Effects of loss of perennial lake ice on mixing and phytoplankton dynamics: insights from High Arctic Canada

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ABSTRACT. Perennially ice-covered lakes are well known from Antarctica and also occur in the extreme High Arctic. Climate change has many implications for these lakes, including the thinning and disappearance of their perennial ice cover. The goal of this study was to consider the effects of transition to seasonal ice cover by way of limnological observations on a series of meromictic lakes along the northern coastline of Ellesmere Island, Nunavut, Canada. Conductivity–temperature profiles during a rare period of ice-free conditions (August 2008) in these lakes suggested effects of wind-induced mixing of their surface freshwater layers and the onset of entrainment of water at the halocline. Sampling of the mixed layer of one of these meromictic lakes in May and August 2008 revealed a pronounced vertical structure in phytoplankton pigments and species composition, with dominance by cyanobacteria, green algae, chrysophytes, cryptophytes and dinoflagellates, and a conspicuous absence of diatoms. The loss of ice cover resulted in an 80-fold increase in water column irradiance and apparent mixing of the upper water column during a period of higher wind speeds. Zeaxanthin, a pigment found in cyanobacteria, was entirely restricted to the <3 μm cell fraction at all depths and increased by a factor of 2–17, with the greatest increases in the upper halocline region subject to mixing. Consistent with the pigment data, picocyanobacterial populations increased by a factor of 3, with the highest concentration (1.65×10^8 cells L^{-1}) in the upper halocline. Chlorophyll *a* concentrations and the relative importance of phytoplankton groups differed among the four lakes during the open-water period, implying lake-specific differences in phytoplankton community structure under ice-free conditions.

INTRODUCTION

Ice-dominated lakes are a common feature of glacial environments in alpine and polar regions, and three classes of such lakes can be distinguished on the basis of their ice characteristics. Firstly, lakes with perennial ice cover are found in several parts of Antarctica and in the coldest parts of the Arctic. In these lakes, the ice persists throughout the year and any open water each year is limited to a narrow moat that may form around the edge of the lake in late summer. The best-known examples of this lake type are the perennially ice-capped lakes of the McMurdo Dry Valleys, Antarctica, that are typically covered by 3–5 m of ice (Green and Lyons, 2009, and references therein), with an extreme ice thickness of 19 m recorded in Lake Vida (Doran and others, 2003). Ward Hunt Lake, located at 83° N at the north of Ellesmere Island in the Arctic, was reported to have an ice cover of 4.1 m in 2003 (Antoniades and others, 2007), and an ice thickness of 5.5 m was measured on a lake in central Ellesmere Island at 830 m a.s.l. in the 1980s (Blake, 1989). Perennial ice cover has also been reported in northwest Greenland where Anguissaq Lake (77° N) has up to 3.4 m of ice (Hobbie, 1984).

The second class of lakes comprises inland waters that intermittently retain their ice cover for >1 year. The best-known examples are High Arctic Char Lake and Meretta Lake that typically lose their ice for 1–2 months each year, but occasionally retain their ice for the entire year (e.g. summer 1972; Schindler and others, 1974a,b). Similarly, Colour Lake, located further north on Axel Heiberg Island, was estimated to retain its ice cover about once every 6 years (Doran and others, 1996). Current warming trends and paleolimnological analyses suggest that multi-year ice cover is becoming increasingly rare in such lakes (e.g. Michelutti and others, 2003). Some Antarctic lakes (e.g. in the Vestfold Hills and Bunger Hills) may also intermittently retain their ice covers (Vincent and others, 2008a).

Most lakes in the Arctic have several months of ice-free conditions per year. In contrast to temperate lakes, these waters are covered by 1–2 m of ice for >8 months of the year. Examples of this third class of lakes include Toolik Lake, lying at 68° N in Alaska, which is usually ice-free from July through September and has an ice-cover thickness that may reach 1.4 m (http://ecosystems.mbl.edu/ARC). Numerous lakes located between the ice-cap margin and the coast in West Greenland (66–67° N) are ice-covered for 9 months a^{-1} (Anderson and others, 2001). Seasonal ice cover also occurs in the warmest parts of Antarctica, including maritime Antarctica and certain coastal areas of the continent (Vincent and others 2008a). For example, Ace Lake and other meromictic (i.e. permanently stratified) lakes in the Vestfold Hills of East Antarctica are known to often lose their ice in the summer (Gibson, 1999).

Lake ice phenology is highly responsive to climatic variations and has been identified as one of the strongest limnological indicators of climate change (Vincent and others, 2008a). Recent warming in the Northern Hemisphere has resulted in shorter lake ice cover duration, with earlier break-up dates and, to a lesser extent, later freezing (Magnuson and others, 2000; Duguay and others, 2006). Thinning of the ice cover of an Antarctic lake has been linked to the extent of air temperatures above freezing (Wharton and others, 1992), while thinning and complete

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Fig. 1. (a) Location map of the study area on northern Ellesmere Island with (b) a close-up of the study area. (c) Map of Lake A and Lake B catchments.

melt of the ice cover of previously perennially ice-capped High Arctic and maritime Antarctic lakes have been attributed to warming climates (Quayle and others, 2002; Van Hove and others, 2006; Mueller and others, 2009).

Our objective in this study was to evaluate the implications for ecosystem structure and function of the increasingly observed loss of perennial lake ice. Specifically, we examined a meromictic High Arctic lake, Lake A, that appears to be in transition from perennial ice to seasonally ice-free conditions. To understand the effects of a shift towards seasonal ice cover, we focused on the water column properties and phototrophic community structure in the section most affected by wind-induced mixing (0–12 m), where almost all interannual variability and most of the in situ production of chlorophyll *a* occurs (Antoniades and others, 2009). We assessed changes in biomass and community composition with high-performance liquid chromatography (HPLC) analysis of photosynthetic pigments and microscopic analysis of the phytoplankton community. We extended these measurements to three other meromictic lakes in the region to investigate whether general trends could be identified.

METHODS

Study area

Lake A (83°00′ N, 75°30′ W), Lake B (82°58′ N, 75°26′ W), Lake C1 (82°51′ N, 78°12′ W) and Lake C2 (82°50′ N, 78°05′ W) (unofficial names) are meromictic lakes located on the northwestern coast of Ellesmere Island, Nunavut, Canada (Fig. 1). They were formed after isostatic rebound caused the isolation of fiords from the Arctic Ocean several thousand years ago; lakes located further inland at a higher elevation became isolated and stratified earlier (Jeffries and others, 1984; Ludlam, 1996a,b). Lake A (4.9 km^2 in surface area) and Lake B (1 km^2) are located in the same valley, and Lake B's outlet flows into Lake A. The catchments of Lake A (37 km^2) and Lake B (5 km^2) contain no glaciers. Lake C1 (1.1 km^2 in surface area) and Lake C2 (1.8 km^2) are located in Taconite Inlet ~40 km to the west. The catchment of Lake C1 is small (3.3 km^2) and contains no glaciers, while that of Lake C2 is glacierized and larger (23.5 km^2).

Climate

Air temperature, incident solar irradiance in the photosynthetically active radiation (PAR) waveband (400–700 nm), and wind speed and direction at Lake A were recorded at 3 m above the ground with a tripod design automatic weather station (Campbell Scientific Inc.) that has been in operation since August 2003 as part of the SILA (in Inuktitut, 'climate and all things around us') monitoring network of Centre d'Études Nordiques (CEN). This was located at 83°0.14′ N, 75°23.38′ W, 10 m from Lake A on the eastern stream delta (Fig. 1c). Measurements were taken every minute by a Campbell Scientific CR10X data logger and output as hourly averages, or hourly maxima (maximum wind speed).

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Table 1. Ice and snow thicknesses for Lake A from 1969 to 2009. – : information not available

Date of profiling	Ice thickness m	Snow depth cm	Source
1 May 1969	2.0	–	Hattersley-Smith and others (1970)
10 May 1982	2.0	–	Jeffries and others (1984)
14 May 1983	2.0	–	Jeffries and Krouse (1985)
5 June 1999	2.0	52	Belzile and others (2001)
1 August 2001	1.0	0	Van Hove and others (2006)
1 August 2003	thin	0	Mueller and others (2009)
4 August 2004	1.0	0	Mueller and others (2009)
26 May 2005	1.5	60	Antoniades and others (2009)
30 May 2006	1.3	50	Antoniades and others (2009)
13 July 2007	1.0	0	Mueller and others (2009)
30 May 2008	1.2	50	This study
20 August 2008	0	0	This study
6 July 2009	1.6	4	This study

Field sampling

We visited Lake A on 30 May and 20 August 2008, and Lakes B, C1 and C2 on 24 August 2008. There was an ice cover of 1.2 m and a snow cover of 50 cm on Lake A at the time of sampling in May while all sampled lakes were ice-free in August. Additional profiling and hydrological measurements at Lake A were done on 13 July 2007 (1 m of ice) and 6 July 2009 (1.6 m of ice and 4 cm of snow). Water column profiles were taken with an XR-420 or XR-620 CTD (conductivity–temperature–depth profiler; RBR Ltd, Ottawa, Ont., Canada) through a drilled hole or from a Zodiac inflatable boat. Water samples for nutrient, pigment and microscopic analyses were taken using a 6.2 L Kemmerer sampler, transferred to acid-washed, opaque 20 L plastic containers and stored in the dark at 4°C until processing. Sampling depths were selected in relation to the salinity profile to target the surface freshwater layer in all lakes (2 m), and additional samples were taken through the freshwater layer, upper halocline and deeper in the water column when logistical conditions were favourable. Lake A inflow and outflow conductivity data were taken with a portable pH–conductivity–temperature probe (Oakton Instruments, Vernon Hills, IL, USA), with the exception of the outflow measurements on 20 August 2008 that were taken with an XR-620 CTD. Measured conductivity normalized at 25°C, C_{25}, was converted to salinity, S, via the algorithm $S = 0.65 \times 10^{-3} C_{25}$ (µS cm^{-1}) (Pawlowicz, 2008). Flow velocities were measured with a Swoffer Instruments 2100 STDX flowmeter (Seattle, WA, USA). Water samples for nutrient (TN, TP, NO_3^-, NO_2^-, SRP) analyses were processed at the National Laboratory for Environmental Testing (NLET, Burlington, Ont., Canada).

