Title:

Changes in trophic state and aquatic communities in high Arctic ponds in response to increasing goose populations.

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Summary

1. The High Arctic, including the Svalbard archipelago in the North Atlantic, has been exposed to direct and indirect drivers of climatic change such as rising temperatures and associated changes in hydrology and nutrient fluxes. In addition, the number of migrating birds, particularly geese, has increased remarkably in the Svalbard archipelago during the second half of the last century. The higher number of breeding birds potentially affects water quality and the biota in ponds and lakes.
2. We aimed to investigate the potential influence of increasing goose abundance on trophic state, taxa richness and species composition of freshwater communities in the high Arctic. We hypothesized that higher goose abundance affects the trophic state of shallow lakes and ponds and their taxon richness and species composition. We conducted a survey of selected ponds at Svalbard along a "goose abundance gradient". We used the number of area-specific goose droppings (range of 0-94 droppings m^2) as a proxy of goose presence and measured proxies for productivity as well as taxon richness and composition of phytoplankton and invertebrate communities.
3. Presence and abundance of geese was associated with higher productivity of ponds. Invertebrate and phytoplankton taxon richness correlated (positively) with goose abundance. Both phytoplankton and invertebrate taxon richness increased with increasing nitrogen (N) concentrations. Goose abundance significantly affected phytoplankton species composition, while concentrations of total-N and total phosphorus (P) did not. Species composition of aquatic invertebrates was most strongly affected by goose abundance, but the effect of total-N concentration was also significant.
4. Increased goose abundance was associated with bird driven nutrient enrichment, increased phytoplankton and invertebrate taxon richness and changes of these biological communities. Thus in addition to climate change, the higher abundances of large migratory water fowl in many polar areas may pose a major additional stress to arctic lakes and ponds. In fact, climate change and bird impact may interact, accelerating ongoing environmental change of arctic freshwater ecosystems.

Introduction

The High Arctic has been exposed to dramatic climate change, and future scenarios predict that this development will accelerate in the years to come (Førland *et al.*, 2011). This change is affecting not only the terrestrial and aquatic ecosystems *per se*, but also the links between the two. The terrestrial-aquatic interface plays an important role for the dynamics of freshwater ecosystems in arctic and temperate regions (Bartels *et al.*, 2012, Soininen *et al.*, 2015).

The increasing impact by waterfowl on high latitude lakes and ponds provides a prime example of how climate change has consequences at the interface of terrestrial and freshwater environments, and also between geographically separated ecosystems such as overwintering grounds and breeding grounds. Migrating birds, particularly geese, have been observed in increasing numbers in many Arctic regions (e.g. Flemming *et al.*, 2016, Jefferies *et al.*, 2006, Pedersen *et al.*, 2013). Likewise, the Svalbard archipelago has experienced a dramatic increase in goose populations during the second half of the last century (Madsen *et al.*, 2017). This is partly a consequence of improved breeding conditions due to increased temperatures and an extended growing season, and partly a consequence of changes in land-use and hunting practices at overwintering sites in Western Europe (Fox *et al.*, 2010, Madsen *et al.*, 1999). The Pink-footed Goose (*Anser brachyrhunchus*) is the most numerous goose species on Svalbard, with a breeding population that has grown from around 10,000 to 88,000 since the mid 1960's, and has doubled during the past 15 years (Madsen *et al.*, 2017, Pedersen *et al.*, 2013). The growing population of breeding geese has also led to a range expansion of their breeding and grazing grounds within the archipelago (Jensen *et al.*, 2008, Wisz *et al.*, 2008), thereby also affecting an increased number of terrestrial and aquatic habitats – and the interaction between these habitats.

Processes in the terrestrial environment supply carbon and nutrients to the aquatic environment and affects productivity and biodiversity in freshwater ecosystems. This transport of resources is directly and indirectly impacted by climate related factors (Finstad *et al.*, 2016, Larsen *et al.*, 2011), but also geese may contribute substantially to this by their fertilization and grazing activities. Increased grazing on the terrestrial vegetation with a subsequent change in runoff and nutrient loadings to the freshwater environment accompanies the direct impact by birds in shore regions or open waters (e.g. Jefferies *et al.*, 2006). The growing population thus leads to rising inputs of nutrients and organic carbon directly from droppings, contributing to bird-mediated eutrophication of the arctic freshwater environment (Côté *et al.*, 2010, Mariash *et al.*, 2018, Milakovic *et al.*, 2001, van Geest *et al.*, 2007), and indirectly by grazing and grubbing. Previous studies have shown that a high impact of seabirds may also affect other water properties, such as pH and conductivity (Gonzalez-Bergonzoni *et al.*, 2017, Keatley *et al.*, 2009), which itself may impact the biodiversity of arctic freshwaters (Gonzalez-Bergonzoni *et al.*, 2017).

Increased goose migration also potentially impacts the transport of aquatic microorganisms and propagules, via gut content or feathers (e.g. Coughlan *et al.*, 2017). It may promote the establishment of protists or invertebrate invaders, as well as infectious organisms (bacteria, fungi, unicellular parasites) both among Svalbard localities and potentially also from mainland Europe to the Arctic. Collectively, the impact of migrating birds that affects water quality and dispersal of aquatic organisms may lead to community shifts in oligotrophic species-poor arctic ponds and lakes, i.e. by increasing species richness as is observed in oligotrophic temperate lakes in response to higher nutrient loadings (e.g., Hessen *et al.*, 2006, Jensen *et al.*, 2013).

Studies of increasing goose populations impacting arctic freshwaters are biased towards ecological function and point to an increase in aquatic productivity (Côté *et al.*, 2010, Hessen *et al.*, 2017, MacDonald *et al.*, 2015, Mariash *et al.*, 2018, Milakovic *et al.*, 2001, van Geest *et al.*, 2007). Although some studies also address the impact of seabirds on the biodiversity of arctic ponds (Gonzalez-Bergonzoni *et al.*, 2017, Keatley *et al.*, 2009, Stewart *et al.*, 2013), only few have assessed the impact on aquatic biodiversity by geese. A recent study described higher genetic (haplotype) diversity in arctic *Daphnia* in nutrient-rich ponds affected by migratory bird populations, notably geese (Alfsnes *et al.*, 2016). However, almost no studies have addressed the potential impact on the diversity at the community level in arctic lakes and ponds.

The aim of this study is to add knowledge on how the goose populations affect arctic freshwater communities. We hypothesize that:

(1) a higher goose abundance increases the trophic state of shallow lakes and ponds (hereafter ponds for simplicity) and enhances the taxon richness of these water bodies; and
(2) the increasing goose abundance and a related increase in nutrients are major drivers of aquatic species composition in these habitats.

To address these hypotheses, we conducted a survey on a set of high arctic lakes and ponds in Svalbard along a “goose abundance gradient”, measuring important proxies for trophic state and examining taxon richness and species composition of their phytoplankton and invertebrate communities.

Methods

A survey of 25 ponds was carried out on Svalbard in August 2014 and August 2015 in different areas around Isfjorden and Kongsfjorden. The 25 sites covered a gradient of goose abundance. As a proxy of goose presence and abundance, we counted the number of area-specific goose droppings (range of 0 - 94 droppings m^2). In the absence of population estimates for geese, which requires far more effort, the droppings are considered a useful proxy of goose abundance (Bos *et al.*, 2005, Owen, 1971, Ydenberg and Prins, 1981). The 25 sites were all located in the same climatic region on the coastal lowland on western Svalbard, and in catchments unaffected by glaciers since 1990. All sites were devoid of fish. Six of the 25 sites were located in the area of Aldegondabreen and Grønfjordbreen (Figure 1), seven were located further east in Isfjorden in the areas of Ymerbukta, Diabassodden, Kapp Napier and Pyramiden. The remaining 12 sites were located further north in the Ny Ålesund area south of Kongsfjorden.

The waterbodies were categorized into three classes according to their approximate average depth (1: ≤ 0.25 m, 2: 0.25 – 1 m, 3: > 1 m) and four classes reflecting area (1: ≤ 0.01 ha, 2: 0.01-0.1 ha, 3: 0.1 – 1.0 ha, 4: > 1 ha). From each of the 25 sites, a single 10 L water sample was taken from approximately 0.2 m below the surface for subsampling and later analysis of phytoplankton species composition, chlorophyll a, total phosphorus (total-P), and total nitrogen (total-N). Conductivity and pH were measured with a Hanna Instrument (model HI98129, range: 0 - 3999 μS cm^{-1}) on site. For quantification of phytoplankton abundance, a subsample of 200 mL from the 10 L water sample was fixed with acid Lugol solution and kept in the dark. For identification of rare phytoplankton species, a concentrated sample was obtained by dragging a plankton net (20 μm mesh size) through the upper part of the water column for approx. 5 min. Phytoplankton composition and richness were based on the 200 ml subsample but supplemented with records of rare species from the plankton net hauls. For chlorophyll a, a known volume of water (typically 1 L) was filtered *in situ* through Whatman GF/C filters, which were folded and wrapped in aluminum foil. Duplicate samples were taken. A 50 ml unfiltered subsample for nutrients (total-P and total-N) was added to an acid-cleaned plastic bottle. Samples for nutrients and chlorophyll filters were kept cold (5-10ºC) and dark for 0-2 days and then stored frozen (-18ºC) until analysis. Droppings were quantified by counting the number in squares of 0.25 m^2 along a transect from 0 to 6 m from the shoreline. For each pond, three randomly selected transects distributed evenly spaced around the pond were quantified, and five squares per transect counted (0, 2, 4, 6, and 8 m from the edge of the pond). Average dropping abundance per pond was calculated from the cumulative number of droppings per transect.

