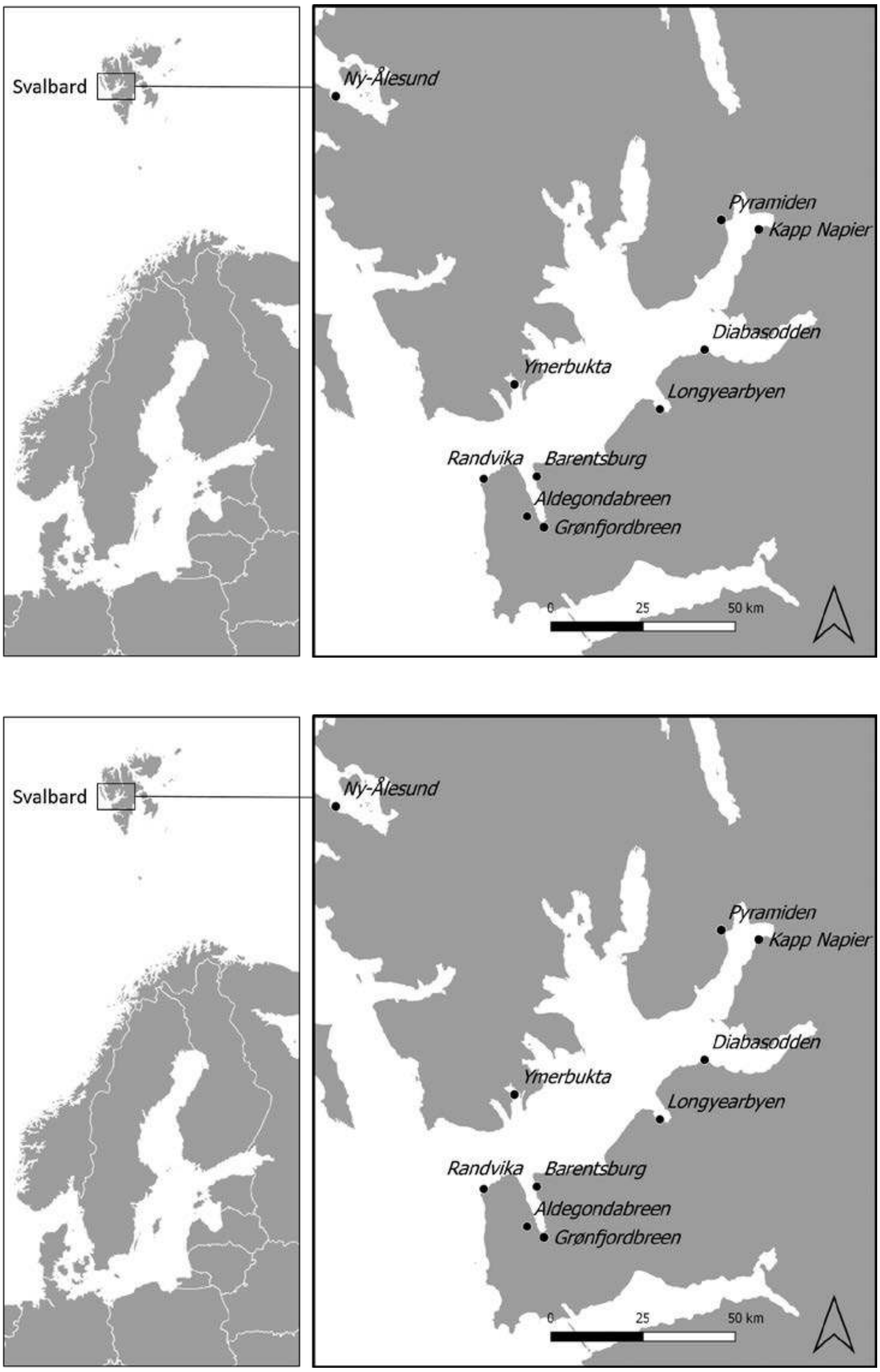

Fig. 1. An overview over the investigated areas in Svalbard, Spitsbergen, in 2014 and 2015.

