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An Exploratory Survey of Summer Water Chemistry and Plankton Communities in Lakes near the Sutton River, Hudson Bay Lowlands, Ontario, Canada

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Abstract

We provide the first assessment of regional water chemistry and plankton (phytoplankton and crustacean zooplankton) for a suite of lakes near the Sutton River region of the north-central Hudson Bay Lowlands (HBL). We use ordination analyses to examine the spatial variation in water chemistry and plankton across lakes, and to explore the factors that may explain this variation. Based on data collected during summer from 2009 to 2011, we found that in addition to geology, water chemistry was strongly influenced by a lake's proximity to salt water and the degree of permafrost development within its catchment. Phytoplankton composition varied across lakes based on differences in water depth and nutrient concentrations, with non-filamentous cyanobacteria and chlorophytes more common in shallow lakes, and deeper lakes dominated by planktonic diatoms or filamentous cyanophytes. Crustacean zooplankton community composition and richness in the HBL lakes was similar to communities found in Ontario lakes in more temperate regions within the Precambrian Shield. These baseline data provide a foundation upon which future surveys in this climatically sensitive region may be compared.

Introduction

The Hudson Bay Lowlands (HBL) of central Canada comprise the second largest contiguous peatlands in the world, containing an estimated 12% of the organic carbon stored in Canadian soils (Humphreys et al., 2014). It is a region characterized by low topographic relief that is overlain with poorly drained glacial and marine silts and clays, with lakes and ponds covering an estimated 25% (Macrae et al., 2004) to >40% of the landscape (Bello and Smith, 1990). Many of these water bodies are shallow and provide excellent habitat for waterfowl and other wildlife (Wolfe et al., 2011). They also influence biogeochemical dynamics at local, regional, and perhaps global scales (Vincent et al., 2013), serving as important sinks or sources of carbon, the balance of which is closely tied to hydrology and climate (Macrae et al., 2004).

Aquatic ecosystems within the HBL are being increasingly threatened by industrial activities and the extraction of natural resources. Large-scale industrial projects (e.g., hydropower generation, mining) have recently commenced or are being considered in the region despite its remoteness, sparse population, and significant logistical challenges. Considerable attention, for example, has been focused on the *Ring of Fire* region of northern Ontario, which contains one of the world's largest nickel-chromium deposits, and which may soon house North America's first major chromite mine. A bi-product of new development will be increased access to this historically remote region, with unknown consequences for aquatic systems. The collection of baseline water quality and ecological data, prior to major development, is an essential step in the management of these vital ecosystems.

Assessments of the effects of industrial development on aquatic ecosystems in the HBL may be confounded by recent, rapid changes in climate. The concentration, extent, and duration of sea-ice cover on Hudson Bay have decreased significantly over the past three decades (Gough et al., 2004; Hochheim et al., 2011; Hochheim and Barber, 2014), resulting in a positive feedback cycle that has accelerated warming over land surfaces (Hochheim and Barber, 2010). While there is little evidence that warmer temperatures have thus far impacted permafrost extent in the HBL, likely because of thermal lags between changes in air temperature and ground ice conditions (Gough and Leung, 2002; but see Wolfe et al., 2011), there are several examples of recent biological changes within aquatic ecosystems in the region.

For example, in a high-resolution paleolimnological study of four lakes near the Sutton River in the HBL, Rühland et al. (2013) observed biological changes that were regionally coherent and coincident with rapidly warming air temperatures since the early 1990s. Using multiple paleoecological indicators, Rühland et al. (2014) provide additional evidence for biological change in HBL lakes. They report early signs of a biological response to warming, but note that the magnitude of change varies across sites and trophic levels. Thus, despite evidence of a coherent tem-

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poral response among primary producers (diatoms) in at least four lakes examined in detail (Rühland et al., 2013), regional stressors may be regulated by local factors (e.g. lake depth, distance to salt water, nutrient status) that moderate the degree of biological response observed.

Climate change scenarios for the Hudson Bay region suggest that annual air temperatures may increase between 3.9 and 4.5 °C by 2040–2069, under a 2 × CO_2 scenario (Gagnon and Gough, 2005). In light of these projections, and increased pressure from industrial development, high quality baseline data are required to permit effective monitoring of environmental change in aquatic ecosystems within the HBL. However, even basic limnological and biological data are uncommon or unavailable for lakes and ponds in this remote region. Characterizations of plankton in remote HBL lakes, for example, are extremely rare (e.g. Symons et al., 2012, 2014), despite their recognition as essential components of environmental assessments in other lake regions (Schindler, 1978; Yan et al., 2008). Existing surveys of water chemistry from shallow tundra ponds in Wapusk National Park (Bos and Pellatt, 2012) and from within the Churchill Wildlife Management Area (White et al., 2014), both in northern Manitoba, reveal that morphometry (i.e. depth) and catchment vegetation are important predictors of variation in chemistry between lakes. These studies also show that limnological conditions are influenced strongly by hydrologic and climatic conditions in the HBL region. Specifically, pond water chemistry often reflects the connectivity of a lake to its adjacent catchment. These connections are often complex in permafrost regions, and are likely to be affected by climate warming as water budgets are altered (Rouse et al., 1997).

Our objectives were threefold. First, we aimed to provide baseline information on water chemistry and plankton (i.e. phytoplankton, zooplankton) for lakes in the Sutton River region of the HBL, Ontario, Canada. This region was initially selected for study because of previous evidence that biological changes are occurring in nearby lakes and in the Sutton River (e.g. Gunn and Snucins, 2010). Second, we used ordination analyses to examine the spatial variation in water chemistry and plankton across lakes, and third, we explored the factors that may explain this variation. An improved understanding of the basic limnological and biological conditions of these lakes will lay a foundation upon which past (Rühland et al., 2014), and possibly future, limnological changes may be interpreted.

Methods

STUDY REGION AND SITE DESCRIPTION

The Hudson Bay Lowlands (HBL) region includes a continuous belt of land with an elevation of less than 200 m (average slope of 0.5 m per km), surrounding the western side of Hudson and James Bays (Martini, 1989; Rouse, 1991). The area is mostly flat and very wet, with countless lakes and ponds, and is traversed by the southern boundaries of continuous and discontinuous permafrost (Gough and Leung, 2002), and the northern tree line (Rouse et al., 1997). The HBL are actively responding to the last glacial retreat, showing very high rates of isostatic rebound (~1.1 m rise per century), resulting in the emergence of approximately 2 km of new coastline per century (Webber et al., 1970).

The region is underlain by Paleozoic and Mesozoic rocks, and covered with a Pleistocene mantle of thin till (Martini, 1989). In the immediate post-glacial period, this was overlain by thin marine and coastal sediments deposited by the Tyrrell Sea, and the subsequent development of up to 3–4 m of peat since the mid-Holocene (Martini, 2006). The geology of the central HBL is predominantly calcareous, underlain by limestone and dolomite (Glaser et al., 2004). The Sutton Ridges, located near the Sutton River, are a geologic anomaly of Precambrian origin, rising up to 120 m above the lowlands.

The HBL climate is subarctic and strongly influenced by circulation patterns and ice dynamics within Hudson Bay (Martini, 2006). Mean annual temperature between 1960 and 1990 was –7.2 °C in Churchill, Manitoba, on the western shore of Hudson Bay. However, increases in temperature of 0.5 to 1.0 °C per decade have been observed in Churchill and at other locations in the HBL since the early 1990s (e.g. Hochheim and Barber, 2010; Galbraith and Larouche, 2011). Total annual precipitation, averaged for the period 1960–1990, was 355.2 mm per year, with approximately 55% falling as snow.

The 17 study lakes are located near the Sutton River in the north-central HBL (Fig. 1). They are positioned within, and to the south of, Polar Bear Provincial Park in Ontario, spanning a north–south transect that extends ~130 km inland from the southern shore of Hudson Bay. The region is dominated by vast peatlands (bogs and fens), although black spruce (*Picea mariana*) are common along lake margins, riparian zones, and gravel beach ridges that run parallel to Hudson Bay. Other common vegetation includes tamarack (*Larix laricina*), sedges, and various *Sphagnum* species, and other mosses. The boundary of continuous and discontinuous permafrost runs approximately east–west through the study region (Fig. 1). Lakes on continuous permafrost are located within the tundra with their catchments largely devoid of trees.

FIELD METHODS

The 17 study lakes were sampled over three years (2009 to 2011), from late July to late August (Table 1). Lakes were selected from topographic maps in a rough transect running parallel to the Sutton River. The objective was to obtain as broad a survey of lakes as possible, given constraints on floatplane time and landing capabilities. As a result, a lake was sometimes added or removed from the sampling plan based on its accessibility, which varied from year to year with changing water levels in the shallowest of sites. A study lake was sampled a maximum of once per year, totaling one to three visits per lake between 2009 and 2011 (Table 1). With the exception of Hawley (4) and Sutton (15) Lakes, which were sampled by motor boat, the study lakes were accessed by floatplane, and sampled from the aircraft's pontoon. Although no bathymetric maps are available for the study lakes, attempts were made to sample within, or near, the deepest basin of each lake. For some lakes, the approximate location of the deepest point was known from local traditional knowledge (Albert Chookomolin, Weenusk First Nation, Peawanuk General Delivery, personal communication), or was identified visually from aerial surveys (i.e. in shallow lakes). For all other lakes, several depth readings were taken using the floatplane's depth sounder, with sampling occurring at the deepest recorded location.

