

1 **Freshwater diversity in Svalbard;**
2 **providing baseline data for ecosystems in change**

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39 [246726]”.

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41

42 **Abstract**

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

58

59

60 **Introduction**

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

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

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

98 Fortunately, there exist some old recordings of the Svalbard freshwater fauna
99 (Brehm 1917, Thor 1930), and the most extensive study dates more than 100 years back
100 to a survey in 1910 (Olofsson 1918). These data, focusing on rotifers and crustaceans,
101 were gathered in the Isfjorden and Van Mijenfjorden area, possessing numerous ponds
102 and a few lakes. Since Olofsson's seminal survey there have only been some scattered
103 studies on crustaceans (e.g., Halvorsen and Gullestad 1976, Jørgensen and Eie 1993
104 Husman et al. 1978, Kubicek and Terek 1991). Some studies have also specifically
105 addressed the clonal diversity of the widespread and dominant cladoceran *Daphnia*
106 (Weider and Hobaek 1994) as well as the impact of birds on species and clonal
107 composition (van Geest et al. 2007; Alfsnes et al. 2016). For other compartments of the
108 freshwater fauna, there is even more scarce information, and some groups are hardly
109 recorded, at least not in any systematic manner. Among the insects, there is a strong
110 dominance of Diptera, which is the most species-rich freshwater group in Svalbard,
111 being 122 species at Svalbard and Bear Island (Coulson and Refseth 2004; Coulson
112 2014). This group is better adapted to the cold and harsh climate in the arctic than any
113 other order of insects (Coulson and Refseth 2004).

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

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

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

130

131 **Material and Methods**

132 Altogether 75 localities were sampled in Svalbard in 2014 and 2015. In the period
133 18–24 August 2014, sampling was conducted in different parts of Isfjorden:
134 Longyearbyen (2 localities), the gradient Aldegondabreen-Grønfjorden (16), Randvika
135 (12), Barentsburg (2), Ymerbukta (4), Pyramiden (6), Kapp Napier (6) and Diabasodden
136 (2) (Fig. 1). In 2015 (17 – 19 August) 15 localities in Ny-Ålesund area (including six
137 localities along the gradient from the sea and to the glacier Midtre Lovèn breen) and 10
138 localities along the gradient from Grønfjorden to the glacier Vestre Grønfjordbreen were
139 sampled. These localities also covered the areas sampled in 1910 (Olofsson 1918).

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

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

153 Monitoring Group for Pan-Arctic Monitoring program and from other literature sources
154 (Culp et al. 2012; Rautio et al. 2011). The localities ranged from 4 m to 166 m above sea;
155 surface area varied from puddles less than 2 m² to 460 ha and depths of 0.25 to 37 m.
156 Lake Linnè was the largest and deepest lake. For the analysis we categorized the sites in
157 four classes according to their size; 1 (puddle): ≤ 0.01 ha, 2 (small pond): 0.01–0.1 ha, 3
158 (large pond): 0.1–1.0 ha, 4: (lake) > 1.0 ha, and three classes according to their average
159 depths (1: ≤ 0.25 m, 2: 0.25–1 m, 3: > 1 m). With a few exceptions, all ponds were
160 shallow and less than 1 m deep. Depth estimates for the lakes are, however, somewhat
161 rough since they for logistic reasons had to be performed without the use of a boat.
162 Examples of these categories are provided in Fig. 2.

163 The past coverage of glaciers on Svalbard is shown in the digital atlas of “Glaciers
164 on Svalbard” published by the Norwegian Polar Institute
165 (<http://svalbardkartet.npolar.no/html5/index.html?viewer=svalbardkartet>). The basis for
166 the atlas is three sets of maps showing the distribution of the glaciers created in the
167 period 1936–72, in 1990 and later in the period 2001–2010. Based on the atlas we
168 grouped the localities into four age classes; 1) 2001/2010 to the present (1 locality), 2)
169 1990–2001/2010 (3 localities), 3) 1936/1972–1990 (19 localities) and 4) < 1936–1972
170 (52 localities). The age of the oldest localities may cover a wider span (i.e Velle et al.
171 2011), but in the absence of proper dating we have pooled them into one category that
172 has been without a permanent ice-cover for an extended period.