Nutrient analysis of pond water was performed with persulfate digestion following Koroleff (1970) for total-P and Solórzano & Sharp (1980) for total-N. Water samples were autoclaved for 30 minutes at 120°C with added potassium peroxydisulphate solution. Total-N was measured in an AutoAnalyzer

158 ALPKEM and total-P was determined by measuring absorbance at 882 nm in a spectrophotometer
159 (Shimadzu UV160A).

160 Chlorophyll a extractions were carried out following Jespersen and Christoffersen (1987). In brief,
161 filters were thawed and placed in 96 % ethanol at room temperature overnight. The extracts were
162 filtered through GF/C filters, the total volume of ethanol was recorded and the absorbance at 665 and
163 750 nm was measured in a spectrophotometer (Shimadzu UV160A).

164 Phytoplankton identification was done using an Olympus IMT/2 inverted microscope (100-400 x
165 magnification) to the lowest possible taxonomic level. The number of individuals of dominant
166 phytoplankton taxa were counted in sedimentation chambers along random transects following
167 Utermöhl (1958).

168 Sampling of the invertebrate fauna was designed to include the entire invertebrate community present
169 in the study sites. The microcrustacean fauna in the water column was sampled with standardized
170 sampling gear in terms of plankton net with mesh size commonly used for zooplankton (100 mm
171 diameter, 50 µm mesh size), but length of net haul was adjusted to the size of the localities. There was
172 no clear relationship between the length of the net haul and microcrustacean taxon richness. Littoral
173 samples of macrobenthos were taken from the shore and down to a depth of ca 1.5 m (or max depth in
174 the shallower sites) with a hemispherical scraper (diameter 16 cm, area 0.02 m^2, mesh size 0.5 mm).
175 Meiobenthic samples were taken with a tube (3 cm^2 surface area) from the upper sediment layer. Both
176 microcrustacean, macro- and meiobenthos samples were fixed *in situ* with 96 % ethanol. Samples
177 were later sorted, identified and counted with the use of binoculars and light microscope in the
178 laboratory. For identification we followed Dussart and Defaye (2011), Bartsch (2006), Alekseev and
179 Tsalolikhin (2010), Wiederholm (1983), Timm (2009) and Makarcgenko (1999). Cladoceran
180 identification literature follow details given in Novichkova et al. (2014).

181 *Statistical analysis*

182 We investigated changes of the biological communities along the goose abundance gradient by
183 examining species composition and taxon richness of the phytoplankton and invertebrate communities.
184 Initially, we tested the effect of goose abundance (i.e. abundance of goose droppings) on
185 phytoplankton and invertebrate taxon richness by one-way ANOVA. For this purpose, the ponds were
186 divided into three categories according to goose abundance (no: no droppings, low: < 5 droppings m^2,
187 high: > 5 droppings m^2). Taxon richness was checked for normality and homogeneity of variances.
188 Pairwise comparisons between categories were made with the t-test using the Bonferroni correction to
189 account for multiple comparisons. We also aggregated taxa at a higher taxonomic level for the
190 genera/groups represented by several species and tested the effect of goose abundance (by category)
191 on taxon richness of different higher level taxonomic groups (invertebrates: cladocerans, copepods,

chironomids; phytoplankton: chlorophytes, chrysophytes, cyanobacteria, diatoms, dinoflagellates; and "others" when the above grouping did not fit.).

We further analyzed the relationship between phytoplankton and invertebrate taxon richness and goose abundance, using absolute dropping abundance, and other selected environmental variables with simple and multiple linear regression. The seemingly most important predictors, in addition to goose droppings, for phytoplankton and invertebrate taxon richness were selected based on correlation coefficients. For both phytoplankton and invertebrates, total-N was chosen in addition to goose droppings. We therefore conducted simple linear regression analyses separately for goose droppings and total-N as predictors, as well as multiple linear regression analyses that included both predictors and their interaction. A backward selection procedure was used to exclude predictors in the multiple regression ($P > 0.1$). Number of goose droppings and total-N were both transformed ($\log_{10}(X + 1)$) prior to analysis due to data skewness.

The relationships between goose abundance and other environmental variables and species composition of phytoplankton and invertebrate communities were analyzed using unconstrained and constrained ordination techniques. Initially, we explored the impact of goose abundance on phytoplankton and invertebrate species composition by non-metric multidimensional scaling (nMDS). For this purpose, the ponds were divided into three categories according to goose abundance (no: no droppings, low: < 5 droppings m^2, high: > 5 droppings m^2). Furthermore, we tested if communities were different in ponds differentially affected by geese. This was done by testing significant differences of Bray-Curtis' similarity indices between goose abundance categories by one-way Analysis of Similarities (ANOSIM). Pairwise comparisons between categories were conducted using the step-down sequential Bonferroni procedure. To further explore how goose abundance and other environmental variables impacted species composition, constrained ordination was applied. Detrended correspondence analysis (DCA, Hill and Gauch, 1980) showed that the first DCA axis spanned gradient lengths of 4.2 and 2.5 SD units for the phytoplankton and invertebrate communities, respectively. Due to the relatively long gradient present in the phytoplankton community data, we applied canonical correspondence analysis (CCA) to the analysis of the phytoplankton community (ter Braak, 1986). In contrast, the relatively short gradient in the invertebrate community data justified the use of redundancy analysis (RDA) for these data (cf. Økland, 1990). The relationship between species and environmental variables was judged by the significance of the canonical axes together with a Monte-Carlo permutation test. A "minimal adequate model" was developed by forward selection of environmental variables with a Monte Carlo test (499 permutations). Only variables that made significant independent contributions to species abundance ($\alpha = 0.05$ level) were included in the model. Multicollinearity of the environmental variables was assessed by checking their Variance Inflation Factors (VIF, ter Braak and Šmilauer, 2012).

Frequencies of phytoplankton taxa (calculated from abundance) and invertebrate taxa (calculated from the aggregated dataset) were categorized into four "dominance classes" reflecting the dominance of species/taxa based on their relative frequencies (0: absent, 1: < 1%, 2: 1–10%, 3: >10%, Walseng *et al.*, 2006). Rare phytoplankton species only recorded in the net hauls was allocated to dominance class 1 (< 1%). The dominance scores of the different taxa were used as input data for the ordination analyses. In the CCA of the phytoplankton community we used abundance of goose droppings, longitude, latitude, elevation, depth class, area class, conductivity, total-P, total-N and pH as environmental variables. The following parameters were used as environmental variables in the RDA of the invertebrate community: abundance of goose droppings, longitude, latitude, elevation, depth class, area class, conductivity, chlorophyll a, total-P, total-N and pH. In both the CCA and the RDA we included sampling year (2014 and 2015) as an additional environmental variable to test if sampling year influenced species composition. All environmental variables, except sampling year, longitude, latitude, depth class, area class and pH, were transformed prior to the analyses ($\log_{10}(X + 1)$).

To address the unique effects of goose dropping abundance and shared effects with other environmental variables selected in the "minimal adequate model" of the CCA and RDA described above we conducted a variance partitioning analysis (VPA) using partial redundancy analysis and partial correspondence analysis (cf. Borcard *et al.*, 1992). This technique may be used to divide variation in ecological data sets between two or three environmental variables (or groups of environmental variables, e.g. Liu, 1997). We included the explanatory variables selected by the minimal model in the CCA and RDA analysis. In this type of analysis, the total variation and the unique contribution of the variables and their joint effects are obtained in several steps. For further description of this method, see for example Liu (1997).

Statistical analyses were conducted in SPSS Statistics 24 (IBM, 2016) and PAST 3.1.8 (Hammer *et al.*, 2001). Ordination analyses were conducted with the software CANOCO 5.0 (ter Braak and Šmilauer, 2012).

253 **Results**

254 *Environmental variables*

255 Although one subset of the ponds was sampled in 2014 and another in 2015, sampling year did not
256 impact the recorded environmental variables except for conductivity (data not shown). The sites
257 sampled in 2015 had slightly higher conductivity than the ones sampled in 2014. The study sites were
258 located between 4 and 166 m a.s.l. (Table 1). All ponds were relatively shallow, and although they
259 spanned a considerable range in surface area, most of the sites were below 2 ha. They all freeze solid
260 during winter and are thus devoid of fish. They varied from very dilute sites with a conductivity
261 between 10 and 1630 µS cm^{-1}. However, most sites were below 500 µS cm^{-1}. The conductivity reflects
262 sea spray and thus proximity to the sea. The abundance of goose droppings at the shores ranged from
263 zero to 94 droppings m^{-2}. The nutrient concentrations ranged from 1.6 to 63 µg $L^{-1,}$ total-P and 7 to
264 1205 µg L^{-1} total-N, but most of the water bodies had total-P and total-N concentrations below 20 µg
265 L^{-1} and 500 µg L^{-1}, respectively. The number of goose droppings was significantly positively correlated
266 with the productivity parameters (total-P, total-N, chlorophyll a, Table 2). The correlation was
267 strongest with total-N. Average (min. and max. values in parentheses) chlorophyll a in the three goose
268 abundance categories were 0.21 µg L^{-1} (0.06 - 0.57), 0.60 µg L^{-1} (0.20 - 2.04) and 0.83 µg L^{-1} (0.06 -
269 1.54) for no goose, low abundance and high abundance respectively. For total-P, the corresponding
270 values were 9.1 µg L^{-1} (2.9 - 23.3), 13.4 µg L^{-1} (1.6 - 44.5) and 26.5 µg L^{-1} (4.6 - 63.0). Finally, for
271 total-N these values were 120 µg L^{-1} (7 - 265), 367 µg L^{-1} (147 - 806) and 643 µg L^{-1} (261 - 1205). pH
272 of the 25 sites ranged from 7.4 to 9.5 and was unrelated to goose dropping abundance.

