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Special Section:
Winter limnology in a changing world

Key Points:

- Phytoplankton biomass was correlated negatively with dissolved organic carbon under ice but positively during the open-water period
- High phytoplankton biomass under ice, coupled with low dissolved organic carbon led to persistent oxic conditions in the hypolimnion
- Algae growing under ice can provide seeding populations for early spring phytoplankton blooms

Supporting Information:

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

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Under Ice and Early Summer Phytoplankton Dynamics in Two Arctic Lakes with Differing DOC

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Abstract We investigated Arctic lake phytoplankton response along vertical gradients in the water column during seasonal succession from ice-covered to open-water conditions. Two oligotrophic lakes in West Greenland with different dissolved organic carbon (DOC) concentrations were selected. We assessed which factors: (1) promote under-ice growth of phytoplankton, and (2) trigger shifts in the community structure. Our results suggest that DOC is an important driver of the seasonal distribution of phytoplankton biomass—high DOC exacerbates light limitation under ice resulting in low phytoplankton biomass, but supports phytoplankton growth during the open-water period when photolytic and biological degradation of organic matter contributes to the pool of available nutrients. Under-ice phytoplankton biomass in a clear, low DOC lake was as high as during the open-water period, suggesting the importance of under-ice processes for lake metabolic balance, also evidenced by persistent oxic conditions in the hypolimnion. Species composition was dynamic, reflecting rapidly changing conditions over the course of the season. Our data suggest that phytoplankton under ice provides seed populations for early spring blooms and that the largest shifts in species composition occur later during the summer, likely as a result of nutrient depletion and intensified grazing pressure. Early spring temperatures in West Greenland have risen rapidly in recent decades, triggering shifts in the timing of lake ice-out and the onset of stratification; therefore, it is important to understand phytoplankton seasonal dynamics to disentangle the effects of climate-driven shifts on aquatic biota.

Plain Language Summary Arctic lakes are ice-covered for a substantial portion of the year. However, despite ongoing changes in winter climate patterns and the length of the ice-covered period, there is only limited understanding of the drivers of under-ice Arctic phytoplankton ecology. Simultaneous with warming winters and shifts in the timing of spring ice melt, concentration of dissolved organic matter that affects water transparency and nutrient content in lakes also changes. To understand how these factors affect phytoplankton communities, we studied their responses to seasonal changes in two lakes with differing dissolved organic carbon (DOC) concentrations located in West Greenland. Under-ice phytoplankton biomass in the low-DOC lake was as high as during the open-water period but it was very low in the high-DOC lake, likely as a result of strong light limitation. High phytoplankton biomass in the low-DOC lake was coupled with oxic conditions under ice, implying consequences for the volume of greenhouse gas emissions upon ice out that are more likely to accumulate under oxygen-depleted conditions. Together, our results suggest that differences in DOC concentration can have consequences for seasonal distribution of phytoplankton, and underscore the importance of under-ice period—especially in clear Arctic lakes

1. Introduction

The Arctic is covered with lakes that freeze over for a significant part of the year. Ice formation leads to the establishment of a distinct environment within the lake relative to the open-water period by limiting gas exchange at the air-water interface, wind-driven mixing (Denfeld et al., 2018), allochthonous input of terrestrial carbon and nutrients (Bertilsson et al., 2013), and also reducing the amount of light penetrating through the water column (Kirillin et al., 2012). All of these factors—light penetration, nutrient concentrations, and thermal structure of the water column—affect biomass and community structure of phytoplankton. Despite the fact that ice covers Arctic lakes for the majority of the annual cycle, most of what we know about phytoplankton communities and biogeochemical dynamics in these lakes is based on the open-water season. Considering the rapid changes in climate affecting phenology, ice-out dates, and abiotic conditions

(Saros et al., 2019), it is desirable to further understand the temporal dynamics of phytoplankton in Arctic lakes because shifts in the magnitude and timing of blooms affect the transfer of energy through aquatic food webs as well as biogeochemical processes—ultimately having consequences for carbon cycling across the landscape.

It has long been recognized that insufficient light penetration through the ice cover is a major factor limiting the growth of phototrophs under ice (e.g., Fritsen & Priscu, 1999; Hampton et al., 2017; Pennak, 1968; Salonen et al., 2009). In high latitudes, irradiance during late winter and early spring hits the surface of lakes at a low angle of incidence, leading to high scattering and overall lower radiation intensity. Further, the quantity of light available to planktonic photosynthetic organisms is dependent on the thickness of snow cover if present, and the quality of ice itself—while clear ice is highly transparent, impurities trapped in ice (e.g., gas bubbles, dust particles) lead to increased scattering (Kirillin et al., 2012; Warren, 2019). Light availability is further diminished through absorption by solutes, such as dissolved organic matter (DOM), present in the water column. Provided that higher concentrations of DOM are expected under the ice as solutes are expelled from freezing water during ice formation (Belzile et al., 2001), and that the humic fraction of DOM is preferentially excluded from ice (Santibáñez et al., 2019), light penetration will likely be substantially affected. At the end of the ice-covered period, the light environment that phytoplankton are exposed to is also affected by under-ice convective mixing which has consequences for growth rates and vertical distribution of primary producers (Bengtsson, 1996; Bouffard & Wüest, 2019; Pernica et al., 2017; Vehmaa & Salonen, 2009).

