

Trends in Ostracoda and Cladocera distribution and water chemistry in subarctic Canada: Churchill (Manitoba) lakes and ponds revisited

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ABSTRACT

Ponds and lakes distributed across northern treeline in the Hudson Bay Lowlands near Churchill (Manitoba) were revisited to analyse and document the local ecoclimatic and limnological changes that occurred over the period 1997-2012. Our analyses revealed that single events may cause significant changes in salinity, pH and silicate content because of the limited buffer capacity of the inter-connected waters. Planktic freshwater microcrustaceans (Cladocera) presented less diverse assemblages and appeared to favour waters that are situated in the boreal forest, while the diversity of benthic species assemblages (Cladocera and Ostracoda) was highest in waters located closer to the coastline and in open tundra vegetation. We identified three species that are distinctive for the boreal ecozone (*i.e.*, *Candona acuta*, *Can. acutula* and *Can. decora*) and two species (*i.e.*, *Tonnacypris glacialis* and *Can. rawsoni*) that are elements of (sub-)arctic landscapes and potentially endangered as the northern treeline expands due to rapid warming. These species are thought to be useful indicators for future ecosystem quality assessments and/or ecosystem service management programs. Our findings were compared to other studies completed in the boreal Yukon Territory and revealed that species diversity is closely linked to landscape history.

Key words: Freshwater Ostracodes; Cladocerans; Hudson Bay Lowlands; subarctic; climate change; biodiversity.

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INTRODUCTION

The latest assessment report of the Intergovernmental Panel on Climate Change 2013 (IPCC AR5) summarized evidence for the warming of arctic and subarctic regions. Studies of the thermal state of permafrost in the southern Hudson Bay lowlands document air temperature increases of up to 2°C within the last 20 years (Smith *et al.*, 2010). The date of sea ice break-up/freeze-up in Hudson Bay changed accordingly, leading to longer periods of open waters (Gagnon and Gough, 2005b) and large-scale environmental changes in areas along ecological transition zones (*e.g.*, northern displacement of ecozones and tree-line) as assessed by satellite imagery time-series data (Piwowar and Ledrew, 1995; Fraser *et al.*, 2012; Mamet and Kershaw, 2012). The densification of vegetation is another consequence of the rapid warming at high latitudes (Elmendorf *et al.*, 2012). Such profound changes in the northern landscapes will alter ecosystem services and wildlife habitat resulting in modifications of species distribution and phenology, as well as biodiversity losses (Dokulil, 2014).

Lakes and ponds are numerous and widespread components of the North that respond sensitively to multiple environmental changes (Vincent and Pienitz, 1996). The limnological and hydrological conditions of surface fresh-

water ecosystems are known to change significantly across several marked ecozones within the subarctic region (SWIPA 2011) (Serreze *et al.*, 2000). Detailed ecological surveys are therefore necessary to quantify changes in aquatic biota and their biodiversity, yet studies on aquatic ecosystems spanning multiple years are still rare (Lougheed *et al.*, 2011). The Churchill Northern Studies Centre (CNSC, Churchill, Manitoba) is one of the few research facilities offering accessibility to the subarctic treeline and permafrost ecozone enabling the monitoring of ecosystems over longer periods of time. Natural sediment archives for reconstructing past environmental conditions over time can be tapped with paleolimnology (Smol, 2008). However, this approach often lacks the necessary temporal and spatial resolution to precisely unravel recent ecosystem changes (Prowse *et al.*, 2006; Bouchard *et al.*, 2013).

In order to document recent limnological and faunal changes in water bodies located across the boreal forest - tundra ecozone, we sampled and re-sampled a selection of lakes and ponds in the northwestern Hudson Bay Lowlands (HBL) in the vicinity of the CNSC in the summers of 1997 and 2006. This allowed us to compare the evolution of limnological conditions within the context of accelerated environmental change (Mamet and Kershaw, 2011, 2012). We also consulted historical ice maps, temperature and precip-

itation records to infer and quantify local environmental shifts over the period from 1978 to 2009. This information served to assess variations that occurred in the water quality and faunal assemblages between our two field surveys.

Freshwater microcrustaceans, in particular Cladocera and, to a lesser degree Ostracoda, are the most abundant species groups in Nordic water bodies and have been extensively used for water quality studies (Rautio, 2001; Sweetman and Smol, 2006; Wetterich *et al.*, 2008; Rautio *et al.*, 2011; Schneider *et al.*, 2016). They are known to respond sensitively to environmental change and show distinct biogeographical distribution patterns (Jeffery *et al.*, 2011; Rautio *et al.*, 2011; Curry *et al.*, 2012; Viehberg and Mesquita-Joanes, 2012). Previous biological studies on cladocerans and ostracods in our study area (Shelford and Twomey, 1941; Hebert and Hann, 1986; Havel *et al.*, 1990a, 1990b; Boileau

et al., 1992; Hann, 1995; Ng *et al.*, 2009; Weider *et al.*, 2010; Jeffery *et al.*, 2011; Abbate and Sagri, 2012) enabled us to use this baseline information as a reference to compare against our most recent limnological survey completed in 2006. Our study aims to provide answers to fundamental questions related to modifications in faunal community composition, range (migration/dispersal) and biodiversity that are forced upon aquatic biota by the observed rapid ecoclimatic and environmental changes in the North.

Study region and sites

Air temperature and ice concentration data

The study region is located on the southwestern shore of Hudson Bay (N58.75° - 58.80°; W94.20° - 93.60°; Fig. 1) and is characterized by the transition of the northern

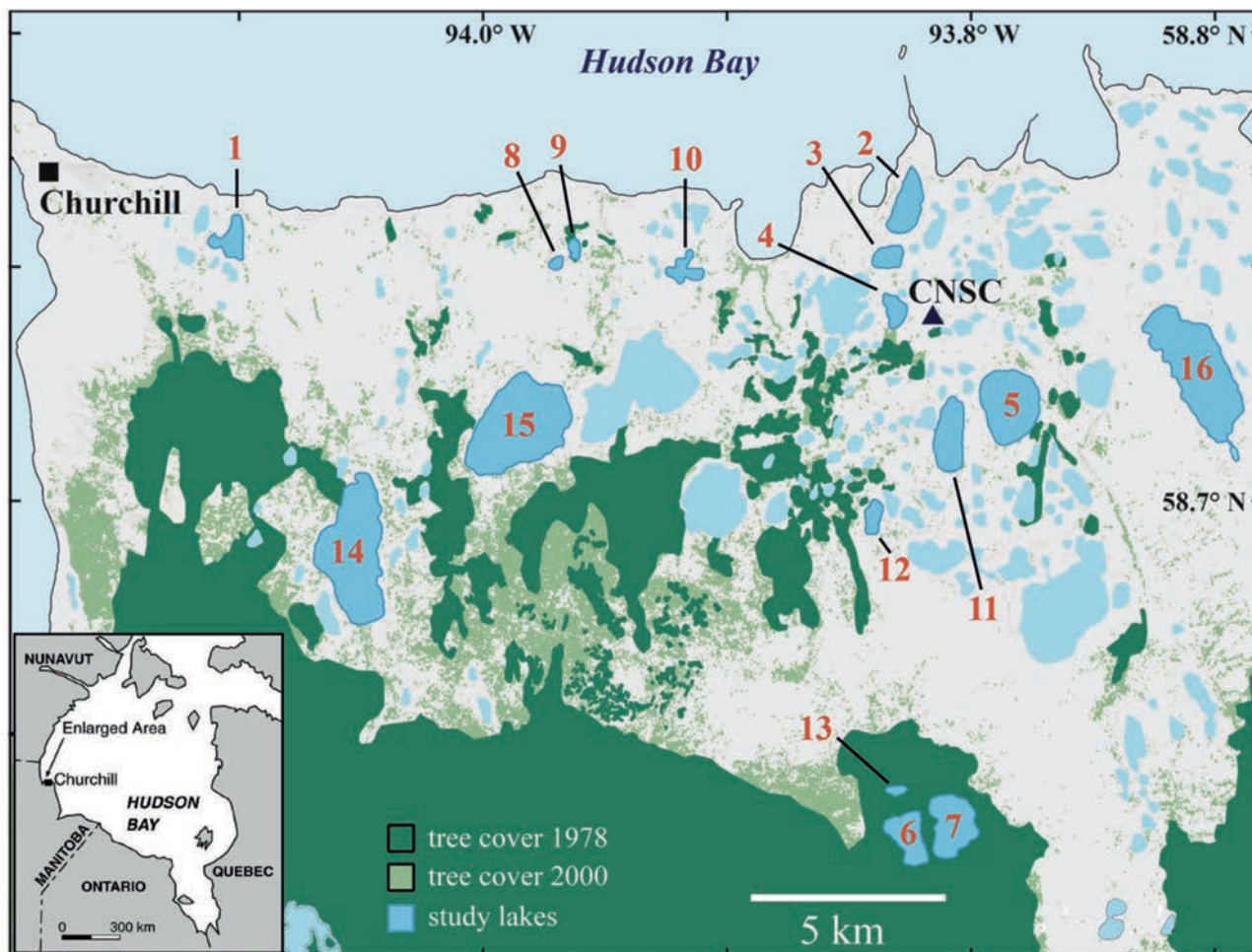


Fig. 1. Study area and location of study sites sampled in 1997 and 2006, numbered consecutively (1-16) - see text and Tab. 1 for details - and shown in dark blue. Tree cover changes in the study area between years 1978 and 2000 are illustrated in dark and pale green, respectively. Data from 1978 obtained from aerial images (A24922 #48-75, recorded 22 June 1978; Department of Energy Mines and Resources - Natural Resources Canada, 1978). Data from 2000 are abstracted from Landsat satellite images (Hansen *et al.*, 2013). Triangle, laboratory facilities of the Churchill Northern Studies Center (CNSC).

limit of the boreal forest biome to the southern boundary of the arctic tundra biome. Churchill is one of the few cities in northern Canada that maintains a weather station since 1929 due to its (former) economic importance. The modern climate conditions in Churchill are characterized by four months with above 0°C mean air temperature (June, July, August and September). During this summer period about half of the mean annual precipitation (435 mm) is recorded (Environment Canada, 2013). The mean July air temperature varies between +8°C and +16°C, while the mean January air temperature varies between -34°C and -19°C. The mean annual air temperature averages -7°C. Consequently, lakes and ponds are covered with ice during eight months.