273 *Phytoplankton and invertebrate taxon richness.*

274 In total 137 phytoplankton taxa and 33 invertebrate taxa were recorded in the study ponds (Table S6
275 and S7). Goose abundance category had a significant effect on taxon richness of phytoplankton and
276 invertebrates (Figure 2, one-way Anova, $F_2 = 3.901$, $p = 0.035$and $F_2 = 5.338$, $p = 0.013$ respectively).
277 For both groups, pairwise comparisons showed that taxon richness in ponds with no geese was
278 significantly lower than in ponds with high abundance (Figure 2). The analysis of taxon richness at a
279 higher taxonomic level showed that taxon richness of cladocerans increased with goose abundance
280 category (Table S1, Figure S1). There was a marginal overall significant effect for cyanobacteria, but
281 pairwise comparisons did not reveal differences between the three categories of goose abundance for
282 cyanobacteria taxon richness (Table S1, Figure S1). Taxon richness of copepods, chironomids,
283 chlorophytes, chrysophytes, diatoms, dinoflagellates and the phytoplankton group "others" were not
284 significantly related to goose abundance category (Table S1, Figure S1).

285 Simple linear regressions were calculated to predict phytoplankton and invertebrate taxon richness
286 based on goose dropping abundance and total-N respectively. Goose dropping abundance showed a
287 trend towards affecting phytoplankton taxon richness (Figure 3, Table 3, $F(1, 23) = 4.042$, $p = 0.056$,

288 $R^2 = 0.149$). Phytoplankton taxon richness was significantly positively correlated with total-N (Figure
289 3, Table 3, $F(1, 23) = 13.491$, $p = 0.001$, $R^2 = 0.370$). The multiple regression of phytoplankton taxon
290 richness with goose droppings, total-N and the interaction between the two only included total-N as a
291 significant predictor, and therefore gave the same result as the simple linear regression of
292 phytoplankton taxon richness with total-N as predictor. Phytoplankton taxon richness thus increased
293 with increasing total-N concentration and tended to increase with goose abundance. Thus, total-N was
294 the most important of the two predictors. Invertebrate taxon richness was also positively correlated
295 with goose droppings (Figure 3, Table 3, $F(1, 23) = 10.473$, $p = 0.004$, $R^2 = 0.313$) as well as total-N
296 (Figure 3, Table 3, $F(1, 23) = 19.854$, $p = 0.000$, $R^2 = 0.463$). Multiple regression of invertebrate taxon
297 richness with goose droppings, total-N and the interaction between the two only included total-N as a
298 significant predictor. Thus, also for invertebrate taxon richness the multiple regression gave the same
299 result as the simple linear regression of invertebrate taxon richness with total-N as predictor.
300 Invertebrate taxon richness therefore increased with increasing goose abundance and increasing total-
301 N concentration, but total-N seemed to be the most important of the two predictors.

302 Sampling year had no significant effect on phytoplankton or invertebrate taxon richness (t-test for
303 independent samples, phytoplankton $t = 0.37$, $df = 23$, $P = 0.714$, invertebrates $t = 0.458$, $df = 23$, $P =$
304 0.651).

305 *Phytoplankton species composition*

306 Goose abundance category tended to affect phytoplankton species composition (Figure S2, Table S2,
307 ANOSIM, $R = 0.112$, $p = 0.071$). Pairwise comparisons revealed significant differences in species
308 composition between ponds with the highest abundance of droppings and ponds without droppings
309 (step-down sequential Bonferroni procedure, $p = 0.024$).

310 In addition to sampling year, goose dropping abundance was the most important driver of
311 phytoplankton species composition as indicated by CCA (Table S4; Figure 4). There was a significant
312 relationship between species composition and the tested environmental variables (i.e. all canonical
313 axes, pseudo-$F = 1.1$, $p = 0.032$). The ‘‘minimal adequate model’’ resulting from the forward selection
314 included the explanatory variables sampling year and goose dropping abundance (year 2014 and 2015
315 pseudo-$F = 2.0$, $p = 0.002$; goose droppings pseudo-$F = 1.7$, $p = 0.002$). The intra-set correlations of
316 environmental variables with the CCA axes (Table S4) and the CCA biplot (Figure 4) showed that the
317 effect of goose droppings on phytoplankton species composition was manifested along CCA axis 2
318 (Figure 4): sites with high goose abundance had high axis 2 scores, while sites with low goose
319 abundance had low axis 2 scores. While total-P and total-N also aligned closest to axis 2, both
320 parameters only had minor effects on the phytoplankton species composition. CCA axis 1 reflected a
321 change in phytoplankton species composition along a time, longitude and conductivity gradient. Water
322 bodies sampled in 2015 with high conductivity and a western location had low axis 1 scores, while

sites from 2014 with low conductivity and an eastern location had high axis 1 scores. Including goose abundance as the only environmental variable in the CCA explained 6.3 % of the total variation in the phytoplankton species composition.

The CCA species plot indicated species sorting along axis 2, i.e. along the goose abundance gradient. *Pediastrum* spp., *Chroococcus disperses*, *Aulacoseira* spp., thecate dinoflagellates (30-40 µm), *Eutreptia* sp., *Closterium parvulum*, *Cosmarium margaritiferum*, *Merismopedia* sp. were associated with high axis 2 scores, i.e. high goose abundance. *Bitrichia chodatii, Chrysochromulina parva* and *Chromulina* spp. are examples of species associated with low axis 2 scores, i.e. low goose abundance. Along CCA axis 1, few phytoplankton taxa, including naked dinoflagellates (10-20 µm) and *Chromulina* spp., were associated with low axis 1 scores (Figure 4), i.e. with the year 2015, a western location and high conductivity. Other taxa such as *Achnanthes* spp., *Navicula* spp. and *Bitrichia chodatii* were associated with higher axis 1 scores, i.e. year 2014, an eastern location and low conductivity.

To analyze the unique and shared effects of the two significant environmental variables (goose dropping abundance and sampling year) on phytoplankton species composition, we conducted a VPA (Figure 6). While the pure effects of goose droppings explained 6.5 % of the total variation in species composition, the "pure" effect of sampling year explained 8.1 %. Goose droppings in combination with sampling year constituted 0 % (the negative value is an artefact in the analysis, Legendre, 2008). We also conducted a VPA using goose abundance category and sampling year, but the results were very similar (results not shown); sampling year was more important than goose droppings.

Invertebrate species composition

The invertebrate community differed significantly between ponds with different categories of goose abundance (Figure S3, Table S3, ANOSIM, $R = 0.217$, $p = 0.006$). Pairwise comparisons showed that species composition in ponds with the highest abundance of droppings differed significantly from that in ponds without droppings (step-down sequential Bonferroni procedure, $p = 0.0039$) and was marginally different from ponds with low abundance of droppings (step-down sequential Bonferroni procedure, $p = 0.045$. Overall, the RDA analysis showed that the most important drivers of invertebrate species composition were goose dropping abundance, trophic state and conductivity. Longitude had a marginal effect (Table S5; Figure 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 of goose dropping abundance (pseudo-$F = 4.3$, $p = 0.002$), conductivity (pseudo-$F = 2.5$, $p = 0.002$), total-N (pseudo-$F = 1.9$, $p = 0.02$) and longitude with a marginal effect (pseudo-$F = 1.7$, $p = 0.046$). The intra-set correlations of environmental variables with the RDA axes (Table S5) and the

RDA biplot (Figure 5) showed that the invertebrate communities were distributed mainly along a gradient of goose dropping abundance and productivity (total-N/ chlorophyll a) on RDA axis 1, from ponds with no or few droppings and low productivity (low axis values) to sites with many goose droppings and higher productivity (high axis values). RDA axis 2 was mainly correlated with conductivity and to some extent with longitude (Table S5, Figure 5). Sites of high conductivity had low axis 2 scores, while sites with low conductivity had high axis 2 scores. Including only goose dropping abundance as environmental variable in the RDA explained 15.7 % of the total variation in the invertebrate species composition.

Among the invertebrate taxa, the cyclopoid *Cyclops abyssorum* and chironomid *Procladius crassinervis* were associated with low axis 1 scores (Figure 5), i.e. no/few droppings and low trophic state. Other taxa such as the cladocerans *Chydorus sphaericus*, *Macrothrix hirsuticornis*, *Daphnia pulex* and *Acroperus harpae* and the chironomid *Orthocladius* s.str. were associated with higher axis 1 scores, i.e. many goose droppings and higher trophic state. The RDA species plot also indicated species sorting along axis 2. The chironomids *Psectrocladius barbimanus* and *Paratanytarsus austriacus* were associated with low axis 2 scores, i.e. high conductivity. The cladoceran *Bosmina longispina*, the notostracan *Lepidurus arcticus* and the chironomid *Micropsectra radiali* are examples of species associated with high axis 2 scores, i.e. low conductivity. It seemed that some of the more common microcrustaceans (*C. abyssorum*, *C. sphaericus*, *M. hirsuticornis*, *D. pulex* and *A. harpae*) were more strongly associated with and driving the variation along the first axis, compared with the chironomids.

