

Permafrost thaw lakes and ponds as habitats for abundant rotifer populations¹

Paschale N. Bégin and Warwick F. Vincent

Abstract: Thermokarst lakes and ponds were sampled across a range of permafrost landscapes in subarctic Québec (Nunavik, Canada) to compare their rotifer and other zooplankton characteristics with a set of rock-basin lakes and ponds in the region. A total of 24 rotifer species were identified, with an average of seven taxa per waterbody. Rotifer abundance was an order of magnitude higher in the thaw ponds than in rock-basin waters. In some thaw ponds, rotifers accounted for >50% of the total zooplankton biomass, but for <10% in all of the rock-basin waters. Neither α - nor β -diversity was significantly different between the two waterbody types. Grazing experiments with microspheres (0.5–6 μm diameter) showed that medium-sized particles (2–3 μm) were preferred to smaller and larger particles; clearance rates were <0.05% of the water column per day, implying that the rotifer populations were unlikely to be bottom-up limited by food availability. Rotifer abundance was negatively correlated with cladoceran densities, suggesting possible interference effects. *Chaoborus* larvae were also present and may exert a top-down control. Thermokarst ponds are currently favorable environments for rotifers, but the rapid change they have begun to experience brings uncertainty about their ongoing capacity to sustain these prolific communities.

Key words: diversity, permafrost, rotifers, thermokarst, zooplankton.

Résumé : Des lacs et des mares thermokarstiques ont fait l'objet de prélèvement d'échantillons dans divers paysages de pergélisol à travers le Québec subarctique (Nunavik, Canada), afin de comparer les caractéristiques de leurs rotifères et autres zooplanctons, et ce, à un ensemble de lacs et de mares d'ombilic glaciaire dans la région. On a identifié un total de 24 espèces de rotifères, avec une moyenne de sept taxons par plan d'eau. L'abondance de rotifères était d'un ordre de grandeur plus élevé dans les mares de fonte que dans les eaux d'ombilic glaciaire. Dans quelques mares de fonte, les rotifères représentaient >50% de l'ensemble de la biomasse du zooplancton, mais elles en représentaient <10% dans toutes les eaux d'ombilic glaciaire. Ni la diversité α ni β ne se distinguait sensiblement entre les deux types de plan d'eau. Des expériences de broutage avec des microsphères (0,5 à 6 μm de diamètre) ont montré que les particules de taille moyenne (2–3 μm) étaient préférées comparativement aux plus petites et aux grandes particules; les taux d'élimination étaient <0,05% de la colonne d'eau par jour, ce qui laisse entendre qu'il était peu probable que les populations de rotifères subissent une limitation ascendante en raison de la disponibilité alimentaire. L'abondance de rotifères était négativement corrélée avec les densités de cladocères, suggérant des effets d'interférence possibles. Des larves *Chaoborus* étaient aussi présentes et pouvaient exercer un contrôle descendant. Les mares thermokarstiques sont

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actuellement des environnements propices aux rotifères, mais le changement rapide que ces environnements ont commencé à subir engendre l'incertitude qu'ils puissent continuer à maintenir ces communautés prolifiques.

Mots-clés : diversité, pergélisol, rotifères, thermokarst, zooplancton.

Introduction

Small lakes and ponds tend to receive less attention relative to larger freshwater ecosystems, but there is an increasing awareness that small shallow waterbodies are globally important sites for aquatic biodiversity, biological production, and biogeochemical processes (Downing et al. 2006; Downing 2009). In northern landscapes, the degradation and subsidence of ice-rich permafrost give rise to shallow depressions that fill with water to produce thermokarst lakes and ponds (hereafter referred to as thaw ponds; the terms lakes and ponds are both used in the thermokarst literature, with no formal distinction). These are among the most abundant freshwater ecosystems across vast areas of the circumpolar subarctic and Arctic regions (Vincent et al. 2013a). These small (areas typically $<10^4$ m²), shallow (typically <5 m) but numerous aquatic environments are known as sites of high bacterial productivity, with a correspondingly high demand for oxygen (Deshpande et al. 2016) and as biogeochemical hotspots for greenhouse gas production (Walter Anthony et al. 2014; Matveev et al. 2016). Thaw ponds also contain high concentrations of photosynthetic cells, spanning a broad range of size classes (Przytulska et al. 2016). Despite these varied and potentially large resources for transfer to higher trophic levels, the food web characteristics of thaw ponds have been little studied to date.

Zooplankton communities in shallow lakes and ponds can be diverse and reach concentrations up to five times of other freshwater environments because of the absence of fish (Rautio et al. 2011). The resultant grazing activity can potentially consume a large portion of the lower food web resources (Kling et al. 1992). Rotifers are known to be an abundant component of zooplankton assemblages in many types of shallow water ecosystems at temperate latitudes, and early observations of lake plankton at high northern latitudes showed that they were present in high concentrations (Arndt 1993). However, little is known about the taxonomic and functional diversity of this group of micro-invertebrates in northern waters, and their ecology in subarctic thaw ponds has not been studied. Planktonic rotifers feed on protists, bacteria, and particulate organic detritus suspended in the water column (Arndt 1993), and in addition to their influence on microbial communities, they can also provide a food source to higher trophic levels.

Our primary aim in the present study was to determine the diversity, community structure, and abundance of zooplankton in a wide range of subarctic thaw ponds, with emphasis on rotifer populations. We hypothesized that given the organic-rich nature of these waters (Breton et al. 2009) and the range of heterotrophic (Comte et al. 2016), chemotrophic (Crevecoeur et al. 2015), and phototrophic (Przytulska et al. 2016) microbial populations that they support, these environments are conducive to high concentrations of picoplankton-feeding taxa within the phylum Rotifera. Productivity and biodiversity are often positively correlated in a range of ecosystem types (Tilman et al. 1996; Cardinale et al. 2006; Ptaschnik et al. 2008). Given the large limnological variability, including productivity variables, among subarctic thermokarst lakes and ponds (Watanabe et al. 2011), we surmised that both the α -diversity (within ponds) and β -diversity (among ponds) of subarctic rotifer communities are likely to be high relative to less productive, more homogeneous systems such as rock-based northern lakes. Finally, we examined the question of whether the thaw pond rotifer populations are controlled by bottom-up or top-down forces; the former would imply that food is limiting and that the thaw pond microbial community could be in turn controlled by rotifer grazing, whereas top-down effects would imply that predation by

carnivorous zooplankton could be considerable in these fishless ecosystems and could thereby limit the total rotifer biomass.

To address these hypotheses and questions, we sampled 41 thaw ponds in subarctic Québec across a gradient of permafrost degradation to maximize the range of limnological conditions. Sampling was during ice-free open water conditions in mid- to late summer, which is likely to be the period of highest productivity and zooplankton community development. Most of the samples were from near the surface, but we also compared deeper populations in five of the ponds. We additionally made parallel measurements in nine rock-basin lakes and ponds that were located within the same region, but were unaffected by permafrost processes, in order to compare thermokarst ponds with a reference set of non-thermokarst waters. To examine the question of controlling variables, we complemented our analyses of the community and environmental data set with experiments to determine the grazing rates of rotifers on pico- and nano-sized particles in the plankton.

Data and methods

Study sites

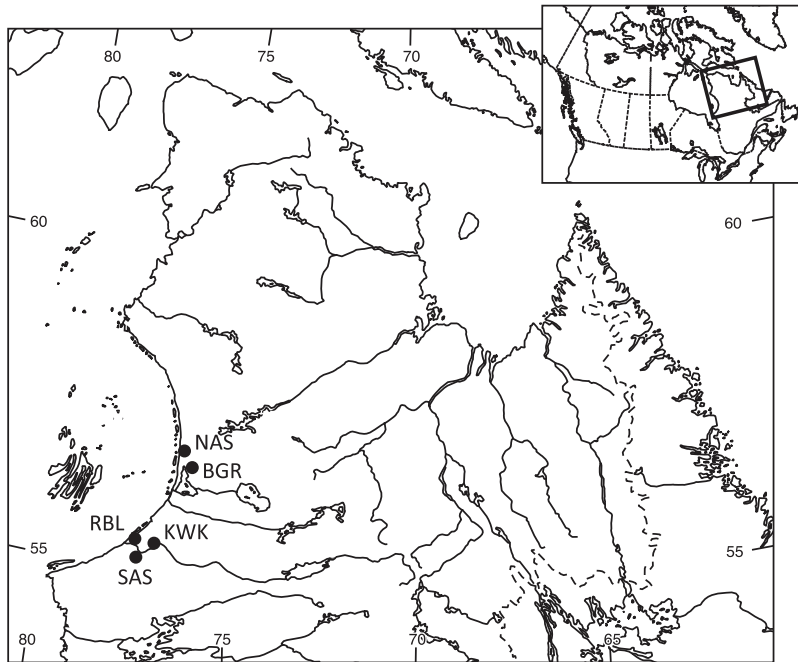
The study was conducted in the vicinity of Whapmagoostui-Kuujjuarapik and Umiujaq villages on the east coast of Hudson Bay, Canada (Fig. 1). These areas are located in sporadic and discontinuous permafrost zones respectively and are subject to a subarctic climate with a cold, dry winter and a short, cool, and humid summer influenced by Hudson Bay. At Kuujjuarapik over the period 1971 to 2000, mean monthly air temperatures ranged from -23.4 °C in January to 10.6 °C in July, and annual precipitation averaged 660 mm, with 40% as snow (Environment Canada 2002).