During the period of ice cover when lakes are largely isolated from atmospheric and terrestrial subsidies, internal biogeochemical cycling becomes the main source of nutrients supporting primary production. Despite the lack of external inputs, concentrations of dissolved, biologically available forms of nitrogen (N) (ammonium, NH_4^+, nitrate, NO_3^-) tend to accumulate in lakes under ice compared to the open-water season (Catalan, 1992; Powers, Baulch, et al., 2017). Bacterial degradation and mineralization of DOM from senescent organisms results in increasing concentrations of NH_4^+, providing a substrate for nitrification. Recent studies show that nitrification under ice is active, stimulated by higher concentrations of NH_4^+ and elevated abundances of microorganisms involved in ammonia oxidation (Cavaliere & Baulch, 2019; Massé et al., 2019), while denitrification rates may remain stable relative to the open-water period (Cavaliere & Baulch, 2018). Both degradation of organic matter and nitrification contribute to the development of anoxia at the water-sediment interface, creating favorable conditions for release of reactive phosphorus (Knowles & Lean, 1987; Mathias & Barica, 1980; Nürnberg et al., 1986; Powers, et al., 2017). If severe light limitation inhibits phytoplankton growth under ice, dissolved nutrients can accumulate and fuel spring phytoplankton blooms; however, if the light environment under ice is favorable, increased nutrient uptake by phytoplankton could alter nutrient availability during the open-water period.

To improve our understanding of temporal shifts in phytoplankton biomass and community structure in Arctic lakes, we also have to consider the dynamics of DOM—a key variable that simultaneously affects both light penetration (Karlsson et al., 2009; Saros et al., 2016) and the nutrient budget (Seekell et al., 2015; Tranvik, 1992; Tranvik & Bertilsson, 2001). In the Arctic, inputs of terrestrial organic matter from degrading permafrost have been increasing in many regions (Wauthy et al., 2018). However, a decreasing trend in lake water dissolved organic carbon (DOC) concentrations was documented in some West Greenland lakes within the past decade, possibly as a result of climate-driven reduction in terrestrial subsidies (Saros et al., 2015, 2019). Besides long-term trends, the quantity and quality of the DOM pool also changes seasonally with inputs of allochthonous and autochthonous OM and losses due to photolysis and bacterial degradation (Cory & Kling, 2018; Guillemette & del Giorgio, 2012; Osburn et al., 2017; Solomon et al., 2015). For example, as a result of low connectivity and high residence time which allow for extended DOM processing, lakes in West Greeenland are essentially colorless despite high concentrations of DOC recorded during the open-water season (Anderson & Stedmon, 2007; Osburn et al., 2017). Even higher concentrations were measured under ice and DOM exhibited signs of a high degree of degradation (Osburn et al., 2017; Whiteford et al., 2016). Although there is some evidence that transformations of DOM occur under ice during winter (Miller & McKnight, 2010; Rue et al., 2020), little is known about how seasonal dynamics of DOM affects composition and growth of primary producers (but see Arvola & Kankaala, 1989).

In lakes covered with ice, the low light environment is coupled with cold temperatures; these harsh conditions likely represent a strong environmental filter for both autotrophs and heterotrophs and have consequences for the community composition of plankton and food web interactions. While low temperatures will curb metabolic rates of heterotrophs, phototrophic organisms are more strongly limited by the lack of light (López-Urrutia et al., 2006; Rose & Caron, 2007). Many Arctic planktonic taxa are adapted to the harsh, cold-water temperatures they are exposed to under ice (Bertilsson et al., 2013; Richardson et al., 2000; Ruuskanen et al., 2020); however, the ability of phytoplankton to withstand cold and low-light conditions is coupled with higher nutrient requirements (Rhee & Gotham, 1981; Spilling et al., 2015). Hence, abiotic conditions associated with the under ice period will likely have consequences for phytoplankton community composition and its seasonal dynamics. For example, mixotrophic algae that are capable of combining phototrophic and heterotrophic metabolic strategies tend to be abundant when resources, either light or nutrient, are limiting (Mitra et al., 2016; Stoecker, 1998). Indeed, mixotrophic algae such as chrysophytes, cryptophytes, haptophytes, and dinoflagellates are common in oligotrophic Arctic lakes, both under ice and during the open water season (Brutemark et al., 2006; St. Pierre et al., 2019; Theroux et al., 2012; Whiteford et al., 2016). Their ability to switch from phototrophy to using organic carbon, either in the form of DOM or prey, not only contributes to internal nutrient cycling, but also allows mixotrophs to connect higher trophic levels to alternative resources (Jones, 2000).