For our study, we used instrumental temperature data with monthly resolution for the last 32 years (1978 to 2009) from Churchill, Manitoba (Climate ID: 5060600

and 5060601, Environment Canada, 2013). For each year, we calculated the mean air temperature of the three months before ice freeze-up (August, September and October; ASO) and ice break-up (May, June and July; MJJ) as the length of this period is determined by ice conditions and consequently controls the duration of the life cycle of microcrustaceans (Fig. 2). For this purpose, weekly sea ice charts from Hudson Bay were re-evaluated for ice concentration during the same time period to estimate the yearly dates of ice freeze-up and ice break-up in SW Hudson Bay. To this end, we followed the methods described by Stirling *et al.* (1999) and Gagnon and Gough (2005b) and used a grid of 0.5° intervals south of 63° latitude and west of 90° longitude (91 grid points). The break-up of the annual sea ice was defined as the date by which half the grid points had a total ice cover of 5/10 or less, whereas the freeze-up was defined as the date by which

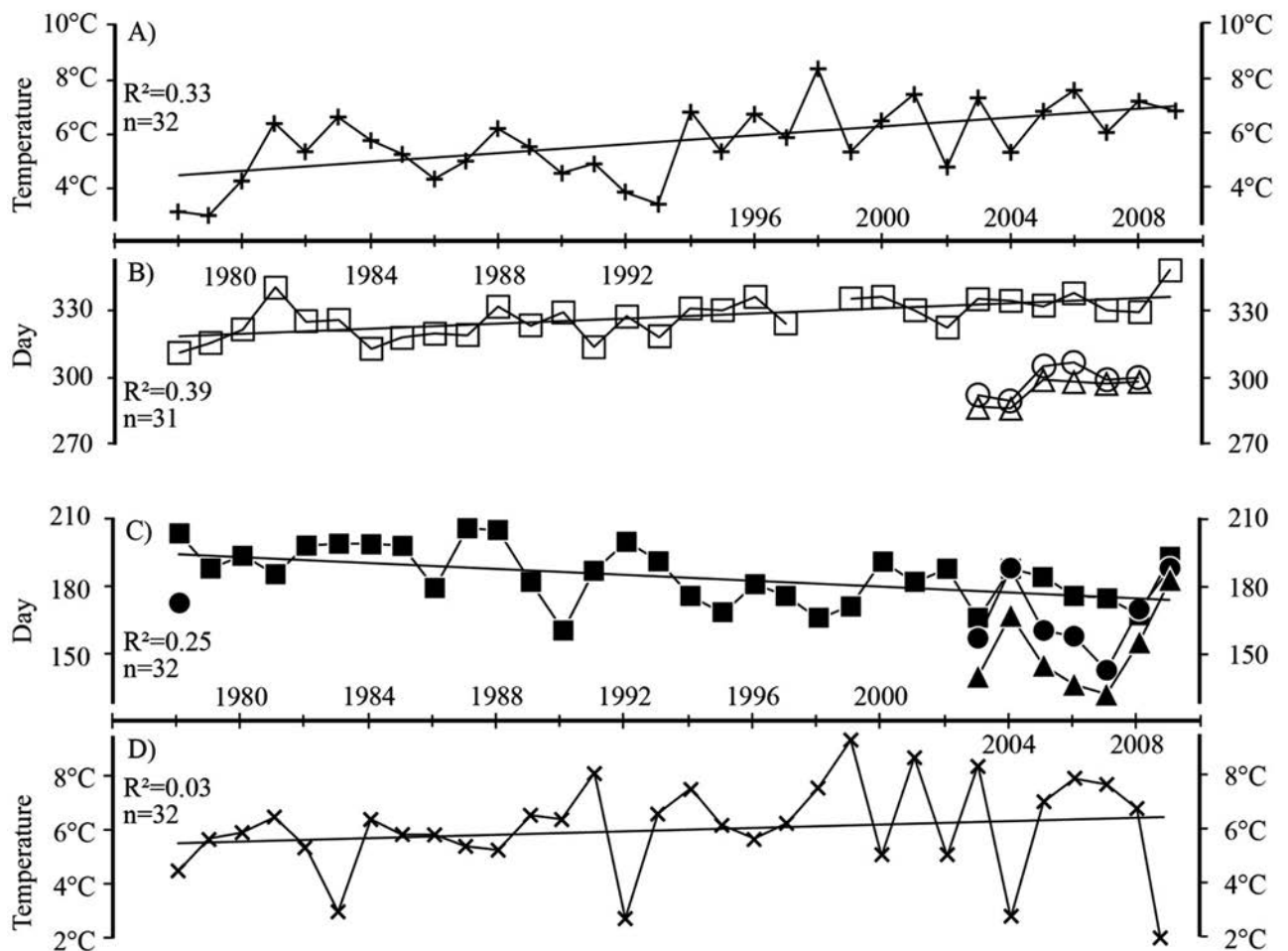


Fig. 2. Trends in Western Hudson Bay ice cover, mean air temperature (MAT) and date of lake and pond ice break-up and freeze-up over the period 1978 to 2009. A) Air temperature during freeze-up; MAT of August, September and October. B) Day of ice freeze-up; open square, Western Hudson Bay; open circle, lakes; open triangle, ponds. C) Day of ice break-up; filled square, Western Hudson Bay; filled circle, lakes; filled triangle, ponds. D) Air temperature during break-up; x, MAT of May, June and July. See text for more details.

half the grid points were equal to or exceeded 5/10 ice concentration (Etkin, 1991). Data on lake and pond ice cover are sparse and archived since 2003 by the staff of the CNSC (Fishback, *personal communication*). Past dates on lake or pond ice break-up can also be inferred from aerial photographs (A24922 #48-75; Department of Energy Mines and Resources - Natural Resources Canada, 1978) or published reports (McClure, 1943). Based on these results, we conclude that ice cover from tundra ponds generally breaks up 6 to 21 days earlier than on deeper and larger lakes in the same area, and that they eventually freeze up 2 to 9 days earlier. The ice cover of freshwater ecosystems follows the ice conditions on Hudson Bay by a lead of up to 48 days in the spring and up to 14 days in the fall.

The temperature and sea ice data provide evidence for increasingly warm mean temperatures in MJJ (+ 2.1°C) and ASO (+ 2.6°C) over the past 32 years, as well as periods of open water conditions on SW Hudson Bay that lengthened by 39 days from 122 to 161 days. Thus, we infer that tundra pond and lake catchments were also subjected to a similar extension in the length of the vegetation (growing) period.

Tundra landscape features

Abundant peatlands in open woodlands characterize the transitional landscape in the Hudson Bay lowlands (HBL). The peatlands are usually fens characterized by wet, dense, amorphous sedge and moss peats. Forested peatlands with thermokarst ponds can be found only on kame and esker sands, which are covered mainly by Black Spruce (*Picea mariana*) and Larch (*Larix laricina*) stands.

The surficial geology is made up of marine and glaciomarine sands and gravel deposits of the postglacial Tyrrell Sea (Dredge, 1992b). The only exception are local kame and esker sands that form prominent ridges of Late Wisconsinan age, as well as prominent ridges composed of aphanitic greywacke of Pre-Quaternary age along the coastline or Silurian dolomitic limestone further inland (Dredge, 1992b). Standing waters of different size are numerous and scattered throughout HBL and characterized by their shallow (<2.5 m depth) and alkaline (pH >8.5) waters can be explained by the underlying (glacio-) marine sediments and bedrocks consisting of Silurian dolomitic limestones (Dredge, 1992a).

The hydrological setting in HBL changes significantly throughout the year and was extensively investigated by Macrae *et al.* (2004) and White *et al.* (2014). During winter, the aquifers are inactive due to frozen soils and hence there is no connection between surficial waters. As air temperature (May) exceeds 0°C in the spring, the soil and aquifer layers are still frozen, but melt water forms non-channeled overland flows that connect ponds and lakes. In the summer, the water levels of ponds and lakes are

mainly controlled by precipitation and evaporative processes that can result in water-level fluctuations of up to 20 cm during periods of drought (Macrae *et al.*, 2004). Strong precipitation events, however, may result in runoff and hydrological connection (White *et al.*, 2014).

METHODS

Limnological studies

In total, 16 lakes and ponds were initially investigated during 29 July to 5 August 1997 by Claude Duguay (University of Waterloo, Ontario) and RP in the surroundings of Churchill, Manitoba, and across the transition zone of the northern treeline (Fig. 1). Nine years later, Ghislain Côté (Université Laval, Québec) and FV revisited eleven localities between 16 and 21 July 2006.

The tree-vegetation cover in the vicinity of each locality was classified according to three types, defined mainly by the presence of *Picea mariana* and *Larix laricina* along the lake shores. Shrub tundra-type (ST) is characterized by the absence of any tree vegetation or singular appearance of a tree along the shore. Forest-tundra-type (FT; open woodland) was described when the tree stands were scattered and open areas were occupied by shrubs and lichens. Boreal forest-type (BF; taiga) was defined when the locality was completely surrounded by closed tree stands.

The water samples were collected at the site of maximum water depth of each site. Profiles of water temperature, pH and specific conductivity were recorded each time with a multisensor Quanta Hydrolab®. Unfortunately, the oxygen sensor failed during the fieldwork campaign in 2006, but first readings presume that all sites were well oxygenated. For chemical analysis, water samples were taken with a Kemmerer sampler and stored in PE-bottles in a cooler box until the samples were split and pre-treated in the laboratories of the CNSC within 12 hours according to the protocol of the *Analytical Methods Manual* of Environment Canada laboratories. The samples were then stored at 4°C, shipped to and analyzed by the National Water Research Center (Burlington, Ontario) successfully for 10 parameters: chlorophyll-a (Chl_a), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total Kjeldahl nitrogen (TKN), total phosphorus (TP; filtered water), sulfate (SO₄), chloride (Cl), silicate ions (SiO₂), calcium (Ca), and sodium (Na).