To analyze the unique and shared effects of the three significant environmental variables (goose droppings, conductivity and total-N) on the invertebrate community, we conducted a VPA (Figure 6). Together the three variables explained 30.5 % of the total variation in the invertebrate community. The "pure" effect of goose droppings explained the largest fraction of the total variation (10.1 %), followed by the pure effects of conductivity (8.7 %) and total-N (6.2 %). Goose droppings in combination with conductivity constituted 0.8 %, goose droppings in combination with total-N 3.7 % and conductivity in combination with total-N 0 %. The combination of all three environmental variables constituted 1.1 % of the total variation. We also conducted a VPA with goose dropping abundance, conductivity and the marginally significant longitude but the results were very similar (results not shown); goose dropping abundance was most important followed by conductivity and longitude.

Discussion

Our study shows how increasing goose abundance, using the presence of goose droppings as a proxy, contributes to nutrient enrichment as well as affects taxon richness and species composition in arctic ponds. While the number of droppings provides an indication of the presence and abundance of the birds over a period of time, it is not a direct assessment of goose impact. Ideally, a quantification of the impact of geese on freshwater habitats will include information on number of geese visiting the location, the duration of the time they spend there, their feeding and defecation rates, etc. Owing to logistic constraints of the remote study sites there is no realistic way to quantify geese activity for the entire season; we took a more practical and resource-efficient way to assess bird influence by an indirect measure through counting drooping. As goose droppings are compacted units resistant to immediate degradation, are not easily moved by wind and are not utilized to any significant extent by other birds or mammals for food, we argue that the droppings can be used as a proxy for the presence and abundance of geese. Moreover, this method has been applied in several other studies (Bos *et al.*, 2005, Owen, 1971, Ydenberg and Prins, 1981) and it is also used in standardized Arctic monitoring programs for the assessment of herbivory occurrence and intensity (International Tundra Experiment, ITEX, see Barrio *et al.*, 2016).

Both phytoplankton and invertebrate taxon richness were positively correlated with goose abundance. However, the correlation was strongest for invertebrates. Likewise, phytoplankton and invertebrate taxon richness both increased with increasing total-N concentrations. An aggregation of taxa at higher taxonomic level showed that taxon richness of cladocerans and cyanobacteria increased with goose abundance. Goose abundance also significantly affected the composition of phytoplankton communities, while total-N and total-P did not. Invertebrate species composition was most strongly influenced by goose abundance, but the effect of total-N was also significant.

In support of other studies (Côté *et al.*, 2010, Mariash *et al.*, 2018, Olson *et al.*, 2005, van Geest *et al.*, 2007), we found that a high abundance of goose droppings was associated with elevated nutrient concentrations as illustrated by the positive correlation between droppings and especially total-N and total-P. Furthermore, the observed ranges of total-N and total-P in goose-impacted and non-impacted ponds correspond well with the range reported in these previous studies. The nutrient concentrations in most of the non-impacted lakes in these previous studies as well as in our study fall within the oligotrophic range (Côté *et al.*, 2010, Mariash *et al.*, 2018, Olson *et al.*, 2005, van Geest *et al.*, 2007). In comparison, most of the impacted ponds in our study fall within mesotrophic or eutrophic range, suggesting that increasing goose impact may lead to eutrophication. Goose droppings had a stronger effect on total-N than on total-P, probably due to the relatively high N content of goose droppings compared to P. van Geest et al. (2007) found N:P ratios of droppings of 6 to 9 (molar ratios). Higher goose abundance and nutrient enrichment were associated with higher chlorophyll *a* concentrations.

While several studies have demonstrated that increasing bird impact can lead to nutrient enrichment in arctic lakes and ponds, there are few studies addressing bird impacts at the community level in the arctic aquatic environment. However, Keatley et al. (2009) found that increasing impact by seabirds affected the diatom communities due to increasing nutrient loadings. Gonzalez-Bergonzoni et al. (2017) observed that increasing impact by seabirds reduced macroinvertebrate taxon richness, due to bird-induced acidification. To the best of our knowledge, the present study is the first to show how the increasing goose population in the Arctic may directly affect aquatic taxon richness and species composition in arctic freshwater bodies. In temperate regions, nutrient status of lakes may affect communities of phytoplankton and invertebrates (Jensen *et al.*, 2013, O'Toole *et al.*, 2008, Ptacnik *et al.*, 2008). However, our results also indicate that other bird-mediated mechanisms may have affected taxon richness and species composition. First, goose abundance was the only significant driver of the phytoplankton species composition (in addition to sampling year) in the CCA. Second, goose abundance was the most important driver of invertebrate species composition in the RDA and alone explained the largest fraction of the variation in the variance partitioning analysis independent of total-N.

In our study, the effect of geese on arctic pond communities was partly due to bird-driven nutrient enrichment. Increasing goose abundance may affect other chemical and physical water properties in addition to nutrient concentration. Bird mediated acidification impacting biodiversity as observed by Gonzalez-Bergonzoni et al. (2017) was an unlikely mechanism in our study as no effect of pH was observed. Increased goose abundance could also potentially impact biodiversity by impacting oxygen concentration due to increased degradation of organic material. However, previous studies did not record any significant differences of oxygen concentrations between control sites and bird impacted sites (Côté *et al.*, 2010, Gonzalez-Bergonzoni *et al.*, 2017). In our study, oxygen was measured in a subset of 13 ponds sampled in 2015 and confirmed a high oxygen saturation > 80 % in all but one pond (oxygen saturation 70 %). Strong oxygen depletion is also unlikely in these shallow, strong wind-mixed sites. Likewise, bird-induced changes in turbidity, for example due to increased erosion or because of mechanical resuspension of material by the geese, was considered low, based on visual inspection.

Direct bird-mediated dispersal of aquatic organisms and propagules may, at least partly, explain the effects of increased goose abundance on taxon richness and species composition. Microcrustaceans, the invertebrate group driving the major part of the variation in invertebrate species composition and most strongly associated with goose dropping abundance, are passive dispersers that may form resistant propagules, dispersed by a variety of vectors including wind, water or animals (e.g. Caceres and Soluk, 2002, Louette and De Meester, 2004, Vanschoenwinkel *et al.*, 2008). Viable propagules of zooplankton have been recovered from waterfowl faeces (Frisch *et al.*, 2007) and evidence is accumulating that ectozoochory by waterfowl is also common, effectively moving zooplankton

between new water bodies (Coughlan *et al.*, 2017, Figuerola and Green, 2002). The parthenogenetic mode of reproduction in cladocera would be expected to facilitate post-dispersal colonization and might partly explain the contrasting relationships of cladoceran and copepod abundance to goose abundance. Cladoceran taxon richness increased with increasing goose abundance, but this was not the case for copepods. Furthermore, cladoceran abundance increased with increasing goose dropping abundance (in particular *C. sphaericus*, *M. hirsuticornis*, *D. pulex* and *A.s harpae*). Many of the chironomid taxa, by far the most important macrobenthos group in this study, appeared to be less impacted by goose abundance than the most common cladocerans as shown in the RDA. Furthermore, chironomid taxon richness was not significantly impacted by goose dropping abundance. In chironomids, the adult stage leaves the aquatic environment, actively flying and dispersing to new sites. Furthermore, chironomids may not necessarily be expected to respond to a goose-mediated nutrient enrichment in shallow well oxygenated arctic ponds (Stewart *et al.*, 2013).

Among phytoplankton, a significant number of taxa has been found to be airborne (Tesson *et al.*, 2016) and may therefore be wind-dispersed. Waterfowl are also vectors for dispersal of algae both externally (on feathers and feet) as well as internally (reviewed in Kristiansen, 1996). However, the relative importance of wind-dispersal and bird-mediated dispersal is hard to judge (Naselli-Flores and Padisak, 2016). For both phytoplankton and invertebrate species composition geographical location had no or only a marginally significant effect, indicating that there is little geographically-induced variation in the communities. Geese may have aided in reducing variation in species composition between geographically distant sites. Overall, bird-mediated dispersal provides a mechanism that might, at least partly, explain variation in taxon richness and species composition along a gradient of increasing goose abundance in our study. Yet, the confounding impacts of nutrient enrichment and dispersal make it difficult to really disentangle their individual effects.

The fieldwork in this study was conducted over two field seasons. The only biological response variable affected by sampling year was phytoplankton species composition. This effect could be explained by several mechanisms. Differences in the environmental variables between years seem less important. There was no difference between years in size (area and depth) of the investigated ponds. Conductivity was the only water chemistry parameter affected by sampling year (slightly higher conductivity in 2015 compared to 2014) and could therefore have contributed to the “year effect” on phytoplankton species composition. Furthermore, the ponds sampled in 2015 had a more western location and we cannot exclude that differences in geology, catchment characteristics and climate may have contributed to the “year effect”.