173 pH was > 7.0 in all waterbodies with a mean of 8.5, and a max of 9.5 (small pond,
174 Diabasodden). The lowest pH, 7.3, was recorded in a small pond in Ymerbukta. Most
175 sites had high conductivity (mean 413, max 1750 μS cm⁻¹). pH, conductivity and
176 temperature were measured by applying Hanna Instruments waterproof tester (HI98129
177 and HI98130).

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

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

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

197 *Meibenthos* was sampled using a plastic tube that was inserted into the uppermost 3–4 cm
198 of the sediment layer. From each site, 2–3 samples were taken randomly, all representing different
199 meiobenthic habitat substrates if possible, and then pooled. Each sample covered an area of 3
200 cm². The samples were preserved with 96 % ethanol and filtered (50- μ m mesh) before
201 identification following Dussart and Defaye (1983), Bartsch (2006) and Alekseev and
202 Tsalolikhin (2010).

203 *Macrobenthos* samples were taken from the shore to a depth of ca 1.5 m (or max
204 depth in the more shallow sites). We used a hemispherical scraper (diameter 16 cm,
205 area 0.02 m², mesh size 0.5 mm) and 5–10 samples (depending on the density of
206 organisms) were merged into one sample. Mud and coarse gravel were eliminated
207 before the sample was preserved with 96 % ethanol. Identification was performed
208 according to Wiederholm (1983), Timm (2009) and Makarchenko (2001).

209 Neither of these samplings allowed for a precise quantitative judgment; hence we
210 applied four “dominance classes” on an ordinal scale to reflect the dominance of species
211 based on frequencies in the individual sample (0: absent, 1: <1%, 2: 1–10%, 3: >10%)
212 (Walseng et al. 2006). The relationship between taxa richness and the environmental
213 variables longitude, latitude, elevation, depth, area, age, presence of fish, pH,
214 conductivity and water temperature was analyzed by univariate multiple linear

215 regression. Due to the high number of possible interactions between environmental
216 variables, interactions were not included in the analysis. Taxa richness was checked for
217 normality and homogeneity of variances. A backward selection procedure was used to
218 exclude predictors from the model ($P > 0.1$). Elevation and conductivity were log-
219 transformed. For pair-wise comparisons of means of taxa richness in the different age
220 classes, t-tests with Bonferroni correction was applied. Hence, the observed significance
221 level is adjusted for multiple comparisons. The youngest age class only contained one
222 water body. Therefore, the pairwise comparisons were only conducted between age
223 classes 2, 3 and 4.

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

243 **Results**

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

250 The two most taxon-rich invertebrate groups were crustaceans and chironomids,
251 both constituting 22 and 21 taxa, respectively. Crustaceans were found in both
252 zooplankton and meiobenthos samples and were represented by four groups; Cladocera
253 (8 taxa), Cyclopoida (4 taxa), Calanoida (2 taxa) and Harpactoida (6 taxa) (Appendix 1).
254 On average 4.3 species of crustaceans were found per locality (from zero to 8 species).
255 The most common cladoceran, *Daphnia cf. pulex*, was found in 39 localities and was
256 often the dominating species. The most common harpactoid, *Maraenobiotus brucei*, was
257 found in nearly half of the localities (34). Another common crustacean was *Lepidurus*
258 *arcticus*, a cold water, primarily benthic notostracan, which was recorded in 27 localities.

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

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

269 The model for taxon richness was statistically significant ($F_{1, 73} = 22.838$, $p =$
270 0.000 , $R^2 = 0.238$ %, $n = 75$) and included significant effects of water body age (Tab.
271 2).