Zooplankton samples were retrieved quantitatively in 2006 by three vertical tows of a conical plankton net (63 µm mesh size) with a mouth diameter of 40 cm from 1.0 m water depth to surface close to the center of the sampling site. In shallow waters, six vertical hauls of 50 cm were sampled instead. The total water volume sampled encompasses approx. 380 L. The captured material was

fixed in the field with 70% ethanol and stored cool.

A set of seven surface sediment samples was collected with an Aqua Research® gravity corer with a discrete sampling area of 44.2 cm² (total 309.4 cm²). The material was used to retrieve abundance data from meiofauna (*i.e.*, ostracods and benthic cladocerans) and organic sediment analyses at each site. It is noteworthy that in some ponds, gravel, stones and boulders dominated the sediment and thus the sampling position was selected based on the presence of penetrable sediment patches. The supernatant water and the top 2-3 cm of sediment from the short cores were conserved with 70% ethanol and stored cool. For each site, the samples were taken from different positions to ensure a representative minimum area for the coverage of the species diversity (Viehberg, 2006).

In the Aquatic Paleoecology Laboratory (APL) at Université Laval, we used a Folsom splitter (McEwen *et al.*, 1954; Van Guelpen *et al.*, 1982) for zooplankton samples when the abundance exceeded 500 individuals per sample. The results of the zooplankton counting were standardized to a water volume of 100 L. Sediment samples were washed over a 125 µm sieve gently under warm water. Ostracods and cladocerans were isolated from the sediment samples by using a flotation technique and an exhaustor device described by Viehberg (2002). All sediment samples were post-screened for remaining individuals using a stereo binocular. Individuals were counted as living species when the soft-body was attached to their carapaces. The abundance of benthic microcrustaceans were standardized to 100 cm². The identification of cladocerans and ostracods followed Benzie (2005), Brooks (1959), Delorme (1969, 1970a, 1970b, 1970c, 1970d, 1971, 2001), Frey (1959, 1962), Meisch (2000), Orlova-Bienkowskaja (1998) and Tressler (1959).

For sediment characterization, a subsample of 15.6 to 25.2 g of wet sediment was analyzed for water content and loss-on-ignition (LOI), following the instructions outlined by Heiri *et al.* (2001). The sediment was weighed before and after drying the sediment at 105°C in the oven overnight to assess the water content. Then the organic matter was estimated by weighing the loss of dry sediment after burning the samples at 550°C for 8h in crucibles. Finally, the inorganic fraction was assessed by burning the previous samples at 950°C for another 8 h and monitoring the total loss.

Numerical analysis and diversity indices

All statistical tests and unconstrained ordination techniques were completed with the software package R version 3.2.5 including the libraries: ade4, vegan (R Core Team, 2016). A paired sample t-test was used to identify significant changes ($P < 0.01$) between environmental variables measured at identical sample sites during the campaigns of 1997 and 2006. In addition, we were interested

in the consistency of the total variance of each environmental variable between the two fieldwork campaigns, therefore we used an one-way ANOVA approach to test on significance. A principal component analysis (PCA) was applied to standardized environmental variables to identify driving factors characterizing the ponds and lakes in our study area and to assess the multivariable change over time. To explore the main spatial and ecological dimensions of species distribution and studied sites, we ran a correspondence analysis (CA). The results are scaled by the weighted average of species abundances (scaling 2) to focus on the ordination of species. The influencing environmental variables whose eigenvalues contribute more than average to the variation in our data set were projected posteriori in the CA biplot by regression on the two axes. A permutation test ($n=999$) assessed the significance of the regression coefficient (r^2). To express the species diversity of the studied lakes and ponds (alpha diversity), we calculated for each site the species richness as the sum of all different species occurrences and converted the entropy to diversity measures (Jost, 2006). The Shannon entropy index (1) was calculated as follows:

$$H' = -\sum p_i \ln(p_i) \quad (\text{eq. 1})$$

where p_i is the relative abundance of the i^{th} species focusing on the abundant species. For direct comparison reasons, we converted the entropy index (1) to a diversity measure, the Shannon diversity index

$$D_1 = \exp(H') \quad (\text{eq. 2})$$

and similarly, we calculated the reciprocal of Simpson diversity indices as

$$1/D^2 = 1/(\sum p_i^2) \quad (\text{eq. 3})$$

to evaluate the diversity in terms of dominating species (Hill, 1973; Jost, 2006). The indices were determined for zooplankton and benthos separately, because the results of the different sampling methods are incomparable. To evaluate the variation of species assemblages between the lakes and ponds, we used two measures, the Sørensen (β_{sor}) similarity index:

$$\beta_{\text{sor}} = \frac{2a}{2a+b+c} \quad (\text{eq. 4})$$

and the Simpson (β_{sim}) similarity index:

$$\beta_{\text{sim}} = \frac{a}{a+\min(b+c)} \quad (\text{eq. 5})$$

where a is the number of species both sites have in common, b and c are the number of species that are exclusive in one

or the other (*sensu* Lennon *et al.*, 2001). Both indices have a lower limit of zero when the sites have no species in common and an upper limit of one when the sites have an identical species inventory. The β_{sor} is more sensitive to detect total differences in richness between sites, while β_{sim} better reveals compositional differences even if the richness is rather asymmetric between sites.

RESULTS AND DISCUSSION

General limnology

The shallow water basins of our study lakes and ponds are representative of tundra lakes from throughout the cir-

cumpolar subarctic landscapes; they were well oxygenized at the bottom and not stratified (Smol *et al.*, 2005) (Fig. 3). The analyzed chemical parameters indicate that all investigated lakes are oligotrophic and dilute (Tab. 1). However, due to their limited volume, the physical and chemical variables are directly influenced by climate forcing mechanisms (*e.g.*, precipitation and temperature) and the development of their catchment (*e.g.*, geochemical leaching from the bedrock, local vegetation, peat accumulation and erosion) (Macrae *et al.*, 2004; Pienitz *et al.*, 2008). In particular, the water temperature is coherent with the air-temperature regime as well as solar radiation. On a daily scale, temperature changes of up to 4°C were observed (Fig. 3; profiles). On a yearly scale, the date of

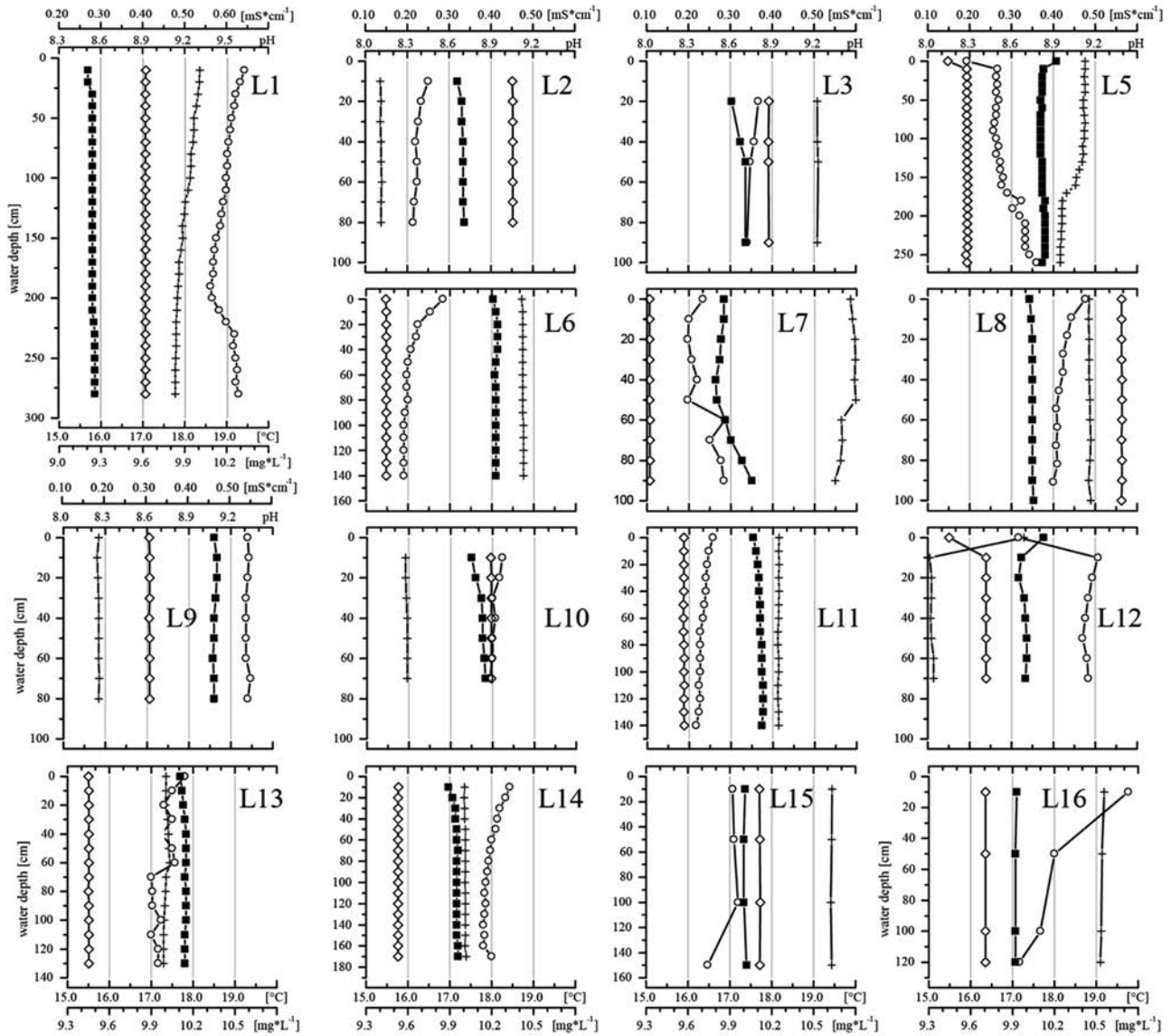


Fig. 3. Graphs showing water column profiles. +, Water temperature (°C); open circle, dissolved oxygen; filled square, pH; open diamond, specific conductivity. Measurements taken in 1997. Lakes are numbered in consecutive order; data for lake 4 is missing.

ice break-up on ponds and lakes in the study is respectively 31 to 48 and 27 to 45 days earlier than that of the sea ice in western Hudson Bay (Fishback LA, *personal communication*; Fig. 2). It has been shown previously that the distinct dates are strongly related to the mean air temperature of the months May, June and July ($r^2=0.33$; $P<0.001$; this study) (Gough *et al.*, 2004; Gagnon and Gough, 2005a, 2005b). Two additional references to ice break-up dates of freshwater ponds in the Churchill area are reported by McClure (1943) as day 162 in 1937, whereas a set of aerial images (National Air Photo Library, Natural Resources Canada, Film A24922) from 22 June 1978 documents the approximate date of ice break-up on lakes (day 173) in our study area. This latter data point corresponds well to the historical temperature record as shown in Fig. 2.