The inundation of coastal lands around Hudson Bay by the Tyrrell Sea ca. 7900 BP (Hillaire-Marcel 1976; Allard and Seguin 1985) resulted in the deposition of a thick layer of marine silts. Postglacial land uplift raised the coast up to its present altitude, by 185 m near Kuujjuarapik and 228 m near Umiujaq. The silts are mainly concentrated in valleys and represent poorly drained deposits that became permanently frozen soon after land emergence. Recent permafrost degradation has created karst-like landforms recalling karst landforms in limestone, from which the term “thermokarst” is derived (landscape erosion caused by permafrost degradation). This region of Nunavik represents one of the densest areas of thermokarst, suggesting active landform erosion due to climate warming (Bhiry et al. 2011). For thaw pond sampling, we selected valleys at each end of the latitudinal gradient from Kuujjuarapik to Umiujaq along the Hudson Bay coast, in order to capture the variability within and among permafrost regimes across this thermal gradient, and included lakes on peatland permafrost (palsa thaw ponds) and on mineral permafrost (lithalsa thaw ponds). A set of shallow rock-basin lakes and ponds near Kuujjuarapik was also studied, as reference environments unaffected by thermokarst. A total of 50 waterbodies were sampled across five sites (Tables S1 and S2²). Fieldwork was conducted in summer 2012 and 2013 during the month of August, since this is the period when these waters reach their warmest temperatures (Deshpande et al. 2015), and is therefore likely to be the optimal time for the development of rotifer communities.

The five sites are within a region where there have been extensive ecological, paleoecological, and geomorphological studies (Bhiry et al. 2011), including the project “Arctic Development and Adaptation to Permafrost in Transition” (ADAPT) (Vincent et al. 2013b) that includes the present study. Although the lakes and ponds at each site shared certain characteristics in their catchment properties, there were often striking differences

²Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/as-2016-0017>.

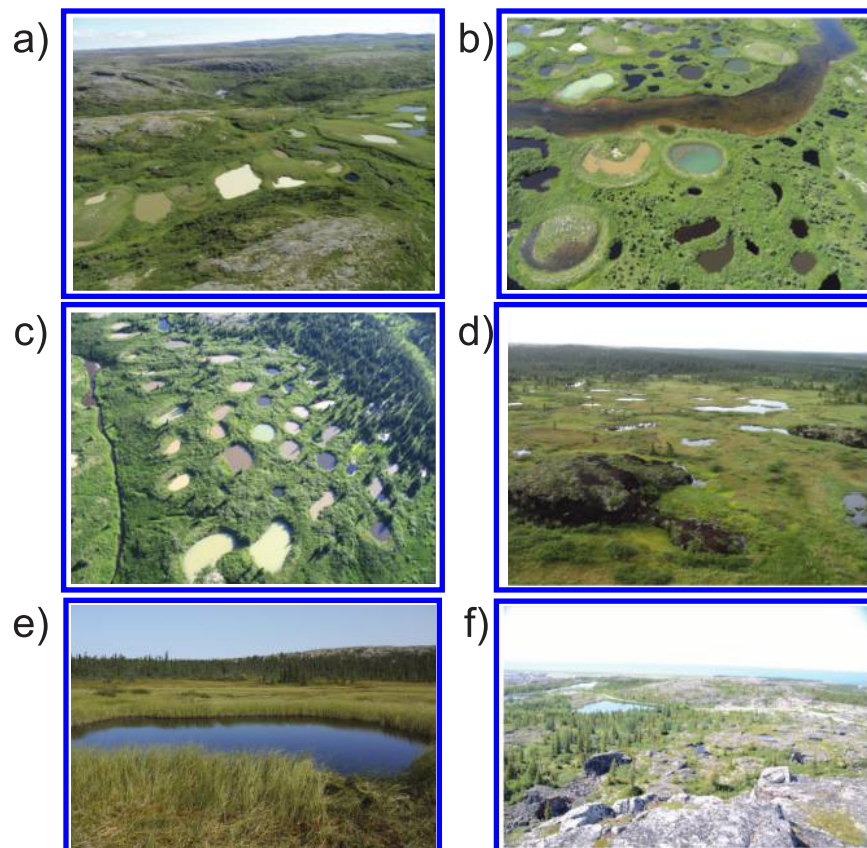
Fig. 1. Map of the study area, eastern Hudson Bay.



among them, even between adjacent waters, including in their appearance (water transparency and colour) (Watanabe et al. 2011) and other limnological properties (Laurion et al. 2010; Przytulska et al. 2016).

In the northern part of the study area (Umiujaq region), the Bundesanstalt für Geowissenschaften und Rohstoffe site (BGR) ($56^{\circ}36'N$, $76^{\circ}12'W$) (Fig. 2b) is within the Sheldrake River valley that contains degrading permafrost mineral mounds (lithalsa, *sensu* Harris 1993). As the permafrost degrades, the pond structure evolves from a crescent shape on the rim of the lithalsa to a circular pond (Calmels et al. 2008). The Nastapoka River ponds (NAS) ($56^{\circ}55'N$, $76^{\circ}22'W$) (Fig. 2a) are also located on degrading lithalsa plateau. Marine silt deposits are close to the ground surface and are easily eroded, and these sediments give many of the lakes an opaque white colour. Long-term studies have been conducted at the NAS and BGR sites (Figs. 2a and 2b) focusing on permafrost dynamics (Seguin and Allard 1984; Calmels and Allard 2004) and sediment transport (Jolivel and Allard 2013). In the southern part of the study area, ponds along the Kwakwatanikapistikw River (KWK) ($55^{\circ}19'N$, $77^{\circ}30'W$) (Fig. 2c), 12 km east of Whapmagoostui-Kuujuarapik, are also formed in depressions left by the subsidence of mineral mounds. They are surrounded by stands of shrubs (*Salix planifolia* Pursh and *Salix glauca* L., *Alnus viridis* [Chaix] DC, and *Myrica gale* L.), with sparse populations of *Picea mariana* Mill., *Picea glauca* [Moench] Voss, *Larix laricina* [Du Roi] K. Koch, *Rhododendron groenlandicum* [Oeder] Kron and Judd, and *Betula glandulosa* Michx (Bouchard et al. 2014). Some areas around the ponds are colonized by *Sphagnum* sp. (mainly *Sphagnum fuscum* [Schimper] H. Klinggraff and *Sphagnum capillifolium* [Ehrhart] R. Hedwig). The Sasapimakwananisikw River site (SAS) ($55^{\circ}13'N$, $77^{\circ}42'W$) (Fig. 2d) is located 8 km southeast of Kuujuarapik, where the ponds are formed in a peatland surrounded by palsas, which collapse and bring organic matter previously trapped in permafrost to the aquatic ecosystem. These black-coloured peatland permafrost waters have especially high rates of methane emission (Matveev et al. 2016). The edges of the ponds are colonized

Fig. 2. Photographs of the subarctic sampling sites. Two sites were located in the vicinity of the Inuit community of Umiujaq: (a) Nastapoka River valley (NAS) and (b) Bundesanstalt für Geowissenschaften und Rohstoffe site in the Sheldrake River valley (BGR). Three additional sites were located in the vicinity of the Cree and Inuit community of Whapmagoostui-Kuujuarapik: (c) Kwakwatanikapistikw River valley (KWK), (d) Sasapimakwananisikw River valley (SAS), (e) lake SAS2A, and (f) the rock-basin reference lakes (RBL). Photo credits: J. Comte, I. Laurion, B. Deshpande, and A. Matveev.



by *Carex* sp., *Eriophorum angustifolium* Honckeny, *Trichophorum* sp., *Rubus chamaemorus* L., *Potentilla palustris* (L.) Scop., *Sphagnum* spp. (*S. capillifolium*, *Sphagnum teres* [Schimper] Ångstrom, and *Sphagnum warnstorffii* Russow), and brown mosses from the *Dicranum* group (Arlen-Pouliot and Bhiry 2005). Rock-basin lakes and ponds were sampled in the vicinity of Whapmagoostui-Kuujuarapik (RBL) (55°17'N, 77°44'W) (Fig. 2e); these waterbodies lie on bedrock and are not influenced by thermokarst processes. The vegetation of their catchments is mixed forest tundra, with *P. mariana*, *B. glandulosa*, *R. groenlandicum*, and lichens.

Physico-chemical measurements

Field measurements of the limnological properties of the ponds were taken in their surface waters. Temperature, dissolved oxygen, redox potential, pH, and conductivity were measured with a Hydrolab DS5X probe (Loveland, Colorado). Fine-scale profiles were made for conductivity and temperature using a RBR XR620 CTD (Richard Brancker Research Ltd.). Water samples were filtered through 0.2 µm cellulose acetate filters (Advantec MFS) and stored at 4 °C until analysis for dissolved organic carbon (DOC) concentration with a Shimadzu TOC-5000A carbon analyzer calibrated with potassium biphthalate. Total suspended solids (TSS) were collected on pre-ashed, pre-weighed glass fiber filters (0.7 µm, Advantec MFS) that were dried for 2 h at 60 °C and reweighed (Breton et al. 2009).

Total phosphorus (TP) and total nitrogen (TN) were measured using unfiltered water samples acidified with sulphuric acid (0.2% final concentration) and stored at 4 °C until a persulfate digestion followed by analysis. TP was measured by spectrophotometry following the method described by Stainton et al. (1977). TN was measured by the determination of nitrate and nitrite by hydrazine reduction using flow injection analysis following the QuickChem method 10-107-04-2-A (Zellweger Analytics Inc., Milwaukee, Wisconsin).

Picoplankton and chlorophyll *a*

Surface water samples were collected using 1 L opaque Nalgene bottles. Water for bacterial abundance was fixed with a filtered solution of glutaraldehyde (1% final concentration) and was stored frozen at –80 °C until further analysis. Cells were stained using SYBR Green I (Invitrogen) and enumerated based on their fluorescence and side-scatter characteristics in a BD FACSCalibur flow cytometer (BD Biosciences) following the procedure described in Rossi et al. (2013). Chlorophyll *a* (Chl *a*) samples were collected on glass fiber filters (GF/F equivalent, Advantec MFS) and kept at –80 °C until extraction in 95% methanol. Chl *a* concentrations were measured by high-pressure liquid chromatography as described in Bonilla et al. (2005).