The sampling location and elevation were recorded using GPS at each lake. After returning from the field, Google Earth™ was used to estimate the distance from each lake to salt water [i.e., to Hudson Bay for most lakes, and to James Bay for Opinnagau (10) and Opinnagau East (9) Lakes]. Temperature and oxygen readings were taken through the water column using a YSI model 58 meter. Composite water samples (i.e. an integrated sample of the water column) for chemical and phytoplankton analyses were collected using a 2 L bottle lowered and raised slowly through the

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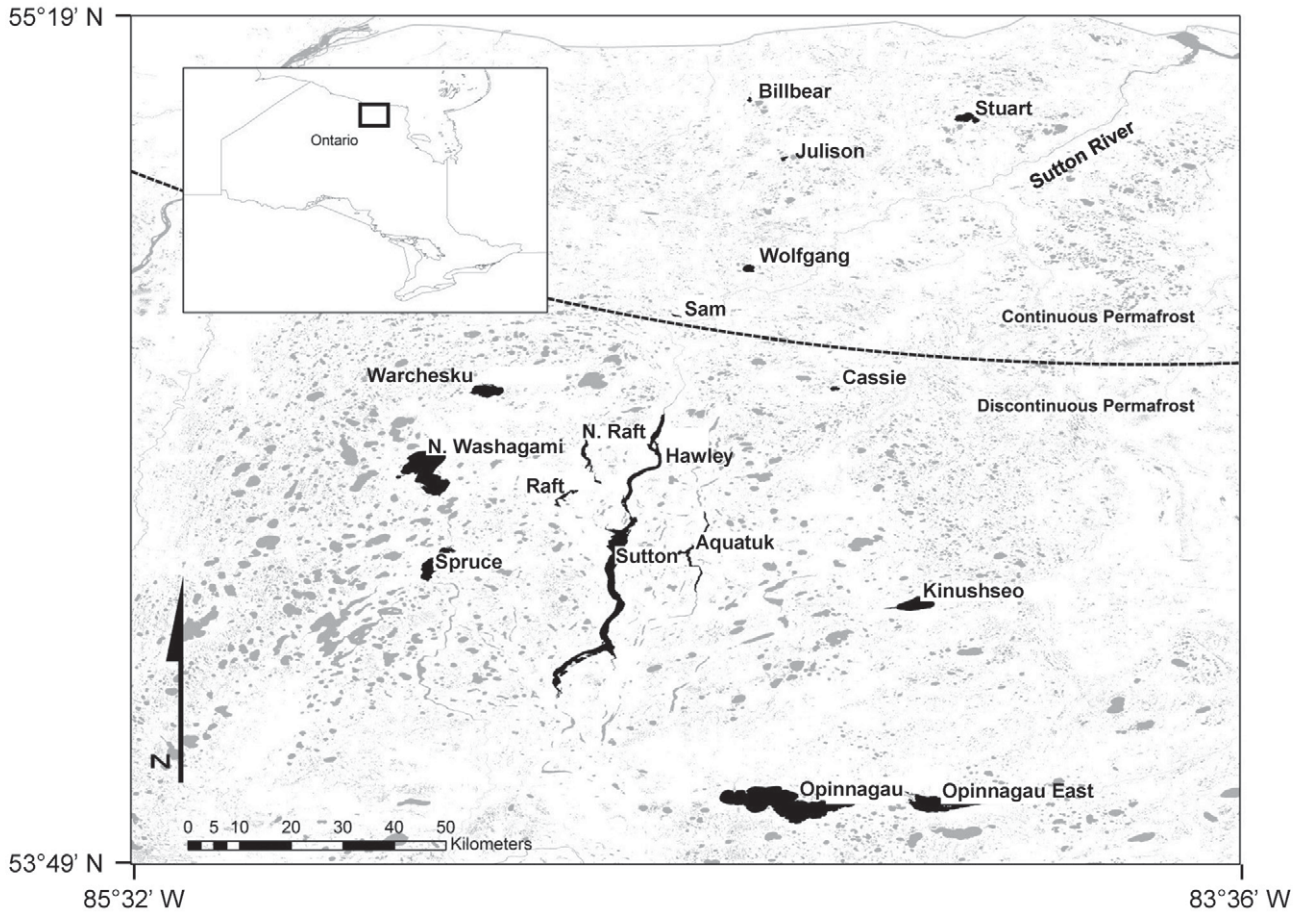


FIGURE 1. Study lakes in the Sutton River region of northern Ontario, Canada.

Secchi transparency depth (also measured), or to a depth of 0.5 m above the lake sediments (i.e. in shallow lakes or in lakes where the Secchi depth was deeper than the lake depth) (Ingram et al., 2013). The water for chemical analyses was coarse-filtered through an 80 µm filter to remove large particles, consistent with standard Ontario Ministry of the Environment lake sampling protocols (Ingram et al., 2013). Water samples for phytoplankton enumeration were sampled to a depth of 2 times Secchi, unfiltered, and fixed with a 1 mL Lugol's iodine solution in the field. No phytoplankton samples were collected from Sutton Lake (15), due to sampling constraints (Table 1). Crustacean zooplankton were sampled using a 30-cm-diameter, 80 µm mesh conical plankton net. A vertical haul from 1 m above the bottom of the lake to the surface was collected from deeper lakes, while shallow (<5 m) lakes were sampled with a 4 m horizontal tow. Zooplankton samples were preserved in the field with 14% buffered formalin.

LABORATORY METHODS

Water chemistry samples were analyzed using standard laboratory protocols at the Ontario Ministry of the Environment's Dorset Environmental Science Centre (Ontario Ministry of the Environment, 1983; http://www.desc.ca). The parameters analyzed included Gran alkalinity (Alk), aluminum (Al), calcium (Ca), chloride (Cl), true color (Col), specific conductance (Cond), dissolved organic carbon (DOC), iron (Fe), potassium (K), magnesium (Mg), sodium (Na), ammonium/ammonia (NH_4/NH_3), nitrate/nitrite (NO_3/NO_2), pH, total phosphorus (TP), reactive silicate (SiO_3), and sulfate (SO_4). Total inorganic nitrogen (TIN) was calculated as the mass sum of ammonium/ammonia and nitrate/nitrite.

Phytoplankton samples were settled and enumerated using standard MOE protocols (Hopkins and Standke, 1992). Briefly, phytoplankton were counted using inverted microscopy and Utermöhl counting chambers following concentration by sedimentation. A minimum of 300 units (singly occurring cells or colonies) were counted and identified to genus level (or occasionally to species level when easily identifiable). Estimates of cell volume for each taxon were obtained by routine measurements of 30 to 50 cells, and application of geometric formula best fitted to the shapes of the cells. A density of 1 g cm^{-3} was assumed for cellular mass, enabling cell counts to be converted to wet weight biomass and expressed as biovolume.

In the laboratory, crustacean zooplankton samples were split into fractions with a Folsom plankton splitter. At a species level, approximately 45–60 adults were enumerated, with a target of ~15–35 juvenile copepods identified as either calanoid or cyclopoid nauplii or copepodids. These targets ensured that no single species comprised more than 20% of the final count. For statistical analyses, phytoplankton and zooplankton data were expressed as relative biovolume and relative abundance, respectively

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TABLE 1

Location of the 17 study lakes, including the years sampled, the distance to salt water, elevation, and the depth at the location of sampling. Note that six of the lakes, shown in parentheses, are presented with unofficial names.

Lake	Code	Latitude (decimal degrees)	Longitude (decimal degrees)	Years sampled	Surface area (ha)	Sampling depth (m; Z)	Distance to salt water (km; Dist. to sea)	Elevation (m a.s.l.; Elv)
Aquatuk	1	54.3281	–84.5686	2009–2011	828	11.7	101	127
(Billbear)	2	55.1378	–84.4688	2010–2011	77	0.8	11	24
(Cassie)	3	54.6368	–84.3203	2010–2011	70	1.0	70	105
Hawley	4	54.5269	–84.6288	2009–2011	1235	34.6	78	95
(Julison)	5	55.0381	–84.4073	2010	156	0.9	24	33
Kinushseo	6	54.2599	–84.1786	2009	868	2.5	110	134
North Raft	7	54.5343	–84.7561	2009–2011	662	11.1	78	113
North Washagami	8	54.5101	–85.0399	2009	2813	2.7	84	119
Opinnagau East	9	53.9083	–84.1452	2009–2010	2723	1.6	118	102
Opinnagau	10	53.9220	–84.4551	2009	5804	1.9	131	120
Raft	11	54.4501	–84.7919	2009	188	1.3	87	130
(Sam)	12	54.7626	–84.5980	2010–2011	32	1.7	53	92
Spruce	13	54.3282	–85.0079	2009–2011	1227	10.9	102	125
(Stuart)	14	55.1135	–84.0842	2010	357	0.7	15	24
Sutton	15	54.2501	–84.7000	2009	3744	19.0	109	95
Warchesku	16	54.6301	–84.9299	2009	3764	2.1	69	129
(Wolfgang)	17	54.8473	–84.4697	2010–2011	157	1.2	43	67

STATISTICAL ANALYSES

All ordination analyses were performed using Canoco version 4.5 (ter Braak and Šmilauer, 2002). Principal components analysis (PCA) was used to examine the variation in water chemistry across lakes. Water chemistry data were collected from one to three years, depending on the lake (Table 1), but were analyzed as a single sample per lake by averaging the values from multiple years. This was deemed appropriate given that the variability in chemistry within lakes over time was much less than the spatial variability among lakes (Appendix Fig. A1). Prior to ordination analysis, environmental data were screened for normality using a Shapiro-Wilk test using SigmatStat version 3.1, and log (x+1) transformed where the fit was improved. As the number of environmental variables (21) exceeded the number of lakes (17), a correlation matrix (not shown) was used to identify highly correlated variables, with redundant variables being removed to reduce the number of predictors ordinated. Variables were removed if they were highly correlated ($r > 0.9$) to "master" variables (e.g. pH, Mg, and Ca were highly correlated to Alk, with Alk retained as the representative variable), thus reducing the data set to six key environmental variables (Alk, TIN, TP, log Cl, DOC, and SiO_3). All remaining variables were run passively in the PCA, to show their relationship to the selected master variables. To explore the possible influence of sampling depth and the distance to the sea on water chemistry, we examined their relationships to PCA Axis 1 scores (the main direction of variation in the chemistry data), generated using the six water chemical variables described above. These explanatory variables were selected because they can be measured with relative ease, and have been shown to be important predictors of pond and lake water chemistry in other areas of the HBL (e.g. Bos and Pellatt, 2012), and in other subarctic regions (e.g. Eilers et al., 1993, Rühland et al., 2003). Lakes were also grouped with respect to their position on either continuous or discontinuous permafrost, and key water chemical variables between groups were compared (i.e. DOC, color, SiO_3, TP, and TN).

Before analyzing biological data, rare taxa were removed from the phytoplankton and zooplankton data sets if they did not occur in at least one sample at >1% biovolume or abundance, respectively. Because only single plankton samples were available from each lake in any year, and inter-annual variability in biological assemblages can be high (e.g. Paterson et al., 2008), we treated each lake-year as a unique sample, with comparisons made to the specific environmental conditions from that year.