272 The pair-wise comparison revealed that mean taxa richness in age class 2 was
273 significantly lower than that of age class 4 (Fig. 4, t-test with Bonferroni correction,

274 difference between means = 4.891, $p = 0.003$). The first two CCA axes in the
275 ordination of the invertebrate community had eigenvalues of 0.1925 and 0.1053,
276 respectively, and explained 10.8 % of the variation in the species' composition and 47.0
277 % of the variation in the species-environment relationship (Table 3; Fig. 5). There was
278 a significant relationship between the set of environmental variables and species'
279 composition (i.e. all canonical axes, pseudo-F = 1.9, $p = 0.002$). The "minimal adequate
280 model" resulting from the forward selection included the explanatory variable water
281 body age (pseudo-F = 3.5, $p = 0.002$), temperature (pseudo-F = 2.2, $p = 0.006$),
282 conductivity (pseudo-F = 2.1, $p = 0.002$), longitude (pseudo-F = 2.1, $p = 0.002$) and
283 latitude (pseudo-F = 2.1, $p = 0.002$). The intra-set correlations of environmental
284 variables with the CCA axes (Tab. 3) and the CCA biplot (Fig. 5) showed that the
285 invertebrate community in the water bodies was distributed mainly along a gradient of
286 age and temperature on CCA axis 1. CCA axis 2 was mainly correlated with
287 conductivity (Tab. 1, Fig. 5).

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

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

304

305 **Discussion**

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

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

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

334 *Community and species responses:* Nematodes and tardigrades were the only taxa
335 represented in the newly established waterbody in front of the glacier in Grønfjorden.
336 Both groups include extremely tolerant forms and have successfully adapted to nearly all

337 ecosystems. Free-living nematodes are a major component of both pelagic and
338 meiofaunal communities (Majdi and Traunspurger 2015) and 95 species have been
339 reported from Spitzbergen inhabiting mosses, soil and water (Coulson 2014). Even from
340 debris-covered glaciers, several species have been reported (Azzoni et al. 2015).

341 Likewise, tardigrades constitute a permanent and ubiquitous faunal component of
342 polar regions (Zawierucha et al. 2016) and have also been recorded in supraglacial
343 ecosystems like small puddles at glaciers (De Smet and van Rompu 1994, Hodson et al.
344 2008). Due to their size and robustness, this group can easily spread to nearby
345 locations by wind and birds. This group has a high tolerance to harsh conditions, such as
346 dehydration, freezing and radiation, and can survive either in anabiosis or an active state
347 where morphological, physiological and molecular adaptations may occur (Wełnicz et
348 al. 2011). According to Pugh and McInnes (1998), arctic tardigrades was probably
349 derived from wind-blown Nearctic propagules that colonized the region during the
350 Holocene.

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

361 Other early colonizers or pioneer species were the cyclopoid copepod *Cyclops*
362 *abyssorum* and a representative for the phylum Annelida (*Lumbricillus* sp.), both
363 represented in age-class 2. *C. abyssorum* was the most common copepod in our study,
364 found in nearly half of the localities. Its preference for cold sites is confirmed by its
365 presence on the mainland Norway, where it is most abundant in alpine lakes (situated >
366 1000 m above sea) and it is also among the most common copepods in the Alps (Jersabek
367 2001).

368 Localities formed in the period 1932–1990 or prior to this contained most taxa

369 among the surveyed sites, and the diversity differed only marginally between these
370 categories, suggesting quite a fast colonization. The localities are, however, closely
371 situated, and repeated transmission of species by birds is likely. For the cladocera, which
372 has asexual formation and resting stages tolerant to freezing and desiccation, wind is
373 also a likely spreading mechanism (Bennike 1999, Incagnone et al. 2015), which is
374 especially effective for small distances in-between sites. Finally, humans may also serve
375 as vectors related to transportation, tourism and scientific fieldwork (Waterkeyn et al.
376 2010; Incagnone et al. 2015).