The ordination analysis of the phytoplankton community had relatively low explanatory power, indicating that important drivers of the phytoplankton were not included in the CCA. Phytoplankton take up N and P from the water in an inorganic form as PO_4, NO_3 or NH_4. We did not measure the

concentration of these inorganic nutrients. Including these variables in the CCA might have explained a higher percentage of the variation in the phytoplankton community. Furthermore, phytoplankton may be limited by other nutrients than N and P, notably Fe (e.g. van Geest *et al.*, 2007).

All ponds in our study were located on the coastal lowland. While being situated well above the tidal zone, they were still to some extent exposed to sea-salt spray, depending on their distance from the sea as well as on prevailing local weather conditions. Conductivity thus reflected distance to the sea, a factor that apparently also impacted invertebrate species composition. The chironomid *P. barbimanus,* the annelid *Marionina* sp. and the harpacticoid *Tahidius discipes* were among the species most strongly associated with high conductivity (i.e. high marine impact), whereas the cladoceran *B. longispina*, the notostracan *L. arcticus* and the chironomid *M. radiali* were the species most strongly associated with low conductivity (i.e. low marine impact). Both *P. barbimanus* and *T. discipes* are indicative of higher salinity (Chen *et al.*, 2009, Dimante-Deimantovica *et al.*, 2016). Some of the other recorded invertebrates are also characterized as brackish water species, such as the harpacticoid *Nitokra spinipes*, although the species also occurs in freshwaters (Dimante-Deimantovica *et al.*, 2016).

While the current study suggests important effects of increasing goose populations at the community level of arctic freshwaters, we are only beginning to decipher this multifaceted issue affecting aquatic ecosystems. An improved understanding of the combined impacts of direct climate effects and indirect effects mediated by an increasing goose population is needed. Detailed information on goose presence, feeding and defecation near arctic freshwater environments will improve the prediction for future changes in these vulnerable ecosystems, and is also important for appropriate management of the goose population both on their overwintering grounds, resting sites during migration and their Arctic nesting and foraging grounds. Ultimately, it will also aid to evaluate the impact of geese on ecosystem services supplied by the arctic aquatic environment (Buij *et al.*, 2017).

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Conflict of interest

The authors declare that they have no conflict of interest.

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714

715 **Tables**

716 Table 1. Major characteristics of the 25 ponds sampled during August 2014 and 2015 in western
717 Svalbard (see Figure 1).

		Mean	Min.	Max.
Elevation	(m a.s.l.)	44	4	166
Depth	(m)	1.3	0.25	2.5
Area	(Ha)	1.781	0.002	15.768
Goose droppings	(No m^{-2})	8	0	94
Conductivity	(µS cm^{-1})	314	10	1630
Chlorophyll *a*	(µg L^{-1})	0.55	0.06	2.04
Total-P	(µg L^{-1})	15.3	1.6	63.0
Total-N	(µg L^{-1})	364	7	1205
pH		8.3	7.4	9.5

718

Table 2. Pearson correlation coefficients for elevation, depth class, area class, goose dropping abundance, categories of goose abundance (based on dropping abundance), conductivity, chlorophyll *a*, total-P, total-N and pH. Elevation, goose dropping abundance, conductivity, chlorophyll *a*, total-P and total-N were transformed ($\log_{10}(X + 1)$). ** = Correlation is significant at the 0.01 level. * = Correlation is significant at the 0.05 level.

	Elevation	Depth-class	Area-class	Goose dr. abundance	Goose abundance category	Conductivity	Chl. *a*	total-P	total-N	pH
Elevation	1									
Depth-class	0.2	1								
Area-class	0.183	0.782**	1							
Goose dr. abundance	-0.128	0.036	0.064	1						
Goose abundance category	-0.085	0,032	0.058	0.850**	1					
Conductivity	-0.357	-0.214	-0.262	0.256	0.115	1				
Chl. *a*	-0.353	-0.05	0.057	0.452*	0.507**	-0.098	1			
total-P	0.003	-0.267	-0.076	0.441*	0.381	-0.301	0.588**	1		
total-N	-0.244	-0.038	0.067	0.616**	0.683**	0.13	0.596**	0.520**	1	
pH	0.191	-0.040	-0.112	0.082	0.196	0.373	-0.146	-0.220	0.159	1

Table 3. Parameter estimates for simple linear regression models relating phytoplankton and invertebrate taxon richness to the environmental parameters goose dropping abundance and total-N (both transformed, $\log_{10}(X + 1)$).

Response variable	Predictor	Coefficients	Estimate (± SE)	t-value	*p*
Phytopl. taxon richness	Goose dr. abundance	Intercept	13.966 (1.382)	10.107	0.000
		Goose dr. abundance	3.877 (1.928)	2.010	0.056
	Total N	Intercept	-1.249 (4.750)	-0.263	0.795
		Total-N	7.138 (1.943)	3.673	0.001
Inv. taxon richness	Goose dr. abundance	Intercept	8.298 (0.660)	12.576	0.000
		Goose dr. abundance	2.980 (0.921)	3.236	0.004
	Total N	Intercept	-0.412 (2.329)	-0.177	0.861
		Total-N	4.246 (0.953)	4.456	0.000

Figure captions

Figure 1. The location of the 25 studied ponds in seven areas in western Svalbard, Spitsbergen. The 25 sites were distributed in the different areas as follows: Aldegondabreen (four sites), Grønfjordbreen (two sites), Ymerbukta (two sites), Diabasodden (one site), Kapp Napier (one site), Pyramiden (three sites) and Ny Ålesund (12 sites).

Figure 2. Average (±S.E.) of phytoplankton and invertebrate taxa richness. Different letters above columns indicate a significant difference between categories of goose abundance (based on dropping abundances, Pairwise t-test with Bonferroni correction, $P<0.05$).

Figure 3. Scatterplot of phytoplankton and invertebrate taxon richness vs. goose dropping abundance ($\log_{10}$(no. goose dr. + 1) and total-N (($\log_{10}$(total-N + 1) in 25 ponds located in western Svalbard (see Figure 1). a) Phytoplankton taxon richness vs. number of goose droppings. b) Phytoplankton taxon richness vs. total-N. c) Invertebrate taxon richness vs. number of goose droppings. d) Invertebrate taxon richness vs. total-N. Also shown are the simple linear regressions.

Figure 4. Canonical correspondence analysis (CCA) of phytoplankton communities in 25 ponds located in western Svalbard (See Figure 1). (a) CCA–ordination plot of the 25 study sites. (b) CCA–ordination plot of phytoplankton taxa showing the 34 best fitting taxa. Environmental variables included in both plots are both significant (sampling year and goose droppings, in bold) and non-significant variables (longitude, latitude, elevation, depth class, area class, conductivity, total-P, total-N, pH). Environmental variables abbreviated as: Goose droppings (Goose dr.), total nitrogen (total-N), total phosphorus (total-P), area-class (Area), depth-class (Depth). Categories of ponds with different abundances of goose droppings indicated as: no droppings – circle, < 5 droppings m^2 – squares, > 5 droppings m^2 – diamonds. Phytoplankton taxa are abbreviated as: *Achnanthes* spp. (AchnaSpp), *Amphora* sp. (AmphrSp), *Aulacoseira* spp., (AulacSpp), *Bitrichia chodatii* (BitrChod), *Chromulina* spp. (ChromSpp), *Chroococcus disperses* (ChroDisp), *Chrysochromulina parva* (ChrsParv), *Chrysolykos skujai* (ChrsSkuj), *Closterium parvulum* (ClosParv), *Cosmarium margaritatum (*CosmMarga*), Cosmarium margaritiferum* (CosmMarg), *Cymbella* spp. (CymblSpp), *Dinobryon sertularia* (DinbSert), *Euglena* sp. (EuglnSp), *Eutreptia* sp. (EutrpSp), *Gymnodinium simplex* (GymnSimp), *Koliella longiseta* (KoliLong), *Korschikovella limnetica* (KosLimn), *Mallomonas* spp. *(MallmSpp), Merismopedia* sp. (MerisSp), Naked dinoflagellates 10-20µm (NakDin10), *Navicula* spp. (NavicSpp), *Nitzschia* spp. (NitzSpp), *Pandorina morum* (PandMorm), *Pediastrum boryanum* (PediBory), *Pediastrum integrum* (PediIntg), *Pediastrum* spp. (PediaSpp), Pennate diatoms 10-40µm

(PenDia10), *Planktothrix* sp. (PlankSp), *Scenedesmus* spp. (ScendSpp), *Staurastrum* sp. (StaurSp), *Tabellaria* spp. (TabelSpp), *Teilingia granulata* (TeilGran), Thecate dinoflagellates 30-40µm (TheDin30).