All ordination analyses involving biological data were run on percent biovolume (phytoplankton, genus-level) or percent abundance (zooplankton, species-level) data. Genus or species percentage data were square root transformed prior to analyses to downweight the importance of dominant taxa. Detrended correspondence analysis (DCA), with detrending by segments, was used to determine the maximum amount of variation in the species data (Hill and Gauch, 1980). Because of the relatively short gradient lengths of the first DCA axes for phytoplankton and zooplankton species data (2.5 and 2.1, respectively), a linear ordination tech-

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nique (Redundancy Analysis, RDA) was used to explore the relationship between species and environmental data.

A forward selection step was used with RDA to reduce the issue of collinearity in the explanatory variables. Monte Carlo permutation tests (999 permutations) were run to determine the significance of each forward selected variable, and to test the significance of the first and all canonical ordination axes defined by the forward selected environmental variables.

Phytoplankton were analyzed qualitatively at the major algal group level (e.g. cyanobacteria). For this analysis, one to three years of phytoplankton data were grouped to create an "average" assemblage for each lake. In Aquatuk Lake (1), the 2010 phytoplankton sample was not included in the lake average as the total biovolume was four times higher than in either 2009 or 2011, likely due to a cyanobacterial bloom at the time of sampling (described below).

Results

TEMPERATURE, OXYGEN, AND LIGHT REGIMES

Twelve of the study lakes are shallow (depths at sampling locations of less than 3 m), and were isothermal and well oxygenated throughout the water column at the time of sampling (late July to late August). Five of the lakes in proximity to the Sutton Ridges had sampling depths of greater than 10 m, and showed evidence of weak thermal stratification at the time of sampling in some years. However, as shown for North Raft and Hawley Lakes (sampling depths = 11.1 m and 34.6 m, respectively; Fig. 2), thermal conditions varied from year to year, including the presence and strength of stratification, and the depth of the thermocline. None of the lakes, regardless of their depths or the years sampled, showed any evidence of deep water hypoxia or anoxia.

Secchi transparency depths varied from 0.6 to 4.5 m in the study lakes and were negatively correlated with DOC concentrations (DOC range: 5.9 to 10.4 mg L^{-1}). However, this was not a true estimate of light availability, as Secchi depth was equal to the sampling depth in many of the shallow lakes.

WATER CHEMISTRY

In general, the study lakes were found to be alkaline at the time of sampling, with relatively high calcium concentrations (mean: 25.1 mg L^{-1}; Table 2). Despite extensive peatlands in the region, and the presence of *Sphagnum* moss commonly associated with high organic acid production, DOC concentrations in the study lakes were lower (Table 2) than those reported for other peat-dominated, subarctic regions (e.g., Kortelainen, 1993) and for ponds in the northwestern HBL (Bos and Pellatt, 2012). Low to moderate total phosphorus concentrations (Table 2) and high mass ratios of TN/TP (available for 15 of the 17 lakes; range: 26 to 99; mean: 43) suggest the lakes were P-limited at the time of sampling (Downing and McCauley, 1992; Guildford and Hecky, 2000; Bergström, 2010). Na and Cl con-

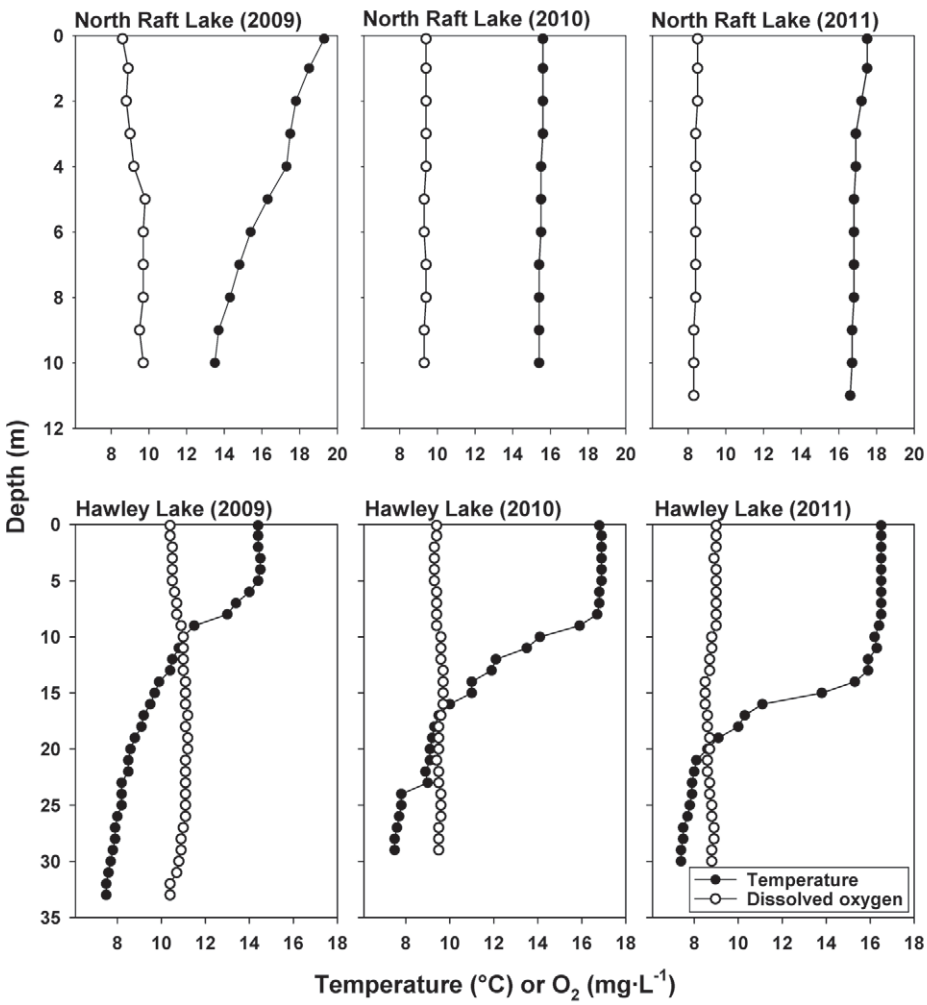


FIGURE 2. Temperature and dissolved oxygen profile data from North Raft Lake (28 July 2009, 11 August 2010, and 19 August 2011), and Hawley Lake (30 July 2009, 5 August 2010, and 20 August 2011).

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TABLE 2

Summary of the general water chemistry measured in 17 study lakes (2009–2011). Chemical parameters were averaged over one to three years for each lake. See Table 1 for the years each lake was sampled.

Lake	Code	Alk ($mg \cdot L^{-1}$ as $CaCO_3$)	Al ($\mu g \cdot L^{-1}$)	Ca ($mg \cdot L^{-1}$)	Cl ($mg \cdot L^{-1}$)	Col (TCU)	Cond ($\mu S \cdot cm^{-1}$)	DOC ($mg \cdot L^{-1}$)	Fe ($\mu g \cdot L^{-1}$)	K ($mg \cdot L^{-1}$)	Mg ($mg \cdot L^{-1}$)	Na ($mg \cdot L^{-1}$)	NH_4/NH_3 ($\mu g \cdot L^{-1}$)	NO_3/NO_2 ($\mu g \cdot L^{-1}$)	pH	TP ($\mu g \cdot L^{-1}$)	SiO_3 ($mg \cdot L^{-1}$)	SO_4 ($mg \cdot L^{-1}$)	TIN ($\mu g \cdot L^{-1}$)
Aquatuk	1	98.7	3.9	32.4	1.4	26.9	188.7	7.6	37.8	0.3	5.0	2.2	21.3	4.0	8.1	13.8	1.5	0.5	25.3
(Billbear)	2	71.5	58.4	27.1	17.3	36.0	193.0	9.0	190.0	0.3	3.3	8.5	45.0	5.0	7.7	28.8	0.2	0.7	50.0
(Cassie)	3	90.3	6.1	33.6	1.9	26.8	184.5	10.4	120.0	0.1	3.1	1.6	13.0	5.0	8.1	4.4	1.6	0.1	18.0
Hawley	4	105.3	2.7	35.1	4.8	15.5	213.3	6.3	8.7	0.5	5.7	4.8	12.7	3.3	8.1	6.8	1.3	1.8	16.0
(Julison)	5	90.7	16.9	32.6	16.0	18.8	229.0	7.5	90.0	0.5	3.3	10.8	22.0	6.0	8.0	14.8	0.2	0.7	28.0
Kinushseo	6	38.9	11.9	13.3	1.0	29.4	78.8	7.0	64.4	0.2	1.5	1.3	2.0	2.0	7.7	9.1	0.4	0.3	4.0
North Raft	7	80.0	8.2	28.9	1.3	21.9	152.3	6.8	26.9	0.2	3.5	1.0	6.7	4.0	7.9	6.4	0.9	0.5	10.7
North Washagami	8	44.6	16.8	14.2	1.4	28.8	88.6	6.4	89.6	0.2	1.8	1.2	4.0	2.0	7.7	9.6	0.3	0.3	6.0
Opinnagau East	9	52.4	36.2	17.4	1.5	43.9	106.7	9.3	144.5	0.2	2.5	2.3	8.0	5.0	7.7	16.4	0.7	0.4	13.0
Opinnagau	10	38.2	66.8	12.7	1.2	63.4	79.2	8.8	203.0	0.2	1.8	1.7	4.0	4.0	7.6	16.1	0.4	0.2	8.0
Raft	11	76.4	9.2	25.8	0.7	61.0	143.0	10.4	133.0	0.1	3.3	1.2	10.0	4.0	7.9	7.0	1.1	0.2	14.0
(Sam)	12	82.4	6.3	27.0	1.8	5.1	160.5	6.7	5.0	0.2	4.1	1.3	17.0	4.0	8.1	8.0	0.5	0.1	21.0
Spruce	13	63.4	7.7	23.0	1.7	21.5	135.3	7.9	108.6	0.2	2.7	1.6	18.0	3.3	7.9	10.8	0.7	0.3	21.3
(Stuart)	14	79.3	61.5	30.4	16.7	15.2	206.0	6.3	150.0	0.3	3.1	8.0	18.0	6.0	8.0	19.6	0.1	0.3	24.0
Sutton	15	98.2	3.2	28.5	5.0	23.2	208.0	6.4	15.3	0.5	5.1	4.7	16.0	6.0	8.0	5.4	1.2	2.2	22.0
Warchesku	16	57.6	25.4	20.0	0.9	21.2	113.0	5.9	107.0	0.1	2.0	0.8	6.0	2.0	7.9	7.4	0.3	0.3	8.0
(Wolfgang)	17	70.1	12.2	24.6	2.9	19.9	146.0	9.1	115.0	0.2	2.5	2.1	27.0	5.0	7.9	15.2	0.8	0.5	32.0
	Min	38.2	2.7	12.7	0.7	5.1	78.8	5.9	5.0	0.1	1.5	0.8	2.0	2.0	7.6	4.4	0.1	0.1	4.0
	Max	105.3	66.8	35.1	17.3	63.4	229.0	10.4	203.0	0.5	5.7	10.8	45.0	6.0	8.1	28.8	1.6	2.2	50.0
	Mean	72.8	20.8	25.1	4.6	28.2	154.5	7.8	94.6	0.3	3.2	3.2	14.8	4.2	7.9	11.7	0.7	0.5	18.9

Alk = Gran alkalinity; Al = aluminum; Ca = calcium; Cl = chloride; Col = true color; Cond = specific conductance; DOC = dissolved organic carbon; Fe = iron; K = potassium; Mg = magnesium; Na = sodium; NH_4/NH_3 = ammonium/ammonia; NO_3/NO_2 = nitrate/nitrite; TP = total phosphorus; SiO_3 = reactive silicate; SO_4 = sulfate; TIN = total inorganic nitrogen.

centrations were very high in the three lakes [Billbear (2), Julison (5) and Stuart (14)] closest to the Hudson Bay shoreline ([Cl] > 15 mg L^{-1}).