It is also important to acknowledge the role of vertical variability for seasonal dynamics in lakes. For phytoplankton, the optimal conditions for phototrophic growth are spatially mismatched—the hypolimnion, where nutrient availability is high is also the most severely light limited (Klausmeier & Litchman, 2001). Under the ice, vertical heterogeneity of the water column is further strengthened by the overall lower light penetration and diffusion of solutes from the sediments, contributing to the establishment of strong physico-chemical gradients (Bengtsson, 1996; Bertilsson et al., 2013). Shifts in environmental conditions, both vertically across the water column, and seasonally, have consequences for phytoplankton community structure and biomass distribution (Litchman et al., 2010; Reynolds, 2006; Sommer et al., 1986), underscoring the importance of studying processes in lakes simultaneously at both spatial and temporal scales.

The objective of our study was to understand seasonal dynamics of phytoplankton biomass and community structure during the succession from ice covered to open-water conditions in two oligotrophic Arctic lakes with different DOC concentrations that are representative of a suite of lakes in West Greenland. Specifically, we assessed which factors promote under-ice growth of phytoplankton and trigger shifts in the community structure over time and along vertical gradients within the water column. First, we hypothesized that under-ice phytoplankton biomass will be lower in a lake with higher DOC, which exacerbates light limitation already imposed by the presence of ice cover. While we expected that phytoplankton biomass under ice will be relatively higher in the low DOC lake, biomass will likely be lower during the open-water period resulting from more severe nutrient limitation. Second, we hypothesized that the largest shifts in phytoplankton community structure would occur upon ice melt when light penetration is deeper and when terrestrial nutrient subsidies can reach the lake, boosting the overall growth of phytoplankton and potentially creating conditions suitable for different phytoplankton species. Lastly, due to the overall lower availability of light under ice in both lakes, we expected greater prevalence of mixotrophic algae relative to the open-water period when autotrophy would be a more favorable way of acquiring carbon.

2. Materials and Methods

2.1. Study Site

The Kangerlussuaq region (Søndre Strømfjord in Danish) is located around 67°N in West Greenland (Figure 1). The region has continental, subarctic climate with negative effective precipitation (precipitation less than 200 mm) and mean June temperature of 10.5°C (Saros et al., 2016, 2019). The bedrock within the area mostly consists of granodioritic gneisses and tundra vegetation dominated by *Betula nana*, *Salix glauca*, *Vaccinium* spp., *Empetrum nigrum*, and grasses prevails across the region. There are about 20,000 lakes in the ice-free area of continuous permafrost between the coast and the Greenland Ice Sheet (Figure 1), most of them oligotrophic and chemically dilute with limited hydrologic connectivity (Anderson & Stedmon, 2007; Anderson et al., 2002; Johansson et al., 2015). The lakes are ice covered on average for 8 months with a short open-water season starting in late May/mid-June and ending usually in late September/early

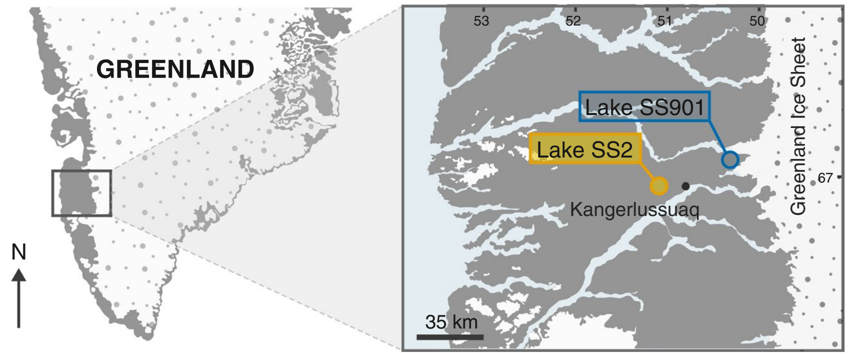


Figure 1. Map of the sampling area. Right panel shows the position of study lakes relative to the Greenland Ice Sheet and the coast. Lake SS901 (low dissolved organic carbon [DOC], in blue) is located closer to the ice sheet in a cooler and wetter microclimate and Lake SS2 (high DOC, in orange) is located in a warmer and drier area inland.

October (Anderson & Brodersen, 2001). Lake ice is usually snow-free due to low precipitation, sublimation, and high-speed katabatic winds from the Greenland Ice Sheet.

The selected study lakes, SS2 and SS901, are located along a temperature-precipitation gradient, with cooler and wetter climate closer by the ice sheet (Lake SS901), and warmer and drier climate inland (Lake SS2) (Figure 1; Fowler et al., 2020). Lakes are comparable in size, depth, and lake water nutrient concentrations, but differ in their concentrations of DOC which affects light penetration (Table 1; Saros et al., 2016). DOC concentrations are generally relatively high across lakes located inland due to high residence time and low effective precipitation; however, during the open-water period, these lakes are not humic-stained (Anderson & Stedmon, 2007; Osburn et al., 2017). Both lakes are fishless.