Figure 5. Redundancy analysis (RDA) of invertebrate communities in the 25 study ponds located in western Svalbard (See Figure 1). (a) RDA–ordination plot of the 25 study sites. (b) RDA–ordination plot of invertebrate taxa. Environmental variables included in both plots are both significant (goose droppings, conductivity and total-N, in bold) and non-significant variables (elevation, depth class, area class, phytoplankton-biovolume, chlorophyll *a*, total-P). Environmental variables abbreviated as: Goose droppings (Goose dr.), total nitrogen (total-N), total phosphorus (total-P), chlorophyll *a* (Pel. Chl. a), area-class (Area), depth-class (Depth). Categories of ponds with different abundances of goose droppings indicated as: no droppings – circle, < 5 droppings m^2 – squares, > 5 droppings m^2 – diamonds. Invertebrate taxa are abbreviated as: *Acroperus harpae* (AcrHar), *Alona guttata* (AloGut), *Alona werestschagini* (AloWer), *Apatania zonella* (ApaZon), *Bosmina longispina* (BosLon), *Camisia foveolate* (CamFov), *Chironomus* sp. (ChirSp), *Chydorus sphaericus* (ChySph), *Cricotopus* s.str (Cricoto), *Cricotopus glacialis* (CriGla), *Cricotopus tibialis* (CriTib), *Cyclops abyssorum* (CycAby), *Daphnia pulex* (DapPul), *Diacyclops crassicaudis* (DiaCra), Diaptomidae sp. (Diapto), *Epactophanes richardi (EpaRic), Eurytemora raboti* (EurRab), *Hydrobaenus conformis* (HydCon), *Lepidurus arcticus* (LepArc), *Macrothrix hirsuticornis* (MacHir), *Maraenobiotus brucei* (MarBru), *Marionina* sp. (MariSp), *Micropsectra radialis* (MicRad), *Micropsectra* sp. (MicroSp), Nematoda (Nematoda), *Nitokra spinipes* (NitSpi), *Orthocladius* s.str. (Orthocla), Ostracoda (Ostracoda), Paratanytarsus austriacus (ParAus), *Procladius crassinervis* (ProCra), *Psectrocladius barbimanus* (PseBar), Tardigrada (Tardigrada),*Tahidius discipes* (TahDis).

Figure 6. Venn diagram based on variance partitioning analyses showing the fraction of the total (a) phytoplankton variation explained by sampling year and goose droppings and (b) the invertebrate variation explained by goose droppings, total-N and conductivity.

Freshwater Biology

SUPPLEMENTARY MATERIAL

Changes in trophic state and aquatic communities in high Arctic ponds in response to increasing goose populations.

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Table S1. Results of one-way Anova of effects of goose abundance category (based on goose dropping abundance) on phytoplankton and invertebrate taxa richness (TR) as well as on major taxonomic groups. F-values and P-values for given in the table. Different letters in columns with averages indicate a significant difference between averages (Pairwise t-test with Bonferroni correction, $P<0.05$).

One-way Anova	F_2	p
Phytoplankton TR	3.901	0.035
Invertebrate TR	5.338	0.013
Cladoceran TR	23.449	0.000
Copepod TR	2.602	0.097
Chironomid TR	1.053	0.366
Chlorophyte TR	0.429	0.657
Chrysophyte TR†	1,419	0.276
Cyanobacteria TR†	4.115	0.041
Diatom TR	1.430	0.261
Dinoflagellate TR	0.159	0.854
Other TR	0.747	0.486

†Welch Anova applied due to inequality of variances, hence the Welch test statistic is written in the column. In this case the Games-Howell test is used for the pairwise comparisosns.

Table S2. Results of the nonmetric multidimensional scaling (three-dimensional solution) using Bray-Curtis dissimilarities between phytoplankton communities from ponds differently affected by geese.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.424	0.327	0.249
Explained variation (cumulative)	42.4	75.1	100.0

Table S3. Results of the nonmetric multidimensional scaling (three-dimensional solution) using Bray-Curtis dissimilarities between invertebrate communities from ponds differently affected by geese.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.446	0.294	0.260
Explained variation (cumulative)	44.6	74.0	100.0

Table S4. Canonical correspondence analysis (CCA) of the taxonomical composition of phytoplankton communities in 25 ponds in western Svalbard. Also given are intra-set correlations of environmental variables with CCA axes.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.464	0.362	0.301	0.257	5.462
Pseudo-canonical correlation	0.975	0.950	0.954	0.954	
Explained variation (cumulative)	8.5	15.1	20.7	25.4	
Explained fitted variation (cumulative)	17.6	31.3	42.7	52.4	
Sum of all eigenvalues					5.462
Sum of all canonical eigenvalues					2.641
Intra-set correlations of environmental variables with axes	Axis 1	Axis 2	Axis 3	Axis 4	
2014	0.9037	-0.2811	0.1991	0.084	
2015	-0.9037	0.2811	-0.1991	-0.084	
Longitude	0.7154	-0.3332	0.1798	-0.0687	
Latitude	-0.4896	0.3649	-0.0008	-0.0654	
Elevation	-0.3146	-0.0745	-0.1599	0.1407	
Depth-class	-0.0016	-0.0528	-0.0474	-0.102	
Area-class	0.2267	-0.0632	-0.122	0.0883	
Goose dr. abundance	0.0563	0.9313	-0.1771	-0.1194	
Conductivity	-0.4937	0.1927	-0.1586	-0.0922	
Total-P	0.2808	0.6512	0.4388	0.0482	
Total-N	0.1594	0.5536	0.2816	0.1837	
pH	-0.2487	-0.1221	0.0808	-0.3519	

Table S5. Redundancy analysis (RDA) of the taxonomical composition of invertebrate communities in 25 ponds in western Svalbard. Also given are intra-set correlations of environmental variables with RDA axes.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.204	0.116	0.069	0.059	1.0000
Pseudo-canonical correlation	0.960	0.956	0.908	0.915	
Explained variation (cumulative)	20.4	32.0	39.0	44.8	
Explained fitted variation (cumulative)	31.1	58.8	59.4	68.3	
Sum of all eigenvalues					1.0000
Sum of all canonical eigenvalues					0.6561
Intra-set correlations of environmental variables with axes	Axis 1	Axis 2	Axis 3	Axis 4	
2014	-0.3021	0.625	-0.3805	0.0359	
2015	0.3021	-0.625	0.3805	-0.0359	
Longitude	-0.3353	0.5532	-0.5762	0.1356	
Latitude	0.4688	-0.0743	0.1535	0.2773	
Elevation	-0.2477	0.2154	-0.024	-0.0417	
Depth-class	-0.2971	0.1074	0.1211	-0.4964	
Area-class	-0.1856	0.416	0.0627	-0.1038	
Goose droppings	0.8365	0.2013	0.1035	-0.2738	
Conductivity	0.488	-0.6248	0.0525	0.1481	
Chlorophyll *a*	0.5476	0.3571	-0.1317	0.0036	
Total-P	0.5026	0.5485	-0.1087	0.0227	
Total-N	0.6187	0.0709	-0.5886	-0.0704	
pH	0.2494	-0.2129	-0.5353	-0.0773	

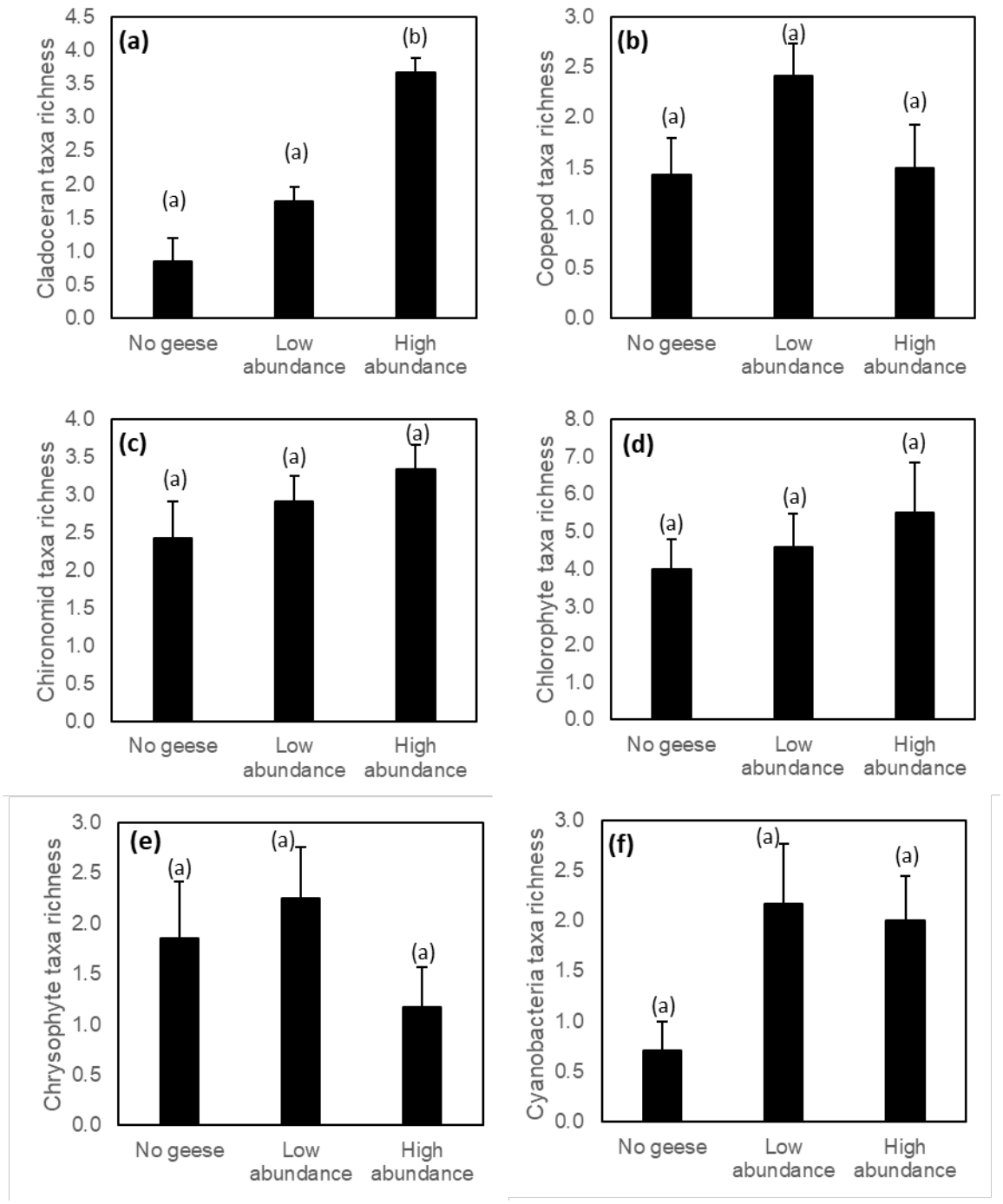

Figure S1. Average (±S.E.) of taxon richness of major taxonomic groups. Different letters above columns indicate a significant difference between categories of goose abundance (based on dropping abundances, Pairwise t-test with Bonferroni correction, $P<0.05$).