Hydrological calculations

Annual discharge of Lake A was estimated by two methods. First, it was calculated assuming complete melting of the end-of-winter snowpack, roughly estimated as the lake snow depth of 0.5 m observed in May each year (Table 1) extrapolated to the whole catchment plus lake, and using a snow water equivalent of 0.21 (Belzile and others, 2001). To this were added the water equivalent precipitation averages for 1971–2000 during June (11.1 mm), July (27.8 mm) and August (21.2 mm) from Alert (the closest weather station of Environment Canada, located 193 km to the east of Lake A; http://www.weatheroffice.gc.ca). For this first-order estimate, surface evaporation was considered negligible. This gave an annual total of 165 mm, similar to the 154 mm average annual precipitation at Alert. Secondly, discharge was estimated from current data measured at the single outflow of Lake A in July 2007. Water residence times of the meltwater layer present during the melt period at Lake A (uppermost 2–3 m of water from the profiles of July 2007 and 2009) and of the entire freshwater layer during open-water conditions (0–10 m) were estimated by dividing the volume of the layer by annual discharge. Mean ice-cover thickness in July was 1.3 m (1.0 m in 2007 and 1.6 m in 2009) and the maximum depth at which the low-conductivity meltwater was detectable was 3 m.

Stability indices

Water column stability indices were calculated to examine the potential of mixing of the entire water column and of the surface layer of Lake A after ice-out. Calculations were made with the profile data of May 2008 and the wind conditions during August 2008. The Brünt–Väisälä frequency, N, was calculated following Caplanne and Laurion (2008), and the Wedderburn number, W, following Kalff (2003). Water density was calculated according to the sea-water equation from UNESCO (1981) since salinity was >0.4 ppt for the surface layer (0–10 m) and >1 ppt below 10 m.

Solar radiation

Solar irradiance (PAR) reaching the water column of Lake A was calculated from the hourly measurements at our weather station at Lake A. Daily totals were summed to calculate the cumulative incident PAR reaching Lake A up to the date of water-column samplings. Then PAR immediately under the ice in May 2008 was calculated from snow albedo and ice attenuation coefficients from Belzile and others (2001). PAR immediately under the water surface in August 2008 was calculated from a water albedo of 8.6% for a solar elevation of 33° at noon at Lake A (Kirk, 1994; Belzile and others, 2001). As another measure of light availability, we calculated mean water-column irradiance for the sampling days for the region 0–12 m (or under the ice to 12 m). This encompasses the section of the water column potentially affected by wind-induced mixing. We calculated mean water-column irradiance with the water extinction coefficient of Belzile and others (2001) and the equation used by Vincent (1983).

Photosynthetic pigment analyses

Water samples (0.35–1.05 L) for pigment analyses were filtered with 25 mm diameter GF/F glass-fibre filters (nominal pore size 0.7 µm) that were frozen immediately in the field in a dry shipper (–80°C) and subsequently stored in a –80°C freezer until analysis. For analysis of the picoplankton fraction, the samples (0.5–2.0 L) were pre-filtered through a 3.0 µm, 47 mm diameter Nuclepore filter prior to being filtered with the GF/F. Pigments were extracted from the frozen phytoplankton filters by sonication in 2.5 mL of 95% methanol, cleared by centrifugation, and filtered with PTFE syringe filters (pore size 0.2 µm) into HPLC vials. The extracts were then put under argon and kept at 4°C in the dark in the HPLC autosampler to prevent pigment degradation. Shortly following extraction, 100 µL of phytoplankton

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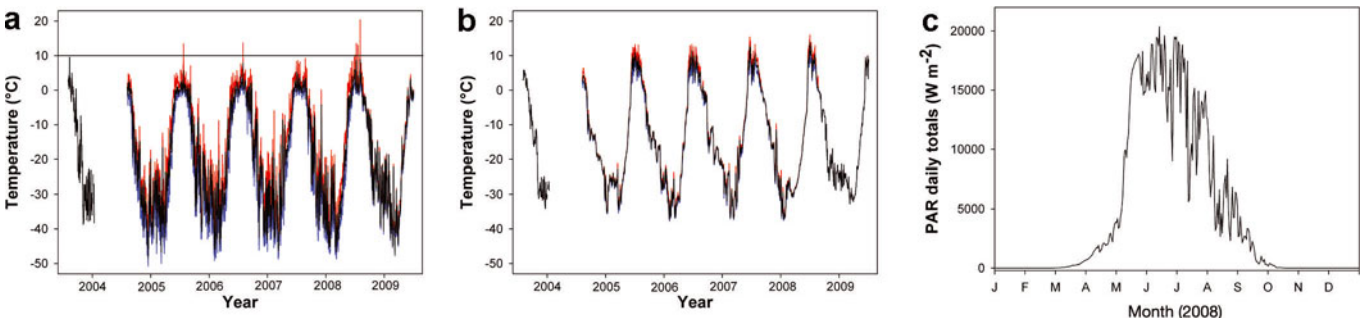

Fig. 2. Mean (black), maximum (red) and minimum (blue) (a) daily air temperatures and (b) daily ground (at 20 cm) temperatures from 2003 to 2009, and (c) the 2008 annual cycle of the daily totals in PAR at the Lake A weather station.

pigment extracts were injected into a Varian ProStar HPLC system equipped with a Symmetry C8 column. The solvent protocol followed that of Zapata and others (2000). Chlorophylls were detected by fluorescence (excitation 440 nm, emission 650 nm) and carotenoids by photodiode-array (PDA) spectroscopy (350–750 nm) set to a slit width of 2 nm. Absorbance chromatograms were obtained at 450 nm for carotenoids and 476 nm for bacteriochlorophylls. Standards for identification (based on PDA spectra and retention times) and quantification (using calibration coefficients) of pigments were obtained from Sigma Inc. (St Louis, MO, USA) (Chl *a*, Chl *b*, β,β-carotene) and DHI Water & Environment (Hørsholm, Denmark) (alloxanthin, Chl c_2, diadinoxanthin, fucoxanthin, lutein, violaxanthin, zeaxanthin) to calibrate our HPLC. Antheraxanthin and MgDVP were identified from a culture of *Micromonas* sp. (CCMP, West Boothbay Harbor, ME, USA); antheraxanthin was quantified using the extinction coefficient from the literature (Jeffrey and others, 1997), and MgDVP using the calibration coefficient of Chl c_2. No commercial standard or culture was available to confirm the identification of Chl c_1 or Chl c_3; these pigments were identified based on PDA spectra (when present in sufficient concentrations) (Jeffrey and others, 1997) and retention times on the fluorometer chromatogram (Zapata and others, 2000), and quantified using the calibration coefficient of Chl c_2. Chlorophyllide *a* was identified based on its retention time on the fluorometer chromatogram (Zapata and others, 2000). No commercial standards for the photosynthetic bacterial pigments bacteriochlorophyll-*e* and isorenieratene were available, and these were identified and quantified from published spectra and coefficients (Borrego and Garcia-Gil, 1994). Concentrations of unknown chlorophylls were calculated using the calibration coefficient of Chl *a*, and concentrations of unknown carotenoids using the calibration coefficient of β,β-carotene.