Zooplankton sampling

Zooplankton was collected at the surface of the 50 ponds: 9 at BGR, NAS, and RBL, 12 at SAS, and 11 at KWK. Surface sampling was by way of a horizontal trawl of a 35 µm mesh zooplankton net (21 cm in diameter) in each waterbody. Zooplankton concentrations were calculated with the estimation of volume filtered with the net according to the distance covered by the net at the surface of the pond. Samples at different depths were collected in five ponds with a 30 L Schindler–Patalas trap (35 µm mesh). The sampling depths were chosen to include the surface waters, the oxycline, and deeper waters.

Diurnal migration was examined in one of the ponds (SAS2A) in August 2013 by sampling with the Schindler–Patalas trap at four depths (surface and 0.8, 1.3, and 1.8 m) over a 24 h period. Zooplankton samples were preserved with ethanol (95% final concentration) and Lugol's iodine (4% final concentration) and the rotifers and other zooplankton were counted using an Utermöhl sedimentation chamber (Utermöhl 1958) with a Zeiss Axiovert inverted microscope at 100 to 400× magnification.

Mean biomass in micrograms per litre was calculated for each species of zooplankton from measurements using microphotographs or, for *Chaoborus* sp., direct measurements of preserved specimens. Rotifer biovolumes were calculated according to McCauley (1984). The wet biomass to biovolume ratio was considered to be 1:1, and these values were converted to dry biomass according to Pauli (1989). Body width and length of the copepods and cladocerans were measured to estimate their biomass according to the regression curves in McCauley (1984), Culver et al. (1985), and Lawrence et al. (1987). *Chaoborus* sp. biomass was estimated with the same method using the front air sac length according to the regression curves in Traina and von Ende (1992).

Grazing experiments

To assess the grazing pressure of rotifers on small-sized particles in thermokarst ponds, an experiment was performed on zooplankton from KWK12. Surface water containing rotifer populations was collected and maintained in dim light in 20 L cubitainers for 12 h, and 500 mL aliquots were then transferred to smaller plastic containers. After a pre-incubation period of 30 min to allow the zooplankton to acclimatize after transfer, these samples were then incubated for 20 min with one of four different sizes of fluorescent microspheres: 0.5, 1.75, 3.0, and 6 µm in diameter (Polyscience). The final concentrations of the added microspheres were 5220, 95, 20, and 3 microspheres µL⁻¹. A control group (T0) was fixed

immediately after the addition of microspheres in order to determine any immediate adsorption or ingestion of beads. After incubation, the zooplankton was filtered onto a 35 μm sieve, narcotized with carbonated water (Alka-Seltzer), and fixed with a solution of formaldehyde (0.06% final concentration) and glutaraldehyde (0.75% final concentration). The rotifers and ingested beads were counted in an Utermöhl sedimentation chamber on an inverted microscope by epifluorescence (Zeiss Axiovert, 100 \times). The suspended bead concentrations were measured using flow cytometry (BD FACSCalibur, BD Biosciences) and the clearance rate (CR) was then calculated as in Ooms-Wilms (1997):

$$(1) \quad \text{CR} = \frac{M_t - M_0}{[M]T}$$

where M_t corresponds to the number of microspheres ingested after the period of the incubation, M_0 is the number of microspheres ingested immediately after the addition of the microspheres (control bottles), $[M]$ is the concentration of microspheres added to the bottles, and T is the period of incubation.

A similar experiment was performed on zooplankton from one of the rock-basin reference lakes (Olsha Lake) in order to compare with grazing rates in a non-thermokarst waterbody. Surface water was collected from the lake and brought back to the laboratory where it was acclimated in 4 L cubitainers for 12h. Water samples were thereafter incubated for 20 min with five different sizes of fluorescent microspheres (1.75, 2, 3, 4.5, and 6 μm in diameter and 311, 37, 108, 38, and 13 microspheres μL^{-1} , respectively) in triplicate.

Statistical analysis

Cluster analysis of rotifer community data was performed with the unweighted pair-group method using arithmetic averages on a chord distance matrix (Borcard et al. 2011). A redundancy analysis (RDA) was performed on surface limnological variables constrained by rotifer assemblages and the Shannon diversity index for 28 thermokarst ponds. We used the “diversity” function of the Vegan package from Borcard et al. (2011) for R version 2.15.1 (R Core Team) to process the RDA. A Hellinger transformation was performed on the rotifer population data matrix using the “Decostand” function from the same package. Environmental data were standardized and centered. A forward selection was run on the data set to reduce co-linearity in explanatory variables (Borcard et al. 2011). The Shannon diversity index was computed for each pond, and the Euclidian distances between the values obtained by the Hellinger transformation of the species data matrix were used as an index of β -diversity. Mean distance values were computed for each site in order to analyze their correlative relationships with the limnological variables. The grazing experiments were analyzed with a two-way ANOVA and a Tukey HSD test for multiple comparisons, after verification of the homogeneity of variance using the Levene’s test in SigmaPlot version 11 (Systat Software Inc., Germany).

Results

Zooplankton community structure and abundance

Twenty-four rotifer taxa were identified at the surface of the 50 sampled lakes and ponds, with an average of seven taxa (range from 2 to 14) per waterbody (Table 1; Fig. 3). Thirteen crustacean zooplankton taxa were observed, with an average of three taxa per lake (range from 0 to 8). Insect larvae of two species of *Chaoborus* were observed in 19 of the waterbodies; these were subsequently identified as *Chaoborus americanus* and *Chaoborus trivittatus*, which were combined in the enumerations.

Table 1. Rotifer taxa identified at the surface of lakes and ponds at the five subarctic sites and their potential food sources as indicated by the literature (Pourriot 1977; Sanders et al. 1989; Walz 1995).

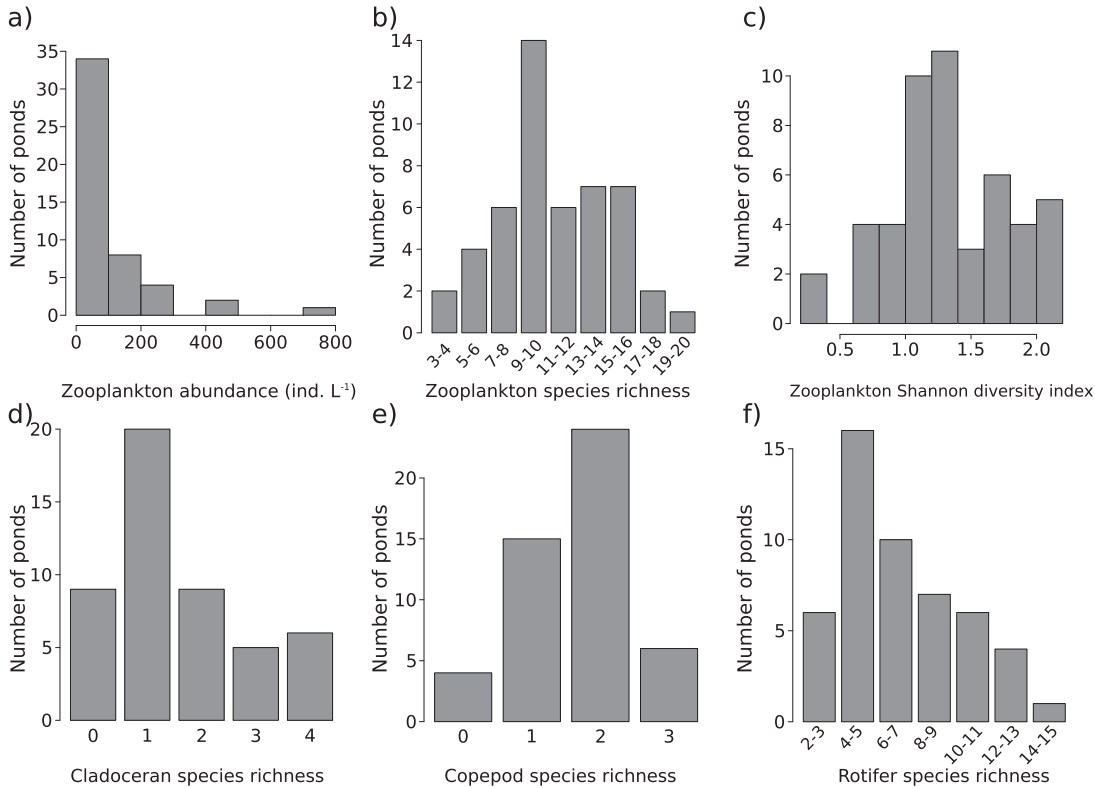
Species	Site					Food source
	RBL	NAS	BGR	KWK	SAS	
Subclass Bdelloida						
<i>Philodina</i> sp.	+	-	-	-	+	D, BA
Subclass Monogononta						
Order Collothecaceae						
<i>Collotheca</i> sp.	-	+	+	+	+	
Order Flosculariaceae						
<i>Conochilus unicornis</i>	+	+	++	+	+	D, BA, SA
<i>Pompholyx</i> sp.	-	+	+	+	+	D, BA
Order Ploima						
<i>Anuraeopsis fissa</i>	+	++	++	+	+	D, BA
<i>Ascomorpha</i> sp.	+	+	+	+	+	DI
<i>Asplanchna</i> sp.	+	+	-	-	+	LA, CI, RO
<i>Colurella</i> sp.	-	+	+	+	+	
<i>Gastropus stylifer</i>	+	+	+	-	+	SA
<i>Kellicottia longispina</i>	+	+	-	-	-	D, BA, SA, LA, DA
<i>Keratella cochlearis</i>	+	+	+	+	+	D, BA, SA, LA, FL, DA
<i>Keratella serrulata</i>	+	+	+	-	+	D, BA, SA, LA, FL, DA
<i>Keratella tecta</i>	+	+	+	+	-	D, BA, SA, LA, FL, DA
<i>Keratella testudo</i>	-	+	+	-	+	D, BA, SA, LA, FL, DA
<i>Lecane</i> sp.	+	-	+	-	+	D, BA
<i>Lepadella</i> sp.	+	+	+	+	+	
<i>Monommata</i> sp.	-	-	-	-	+	
<i>Monostyla copeis</i>	+	+	+	+	+	
<i>Ploesoma</i> sp.	+	+	+	-	+	RO
<i>Polyarthra euryptera</i>	-	+	+	+	++	SA, LA, DA
<i>Polyarthra remata</i>	+	++	++	++	+	SA, LA
<i>Synchaeta</i> sp.	-	+	+	+	+	SA, LA, DA
<i>Trichocerca</i> sp.	-	+	+	+	+	SA, RO
<i>Trichotria</i> sp.	+	+	-	-	+	

Note: Key: -, absent in all samples; +, present in at least one pond; ++, >100 ind L⁻¹ in at least one pond; D, detritus; BA, bacteria; SA, small algae; LA, large algae; FL, flagellates; CI, ciliates; DA, diatoms; DN, dinoflagellates; RO, other rotifers.