The first ($\lambda = 0.42$) and second ($\lambda = 0.31$) PCA axes captured 73% of the variation in the environmental data (Fig. 3). The first axis showed strong positive correlations with chloride and nutrient concentrations (TP and TIN) (Fig. 3, left panel). These variables were negatively correlated with elevation and the distance to salt water (plotted passively). The second PCA axis was positively correlated with alkalinity, pH, specific conductance, and ion concentrations (Fig. 2, left panel). Metal concentrations (i.e. Al and Fe; plotted passively) were negatively correlated to the second PCA axis. With some exceptions [e.g. Cassie Lake (3)], the PCA effectively separated the lakes into three broad categories: (a) shallow coastal lakes [e.g. Billbear (2), Julison (5), and Stuart (14) Lakes]; (b) deep inland lakes [e.g. Aquatuk (1), Hawley (4), and Sutton (15) Lakes]; and (c) shallow inland lakes (e.g. Kinushseo (6), North Washagami (8), Opinnagau (10), and Warchesku (16) Lakes]. The shallow coastal lakes were generally similar to the shallow inland lakes with respect to acidity, ion concentrations, and DOC, but had higher concentrations of Cl, Na, and nutrients (TP and TIN). The deep inland lakes were characterized by higher ion concentrations, and recorded higher alkalinity, conductivity, and pH. These lakes also had higher concentrations of SiO_3 than the shallow lakes.

A further examination of the relationship between PCA Axis one scores, which describe the main direction of variation in the chemistry data, and lake depth and the distance to salt water (i.e. Dist. to sea) revealed some interesting patterns (Fig. 4). Distance to salt water showed a strong negative, curvilinear relationship with PCA Axis one scores (Fig. 4, part b). Water chemistry, as described by the first PCA axis, showed very little variation among lakes beyond a distance of ~50 km from the coast. In contrast, lake depth was not strongly correlated to PCA Axis one scores (Fig. 4, part a). However, the shallowest lakes were generally associated with higher nutrient concentrations, although there was a fair degree of scatter among lakes.

There was no significant difference in DOC concentrations among lakes on continuous and discontinuous permafrost. However, lakes situated within the continuous permafrost zone were found to have significantly lower color and SiO_3 concentrations, and higher concentrations of total phosphorus and total nitrogen, than lakes in the discontinuous zone (Fig. 5).

PHYTOPLANKTON

Eighty-two phytoplankton taxa were identified in at least one lake at a relative biovolume of >1% (Table 3). These taxa represented six algal divisions: cyanophytes, dinoflagellates, cryptophytes, chrysophytes, chlorophytes, and bacillariophytes (herein called diatoms). The Euglenophyceae, Xanthophyceae, and Raphidophyceae were identified occasionally, but at very low biovolumes, and so were excluded from subsequent analyses.

Some general patterns emerged when phytoplankton were examined at a major algal group level (Fig. 6). The shallow lakes [e.g. Billbear (2), Stuart (5), and Wolfgang (17) Lakes], which had the highest TP and TIN concentrations, also showed the highest algal biovolume, with some exceptions [e.g. deep, inland Aquatuk Lake (1) also had high biovolume]. Shallow lakes, regardless of their location, also had higher relative biovolumes of chlorophytes and non-filamentous cyanophytes (e.g. *Chroococcus)*, relative to the deeper inland lakes that were dominated by filamentous cyanophytes, such as *Aphanizomenon*, *Anabaena*, and *Planktothrix*. Planktonic diatom taxa (e.g. *Asterionella*, *Cyclotella*, *Stephanodiscus*) were most common in the deeper inland lakes, but were also found at high relative biovolumes in some of the shallow lakes. For example, *Asterionella* taxa reached relative biovolumes of 55% in

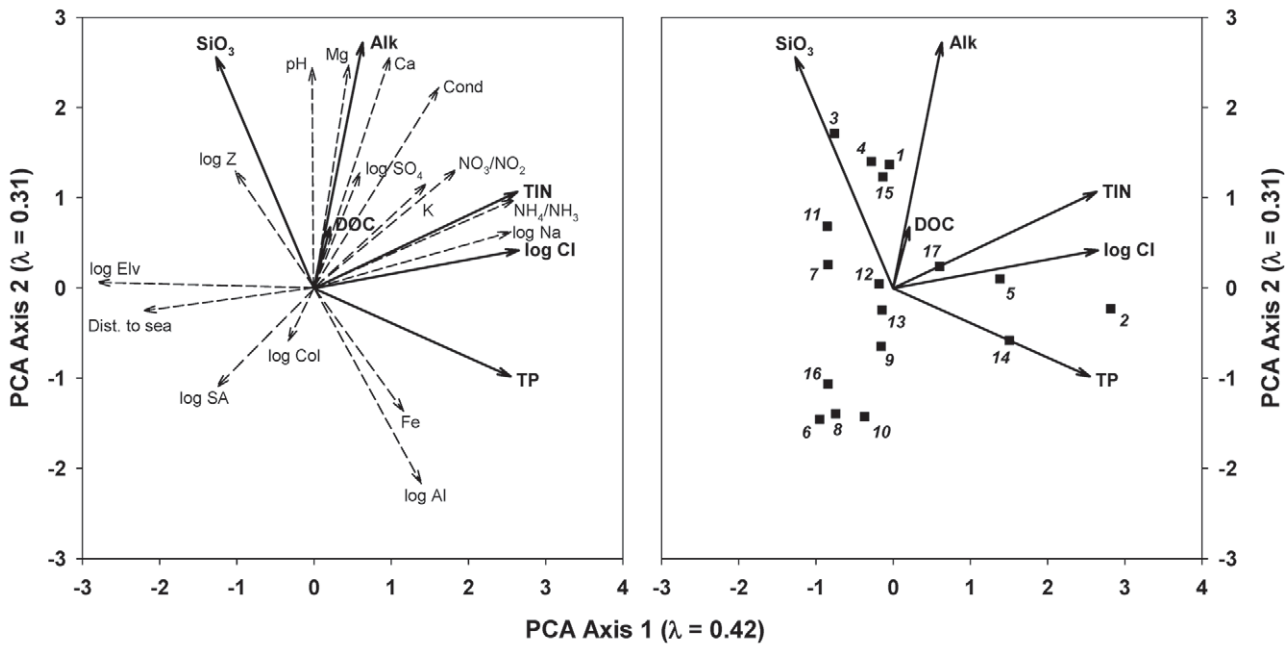


FIGURE 3. Biplots generated from principal components analysis of physical and chemical variables from 17 lakes in the Sutton River region of northern Ontario, Canada. The biplots were created using six active variables (shown with solid arrows). All other variables were run passively in the analysis (dashed arrows, left panel). For plotting purposes, the environmental vectors have been multiplied by a factor of 3. Sites in ordination space are shown as squares (right panel), with site codes described in Table 1.

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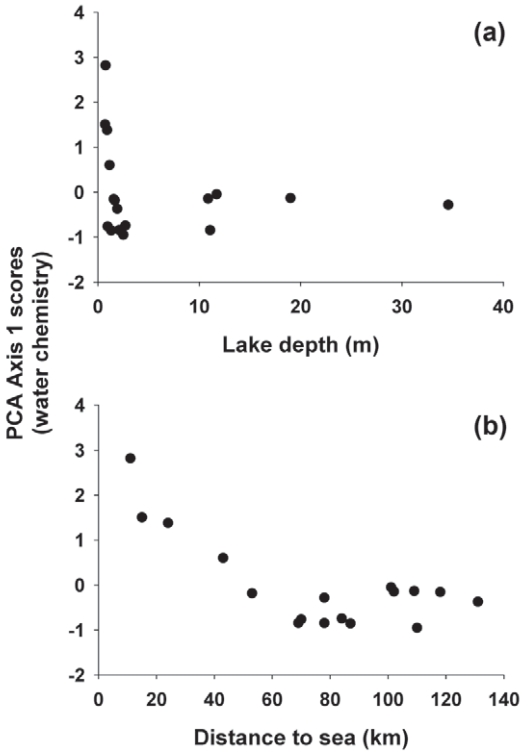


FIGURE 4. For the 17 study lakes, the relationship between PCA Axis 1 scores generated from the analysis of six chemical variables (shown in Fig. 2), and lake depth at the sampling location and the distance to salt water.