Fig. 2. Examples of puddle (Aldegondabreen glacier up left), small pond (Longyearbyen up right), large pond (Aldegondabreen glacier down left) and a lake west of Pyramiden. Photos: Bjørn Walseng

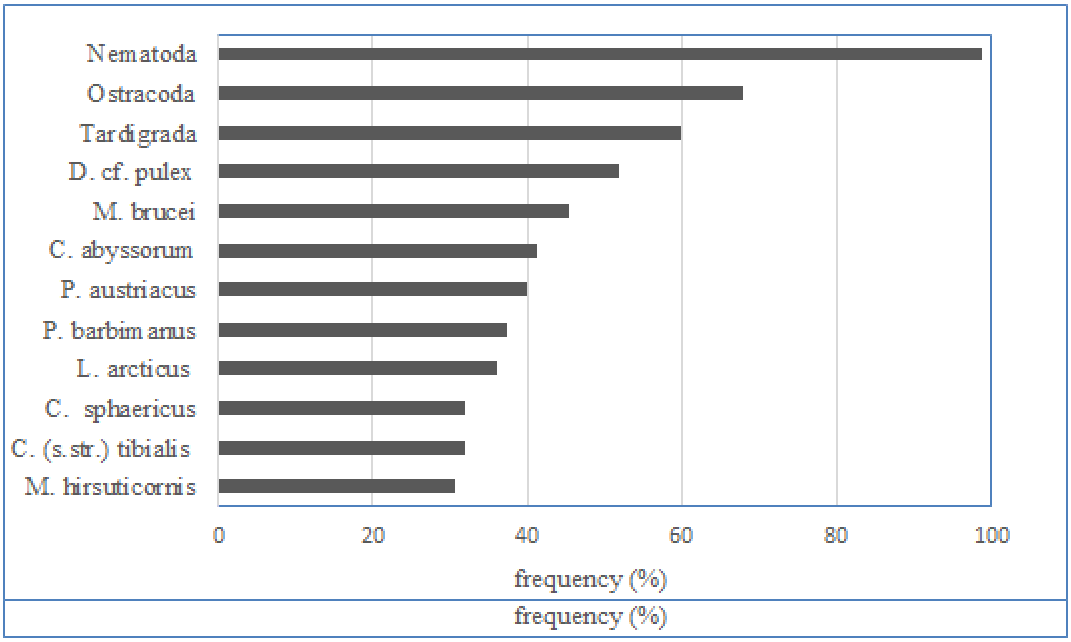

Fig. 3. Taxa which occurred in more than 30% of the localities (n=75).