Rotifers were present in high densities in almost all of the thaw ponds. The maximum concentration at the surface was 660 ind L⁻¹ at the BGR site (Fig. S1A) and up to 1520 ind L⁻¹ at the KWK site (see Fig. 7c). Rotifers were significantly more abundant in thaw ponds than in the reference lakes (Fig. 4a) (ANOVA: $F_{4,45} = 4.29$, $p = 0.005$). Rotifer abundance was significantly higher at BGR, NAS, and SAS than at KWK and RBL (Tukey's HSD test). However, rotifer abundance was exceptionally low in two milky coloured (high sediment content) thaw ponds at the NAS site (NASB and NASD, 0.39 and 0.53 ind L⁻¹, respectively) (Fig. S1A).

The α -diversity of the rotifer community, as measured by species richness, Shannon diversity index, and Simpson index, did not vary significantly among the five sites (ANOVA: $F_{4,45} = 2.18$, $p = 0.09$, $F_{4,45} = 2.01$, $p = 0.11$, and $F_{4,45} = 1.26$, $p = 0.30$, respectively) (Figs. 4b, 4c, and 4d). Mean β -diversity was significantly higher at BGR, NAS, and SAS than at the reference site, whereas it was lower in KWK (ANOVA: $F_{4,224} = 12.37$, $p < 0.001$) (Fig. 4e). Rotifers were the dominant zooplankton group in terms of abundance in the majority of the waterbodies with the exception of SAS1H, which was largely dominated by *Daphnia pulex* (Figs. S1B and S2), and some RBL reference lakes (RBL4KM, RBLPOOL1, RBLPOOL2, and RBLWP1).

Fig. 3. Distribution of zooplankton in the 50 surveyed thaw ponds: (a) total zooplankton abundance, (b) total zooplankton species richness, (c) total zooplankton Shannon diversity, (d) cladoceran species richness, (e) copepod species richness, and (f) rotifer species richness.



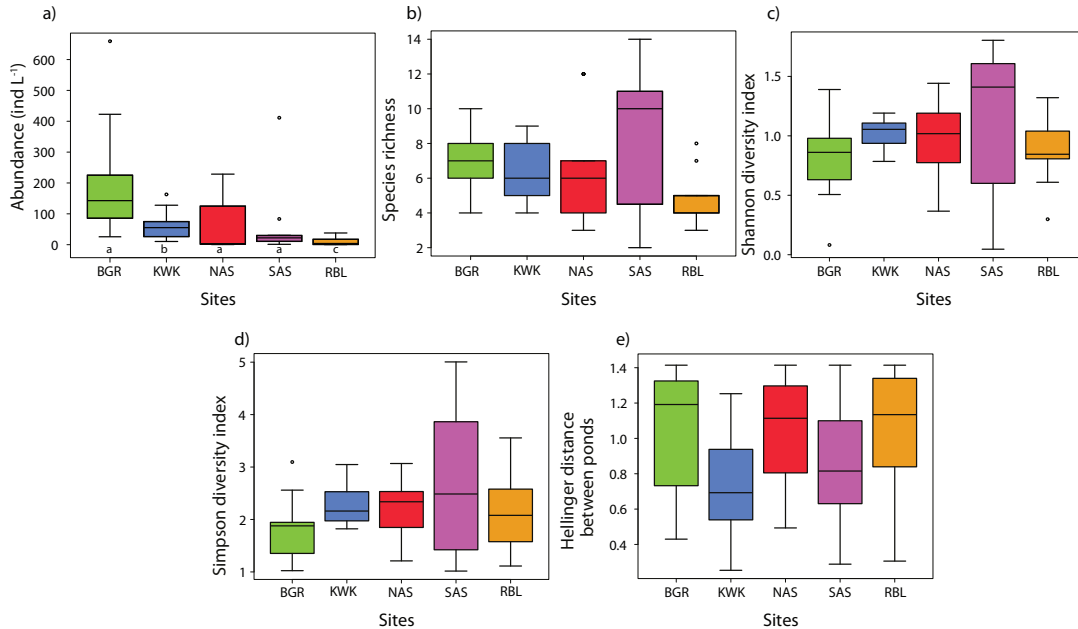
In terms of biomass, rotifers were dominant (>50% biomass) in eight of the 41 thaw ponds. Cladocerans were dominant in five out of the nine NAS ponds and in seven out of 12 SAS ponds. In the RBL reference lakes and ponds, rotifers represented less than 10% of the total zooplankton biomass and were a minor constituent (<1%) in four of the RBL waterbodies. Zooplankton biomass was dominated by cladocerans in NAS, BGR, and SAS, by *Chaoborus* sp. in KWK, and equally by copepods and cladocerans in RBL.

Zooplankton diversity

Five species dominated the rotifer communities: *Anuraeopsis fissa*, *Polyarthra remata*, *Keratella cochlearis*, *Polyarthra euryptera*, and *Conochilus unicornis* (Fig. 5). The waterbodies showed some clustering according to site, but in many cases, ponds of distant sites were more closely related to the ones nearby. SAS lakes were clustered, with the exception of two that had high concentrations of *D. pulex* and rotifer communities dominated by the genera *Monostyla* and *Lecane*. The zooplankton assemblages at other sites showed little clustering, and their limnological properties were more variable than in the SAS ponds (Table 2; Tables S1 and S2).

The RDA analysis of the rotifer community was statistically significant (permutation test: $F_{10,17} = 1.955$, adjusted $R^2 = 0.261$, $p = 0.002$), with three significant canonical axes (RDA 1: $p = 0.001$, RDA 2: $p = 0.003$, RDA 3: $p = 0.018$); however, they explained only a small percentage of the total variation in rotifer community structure (10.2%, 6.1%, and 3.7%, respectively). For this analysis, picoeukaryote abundance and latitude were removed because of their strong correlation with the abundance of picocyanobacteria and DOC, respectively.

Fig. 4. ANOVA of the rotifer data with the different sites as factors: (a) abundance (the boxplots with different letters show significant differences between sites), (b) species richness, (c) Shannon diversity index, (d) Simpson diversity index, and (e) Hellinger mean distance between ponds (β -diversity).

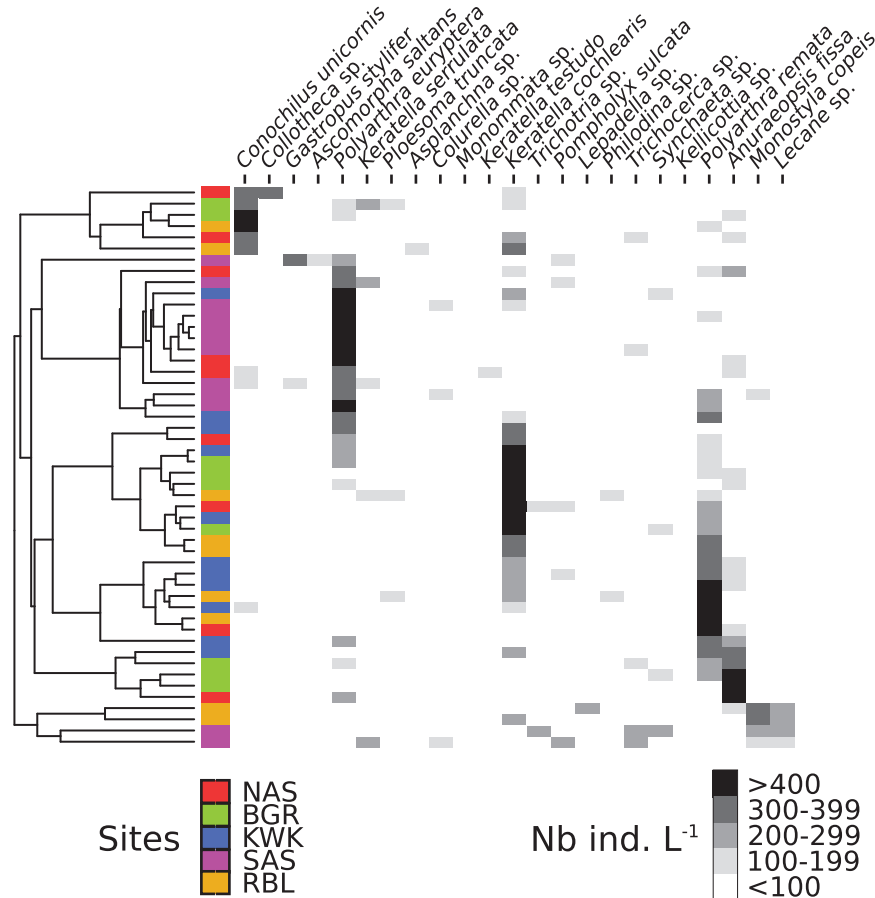


The RDA analysis indicated that Shannon diversity was positively correlated with copepod, cladoceran, TP, and Chl *a* concentrations (Fig. 6). *Conochilus unicornis* was positively correlated with TP and Chl *a* concentrations, while *P. euryptera* was positively correlated with temperature, DOC, and bacterial abundance. *Polyarthra remata* was positively correlated with oxygen concentration and *Chaoborus* abundance but negatively with copepod abundance (Fig. 5). Both *K. cochlearis* and *A. fissa* were positively correlated with picocyanobacteria, oxygen concentration, and *Chaoborus* abundance (Fig. 6). The clustering of sites in the RDA implied that the KWK group was more related to *Chaoborus*, picocyanobacteria, and high oxygen concentrations, whereas the NAS sites were more related to high phosphorus concentrations and SAS sites were related to high DOC, bacterial abundance, and temperature (Fig. 6).