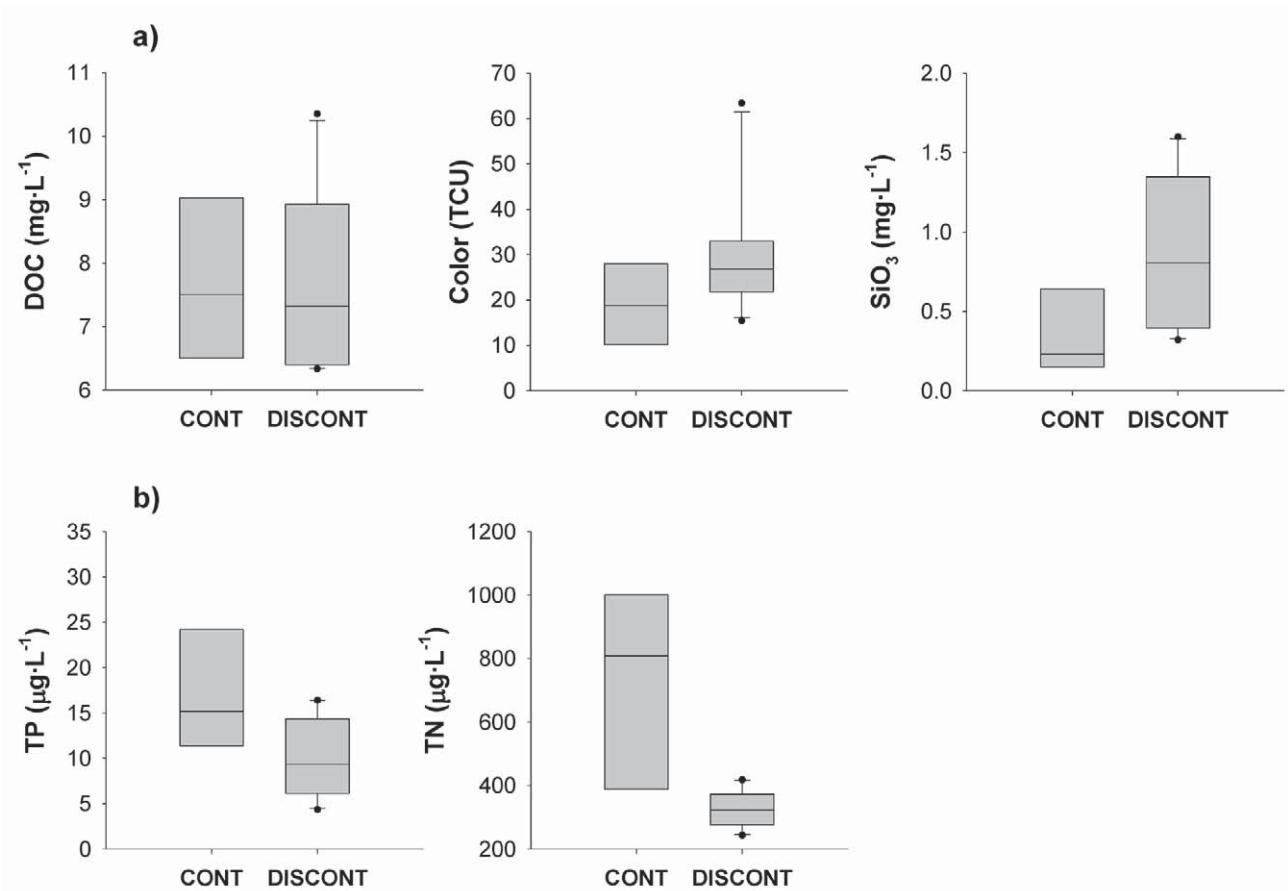


FIGURE 5. Boxplots comparing the distributions of (a) dissolved organic carbon (DOC), color, reactive silicate (SiO_3); and (b) total phosphorus (TP) and total nitrogen (TN) for lakes within continuous (CONT) versus discontinuous (DISCONT) permafrost. Five and twelve lakes were located within the zones of continuous and discontinuous permafrost, respectively (see Fig. 1). Significant differences (based on Mann Whitney U tests) were found in the distributions of all variables shown, with the exception of DOC.

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TABLE 3

A list of algal genera and their associated codes for taxa found in at least one study lake at a relative biovolume of more than 1%.

Genus (species)	Code	Group	# occurrences	Maximum biovolume (%)	Mean biovolume (%)
Anabaena	sp3	cyanophyte	29	33.0	7.2
Aphanizomenon	sp5	cyanophyte	10	86.7	5.4
Aphanothece	sp7	cyanophyte	28	33.8	3.9
Chroococcus	sp20	cyanophyte	29	17.1	3.2
Coelosphaerium	sp36	cyanophyte	2	19.7	0.7
Cyanophyte, unidentified	sp13	cyanophyte	14	1.6	0.2
Gomphosphaeria	sp69	cyanophyte	16	4.0	0.5
Microcystis	sp87	cyanophyte	14	3.1	0.3
Nostoc	sp96	cyanophyte	2	1.3	0.1
Oscillatoria (limnetica)	sp102	cyanophyte	10	28.1	1.3
Planktolyngbya	sp113	cyanophyte	19	22.2	3.0
Planktothrix	sp115	cyanophyte	9	34.8	2.6
Pseudanabaena	sp118	cyanophyte	22	7.4	0.6
Scytonema	spSCY	cyanophyte	1	2.5	0.1
Snowella	sp142	cyanophyte	12	2.7	0.2
Woronichinia	spWOR	cyanophyte	15	8.6	0.5
Ceratium	sp16	dinoflagellate	9	10.1	0.9
Gymnodinium	sp71	dinoflagellate	26	6.0	1.7
Peridinium	sp107	dinoflagellate	23	9.7	2.1
Chroomonas	sp21	cryptophyte	16	2.8	0.3
Cryptomonas	sp41	cryptophyte	26	21.4	3.5
Katablepharis	sp76	cryptophyte	28	2.1	0.7
Katablepharis (ovalis)	sp77	cryptophyte	1	2.0	0.1
Rhodomonas	sp125	cryptophyte	26	13.9	2.2
Chromulina	sp19	chrysophyte	29	25.5	4.8
Chrysidiastrum	sp22	chrysophyte	8	3.1	0.3
Chrysochromulina	sp23	chrysophyte	9	1.6	0.2
Chrysochromulina (parva)	sp25	chrysophyte	22	5.0	0.5
Chrysophyte, unidentified	sp28	chrysophyte	28	9.1	2.6
Dinobryon	sp50	chrysophyte	28	9.7	1.6
Ellipsoideon	sp52	chrysophyte	11	3.2	0.5
Epipyxis	sp53	chrysophyte	16	1.7	0.2
Isthmochloron (Xantho)	sp75	chrysophyte	5	3.3	0.2
Mallomonas	sp82	chrysophyte	20	4.7	0.8
Rhizochrysis	sp123	chrysophyte	3	1.9	0.1
Spiniferomonas	spSPI	chrysophyte	4	1.2	0.1
Uroglena	sp152	chrysophyte	8	4.0	0.3
Arthrodesmus	sp8	chlorophyte	4	1.1	0.1
Botryococcus	sp14	chlorophyte	24	5.4	0.8
Carteria	sp15	chlorophyte	3	1.1	0.1
Chlamydomonas	sp17	chlorophyte	26	2.2	0.5

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TABLE 3

Continued.

Genus (species)	Code	Group	# occurrences	Maximum biovolume (%)	Mean biovolume (%)
Chlorophyte, unidentified	sp70	chlorophyte	19	1.7	0.2
Chodatella	sp18	chlorophyte	13	1.0	0.2
Coelastrum	sp34	chlorophyte	21	6.8	0.7
Cosmarium	sp38	chlorophyte	25	6.6	1.3
Crucigenia	sp39	chlorophyte	16	8.0	0.9
Gloeotila	sp66	chlorophyte	15	1.8	0.2
Golenkinia	sp68	chlorophyte	6	1.9	0.1
Mougeotia	sp90	chlorophyte	7	2.2	0.2
Oedogonium	sp98	chlorophyte	16	19.4	1.9
Oocystis	sp99	chlorophyte	29	21.7	4.5
Pediastrum	sp105	chlorophyte	24	9.3	1.1
Planctonema	sp112	chlorophyte	9	3.0	0.2
Planktosphaeria	sp114	chlorophyte	3	2.3	0.1
Quadrigula	sp119	chlorophyte	23	1.1	0.1
Scenedesmus	sp130	chlorophyte	27	10.3	2.4
Sphaerellopsis	sp133	chlorophyte	6	1.1	0.1
Sphaerocystis	sp134	chlorophyte	29	6.6	0.8
Spirogyra	spSPI	chlorophyte	1	45.0	1.6
Spondylosium	sp136	chlorophyte	15	6.6	0.4
Staurastrum	sp137	chlorophyte	22	3.7	0.6
Tetraëdron	sp147	chlorophyte	27	4.0	0.6
Tetrastrum	sp148	chlorophyte	18	2.0	0.4
Zygnema	spZYG	chlorophyte	1	12.3	0.4
Achnanthes	sp1	diatom	16	1.3	0.1
Asterionella	sp9	diatom	17	55.1	2.8
Aulacoseira	sp83	diatom	12	19.9	1.8
Cyclotella	sp43	diatom	29	54.7	5.9
Cymbella	sp44	diatom	19	2.8	0.5
Diatoma	sp48	diatom	7	17.3	0.7
Eunotia	sp60	diatom	4	2.4	0.1
Fragilaria	sp61	diatom	23	7.3	1.4
Navicula	sp91	diatom	26	6.3	1.5
Neidium	sp92	diatom	2	1.4	0.1
Nitzschia	sp95	diatom	26	4.5	0.6
Pinnularia	sp111	diatom	7	2.6	0.2
Rhizosolenia	spRHI	diatom	5	2.4	0.2
Rhopalodia	sp126	diatom	4	2.9	0.1
Stephanodiscus	sp140	diatom	10	51.6	2.7
Surirella	sp141	diatom	11	2.4	0.2
Synedra	sp144	diatom	29	14.5	2.8
Tabellaria	sp146	diatom	23	15.9	2.7

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Sam Lake (12) in 2010 (sampling depth = 1.7 m), but were not present in 2011 at the time of sampling, suggesting the existence of a bloom in 2010.