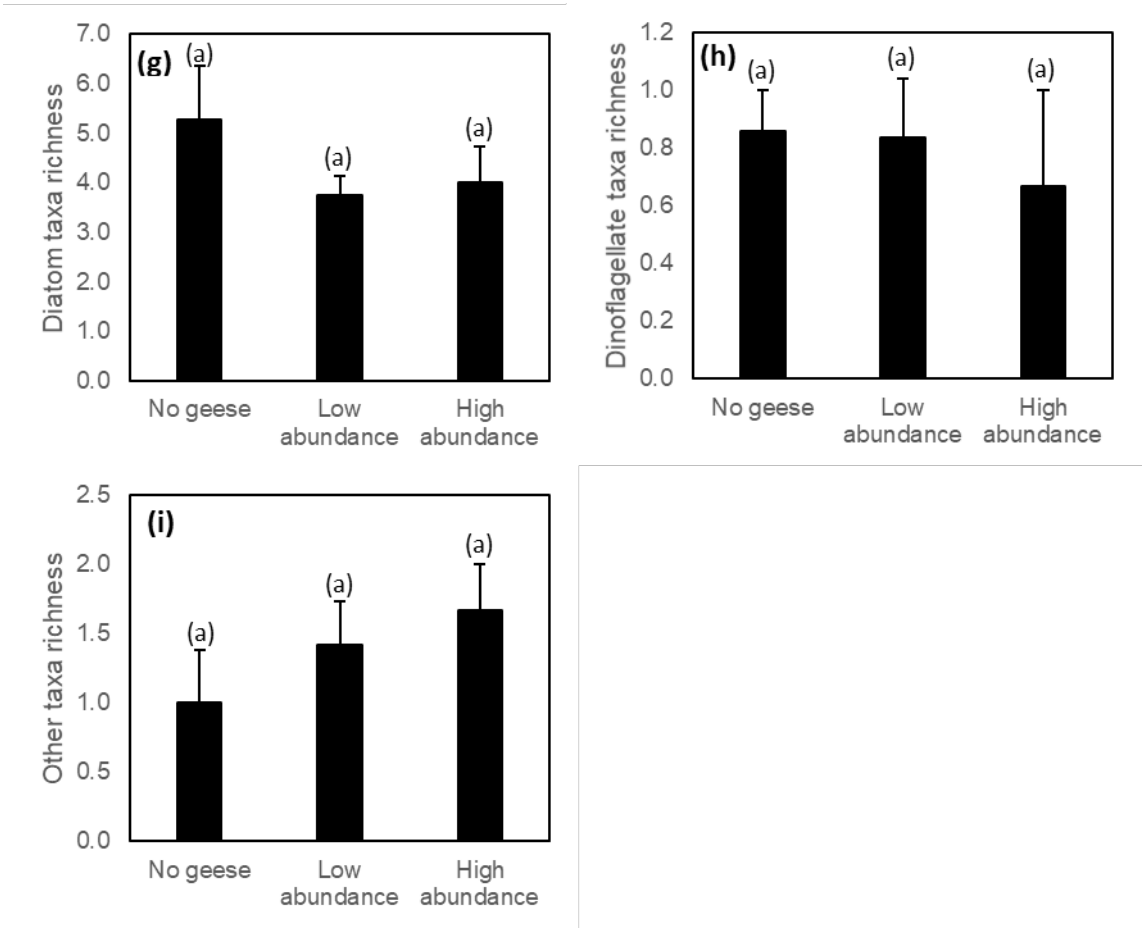

Figure S1 continued

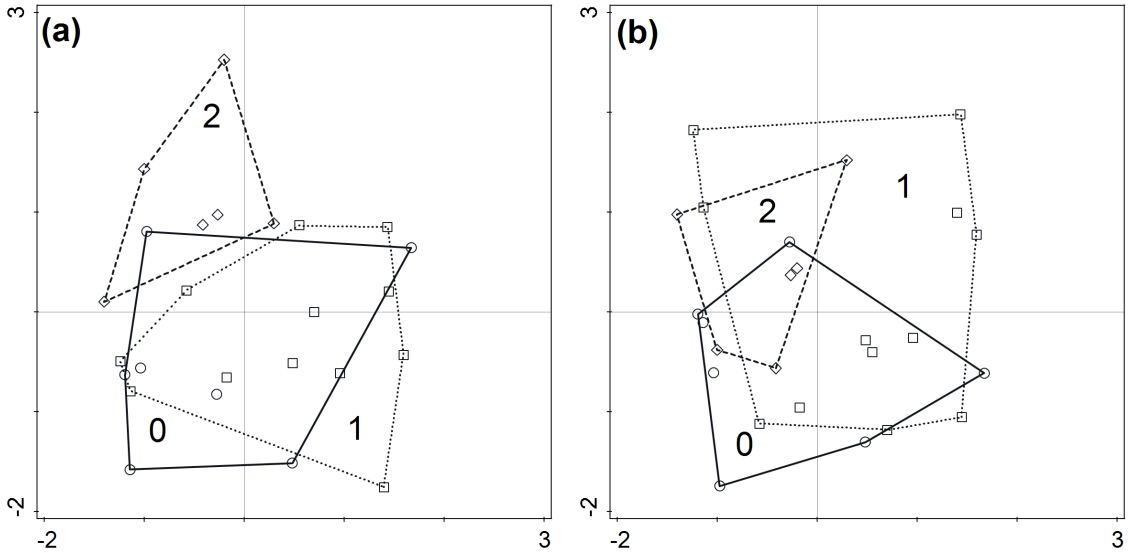

Figure S2 Sample scores from nonmetric multidimensional scaling (three-dimensional solution) using Bray-Curtis dissimilarities between phytoplankton communities from ponds differently affected by geese. (a) Axis 1 and 2. (b) Axis 1 and 3. Categories of ponds with different abundances of goose droppings indicated as: no droppings – circle (0) enveloped by solid line, < 5 droppings m^2 – squares (1) enveloped by dotted line, > 5 droppings m^2 – diamonds (2) enveloped by dashed line.

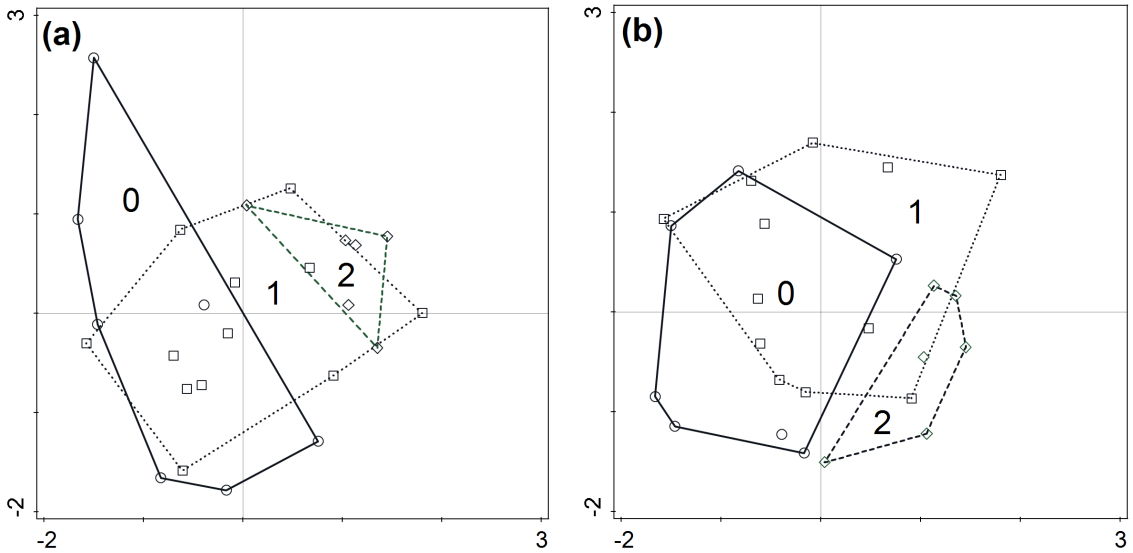

Figure S3. Sample scores from nonmetric multidimensional scaling (three-dimensional solution) using Bray-Curtis dissimilarities between invertebrate communities from ponds differently affected by geese. (a) Axis 1 and 2. (b) Axis 1 and 3. Categories of ponds with different abundances of goose droppings indicated as: no droppings – circle (0) enveloped by solid line, < 5 droppings m^2 – squares (1) enveloped by dotted line, > 5 droppings m^2 – diamonds (2) enveloped by dashed line.