A significant positive correlation ($r^2=0.48$; $P<0.001$) also exists between mean air temperatures of August, September and October and the date of ice freeze-up (Fig. 2). The time of ice freeze-up of the ponds and lakes is simultaneous or up to 33 to 48 days earlier than the formation of sea ice in western Hudson Bay. As a result, the time of open water and increased biological production varies between 118 and 165 days in ponds and 100 and 156 days in lakes, thereby influencing also the development of the microcrustacean fauna (Wetterich *et al.*, 2008). In this study, we conclude from the measured data that the average monthly winter air temperature increased by approx. 2°C during the investigated time span of 30 years (Fig. 2), while average monthly precipitation over the past decades increased by approx. 5 mm (Environment Canada, 2013). In case this trend is continuous, we anticipate an increase of ice-free waters in ponds and lakes by approx. 12 days per decade.

Historical changes in water quality

The general hydrology of ponds and lakes in the study area varies substantially after pronounced precipitation and/or snowmelt events (Macrae *et al.*, 2004). To compare data, it is important to highlight the meteorological setting before and during the fieldwork campaigns in 1997 and in 2006. The mean air temperature during the campaigns was comparable, 15.5°C (min. 8.0°C; max. 28.5°C) in 1997 and 15.6°C (min. 8.8°C; max. 24.0°C) in 2006. In contrast, the precipitation that accumulated during the week preceding the start of the fieldwork missions in 1997 and 2006 was different. Precipitation totalled 19.5 mm and 82.5 mm in 1997 and 2006, respectively, but no major rain event occurred during both sampling periods. The measured specific conductivity of the ponds was systematically and significantly ($P=0.004$) lower in 2006 than in 1997, but the general trend shows increased values with proximity to the Hudson Bay shoreline (Tab. 1), likely caused by sea spray inputs (Pienitz *et al.*, 1997). As a re-

sult, the ponds within a distance of 2 km have an increased specific conductivity between 252 and 563 $\mu\text{S cm}^{-2}$, while distant ponds are more dilute between 100 and 148 $\mu\text{S cm}^{-2}$. As a consequence, the main variance in the PCA is associated with the conductivity (salinity) gradient (PC-axis 1; eigenvalue=6.54; explained proportion=54.5%) and showing the dilution effect in water bodies revisited in 2006 (Figs. 4 and 5).

The PCA-analysis also reveals changes that evolve along PC-axis 2 (eigenvalue=1.83; explained proportion=15.2%) (Fig. 4) that is loaded mainly by pH variations (score=0.94). Almost all studied water bodies are affected by this trend, with the exception of sites 9 and 12. Correspondingly, we measured systematically and significantly higher pH values in pond waters in 1997 (mean 8.7, sd. 0.2; Fig. 5) compared to field data in 2006 (mean 8.0, sd. 0.2; Fig. 5). We believe that the resulting lower pH values are due to several causes. Heavy precipitation events prior to the 2006 field campaign must have led to acidification and general ion-dilution in our studied waters as mentioned above (Galloway *et al.*, 1984).

A slight eutrophication of the pond waters over the years may be interpreted based on the higher mean DOC and Chla concentrations in 2006, while nutrients and silicate appear to have been metabolized and taken up by

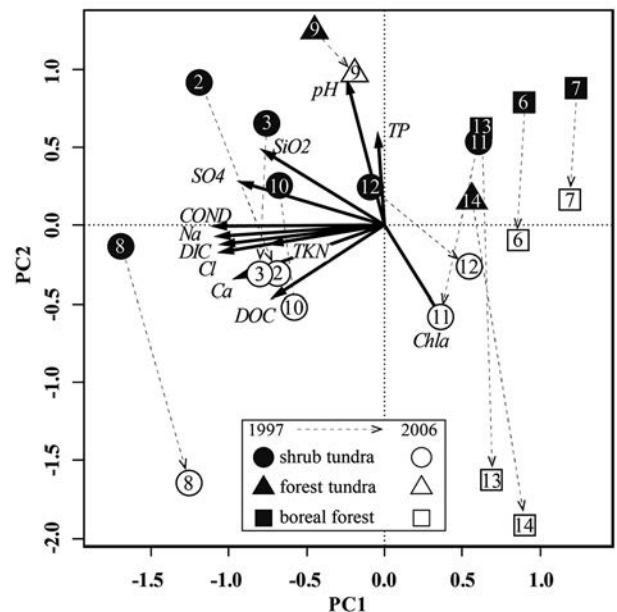


Fig. 4. Principal Components Analysis (PCA) of water quality data from measurements taken in 1997 (filled symbols) and 2006 (open symbols). Circle, shrub tundra-type; triangle, forest-tundra-type; square, boreal forest-type. Dotted arrows indicate trends over time. Physical and chemical parameters are scaled proportional to their eigenvalues in the PCA.

Tab. 1. Summary data of the geographic, chemical, and physical parameters of the 16 study lakes and ponds.

Site	Coordinates °N	°W	Distance coast km	Area km ²	Max. depth m	Date	Catchment vegetation	Temp °C	*COND µS*cm ⁻¹	*pH	DOC mg L ⁻¹	DIC mg L ⁻¹	TP µg L ⁻¹	TKN µg L ⁻¹	Cl mg L ⁻¹	SO ₄ mg L ⁻¹	Ca mg L ⁻¹	Na mg L ⁻¹	*SiO ₂ mg L ⁻¹	Chl <i>a</i> µg L ⁻¹	LOI ₅₅₀ mg/g
1	58.756	94.102	0.5	0.69	3.3	04.08.1997	ST	18.3	407	8.5	7.6	22.0	12.8	714	70.7	4.8	27.5	34.3	0.84	1.8	1.8
2	58.764	93.828	0.3	0.79	1.5	01.08.1997	ST	15.4	451	8.7	8.8	29.5	6.8	697	56.9	19.1	24.1	38.9	2.29	0.5	0.5
3	58.752	93.835	1.2	0.51	1.7	17.07.2006	ST	20.4	345	8.3	12.0	25.0	6.7	979	53.6	16.4	21.1	28.4	0.66	1.1	670
4	58.741	93.832	2.4	0.78	0.6	18.07.2006	ST	19.1	392	8.6	7.5	26.6	7.3	745	48.4	15.8	23.4	31.7	1.54	0.9	810
5	58.722	93.785	4.8	2.02	3.1	31.07.1997	FT	17.4	315	8.3	13.9	27.4	10.5	1340	41.3	9.0	24.6	23.1	0.40	0.5	810
6	58.629	93.827	13.8	0.86	1.8	30.07.1997	BF	21.7	544	8.2	9.2	46.4	7.7	745	57.1	6.7	50.0	34.3	1.95	1.4	170
7	58.630	93.809	13.6	1.22	1.3	29.07.1997	BF	18.8	194	8.8	5.4	18.8	9.4	580	13.5	3.0	18.5	8.2	0.16	1.8	60
8	58.750	93.970	2.0	0.12	1.0	02.08.1997	ST	18.7	148	8.9	5.0	16.1	11.1	559	5.7	1.1	18.1	3.1	0.12	2.0	40
9	58.754	93.963	1.3	0.04	1.2	02.08.1997	FT	19.0	128	8.1	5.3	17.3	4.8	581	5.4	1.0	19.0	2.6	0.50	0.8	610
10	58.748	93.922	1.2	0.20	1.0	01.08.1997	ST	19.9	101	8.6	3.5	11.5	6.2	418	2.8	3.3	12.2	1.6	0.12	0.9	460
11	58.714	93.810	5.1	0.67	2.0	31.07.1997	ST	18.1	100	7.9	5.1	13.5	7.7	386	2.9	3.1	13.5	1.8	0.02	1.0	40
12	58.697	93.841	6.2	0.20	0.8	02.08.1997	ST	13.9	563	8.7	13.4	26.4	7.6	1020	103.0	10.5	30.2	57.2	1.64	0.9	610
13	58.639	93.832	13.0	0.11	1.5	02.08.1997	BF	15.5	476	7.9	11.4	26.6	6.5	738	101.0	10.7	35.1	48.4	0.89	2.2	610
14	58.690	94.053	6.3	3.53	2.2	03.08.1997	FT	15.8	306	9.1	7.7	20.7	8.2	655	37.3	10.7	24.9	21.2	2.77	1.5	460
15	58.719	93.984	4.3	3.90	2.1	05.08.1997	FT	17.1	252	8.3	10.5	18.6	16.3	506	33.2	14.2	23.3	21.1	1.13	0.8	460
16	58.729	93.706	3.6	3.85	1.5	05.08.1997	ST	15.9	396	8.8	9.7	24.0	5.7	868	58.1	9.7	21.9	38.0	0.87	0.8	490
						19.07.2006	ST	20.0	342	8.1	10.1	25.1	5.1	740	56.2	11.9	23.7	32.9	0.75	1.1	490
						18.07.2006	FT	18.2	187	8.8	6.0	18.3	7.2	602	12.8	2.2	18.1	8.7	0.51	1.5	660
						19.07.2006	BF	18.5	208	8.0	7.9	21.8	5.3	524	21.4	3.2	22.5	12.0	0.21	1.3	660
						19.07.2006	FT	15.1	239	8.7	11.1	21.6	5.1	935	19.9	3.7	19.9	12.1	1.48	0.9	700
						19.07.2006	BF	19.5	138	8.1	10.0	17.7	4.7	621	9.6	2.5	18.3	5.3	0.72	0.8	700
						19.07.2006	BF	17.3	151	8.8	10.3	15.6	14.3	773	8.6	3.3	17.3	4.8	0.15	2.0	130
						19.07.2006	BF	19.5	138	7.9	11.7	16.9	4.2	708	7.3	1.1	19.9	4.4	0.04	2.7	130
						19.07.2006	BF	17.4	177	8.6	8.7	18.1	9.8	726	11.0	1.2	19.1	6.4	0.27	1.7	170
						19.07.2006	BF	14.5	143	7.5	8.4	17.4	3.6	505	10.3	1.1	20.1	5.3	0.10	3.1	40
						19.07.2006	FT	19.4	371	8.7	10.2	23.1	7.2	766	51.4	7.7	23.5	34.5	1.10	1.9	282
						19.07.2006	ST	19.2	235	8.6	7.5	20.1	6.3	851	23.8	1.3	20.5	13.9	0.92	2.6	282