Despite inter-annual variability in phytoplankton composition, RDA suggested that phytoplankton composition was more similar within lakes (across years), than it was among lakes (Fig. 7, left panel). As identified using a forward selection procedure in the RDA, six variables (TP, Col, Dist. to sea, Z, SiO_3, and Mg) explained significant, independent sources of variation in the phytoplankton data. Constrained to the forward-selected variables,

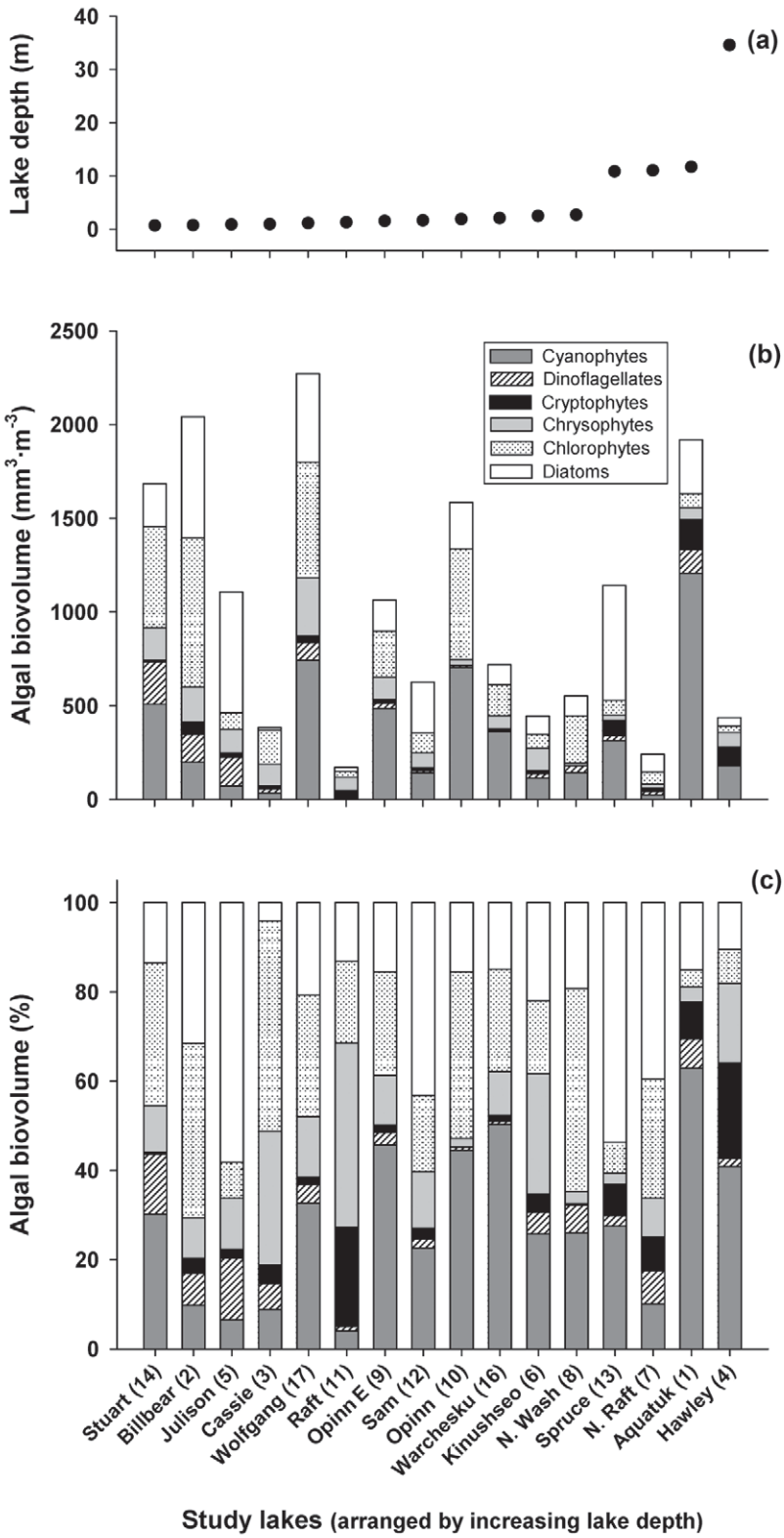


FIGURE 6. For the 16 lakes with phytoplankton data, plots showing (a) water depth at the sampling location; (b) the absolute biovolume of major algal groups; and (c) the relative biovolume of major algal groups.

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the first (λ = 0.18) and second (λ = 0.08) RDA axis explained 26.2% of the cumulative variation in the species data. Species-environmental correlations of the first two axes were high (0.94 and 0.92, respectively), suggesting that the forward-selected environmental variables explained major directions of variation in the species data.

RDA Axis 1 of the phytoplankton-environment relationship captured a gradient of sampling depth, SiO_3, and Mg. The deeper, more alkaline lakes [e.g. Aquatuk (1), Hawley (4), North Raft (7), and Spruce (13) Lakes] were clustered to the right side of the ordination biplot (Fig. 7, left panel). The shallow coastal and inland lakes were clustered to the left side of the ordination biplot, with generally higher relative abundances of chlorophytes and non-filamentous cyanophytes (Fig. 7, right panel). The shallow lakes were effectively separated into inland and coastal groups along the second RDA axis, which captured a nutrient gradient. Inland shallow lakes, with lower TP concentrations, showed higher relative biovolumes of the diatom *Cyclotella*, and several chrysophytes (e.g. *Chromulina, Mallomonas*).

ZOOPLANKTON

Over the three study years, 30 species of crustacean zooplankton were collected from the 17 lakes, with 15 species reaching relative abundances of >1% in at least one lake-year (Table 4). The most common species were *Bosmina freyi*, *Bosmina liederi*, *Chydorus sphaericus*, *Daphnia mendotae, Diacyclops bicuspidatus thomasi*, *Epischura lacustris*, *Eubosmina* spp., *Leptodiaptomus minutus*, and *Skistodiaptomus oregonensis*, all of which occurred in more than 50% of the lakes. Within individual lakes, the species richness per collection ranged from 6 to 12.

RDA with forward selection identified five environmental variables (Dist. to sea, Z, SO_4, TP, and Col) that explained independent and significant portions of the variance in the zooplankton abundance data. Constrained to these variables, the first (λ = 0.26) and second (λ = 0.11) RDA axes explained 37.7% of the cumulative variation in the species data (Fig. 8). The species-environment correlations were somewhat stronger along the first (0.92) than the second (0.74) RDA axis, with the first axis negatively correlated to both the distance to salt water (–0.75) and sampling depth (–0.67) (Fig. 8, left panel). The second axis showed generally weaker correlations overall, and was related to the distance to salt water (–0.39) and TP (0.35). Sulfate, which in our study was significantly correlated to alkalinity and other measures of ionic strength (e.g. specific conductance), was weakly associated with the second RDA axis (0.25). Furthermore, despite some evidence of interannual variation in zooplankton assemblages, lakes showed similar positions in ordination space regardless of the year of collection (Fig. 8, left panel).

RDA axis 1 of the zooplankton-environment relationship was associated with higher relative abundances of *Bosmina* and *Eubosmina* spp. in shallow lakes with higher Cl concentrations, and higher abundances of *Daphnia* spp. and *Diacyclops bicuspidatus thomasi* in deeper, clear lakes of lower ionic strength (Fig. 8, right panel). *Bosmina freyi* comprised more than 50% of the relative abundances of the three lakes with the highest Cl concentrations [Billbear (2), Julison (5), and Stuart (14) Lakes]. The second axis separated some groups at the species level. As mentioned, for example, *Bosmina freyi* was more common in lakes with higher Cl and TP concentrations, with *Bosmina liederi* more abundant in somewhat less productive lakes. Similarly, *Holopedium gibberum* and *Daphnia catawba* were found

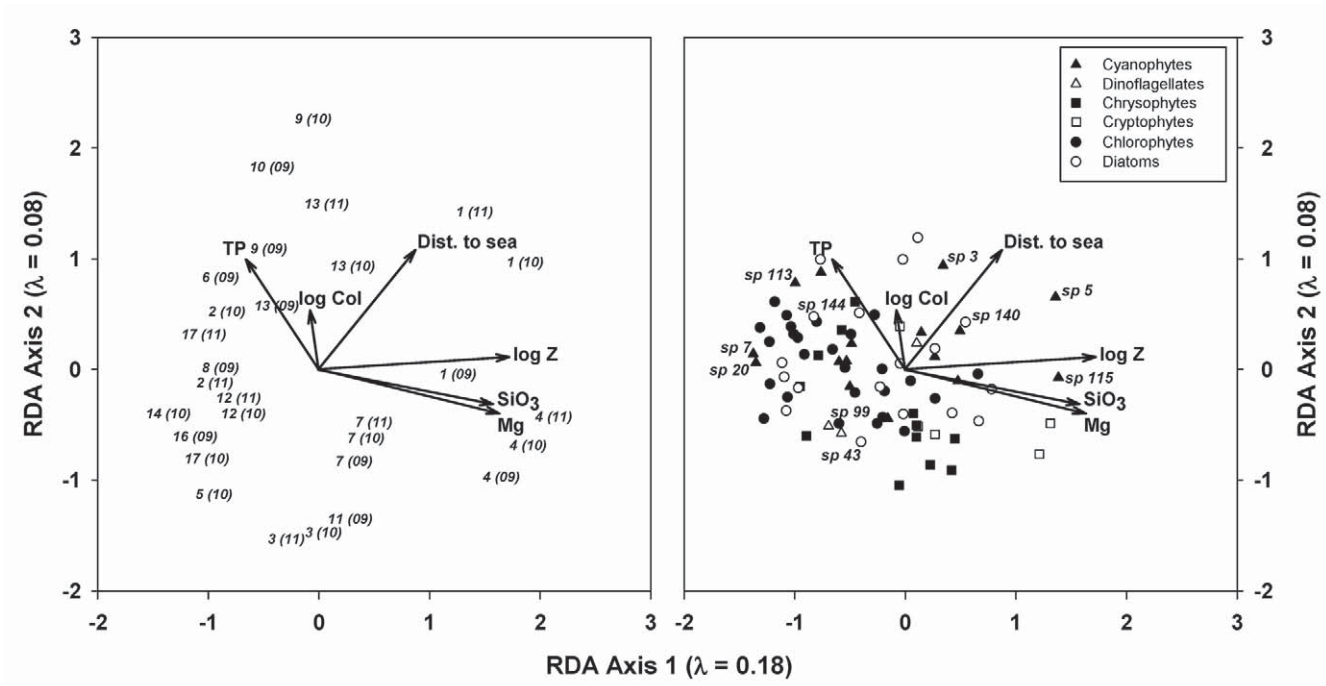


FIGURE 7. Biplots generated from redundancy analysis of relative biovolume of phytoplankton and six forward-selected environmental variables from 16 sites near the Sutton River in northern Ontario, Canada. The left and right panels show the relationships of lake-years (shown as lake code with year in parentheses) and genera (coded by major algal group), to the environmental variables, respectively. Taxa codes (found in Table 3) are shown for dominant genera, as described in the manuscript. For plotting purposes, environmental vectors and species scores have been multiplied by a factor of 2.