2.2. Collection of Samples

Sampling of both lakes was conducted in 2019 from April to July, from late under-ice period to midsummer. Lake ice-out in 2019 occurred more than 2 weeks earlier than usual and it was followed by an immediate establishment of thermally stratified conditions. Ice-out in Lake SS2 happened on May 21 and on May 25 in Lake SS901. During the first visit to lakes in April, high frequency in situ monitoring sensors were deployed, attached to an under-ice string with a buoy below the maximum ice thickness depth to reduce drag associated with ice breakup (Block et al., 2019). With lakes by the ice sheet having thicker ice, the buoy in Lake SS901 was deployed about 1 m deeper relative to that in Lake SS2. Each string had a light sensor (PME miniPAR) attached 1 m below the buoy, a dissolved oxygen (DO) sensor (PME miniDOT) attached 1 m above the sediments, and temperature/light loggers (Onset HOBO pendants) were clipped every 1 m along the length of the string. All loggers recorded measurements hourly. In Lake SS2, the sensors were deployed on April 16 (ice thickness = 87 cm) and retrieved on July 6. In Lake SS901, the sensors were deployed on April 17 (ice thickness = 120 cm) and retrieved on July 4. Considering the difference in miniPAR sensor depths in the two lakes, absolute photosynthetically active radiation (PAR) values should not be directly compared between the two lakes; however, these high-quality measurements offer relative comparison of seasonal

Table 1

Summary of Physical and Chemical Variables Measured in Epilimnion During Stratified, Open-Water Conditions Between 2013 and 2018

Lake	Surface area (km^2)*	Depth (m)*	1% PAR (m)	Z epi (m)	DOC (mg.L^{-1})	Chl-*a* (μg.L^{-1})	DIN (μg.L^{-1})	TP (μg.L^{-1})
SS2	0.368	12	9.0 ± 1.1	5.4 ± 1.5	25.9 ± 1.8	1.7 ± 0.6	7 ± 3.8	4.9 ± 2.2
SS901	0.106	15	11.8 ± 1.6	5.5 ± 1.7	7.8 ± 0.2	1.3 ± 0.5	7.25 ± 3.8	6 ± 2.2

Note. Variables are summarized as mean ± SD when applicable. * denotes data from Saros et al. (2016). 1% PAR = depth of 1% attenuation of photosynthetically active radiation; Z epi = depth of epilimnion; DOC = dissolved organic carbon; Chl-*a* = concentration of chlorophyll-*a*; DIN = dissolved inorganic nitrogen (NH_4^+ + NO_3^-); TP = total phosphorus.

trends in irradiance between lakes. For relative comparison of irradiance at different depths, we used light data collected by HOBO light sensors. We also used these measurements to calculate light attenuation coefficient (K_d) using the following equation (Kirk, 2011):

$$K_d = \frac{1}{z_2 - z_1} \times ln \frac{E_d(z_1)}{E_d(z_2)}$$

where E_d is irradiance measured at depths z_1 (3 m) and z_2 (8 m).

We visited lakes on an approximately weekly basis to collect water samples for phytoplankton enumeration and for water chemistry analyses; however, sampling was bound to logistical and safety constraints. Since ice-out happened unusually early in 2019, we were able to sample lakes twice under the ice as moating started in early May, making further under-ice sampling unsafe. We started collecting samples immediately after ice-out in Lake SS901 on May 25, and one day before ice-out in Lake SS2 on May 20. Lake SS2 was sampled 3x after ice-out in late May, and 3x during midsummer sampling (June/July). Lake SS901 was sampled 2x shortly after ice-out, and only 1x in early July because the area was temporarily inaccessible due to the presence of a polar bear. These periods of sampling are hereafter referred to as “under ice”: April 22–29, “early”: May 20–31, and “midsummer”: June 24–July 6. Water samples were collected using a Van Dorn bottle from three depths that were selected to correspond to typical depths of the epilimnion, metalimnion, and hypolimnion during stratified conditions. During each sampling event, we also profiled lakes using a TurnerDesigns C3 probe fitted with chlorophyll (fluorescence in red and blue light spectra) and fDOM sensors.

2.3. Water Chemistry Analysis

To estimate concentrations of dissolved inorganic nutrients (NH_4^+, NO_3^-, and SRP) and DOC, water was filtered through 0.7 μm Whatman glass fiber filters prerinsed with deionized water. Water samples for dissolved silica were filtered through 0.45 μm polypropylene filters. Following standard methods, the phenate method was used to determine the concentration of NH_4^+, cadmium reduction method was used for NO_3^-, ascorbic acid method for SRP, and heteropoly blue method for dissolved Si. Total nutrient concentrations (TN, total phosphorus [TP]) were estimated from an unfiltered, whole water sample using persulfate digestion (American Public Health Association (APHA), 2000). Concentrations were determined on a Lachat QuickChem 8500 analyzer. Concentration of DOC was determined using a Shimadzu TOC-5000 total organic carbon analyzer by high-temperature catalytic oxidation. For each DOC sample, spectral absorbance between 220 and 700 nm was measured on a Varian Cary-300 UV spectrophotometer (Agilent Technologies, Santa Clara, CA) using 1 cm quartz cells and common qualitative metrics were calculated (for complete methods, see Text S1). Only acid-washed labware was used to handle water samples for nutrient and DOC analyses and samples were refrigerated until analysis at the University of Maine. Specific conductivity was measured at 25°C using a YSI 3253 conductivity cell (Yellow Springs, OH).