Test statistics

Mean 1997	283	8.8	8.3	20.8	8.1	727	33.1	7.3	20.8	20.3	1.07	1.2	-
SD 1997	149	0.2	2.8	5.5	2.7	172	31.1	6.2	4.8	18.5	0.93	0.5	-
Mean 2006	235	8.0	9.6	20.7	6.9	694	31.1	6.5	21.9	16.9	0.45	1.4	403
SD 2006	121	0.2	2.7	4.7	3.7	268	30.2	6.0	5.4	15.2	0.39	0.9	282
<i>t</i> -test (paired)	< 0.01	< 0.01	0.11	0.90	0.42	0.68	0.18	0.34	0.17	0.03	0.01	0.51	-
ANOVA (one-way)	0.42	< 0.01	0.26	0.96	0.37	0.73	0.88	0.82	0.61	0.63	0.05	0.60	-

Site number studied sites are consecutively numbered; distance coast, shortest aerial distance to western Hudson Bay coast; area, lake and pond surface area; max. depth, maximum water depth; ST, shrub tundra; FT, forest tundra; BF, boreal forest; Temp, temperature below water surface; COND, specific conductivity; DOC, dissolved organic carbon; DIC, dissolved inorganic carbon; TP, total phosphorus; TKN, total Kjeldahl nitrogen; Cl, chloride; SO₄, sulfate; Ca, calcium; Na, sodium; SiO₂, silicate; Chl *a*, chlorophyll-*a*; SD, standard deviation; *parameters with a significant change over time (*p*<0.01).

aquatic biota at the time of sampling (Fig. 5). Other studies have shown the fertilizing impact of DOC on primary productivity in northern Swedish lakes (Seekell *et al.*, 2015). Future investigations may test this hypothesis by extending the seasonal coverage of limnological surveys and by putting special emphasis on the impact of prolonged ice-free periods on lake trophic changes.

Species inventory - Alpha diversity

In our samples from 2006, microcrustaceans are the dominant meiofauna group. For reasons of comparison, we focused on Cladocera and Ostracoda as both groups were subject of previous published (partly molecular biology) studies in HBL (Shelford and Twomey, 1941;

Hebert and Hann, 1986; Havel *et al.*, 1990a, 1990b; Boileau *et al.*, 1992; Hann, 1995; Weider *et al.*, 1999a, 1999b; Marková *et al.*, 2007; Ng *et al.*, 2009; Xu *et al.*, 2009; Weider *et al.*, 2010; Jeffery *et al.*, 2011). In addition, both microcrustacean groups have potential value for paleoenvironmental assessment studies and this study is intentionally necessary to interpret future analyses of faunal assemblages in the HBL.

We identified a total of 44 species (Tab. 2; Cladocera: 18, Ostracoda: 26), of which nine species are known to be planktic (*sensu strictu*) (Dodson and Frey, 2001). Our sampling effort resulted in eleven species that were previously not reported from HBL waters (*Alona (A.) circumfimbriata*, *A. guttata*, *A. quadrangularis*, *Candona (Can.) acuta*, *Can. decora*, *Cypria ophtalmica*, *Graptoleberis*

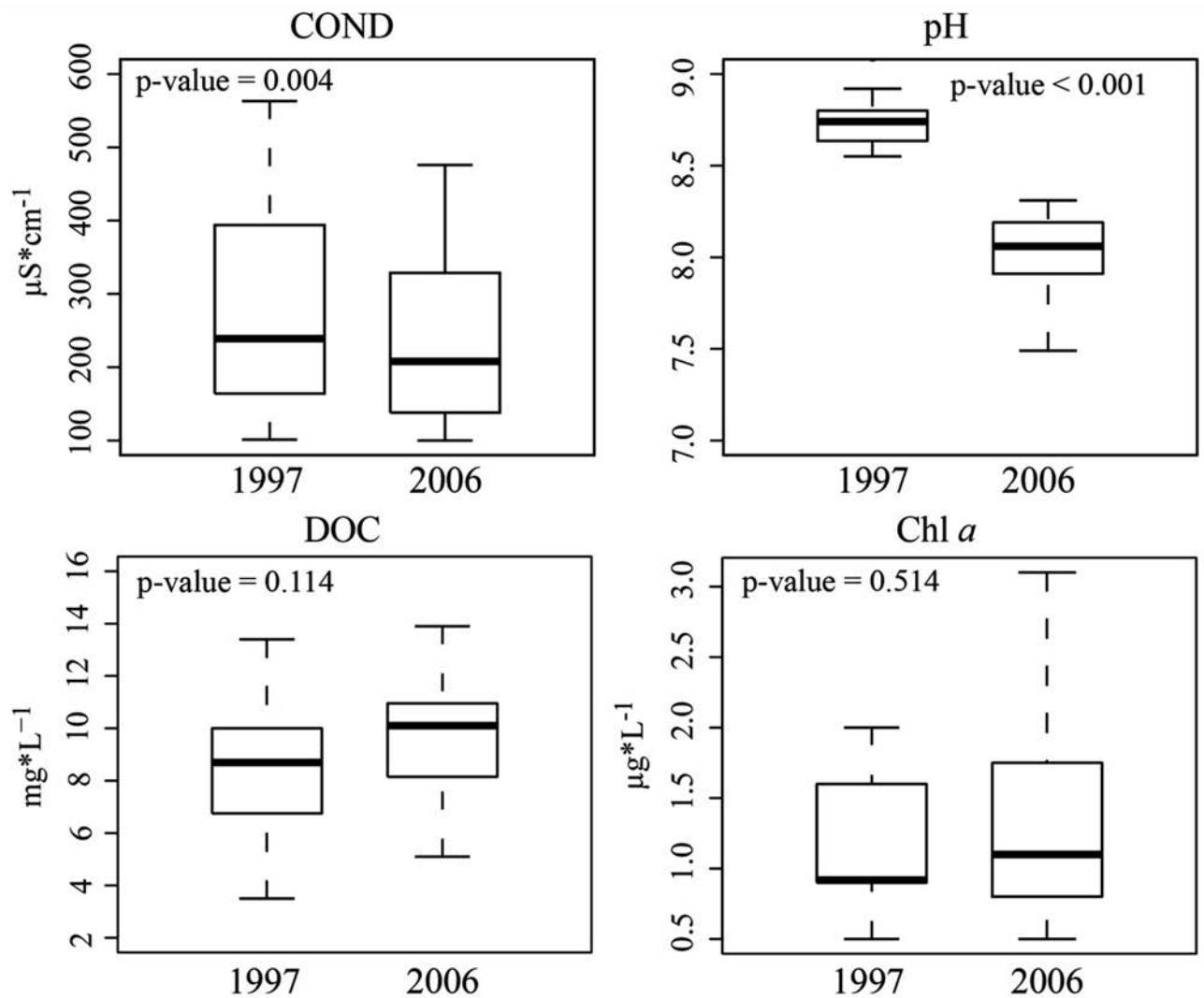


Fig. 5. Water quality changes for select physical and chemical water parameters from measurements taken in 1997 (left/pale) and 2006 (right/dark). P-values determined by paired t-test. COND, specific conductivity; DOC, dissolved organic carbon; Chl a, chlorophyll a.

Tab. 2. Abundance of species in the study lakes and ponds and published presence/absence data from waters from Hudson Bay Lowlands (HBL; Shelford and Twomey, 1941; Hebert and Hann, 1986; Havel *et al.*, 1990a, 1990b; Boileau *et al.*, 1992; Hann, 1995; Jeffery *et al.*, 2011; Abbate and Sagri, 2012) and waters in the Yukon boreal forest (Yukon; Swadling *et al.*, 2000; Bunbury and Gajewski, 2005).