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TABLE 4

A list of zooplankton species and their associated codes for taxa found in at least one study lake at a relative abundance of more than 1%.

Species	Code	# occurrences	Maximum abundance (%)	Mean abundance (%)
Acanthocyclops vernalis complex	Aca ver	2	2.4	0.1
Bosmina freyi	Bos fre	26	51.9	7.0
Bosmina liederi	Bos lie	28	68.5	6.1
Chydorus sphaericus	Chy sph	23	10.2	1.4
Daphnia catawba	Dap cat	2	4.7	0.2
Daphnia longiremis	Dap lon	11	12.5	1.1
Daphnia mendotae	Dap men	21	65.5	5.9
Daphnia tenebrosa	Dap ten	2	6.1	0.4
Diacyclops bicuspidatus thomasi	Dia bic	26	11.3	2.5
Diaphanosoma birgei	Dia bir	7	1.5	0.1
Epischura lacustris	Epi lac	25	5.5	1.5
Eubosmina spp.	Eubos	15	4.9	0.8
Holopedium gibberum	Hol gib	7	4.0	0.3
Leptodiaptomus minutus	Lep min	24	26.0	3.3
Skistodiaptomus oregonensis	Ski ore	16	3.1	0.4

at higher relative abundances than other *Daphnia* spp. in the less productive lakes, of generally lower ionic strength (Fig. 8, right panel).

Discussion

As observed in other Arctic and subarctic regions (Rühland and Smol, 1998; Rautio et al., 2011), summer chemistry of lakes in the Sutton River region of the HBL is strongly influenced by catchment bedrock and soil composition. Primarily calcareous in nature, the central HBL is underlain by Paleozoic and Mesozoic limestone and dolomite (Glaser et al., 2004), and covered with a mantle of glacial and marine soils, leading to the relatively hard water nature of these lakes. The presence or absence of Precambrian bedrock in some catchments (i.e. the Sutton Ridges) appears to have little influence on surface water chemistry, likely because of its sporadic appearance within catchments, and its high resistance to weathering relative to overlying, calcareous soils. The relatively high alkalinity and conductivity of the shallow lakes may also be influenced, in part, by evaporative enrichment at the time of sampling in mid-summer. White et al. (2014) observed distinct, seasonal changes in water chemistry in ponds near Churchill, Ontario, with the concentrations of major ions peaking in the summer months, and stabilizing or declining following replenishment by precipitation events in late summer.

At the time of sampling, we observed isothermal, well-oxygenated conditions in many of the deeper (but see Hawley Lake in Fig. 2) and all of the shallow study lakes. This is in contrast to shallow, subarctic ponds in the northeastern HBL that showed strong thermal stratification and hypoxic conditions within their hypolimnia in July of 2006 and/or 2007 (Laurion et al., 2010). Differences in DOC concentrations, and thus light attenuation, across the regions cannot explain this difference, as values were within a similar range. However, the subarctic ponds studied by Laurion et al. (2010) were of a much smaller size (surface areas between 1 and 7 ha) than our study lakes (surface areas between ~30 and 5800 ha), suggesting that the observed differences in thermal regimes across regions were the result of much larger fetches and stronger mixing in lakes near the Sutton River of northern Ontario.

PCA revealed that the shallow coastal lakes are distinct in terms of water chemistry. Positioned within 25 km of the coast and in the zone of continuous permafrost (Fig. 1), these lakes are potentially relatively young in age due to their recent emergence from the sea because of high rates of isostatic rebound. With elevated Cl and Na concentrations, and molar Na to Cl ratios (0.76 to 1.04) similar to that of seawater (0.86), the coastal lakes appear to be strongly influenced by sea salt in precipitation. Interestingly, Sam (12) and Wolfgang (17) Lakes, also located within the zone of continuous permafrost, but at distances approaching 50 km from the coast (Fig. 1), have similar ratios of Na to Cl (1.06 and 1.10, respectively), albeit at lower absolute concentrations. This suggests that the influence of the coast may extend further inland in the HBL than reported for other subarctic regions (Kling et al., 1992; Eilers et al., 1993; Pienitz et al., 1997).

In our data set, the presence of continuous permafrost clearly separated lakes based on summer water chemistry (Fig. 5), possibly through its influence on the hydrological connectivity between lakes and their local catchments (Wolfe et al., 2011). While there was no significant difference in DOC concentrations of lakes within continuous and discontinuous permafrost, lakes in the former region were significantly clearer (i.e. lower color) and lower in SiO_3, suggesting a reduced surface water–groundwater

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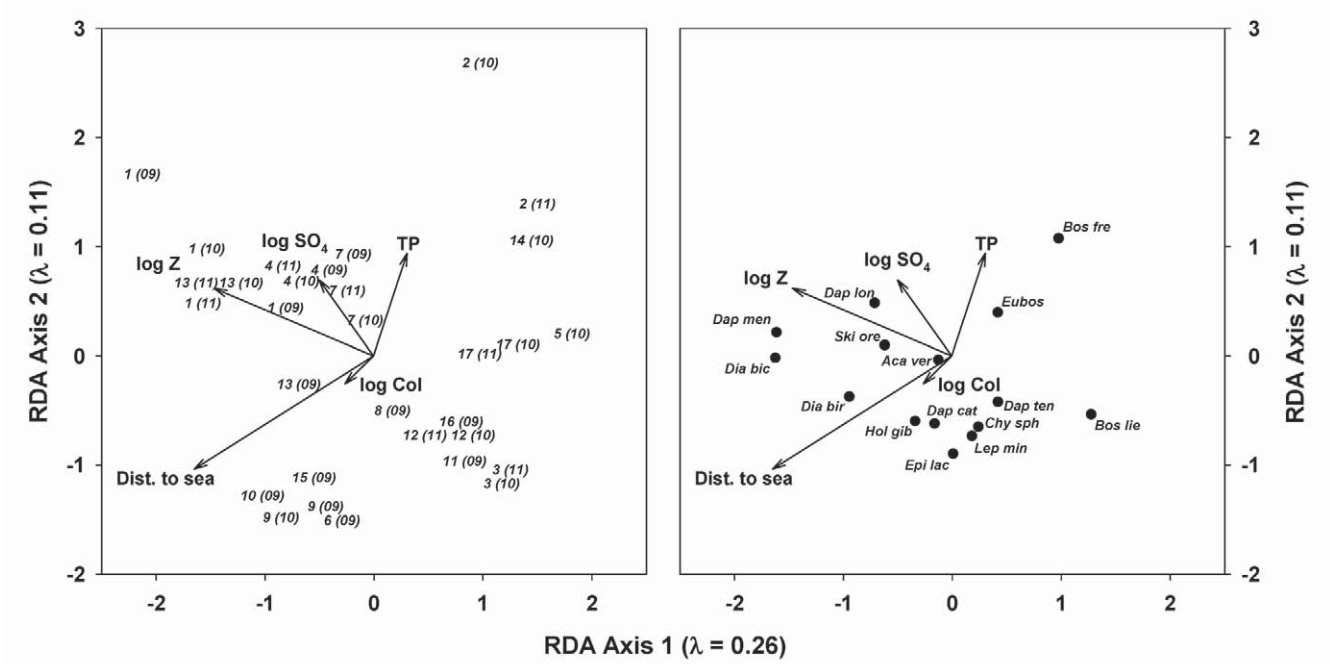


FIGURE 8. Biplots generated from redundancy analysis of relative abundance of zooplankton species and 5 forward-selected environmental variables from 17 sites near the Sutton River in northern Ontario, Canada. The left and right panels show the relationships of lake-years (shown as lake code with year in parentheses) and taxa (codes presented in Table 4), to the environmental variables, respectively. For plotting purposes, the environmental vectors and species scores have been multiplied by a factor of 2.

interaction (Eilers et al., 1993) (Fig. 5). However, in contrast to findings in other subarctic regions (e.g., Fallu et al., 2002; Rühland et al., 2003) where ionic concentration was also related to the degree of permafrost development (and related factors such as the degree of soil development and vegetation), we found no significant difference in alkalinity or conductivity among lakes within the continuous and discontinuous permafrost zones (not shown). It is possible that the reduced ionic inputs from the surrounding catchment in the shallow coastal lakes were offset by sea salt inputs in precipitation, resulting in relatively higher conductivity and ion concentrations.

Lakes within continuous permafrost also had significantly higher nutrient concentrations at the time of sampling (Fig. 5). This is in contrast to observations from the western HBL, where declines in concentrations of suspended solids and nutrients (e.g., total Kjeldahl nitrogen) were reported in lakes as hydrological connectivity was lost during periods of lower water levels and low flow (White et al., 2014). As suggested by Welch and Legault (1986) for high solute lakes near the northwestern shore of Hudson Bay, residual sea salt in the local catchments of these relatively young lakes may have resulted in both higher salinities and increased phosphorus inputs. However, in the absence of detailed catchment data for our study lakes, the specific mechanisms causing higher nutrient levels in the shallow coastal lakes remain unclear. Furthermore, differences in nutrient concentrations among lakes could not be explained by differences in lake depth, as shallow and deeper inland lakes did not differ significantly in TP and TIN concentrations.

Phytoplankton composition in subarctic ponds and lakes may be influenced by several factors, including a short growing season, low temperatures, freezing, and desiccation during the ice-on season, high PAR and UV radiation in summer, low nutrient inputs, and high zooplankton grazing pressure in shallow, fishless ponds (Rautio et al., 2011). As these factors may manifest themselves differently in deeper lakes, it is not surprising that we observed differences in both total biomass and composition in deeper versus shallower lakes. In the well-mixed shallow ponds, where Secchi depths commonly exceeded sampling depths, non-filamentous cyanophytes and chlorophytes were common, and benthic algal mats were observed in some cases. In contrast, the euphotic zone of deeper lakes was more commonly dominated by small centric and pennate, planktonic diatom taxa, or filamentous cyanophytes.

Small diatoms and buoyant cyanobacteria have a distinct competitive advantage during periods of relative stability in lakes, as they experience reduced sinking velocities (Paerl, 1988; Winder et al., 2008) and may be able exploit subsurface habitats in the metalimnia of stratified lakes where nutrients are elevated (Fahnenstiel and Glime, 1983; Rühland et al., 2010). In our study, the deeper inland lakes showed evidence of weak to moderate stratification and, in at least one year (2001; described in Gunn and Snucins, 2010), strong thermal stratification has been observed in August in Hawley Lake. Furthermore, because subarctic lakes and ponds may stratify for very short periods of time (hours to days; Rautio et al., 2011), and algae may exploit these brief periods of optimal growth, our sampling visits may not adequately capture the physical conditions present in the study lakes. For example, the presence of algal blooms at the time of sampling in some lakes [e.g., Aquatuk (1) and Spruce (13) Lakes in 2010, a particularly hot summer] may have been a response to a prolonged period of higher stability in the days to weeks prior to sampling (e.g., Soranno, 1997).

Although more commonly associated with deeper lakes, the presence of *Cyclotella* taxa and planktonic chrysophytes

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(e.g. *Mallomonas*) in the shallow inland lakes is consistent with findings from recent paleoecological studies from the same lakes (Rühland et al., 2014) and may be associated with climate-driven changes in lake water properties (Sorvari et al., 2002; Rühland et al., 2008). Recent evidence from our study lakes suggests that regional warming since the mid-1990s has resulted in increased diatom diversity, including increases in the relative abundances of planktonic diatoms and cladocerans (i.e. *Bosmina* spp.), although this trend was more modest in the shallow study lakes. Rühland et al. (2014) argue that a longer ice-free season may result in an enhanced period of radiative heating, and changes in light habitat (and associated physical changes) that favor planktonic taxa.

In the shallow coastal lakes on continuous permafrost, however, higher nutrient and lower silica concentrations (Fig. 5) may explain why chlorophytes and non-filamentous cyanophytes dominate over siliceous groups (i.e. diatoms and some chrysophytes). Cyanobacteria, in particular, may be favored in these very clear lakes because of their ability to tolerate higher UV exposure (Laurion and Vincent, 1998); the presence of colorful benthic mats in these shallow lakes also suggest that phytoplankton, in general, may be a relatively minor component of total autotrophic productivity.

The crustacean zooplankton species that were common in the HBL lakes (taxa occurring in more than one lake) have been reported in synoptic lake surveys from central Ontario, several hundred kilometers farther south (Keller and Pitblado, 1984; Keller and Conlon, 1994). *Daphnia tenebrosa* is an exception, although it has been found in a few Ontario lakes within the Arctic watershed (reported as *D. middendorfiana*; Keller and Pitblado, 1989). It is uncertain why this Arctic-subarctic species was restricted to only two of the inland shallow lakes [Raft (11) and Warchesku (16) Lakes] as these were not distinct in terms of water chemistry or general morphometry, and it occurs frequently in lakes and ponds of Wapusk National Park on the western shore of Hudson Bay in Manitoba (Symons et al., 2014). *Tropocyclops extensus*, usually quite common in the plankton of Ontario lakes (Keller and Pitblado, 1989; Keller and Conlon, 1994), was conspicuously absent from our HBL collections for reasons that remain unclear.

Crustacean zooplankton communities in the HBL lakes were generally similar to communities found in Ontario lakes within the Precambrian Shield. The three taxa showing the highest average abundance in the HBL lakes (*Bosmina* spp., *Daphnia mendotae*, and *Leptodiaptomus minutus*) are also common and numerically important in other Ontario lakes. For example, *D. mendotae* was ranked the first to third most important contributor to crustacean zooplankton biomass in lakes across the Precambrian Shield of Ontario (Keller et al., 1990).

The species richness per collection of our HBL lakes (6 to 12) was also comparable to richness reported in other, more extensive synoptic lake surveys from Ontario (e.g. 8.5 to 10.5 for averages of non-acidic lakes in northeastern Ontario; Keller and Pitblado, 1984). Our survey only included 17 lakes, and thus we cannot definitively assume that we have captured representatives of all the crustacean zooplankton in the HBL lakes. However, our list of 30 recorded taxa is only slightly less than total species lists for much more extensive regional surveys in the province (northeastern Ontario, 161 lakes, 35 species; northwestern Ontario, 137 lakes, 36 species; Keller and Pitblado, 1989), suggesting that our survey is an important initial step to characterizing the diversity of crustacean plankton communities in HBL lakes.

While the proximity to salt water, geology, and degree of permafrost development make the HBL unique in Ontario, many of the physico-chemical factors affecting zooplankton community structure appear to be similar to those in Precambrian Shield lakes. In particular, the observed importance of sampling depth, TP, and color in explaining zooplankton community composition in HBL lakes agrees with the results of various other Ontario surveys that have identified factors related to depth, transparency, and nutrient status as important environmental correlates with zooplankton communities (e.g. Keller and Conlon, 1994; Keller et al., 2002; Yan et al., 2008).

Conclusions

Baseline data are required to effectively monitor environmental change in aquatic ecosystems. However, even basic limnological and biological data are unavailable for most lakes and ponds in the remote HBL. We have provided an exploratory assessment of regional water chemistry and plankton for a suite of lakes near the Sutton River region of the north-central HBL. We report that lake water quality, as observed in other subarctic regions, is strongly controlled by bedrock geology and soil composition, but perhaps more so by the proximity of the study lakes to salt water. We also found significant differences in water chemistry between lakes of the continuous and discontinuous permafrost zones, likely related to the degree of hydrological connectivity with their surrounding catchments. This is particularly important given that the HBL houses the southernmost boundary of continuous permafrost in North America, a boundary that is expected to shift northwards with warming. Gagnon and Gough (2005) predicted that, in the short to medium term, permafrost will diminish in this region, thereby thickening the active layer that experiences seasonal thawing and freezing, and possibly increasing nutrient inputs from catchments to lakes (Rautio et al., 2011). Moreover, a longer ice-free season may increase summer evaporation (Smol and Cumming, 2000; Wolfe et al., 2011) and, when combined with reduced overland flow during the spring melt period (Rouse et al., 1997), may reduce hydrological storage in aquatic ecosystems. While it is difficult to predict lake- or pond-specific hydrological responses to warming (Wolfe et al., 2011), the variation in limnological conditions we report among lakes suggests that HBL lakes have the potential to undergo significant changes in water chemistry with warming.

Warmer temperatures in recent decades and associated changes to water column properties are also affecting biological communities across trophic levels within HBL lakes, as supported by recent paleoecological studies from the region (e.g. Rühland et al., 2014). Climate models for the HBL project further significant increases in air temperature over the next several decades (Gagnon and Gough, 2005), suggesting that physical changes in these lakes may accelerate and become more pronounced over time. This may lead to increased periods of stratification in all lakes, with strong and sustained thermal stratification likely becoming more important in deeper lakes (e.g. Gunn and Snucins, 2010). In turn, this may result in changes to algal and zooplankton composition, such as favoring the development of cyanobacterial blooms, as were observed in some lakes [e.g. Aquatuk Lake (1)] in 2010 when air temperatures were warm at the time of sampling. Given the potential for further biological change with warming, we recommend that baseline data on other communities (e.g., cyanobacterial mats, picoplankton, and ben-

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thic macroinvertebrates) be collected in this region in the near future, as these communities play important roles in the transfer and fate of nutrients, energy, and organic material through the food web (Rautio et al., 2011).

The baseline data presented here, which include water chemistry and plankton data collected over three years, represent a synopsis of what is currently known for remote lakes near the Sutton River in the HBL. These data provide a foundation on which future surveys may be compared in this climatically sensitive region.

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APPENDIX

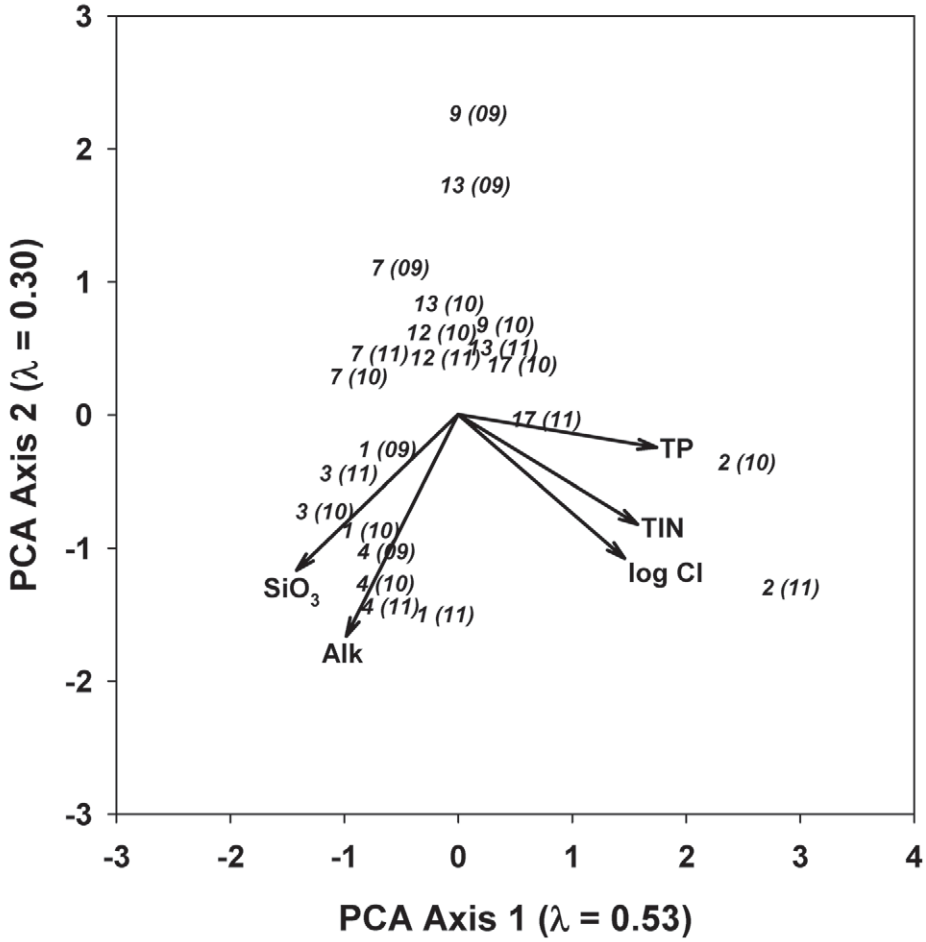


FIGURE A1. PCA of water chemistry from the nine study lakes for which more than one year of data exists. Lakes are shown by their site numbers (see Table 1), and by the year of sampling (in parentheses). The biplot shows that inter-annual variability in water chemistry within lakes is less than the spatial variability among lakes, suggesting that chemistry could be averaged across years to obtain an average chemical condition for each lake.

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