Four environmental variables were identified in a multiple linear regression by forward selection (999 permutations) as the most influential on rotifer diversity. The strongest explaining variables were surface oxygen concentration (positive relationship: adjusted $R^2 = 0.068$, $F = 2.96$, $p = 0.009$) and DOC (negative relationship: adjusted $R^2 = 0.064$, $F = 2.91$, $p = 0.013$). The two additional variables were Chl *a* (adjusted $R^2 = 0.046$, $F = 2.41$, $p = 0.021$) and *Chaoborus* abundance ($R^2 = 0.046$, $F = 2.43$, $p = 0.035$), both with positive relationships. The combined variance explained by these variables was significant but small (22%).

The zooplankton showed large differences in vertical distribution in three of the four thaw ponds profiled (KWK01, KWK12, and KWK23) (Fig. 7). In KWK01, a higher cladoceran biomass value was observed at 1.0 m, while the rotifer biomass increased to maximum values deeper in the water column, even in the presence of *Chaoborus* and low concentrations of oxygen. In KWK06, rotifer biomass was relatively constant with depth at around $15 \mu\text{g L}^{-1}$, including deeper in the water column at low oxygen concentrations ($<2 \text{ mg L}^{-1}$). *Chaoborus* biomass was high throughout the whole water column, whereas cladocerans were absent and a low biomass of copepods was present at 1.7 m depth. *Chaoborus* was abundant at the surface and at 2.2 m.

Fig. 5. Heat map of the rotifer community composition and their clustering according to the unweighted pair-group method using arithmetic averages performed on a chord distance matrix (Borcard et al. 2011). The darker shading represents the dominant species.



Rotifer concentrations increased with depth in the water column of KWK12 and rose to a maximum at 2.4 m (1520 ind L^{-1} , the highest concentration recorded in this study), despite the presence of high concentrations of *Chaoborus* (Fig. 7c). Copepod biomass (dominated by nauplii) also increased with depth. KWK23 was slightly different from the three previous ponds in that although *Chaoborus* was abundant at the surface, rotifer and cladoceran densities decreased with depth (Fig. 7d).

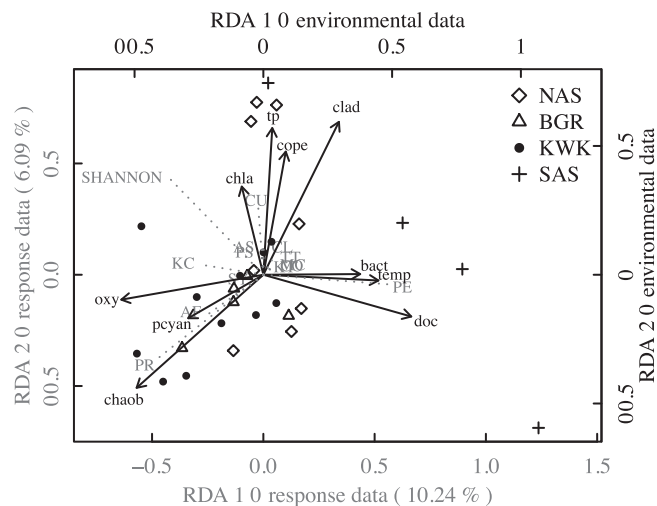
The analysis of zooplankton distribution in Iqalussiuvik Lake (an RBL site) showed that copepods dominated the biomass (55% of total zooplankton biomass at the surface) and that rotifers were present throughout the water column, but at concentrations three to five times lower than in KWK thermokarst ponds (Fig. 7e). The rotifer communities in KWK01, KWK06, and KWK12 were dominated by *K. cochlearis* (respectively 76%, 45%, and 68% of the total rotifer abundance at the surface), whereas *P. remata* was dominant in KWK23 (56% of the total rotifer abundance at the surface), with subpopulations of *A. fissa* (15% abundance) and *K. cochlearis* (24% abundance). The rotifer community in Iqalussiuvik Lake was dominated by *C. unicornis* (72% of the total rotifer abundance at the surface).

Table 2. Median and range of the physical and biological variables for the surface waters of 50 ponds sampled in August 2012.

	RBL		NAS		BGR		KWK		SAS	
	Median	Range	Median	Range	Median	Range	Median	Range	Median	Range
Temperature (°C)	18.3	14.7–20.5	17.0	13.8–18.3	14.6	13.4–17.2	14.7	12.0–18.3	15.6	12.4–19.9
pH	6.7	6.1–7.4	7.3	6.8–7.6	6.7	6.5–7.0	6.4	5.9–8.3	6.0	5.9–7.7
Conductivity ($\mu\text{S cm}^{-1}$)	82	33–231	195	3–457	168	38–230	70	55–89	104	76–945
TP ($\mu\text{g L}^{-1}$)	10.2	1.6–17.2	49.5	7.9–994.5	25.6	7.3–391	71.7	27.4–197.3	18.6	11.7–197.3
TN (mg L^{-1})	0.8	0.2–1.4	0.4	0.3–4.2	0.3	0.2–1.1	0.4	0.2–0.6	0.7	0.3–2.3
DOC (mg L^{-1})	9.2	3.6–15.8	4.1	1.5–7.3	5.3	2.0–14.3	10.6	5.2–13.4	16.5	10.5–33.0
Oxygen (mg L^{-1})	8.9	6.4–10.0	9.1	4.3–9.7	7.0	4.2–8.0	9.9	8.3–12.0	6.6	1.9–10.0
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	2.2	0.3–5.5	1.4	0.2–2.2	1.7	1.0–7.0	7.4	1.6–31.6	2.1	0.9–72.0
BA (10^6 cells mL^{-1})	3.4	1.6–7.3	4.8	0.8–15.6	2.4	1.4–13.7	2.2	0.9–5.0	2.5	1.5–24.3
PA (10^3 cells mL^{-1})	66.7	2.5–441.2	0.2	0–17.7	0.04	0–358.2	48.0	0.2–120.4	2.0	0.3–40.5

Note: TP, total phosphorus; TN, total nitrogen; DOC, dissolved organic carbon; BA, bacterial abundance; PA, picocyanobacterial abundance. Study sites: Rock Basin Lakes (RBL), Nastapoka River ponds (NAS), Bundesanstalt für Geowissenschaften und Rohstoffe ponds (BGR), Kwakwakaikwak River ponds (KWK), and Sasipamakwananiskw River ponds (SAS).

Fig. 6. Redundancy analysis of rotifer species and the Shannon diversity index (dashed grey lines) constrained by environmental variables (solid black lines) in 33 thermokarst ponds. Rotifer species: AN, *Anuraeopsis fissa*; AS, *Ascomorpha* sp.; CO, *Conochilus unicornis*; KC, *Keratella cochlearis*; MO, *Monostyla copeis*; PR, *Polyarthra remata*; PE, *Polyarthra euryptera*; PM, *Pompholyx sulcata*; SY, *Synchaeta* sp.; TR, *Trichocerca* sp. SHANNON, Shannon diversity index. Environmental variables: lat, latitude; tp, total phosphorus; temp, temperature; oxy, oxygen concentration; cond, conductivity; pH, pH; orp, oxydoreduction potential; bact, bacterial abundance; pcyan, picocyanobacterial abundance; clad, cladoceran abundance; cope, copepod abundance; chaob, *Chaoborus* sp. abundance.



Vertical migration

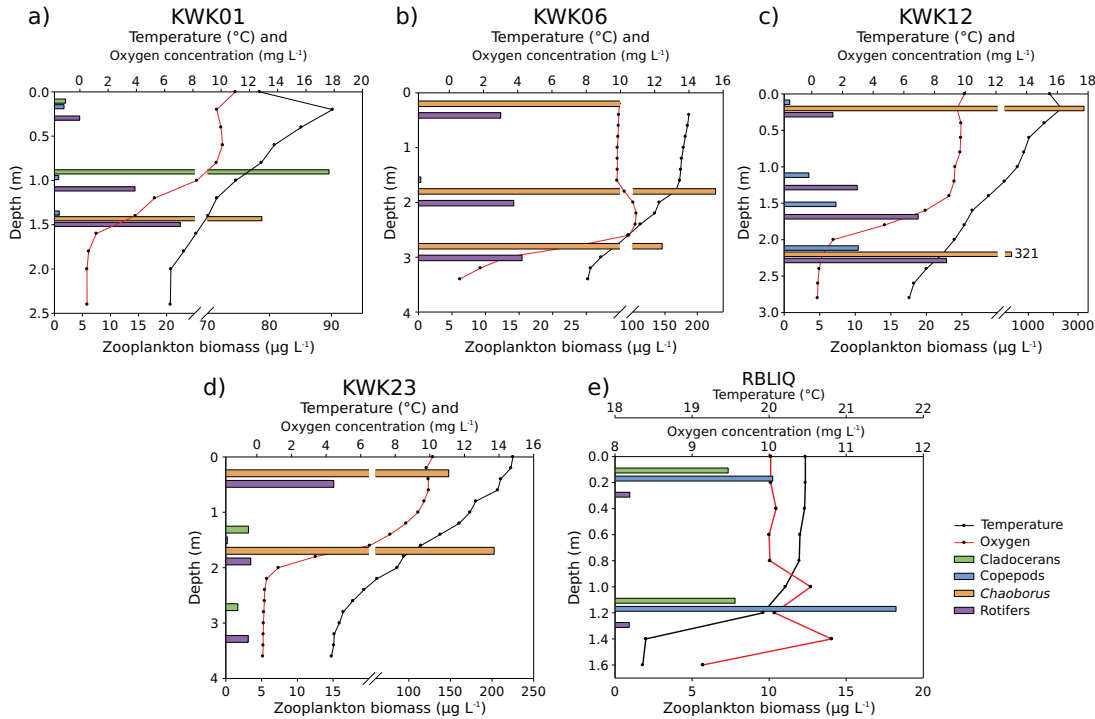
The 24 h migration study in SAS2A showed that cladocerans were concentrated at around 0.8 m at night and spread throughout the water column at 06h00, falling to non-detectable concentrations at all sampled depths by midday (Fig. 8a). The copepod populations were more concentrated at the surface at 06h00 and 18h00. They became more evenly distributed throughout the water column by midnight and more concentrated at around 0.8 m at midday (Fig. 8b). *Chaoborus* populations were concentrated at the surface at 18h00 and at 0.8 m at midnight. They were not observed at 06h00 and midday the next day (Fig. 8c).