Table S6. Occurrence of phytoplankton taxa identified in the 25 investigated ponds in seven areas in western Svalbard, Spitsbergen. The 25 sites were distributed in the different areas as follows: Aldegondabreen (four sites), Grønfjordbreen (two sites), Ymerbukta (two sites), Diabasodden (one site), Kapp Napier (one site), Pyramiden (three sites) and Ny Ålesund (12 sites).

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Achnanthes minutissima							X		X		X			X	X				X	X	X		X	X	
Achnanthes spp.		X	X	X			X	X		X															
Amphora sp.																				X		X			
Anabaena spp.					X	X					X		X		X						X	X			
Aphanizomenon sp.				X																					
Aphanocapsa compacta																							X		
Aphanocapsa delicatissima											X														
Asterionella formosa	X	X		X								X							X		X	X			
Aulacoseira spp.																					X				
Bitrichia chodatii				X	X																				
Bitrichia granulata									X																
Bitrichia sp.													X												
Botryococcus braunii											X														
Carteria spp.		X								X		X		X	X	X		X					X		
Centric diatoms 10-20µm		X		X																			X		
Centric diatoms 20-30µm			X																						
Chlamydomonas spp.				X							X			X						X				X	
Chlorogonium sp.																	X					X			
Chromulina spp.													X	X	X	X							X		
Chroococcales 2-5µm													X												
Chroococcus dispersus																				X					
Chroococcus limneticus										X			X												
Chroococcus spp.												X													
Chroomonas acuta													X	X				X							
Chrysochromulina parva		X		X	X		X		X	X															
Chrysochromulina sp.																		X							

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Chrysococcus minutus					X																				
Chrysococcus sp.	X						X	X	X	X					X				X						
Chrysolykos skujai														X		X									X
Chrysolykos sp.															X										
Chrysophytes												X		X											X
Closterium parvulum																					X				
Closterium spp.											X														
Closterium venus											X														
Coelosphaerium kuetzingianum												X													
Cosmarium abbreviatum											X														
Cosmarium granatum															X								X		
Cosmarium granatum v. *granatum*												X													
Cosmarium margaritatum				X	X																				
Cosmarium margaritiferum																					X				
Cosmarium punctulatum																							X		
Cosmarium pygmaeum																							X		
Cosmarium reniforme	X																								
Cosmarium spp.						X	X	X	X	X	X	X		X	X			X		X	X	X			X
Cryptomonas spp.					X		X		X	X	X	X					X		X		X		X	X	
Cyclotella sp.										X															
Cymbella spp.	X		X	X	X	X		X	X	X	X	X											X		
Diatoma sp.			X																						
Dictyosphaerium elegans											X														
Dinobryon cylindricum		X																							
Dinobryon sertularia														X		X			X						
Dinobryon sociale v. *americana*		X			X				X									X							
Dinobryon spp.		X			X											X							X		
Elakatothrix gelatinosa				X																					
Elakatothrix genevensis cells						X	X		X																
Euastrum spp.						X																			

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Euglena sp.					X						X		X							X	X				
Eutreptia sp.																					X				
Filamentous diatoms 10-15µm				X																					
Filamentous diatoms 5-10µm			X																						
Flagellates 2-5µm									X			X							X					X	
Flagellates 5-10µm	X											X						X							
Fragilaria nanana														X											
Fragilaria spp.				X				X	X		X			X											
Fragilaria ulna			X								X														
Golenkinia radiata															X										
Gymnodinium simplex		X	X				X																		
Gymnodinium sp.	X			X																					
Kephyrion sp.																			X					X	
Keratococcus komarkovae																									X
Koliella longiseta	X	X		X	X				X			X					X								
Koliella spiculiformis															X							X	X		
Korschikovella limnetica						X														X	X				
Limnothrix sp.				X																					
Mallomonas spp.		X	X										X	X	X				X					X	
Meridion circulare											X		X												
Merismopedia punctata													X	X											
Merismopedia sp.																					X				
Microcystis natans subcolonies												X													
Monoraphidium komarkovae																			X		X				
Monoraphidium sp.								X																	
Mougeotia sp												X					X		X	X		X			
Naked dinoflagellates 10-20µm												X	X	X		X		X						X	X
Naked dinoflagellates 20-30µm											X				X						X				
Navicula spp.	X		X	X	X	X	X	X		X															
Nephroselmis sp.									X																

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Nitzschia acicularis													X												
Nitzschia spp.												X								X					
Nostoc kihlmanni																								X	
Ochromonas acuta																						X			
Oocystis spp.	X			X	X			X	X	X	X	X			X								X		
Ophiocytium parvulum							X																		
Oscillatoria sp.															X										
Pandorina morum												X									X				
Pediastrum biradiatum										X															
Pediastrum boryanum									X											X	X	X			
Pediastrum integrum					X															X					
Pediastrum spp.																				X					
Pennate diatoms 10-40µm				X			X		X		X	X	X	X	X	X	X	X	X		X	X	X	X	X
Pennate diatoms 40-150µm			X										X		X	X	X				X	X		X	
Phacus pyrum				X								X													
Pinnularia sp.								X																	
Planktolyngbya limnetica																							X		
Planktolyngbya sp.										X															
Planktothrix sp.							X			X								X	X	X	X	X			
Pseudanabaena limnetica											X	X													
Pseudanabaena sp.																		X						X	
Pseudopedinella elachista									X																
Pseudopedinella sp.					X										X			X	X						X
Pyramimonas sp.								X																	
Rhodomonas lacustris	X	X		X	X		X	X		X					X	X			X		X		X	X	X
Romeria sp.													X										X		
Round flagellates 5-10µm																						X	X		
Scenedesmus spp.	X				X															X	X	X			
Sphaerellopsis sp.																			X						
Sphaerocystis sp.		X																							

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Spondylosium sp.						X																			
Staurastrum sp.												X									X				
Synedra acus		X													X										
S*ynedra* spp.				X																					
Synura sp.						X																			
Tabellaria flocculosa				X						X							X					X			
Tabellaria flocculosa v. *asterionelloides*	X				X																				
Tabellaria spp.		X					X													X	X		X		
Teilingia granulata				X		X		X	X		X														
Tetraëdron caudatum							X		X																
Tetraëdron minimum											X														
Tetrastrum komarekii																						X			
Thecate dinoflagellates 10-20µm															X		X								
Thecate dinoflagellates 20-30µm																		X							
Thecate dinoflagellates 30-40µm																					X				
Thecate dinoflagellates 40-50µm					X																				
Trachelomonas spp.				X							X										X				
Trachelomonas varians											X														
Unidentified oval algae							X			X				X	X							X	X		
Woronichinia compacta										X		X													
Zygnema sp.		X										X							X						

Table S7. Occurrence of invertebrate taxa identified in the 25 investigated ponds in seven areas in western Svalbard, Spitsbergen. The 25 sites were distributed in the different areas as follows: Aldegondabreen (four sites), Grønfjordbreen (two sites), Ymerbukta (two sites), Diabasodden (one site), Kapp Napier (one site), Pyramiden (three sites) and Ny Ålesund (12 sites).

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Acroperus harpae												X								X	X				
Alona guttata			X															X							
Alona werestschagini																								X	
Bosmina longispina	X					X	X	X	X		X														
Chydorus sphaericus							X			X	X	X						X		X	X	X	X		
Daphnia cf. *pulex*	X			X	X	X	X		X	X	X	X	X	X	X			X	X	X	X	X	X		X
Macrothrix hirsuticornis										X	X	X	X	X	X					X	X	X			
Diacyclops crassicaudis			X																X	X	X	X			
Cyclops abyssorum		X	X	X		X	X	X	X	X				X	X				X			X		X	X
Eurytemora raboti		X					X		X	X			X							X					
Diaptomidae sp.	X					X	X																		
Epactophanes richardi								X		X								X	X				X		
Maraenobiotus brucei	X			X					X	X		X		X		X		X	X	X				X	
Tahidius discipes													X										X	X	
Nitokra spinipes													X												
Ostracoda	X	X	X	X	X		X	X	X	X	X	X	X	X					X	X	X	X	X	X	
Nematoda	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tardigrada			X		X	X	X	X	X	X					X	X	X	X	X	X	X	X		X	
Camisia foveolata																		X						X	
Lepidurus arcticus	X	X	X		X	X	X		X		X	X													
Apatania zonella		X					X	X																	X
Cricotopus (s. str.) *tibialis*		X	X			X		X	X		X		X						X	X	X	X	X		
Cricotopus s.str.													X	X						X		X			
Cricotopus (Isocladius) glacialis											X	X													
Psectrocladius barbimanus	X		X							X	X			X	X			X				X	X	X	
Hydrobaenus conformis										X							X								
Orthocladius s.str.			X												X			X		X	X		X		
Procladius crassinervis		X		X			X	X	X					X	X	X		X	X					X	
Paratanytarsus austriacus	X		X	X								X		X	X	X			X		X		X	X	X
Micropsectra radialis		X	X				X	X	X															X	

Taxa/Locality	8	9	10	23	45	46	49	50	53	54	62	65	66	67	68	69	70	71	72	74	75	81	82	85	86
Micropsectra sp.								X																	
Chironomus sp.					X	X				X										X	X	X			
Marionina sp.													X												