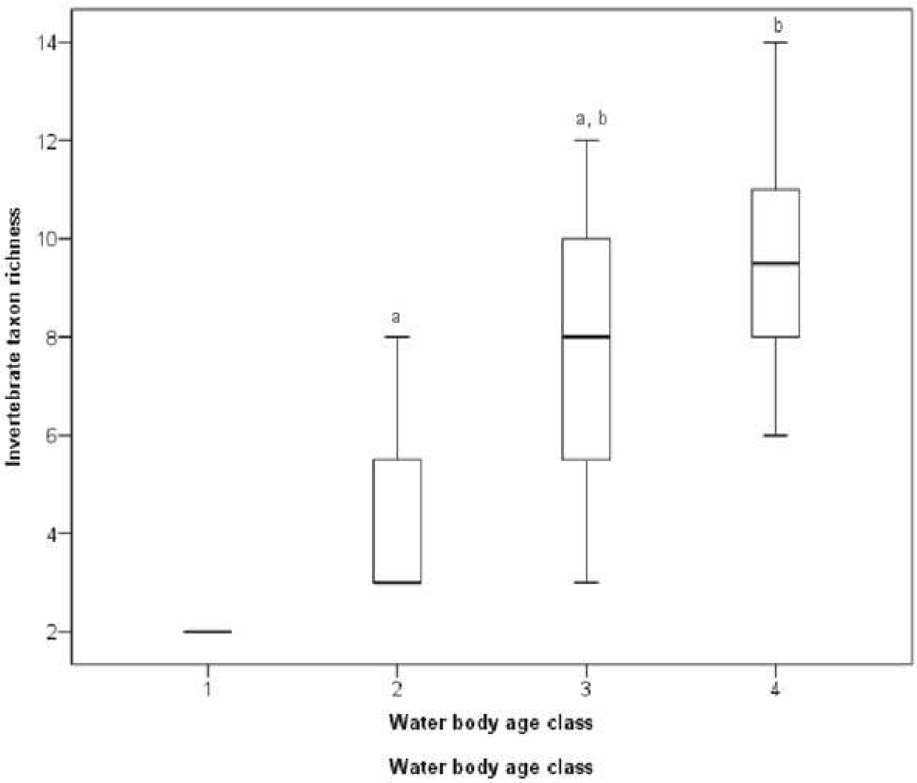

Fig. 4. Box-plot showing invertebrate taxa richness in four groups of water bodies according to age (1: 2001/2010 to the present, 2: 1990–2001/2010, 3: 1936/1972–1990 and 4: < 1936/1972). For an explanation of water body age class, see material and methods section. Different letters above columns indicate a significant difference between means (t-test with Bonferroni correction, $p<0.05$). The youngest age-class only contained one water body. Hence, a pairwise comparison was only conducted between age-classes 2, 3 and 4.