Nr.	Species name	Species ID	P/B	2	3	4	6	7	8	9	10	11	12	13	14	HBL	Yukon
Cladocera																	
1	<i>Acroperus</i> sp.	ACSP	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2	<i>Alona circumfimbriata</i> Megard, 1967	ALCI	B	11	0	4	2	0	37	0	12	0	16	0	0	0	0
3	<i>Alona guttata</i> Sars, 1862	ALGU	B	15	4	56	8	10	25	2	12	18	4	33	44	0	0
4	<i>Alona lapidicola</i> Chengalath and Hann, 1981	ALLA	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
5	<i>Alona quadrangularis</i> (O.F. Müller, 1776)	ALQU	B	0	0	23	0	2	34	0	27	6	23	0	0	0	0
6	<i>Alona</i> sp.	ALSP	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
7	<i>Alonella excisa</i> (Fischer, 1854)	ALEX	B	15	23	19	6	11	21	3	13	17	3	27	32	1	0
8	<i>Bosmina liederi</i> De Melo and Hebert, 1994	BOLI	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
9	<i>Bosmina</i> sp.	BOSP	P	21	54	12	4	0	15	7	9	17	34	0	3	0	1
10	<i>Ceriodaphnia</i> cf. <i>laticaudata</i> P.E. Müller, 1867	CECF	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
11	<i>Ceriodaphnia pulchella</i> Sars, 1862	CEPU	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
12	<i>Ceriodaphnia quadrangula</i> (O.F. Müller, 1785)	CEQU	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1
13	<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	CERE	P	0	0	5	1	0	6	0	0	0	0	12	14	1	0
14	<i>Ceriodaphnia</i> sp.	CESP	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1
15	<i>Chydorus brevilabris</i> Frey, 1980	CHBR	B	7	0	12	0	0	8	0	7	0	0	0	0	1	0
16	<i>Chydorus</i> cf. <i>linguilabris</i> Frey, 1982	CHCF	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
17	<i>Chydorus ovalis</i> Kurz, 1875	CHOV	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
18	<i>Chydorus sphaericus</i> (O.F. Müller, 1776)	CHSP	B	12	5	0	4	0	23	78	52	0	12	0	16	1	1
19	<i>Daphnia ambigua</i> Scourfield, 1947	DAAM	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1
20	<i>Daphnia galeata</i> Sars, 1864	DAGA	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1
21	<i>Daphnia magna</i> Straus, 1820	DAMA	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
22	<i>Daphnia middendorffiana</i> Fischer, 1851	DAMI	P	57	60	89	13	21	132	0	12	75	0	146	178	1	1
23	<i>Daphnia obtusa</i> Kurz, 1875	DAOB	P	0	0	0	0	0	0	0	0	0	0	0	0	0	1
24	<i>Daphnia pulex</i> Leydig, 1860	DAPU	P	4	0	6	3	7	6	1	3	5	0	8	10	1	0
25	<i>Daphnia pulicaria</i> Forbes, 1893	DAPA	P	4	0	6	0	6	4	0	4	0	0	0	4	1	0
26	<i>Daphnia tenebrosa</i> Sars, 1898	DATE	P	674	186	795	25	15	851	402	601	737	240	21	950	1	0
27	<i>Eubosmina</i> sp.	EUSP	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
28	<i>Eurycerus glacialis</i> Lilljeborg, 1887	EUGL	B	14	23	0	0	0	8	3	4	12	17	0	0	1	0
29	<i>Graptoleberis</i> sp.	GRSP	B	5	7	0	0	0	0	0	0	4	5	0	0	0	0
30	<i>Holopedium gibberum</i> Zaddach, 1855	HOGI	P	141	0	242	20	35	290	0	91	189	0	23	392	1	0
31	<i>Lathonura</i> sp.	LASP	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
32	<i>Lynceus</i> sp.	LYSP	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
33	<i>Macrothrix hirsuticornis</i> Norman and Brady, 1867	MAHI	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
34	<i>Macrothrix</i> sp.	MASP	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
35	<i>Moina macrocopa</i> (Straus, 1820)	MOMA	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
36	<i>Moina rectirostris</i> (Leydig, 1860)	MORE	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
37	<i>Picripleuroxus striatus</i> (Schoedler, 1863)	PIST	B	4	4	3	0	0	2	0	12	6	3	6	4	1	0
38	<i>Pleuroxus procurvus</i> Birge, 1879	PLPR	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
39	<i>Polyphemus pediculus</i> (Linnaeus, 1761)	POPE	P	2	1	3	1	1	2	0	2	2	1	5	6	1	1
40	<i>Scapholeberis</i> sp.	SCSP	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
41	<i>Sida crystallina</i> (O. F. Müller, 1776)	SICR	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
42	<i>Simocephalus</i> cf. <i>serrulatus</i> (Koch, 1841)	SICF	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
43	<i>Simocephalus punctatus</i> Orlova-Bienkowskaja, 1998	SIPU	P	7	0	9	0	5	10	0	7	8	0	11	12	1	0
44	<i>Simocephalus vetulus</i> (O. F. Müller, 1776)	SIVE	P	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ostracoda																	
45	<i>Bradleystrandesia reticulata</i> (Zaddach, 1844)	BRRE	B	0	0	0	6	7	0	0	0	12	0	11	0	1	0
46	<i>Candocyprinotus ovatus</i> Delorme, 1970	CAOV	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
47	<i>Candona acuta</i> Hoff, 1942	CAAC	B	0	0	0	0	0	0	0	0	0	0	7	0	0	0

To be continued on next page

Tab. 2. Continued from previous page.

Nr.	Species name	Species ID	P/B	2	3	4	6	7	8	9	10	11	12	13	14	HBL	Yukon
48	<i>Candona acutula</i> Delorme, 1967	CAAL	B	0	0	0	4	0	4	5	0	0	0	0	7	1	1
49	<i>Candona candida</i> (O.F. Müller, 1776)	CACA	B	0	0	0	12	15	0	6	12	11	9	13	0	1	1
50	<i>Candona decora</i> Furtos, 1933	CADE	B	0	0	0	4	2	0	0	0	0	0	0	2	0	1
51	<i>Candona distincta</i> Furtos, 1933	CADI	B	0	0	0	1	0	0	0	0	0	0	6	2	1	1
52	<i>Candona ikpikukensis</i> (Swain, 1963)	CAIK	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
53	<i>Candona ohioensis</i> Furtos, 1933	CAOH	B	0	0	0	0	3	0	0	0	5	0	0	9	1	0
54	<i>Candona paraohioensis</i> Staplin, 1963	CAPO	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
55	<i>Candona</i> sp.1	CAS1	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
56	<i>Candona</i> sp.2	CAS2	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
57	<i>Candona subtriangulata</i> Benson & Macdonald, 1963	CAST	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
58	<i>Cyclocypris ampla</i> Furtos, 1933	CYAM	B	12	16	18	0	0	0	0	13	0	12	0	0	1	1
59	<i>Cyclocypris globosa</i> (Sars, 1863)	CYGL	B	7	9	12	0	0	4	0	11	0	14	0	4	1	0
60	<i>Cyclocypris ovum</i> (Jurine, 1820)	CYOV	B	25	5	8	0	0	17	21	0	7	15	0	0	1	0
61	<i>Cyclocypris serena</i> (Koch, 1838)	CYSE	B	0	0	0	0	0	13	9	0	5	0	0	0	1	0
62	<i>Cyclocypris sharpei</i> Furtos, 1933	CYSH	B	0	0	0	10	12	0	0	17	0	0	0	8	1	1
63	<i>Cyclocypris</i> sp. 1	CYS1	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
64	<i>Cypria ophthalmica</i> (Jurine, 1820)	CYOP	B	9	14	6	0	0	0	0	13	0	12	0	0	0	1
65	<i>Cypria</i> sp.1	CYS6	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
66	<i>Cypria turneri</i> Hoff, 1942	CYTU	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
67	<i>Cypricerus horridus</i> Sars, 1926	CYHO	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
68	<i>Cypridopsis</i> sp. 1	CYS8	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
69	<i>Cypridopsis vidua</i> (O.F. Müller, 1776)	CYVI	B	6	5	8	0	0	0	0	7	9	0	0	0	1	1
70	<i>Cyprinotus pellucidus</i> Sharpe, 1897	CYPE	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
71	<i>Cyprinotus</i> sp. 1	CYS2	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
72	<i>Cypris pubera</i> (O.F. Müller, 1776)	CYPU	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
73	<i>Cypris marginata</i> (Straus, 1821)	CYMA	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
74	<i>Cytherissa lacustris</i> (Sars, 1863)	CYLS	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
75	<i>Dolerocypris fasciata</i> (O.F. Müller, 1776)	DOFA	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
76	<i>Eucypris foveata</i> Delorme, 1967	EUFO	B	0	0	0	0	0	0	0	5	0	5	5	0	1	0
77	<i>Fabaeformiscandona caudata</i> (Kaufmann, 1900)	FACA	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
78	<i>Fabaeformiscandona protzi</i> (Hartwig, 1898)	FAPR	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
79	<i>Fabaeformiscandona rawsoni</i> (Tressler, 1957)	FARA	B	4	5	4	0	0	9	0	2	0	0	0	6	1	1
80	<i>Fabaeformiscandona rectangulata</i> (Alm, 1914)	FARE	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
81	<i>Herpetocypris reptans</i> (Baird, 1835)	HERE	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
82	<i>Heterocypris incongruens</i> (Ramdohr, 1808)	HEIN	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
83	<i>Ilyocypris bradyi</i> Sars, 1890	ILBR	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
84	<i>Ilyocypris gibba</i> (Ramdohr, 1808)	ILGI	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
85	<i>Limnocythere inopinata</i> (Baird, 1843)	LIIN	B	3	4	0	0	0	0	0	3	0	0	0	5	0	1
86	<i>Limnocythere itasca</i> Cole, 1949	LIIT	B	0	0	5	5	4	0	0	0	4	0	0	5	0	1
87	<i>Limnocythere liporeticulata</i> Delorme, 1968	LILI	B	0	0	0	0	0	0	0	0	0	0	5	0	0	0
88	<i>Limnocythere</i> sp.1	LIS1	B	0	0	0	0	0	0	0	0	0	0	0	0	0	1
89	<i>Limnocythere varia</i> Staplin, 1963	LIVA	B	0	0	2	0	0	0	0	0	1	0	1	0	0	1
90	<i>Megalocypris alba</i> (Dobbin, 1941)	MEAL	B	0	0	0	0	0	0	0	0	0	10	0	0	1	0
91	<i>Notodromas monacha</i> (O.F. Müller, 1776)	NOMO	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
92	<i>Potamocypris granulosa</i> Daday, 1902	POGR	B	0	0	0	5	0	0	0	0	0	3	0	7	1	0
93	<i>Pseudocandona albicans</i> (Brady, 1864)	PSAL	B	0	0	6	0	0	0	0	0	0	0	0	0	1	0
94	<i>Pseudocandona compressa</i> (Koch, 1838)	PSCO	B	5	4	3	0	0	9	17	0	0	1	0	9	1	1
95	<i>Pseudocandona rostrata</i> (Brady & Norman, 1889)	PSRO	B	0	0	0	7	9	0	0	1	7	0	0	0	1	0
96	<i>Sarscypridopsis aculeata</i> (Costa, 1847)	SAAC	B	0	0	0	0	0	0	0	0	0	0	0	0	1	0
97	<i>Tonnacypris glacialis</i> (Sars, 1890)	TOGL	B	0	3	0	0	0	0	0	3	5	1	5	0	1	0

SpeciesID, abbreviation of species names; P, planktic species; B, benthic species. Studied sites are consecutively numbered; abundance of planktic species refers to n individuals * 100 L⁻¹, abundance of benthic species refers to n individuals * 100 cm⁻¹.

sp., *Limnocythere (L.) inopinata*, *L. itasca*, *L. liporeticulata* and *L. varia*). On average, our study sites comprised 21 species (Benthic: 14, Planktic: 7). Due to the shallow water depth, we collected several benthic chydorids in the plankton net samples. However, the abundance data from the parallel sediment samples were less variable. Therefore, they are more reliable and representative to interpret species occurrences and to calculate diversity and similarity indices (Tabs. 3 and 4). It is noteworthy that the species richness is in favour of the benthic species assemblage, mainly because the complete ostracod fauna is exclusively benthic and comprises 26 species.