377 Conductivity was an important driver along axis 2, most probably due to high
378 marine impact because of the close distance to the sea. The harpacticoid *Tahidius*
379 *discipes* and the annelid *Marionina* sp. were both strongly associated with high
380 conductivity. *T. discipes* is a brackish water species (Song et al. 2009), while *Marionina*
381 sp., among others, includes two species (*M. macgrathi* and *M. ulstrupae*) that live on
382 wave-exposed rocky shores (Healy 2007). Micro sp., *Micropsectra radiali* and the
383 trichoptera *Apatania zonella* were, in contrast, strongly associated with low
384 conductivity. The latter is associated with the outlet from lakes (Lods-Crozet et al.
385 2007).

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

397 The strong increase in temperatures and extended growing season over the past
398 few decades in the high Arctic (Holm et al. 2012; Xu et al. 2013) will undoubtedly
399 affect freshwater ecosystems with respect to productivity, community composition and
400 the establishment of new species. For example, five copepods and two cladocerans new

401 to Svalbard were recorded during our samplings: *Diacyclops abyssicola*, *Epactophanes*
402 *richardi*, *Geeopsis incisipes*, *Nitokra spinipes*, *Diaptomus* sp., *Alona werestchagini* and
403 *Polyphemus pediculus* (details in Dimante-Deimantovica et al. in prep). *Epactophanes*
404 *richardi* was the most common of the newcomers found in 15 localities, often in high
405 number. The others were all found in less than four localities, but then commonly in high
406 number. It should be noted, however, that since previous studies to our knowledge did
407 not search specifically for harpacticoid species, “new to Svalbard” may not, in this case,
408 imply that they have become established over the past 100 years.

409 Among cladocerans, a recent and prominent trend is a widespread establishment of
410 *Bosmina longispina*. This is by far the most common species in mainland lakes in
411 Norway (Hessen and Walseng 2006) but has previously not been positively identified at
412 Svalbard. We cannot exclude the possibility that it has been mistaken for *B. longirostris*
413 for which there exists a couple of observations (Zawisza and Szeroczynska 2011; Luoto
414 2015). Neither of these species was recognized by Olofsson (1918), and since *B.*
415 *longispina* is now occurring in some of the sites he visited as well as 15 of the localities
416 that were sampled during our campaign in 2014/15, it very likely has benefited from the
417 elevated temperatures and extended growing season. None of the previously recorded
418 species has disappeared; hence the total species richness will potentially continue to
419 increase over the coming years.

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

429 Generally, all macrobenthic communities in Svalbard have a simple and very
430 similar taxonomical structure, with dominance of chironomids larvae (Brooks and Birks
431 2004, Lods-Crozet et al. 2007). Except for *M. insignilobus* which was for the first time
432 reported from Svalbard in 2011 (Velle et al. 2011), most taxa seem to be rather common.