The total rotifer community showed little change though the water column over 24 h, with slightly lower biomass densities at the surface at midday and midnight (Fig. 8d). *Keratella serrulata* and *Keratella testudo* showed the strongest evidence of vertical migration, with higher concentrations at the surface at midnight and at lower depths during the daylight hours (Figs. 8f and 8g). In contrast, *K. cochlearis* showed no discernable pattern of vertical migration. *Lepadella* sp. peaked lower in the water column at midnight and 18h00 but was more evenly distributed at midnight and 06h00 (Fig. 8h).

Top-down versus bottom-up controls

The microspheres were ingested by the rotifers (clearance rate up to 2244 nL ind⁻¹ h⁻¹), indicating the grazing potential on small particles. The two-way ANOVA of grazing rates in thaw pond water (Table 3) revealed significant effects of species ($F_{3,32} = 13.56$, $p < 0.001$) and microsphere diameter ($F_{3,32} = 3.95$, $p = 0.017$) as well as significant interaction between species and microsphere diameter ($F_{9,32} = 3.72$, $p = 0.003$). Tukey HSD tests showed that differences in size of microspheres ingested were significant for the *Synchaeta* sp. only and that the 3 μ m microspheres were preferred. Differences among species were observed for 1.75 and 3 μ m microspheres, with *Synchaeta* sp. filtering at the fastest rate: 14, 22, and 318 times faster than *K. cochlearis*, *Polyarthra* sp. and *Trichocerca* sp., respectively.

Fig. 7. Vertical distribution of zooplankton and associated temperature (black) and oxygen (red) profiles in four thermokarst ponds and the reference rock-basin waterbody Iqalussivik Lake: (a) KWK01, (b) KWK06, (c) KWK12, (d) KWK23, and (e) RBLIQ.



The two-way ANOVA of rotifer grazing rates in the reference RBL water (Table 4) also showed significant effects of species ($F_{3,39} = 29.14$, $p < 0.001$), microsphere diameter ($F_{4,39} = 7.08$, $p < 0.001$), and interaction between species and microsphere diameter ($F_{12,39} = 6.15$, $p < 0.001$). The Tukey HSD analysis showed that differences in size of microsphere ingested were significant only in one species (*C. unicornis*) and with preference for the 2 μm microspheres. Differences among species were observed for 2 and 4.5 μm microspheres only, with *C. unicornis* filtering at rates that were 33, 87, and 106 times faster than *K. cochlearis*, *Polyarthra* sp., and *Pompholyx sulcata*, respectively.

To assess the maximum grazing potential in the waterbodies, we multiplied the maximum filtering rate per hour for each species and each microsphere size to give a daily maximum filtering rate in nanolitres per individual per day. We then multiplied this value by the maximum concentration of rotifers observed in the waterbodies in order to estimate an upper bound to the percentage of the water column filtered by each species (Tables 5 and 6). These calculations gave values that convert to percentages of total lake volume filtered of 0.029% day^{-1} in the reference lake (RBLOL) and 0.035% day^{-1} in KWK12.

Discussion

Zooplankton community structure and abundance

In accordance with our hypothesis, the thaw ponds sampled across a broad range of permafrost conditions contained high population densities of rotifers. These productive waters, as indicated by their Chl *a* and TP concentrations, supported orders of magnitude higher rotifer concentrations than the shallow rock-basin waterbodies in the same region; for example, the mean rotifer abundance at the BGR site was 20 times higher than at the

Fig. 8. Zooplankton diurnal vertical profiles from 18h00 on August 2 to 12h00 on August 3, 2013, in SAS2A pond. The band widths are proportional to the percentage of biomass found at the discrete depths. Macrozooplankton groups: (a) cladocerans, (b) copepods, (c) *Chaoborus* sp. Rotifer species: (d) total rotifer community, (e) *Keratella cochlearis*, (f) *Keratella serrulata*, (g) *Keratella testudo*, and (h) *Polyarthra* sp. *n* is the number of species found in samples.

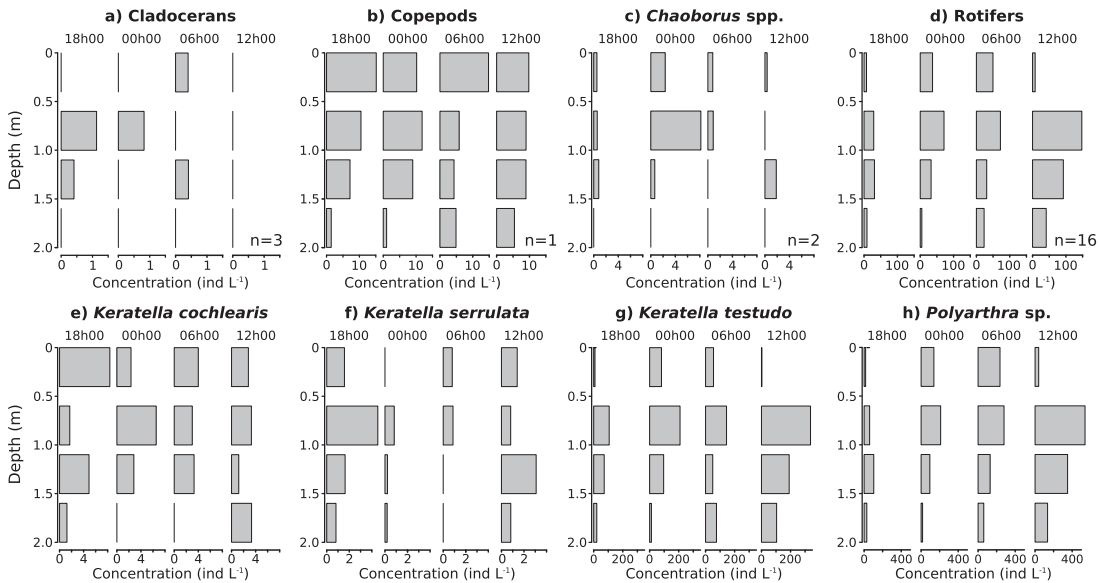


Table 3. Mean clearance rates (mean of triplicates (SE in parentheses)) determined with microspheres (0.5 to 6.0 μm diameter) for four rotifer species in samples from thermokarst pond KWK12, August 2013.

Taxon	Clearance rate ($\text{nL ind}^{-1} \text{h}^{-1}$)			
	0.5 μm	1.75 μm	3 μm	6 μm
<i>Keratella cochlearis</i>	0.0 (0.0)	6.6 (2.4) ab	0.0 (0.0) b	4.1 (4.1)
<i>Polyarthra</i> sp.	0.3 (0.2)	0.6 (0.4) B	3.7 (2.1) b	0.0 (0.0)
<i>Synchaeta</i> sp.	6.9 (1.7) B	30.7 (19.7) Ba	64.6 (18.3) Aa	7.0 (7.0) B
<i>Trichocerca</i> sp.	0.5 (0.3)	0.3 (0.3) B	0.0 (0.0) b	0.0 (0.0)

Note: Means with different uppercase letters are significantly different within a column (significant difference among microsphere sizes for a given species); means with different lowercase letters are significantly different within a row (significant difference among species for a given microsphere size). For the values without letters, there were no significant differences from any other mean in the table (Tukey HSD test, $\alpha = 0.05$).

reference sites. The maximum rotifer abundances recorded in these Nunavik thermokarst lakes (up to 1470 ind L^{-1}) are well above values recorded in the deep lakes of James Bay, just to the south, for example up to 200 ind L^{-1} in Desaulniers Lake (Pinel-Alloul et al. 1982), and the values also lie well above those in the Alaskan Arctic LTER site, Toolik Lake, where concentrations were recorded in the range 100 and 400 ind L^{-1} (Ruble 1992).

Rotifers are often the numerically most abundant component of the zooplankton in temperate lakes, but because of their small size, they normally account for a much smaller fraction of total zooplankton biomass (e.g., 10%–44% of the zooplankton biomass) (Herzig 1987). However, in thaw ponds sampled here, rotifers were so abundant that they made a substantial biomass contribution, and in several of the ponds, they accounted for more than 50% of the zooplankton biomass.

Zooplankton diversity

Contrary to our hypothesis, the high rotifer abundance for the thaw ponds was not accompanied by a significantly higher diversity than in the oligotrophic rock-basin lakes.

Table 4. Mean clearance rates (mean of triplicates (SE in parentheses)) determined with microspheres (0.5 to 6.0 μm diameter) for four rotifer species in reference rock-basin lake RBROL, August 2013.