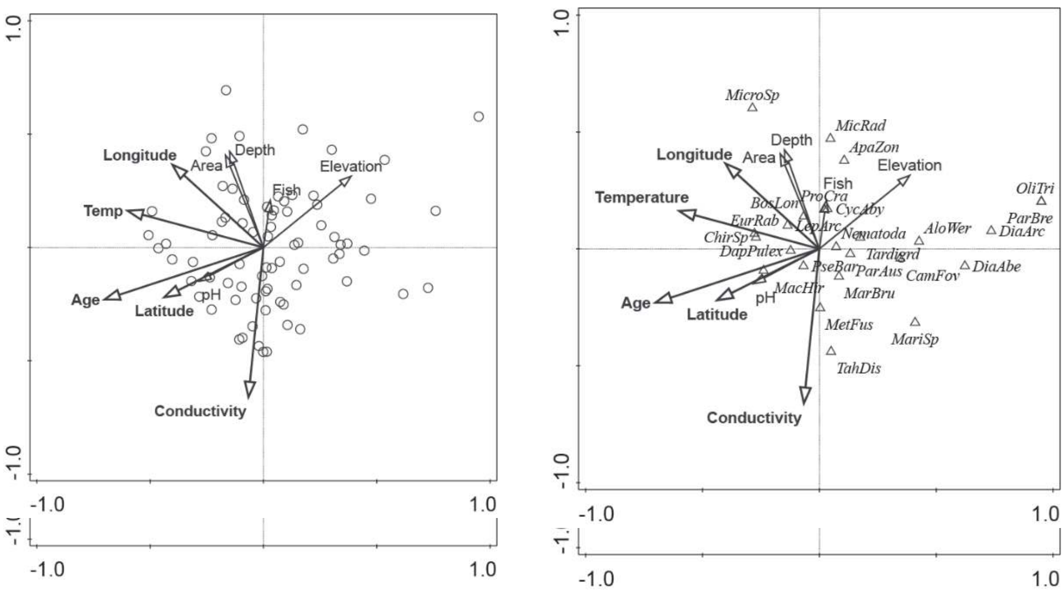

Fig. 5. CCA of the invertebrate community in the surveyed water bodies on Svalbard. Left panel: CCA–ordination plot of the 75 study sites. Right panel: CCA–ordination plot of invertebrate taxa showing the 25 best fitting invertebrate taxa in the ordination space. Environmental variables included in both plots are both significant (in bold: age, temperature, conductivity, longitude and latitude) and non-significant variables from the minimal model (all other environmental variables). Species are abbreviated as MicroSp: *Micropsectra* sp., MicRad: *Micropsectra radialis*, ApaZon: *Apatania zonella*, OliTri: *Oliveridia tricornis*, ParBre: *Paraphaenocladius brevinervis*, DiaArc: *Diamesa gr. arctica*, AloWer: *Alona werestschagini*, Nematoda: nematodes, CycAby: *Cyclops abyssorum*, ProCra: *Procladius crassinervis*, LepArc: Lepidurus arcticus, BosLon: Bosmina longispina, DapPulex: *Daphnia pulex*, ChirSp: *Chironomus* sp., EurRab: *Eurytemora raboti*, MacHir: *Macrothrix hirsuticornis*, PseBar: *Psectrocladius barbimanus*, Tardigrd: tardigrades, ParAus: *Paratanytarsus austriacus*, CamFov: *Camisia foveolata*, Dia Abe: *Diamesa aberrata*, MarBru: *Maraenobiotus brucei*, MetFus: *Metriocnemis gr fuscipes*, TahDis: *Tahidius discipes*, MariSp: *M* .

Tab 1. Correlation coefficient and significance level e (Pearson correlation) for longitude, latitude, elevation, depth class, area class, water body age class, presence/absence of fish, pH, conductivity, water temperature and invertebrate taxa richness. Elevation and conductivity were transformed (log10(X + 1)). **Correlation is significant at the 0.01 level. * Correlation is significant at the 0.05 level.

	Longitude	Latitude	Elevation	Depth class	Area class	Age class	Fish	pH	Conductivity	Temperature	Taxon richness
Longitude	1										
Latitude	-0.257*	1									
Elevation	-0.302**	0.171	1								
Depth class	-0.144	0.099	0.083	1							
Area class	-0.136	0.141	0.089	0.905**	1						
age	0.1306	0.296**	-0.226	0.111	0.100	1					
Fish	-0.031	-0.211	-0.145	0.325**	0.357**	0.073	1				
pH	0.123	0.189	0.084	0.194	0.126	0.073	0.050	1			
Conductivity	0.120	0.176	-0.369**	-0.363**	-0.410**	-0.031	-0.003	0.115	1		
Temperature	0.227	-0.070	-0.310**	0.061	0.034	0.403**	-0.046	-0.023	-0.042	1	
Taxon richness	0.005	0.171	0.013	0.133	0.162	0.488**	-0.007	0.146	-0.063	0.193	1

Tab 2. Parameter estimates for multiple regression models relating invertebrate taxa richness to longitude, latitude, elevation, depth class, area class, water body age class, presence/absence of fish, pH, conductivity and water temperature. For an explanation of depth-, area- and age-class, see methods chapter. Elevation and conductivity were transformed (log10(x+1)). A backward selection procedure was used to select predictors and two-way interactions from the full model (p > 0,1). However, none of the interactions were significant.

Response variable	Coefficients	Estimate (± SE)	t-value	*p*
Invertebrate taxon richness	Intercept	1.224 (1.623)	0.754	0.453
	Age	2.107 (0.441)	4.779	0.000

Tab. 3. Results of the CCA of the taxonomical composition of the invertebrate community in lentic water bodies on Svalbard. Also given are intra-set correlations of environmental variables with CCA axes.