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

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

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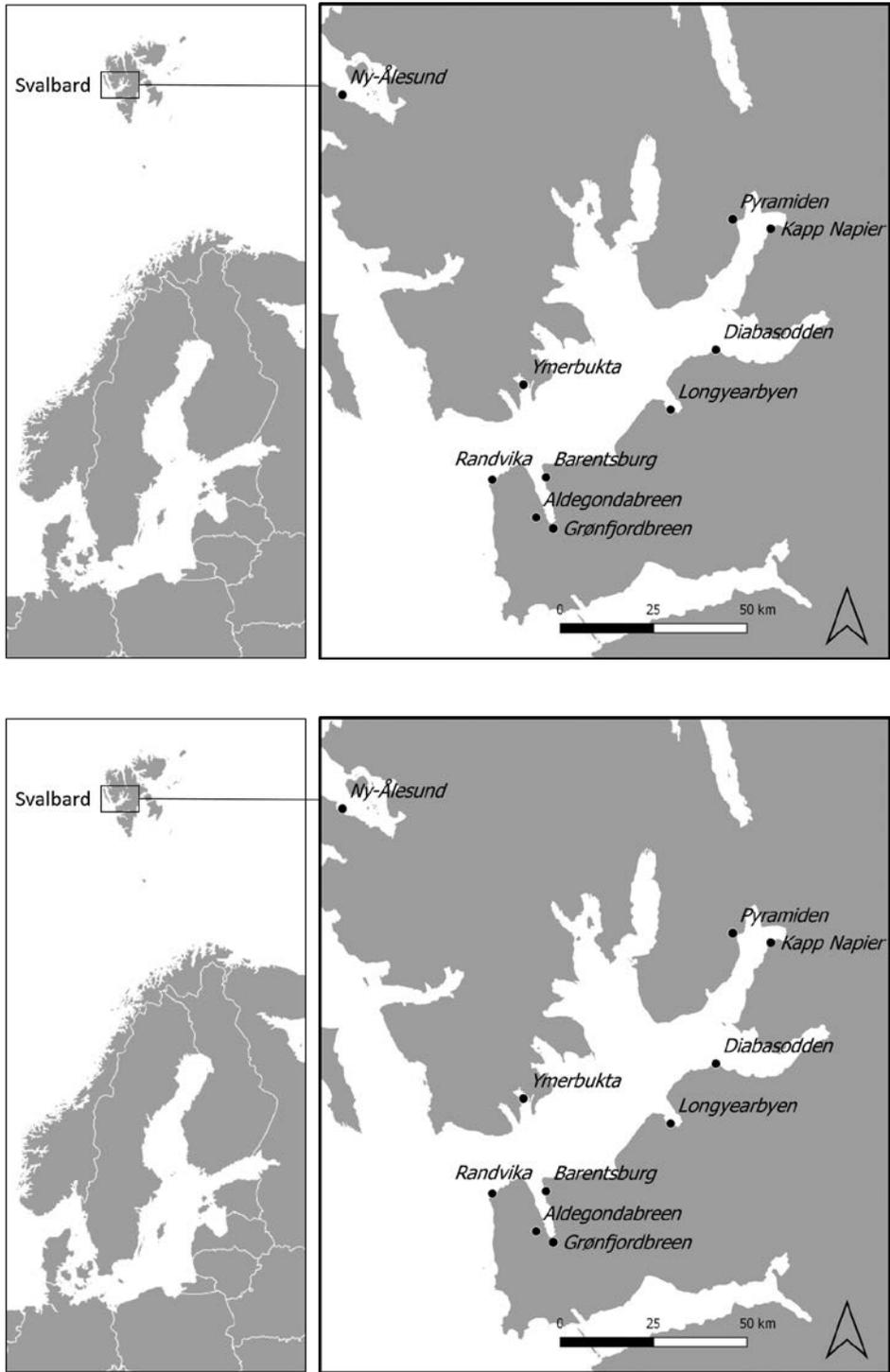
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689 Fig. 1. An overview over the investigated areas in Svalbard, Spitsbergen, in 2014 and
690 2015.

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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