2.4. Pigment Analysis

Water samples for determining the concentration of chlorophyll-*a* and accessory pigments were filtered through 0.7 μm Whatman glass fiber filters, one filter was used for determining chlorophyll-*a* concentration, and the second for quantification of pigments using high-performance liquid chromatography (HPLC). Pigment concentrations were not quantified for the first under-ice sampling events, instead, chlorophyll-*a* concentration was duplicated. Filters were immediately wrapped in aluminum foil and stored at −20°C at the field station in Kangerlussuaq until analysis at the University of Maine. Using standard methods (American Public Health Association (APHA), 2000), chlorophyll-*a* was extracted in 90% acetone, purified by centrifugation and its concentration was determined with a Varian Cary-50 UV-VIS spectrophotometer (Agilent Technologies, Santa Clara, CA).

Accessory algal pigments were quantified using HPLC, following a modified methodology in Chen et al. (2001). Briefly, pigments were extracted overnight at 4°C in a solvent mixture of acetone, methanol, and water (80:15:5), followed by filtration through 0.22 μm PTFE syringe filters. Filtered extracts were dried under N_2 gas and stored at −20°C until injection (no longer than 2 weeks). Prior to injection into the Agilent 1200 Series HPLC unit (Agilent Technologies, Santa Clara, CA) equipped with Hypersil ODS column (5 μm particle size, 250 × 4.6 mm; ThermoFisher Scientific; Waltham, MA), dried extracts were redissolved in 600 μL of a 70:25:5 mixture of acetone, ion pairing reagent (0.75 g tetrabutyl ammonium acetate and 7.7 g ammonium acetate in 100 ml water), and methanol. We quantified the following pigments: chlorophylls *a*, *b*, c_2, c_3, phaeophytins *a*, *b*, β-carotene, phaeophorbide *a*, neoxanthin, violaxanthin, lutein/zeaxanthin, fuxoxanthin, diadinoxanthin, diatoxanthin, alloxanthin, peridinin, aphanizophyll, myxoxanthophyll, canthaxanthin, and echinenone. The analysis of common photosynthetic algal pigments provides an additional proxy for phytoplankton biomass, an especially useful one when biomass is low. Moreover, some pigments are specific to phytoplankton groups (e.g., alloxanthin (Cryptophyta), peridinin (Dinophyta); McGowan, 2007), allowing us to glean insight into community structure. Commercial standards were used to calibrate peak areas (DHI Denmark). Pigment concentrations are reported in nmol. L^{-1}.

2.5. Phytoplankton and Zooplankton Sampling and Enumeration

Approximately 50 ml of sample from each sampling depth was preserved in Lugol's solution and stored in the dark for phytoplankton identification. Depending on phytoplankton cell density, between 20 and 30 mL of sample was settled in an Utermöhl chamber overnight. Phytoplankton was counted along two transects at 600x using a Nikon TS100 inverted microscope. More transects were counted in samples, where phytoplankton cell density was very low (e.g., under-ice samples) to better characterize the community. Between 200 and 500 cells were counted for the majority of the samples; however, cell counts were lower for under-ice samples (median = 65 cells) and higher during blooms (>1,000 cells). Cell counts were converted to cell densities per mL and biovolume, taking into account the number of transects counted and volume of water settled (Hillebrand et al., 1999). Individuals were identified to the lowest taxonomic level possible—in most cases to species level; however, when it was not possible we at least distinguished between morphotypes. The final list included 136 taxa. For identification of phytoplankton, we used Komárek and Fott (1985), Komárek and Anagnostidis (1999, 2005), Komárek (2013), Kristiansen and Preisig (2007), Coesel and Meesters (2007), Carty (2014). For each identified alga, we determined its capacity for mixotrophy based on available literature (Reynolds, 2006; Sanders, 1991). We chose to focus on these traits as they can provide further insight into factors structuring the communities throughout the season. Contributions of mixotrophs in each sample were calculated as proportions from total biomass and cell density.