The most abundant and common planktic species was *Daphnia (D.) tenebrosa* (DATE), which occurred in all studied sites and in high abundance particularly in waters with higher concentrations of Chla (*i.e.*, high phytoplankton concentration) of up to 950 n/100L (Fig. 6). Similarly, other abundant planktic species, *D. middendorffiana* (DAMI) and *Holopedium gibberum* (HOGI), also show a positive correlation to increased concentrations of Chla (Fig. 6). In three sites (4, 8 and 14), all planktic species were found, but their faunal assemblage was dominated by *D. tenebrosa* and *D. middendorffiana* thus resulting in relatively low diversity indices (Tab. 3). In contrast, a

Tab. 3. Species richness and diversity indices split for plankton and benthos species; studied sites are consecutively numbered, cumulative results of this study = FV2006, published presence/absence data from waters from Hudson Bay Lowlands (HBL; for references see Tab. 2) and waters in the Yukon boreal forest (Yukon; for references see Tab. 2), Shannon entropy (H'), Shannon Diversity (D¹), inverse Simpson Diversity (1/D²).

Catchment vegetation	Site 2 ST	Site 3 ST	Site 4 FT	Site 6 BF	Site 7 BF	Site 8 ST	Site 9 FT	Site 10 ST	Site 11 ST	Site 12 FT	Site 13 BF	Site 14 BF	FV2006 ST, FT, BF	HBL ST, FT, BF	Yukon BF
Species richness	24	19	25	19	16	23	12	27	22	21	17	24	44	64	37
Benthos species	16	15	16	12	9	14	9	19	15	18	10	15	35	42	29
H' _{Plankton}	0.870	0.946	0.961	1.480	1.595	1.011	0.103	0.653	0.885	0.398	1.241	1.057	1.014	NA	NA
D ¹ _{Plankton}	2.388	2.576	2.616	4.392	4.929	2.747	1.109	1.921	2.423	1.488	3.460	2.879	2.758	NA	NA
1/D ² _{Plankton}	1.733	2.204	1.949	3.676	4.046	2.096	1.040	1.437	1.824	1.287	2.256	2.262	1.991	NA	NA
H' _{Benthos}	2.615	2.458	2.347	2.429	2.119	2.390	1.508	2.601	2.612	2.645	2.062	2.288	3.084	NA	NA
D ¹ _{Benthos}	13.672	11.686	10.458	11.353	8.327	10.915	4.519	13.483	13.627	14.089	7.860	9.858	21.844	NA	NA
1/D ² _{Benthos}	11.942	9.466	7.265	10.293	7.470	9.338	2.972	10.039	12.050	12.358	6.144	6.983	15.884	NA	NA

Tab. 4. Beta diversity matrix of studied sites. Sørensen (β_{sor}) and Simpson (β_{sim} ; grey shaded) similarity indices (see text for details), study sites are numbered consecutively, FV2006 are the cumulative results of this study, published presence/absence data from waters from Hudson Bay Lowlands (HBL; for references see Tab. 2) and waters in the Yukon boreal forest (Yukon; for references see Tab. 2).

	Site 2	Site 3	Site 4	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13	Site 14	FV2006	HBL	Yukon
Site 2	1.000	0.837	0.816	0.455	0.439	0.809	0.500	0.824	0.596	0.667	0.429	0.667	0.706	0.404	0.328
Site 3	0.947	1.000	0.636	0.359	0.278	0.619	0.516	0.696	0.571	0.750	0.378	0.558	0.603	0.333	0.357
Site 4	0.833	0.737	1.000	0.489	0.524	0.792	0.378	0.731	0.625	0.565	0.512	0.653	0.725	0.400	0.323
Site 6	0.500	0.368	0.550	1.000	0.703	0.558	0.500	0.553	0.558	0.439	0.579	0.727	0.625	0.353	0.351
Site 7	0.529	0.294	0.647	0.765	1.000	0.500	0.345	0.591	0.700	0.316	0.571	0.634	0.557	0.317	0.222
Site 8	0.826	0.684	0.826	0.600	0.588	1.000	0.629	0.720	0.609	0.591	0.488	0.723	0.687	0.432	0.233
Site 9	0.750	0.667	0.583	0.667	0.417	0.917	1.000	0.410	0.514	0.545	0.333	0.444	0.429	0.260	0.204
Site 10	0.875	0.842	0.760	0.650	0.765	0.783	0.667	1.000	0.640	0.667	0.533	0.627	0.761	0.457	0.344
Site 11	0.609	0.632	0.652	0.600	0.824	0.609	0.750	0.696	1.000	0.545	0.634	0.511	0.687	0.386	0.233
Site 12	0.714	0.789	0.619	0.450	0.353	0.619	0.750	0.762	0.571	1.000	0.410	0.444	0.646	0.349	0.241
Site 13	0.500	0.389	0.611	0.611	0.588	0.556	0.417	0.667	0.722	0.444	1.000	0.524	0.581	0.337	0.182
Site 14	0.667	0.632	0.667	0.800	0.765	0.739	0.667	0.667	0.522	0.476	0.611	1.000	0.706	0.427	0.393
FV2006	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.587	0.420
HBL	0.750	0.737	0.720	0.750	0.765	0.826	0.833	0.778	0.739	0.714	0.778	0.792	0.727	1.000	0.216
Yukon	0.417	0.526	0.400	0.500	0.353	0.304	0.417	0.407	0.304	0.333	0.278	0.500	0.459	0.297	1.000

minimum of only three planktic species were found in sites 9 and 12 and thus resulting in the minimal diversity indices of $D^1_{\text{Plankton}}=1.11$ or $1/D^2_{\text{Plankton}}=1.04$ and $D^1_{\text{Plankton}}=1.49$ or $1/D^2_{\text{Plankton}}=1.29$, respectively. An explanation for the low diversity in planktic Cladocera could be limited food availability inferred from low Chl-a concentrations and increased DOC and TP concentrations (Tab. 1). Another explanation may be due to competition by Copepoda (Gliwicz and Umana, 1994), which were not in focus of this study. Highest diversity indices were found in sites located within the boreal forest zone (6, 7, 13 and 14) ranging between $D^1_{\text{Plankton}}=2.88 - 4.93$ and $1/D^2_{\text{Plankton}}=2.26 - 4.05$, respectively.

Alonella excisa (ALEX) and *Alona guttata* (ALGU)

are the most common benthic microcrustaceans, which were caught in all studied sites with abundances of up to 56 n/100cm². Followed by *Picripleuroxus striatus*, *Chydorus sphaericus*, *Cyclocypris (Cyc.) globosa*, *Cyc. ovum* and *Pseudocandona (Psc.) compressa* (Tab. 2) that are found in the majority of the sites. Again, site 9 holds the lowest species richness with a total of nine benthic species and thus resulting in overall low diversity indices in benthic microcrustaceans: respectively $D^1_{\text{Benthos}} = 4.52$ or $1/D^2_{\text{Benthos}}=2.97$. The neighboring sites and measured variables give no reasonable explanation for the minimal diversity. In general, sites in the boreal forest zone (6, 7, 13 and 14) yield a low number of benthic species (Tab. 3), whereas waters with higher conductivity and closer prox-