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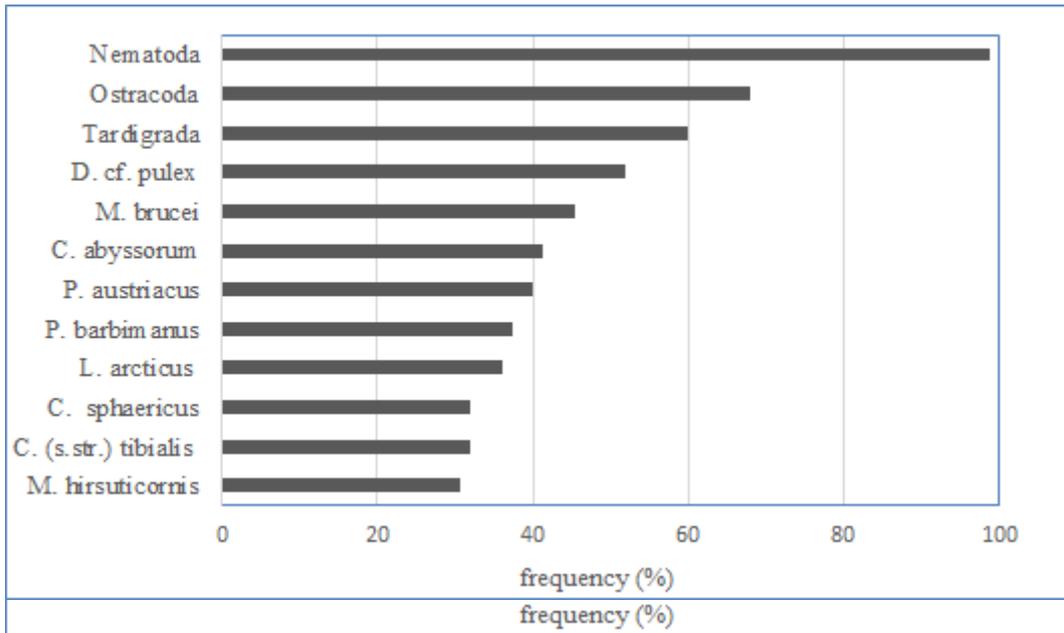


Fig. 3. Taxa which occurred in more than 30% of the localities (n=75).

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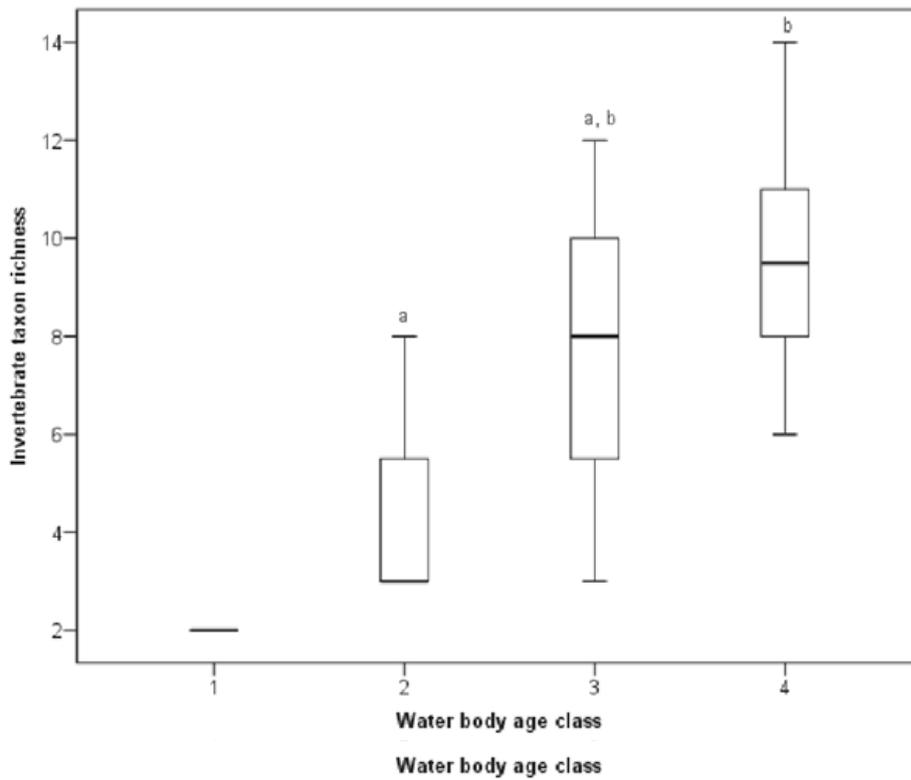


Fig. 4. Box-plot showing invertebrate taxa richness in four groups of water bodies according to age (1: 2001/2010 to the present, 2: 1990–2001/2010, 3: 1936/1972–1990 and 4: < 1936/1972). For an explanation of water body age class, see material and methods section. Different letters above columns indicate 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.