Microscopy counts and identifications

Protist samples were preserved with paraformaldehyde (0.1% final concentration) and glutaraldehyde (1% final concentration) in duplicate 50 mL polypropylene centrifuge tubes and stored at 4°C for up to 6 months in the dark until analysis; cellular features were well preserved and showed no evidence of degradation during storage. Protists were counted and identified using a combined system of fluorescence, Nomarski interference and Utermöhl sedimentation (FNU; Lovejoy and others, 1993). 60 mL samples (16 mL for Lake B) were concentrated in Utermöhl sedimentation chambers for 24 hours and stained with DAPI (0.1 $\mu g\,mL^{-1}$). Counts and identifications were made with a Zeiss Axiovert 100 inverted epifluorescence microscope under 400 and 1000× magnification (cells >2 µm in diameter). Cells were identified to genus wherever possible and were classified as heterotrophic when no chloroplast was observed. Picocyanobacteria concentrations were determined by filtering 25–40 mL of the samples preserved for protists through Anodisc 0.2 µm filters under gentle pressure, and mounting on microscope slides using immersion oil that were then stored at –20°C until analysis. The cells were counted by epifluorescence microscopy at 1000× magnification with an Olympus 1X71 inverted microscope fitted with blue and green excitation filters to detect the autofluorescence of photosynthetic pigments (MacIsaac and Stockner, 1993). A minimum of 400 cells and 15 fields were counted wherever possible.

RESULTS

Climate

The mean overall temperature from 2005 to 2008 was –18.27°C, and the mean summer (June–August) temperature for this 4 year period was 0.4°C. Summer air temperatures were typically between –7 and 9°C, but a maximum temperature of 20.5°C was recorded on 2 August 2008 (Fig. 2a), and ground temperatures at 20 cm at Lake A rose above 0°C from early June to late August every year (Fig. 2b). Given the extreme latitude, daily totals of PAR fluctuated greatly over the year, with complete darkness from October until March (Fig. 2c). Cumulative PAR reaching Lake A was

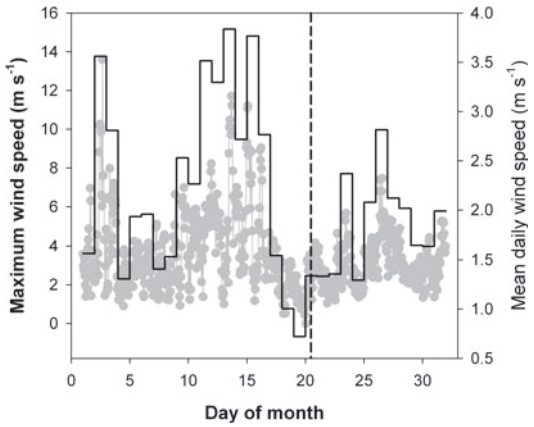

Fig. 3. The wind regime at Lake A during August 2008. Grey filled circles: maximum wind speed each hour. Black line: mean daily wind speed. The dashed line shows the time and date of profiling.

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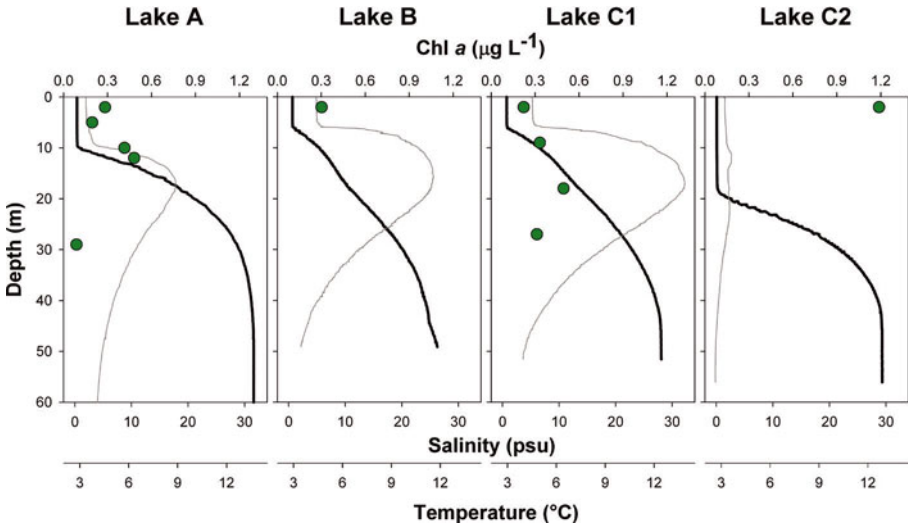

Fig. 4. Mixing in August 2008 for Lakes A, B, C1 and C2 from salinity (dark curves) and temperature (grey curves) profiles. Filled circles: Chl *a* concentrations, including the sum of all allomers, epimers and chlorophyllide *a*-like pigments.

1498 mol photons m^{-2} prior to sampling on 30 May and 5329 mol photons m^{-2} prior to 20 August 2008. For 30 May 2008, the incident PAR was 53 mol photons m^{-2} d^{-1} and 0.38 mol photons m^{-2} d^{-1} reached underneath the ice, while on 20 August 2008 incident PAR was 33 mol photons m^{-2} d^{-1} and 30 mol photons m^{-2} d^{-1} immediately below the surface water. Mean water column PAR for the region 0–12 m (or from just under the ice to 12 m) on the sampling days was 24% of the PAR under the ice or just below the water surface: 0.09 mol photons m^{-2} d^{-1} for 30 May and 7.23 mol photons m^{-2} d^{-1} in August during open-water conditions. Wind observations for the latter period in 2008 at Lake A showed two main episodes of high average wind speeds prior to the date of profiling (Fig. 3). Peak winds of up to 50 km h^{-1} were recorded in early August, and a second more prolonged episode of high average winds occurred in the period 9–17 August, with recorded maxima up to 43 km h^{-1}. For the summer months July–September, the prevailing winds were from the north-northeast (0–45°), while the dominant winds (>30 km h^{-1}) were from the west-northwest (270–315°).

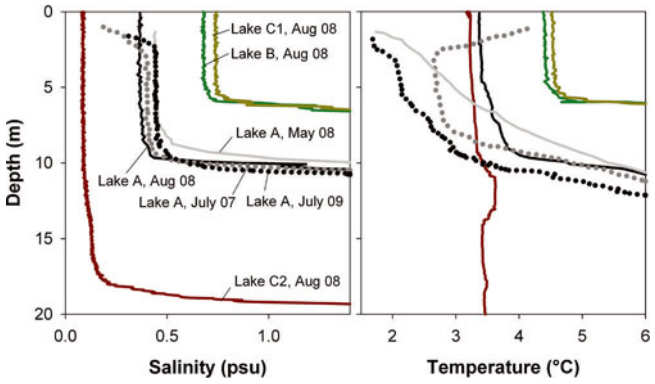

Fig. 5. CTD profiles for Lakes A, B, C1 and C2. Lake A had an ice cover of 1 m in July 2007, an ice cover of 1.2 m and 50 cm of snow in May 2008, and an ice cover of 1.6 m and 4 cm of snow in July 2009.

Ice cover

Previous measurements have shown that ice cover varies greatly between and within years on the northern Ellesmere Island meromictic lakes. Lake A had a perennial, 2 m thick ice cover during late spring between 1969, when it was first measured, and 1999 (Table 1). Thinner ice covers were recently reported with thicknesses of 1.2–1.6 m before the onset of melt, and the lake was completely ice-free in August 2000 and 2008 and partially ice-free in 2003, 2006 and 2007 (Mueller and others, 2009; this study). Lakes B, C1 and C2 were also completely ice-free during the summers of 2000 and 2008 (Mueller and others, 2009; this study). Lake B was partially ice-free in 2003 and 2007, Lake C1 was partially ice-free in 2003 and completely ice-free in 2006, and Lake C2 was partially ice-free in 2003, 2006 and 2007 (Mueller and others, 2009).

Water column structure and dynamics

All four lakes had strong salinity gradients, with an upper layer of fresh water overlying salt water (Fig. 4). This upper layer had homogeneous salinity and temperature values during the open-water conditions of August 2008, suggestive of mixing (Figs 4 and 5). The freshwater layers of Lakes B and C1 were shallower (~6 m) and slightly warmer (~4.5°C) than those of Lakes A and C2 (10 and 19 m respectively; ~3.2°C). Profiles of Lake A taken between July 2007 and July 2009 presented a continuum of conditions, from the presence of stratification through a completely homogeneous freshwater layer (Fig. 5). A stepped temperature profile in August 2008, compared to the monotonic increase in temperature observed in May 2008, suggests that mixing occurred between May and August 2008, and the salinity profiles suggest some erosion of the halocline to 11 m, where the salinity values converge (Fig. 6). RADARSAT satellite images show that Lake A became entirely ice-free at some point between 6 and 12 August 2008 (D.R. Mueller, unpublished data), implying that the lake was potentially exposed to wind-induced mixing for up to 2 weeks prior to sampling. A slight decrease in salinity of the freshwater layer in August 2008 (0.37 psu) compared to May 2008 (0.44 psu) likely reflects the input of meltwater during summer; by July

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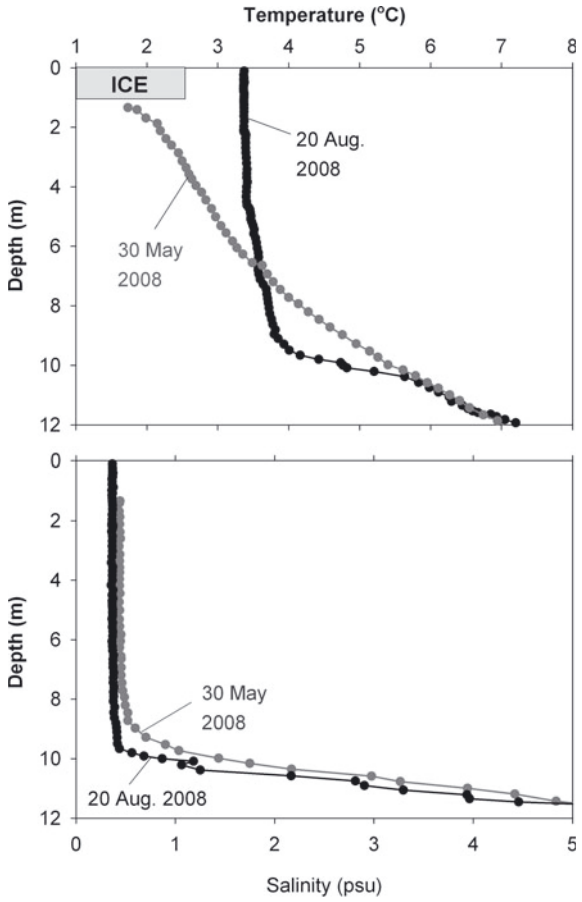

Fig. 6. CTD profiles for Lake A before (May) and during (August) open-water conditions in 2008.

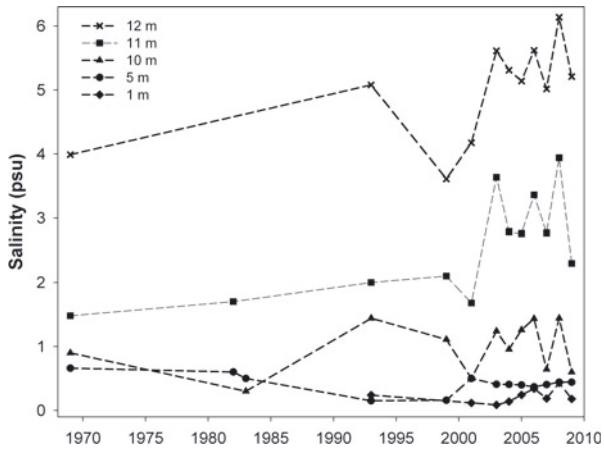

Fig. 7. Time series of salinity at different depths of Lake A from 1969 to 2009. All measurements were made with an ice cover (Table 1) and are the earliest available for every year. The vertical dashed lines indicate complete open-water conditions.

2009 the salinity had returned to higher values (0.45 psu). Isohaline waters from 5 to 10 m in 2001 and 2008 suggested that mixing in Lake A extended to 10 m depth (Fig. 7), while reduced salinities at 11 and 12 m implied the penetration of mixing into the upper halocline during these years. As illustrated by the time series at 10 m, due to diffusion the upper halocline returned to its prior salinity following mixing events. However, the highest salinities at 11 and 12 m were measured in May 2008; the mixing of August 2008 did not return them to the values measured in 2001 following the mixing of 2000. Salinity at 5 m appears to have remained relatively stable over the last 40 years, while variations in salinity at 1 m are likely the result of seasonal inflow of stream water, combined with inputs from the melting lake ice.

The inflow and outflow salinities provided additional information about water movement (Table 2). The low salinity of inflows in July 2007 indicated that they were composed of water from the melting winter snowpack. However, the outflow of Lake A in July 2007 had a higher salinity than the lake water just underneath the ice (0.41 versus 0.19 psu). This has been observed in other Arctic lakes and has been suggested to be caused by the widening and thickening of the through-flow layer before exiting the lake, with the meltwater layer mixing with the upper meters of the water column (Bergmann and Welch, 1985). The high salinity of the outflows of Lakes B and A in August 2008 (0.83 and 0.39 psu) was consistent with mixing of their freshwater surface layers.

The estimated annual discharge of Lake A calculated from snowmelt and precipitation (but not including evaporation) was $6.96 \times 10^6\,m^3\,a^{-1}$, while that calculated with the discharge data was $4.00 \times 10^6\,m^3\,a^{-1}$ for a melt period of 2 weeks or $6.00 \times 10^6\,m^3\,a^{-1}$ for a melt period of 3 weeks. The water residence time of the meltwater layer underneath the ice (from beneath the ice to 3 m depth) was estimated to be 1.2 years. This estimate must be considered an average

Table 2. Description of the inflows and outflow of Lake A, during or following the peak melt period. Inflow at the delta on 12 July 2007 was divided into two main streams, but the inflow at full freshet would be ~100 m wide. Water salinity in Lake A just underneath the ice cover on 12 July 2007 was 0.19 psu, and the freshwater layer salinity was 0.37 psu on 24 August 2008

Site	Date	Width		Max. depth	Salinity	Discharge
		Flowing	Freshet			
		m	m	m	psu	$m^3\,s^{-1}$
Inflow at delta	12 Jul 2007	(1) 6.8	100	(1) 0.24	0.06	4.901
		(2) 4.0		(2) 0.30		
Inflow from Lake B	12 Jul 2007	32.0	32	0.34	0.08	None
	20 Aug 2008	1.1	8	0.09	0.83	0.064
Outflow to sea	14 Jul 2007	9.0	9	0.38	0.41	3.306
	20 Aug 2008	7.0	9	0.30	0.39	1.449

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Table 3. Concentration of nutrients in Lakes A, B, C1 and C2 measured in 2008. Unusually high values (in italics) were recorded at 10 m in Lake A (May) for TN, and at 9 m in Lake C1 for NO_3^-–NO_2^-

Lake	Depth	TN	TP	TN:TP ratio	NO_3^-–NO_2^-	SRP
	m	µg L^{-1}	µg L^{-1}		µg N L^{-1}	µg L^{-1}
A (May)	2	97	2.7	35.9	<5	1.1
	5	105	1.2	87.5	<5	2.2
	10	*468*	1.4	*334.3*	6	2.0
	12	72	2.9	24.8	16	1.9
	20	<14	15.9	0.9	6	10.7
	29	337	157	2.1	11	29.3
	32	467	401	1.2	10	297
	60	496	1200	0.4	8	1260
A (Aug.)	2	80	2.5	32.0	13	1.1
	5	93	2.5	37.2	<5	1.0
	10	107	3.4	31.5	8	1.4
	12	109	3.6	30.3	10	1.7
	29	4670	60.3	77.4	102	51.5
B (Aug.)	2	113	1.5	75.3	7	1.3
C1 (Aug.)	2	104	2.1	49.5	13	1.8
	9	143	3.2	44.7	*388*	2.9
	18	144	4.4	32.7	47	5.7
	27	1610	13.8	116.7	21	8.5
C2 (Aug.)	2	50	5.9	8.5	5	1.4

value, as the meltwater layer immediately underneath the ice would be present throughout the melt season and therefore be renewed probably more than once during the same summer, while meltwater at 3 m would be present only at the climax of the melt season and therefore likely renewed more slowly than the 1.2 year average. Under perennially ice-cover conditions and no wind-induced mixing, there would be negligible renewal of water in the layer between 3 and 10 m, while in the absence of ice and wind-induced mixing at least once per year to 10 m, this layer would be replaced every 5.0 years.

The Brünt–Väisälä frequency, N^2, for the entire water column was 0.043 s^{-2}. It rose to 0.103 s^{-2} when only the halocline (10–30 m) was considered, and was 0.030 s^{-2} for the surface layer. Relative to a reference criterion of stability of 0.020 s^{-2} (Caplanne and Laurion, 2008), these estimates indicate that the surface layer is much more prone to mixing than the entire water column due to the high stability of the halocline. *W* values of 231 and 0.092 for the entire water column and the surface layer, respectively, were calculated. Values more than 100 generally suggest that wind energy is small compared to the strength of stratification while values less than 10 imply sensitivity to mixing.

Nutrient concentrations were low in the surface waters of the four sampled lakes (Table 3). Total nitrogen (TN) in August 2008 was ~100 µg L^{-1}, total phosphorus (TP) varied between 1 and 6 µg L^{-1}, nitrate–nitrite ranged from below detection to 13 µg N L^{-1}, and soluble reactive phosphorus ranged from 1 to 2 µg L^{-1}. The ratios of TN to TP in Lake A in May 2008 suggested phosphorus limitation in the surface waters but nitrogen limitation deeper in the water column. Nutrient concentrations were much higher in deeper water than in the surface waters, with TN five times greater and TP 400 times greater at 60 m than at 2 m at Lake A in May 2008. Total phosphorus stocks were estimated by trapezoidal integration for the depth region 2–12 m for the two sampling times at Lake A. These increased by 76% from May (16.65 mg TP m^{-2}) to August (29.25 mg TP m^{-2}), implying entrainment of the deeper P-rich waters.

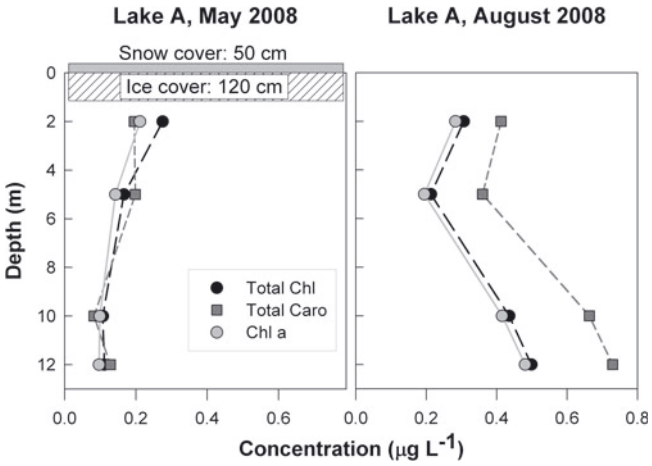

Fig. 8. Freshwater layer photosynthetic pigment concentration profiles for Lake A in May and August 2008. Chl *a* includes the sum of all allomers and epimers, and chlorophyllide *a*-like, and total chlorophylls and carotenoids include low concentration of unidentified chlorophylls and carotenoids, respectively.

Phototrophic communities

The chlorophyll *a* (Chl *a*) profile of Lake A from May 2008 showed higher concentrations just under the ice (0.21 µg L^{-1}) that then decreased with depth to 0.10 µg L^{-1} at 10 and 12 m, with lower concentrations below, although there was a maximum in Chl *a* at 29–32 m (Fig. 8; Table 4). August 2008 was distinctly different, with peak concentrations of Chl *a* present at the bottom of the freshwater layer (0.42 µg L^{-1}) and in the upper halocline (0.48 µg L^{-1}), and minimal concentrations at 5 m (0.20 µg L^{-1}) and deeper in the water column (Figs 4 and 8; Table 4). Lake B (0.30 µg L^{-1}) and Lake C1 (0.22 µg L^{-1}) had surface Chl *a* concentrations in August similar to Lake A, but Lake C2 had the highest value (1.19 µg L^{-1}; Fig. 4). Our Chl *a* profiles for August indicated the presence of deep chlorophyll maxima in Lake A at 12 m and in Lake C1 at 18 m (Fig. 4). Total chlorophyll and total carotenoid concentrations were lower in May than in August in Lake A and followed the same pattern as Chl *a* with depth (Fig. 8). Cell abundances are another indicator of trophic status and generally reflected the same trends as Chl *a*, except for an anomalously low value at 12 m in August 2008 for Lake A (Table 5). On average, 86% of Chl *a* was in the picoplankton size fraction (73–104%) in the topmost 12 m of Lake A in May 2008; all zeaxanthin was in this size fraction (≥100%), while fucoxanthin picoplanktonic percentage varied greatly with depth (45% to >100%, the latter reflecting analytical error at the limits of detection). Chl *b* in the topmost 5 m was contained in larger cells (average 43%) than at the bottom of the freshwater layer and in the upper halocline (average 105%), and Chl *c*-related pigments were less associated with the picoplankton (39–78%; Table 4). Picoplankton contributions equal to or greater than 100% indicate that this pigment is likely all within this size fraction. From 4% to 12% of chlorophylls were degradation products in the freshwater layers, indicating that the vast majority of production was occurring in situ, in contrast to

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Table 4. Pigment concentrations (μg L^{-1}) measured in the water column of Lake A in May and August 2008. The values in italics give the % in the picoplankton fraction (<3 μm). Note that Chl *a* includes the sum of all allomers and epimers, and chlorophyllide *a*-like; Chl *b* includes the sum of all allomers and epimers. Chl c_1: Chl c_1-like. Chl c_3: Chl c_3-like. MgDVP: magnesium-2,4-divinyl phaeoporphyrin a_5 monomethyl ester. BChl *e*: bacteriochlorophyll-*e*. Fuco: fucoxanthin. Zea: zeaxanthin. β,β-Car: β,β-Carotene. Iso: isorenieratene-like. Degr. indicates the molar ratios in % of degraded (i.e. allomers, epimers, chlorophyllide *a*, phaeophytin *a*) to undegraded chlorophylls (i.e. Chl and unknowns). ND: not detected

Depth	Chlorophylls								Carotenoids				Total
	Chl *a*	Chl *b*	Chl c_1	Chl c_2	Chl c_3	MgDVP	Degr.	BChl *e*	Fuco	Zea	β,β-Car	Iso	
May 2008													
2 m	0.211	0.015	0.017	0.018	<0.001	<0.001	12	ND	0.112	0.076	0.004	ND	0.470
	73	*44*	*41*	*39*	*41*	*44*	12	ND	*86*	*106*	*223*		
5 m	0.143	0.003	0.007	0.009	<0.001	ND	12	ND	0.110	0.077	0.011	ND	0.364
	78	*41*	*41*	*38*	*28*				*45*	*102*	*129*		
10 m	0.099	0.001	0.003	0.002	ND	ND	10	ND	0.016	0.058	0.009	ND	0.190
	104	*106*	*68*	*78*					*230*	*100*	*103*		
12 m	0.097	0.001	0.005	0.006	ND	ND	11	ND	0.083	0.037	0.006	ND	0.240
	87	*104*	*57*	*49*					*56*	*118*	*126*		
20 m	0.032	0.006	ND	ND	ND	ND	19	0.316	ND	ND	ND	0.005	0.393
	102	*53*						*88*				*136*	
29 m	0.236	0.115	<0.001	ND	ND	<0.001	54	8.746	ND	ND	0.083	0.224	9.912
	102	*96*	*0*			*0*		*104*			*101*	*115*	
32 m	0.244	0.101	ND	ND	ND	ND	56	3.509	ND	ND	0.079	0.120	4.396
	85	*77*						*84*			*73*	*76*	
60 m	0.073	0.030	ND	ND	ND	ND	42	0.556	ND	ND	0.008	0.015	0.738
	79	*68*						*98*			*162*	*66*	
August 2008													
2 m	0.283	0.004	0.010	<0.001	0.002	ND	12	ND	0.193	0.199	0.021	ND	0.719
5 m	0.195	<0.001	0.007	<0.001	<0.001	ND	16	ND	0.145	0.199	0.016	ND	0.573
10 m	0.416	0.002	0.007	0.003	ND	ND	8	ND	0.113	0.489	0.036	ND	1.099
12 m	0.481	0.002	0.003	0.002	ND	ND	9	ND	0.043	0.632	0.040	ND	1.228
29 m	0.088	0.031	ND	ND	ND	ND	63	3.910	ND	ND	0.026	0.097	4.357

deeper samples (below 29 m in Lake A and 27 m in Lake C1) where up to 63% of chlorophylls were degradation products, and likely resulted from phytoplankton senescence during sinking and accumulation in the salinity gradient.

The freshwater mixed layer contained a similar assemblage of pigments in May and August 2008, but their concentrations and relative importance differed over both time and depth (Fig. 9). Zeaxanthin concentrations were 2- to 17-fold higher in August, with the greatest increases in the upper halocline region subject to mixing and nutrient enrichment. Conversely, Chl *b*, Chl c_1 and Chl c_2 were detected in higher ratios relative to Chl *a* in May than in August at every depth. The fucoxanthin to Chl *a* ratio was similar in the uppermost 10 m in May and in August but was much greater at 12 m in May. Low concentrations of Chl c_3 were detected at 2 and 5 m at both sampling times, and MgDVP was only detected in trace amounts underneath the ice cover in May. Antheraxanthin was detected only at the bottom of the freshwater layer and in the upper halocline in August, where pigment peak concentrations occurred.

Microscopy enumerations of autotrophs in Lake A revealed some differences between May and August samples (Table 5). Chrysophytes were much more abundant in the uppermost 10 m in August, largely due to the widespread representation of cf. *Kephyrion* sp. Cryptophytes (*Rhodomonas* sp.), and dinoflagellates were also more abundant in August at every depth. *Chlamydomonas* sp. (chlorophyta) was identified at most depths at both sampling times, while a few *Chroococcus* sp. (cyanobacteria) were present in the May surface sample. A large number of small, unidentified autotrophic cells were observed in Lake A from May samples. The picocyanobacterial enumerations for Lake A revealed large differences between the two sampling dates. Populations increased by a factor of 3, with highest concentrations (1.65×10^8 cells L^{-1}) in the upper halocline (Table 5).

The photosynthetic pigment assemblages measured in the freshwater layers of Lakes A, B, C1 and C2 in August 2008 during ice-free conditions were similar, although some differences were also apparent (Fig. 10). Zeaxanthin was present in surface waters of all lakes, but its ratio to Chl *a* in Lake A (0.70) was twice those of the other lakes (0.25–0.31). Chl *b* was also detected in the surface waters of all lakes, but its relative importance was greater in Lake C2 (0.07) compared to Lakes A, C1 and C2 (0.01–0.03). Chl c_1 was present in similar proportions in all lakes, but Chl c_2 ratios to Chl *a* were more than ten times greater in Lakes B, C1 and C2 compared to Lake A. Chl c_3 was detected in only small amounts in Lakes A and C2, while trace concentrations of MgDVP were recorded only in Lake C2. The fucoxanthin contribution to total pigments was substantial in all lakes, but especially so in the surface waters of Lake C1. Violaxanthin was not detected in Lake A at any time of sampling but it was present in each of the other lakes. Diadinoxanthin and lutein were only detected in Lake C1, alloxanthin was present only in Lakes C1 and C2, and antheraxanthin was absent from Lake B.

Consistent with the observed differences in pigment composition, there were also large differences in the

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Table 5. Abundance of phytoplankton and other protists (in 10^3 cells L^{-1}) and picocyanobacteria (in 10^6 cells L^{-1}). Lakes B, C1 and C2 were sampled in August

Taxa	Details	A (May)				A (August)				B	C1		C2
		2 m	5 m	10 m	12 m	2 m	5 m	10 m	12 m	2 m	2 m	9 m	2 m
Bacillariophyceae	Pennales	0	0	0	0	0	0	0	0	3	0	0	0
	Centrales	0	0	0	0	0	0	0	0	0	0	0	57
Chlorophyceae	*Chlamydomonas* sp.	12	1	1	0	3	7	1	3	2	0	0	13
	cf. *Dictyosphaerium* sp.	0	0	0	0	0	0	0	0	0	0	0	30
	Tetraedron sp.	0	0	0	0	0	0	0	0	65	0	1	8
Choanoflagellates	cf. *Monosiga* sp.	1	4	11	0	0	0	0	0	0	0	0	0
Chrysophyceae	*Chrysoikos* cf. *bicornis*	0	0	0	0	0	0	0	0	5	0	0	0
	Chrysolykos planctonicus	0	0	0	0	0	0	0	0	0	29	0	7
	Chrysolykos skujae	0	0	0	0	0	1	0	0	0	0	0	0
	cf. *Erkenia subaequiciliata*	0	3	2	0	16	17	2	0	98	87	3	12
	(Pseudo) Kephyrion sp.	0	0	0	0	199	126	215	3	217	146	0	108
	cf. *Pseudopedinella* sp.	0	0	0	0	0	0	0	1	2	13	0	5
	Smooth cyst	2	3	1	5	32	52	37	42	15	8	7	9
	Spiny cyst	0	0	0	0	2	5	7	4	7	0	0	0
Ciliate	Peritrichs	0	0	0	0	0	0	0	1	3	3	0	0
	Holotrichs	0	0	0	0	0	0	0	0	0	0	0	2
Cryptophyceae	cf. *Rhodomonas* sp.	2	3	1	2	9	9	19	6	44	47	30	97
	5–10 µm	0	0	0	0	0	0	0	0	0	0	16	0
Cyanobacteria	cf. *Chroococcus* sp.	3	0	0	0	0	0	0	0	0	0	0	0
	Filament	0	0	0	0	0	0	0	0	0	0	0	16
Dinophyceae	*Gymnodinium* sp.	0	0	0	2	1	0	3	1	0	2	1	27
	Peridinium sp.	0	1	0	0	4	3	1	4	41	19	2	54
Auto. cells	Non-flagellate	120	49	20	40	10	6	4	6	111	92	347	196
	Flagellate	0	0	1	2	4	3	2	2	5	0	1	0
Hetero. cells	Non-flagellate	1	0	0	0	5	1	1	1	3	4	1	1
	Flagellate	0	0	0	0	29	36	8	0	0	1	0	3
	Heliozoan	1	1	0	0	0	0	0	0	0	0	0	0
Total		143	65	38	54	315	264	299	74	634	449	410	700
Picocyanobacteria		23	23	–	9	60	74	165	13	–	–	–	–

–: not determined.

microscopy enumerations among lakes (Table 5). Chrysophytes were abundant in all samples, except in the upper haloclines of Lakes A and C1. Diatoms were observed only in Lakes B and C2, while identified chlorophytes were largely absent from Lake C1. Cryptophytes and dinoflagellates were present in all samples but less abundant in Lake A, with maximal concentration in Lake C2. As in the surface sample for Lake A in May, there were a large

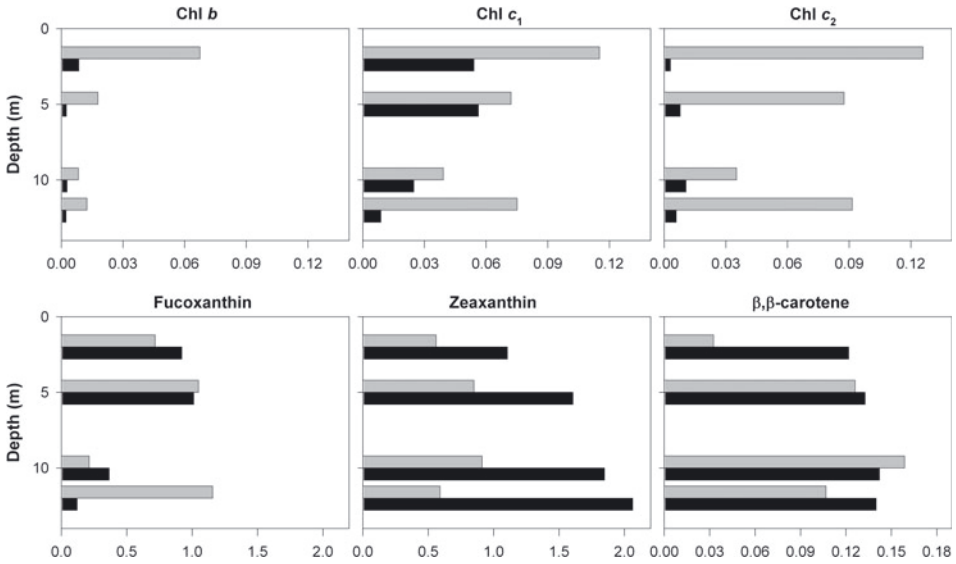

Fig. 9. Concentrations of photosynthetic pigments in Lake A in May and August 2008 expressed as molar ratios to Chl *a*. Grey bars represent May; black bars represent August. Note the different *x*-axis scales. Chl *b* includes the sum of all allomers and epimers. Chl c_1: Chl c_1-like.

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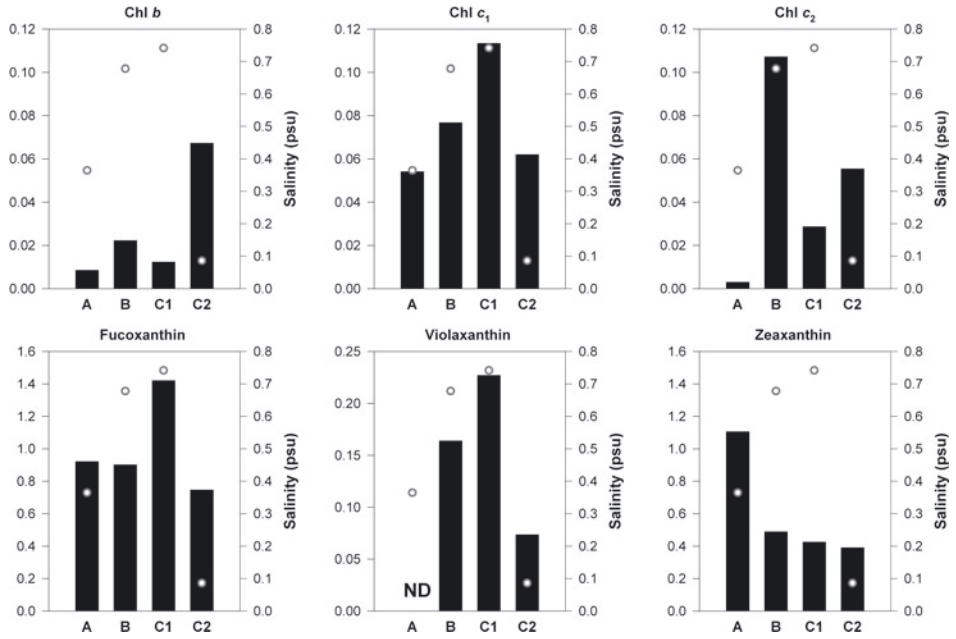

Fig. 10. Differences in surface (2 m) photosynthetic pigments of Lakes A, B, C1 and C2 in August 2008 expressed as molar ratios to Chl *a* on the left *y*-axis (note the differences in scales). Chl *b* includes the sum of all allomers and epimers. Chl c_1: Chl c_1-like. ND: not detected. Open circles: salinity in each lake at the depth of sampling.

number of small, autotrophic cells in Lakes B, C1 and C2 in August that could not be identified. Sediments were observed in the samples of Lakes A and C2 in August, suggesting the turbulent suspension of abiotic materials brought into the lakes from their catchments. Heterotrophic protists were identified in all samples (Table 5). *Monosiga* sp. (choanoflagellate) was the only heterotrophic flagellate observed in the freshwater layer of Lake A in May while ciliates were observed in low abundance in the August samples.

DISCUSSION

Water column stratification

The Ellesmere Island lakes are highly stratified as a result of strong salinity gradients and, until recently, perennial ice cover that prevented wind-induced mixing. Their freshwater oxic mixolimnia are derived from meltwater (e.g. Lake A: 0–10 m) and are separated by haloclines from their marine-derived anoxic monimolimnia (e.g. Lake A: >30 m), that are close to the salinity of sea water. The temperature profiles of these lakes can have two maxima: a small peak that is sometimes present just underneath the ice cover, likely resulting from solar heating or warm inflowing water (e.g. Lake A in July 2007, Fig. 5), and a deep water maximum (e.g. 8.88°C at 16.77 m in August 2008 in Lake A) as a result of solar radiation absorbed in the high-salinity water (Vincent and others, 2008b). It is notable that Lake A's thermal profile is strikingly similar to that of Lake Bonney, a perennially ice-capped lake in the McMurdo Dry Valleys, which has a temperature maximum of 6.4°C at 14–16 m (Spigel and Priscu, 1998). While Lake C2 did not show a deep temperature maximum in 2008, it had a relatively small maximum in 2001 (Mueller and others, 2009). This is consistent with the deeper halocline of Lake C2 and the observation that it loses its ice cover more frequently than Lakes A, B and C1.

Water column dynamics

The depth of the mixed layer of a lake depends on its exposure to wind, and additionally on the strength of its density stratification (Wetzel, 2001). Wind exposure is a function of fetch, wind speed and ice cover, with greater duration of ice-free conditions increasing the probability of mixing via high-wind events as well as by convective circulation. The duration of ice cover is likely to be a complex function of lake depth, snow cover, climate and topography (Vincent and others, 2008a). The importance of the latter factor is supported by comparisons with Lakes C1 and C2, which lose their ice covers more frequently than Lakes A and B despite a slightly cooler climate (Mueller and others, 2009). Lakes A and B are surrounded by steeper terrain that causes greater topographic shading and wind protection than at the C lakes. Differences in catchment size and the amount of relatively warm water that flows beneath the ice each year may also contribute to the differences in ice-out. The difference in mixing depth between Lake A (10 m) and Lake B (6 m) may similarly reflect a topographic control, with Lake A being less wind-protected than Lake B. However, it may also reflect differences in wind fetch: 3.5 km for Lake A but only 1 km for Lake B.

The depth and strength of the halocline in meromictic lakes is an additional control on the potential extent of wind-induced mixing after ice-out. The deeper mixed layer of Lake C2 (19 m) compared to Lake C1 (6 m) is likely a consequence of a larger catchment that contains glaciers, resulting in greater flushing of salts and erosion of the halocline. Similarly, the larger catchment of Lake A compared to Lake B contributes to its deeper mixing depth.

It has been suggested that Romulus Lake, a meromictic lake on Ellesmere Island located 300 km south of Lake A, has become hypersaline as a result of its seasonal ice cover; saline entrainment from the halocline results in brine plumes during freeze-up that sink to the monimolimnion (Van Hove and others, 2006). Could such processes also be occurring in

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northern coastal Ellesmere Island lakes? The salinity of the mixed layer is a balance between salt entrainment from the halocline and flushing via the outflow. The salinity of Lake A at 5 m appears to have been stable at ~0.37 psu since 1970, which indicates that, up to now, freshwater inflows are sufficient to flush the salts entrained from the halocline during the episodic wind-induced mixing. Moreover, increases in annual precipitation over the Arctic are predicted with ongoing climate change (Walsh and others, 2005), which would increasingly flush out any salts entrained into the surface mixed layer. The salinity of the mixed layers of Lakes B, C1 and C2 is also low (i.e. <1 psu). Ellesmere Island's meromictic lakes range from those with low precipitation and catchment:volume (e.g. Romulus Lake) to those with much higher precipitation and catchment:volume (e.g. Lake C3), with the former potentially becoming hypersaline and the latter moving from meromixis to freshwater status (Van Hove and others, 2006). Over the long term, Lake A might become a freshwater lake if catchment inputs and precipitation remain sufficient to flush the salts from the mixed layer and reduced ice cover permits increased mixing and entrainment of salts from the monimolimnion.

The two different stability indices yielded similar estimates: the overall water column of Lake A was highly stratified, and full wind-induced mixing is unlikely; however, the surface layer is readily mixed. N^2 is a simple index but does not take into account the density profile of the full water column, nor the morphometry of the lake basin and wind conditions. The *W* index includes these parameters in its calculation and is therefore more informative. None of these indices considered possible convection currents created by warming, including in the shallow moat region during summers when Lake A does not ice out completely. Thermohaline convection is another potential mixing mechanism under the ice in some meromictic lakes (e.g. Lake Vanda, Antarctica; Vincent and others 2008b). However, earlier data from Lake A during its perennial-ice phase provide no evidence of such effects. For example, in 1999 there was a gradient in salinity throughout the upper water column, and RADARSAT observations showed that the lake had been continuously covered by ice for at least the previous 5 years; however, after complete ice-out in 2000, the upper water column had homogeneous salinities, indicative of wind-induced mixing at that time (Mueller and others, 2009).

The nutrient profiles revealed that the monimolimnia of these meromictic lakes are huge nutrient reservoirs, compared to their surface waters where solar energy is in greatest supply for primary production. Similar nutrient levels have been previously reported from these lakes (Gibson and others, 2002; Van Hove and others, 2006) indicating that concentrations are stable on at least decadal timescales. The higher TP concentrations and total stocks in August than in May for Lake A could imply the entrainment of saline water, replete with nutrients, from the halocline, and rapid uptake by cells; however, the concentration changes are small in absolute terms and should be interpreted with caution. Predicted future warming is also projected to enhance surface runoff and increase external nutrient loading in Arctic lakes, which could enhance overall primary production (Wrona and others, 2006). The timing of melt is critical for these coastal lakes, and as long as freshet occurs while the lakes are ice-covered the through-flow conduit will deliver most of these nutrients directly to the outflow with minimal retention within the lake (Vincent and others, 2008a). Increases in optical constituents of the water (e.g. abiotic particles and dissolved materials) could greatly affect water transparency, reducing PAR penetration, but also protect the cells from damage caused by increased ultraviolet (UV) radiation (Vincent and others, 1998).

The cumulative PAR reaching Lake A was 3.6 times greater by August than by May, and this length of growing season up to the time of sampling may influence the observed phytoplankton community structure. The differences observed between May and August may therefore, at least in part, represent successional changes over the season. Differentiating these under-ice seasonal effects from the impacts of ice-out will require a comparison of late-summer profiles between years with and without ice cover. However, the effects of ice-out vastly exceeded the cumulative change in incident irradiance. PAR availability in the water column on 20 August 2008 was 80 times higher than on 30 May 2008, and the loss of perennial ice therefore has a dramatic effect on underwater energy supply for photosynthesis. This would allow the euphotic zone to extend deeper into the nutrient-rich waters of the monimolimnion, and this effect has been previously suggested to explain the long-term variations in photosynthetic bacterial populations in Lake A (Antoniades and others, 2009)

Changes in phototrophic community structure during summer 2008 at Lake A

Maximum Chl *a* concentrations in the freshwater layer of Lake A in August were more than twice those in May; however, this increase was modest relative to the pronounced change in water-column PAR in August caused by open-water conditions. The difference in the Chl *a* profiles between May and August implies resource limitation. In May, light may be the limiting variable as maximum Chl *a* concentrations occurred immediately below the ice, as observed in May 2005 and 2006 (Antoniades and others, 2009). In August, however, Chl *a* concentrations were much higher at the bottom of the freshwater layer and in the upper halocline, possibly due to entrainment of nutrient-rich deeper waters, while a Chl *a* maximum centered at 29–32 m may be the result of sinking and decomposing phytoplankton, given the high ratio of degraded to undegraded chlorophylls at these depths (Table 4).

Changes in the vertical distribution of phytoplankton in response to changing irradiances later in summer have also been observed in Antarctic meromictic lakes (Burch, 1988; McKnight and others, 2000). Under scenarios of reduced ice cover and higher wind-induced mixing, nutrient entrainment in the freshwater layer from bottom waters will become more frequent and may contribute to the presence of deep chlorophyll maxima at the bottom of the freshwater layer/upper halocline. Such populations will also be favoured by increased light penetration (see above). Deep chlorophyll maxima have been reported along the chemoclines in many meromictic lakes elsewhere, including in Antarctica (e.g. Roberts and others, 2000, 2004; reviewed in Lizotte, 2008). The components of the microbial food web (i.e. picocyanobacteria, phytoplankton, bacteria, nanoflagellates, ciliates and rotifers), given sufficient resource availability, and especially the picoplankton fraction (0.2–2 μm), may also be positively influenced by warmer water temperatures, indicating that warmer climates will

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result in higher primary production (Rae and Vincent, 1998; Wrona and others, 2006). A study on the ecological implications of ice-cover decline of maritime Antarctic lakes since the 1950s also revealed increases in Chl *a* concentrations (1981–95), along with increases in water temperature and nutrient concentrations (Quayle and others, 2002). Grazing, diseases and flushing rates are likely to exert additional controls on primary production in polar lakes (Lizotte, 2008).

Photosynthetic pigment analyses showed that the composition of Lake A's phytoplankton community changed markedly between May and August (Fig. 9). Zeaxanthin, a signature pigment of cyanobacteria (also present in prochlorophytes and chlorophytes), was prevalent in Lake A during both sampling periods, and was significantly correlated with Chl *a* ($r = 0.96$, $p < 0.01$, $n = 8$), indicating the importance of cyanobacteria in Lake A. Cyanobacteria are a ubiquitous component of polar fresh and saline waters (Vincent, 2000; Powell and others, 2005; Van Hove and others, 2008). The increased zeaxanthin:Chl *a* ratios in August also suggested that cyanobacteria represented an even larger proportion of the phototrophic community during open-water conditions, although this may have been amplified by the greater zeaxanthin production relative to Chl *a* as a photoprotection strategy under increased irradiance (Schlüter and others, 2006). The large majority of cyanobacteria in Lake A are in the picoplankton size fraction (Table 4) as reported in numerous polar lakes (Hobbie and Laybourn-Parry, 2008), although the larger species *Chroococcus* sp. was also observed in low concentrations underneath the ice in May 2008 (Table 5). Picocyanobacterial counts for August 2008 (Table 5) were 60-fold and 6-fold greater at 2 and 10 m, respectively, than those reported for 1 August 2001 at the same depths (Van Hove and others, 2008) when Lake A had an ice cover of 1 m. However, Chl *a* concentrations reported for the freshwater layer in August 2001 (0.2–0.3 μg L^{-1}; Van Hove and others, 2008) were similar to those reported in August 2008 (0.2–0.4 μg L^{-1}), suggesting that while picocyanobacteria had increased in abundance, total phytoplankton biomass remained largely unchanged. In meromictic Ace Lake, Antarctica, picocyanobacteria have been observed to similarly increase in abundance during improved irradiance conditions, and especially in the deeper waters (Powell and others, 2005), as in Lake A.

Potential sources of the Chl *b* and antheraxanthin detected in Lake A are chlorophytes, prasinophytes and/or euglenophytes, although these pigments are also produced by terrestrial higher plants. Chlorophytes, however, were the only one of these groups identified during microscopy. The maximum concentrations of Chl *b* immediately below the ice in May therefore reflect the importance of flagellated *Chlamydomonas* during low-light, low-turbulence conditions (Table 5). Motile organisms capable of positioning themselves near the ice bottom have competitive advantages when ice cover limits turbulence and light penetration. The main source of fucoxanthin and Chl *c*-related pigments was likely chrysophytes, as diatoms were not observed by microscopy in the present study nor reported in previous studies of Lake A (Antoniades and others, 2009). Chrysophyte abundances were higher in August than in May, as indicated by fucoxanthin concentrations and microscopy counts (Tables 4 and 5), although ratios of fucoxanthin to Chl *a* changed little from early to late summer, indicating that the proportion of chrysophytes relative to total Lake A biomass was relatively stable. This success of chrysophytes through the summer may be related to their competitive ability at low phosphorus concentrations such as those found in Lake A. The detection of MgDVP, a Chl *c*-related pigment diagnostic of prasinophytes, underneath the ice cover in May 2008 indicates their likely presence in Lake A, although prasinoxanthin, another pigment diagnostic of prasinophytes, was below the detection limits of our HPLC.

Phototrophic differences among lakes

Surface Chl *a* concentrations measured in Lakes A, B and C1 in August 2008 were in the ultra-oligotrophic range and amongst the lowest reported concentrations for polar lakes (Lizotte, 2008). Many of the values of the present study are in the same range as those reported in previous studies of the same sites (Van Hove and others, 2008; Antoniades and others, 2009), indicating minimal interannual variability. However, the August 2008 Lake C2 Chl *a* concentration (1.19 μg L^{-1}) falls at the lower range of oligotrophic lakes (Lizotte, 2008), in contrast to the ultra-oligotrophic value reported previously (0.35 μg L^{-1} in July 2001; Van Hove and others, 2008). The greater biomass in Lake C2 may be explained by its greater TP concentration and by the observation that this lake loses its ice cover more frequently than Lakes A, B and C1.

Pigment signatures and microscopy enumerations from the surface waters of all lakes sampled in August suggest that they contained cyanobacteria (zeaxanthin), green algae (Chl *b*, MgDVP, violaxanthin, lutein, zeaxanthin), chrysophytes (Chl c_2, Chl c_3, fucoxanthin, diadinoxanthin), cryptophytes (Chl c_2, alloxanthin) and dinoflagellates (Chl c_2, diadinoxanthin). Diatoms were identified from microscopic analysis of Lakes B and C2 and confirmed by the presence of diatom pigment groups (Chl c_1, Chl c_2, diadinoxanthin, fucoxanthin). Diatoms are currently rare in the plankton of these ecosystems but could become increasingly common in these lakes as reduced annual ice covers permit increases in wind-induced turbulence, thus keeping heavy siliceous diatoms suspended in the water column (Roberts and others, 2004). Although most phytoplankton groups were present in every lake, they differed in their relative importance. Cyanobacteria were important in all these lakes, but especially in Lake A, consistent with the abundance of picocyanobacteria in many lakes throughout the polar regions (Vincent, 2000). Green algae were another common phytoplankton component that were slightly more abundant in the surface waters of Lake C2 (i.e. high ratio of Chl *b* to Chl *a*, detection of MgDVP, many small autotrophic cells and identified chlorophytes). In Lake Bonney, Antarctica, green algae are similarly important, in particular the cold-adapted taxon *Chlamydomonas* (Morgan-Kiss and others, 2006). Chl c_2 was relatively much more important in Lakes B, C1 and C2 than in Lake A and indicated the greater representation of diatoms, chrysophytes, cryptophytes or dinoflagellates in these lakes. Lake C2 had high ratios of Chl c_2 and alloxanthin to Chl *a*, agreeing with the observation of numerous individuals of *Rhodomonas* sp. (cryptophyte). One or more similar species of cryptophytes also occur as co-dominants in McMurdo Dry Valley lakes (Lizotte, 2008).

The large differences between the lakes in the present study are consistent with the variation in phytoplankton groups and taxa throughout the Arctic and Antarctica, even within specific regions such as the McMurdo Dry Valley

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lakes (Lizotte, 2008). These differences are likely the result of the interplay of many factors including seasonal and interannual variation, catchment and local climatic characteristics, species colonization, nutrient supply and trophic interactions. In addition to photosynthesis, several of these taxa could also use heterotrophy to supplement their supply in dissolved organic matter and nutrients (Hobbie and Laybourn-Parry, 2008) and to survive through the winter darkness (McKnight and others, 2000). Mixotrophic species are common among the phytoflagellates such as cryptophytes, chrysophytes, dinoflagellates and phototrophic ciliates and may respond to additional variables such as organic carbon availability and prey densities.

Phytoplankton dynamics as an indicator of climate change

Changes in primary productivity and in species composition can be reflective of climate change as polar lake ecology is typically dominated by bottom-up processes; the communities respond rapidly to changes in physicochemical characteristics (Roberts and others, 2004; Adrian and others, 2009). The changes in the phototrophic community structure associated with open-water conditions in Lake A provide a first representation of seasonal variability under conditions of extreme ice-cover variation. Although changes in population density and species composition have been observed over annual cycles in Antarctic lakes (Burch, 1988; Butler and others, 2000) and also in High Arctic Char Lake and Meretta Lake (Schindler and others, 1974a,b), this is the first time that such changes have been observed in a heretofore perennially ice-covered lake. Although one summer is too short a time frame to detect significant changes related to climate, this study provides insights into potential future changes associated with transition to seasonal ice cover in these ecosystems. Large interannual variability in phytoplankton species composition is common in polar lakes (Butler and others, 2000; McKnight and others, 2000). However, the phytoplankton communities in Lake A appear to be stable, based on photosynthetic pigment analyses from this and previous years (Antoniades and others, 2009), a fact likely related to the relative stability of stratification, limnological conditions, and ice-cover regimes until recent changes. The phytoplankton assemblage responses to climate change in these meromictic Ellesmere Island lakes are likely to be lake-specific, although general trends (e.g. increased biomass and productivity) are expected. Similarly in Antarctica, there are likely to be large differences in the response to loss of perennial ice cover (e.g. Lake Bonney and Lake Fryxell which lie in the same McMurdo dry valley but differ greatly in geochemistry and phytoplankton composition (Lizotte and Priscu, 1998)).

The linkages between climate change and lake biota are complex, as many factors such as light and nutrient availability, temperature, biotic interactions and species succession play a role in structuring the abundance and distribution of species, and responses can vary between systems. Despite these limitations, paleolimnological records from lakes in the circumpolar Arctic indicate extensive species changes in algae and invertebrate communities since 1850 that have been attributed to climate change (Smol and others, 2005; Antoniades and others, 2007). Loss of perennial ice cover may change or even destroy the vertical gradients in physical and chemical variables in polar meromictic lakes that allow niche partitioning down the water column (e.g. Pouliot and others, 2009). Shifts in phytoplankton community composition are also likely to have repercussions for higher trophic levels through changes in food availability (Prowse and others, 2006).

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