	Axis 1	Axis 2	Axis 3	Axis 4	Total
Eigenvalues	0.1925	0.1053	0.0862	0.0712	2.7664
Pseudo-canonical correlation	0.8338	0.7462	0.7066	0.7666	
Explained variation (cumulative)	6.96	10.76	13.88	16.45	
Explained fitted variation	30.41	47.04	60.67	71.92	
Sum of all eigenvalues					2.7664
Sum of all canonical eigenvalues					0.63
Intra-set correlations of environmental variables with axe	Axis 1	Axis 2	Axis 3	Axis 4	
Longitude	-0.4017	0.3647	-	-0.4355	
Latitude	-0.4378	-	-	0.4514	
Elevation	0.3864	0.314	0.3466	0.1075	
Depth	-0.1671	0.4061	0.3471	0.0778	
Area	-0.1491	0.4232	0.2791	-0.0555	
Age	-0.7016	-	0.1707	-0.4507	
Fish	0.0302	0.2073	0.0573	-0.2888	
pH	-0.282	-	0.2918	0.2865	
Conductivity	-0.0662	-	-	-0.0701	
Temperature	-0.5999	0.1621	0.4216	-0.0301	

Appendix 1. Coordinates, surface area (km2), elevation (m asl) and depth categories (1: < 0,25 m, 2: 0,25-1 m and 3: >1 m) for the 75 investigated localities.

Loc	East	North	Area km²	m asl	depth	Loc	East	North	Area km²	m asl	depth
1	1545,8	7812,2	0,0000045	13	1	52	1612,2	7839,2	0,0002	52	2
5	1542,4	7813,1	0,00039	8	2	53	1607,1	7838,4	0,027	166	3
6	1411,1	7759,5	0,0000019	12	1	54	1644,1	7838,3	0,017	6	1
7	1411,0	7759,4	0,0000019	18	1	55	1644,5	7838,3	0,000105	8	2
8	1410,8	7759,5	0,00002	25	1	56	1644,0	7838,2	0,0065	8	3
9	1410,1	7759,4	0,015	50	3	57	1644,2	7838,1	0,00004	15	1
10	1411,6	7759,5	0,004756	6	3	58	1644,2	7837,9	0,0003	15	2
11	1411,7	7759,5	0,000008	8	1	59	1644,6	7838,1	0,00007	10	1
13	1410,6	7759,2	0,000006	46	1	60	1620,5	7839,1	0,00007	8	1
14	1409,2	7759,2	0,000015	41	1	62	1606,5	7821,7	0,0004	28	2
15	1409,0	7759,2	0,000025	41	1	64	1610,1	7821,5	0,00015	4	2
19	1408,7	7758,9	0,000045	44	1	65	1152,7	7855,4	0,0156	49	3
21	1410,6	7759,1	0,01075	28	3	66	1203,5	7854,9	0,027	18	3
23	1411,2	7759,1	0,006612	4	3	67	1204,3	7854,3	0,00075	42	2
25	1414,0	7758,2	0,002	5	2	68	1203,8	7854,3	0,002625	29	3
26	1414,5	7757,9	0,0006	6	2	69	1204,0	7854,0	0,0048	73	3
27	1414,9	7757,6	0,007918	12	3	70	1203,7	7853,9	0,0014	69	2
29	1347,5	7805,0	0,0009	42	2	71	1204,7	7854,2	0,00016	38	2
30	1347,6	7804,9	0,0004	16	2	72	1151,8	7855,0	0,0296	56	3
31	1348,2	7804,9	0,0015	15	3	74	1156,3	7855,5	0,01125	23	3
32	1347,9	7805,0	0,0021	23	2	75	1155,4	7855,5	0,00025	27	2
33	1348,8	7804,4	0,0018	73	2	76	1157,2	7855,2	0,000015	77	1
34	1348,5	7804,1	0,007	41	3	77	1157,7	7855,1	0,000036	18	1
36	1347,0	7804,0	4,6	11	3	78	1158,5	7854,9	0,00005	19	1
37	1347,7	7804,2	0,016872	27	3	81	1148,0	7856,1	0,002	60	2
38	1347,9	7804,3	0,016	28	3	82	1149,0	7856,1	0,0015	54	2
39	1347,9	7804,5	0,0035	30	3	84	1415,6	7757,4	0,00004	37	1
40	1348,0	7804,5	0,0003	34	2	85	1415,6	7757,4	0,000096	37	1
41	1347,1	7804,4	0,0035	34	3	86	1415,8	7757,3	0,0026	34	3
42	1413,0	7804,2	0,0009	92	2	87	1416,0	7757,2	0,00008	47	1
43	1411,6	7805,7	0,0004	51	2	88	1416,9	7757,3	1,3299	12	3
45	1404,7	7816,8	0,15768	15	2	89	1416,9	7757,2	0,000006	27	1
46	1405,5	7816,8	0,045	16	2	90	1415,6	7757,0	0,000024	52	1
47	1407,0	7817,0	0,0192	15	2	91	1415,6	7756,4	0,01113	35	3
48	1406,9	7816,9	0,0005	21	2	92	1415,0	7756,6	0,0001	61	2
49	1611,0	7839,4	0,0345	110	3	93	1415,6	7757,8	0,00004	26	1
50	1611,4	7839,3	0,0377	61	3	98	1410,3	7800,1	0,00035	34	2
51	1612,5	7839,3	0,0003	50	2						

Appendix 2 Occurrence of invertebrate taxa along the water body age gradient.

Taxa		Age class 1	Age class 2	Age class 3	Age class 4
Nematoda	Nematoda	X	X	X	X
Tardigrada	Tardigrada	X	X	X	X
Oligochaeta	Enchytraeus sp.				X
Oligochaeta	Lumbricillus sp.		X	X	X
Oligochaeta	Marionina sp.			X	X
Cladocera	Acroperus harpae			X	X
Cladocera	Alona guttata			X	X
Cladocera	Alona werestschagini			X	
Cladocera	Bosmina longispina			X	X
Cladocera	Chydorus sphaericus			X	X
Cladocera	Daphnia cf. pulex			X	X
Cladocera	Macrothrix hirsuticornis			X	X
Cladocera	Polyphemus pediculus			X	
Ostracoda	Ostracoda			X	X
Calanoida	Eurytemora raboti			X	X
Calanoida	Diaptomidae sp.			X	X
Cyclopoida	Diacyclops crassicaudis			X	X
Cyclopoida	Cyclops abyssorum		X	X	X
Cyclopoida	Diacyclops abyssicola				X
Cyclopoida	Eucyclops sp.			X	
Harpacticoida	Epactophanes richardi			X	X
Harpacticoida	Maraenobiotus brucei			X	X
Harpacticoida	Tahidius discipes			X	X
Harpacticoida	Nitokra spinipes				X
Harpacticoida	Geeopsis incisipes				X
Harpacticoida	Nannopus didelphis				X
Notostraca	Lepidurus arcticus			X	X
Acari	Ameronothrus lineatus				X
Acari	Thalassarachna sp.				X
Acari	Halacarellus sp.				X
Acari	Camisia foveolata			X	X
Trichoptera	Apatania zonella			X	X
Chironomidae	Diamesa aberrata		X	X	X
Chironomidae	Diamesa bertrami			X	X
Chironomidae	Diamesa gr arctica		X		X
Chironomidae	Paraphaenocladius				X
Chironomidae	Smittia sp.				X
Chironomidae	Cricotopus (s. str.) tibialis			X	X
Chironomidae	Cricotopus s.str.			X	X
Chironomidae	Cricotopus (Isocladius)			X	X
Chironomidae	Psectrocladius barbimanus			X	X
Chironomidae	Metriocnemis gr fuscipes			X	X

Taxa		Age class 1	Age class 2	Age class 3	Age class 4
Chironomidae	Oliveridia tricornis		X		
Chironomidae	Hydrobaenus conformis		X	X	X
Chironomidae	Paraphaenocladius		X		
Chironomidae	Orthocladius s.str.			X	X
Chironomidae	Chaetocladius s.str.			X	
Chironomidae	Procladius crassinervis			X	X
Chironomidae	Paratanytarsus austriacus			X	X
Chironomidae	Micropsectra insignilobus			X	X
Chironomidae	Micropsectra radialis Goetghebuer			X	X
Chironomidae	Micropsectra sp.				X
Chironomidae	Chironomus sp.				X