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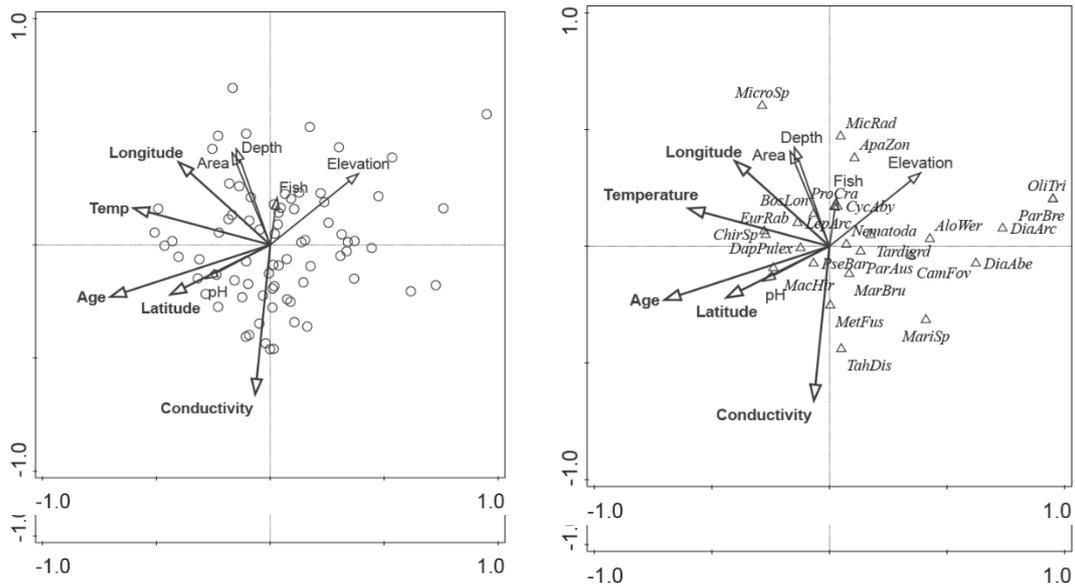


Fig. 5. CCA of the invertebrate community in the surveyed water bodies on Svalbard. Left panel: CCA–ordination plot of the 75 study sites. Right panel: CCA–ordination plot of invertebrate taxa showing the 25 best fitting invertebrate taxa in the ordination space.

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: *Paraphaenocladus brevinervis*, DiaArc: *Diamesa gr. arctica*, AloWer: *Alona werestschagini*, Nematoda: nematodes, CycAby: *Cyclops abyssorum*, ProCra: *Procladius crassinervis*, LepArc: *Lepidurus arcticus*, BosLon: *Bosmina longispina*, 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 r (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 ($\log_{10}(X + 1)$).
 ** 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

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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 ($\log_{10}(x+1)$). 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 (\pm 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

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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 axes	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	

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837 Appendix 1. Coordinates, surface area (km²), elevation (m asl) and depth categories (1: <
838 0,25 m, 2: 0,25-1 m and 3: >1 m) for the 75 investigated localities:-

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Loc	East	North	Area km ²	m asl	depth	Loc	East	North	Area km ²	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						

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845 **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	Paraphaenocladus				X
Chironomidae	Smittia sp.				X
Chironomidae	Cricotopus (s. str.) tibialis			X	X
Chironomidae	Cricotopus s.str.			X	X
Chironomidae	Cricotopus (Isocladus)			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		X	X
Chironomidae	Goetghebuer			
Chironomidae	Micropsectra sp.			X
Chironomidae	Chironomus sp.			X

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