Taxon	Clearance rate ($\text{nL ind}^{-1} \text{h}^{-1}$)				
	1.75 μm	2 μm	3 μm	4.5 μm	6 μm
<i>Keratella cochlearis</i>	17.4 (0.0)	90.5 (2.4) b	8.0 (1.5)	6.6 (1.8) b	5.5 (1.7)
<i>Polyarthra</i> sp.	15.4 (6.6)	31.6 (31.6) b	1.6 (1.6)	4.9 (2.7) b	1.8 (1.8)
<i>Conochilus unicornis</i>	210 (59) C	2244 (670) Aa	409 (25) BC	948 (384) Ba	310 (87) BC
<i>Pompholyx sulcata</i>	3.2 (1.0)	20.9 (3.8) b	12.8 (7.1)	9.0 (3.4) b	17.7 (9.4)

Note: Means with different uppercase letters are significantly different within a column (significant difference among microsphere sizes for a given species); means with different lowercase letters are significantly different within a row (significant difference among species for a given microsphere size). For the values without letters, there were no significant differences from any other mean in the table (Tukey HSD test, $\alpha = 0.05$).

Table 5. Maximum filtering rate, density, and daily filtration as a percentage of the water column in thermokarst pond KWK12.

Taxon	MF ($\mu\text{L ind day}^{-1}$)	MD (ind L^{-1})	DMF (% of lake)
<i>Keratella cochlearis</i>	0.16	1470	0.023
<i>Polyarthra</i> sp.	0.09	694	0.006
<i>Synchaeta</i> sp.	1.55	371	0.006
<i>Trichocerca</i> sp.	0.01	13.6	<0.001
Total			0.035

Note: Daily maximum filtration (DMF) is expressed as a percentage of total lake volume and calculated as the product of maximum filtering rate (MF) and maximum density (MD).

Table 6. Maximum filtering rate, density, and daily filtration as a percentage of the water column in the reference rock basin lake.

Taxon	MF ($\mu\text{L ind day}^{-1}$)	MD (ind L^{-1})	DMF (% of total water)
<i>Keratella cochlearis</i>	0.42	187	0.008
<i>Polyarthra</i> sp.	0.37	88.5	0.003
<i>Conochilus unicornis</i>	9.82	17.5	0.017
<i>Pompholyx sulcata</i>	0.42	11.1	<0.001
Total			0.029

Note: Daily maximum filtration (DMF) is expressed as a percentage of total volume and calculated as the product of maximum filtering rate (MF) and maximum density (MD).

Rotifer diversity was highly variable, particularly among the SAS lakes where the limnological properties also varied greatly among waterbodies. The SAS waters lie directly on a peatland with palsas and therefore receive large quantities of organic matter as the palsas collapse into the ponds (Deshpande et al. 2016). In Scandinavian subarctic waters, addition of allochthonous DOC can stimulate bacterial production and abundance (Forsström et al. 2013), which in turn could influence the rotifer growth and diversity. However, the dominant taxon of the SAS waters, *P. euryptera*, is known to be a selective feeder on larger prey items (Pourriot 1977). Much of the bacterial community in these thaw ponds is associated with particles (Deshpande et al. 2016), and phytoplankton of diverse phyla and sizes also occurs in these waters (Przytulska et al. 2016), providing a variety of food options for rotifers such as *P. euryptera*.

On average, seven rotifer taxa occurred per sample from the thaw ponds. This contrasts with an average of 13 found in southern Québec lakes (Pinel-Alloul et al. 1990), 21 species per lake and pond sample on Devon Island in the Canadian High Arctic

(De Smet and Beyens 1995), and seven to 30 species per sample in average in Greenland waterbodies (De Smet et al. 1993). The mean Shannon diversity for zooplankton in the thermokarst ponds was 2.97 (range from 1.04 to 6.07), which is higher than that observed in subarctic ponds on the western side of Hudson Bay (mean 0.5, ranging from 0.06 to 1.02) (Symons et al. 2014) but similar to the rock-basin reference lakes (mean 2.51, ranging from 1.34 to 3.75). The abundant rotifer communities in the thermokarst ponds were dominated by few species. A total of 13 crustacean taxa were observed, which contrasts with 30 such taxa in lakes of the western Hudson Bay Lowlands (Paterson et al. 2014). This lower species diversity might make these thaw ecosystems more vulnerable to the arrival of new taxa from the south with ongoing climate change, since low-diversity systems in general are less resistant to invasive species (Shurin 2000).

Five species dominated the thermokarst rotifer assemblages: *K. cochlearis*, *P. remata*, *P. euryptera*, *C. unicornis*, and *A. fissa*. These taxa are known to be common throughout the Canadian province of Quebec (Pinel-Alloul et al. 1982; Rublee 1992), and at least two of these species, *K. cochlearis* and *C. unicornis*, have been identified as filter feeders that graze efficiently on bacteria (Arndt 1993).

The forward selection that was performed before the RDA showed that the rotifer community composition was statistically related to oxygen, DOC, Chl *a*, and *Chaoborus*. DOC and latitude were strongly negatively correlated in our limnological data set ($r = -0.67$, $p < 0.001$), consistent with changes in vegetation in the watershed (Pienitz and Vincent 2000 and references therein), and therefore, the abundance and diversity of rotifers are also likely to be a function of latitude. This is consistent with observations from lakes in Norway where zooplankton diversity and biomass are negatively correlated with latitude (Hessen et al. 2006). However, this latter study showed a positive relationship between zooplankton abundance and Chl *a*, which was not the case for our analysis of subarctic thermokarst ponds.

Surface sampling in the present study allowed a comparison of the zooplankton communities among a wide range of thaw ponds; however, the depth variation in population abundance, as observed in the KWK lakes, limits the estimation of the total population size. Our depth profiling of rotifer abundance showed that lower population densities occurred near the surface, possibly as a result of bright light avoidance, and there were unexpectedly high concentrations of rotifers at lower depths, including in low-oxygen waters (e.g., KWK12). Reflecting these depth distributions, there was a negative relationship between rotifer abundance and temperature ($r = -0.46$, $p = 0.05$), but this relationship was not significant for oxygen concentration ($r = -0.43$, $p = 0.06$). High rotifer populations have been reported from low-oxygen waters elsewhere, for example, up to 7690 ind L⁻¹ at 1.0 mg O₂ L⁻¹ in Lake Lunzer Obersee, Austria (Mikschi 1989), whereas the maximum concentration observed in this study is 1520 ind L⁻¹. The species we found in hypoxic layers (*K. cochlearis*, *P. remata*, *A. fissa*, and *P. euryptera*) have been previously reported from a wide range of oxygen concentrations, including low-oxygen environments (Berzins and Pejler 1989).

Diurnal vertical migration patterns are well documented for zooplankton and can be driven by physical and biological factors such as temperature, light, oxygen, food availability, and predation (Dodson 2005). Small lakes and ponds have a large ratio of shoreline (circumference) to surface area, and littoral macrophytes can therefore play a substantial role, including as refuges for zooplankton that may migrate horizontally between the littoral and offshore zones over the 24 h cycle (Kuczynska-Kippen 2001). This may likely explain the complete absence of *D. pulex* at midday in the water column of SAS2A. *Chaoborus* larvae were also absent from the water column at certain times in the diurnal cycle (06h00 and midday), which also may result from horizontal migration or from downward migration onto the sediments during the daylight hours (Voss and Mumm 1999).

The rotifer populations in SAS2A showed some generally limited change in vertical distribution over the course of the 24 h sampling. This may reflect the short swimming range of these small-sized zooplankton and the coarse resolution of the Schindler–Patalas trap (40 cm). Finer scale sampling, for example across the oxycline, could provide insight into the local depth range of conditions accessed by rotifers in these ecosystems over the 24 h cycle. There was some evidence of migration by the taxa *K. testudo* and *K. serrulata* in the present study. This might relate to the presence of cladocerans, mainly *D. pulex*, which are known to exert a strong competition pressure on *Keratella* (MacIsaac and Gilbert 1989). Few studies have identified vertical migration behaviour in rotifer populations. In a study of Johnson Pond in Norwich, Vermont, Gilbert and Hampton (2001) observed vertical migration by *P. remata* but not by other rotifer species in the zooplankton community, and they attributed this migration to an avoidance response to predation by the copepod *Tropocyclops extensus*.

Grazing rates and size dependency

The ingestion rates on the fluorescent microspheres varied enormously, over the range 0 to 2244 nL ind⁻¹ h⁻¹. Large differences among taxa have been measured in other systems, e.g., 70 nL ind⁻¹ h⁻¹ for *K. cochlearis* and 500 nL ind⁻¹ h⁻¹ for *C. unicornis* on fluorescent microspheres in oligotrophic Toolik Lake, Alaska (Ruble 1998). Rates were lower in the thaw pond than in the reference lake, perhaps reflecting effects of high bacterial densities (9.7 and 2.8×10^6 cells mL⁻¹ in KWK12 and RBLOL, respectively). Clearance rates typically follow a saturating exponential curve as a function of food concentrations (Walz 1995), but there is also evidence of declining rates beyond a certain threshold concentration of bacterial cells (Pourriot 1977).

In the experiments conducted here, the most rapid rate of microsphere ingestion was for the 2 µm sized particles for all of the rotifer species except *Polyarthra* sp. (3 µm) and *Trichocerca* sp. (0.5 µm). *Keratella cochlearis* maintained a filtration rate over 5 nL ind⁻¹ h⁻¹ for every size of microsphere in the lakewater, unlike the other species. *Keratella* and *Conochilus* spp. are known to feed on a broad range of particle sizes that is only limited by the size of their corona and mastax (Pourriot 1977; Bogdan and Gilbert 1982, 1984). *Synchaeta* and *Polyarthra* are usually restricted to larger cells, as they capture their prey and suck their cellular content (Pourriot 1977; Stemberger and Gilbert 1985). The results obtained here must be interpreted with caution given the known limitations of microsphere assays including differences in gut passage time among taxa and in discrimination between artificial and natural particles, as observed with copepod species (DeMott 1986).

Bottom-up versus top-down controls

One of the questions in the present study was whether rotifer populations in thaw ponds are controlled by resource availability from below or by predation from above. The microsphere analyses indicated that even for maximum population densities, the rotifer community would filter less than 0.05% of the pond water volume each day (Tables 5 and 6). Bacterial and picocyanobacterial growth rates in oligotrophic waters are typically of the order of 0.12–1.73 day⁻¹ (Schallenberg and Burns 2001; Lavallée and Pick 2002; Tarbe et al. 2011) and 0.04–2.6 day⁻¹ (Coveney and Wetzel 1995; Ducklow 1999; Cotner and Biddanda 2002) and may be even faster in these productive thaw waters. This implies that picoplanktonic production would greatly exceed the feeding demands by the rotifers, even under the highest population densities. It is possible that feeding rates would be higher on natural prey than on the beads (DeMott 1986), but orders of magnitude greater rates would be required for there to be food limitation and seems unlikely. These calculations also imply that rotifer grazing would have minimal effects on standing stocks of bacteria and picophytoplankton.

Some observations of total zooplankton grazing impact on bacteria-sized particles (0.57 μm) have shown that heterotrophic and mixotrophic flagellates dominate this process (55%–99% of total grazing impact in Lake Oglethorpe, USA) and potentially have a strong impact on bacterial communities (Sanders et al. 1989). It is possible that these protists play a greater role than rotifers in controlling bacterial populations in thermokarst lakes; however, the bacterial cell densities were consistently $\geq 10^6$ cells mL^{-1} , implying that such control is limited and the bacterial food stocks are consistently high.

Given the low grazing rates relative to picoplanktonic production, factors other than food limitation would appear to be responsible for the control of rotifer biomass and community composition. Such factors would include predation (Stemberger and Evans 1984) and interference competition with larger zooplankton such as *Daphnia* (Gilbert and Stemberger 1985), the short duration of the growing season, and inhibitory effects of UV exposure, at least in clearer waters.

Brandl and Fernando (1979) observed that predation by the copepod *Mesocyclops edax* on rotifer populations ranged from 13.5% to 23.9% in three lakes in Ontario, Canada. In our data set, there was no significant correlation between rotifer abundance and copepod abundance, although rotifer diversity was positively (albeit weakly) correlated with copepod abundance ($r = 0.24$, $p = 0.05$). Copepods can shape rotifer communities by feeding selectively on some species; for example, illoricate rotifers are known to be vulnerable to copepod predation (Stemberger and Evans 1984). Copepods could potentially exert a top-down control by selective feeding and shape the rotifer community by changing the proportions of species.

The diversity patterns in the rotifer communities could also potentially be explained by top-down controls, specifically by predation from copepods and *Chaoborus* larvae. Two species of copepods were observed in the thaw ponds, *Leptodiaptomus minutus* and *Microcyclops rubellus*. The diet of *L. minutus* generally excludes rotifers (Williamson et al. 2015); however *Microcyclops* spp. have been directly observed ingesting small rotifers (Fryer 1957). *Chaoborus* larvae are likely to be the main predators of rotifers in the thaw ponds, since they were observed in high abundance (Fig. S1C), and rotifers are known to contribute to a large part of their diet at different developmental stages (Moore et al. 1994). There is evidence that boreal species of *Chaoborus* are moving northwards and colonizing tundra ponds, with strong potential impacts on northern aquatic food webs (Taylor et al. 2016).

There was a strong negative correlation between rotifer and cladoceran abundance ($r = -0.54$, $p < 0.001$) and no correlation between cladoceran abundance and rotifer diversity. This would be consistent with indiscriminate mechanical interference by *Daphnia* on rotifers. Experiments conducted on four *Daphnia* spp. by Burns (1969) gave filtration rates at 15 °C (similar to the mean surface temperature of waters sampled in the present study, 15.7 °C) as a function of body size as

$$(2) \quad F = 0.153L_b^{2.16}$$

where F is the filtering rate in $\text{mL ind}^{-1} \text{h}^{-1}$ and L_b is *Daphnia* body length in mm. The mean length of *Daphnia* that we measured in our sampled subarctic waters was 1.58 mm, giving a mean estimated filtering rate of $0.41 \text{ mL ind}^{-1} \text{h}^{-1}$. Multiplication of this rate by the maximum observed population density of *Daphnia* (15.5 ind L^{-1}) gives a maximal percentage of the water column filtered of $15.3\% \text{ day}^{-1}$, which would equate to the entire water column filtered each week. This filtration rate could potentially be to the detriment of the rotifer communities by mechanical interference; experiments by Gilbert and Stemberger (1985) showed that *Keratella* populations can be swept into the branchial chamber of filtering *Daphnia* where they may be injured, killed, or lose attached eggs.

Table 7. First-order estimates of carbon stocks in different compartments of the planktonic food web in thaw pond SAS2A.

Trophic group	Biomass ($\mu\text{g C L}^{-1}$)		
	Mean	Min.	Max.
Bacteria	30.0	28.4	31.7
Phytoplankton			
Picrocyanobacteria	13	12	14
Picoeukaryotes	0.8	0.8	0.8
Nano-/microplankton	480	327	920
Mixotrophs	399	46	1172
Total	893		
Zooplankton			
Ciliates	18	0	64
Rotifers	94	10	191
Cladocerans	5.4	1.5	11.7
Copepods	0.9	0.6	1.0
<i>Chaoborus</i> spp.	42	0	140
Total	160		
Total	1083		

Note: Bacteria and picocyanobacteria were collected in August 2014 at noon at two depths (surface and bottom). Picoeukaryotes were collected at the surface in August 2012. Phytoplankton, mixotrophs, and ciliates were collected at five depths (surface and 0.5, 1, 1.5, and 2 m) in August 2015. Rotifers, cladocerans, copepods, and *Chaoborus* sp. were sampled in August 2013 from four depths (surface and 0.8, 1.3, and 1.8 m). Bacterial biomass was calculated using a carbon content of $18.1 \text{ fg cell}^{-1}$ and bacterial cell counts by flow cytometry (Roiha et al. 2015). Picocyanobacteria and picoeukaryote abundance were converted to carbon biomass using a mean of 138.1 and $709.0 \text{ fg C cell}^{-1}$, respectively (Roiha et al. 2015). Phytoplankton biovolume was calculated from measurements taken by microphotography (Hillebrand et al. 1999) and converted to carbon following the equations in Rocha and Duncan (1985). Rotifer lengths were measured and converted to carbon content following the equations in Telesh et al. (1998). The dry mass of crustacean zooplankton and *Chaoborus* was converted to carbon biomass using a ratio of 0.48 (Andersen and Hessen 1991).

Food web estimates

In order to place our rotifer observations in a broader ecosystem context, we compiled data from various sources for one of the thaw ponds, SAS2A, to make a first-order estimate of carbon stocks in each of the food web compartments. Rotifers dominated the zooplankton, accounting for 59% of zooplankton biomass, including ciliates (Table 7). The biomass level of $94 \mu\text{g C L}^{-1}$ is vastly in excess of the $2 \mu\text{g C L}^{-1}$ measured for rotifers in Toolik Lake, an oligotrophic lake in Arctic Alaska (Ruble and Bettez 2001). This also contrasts with the situation in tundra ponds at Barrow, Alaska, where rotifers were described as present but rare, while copepods dominated and cladocerans were also present (Hobbie 1980). However, the rotifers were a minor constituent relative to the phytoplankton (including mixotrophic taxa), which contributed 84% of the total carbon biomass of the ecosystem (Table 7). Phytoplankton and bacterial biomasses were up to 50-fold higher than reported in tundra ponds of Barrow, Alaska, where Hobbie (1980) measured biomass values from 5 to $10 \mu\text{g C L}^{-1}$. These comparisons must be made with caution given that the data in Table 7 are based on limited sampling in August and in only one waterbody in different years for the different trophic components; however, they reinforce the conclusion that subarctic thaw pond ecosystems are unusually productive and conducive to rotifer proliferation relative to other aquatic ecosystem types at northern latitudes.

Permafrost thaw ponds are described as net heterotrophic environments (Laurion et al. 2010; Deshpande et al. 2015) and contain a high abundance and diversity of bacteria (Comte et al. 2016; Deshpande et al. 2016) that are likely to provide a rich food source for rotifers. However, these ecosystems are also phototrophic in that their limnological properties make them prolific environments for abundant and diverse phytoplankton communities

(Przytulska et al. 2016), which further support the rotifers and other zooplankton. Additionally, these environments contain a high proportional abundance of methanotrophic bacteria (Crevecoeur et al. 2015) that would constitute an additional food source, in this case derived from methane oxidation; methanotrophs have been previously identified as a potentially important carbon source for zooplankton, especially in shallow lakes during the autumn overturn (Kankaala et al. 2010, 2013).

Conclusions

Subarctic thaw ponds appear to be ideal environments for rotifer proliferation. Pico-plankton concentrations are high and volume clearance rates by the rotifers are relatively low, implying the absence of strong bottom-up control. The rotifer populations sampled in the present study achieved much higher densities than in many other types of aquatic ecosystems, including nearby rock-basin lakes and ponds. Top-down and interference effects may impose an overall limit on their maximum population size, but this will require much closer attention and experimental analysis in the future. Contrary to expectation, the α -diversity of rotifer communities in the thaw ponds was not high and was not significantly higher than in rock-basin lakes and ponds of the region or in waterbodies elsewhere, including lakes farther to the north. This implies that species richness may be constrained by factors other than dispersal, for example, tolerance to the low oxygen tensions that are a common feature of these environments or to the effects of predation and interference.

Permafrost landscapes are currently undergoing rapid change as a result of climate warming. Changes in hydrological regimes (decrease in ice cover duration, further permafrost degradation, increase in riparian vegetation, increase in precipitation) are likely to affect light availability, nutrient inputs, and concentrations of coloured dissolved organic matter (Wrona et al. 2016). These variables in turn may have a strong influence on biological productivity and community composition (e.g., Williamson et al. 2015). Warmer water temperatures will result in increased water column stability that may exacerbate oxygen depletion in these waters (Deshpande et al. 2015). It remains to be seen whether the thermokarst aquatic ecosystems will continue to support their prolific rotifer communities despite these changes in their physical and chemical environment.

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