Zooplankton vertical tow samples were collected with a plankton net (80 μm mesh size) during every sampling event from the same depth as hypolimnetic Van Dorn samples. During most sampling events that was 8 m in Lake SS2 and 10 m in Lake SS901. Vertical tow samples were used to describe species composition of the zooplankton community and structural changes over the course of the sampling season. Zooplankton were counted in Bogrov chambers under 100x magnification identified to the lowest taxonomic level possible (usually species-level), but some individuals could only be reliably identified to the family level (e.g., female Copepoda, nauplii). At minimum, 100 individuals were counted. We used Haney et al. (2013) to identify zooplankton. In order to have a better understanding of quantitative changes, we counted individuals that were filtered onto a 150 μm Nitex mesh from 2 L of water collected using a Van Dorn bottle at each sampling depth. These individuals were only identified to the level of phylum (as either Cladocera or Copepoda; Rotifera were not retained on a mesh this size) and reported as ind. L^{-1}. Density and composition of zooplankton has an effect on size distribution of phytoplankton (Bergquist et al., 1985). Therefore, to describe the effect of zooplankton on phytoplankton communities, we characterized each sample by an abundance-weighted average of the greatest axial linear dimension (GALD, μm). GALD was measured for each phytoplankton taxa (~10 cells per taxon were measured if possible).

2.6. Statistical Analyses

To visualize seasonal variability of phytoplankton assemblages in 2D space, a nonmetric multidimensional scaling (nMDS) with Morisita-Horn distance measure was computed by function *metaMDS* as implemented in the vegan package (Oksanen et al., 2017). Morisita-Horn is a suitable measure of similarity for datasets where under-sampling might be an issue as it places more emphasis on dominant species (Jost et al., 2011). Differences in phytoplankton community composition between lakes and across time periods, under ice, early, midsummer, were assessed by PERMANOVA with 999 permutations using function *adonis2* (Anderson, 2017; Oksanen et al., 2017). To test if the assumption of within-group homogeneity of variance was violated, we used *betadisper* with bias correction (i.e., multivariate analogue to Levene's test; Oksanen et al., 2017). *Betadisper* function calculates within group distance between centroids (i.e., dispersion) and compares mean distances across groups. Whether there were significant differences across groups was assessed using pair-wise permutations. Ordinations were also performed separately for each lake to grasp differences in the structure of phytoplankton across seasons. To reduce variability associated with rare taxa, only species with more than two occurrences or more than 20% of relative abundance in one sample were used for lakewise ordinations. To ease the interpretation of the ordinations, *envfit* function (*vegan* package) was used to fit vectors of environmental and biological variables ($p < 0.05$) onto the plot, their significance was assessed using permutations ($n = 999$).

In order to further understand shifts in species composition in each lake over the course of the sampling season and to address our second hypothesis, we calculated temporal changes in β-diversity between sampling events (i.e., similarity between first and second and second and third, …) from each lake using Jaccard dissimilarity index based on presence-absence of taxa. To alleviate issues with uneven characterization of the community, we binned samples from epilimnion, metalimnion, and hypolimnion for each sampling event to better capture the community composition in each lake at each sampling point. However, seasonal changes in phytoplankton cell density can partly contribute to the estimates of β-diversity shifts. We used the *betapart* package (Baselga et al., 2018) to decompose β-diversity into nestedness (i.e., losses of species over time as a result of changes in species richness), and replacement (i.e., simultaneous losses and gains of different species) components (Legendre, 2014). While nMDS helps us understand how do phytoplankton assemblages vary between lakes and over time, this approach allows us to glean further insight in how the dynamics of phytoplankton vary between each time points, providing an opportunity to assess how major environmental changes, for example, ice-out, affect species composition.

To provide insight into relationships between environmental variables and phytoplankton metrics and to assess our first hypothesis, we used Spearman rank correlation. To understand whether these relationships change in magnitude and/or direction over the course of the season, the correlations were performed separately for under ice ($n = 12$) and open-water periods (early, $n = 15$, midsummer, $n = 12$), using samples from both lakes and depths. We treat samples from different depths of the water column, as if they were independent for the sake of this exploratory analysis as it is often the case that both environmental conditions and metrics of phytoplankton vary substantially from top to bottom of lakes. We calculated Spearman's ρ because relationships between variables were not monotonic and environmental data were not normally distributed; therefore, nonparametric approach was suitable to describe the covariance between variables of interest (Sokal & Rohlf, 2012). All statistical analyses were performed using R version 3.5.1 (R Development Core Team, 2018).

3. Results

3.1. Seasonal and Vertical Changes in Physico-Chemical Factors

Mean under-ice PAR was about 37% of mean open-water irradiance in both lakes; however, the level of irradiance under ice was dynamic. It was comparable to open-water values about three weeks before ice-out followed by very low light environment shortly before ice-out (Figure 2a). After ice-out, PAR increased and was relatively stable in both lakes with the photic zone extending to 50%–98% of the water column in Lake SS2 and 81%–100% in Lake SS901. Compared to Lake SS2, HOBO light measurements suggest that under-ice irradiance was only slightly higher at 3 m depth in SS901, on average 1.2-fold higher during the under-ice sampling period but doubled if the whole under-ice period was considered (Figure 2a; complete HOBO vertical profiles in Figure S1a). Light attenuation was greater in Lake SS2 relative to Lake SS901 ($K_d = 0.53$, and 0.23 m^{-1}, respectively) and irradiance recorded at 9 m depth of the water column was almost 3x higher in Lake SS901 during the period of under-ice sampling. The hypolimnion of Lake SS2 was anoxic under ice, while in Lake SS901 the mean DO concentration was 9.2 ± 2.7 $mg.L^{-1}$ which further increased to ∼12 $mg.L^{-1}$ 3 weeks before ice-out, coinciding with the under-ice peak in irradiance (Figure 2b). Hypolimnetic DO in Lake SS2 increased to a mean concentration of 5.7 ± 1.1 $mg.L^{-1}$ upon ice-out which was likely a result of an incomplete mixing event (Figure S1b). Both lakes were clearly stratified within a week after ice-out (Figures 3c and 3f).

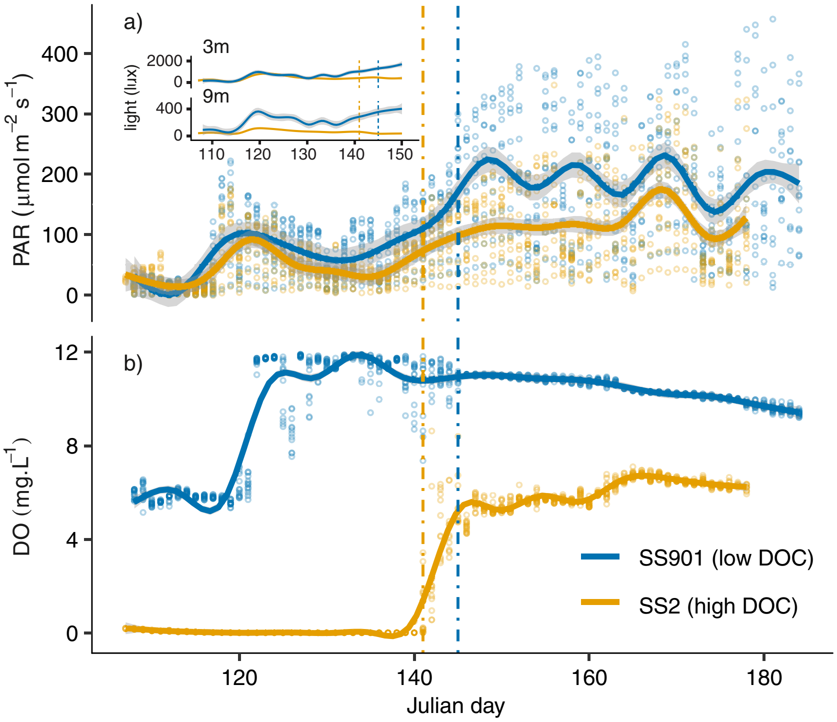


Figure 2. Time series of (a) photosynthetically active radiation (PAR), and (b) hypolimnetic dissolved oxygen (DO) data collected from each lake (SS901 = blue, SS2 = orange) from April 17 to July 3, 2019. The depth of the PAR sensor was approximately 4 m in Lake SS901 and 3 m in Lake SS2. Inset of panel (a) shows relative light intensity measured by HOBO sensors at 3 and 9 m in each lake. Dashed vertical lines designate timing of ice-out for each lake (SS901 = blue, SS2 = orange). Only daytime (defined as between 7:00 and 20:00) data are shown.

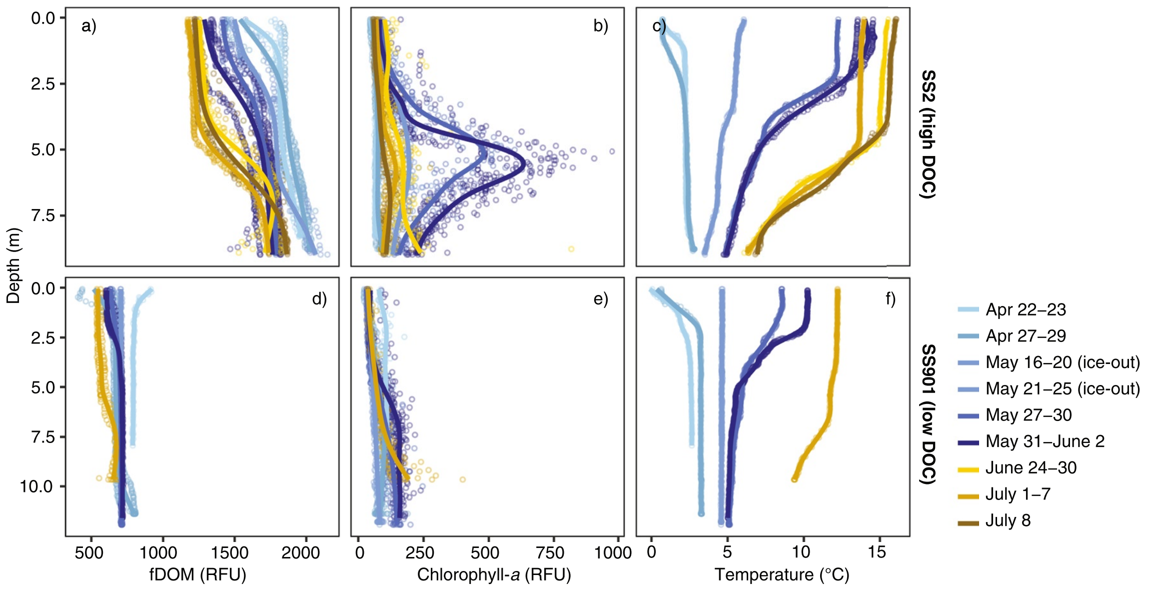


Figure 3. Vertical profiles of fDOM (a, d), chlorophyll-*a* fluorescence (b, e), and temperature (c, f) collected from Lake SS2 (upper panels) and Lake SS901 (lower panels). Fluorescent DOM decreases over the course of the season in both lakes (a, d), while chlorophyll fluorescence reaches peak at mid-depths within 2 weeks from ice-out (b, e). Both lakes thermally stratified immediately following ice-out (c, f). Note that only one midsummer profile is available for Lake SS901 due to logistical constraints in the field (see Section 2.2).

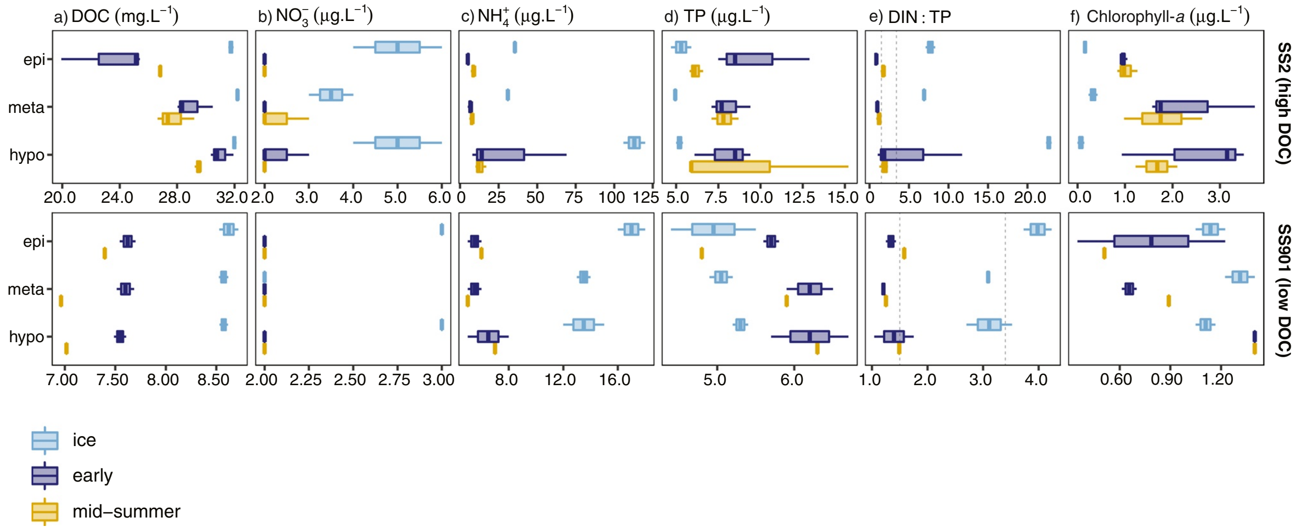


Figure 4. Summary of vertical and seasonal changes in key variables between the two studied lakes; top panels are Lake SS2, lower panels are Lake SS901. Ice period (light blue) includes all sampling events collected under ice, early period includes sampling within 2 weeks since ice-out, and midsummer period corresponds to data collected at the end of June/beginning of July. In panel (e), we added dotted vertical lines to mark thresholds for nutrient limitation status sensu Bergström (2010): dissolved inorganic nitrogen (DIN):TP < 1.5 indicates N-limitation, DIN:TP > 3.4 P-limitation, and the space between the lines indicates colimitation by N and P. Panel (f) is extracted chlorophyll-*a*. Lines in the boxes show medians, the outer rims of the boxes represent first and third quartiles, whiskers reach 1.5x interquartile range. Note different scales on *x*-axes between lakes.

DOC reached the highest concentrations under ice followed by a rapid decline after the ice breakup. In Lake SS2, where DOC concentration under ice was almost 4x higher relative to Lake SS901, DOC losses were highest in the epilimnion (−37.5%) and decreased with depth. In Lake SS901, DOC declined across the whole water column by approximately −10% (Figure 4a). While conductivity declined with ice-out, DOM quality metrics (a_{380}, S_R, $SUVA_{254}$) generally did not substantially change until the midsummer period (Figure S2b–S2e). