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Winter limnology in a changing world

Hidden Stores of Organic Matter in Northern Lake Ice: Selective Retention of Terrestrial Particles, Phytoplankton and Labile Carbon

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Abstract Around 50% of the world's lakes freeze seasonally, but the duration of ice-cover is shortening each year and this is likely to have broad limnological consequences. We sampled freshwater ice and the underlying water in 19 boreal and polar lakes to evaluate whether lake ice contains an inoculum of algae, nutrients, and carbon that may contribute to lake ecosystem productivity. Boreal and Arctic lakes differed in ice duration (6 vs. >10 months), thickness (70 vs. 190 cm), and quality (predominantly snow ice vs. black ice), but in all lakes, there were consistent differences in biological and biogeochemical composition between ice and water. Particulate fractions were often more retained while most dissolved compounds were excluded from the ice; for example, the ice had more terrestrial particulate carbon, measured as fatty acid biomarkers (averages of 1.1 vs. 0.3 $\mu g\ L^{-1}$) but lower dissolved organic carbon (2.2 vs. 5.7 mg C L^{-1}) and inorganic phosphorus concentrations (4.0 vs. 7.5 $\mu g\ C\ L^{-1}$) than the underlying water. The boreal ice further had three times higher chlorophyll-*a,* than the water (0.9 vs. 0.3 $\mu g\ L^{-1}$). Of the dissolved fractions, the contribution of protein-like compounds was higher in the ice, and this in all lakes. These labile compounds would become available to planktonic microbes when the ice melts. Our results show that freshwater ice has an underestimated role in storage and transformation in the biogeochemical carbon cycle of ice-covered lake ecosystems.

Plain Language Summary Winter ice cover of 1–2 m thickness can comprise 20%–70% of the total lake depth in boreal and Arctic lakes. While sea ice is known to contain substantial quantities of carbon and organisms that at ice melt contribute to biological production in the underlying water column, little is known about the composition of lake ice and its role in storage of organic carbon. Our analyses of 19 boreal and Arctic lakes revealed large but different stores of organic material in lake ice versus the underlying water. The ice inclusions were composed predominantly of particulate materials, but also of dissolved materials dominated by biolabile compounds that would likely stimulate metabolic pathways and aquatic food webs when they are released into the water at ice melt. This study underscores the pressing need for greater attention to winter as the dominant season at northern latitudes, and to the consequences of rapid contraction of lake ice on microbial and whole lake production.

Elise Imbeau, Warwick F. Vincent, Maxime Wauthy, and Mathieu Cusson are co-authors.

Key Points:

- Ice covers northern lakes for much of the year and has biogeochemical properties that differ from those in the underlying water
- Boreal and Arctic lake ice contains large stocks of particulate material composed of detritus, bacteria, and a subset of lake phytoplankton
- Dissolved organic matter in the ice is dominated by biolabile compounds that may stimulate microbial production at ice-off

Supporting Information:

Supporting Information may be found in the online version of this article.

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1. Introduction

Over the last few decades, global warming has led to widespread shrinking of the cryosphere and has brought a sense of urgency toward the study of ice habitats. One of the most heavily impacted cryospheric habitats is freshwater ice. Climate change is leading to substantial reductions in the thickness and duration of lake and river ice cover worldwide (Sharma et al., 2019; Wrona et al., 2016). In the northern hemisphere, ice in lakes and rivers freezes an average of 5.8 days later and melts 6.5 days earlier than 100 years ago, based on the measurements taken between the years 1846 and 1995 (Magnuson, et al., 2000). Global air temperatures increased 1.2°C during this period. The majority of boreal and Arctic lakes are still ice-covered for six to ten months a year, and the potential importance of this cold and dark period on ecosystem structure and function is increasingly recognized (Grosbois & Rautio, 2018; Hampton et al., 2017; Schneider et al., 2017). Considering that ice-covered lakes include nearly 50% of the world's lakes, there is a pressing

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need to conduct research on ice ecosystems in order to predict the after-effects of ice-cover loss on the ecology and productivity of lakes (Campbell et al., 2005; Hampton et al., 2017).

Few studies have examined the winter ecology of lakes, and even less is known about freshwater ice, which has been considered a limited habitat for organism growth because it does not contain the brine channels found in sea ice (Vincent, 2004). However, studies have found diverse microbial communities within slush layers in Pyrenean lakes (Felip et al., 1995), viable algal cells in Lake Baikal ice (Bondarenko et al., 2006; Obolkina et al., 2000), viable complex microbial assemblages living within lake ice microhabitats in Antarctica (Priscu et al., 1998), and ice algae living within freshwater lake ice in fluvial Lake Saint-Pierre (Frenette et al., 2008). While the cell numbers and biomass of these communities may be low, the ice habitat where they live can account for more than half of the total lake volume (e.g., Santibáñez et al., 2019) and may persist throughout much or even all of the year (e.g., Bégin, Tanabe, Kumagai, et al., 2021), making survival in ice a potential benefit to these ice-tolerant species.

The biogeochemistry of organic matter in lake ice is another area of uncertainty, yet may play an important role in aquatic ecosystems. Dissolved organic carbon (DOC) supports heterotrophic growth, and its colored fraction (CDOM) alters contaminant toxicity and nutrient availability (Williamson et al., 1999) and attenuates light penetration in the water (Laurion et al., 1997; Thrane et al., 2014), which affects primary production (Arrigo & Brown, 1996), thermal stratification and oxygen dynamics (Pilla & Couture, 2021). Despite the central role that organic carbon plays in the aquatic ecosystems, very few studies have been conducted on this component in lake ice. Priscu et al. (1999) reported that DOC concentration in Antarctic Lake Bonney ice was higher than in the underlying water, Belzile et al. (2002) observed the differential exclusion of different fractions of dissolved organic matter (DOM) from Arctic lake ice and Salonen et al. (2010) described colored water pockets migrating through boreal lake ice. The biogeochemistry of DOC is of special relevance in the context of warming climate and brownification of boreal and Arctic lakes (Wauthy et al., 2018; Williamson et al., 2015) but there is limited information about how much dissolved as well as particulate organic carbon are stored in freshwater ice in winter and whether the composition of these carbon pools change during winter.

The overall objectives of the present study were to better understand the biological and biogeochemical composition of lake ice. More specifically, we aimed to: (a) measure the partitioning of phytoplankton between ice and water to evaluate lake ice as an overwintering habitat for algae that could contribute to lake ecosystem productivity; (b) compare the particulate and dissolved fractions of organic matter within the ice and the water to evaluate how carbon and nutrients are stored in lake ice; and (c) measure temporal changes in organic matter quantity and quality between the ice and water throughout the winter. To address these objectives, we sampled the ice and water column of 19 northern lakes over a broad latitudinal range of landscapes, from boreal forest at 48°N to High Arctic polar desert at 83°N.

2. Materials and Methods

2.1. Study Sites

Lakes were sampled along a latitudinal gradient from the southern coniferous forest in boreal Quebec (48°N, 71°W) where lakes are ice-covered for 6 months a year with a maximum ice thickness of about 70–100 cm, to the Arctic on Victoria Island (69°N, 105°W) where lakes are ice-covered for 10 months a year with a maximum ice thickness of 2 m, and finally to the High-Arctic in northern Ellesmere Island and Ward Hunt Island (83°N, 74°W) where perennially ice-covered lakes are found (Figure 1, Table S1).

Eleven boreal lakes in Saguenay (SAG), six Arctic lakes in the vicinity of Cambridge Bay (CB), and two High Arctic lakes (Ward Hunt Island region [WH]), one on northern Ellesmere Island and another on Ward Hunt Island, were sampled to compare the biogeochemical composition between ice and water across a large spatial scale. The SAG lakes were sampled in February 2018 before the spring melt began and more than 2 months before the ice out, the CB lakes were sampled in April 2018, also 2 months before the ice out, while the multi-year ice and the underlaying water from WH lakes were sampled in July 2018. Additionally, to study seasonal changes in ice and water biogeochemistry, boreal Lake Simoncouche (SAG) and Arctic lakes in (CB) were sampled in fall before freeze-up, several times during winter, and immediately after ice-out.

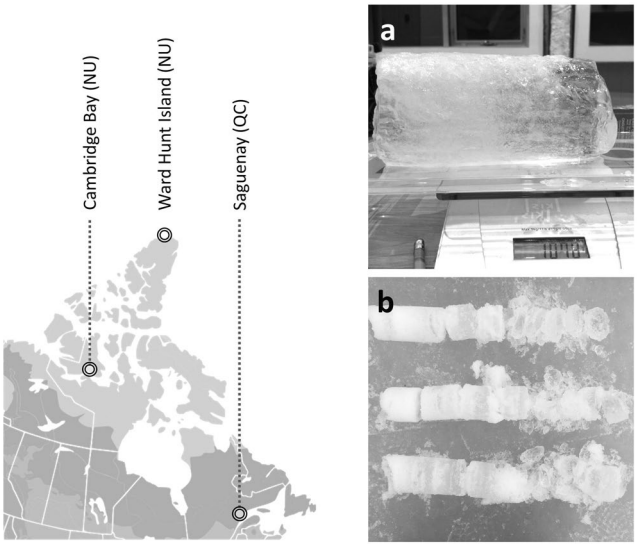

Figure 1. Locations of the three lake ice study regions in Canada. In the Cambridge Bay and Ward Hunt Island regions (Nunavut, NU), the ice was made of black ice throughout the thickness of the ice core (a). In the Saguenay region (Quebec, QC), the ice cores consisted of several sections of different qualities; the water-ice interface comprised 5–10 cm of black ice, while the rest of the core collapsed into several discs of white ice separated by snow, slush and sometimes water (b).

2.2. Water and Ice Sampling

For all water and ice collections, sampling was in the middle of the lake. A hole was made with a power ice auger of 25 cm diameter and depending on lake depth, water was sampled from 1 to 5 different equally spaced depths between the bottom and the surface using a 2 L transparent Plexiglas water sampler (Limnos Ltd, Turku, Finland) (Table S1). The water was mixed to obtain a representative sample of the whole water column and stored in 4 L Nalgene containers.

The ice was sampled using a 9 cm diameter Mark II ice corer (Kovacs Enterprise, Lebanon, NH, USA). Ice thickness and snow depth were measured, and the ice classified into two types: transparent black ice, and opaque white ice that included ice and snow. Three ice cores were collected and vertically subsectioned into two to six parts to study the distribution of chlorophyll-*a* (Chl-*a*) in the ice. The subsections always included a 4–10 cm thick black ice layer at the water-ice interface while the remaining ice core, whether made of transparent black ice or opaque white ice, was in the field cut to sections of equal thickness that varied between 10-25 cm depending on total ice thickness. All subsections were analyzed separately. One to three additional ice cores, depending on the ice thickness, were sampled and combined for all other analysis. These ice cores were not subsectioned but the analyses were performed on melted ice that was from the total ice core(s). To avoid contaminating the ice, it was manipulated wearing gloves, transported to the laboratory frozen in clean (new) opaque polyethylene bags (subsections in different bags), and in the laboratory left to melt in clean polypropylene boxes that were covered with a lid. Blanks (DOC, CDOM, nutrients) were made as part of our normal laboratory procedure, including MQ water kept in the containers where the ice melted. These showed no evidence of contamination from the manipulations.

Light penetration through the ice and water column were quantified as photosynthetically active radiation (PAR) using an underwater radiometer Li-192 attached to a graduated pole (Li-Cor Biosciences, Lincoln, NE, USA). The ice hole was covered with an opaque plate when taking the measurement. PAR was further continuously measured in boreal Lake Simoncouche, and Arctic Lake Greiner using a Li-Cor Li-192 underwater quantum sensor attached to a RBR Maestro automated logger (RBR Ltd., Ottawa, ON, Canada). The logger was located at the depth of 1.4 m in Lake Simoncouche, and at 3.3 m in Lake Greiner, which were 65 and 140 cm below the maximum ice thickness in these two lakes, respectively.

2.3. Algal Biomass and Community Characterization

Chl-*a* was analyzed in ice and water as a proxy of algal biomass. 100–1,000 ml of water from melted ice or from the water column under the ice was filtered through GF/F glass microfiber filters (Whatman, Maidstone, United Kingdom) and kept frozen. Filters were later extracted in hot ethanol (95% EtOH; 70°C, 5 min) and analyzed with a Cary Eclipse spectrofluorometer (Agilent Technologies) following Nusch (1980).

To characterize the algal communities in the ice and the water, phytoplankton enumeration, identification, and biomass estimations were conducted by Biologica Environmental Services Ltd. (Victoria, Canada) on 11 individual samples. These included water and ice from Lake Simoncouche (SAG) at three dates between January and April 2018, Lake Allen (SAG), and Greiner Lake (CB). Samples were preserved with acid Lugol solution. Before counting, samples were mixed gently, and subsamples (100 mL) were dispensed into an Utermöhl sedimentation chamber, and allowed to settle for 48 h. The subsamples were then systematically examined using a Zeiss Axio Vert A.1 inverted phase contrast microscope (Carl Zeiss, Oberkochen, Germany) at 400× magnification. All algal cells were counted in a series of randomly located fields of view until a minimum of 400 algal units were enumerated. Only viable cells (cells with intact contents, implying that they were alive at the time of collection) were identified and enumerated (Grace Analytical

Lab, 1994). Algae were identified to genus, where possible. Species-level identifications were made for taxa for which there are reliable taxonomic references that encompass species-level morphological diversity in North America. Biovolume calculations were also performed for all algal taxa by measuring at least 10 cells of each taxon (when possible) and applying standard geometric formulas best fitted to the shape of the cell (Hillebrand et al., 1999).

2.4. Fatty Acid and Dry Weight Analyses

Ice and seston samples were analyzed for fatty acids (FAs) at Université du Québec à Chicoutimi (SAG, QC, Canada). Replicated (2–3 replicates) subsamples of about 1,000 ml of water from each sample were filtered through preweighed and precombusted GF/F filters (nominal pore size 0.7 μm) and stored at −80°C. Frozen filters were freeze-dried and weighed (to obtain dry weight, DW), and lipids were extracted and methylated. In brief, the filter was added to a mixture of HPLC grade methanol, toluene, and acetyl chloride (4:1:0.125) with internal standard (nonadecanoic acid C19:0, N5252, available from Sigma-Aldrich, Saint Louis, MS, USA). Samples were centrifuged and incubated at 90°C for 20 min. Transesterified FA were extracted with hexane and were scanned through a 7890A gas chromatograph (Agilent) coupled to a 5975C mass spectrometer with a triple-axis detector (Agilent) and a J&W DB-23 column (Agilent). The gas flow was 1.0032 ml min^{-1} and splitless mode was used with a specific temperature ramp of 70°C for the first 1.5 min, followed by an increase of 20°C min^{-1} until 110°C, then 12.5°C min^{-1} until 160°C and 2.5°C min^{-1} until 230°C, with a 6.5-min holding time (42 min total run time). To ensure maximum quantification precision and lowest detection limits, the GC-MS was run in Single Ion Monitoring mode. FA methyl esters (FAME) were identified using retention time and ion composition, based on FAME and bacterial acid methyl esters mix standards (Supelco 37 Component FAME MIX, CRM47885, and Bacterial Acid Methyl Ester BAME MIX, 47080-U, Sigma-Aldrich). They were quantified from the peak area of the most abundant FA-specific ion (m/z 74, 79, 81, and 87) against the known concentration of internal standard C:19. Biomarkers documented only for a unique taxa were selected from the freshwater, marine, and terrestrial literature (phytoplankton biomarkers: C18:4n-3, C20:1n-9, C20:4n-6, C20:5n-3, C22:6n-3, C24:1n-9, terrestrial biomarkers: C20:0, C22:0, C23:0, C24:0, and bacterial biomarkers: aC15:0, iC15:0, iC17:0, C15:0), as in Grosbois et al. (2017).

2.5. Dissolved Chemical Analyses

Lake water and water from the melted mixed total ice cores were filtered through precombusted GF/F filters and subsampled for soluble reactive phosphorus (SRP) and nitrate (NO_3^-). NO_3^- refers to our measurements of nitrate plus nitrite (expressed in terms of nitrogen). These were not separated in the analyses because nitrite was expected to be negligible in the well-oxygenated lake waters at all our sites. Nutrient analyses were conducted at the GRIL analytical lab of Université du Québec à Montréal (Montreal, QC, Canada).

Subsamples of the GF/F filtered water from lake water and the melted mixed total ice cores were collected for carbon characterization. Quantification of DOC was carried out using an Aurora 1030W TOC Analyzer (OI Analytical, College Station, Texas) at the GRIL analytical lab (Montreal, QC, Canada). Absorbance of CDOM was measured using a UV-visible Cary 100 spectrophotometer (Agilent Technologies, Santa Clara, California), recording absorbance between 250 and 800 nm at 1 nm intervals. Milli-Q water was used as a blank and sample spectra were null-point adjusted by subtracting the mean value from 750 to 800 nm to correct for offsets due to instrument baseline effects (Helms et al., 2008). The absorbance measured at 254 nm (A_{254}) was normalized to DOC as specific ultraviolet absorbance at 254 nm (SUVA), as a proxy of aromaticity and the relative proportion of terrestrial versus algal carbon sources in DOM (Weishaar et al., 2003). The absorption coefficient at 320 nm (a_{320}) was used as an index of CDOM concentration and determined following the equation:

$$a_{320} = 2.303 \times A_{320}/L, \quad (1)$$

where a_{320} is the absorption coefficient (m^{-1}) at 320 nm, A_{320} the absorbance at 320 nm, and L the path length of the cuvette. The cuvette length was 10 cm for all the ice core samples and for water samples from polar lakes, while we used a 1-cm cuvette for the boreal water samples.

The fluorescence spectra were recorded on a Cary Eclipse spectrofluorometer (Agilent Technologies, Santa Clara, California) across the excitation waveband from 265 to 450 nm (5 nm increments) and the emission waveband of 250–600 nm (2 nm increments). The fluorescence spectra were corrected for Raman and Rayleigh scattering and inner filter effects, and standardized to Raman units using the FDOMcorr 1.4 toolbox (Murphy et al., 2010). To identify and quantify the main DOM components, a parallel factor (PARAFAC) model was run on MATLAB v R2013a (MathWorks, Natick, MA, USA) as in Murphy et al. (2013), modeling on 77 excitation-emission matrices developed in this research combined with 119 extra-matrices collected from previous studies carried out on 52 boreal and Arctic freshwaters. The model was validated by split-half analysis (Figure S1) using the drEEM toolbox (Murphy et al., 2013). The maximum fluorescence values [Cx] of each component x for each particular sample were summed to determine the total fluorescence (F_T) and then the relative abundance of each component x was calculated according to the equation:

$$\%Cx = \left(\left[Cx\right] / F_T\right) \times 100 \quad (2)$$

To identify the components (humic-like, protein-like) of the model, their respective excitation and emission spectra were compared to published components from 70 models available in the OpenFluor database according to Murphy et al. (2014). Fluorescence signatures of the four components identified by the PARAFAC model and spectral characteristics of the components are shown in Figure S2 and Table S2.

2.6. Data Analysis

Spatial comparisons were made on the data collected from 11 boreal lakes in SAG in February 2018, three Arctic lakes in CB in April 2018, and two High Arctic lakes in the WH sampled in July 2018. Within ice cores, Chl-*a* values were compared among the water-ice interface, the upper sections and the total core with a permutational analysis of variance (PER-ANOVA; Anderson et al., 2008). Euclidian distance matrices between pairs of samples were used, and the number of permutations was fixed at 999. The same approach was also used to compare values of different particulate and dissolved variables between water and ice within each region (SAG, CB, and WH). The variables tested included Chl-*a* concentration (μg L^{-1}), dry weight concentration (mg DW L^{-1}), total FAME concentration (μg L^{-1}), algal FA concentration (μg L^{-1}), terrestrial FA concentration (μg L^{-1}) and bacterial FA concentration (μg L^{-1}), SRP concentration (μg P L^{-1}), NO_3^- concentration (mg N L^{-1}), DOC concentration (mg C L^{-1}), percentage of protein-like compounds (%), SUVA (L mg C^{-1} m^{-1}), and a_{320} (m^{-1}). Chl-*a* and a_{320} variables were log-transformed prior to the statistical analyses. All limnological data are archived in Rautio et al. (2021).

We examined phytoplanktonic community composition (presence-absence data) among the compartment factors (two levels; ice and water) using a Bray-Curtis similarity matrix with a one-way permutational multivariate analyses of variance (PERMANOVA, Anderson et al., 2008) run with 999 permutations. We compared the multivariate structure of dissolved and particulate properties (listed above) among the region (three levels; SAG, CB, and WH) and compartment (two levels; ice and water) factors using Euclidian distance matrices with a two-way PERMANOVA (999 permutations). Following the shade plot method (Clarke et al., 2014), the environmental data were log-transformed and normalized prior to analyses. In both univariate and multivariate analyses, when only few permutations were available (in the case of WH region for example) we used a Monte-Carlo procedure to obtain P values. Pairwise (t-test) comparisons were done with the PERMANOVA routine (999 permutations) when differences were detected. We visualized the effects of the treatments using non-metric multidimensional scaling ordinations. We evaluated the contribution of each particulate and dissolved property to the observed distances between water and ice compartments and among regions using a similarity percentage analysis (SIMPER). Analyses were run using PRIMER + PERMANOVA v.7.0.1 (PRIMER-E Ltd., Plymouth, United Kingdom), with a significance level of $\alpha = 0.05$ for all analyses.

3. Results

3.1. Chl-*a* and Algal Species Composition in Ice

Within the ice cores, Chl-*a* was present in all sections in concentrations that varied between 0.01 and 3.0 μg L^{-1} (median and mean values 0.33 and 0.46 μg L^{-1}, respectively; $N = 285$) but the concentrations

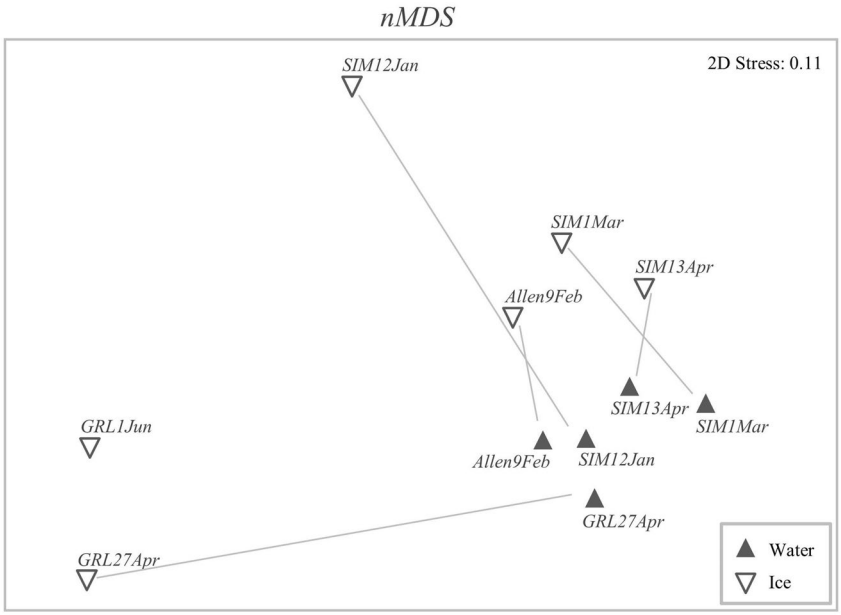

Figure 2. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity (presence-absence of phytoplankton taxa) among samples from water (filled symbols) and ice (empty symbols) for Arctic Lake Greiner (GRL) and boreal lakes Simoncouche (SIM) and Allen. The sampling date is indicated for each sample, and water-ice pairs from the same date are joined with a line. Note that on June 1, 2018, only ice was sampled from Lake Greiner.

did not significantly differ among the water-ice interface, the upper sections and the values for the total core (PER-ANOVA, $F_{3,36} = 1.9$, $P = 0.149$). We therefore show the results from the total ice cores only. The concentrations of Chl-*a* (mean ± SE; μg L^{-1}) in the ice from lakes sampled in SAG, CB, and Ward Hunt were, respectively, 0.85 ± 0.16, 0.03 ± 0.002 and 0.23 ± 0.21 μg L^{-1}. In SAG, the concentration in the ice (0.85 ± 0.16 μg L^{-1}) was significantly higher (*t*-test, $N = 11$, $P = 0.006$) than the concentration in the underlying water (0.3 ± 0.07 μg L^{-1}) (Figure 3a, Table S5).

Phytoplankton taxonomic richness, abundance and biovolume differed between the water and ice (Figure 2, Table S3). A total of 42 taxa were found in the water column and 27 in the ice in the samples that were collected from Lake Simoncouche in January, March, and April. In another boreal lake, Lake Allen, that was sampled for phytoplankton in February, 23 taxa were found in the water and 17 in ice. In Arctic Greiner Lake, 23 taxa were found in the water and only 8 in the ice samples from April to 10 in June. The phytoplankton composition between water and ice compartments was statistically significantly different (PERMANOVA, $P = 0.021$) with compartments explaining 35% of the total variability. Similarity in species composition between ice and water in Lake Simoncouche increased significantly ($N = 3$, Pearson correlation = 0.96; $P < 0.001$) with time with values of 32.4%, 54.2%, and 61.5% for January, March, and April, respectively (Figure 2). All lakes together, 19 taxa were found only in water and 9 only in ice, but no consistent preference for one habitat over the other was observed for any phylum (Table S4). Further, the abundance in ice was often ten-fold less than in water and the ice phytoplankton biovolume was 22%–68% of that in water (Table S3), but Chl-*a* per unit biovolume was higher in ice (Figure S3).

3.2. Particulate and Dissolved Matter in Ice

Particulate matter concentrations in the ice in the SAG and Ward Hunt region lakes were significantly higher (1.81 ± 0.28 and 1.54 ± 0.08 mg DW L^{-1}) than concentrations in the underlying water (0.94 ± 0.15 and 0.48 ± 0.07 mg DW L^{-1}) (Figure 3b, Table S5), indicating that ice may act as carbon pool. Apart from the higher Chl-*a* concentrations in the boreal ice, this organic matter in the ice of all lakes was largely composed of terrestrial carbon, as suggested by the FA composition (Figure 4). The algal FA in the ice had low values (SAG 6%, CB 10%, and WH 12%) and terrestrial FA contributed more (SAG 47%, CB 27%, and WH 16%). In the water, the carbon source was different and dominated by algal FA origin; SAG 39%, CB 67%, and WH

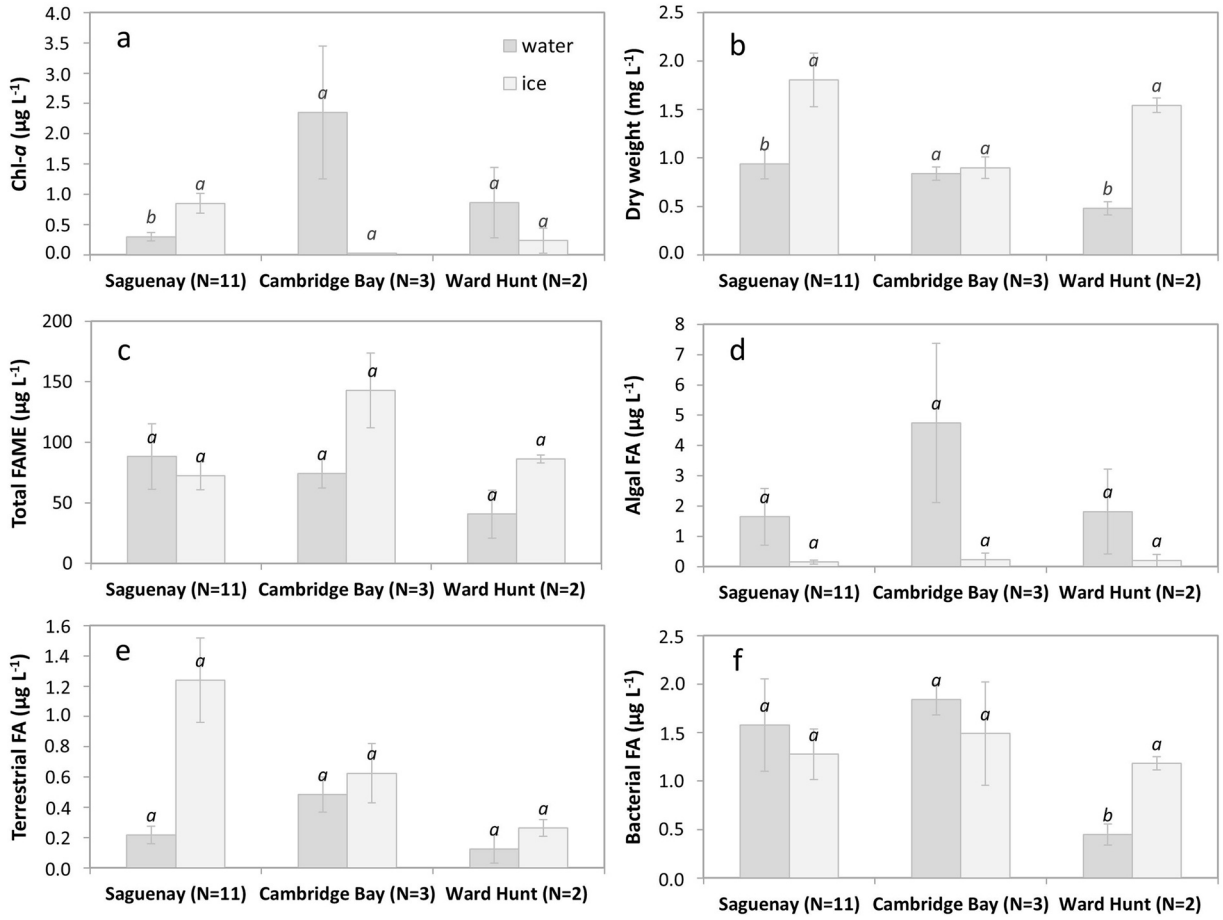

Figure 3. Particulate fraction properties of the water and ice at Saguenay, Cambridge Bay and Ward Hunt areas. Water (dark gray bars) and ice (pale gray bars) concentration of (a) Chl-*a* (µg L^{-1}), (b) dry weight (mg L^{-1}), (c) total fatty acid methyl esters (FAME) (µg L^{-1}), (d) algal fatty acid (FA) (µg L^{-1}), (e) terrestrial FA (µg L^{-1}), and (f) bacterial FA (µg L^{-1}). Ice values are from the total ice cores. Values are means ± standard error. *N* is the number of lakes. Letters above bars indicate the statistically significant differences between ice and water within each region.

76%, indicating an important autochthonous source of the carbon and was composed of a small proportion of terrestrial FA; SAG 24%, CB 7%, and WH 5%, related to a minor allochthonous carbon source (Figure 4).

The dissolved nutrients (SRP and NO_3^-) and dissolved organic carbon were, when significantly different, more concentrated in the water than in the ice (Figure 5, Table S5), indicating exclusion of materials during freeze-up or mineralization beneath the ice cover. The dissolved organic carbon mean values of the water in SAG and CB were significantly higher (6.74 ± 0.78 and 5.31 ± 0.13 mg C L^{-1}) than concentrations in the ice (2.92 ± 0.46 and 0.72 ± 0.08 mg C L^{-1}). In the High Arctic Ward Hunt lakes, DOC concentration was low both in water and ice (0.73 ± 0.11 and 0.31 ± 0.06 mg C L^{-1}). Of the dissolved fractions, the percentage of

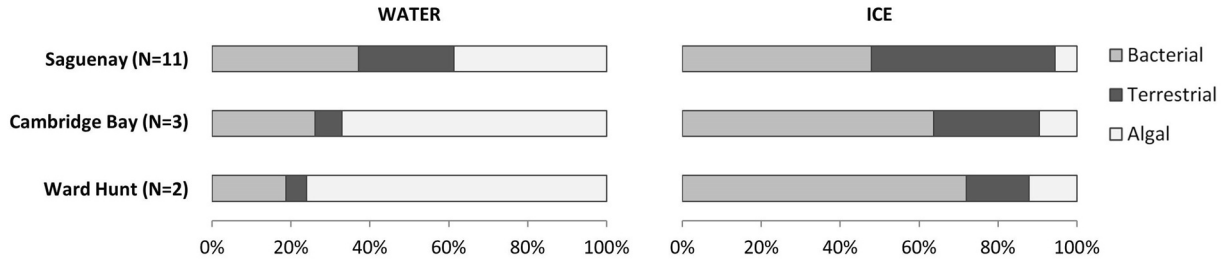

Figure 4. Fatty acid composition (bacterial, terrestrial and algal compounds) of the water and ice of Saguenay, Cambridge Bay, and Ward Hunt areas.

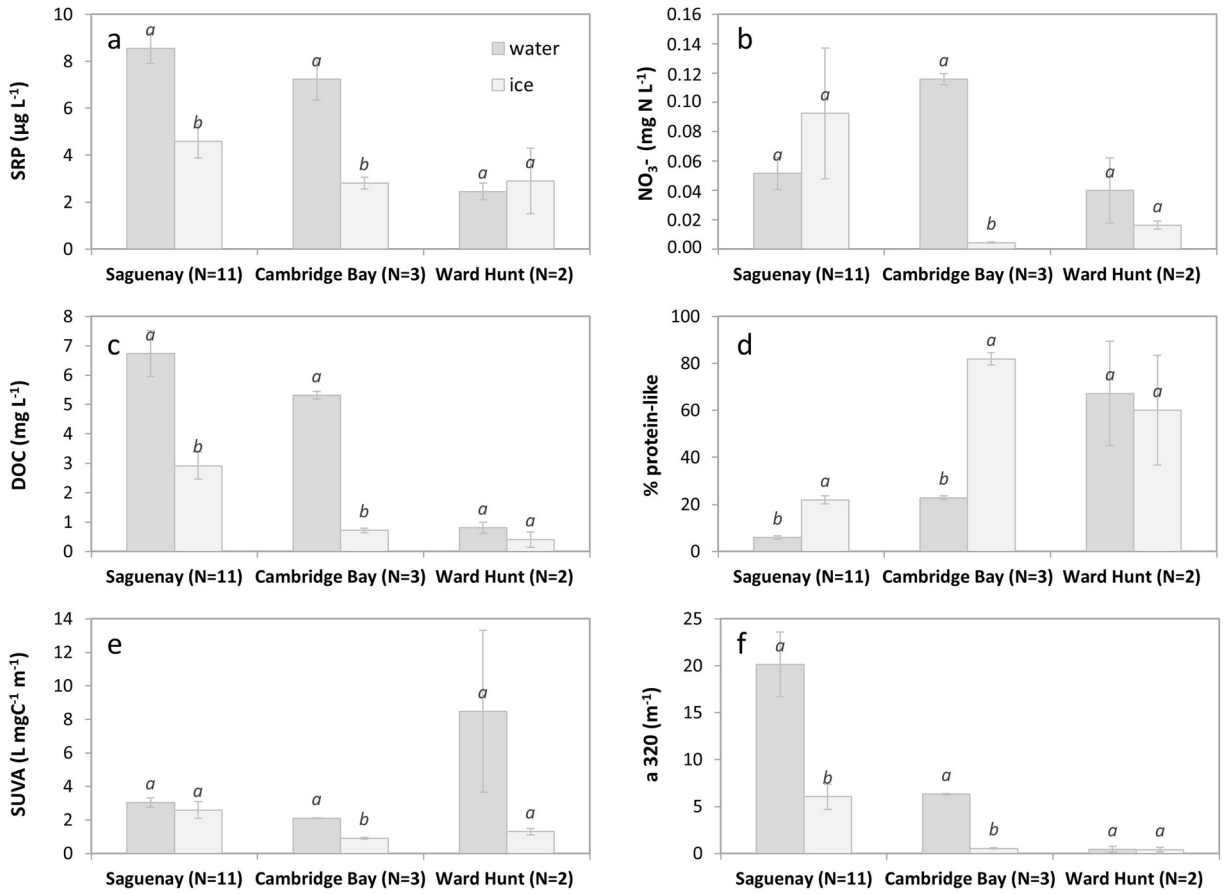

Figure 5. Dissolved fraction properties of the water and ice at Saguenay, Cambridge Bay, and Ward Hunt areas. Water (dark gray bars) and ice (pale gray bars) concentrations of (a) soluble reactive phosphorus (SRP) (µg P L^{-1}), (b) nitrate (NO_3^-) (mg N L^{-1}), (c) dissolved organic carbon (DOC) (mg C L^{-1}), (d) percentage of protein-like compounds, (e) specific ultraviolet absorbance at 254 nm (SUVA, L mgC^{-1} m^{-1}), and (f) absorption coefficient at 320 nm (a_{320}) (m^{-1}). Ice values are from the total ice cores. Values are means ± standard error. *N* is the number of lakes. Letters above bars indicate the statistically significant differences between ice and water within each region.

protein-like compounds was substantially higher in the ice (SAG: 23.0 ± 1.8 vs. 6.2 ± 0.8%; CB: 75.3 ± 2.5 vs. 31.1 ± 0.9%). This shows that a large proportion of the carbon in the ice was composed of biolabile compounds of low molecular weight, while organic carbon in the water was dominated by recalcitrant chromophoric terrestrial compounds (Figures 5d–5f, Table S6). For the Ward Hunt lakes, both the water and ice had a prevalence of protein-like compounds (68.9 ± 5.1%), reflecting the low allochthonous inputs from their polar desert catchments (Bégin, Tanabe, Rautio, et al., 2021).

Collectively, according to the 12 particulate and dissolved properties measured, ice and water from all regions were significantly different (PERMANOVA, $F_{2,24} = 2.94$; $P < 0.001$) (Figure 6). Within regions, the ice and water compartments were different in SAG and in CB (pairwise, $P < 0.001$ and $P = 0.01$ respectively) but not in Ward Hunt region lakes ($P = 0.135$). Overall, the ice and water were mainly differentiated (25% of the difference explained) by the terrestrial FA proportion, dry weight and SRP (Table S7).

3.3. Effect of Seasonality

Light penetration through boreal and Arctic ice followed the same general pattern but with large differences in timing in these two systems, which are located at different latitudes and hence have different exposures to incident light. In boreal Simoncouche Lake (SAG), the ice formed in mid-November (November 12, 2017) and a portion of the light continued to penetrate the ice for about a month until the accumulating snow cover absorbed all light. During the winter, some warming events and rain melted the snow and allowed

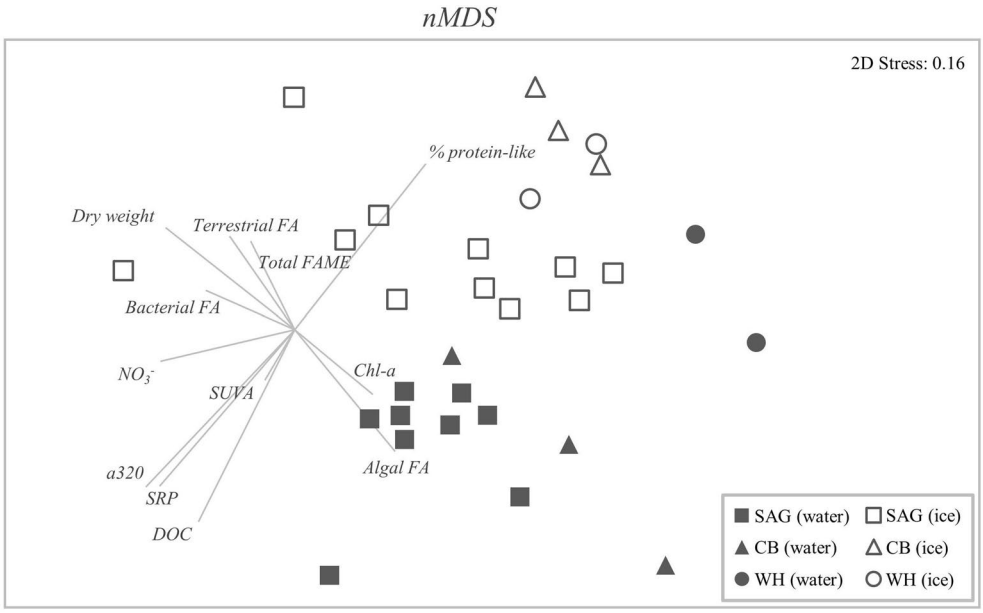

Figure 6. Non-metric multidimensional scaling (nMDS) plot of dissolved and particulate fractions properties of water (filled symbols) and ice (empty symbols) at Saguenay (SAG; squares), Cambridge Bay (CB; triangles), and Ward Hunt Island regions (WH; circles). The length of the vectors represent the Pearson correlation values of contributed variables on the ordination coordinate positions. Data were log transformed and standardized and Euclidian distances were used. Abbreviations are defined in the text.

increased light penetration, as observed on January 12, 2018 (Figure 7a, Figure S4). In late April, when snow melted and the ice became thinner, the light penetration increased, about one month before ice breakup on 11 May. In Arctic Greiner Lake (CB), the ice formed on September 25, 2017 and the light penetration decreased within a month (Figure 7b). In this polar desert region at 69°N, the sun stays below the horizon between November 25 and January 18, and the declining light was a result of a combination of the low zenith angle of the sun and presence of ice. In late May, when the ice started to melt, we measured a rapid increase of the light in the water. The lake was ice-free on June 17, 2018.

Our measurements of dissolved and particulate materials in the ice and water in these northern lakes revealed interesting temporal patterns in winter. Following the diminishing PAR, Chl-*a* concentration in the boreal Lake Simoncouche water decreased from early winter (1.0 μg L^{-1}) to mid-winter (0.3 μg L^{-1}), increasing again just before ice-out (0.7 μg L^{-1}) (Figure 8a). However, only 2 weeks after the ice-out, concentrations were an order of magnitude higher (3.7 μg L^{-1}). The Chl-*a* concentration in the ice in Lake Simoncouche also increased through winter and was higher in the ice than in the water in mid- and late winter with a maximum value of 1.9 μg L^{-1}. In the Arctic lakes, the Chl-*a* concentration in the water was at the same level between September (1.1 μg L^{-1}) and winter (mean winter 1.5 μg/L), and the ice was stable and very low (mean winter 0.1 μg L^{-1}) (Figure 8e).

Seasonal variability in the carbon variables in the ice was greater than that of Chl-*a*, especially in boreal Lake Simoncouche. Over the winter and as the ice cover thickened, we measured in this lake an increase in the terrestrial FA concentration (Figure 8b), a decrease in DOC concentrations (Figure 8c) and increasing proportions of protein-like compounds toward the end of winter (Figure 8d). In other lakes also, protein-like compounds predominated in the ice throughout the winter (Figures 8d and 8h).

4. Discussion

Our observations indicate that biological and biogeochemical materials are present in substantial quantities in the ice cover of northern lakes, and that the particulate and dissolved materials in the ice differ in concentration and composition from those in the underlying lake water. Particulate materials in the ice were

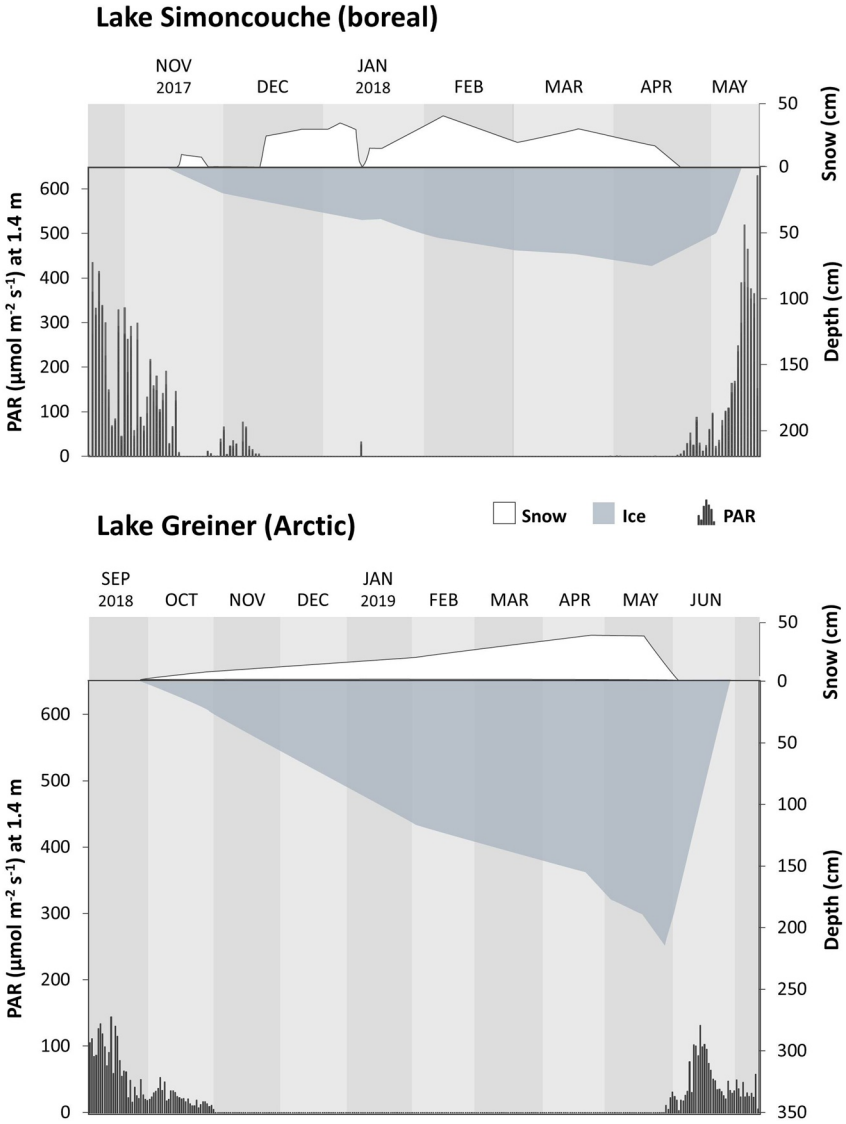

Figure 7. Ice and snow thickness (cm) and photosynthetically active radiation (PAR, µmol m^{-2} s^{-1}) in (a) boreal Lake Simoncouche (mean depth 2.2 m) and (b) Arctic Greiner Lake (mean depth 3.5 m) in winter 2017–2018. PAR data were recorded every 30 min with a Ruskin RBR Maestro at the depth of 1.4 m in Lake Simoncouche and 3.3 m in Lake Greiner.

more concentrated or had similar concentrations than in the water, while dissolved nutrients were mostly excluded from the ice. Ice contained Chl-*a*, phytoplankton, and algal FAs but the dominance of terrestrial and bacterial FAs and microbially derived carbon compounds showed that freshwater ice retains most efficiently detritus and microbes. Overall, these data support the views of Timoshkin (2001) and Hampton et al. (2015), that lake ice acts as a "second bottom," providing habitat complexity and harboring diverse materials and organisms.

Lake ice in all three regions contained around 1 µg L^{-1} of Chl-*a*, which for the boreal lakes was more than in the water but for the Arctic lakes not different from the concentrations in water (Figure 3). Another indicator of algal presence, algal FA biomarkers, showed consistently lower concentrations, by more than an order of magnitude, in the ice versus the water beneath. The large differences among lake waters in seston Chl-*a* and algal FA concentrations are most likely the result of differences in ice quality and PAR penetration. Light transmission through the ice is moderated by the presence or absence of snow cover and the type of ice (Jewson et al., 2009; Leppäranta, 2015). The boreal ice was snow covered and dominated by white

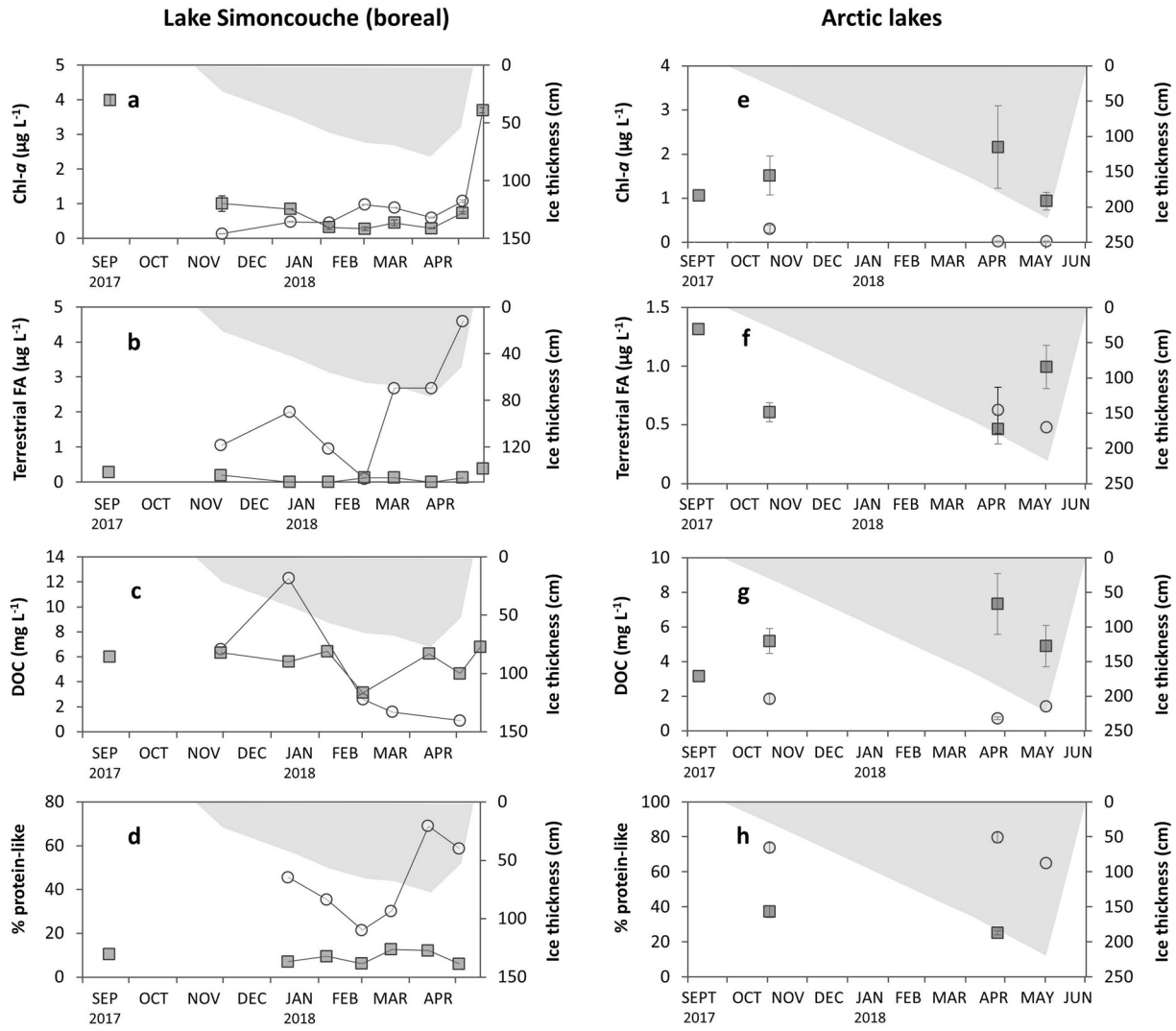

Figure 8. Seasonal changes in boreal Lake Simoncouche and the mean for three Arctic lakes (Greiner Lake, First Lake, and Second Lake, as in Table S1) in (a and e) Chl-*a* concentration (µg L^{-1}), (b and f) terrestrial fatty acid (FA) concentration (µg L^{-1}), (c and g) dissolved organic carbon (DOC) concentration (mg L^{-1}), and (d and h) percentage of protein-like compounds. Dark gray squares are for water and pale gray dots for ice. Ice values are from the total ice cores. The ice cover period, shown as the gray area, was from November to May in Lake Simoncouche and from September to June 2018 in the Arctic lakes.

ice (Figure 1) that has high internal light scattering while the stable sub-zero temperatures and low winter precipitation, typical of polar desert regions in High Arctic Canada, result in the formation of transparent ice observed in CB and WH lakes. Hence, despite the thick ice, PAR penetrated into the water column of the Arctic lakes (Table S1) providing required solar energy to phytoplankton and allowing the higher Chl-*a* concentrations in Arctic lakes than in boreal lakes. Earlier studies have shown light limitation occurs when PAR values fall below the critical light intensity thresholds for photosynthesis (7.6 µmol m^{-2} s^{-1}) and biomass accrual (20 µmol m^{-2} s^{-1}) (Gosselin et al., 1985; Pernica et al., 2017). According to these values, PAR was limiting photosynthesis in all lakes during the main campaign that was in February for the boreal lakes, April for Arctic lakes in CB and July for the lakes at Ward Hunt, however, some of the measures were taken under overcast skies and higher under-ice PAR values have been reported to Arctic lakes in other studies. Continuous PAR recordings under the ice of Ward Hunt Lake have shown that the PAR often reaches levels as high as 100–200 µmol m^{-2} s^{-1} in summer (Bégin, Tanabe, Kumagai, et al., 2021). The under ice Chl-*a* concentrations in Arctic CB lakes were also almost two times higher than values in these lakes in summer (Ayala Borda et al., 2021), further indicating the importance of winter for northern aquatic ecosystems despite the overall low light levels.

Chl-*a* was evenly distributed throughout the lake ice, with no significant difference among the water-ice interface and the upper ice sections. This is different from the usual pattern observed in marine ice where algae are mainly concentrated in a growing ice layer at the interface, resulting in much higher Chl-*a* concentrations near the bottom of sea ice cores than in the upper ice layers (Hsiao, 1980; Leu et al., 2015). Some studies on lake ice have also measured higher Chl-*a* concentrations at the bottom of the ice. String-like diatom aggregations, hanging from the lower side of the ice, have been found in Lake Baikal (Obolkina et al., 2000) and high Chl-*a* concentrations (up to 169 μg L^{-1}) have also been found at the ice-water interface in a shallow fluvial lake in southern Canada (Lake Saint-Pierre, Québec; Frenette et al., 2008) where turbulent resuspension of algae from the lake sediments results from a combination of currents and the shallow depth of the lake. In perennially ice-covered lakes in Antarctica (McMurdo Dry Valley lakes; Priscu et al., 1998), Chl-*a* is most concentrated (1.25 μg L^{-1}) in organic matter aggregates that have been brought to the ice by aeolian processes from outside the lake and which move vertically according to seasonally changing partial melting and freezing of the ice. Thus Chl-*a* concentrations in lake ice can differ enormously among lakes in terms of location within the ice, origin of the cells, and the resultant algal composition. The lack of differences in Chl-*a* concentrations among different sections of the ice in our study may be a result of the homogenizing effect of freeze-up, with continuous formation of black ice from the bottom of the initial ice layers downwards (Leppäranta et al., 2015). In boreal lakes, the alternance of snow and rain precipitation may also have a homogenizing effect if the weight of slush and snow pressing down on the ice results in the upwelling of liquid water through cracks in the ice (Leppäranta, 2015; Saloranta, 2000). It is also possible that Chl-*a* accumulates differently in the ice in different years. For instance, our observations from Lake Simoncouche in March 2016 showed a higher concentration at the ice-water interface (3.3 μg L^{-1}) compared to the upper ice core (<1 μg L^{-1}).

The concentrations of Chl-*a,* we measured in the ice were well below those of usually measured for sea ice. When converted to mg m^{-2} to be able to compare with the sea ice literature, we obtained Chl-*a* values from 0.034 mg m^{-2} in the black ice in Thores Lake (WH region) to 0.94 mg m^{-2} in the more frazil white ice in Lake Allen (SAG region). These values are about a magnitude of order lower than those measured in sea ice. In high-latitude marine systems, ice microalgae are present as soon as the ice forms in the fall (Horner & Schrader, 1982) and the Chl-*a* concentrations vary greatly depending upon the time of the year, location, and portion of the ice core sampled. In Canadian Arctic sea ice sampled by Hsiao (1980), Chl-*a* concentrations varied from 0.023 mg m^{-2} November to 7.58 mg m^{-2} in late May (Hsiao, 1980). These quantities are comparable to other sea ice systems (Leu et al., 2015). The greater presence of algae in sea ice is most likely explained by the difference in ice structure, especially the brine channels that provide favorable microhabitats for the growth of marine ice organisms. With warming winters and increasing prevalence of slush in lake ice (Dibike et al., 2012), the space between icy crystals increases (Ashton, 2011), which may lead to a higher number of microhabitats and subsequent increases in algal abundances in lake ice. In addition, more frequent rain-on-snow events decrease or remove the snow layer that blocks light, which should benefit ice algae. In our study, when snow melted from Lake Simoncouche in January after rain, PAR increased from zero to >20 μmol m^{-2} s^{-1} in the moored underwater radiometer at the depth of 1.4 m, despite cloudy weather (Figure 7).

The higher number of phytoplankton taxa found in boreal ice (23 taxa) compared to Arctic Greiner Lake ice (13 taxa) (Table S3) goes in hand with the regional ice characteristics, and further suggests that the black Arctic ice may be too dense to furnish potential algal habitats while the porous white boreal ice might offer more space for protist communities. A total of 53 phytoplankton taxa were encountered and out of these nine were only found in the ice (Table S4) contributing to separating the ice and water to two different phycological compartments (Figure 2). One possibility is that the taxa unique to ice were seeded by aeolian processes and had their origin outside the lake, as is the case for ice algae in some perennially ice-covered Antarctic lakes (Priscu et al., 1998). A more likely explanation is that these taxa were incorporated into the ice in early winter from the phytoplankton community in the lake at the time, which did not persist in the water at the times of sampling later in winter. We analyzed only 11 phytoplankton samples and some caution is in place due to the low sample number, but it is possible that ice provides an overwintering habitat to certain taxa. The fact that the number of taxa in water declined during the course of winter from 31 to 23 (Lake Simoncouche, Table S3) but remained constant or increased in the ice (16 in the end of winter) indicates that ice is a stable and potentially beneficial habitat to some algae in winter. The high Chl-*a* to

biovolume ratio (Figure S3) further suggests that algae incorporated into ice are smaller but have a higher Chl-*a* content. Small cell size with a high cellular concentration of photosynthetic pigments may be a strategy to persist in cold and low light, as has been previously observed for winter under-ice phytoplankton (Figure 3 in Fournier et al., 2021). It is, however, noteworthy that 19 phytoplankton taxa were entirely missing from the ice and that the overall cell abundance and biovolumes were higher in the water, indicating that not all phytoplankton could be incorporated and potentially overwinter in the ice.

The nine taxa unique to ice were phylogenetically and morphologically diverse, including small diatoms (*Diatoma* sp., *Navicula* sp.), flagellated cells (e.g., *Chrysococcus*), and colonial cyanobacteria (*Coelosphaerium* sp., *Gloecapsa* sp.) (Table S4). We expect the small flagellated, hence motile species, to have been high up in the water column as close to the ice as possible in early winter to harvest the last light that is penetrating through the ice cover, and they might then have been incorporated to the ice as it formed. Bacterial cells are known to be preferentially incorporated into the ice during progressive freezing (Santibáñez et al., 2019), but the incorporation of colonial cyanobacteria was unexpected. Despite the presence of some diatoms in the ice, the generally small algae that were most abundant in lake ice were quite different from the large diatom colonies found in sea ice (Leu et al., 2015). The Arctic Ocean ice harbors diverse algal communities, strongly dominated by pennate diatoms (Poulin et al., 2011; Syvertsen, 1991), with the genera *Nitzschia*, *Navicula,* and *Fragilariopsis* occupying a particularly prominent role (Horner et al., 1992; von Quillfeldt et al., 2009).

The lake ice studied here also stored a substantial amount of nonalgal particulate material. The total dry weight of particulate materials was higher in the ice than in the underlying water in boreal SAG and Arctic WH lakes and equally high between the compartments in CB lakes (Figure 3). Terrestrial and bacteria FA biomarker concentrations and composition between water and ice (Figures 3 and 4) indicated that a large part of the material was terrestrial detritus and heterotrophic bacteria, which with the above algal proxies suggest that lake ice and water are substantially different in the material that they store in winter, with the ice containing more heterotrophic versus autotrophic particulate material (Figure 6).

In places with high snow precipitation such as the SAG boreal lakes region, the mass of snow cover may exceed ice buoyancy, forcing the water to penetrate to the top of the ice through cracks. When the wet snow freezes on top of the ice, it creates snow ice that contains organic carbon from the lake water. The freezing of this slush layer concentrates impurities, creating colored horizontal bands in snow ice that are called humic fingers (Salonen et al., 2010). These humic fingers are not interconnected like the brine channel network in the sea ice and thus do not provide a comparable environment, but they imply that freshwater ice may contain organic carbon that sustains microbial communities. Santibáñez et al. (2019) showed experimentally that bacteria were preferentially incorporated into lake ice during freezing and that this was mainly controlled by the solute concentration of major ions in the liquid water source; the higher the ion concentration in water the more readily the bacteria were incorporated into the ice. Cryoconcentration, the exclusion of solutes when ice freezes, contributes to an increased solute concentration at the ice-water interface (Jansen et al., 2021), which in turn may favor bacterial incorporation into the ice.

Organic material can also come from outside the lake, brought by precipitation, wind or water inflows. Atmospheric dispersal of bacteria is increasingly acknowledged as an important factor influencing bacterial community biodiversity. For example, studies on microbes in High Arctic air and snow have shown that microbiota are widely dispersed via wind and precipitation across the High Arctic and are a common feature of the snow-pack environment (Cuthbertson et al., 2017; Harding et al., 2011). These observations revealed that microbial communities in air and snow contain a mixture of nonliving and living cells. We did not study bacterial sources here, but it is likely that the high proportion of bacterial FA we measured in the ice came from a combination of living and nonliving bacteria that were incorporated into the ice during freezing, deposited onto it with snow precipitation as well as flushed from the watershed with other terrestrial materials during warm temperature events (Figure S4 and Movie S1). The watershed as origin is probably nonnegligible, which would also explain the differences in terrestrial and bacteria FA ratios (Figure 4) among the studied regions. The boreal SAG watersheds comprise trees, plants and high relief, whereas the Arctic CB watersheds are constituted of low-relief tundra and WH region is constituted of bare polar desert soils and high relief. These landscape differences were reflected in the organic matter inputs and the different FA composition of ice among the three regions. The boreal ice was dominated by

terrestrial FA (47%) and toward the treeless Arctic regions, the bacteria FA proportion increased being 72% in the WH region lakes.

Although particulate matter accumulated in the ice during freezing, our results show that dissolved matter was mostly excluded, and separated the ice and water as two distinct compartments (Figure 6). Solute exclusion during the freezing process has long been well known. Belzile et al. (2002) studied different exclusion factors of impurities from ice during freezing process in Canadian lake waters. Their results showed that higher molecular weight DOC was strongly excluded from lake and river ice, which is consistent with our results: we measured higher DOC values in SAG and CB waters than in the ice. Only in January 2018, DOC concentration in the ice exceeded that in water (12.3 vs. 6.4 mg L^{-1}), reflecting the preceding rain event and associated DOM input from the watershed (Figure 8c and Figure S4). The exclusion process also affected other solutes, concordant with the higher SRP and NO_3^- values we measured in the water compared to the ice. As the ice tends to form as pure crystals, it rejects impurities in the freezing process (Schmidt et al., 1991; Wharton et al., 1993). In sea ice, DOM is also partly excluded from ice during freezing, although organic carbon derived from ice algae results in DOC values that are orders of magnitude higher than in the underlying waters (Belzile et al., 2000; Perovich et al., 1998).

The composition of DOM was different between ice and water, and interestingly the DOM in the ice was mostly composed of protein-like low molecular weight compounds (Figures 5 and 6) that are considered biolabile and often attributed to algal production (Stedmon & Markager, 2005) but can also have a microbial origin (Osburn & Stedmon, 2011). While the higher value in ice could be partly explained by the breakup of phytoplankton cells and the release of biolabile compounds, the high bacterial prevalence in the ice (Figure 4) indicates that some of these compounds were from freshly produced organic matter of microbial origin. Santibáñez et al. (2019) recently reported a similar differential incorporation of labile DOM into the ice. It is also known that only low molecular weight compounds are retained when lake water without bacteria freezes (Belzile et al., 2002). This suggests that the dominance of labile low molecular weight compounds in the ice results from a combination of molecular partitioning during ice formation and the initial organic matter composition of the liquid water source. These biolabile carbon compounds in the ice, despite their low concentrations, would likely stimulate microbial production when released from the ice, and subsequently contribute to pelagic food web processes at ice out.

The seasonal observations showed that lake ice and water were biologically and biogeochemically distinct compartments of the lake ecosystem through the entire winter (Figure 8). In boreal Lake Simoncouche and Arctic Greiner Lake, the ice cover reached its maximum about a month before the ice-out when it represented 34% and 61% of the entire water column (ice plus liquid water), as calculated from mean lake depths. In both lakes, the light under the ice increased rapidly when ice started to melt and especially following snowmelt (Figure 7). There was, however, no indication of a spring bloom and higher Chl-*a* concentrations, despite the known light limiting effects of ice and snow cover on phytoplankton growth (Hrycik & Stockwell, 2021). It is likely that our water samples that were taken from the integrated water column prevented us from measuring increases in Chl-*a* that may have been restricted to close to the lit surface by radiative convection that initiates in late winter (Cortés & MacIntyre, 2019), or in subsurface convective cells (Bégin, Tanabe, Rautio, et al., 2021). In the ice, Chl-*a* concentration also remained constant and low through the winter and we did not detect blooms of ice algae that are characteristic of sea ice. Nevertheless, despite the low abundance and biovolume of microalgae in lake ice (Table S3), the phytoplankton cells in the lake ice may be responsible for the initiation of spring phytoplankton production. The phytoplankton composition between water and ice became more similar as the winter advanced and was most similar in mid-April in Lake Simoncouche (Figure 2). This may suggest that the taxa that survived winter in water and ice are key contributors to the spring phytoplankton in this lake, but this requires further study. The cells likely begin to be released from the ice when it begins to melt. Frenette et al. (2008) concluded with growth experiments that the phytoplankton cells that were trapped in the ice in winter were viable and contributed to the spring growth. Future studies are required to test the role of these cells for the initiation of spring phytoplankton production. In the Arctic Ocean, ice microalgae can account for 10%–25% of total annual Arctic primary production (Michel et al., 2002) and play an important role in food webs (Horner & Alexander, 1972; Meguro et al., 1966; Michel et al., 2002), whereas their direct contribution to primary production in lakes is likely to be small.

The seasonality of carbon was more pronounced in winter than that of algae. In boreal Lake Simoncouche, we observed increases in terrestrial FA biomarker concentration in the ice during the winter (Figure 8b). This suggests that new terrestrial materials were frequently incorporated in the ice, probably as organic dust from the surrounding trees as well as from the soils during warm spells. The most apparent of these warm spells occurred on January 12, 2018 when all snow melted from the ice exposing organic matter pools on the ice (Figure S4). The contribution of protein-like dissolved carbon compounds also increased through winter (Figure 8g), pointing to biogeochemical or photochemical (once the snow cover is reduced) transformations that break carbon compounds to more labile forms (Laurion & Mladenov, 2013) that likely become available to microbes in the water column when the ice melts. Clear lake ice such as that found on Ward Hunt Lake allows high transmission of solar ultraviolet radiation (Figure 4 in Bégin, Tanabe, Rautio, et al., 2021), and may be an efficient medium for photochemical breakdown of refractory organic carbon to labile organic carbon, unlike a mixing water column where the exposure to high UV fluxes is intermittent.

5. Conclusions

Winter is the least explored season in ecology, especially for ice-covered ecosystems. Because most northern lakes are shallow (mean depth 3–5 m) with most of their volume freezing during the long winter period, the compounds and organisms trapped in the ice may make a large contribution to the total lake ecosystem. Further, the ice-water interface provides a habitat that sustains biological productivity, much like a secondary benthic environment (Hampton et al., 2015). Collectively, the results showed that lake ice contains Chl-*a*, an inoculum of algal biomass, FAs of diverse origins and potentially biolabile dissolved organic carbon. These materials are released from the ice when the ice melts and may then be incorporated into the planktonic food web. This sudden release of microbial cells and carbon substrates may play a decisive role in the biogeochemical and production cycles of northern lakes and requires closer attention in future studies.

The accumulated materials released from the ice may also increase in the future, as winter rain events and associated runoff from the catchment increase in the boreal regions, and as the permafrost continues to thaw rapidly in the Arctic, exposing new ground to the effect of the wind and wind-blown organic carbon. Rapidly changing freshwater ice may have consequences at a global scale. On average, lake freeze-up has been delayed by approximately one week per hundred years and break-up advanced by a similar or higher rate, resulting in an ice-covered season for northern lakes that is at least two weeks shorter (Magnuson et al., 2000). The ecological and economic consequences of shorter winters and thinning ice and snow cover are some of the key questions in the context of climate change. An important consequence of the decreasing duration of ice cover is its influence on the biological productivity of lakes through carry-over effects from winter to summer (Hampton et al., 2017). The selective retention of particles and labile organic matter observed here indicates that lake ice may set-up effects on ecological processes during the winter-summer transition period of northern lakes.

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Data Availability Statement

The limnological data are available in the northern data repository Nordicana D (http://doi.org/10.5885/45717CE-5A9BFDF1C9064936), CDOM data are archived in OpenFluor (https://openfluor.lablicate.com/of/measurement/4763), and the phytoplankton data are provided in the supporting information.

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