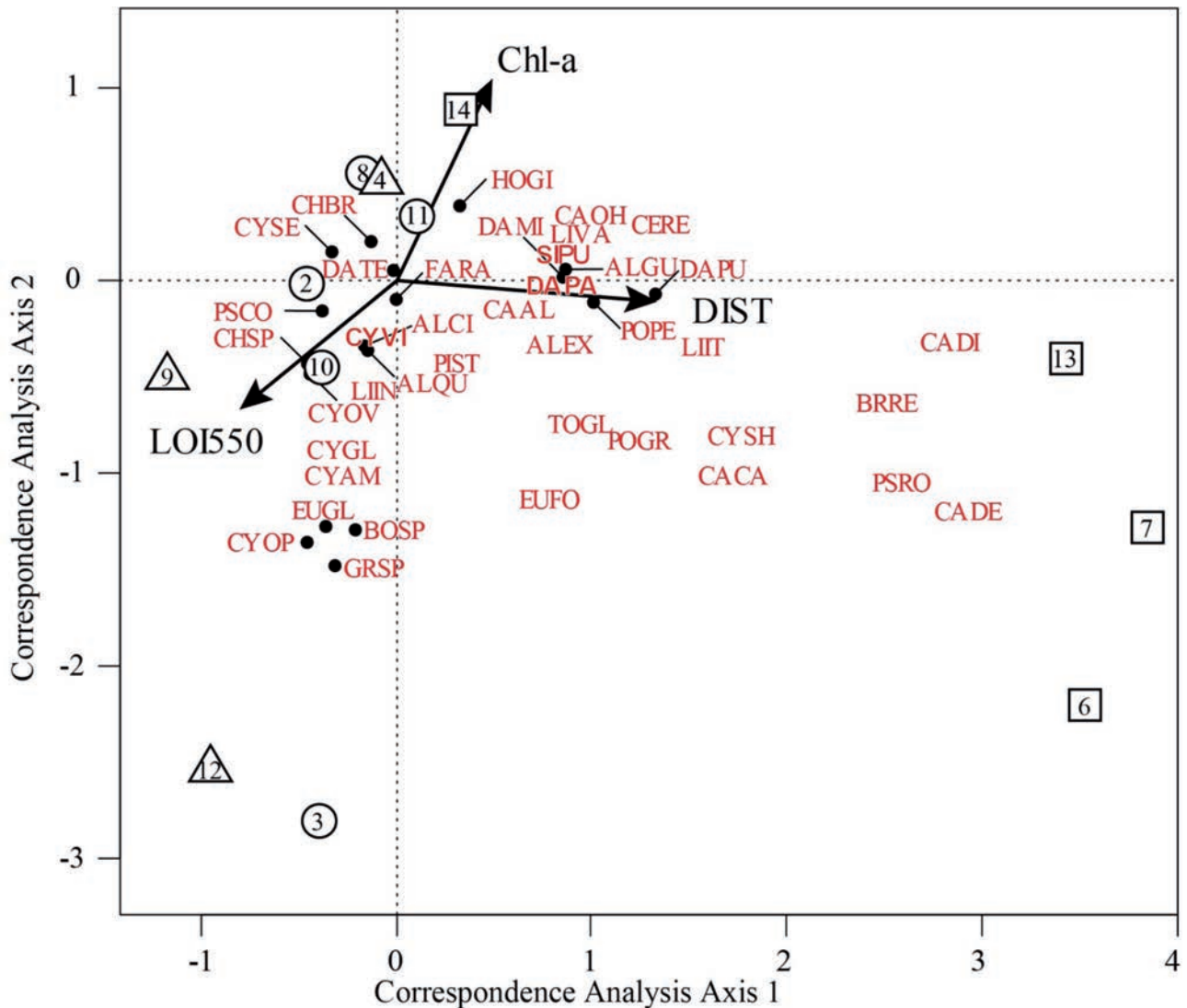


Fig. 6. Correspondence Analysis (CA) of species and water quality data from measurements taken in 2006. Species names are abbreviated and the four-letter code follows Tab. 2. Circle, shrub tundra-type; triangle, forest-tundra-type; square, boreal forest-type.

imity to the coastline tend to have higher diversities up to $D^1_{\text{Benthos}}=14.09$ or $1/D^2_{\text{Benthos}}=12.36$ (Tabs. 2 and 3), while site 9 is an exception.

The axis 1 of the correspondence analysis (CA) explains 34.0% of the total inertia (0.660) in the dataset and that axis is highly loaded with inland sites and their species inventory, especially ostracod species, such as *Bradleystrandesia reticulata* (BRRE), *Can. candida* (CACA), *Can. decora* (CADE), *Can. distincta* (CADI), *Cyc. sharpie* (CYSH), *Limnocythere (L.) itasca* (LIIT) and *Psc. rostrata* (PSRO) (Fig. 6). As expected, the projection of the environmental variable distance from the coast (DIST) is significantly correlated ($r^2=0.71$; $P=0.002$) to the CA results.

CA Axis 2 explains a further 19.5% and is loaded with sites that are characterized by their high Chla concentrations ($r^2=0.53$; $P=0.026$) and/or high LOI₅₅₀ values ($r^2=0.43$; $P=0.034$). In particular, the abundance of *Holopedium gibberum* (HOGI) is positively correlated to higher Chla concentrations. In contrast, benthic species such as *Cyp. ophthalmica* (CYOP), *Gryptoleberis* sp. (GRSP), *Cyc. ampla* (CYAM), *Eurycercus glacialis* (EUGL) and *Bosmina* sp. (BOSP) seem to favour sites with organic-rich sediment type (increased LOI₅₅₀).

Site evolution – Beta diversity

The similarity matrix enabled us to compare the species inventory between sites more generally (Tab. 4). In the study area, sites in close geographical vicinity often show high β_{sor} or β_{sim} values such as neighboring sites 6 and 7 ($\beta_{\text{sor}}=0.703$, $\beta_{\text{sim}}=0.765$) or the cluster of sites 2, 3 and 4 ($\beta_{\text{sor}}=0.837-0.636$, $\beta_{\text{sim}}=0.947-0.737$). Lower values found in the cluster of sites 8, 9 and 10 ($\beta_{\text{sor}}=0.720-0.410$, $\beta_{\text{sim}}=0.917-0.667$) are partly caused by the overall low diversity in site 9, as discussed above.

Focusing on the closest similarities, sites located within the boreal forest (6,7,13 and 14) show a distinct cluster ($\beta_{\text{sor}}=0.727-0.524$ and $\beta_{\text{sim}}=0.800-0.588$) while the fauna of site 13 is least similar in this context, partly because of the overall low species diversity of benthic microcrustaceans at this site.

A further cluster of sites with similar species assemblages are sites close to the HBL coastline (2, 3, 4, 8, 10) with $\beta_{\text{sor}}=0.837-0.618$ and $\beta_{\text{sim}}=0.947-0.684$. It is noteworthy that these sites also show high alpha diversity indices (Tab. 3). According to previous reports on microcrustacean from HBL, the species richness in the coastal rock pools is higher than in the present study of lakes and ponds, including 34 species that were not sampled in the present study (Havel *et al.*, 1990a,1990b; Jeffery *et al.*, 2011). We suggest two main causes for the substantial differences in species richness: i) The dramatic variation in salinity 150-13,650 $\mu\text{S}/\text{cm}^{-1}$ in rock pools expresses a greater ecological gradient to host a more diverse micro-

crustacean fauna (Weider and Hebert, 1987; Havel *et al.*, 1990a, 1990b; Weider *et al.*, 2010); ii) The intense sampling effort of numerous rock pools by various studies focussing on cladocerans covers a time span of 25 years and includes also rare species (Weider *et al.*, 2010). Therefore, a direct comparison of species diversity or similarities is a matter of scaling (Chase and Knight, 2013).

Sites in boreal forest – gamma diversity

The knowledge of the (genetic) biodiversity and ecology of Arctic and Subarctic Cladocera and Ostracoda species is based on numerous studies that were motivated by different research goals, starting with biological expeditions near the end of the 19th century (Sars, 1899). We present a species list of studies completed in the Subarctic and Arctic realms of North America (Supplementary Tabs. 1 and 2). Surprisingly, we found no evidence that both Cladocera and Ostracoda were investigated in the same study. Hence, to assess the species diversity of the studied lakes and ponds, we compared the fauna with two surveys which investigated separately the ecology of cladocerans and ostracods in lakes and ponds in the boreal forest biome in southwest Yukon with similar hydrological settings in terms of the physical and chemical water quality parameters (Swadling *et al.*, 2000; Bunbury and Gajewski, 2005). The species richness in total numbers is comparable (Tab. 3), while the relatively low similarity indices ($\beta_{\text{sor}}=0.420$ and $\beta_{\text{sim}}=0.459$) indicate distinct biogeographical distribution of individual species (Tab. 2; Adamowicz *et al.*, 2009; Curry *et al.*, 2012). Weider and Hobæk (2003) suggested that the asynchronous deglaciation history of the Cordillerian and Laurentide ice sheets resulted in different recolonization patterns of the species in the Arctic and Subarctic that caused species-dependent phylogeography. Thus, it appears that proglacial aquatic ecosystems in the Yukon evolved when the landscape became ice-free already at ca. 13,000 years BP (Dyke and Prest, 1987; Bunbury and Gajewski, 2009b; Bunbury, 2012). In contrast, HBL deglaciated and was submerged by marine waters of the postglacial Tyrell Sea around 8000 years BP. However, freshwater ecosystems established not earlier than 5000 years BP as the landscape gradually emerged above sea-level through glacio-isostatic rebound (Dyke and Prest, 1987; Dredge, 1992b).

CONCLUSIONS

We showed that lake and pond ecosystems in HBL are exposed to similar climate stresses as shown also for arctic tundra ponds (Smol *et al.*, 2005). The waters including the rock pools are identified to be vulnerable, as they have little to no buffer capacity to changes in temperature and precipitation rates (Weider *et al.*, 2010; White *et al.*,

2014). The evident climate warming will shorten the period of ice cover and inversely extend the vegetation period, which will impact phyto- and zooplankton life cycles, but also alter the hydrology due to increased evapotranspiration and absorption of solar radiation (Arp *et al.*, 2015). Consequently, we will experience the densification of the vegetation in the catchment, *i.e.* the northward displacement of the northern treeline and dispersal of boreal (aquatic and terrestrial) species and a retreat of arctic and subarctic (aquatic and terrestrial) species (Jacques *et al.*, 2016).

In this context, long-term ecological research (LTER) is essential to detect systematic floral or faunal changes and assess the resilience, reactivity, and variance of ecosystems based on abiotic and biotic factors (Haase *et al.*, 2016). Our assessment of the faunal similarity and diversity of cladoceran and ostracod species in freshwaters within the boreal forest and shrub tundra catchments revealed distinct faunal assemblages. Markedly, only certain ostracod species (*i.e.*, *Can. acuta*, *Can. acutula*, *Can. decora*, *Can. distincta* and *L. liporeticulata*) appear exclusively in boreal forest sites. Considering also previous studies (Supplementary Tabs. 1 and 2), we suggest especially *Can. acuta*, *Can. acutula* and *Can. decora* as indicator species of proceeding warming and eventually following the northern treeline and identified *Can. rawsoni* and *Ton. glacialis* as subarctic and arctic faunal elements. Both species were reported also from other Arctic sites (Røen, 1962, 1968; Wojtasik, 2008; Bunbury and Gajewski, 2009a). Despite single indicative species, overall it appears that waters in boreal settings have a higher alpha diversity in zooplankton, whereas waters in the shrub tundra display a higher diversity in benthos faunal assemblage. Further research is needed to monitor these trends and to specify implied consequences to the food web (Thienpont *et al.*, 2015).

We conclude that our study contributes quantitative results that are important to understand the decadal hydrochemical and species variation of subarctic waters that are extremely abundant in the northern Manitoba landscape. In combination with other regional reference datasets (Jacques *et al.*, 2016), the resilience, reactivity, and variance of these aquatic ecosystems may be assessed in detail to predict ecosystem changes. Meanwhile, complementary palaeolimnological studies (including remains of diatoms, cladocerans and ostracods) may hindcast the ecosystem dynamics of the past.

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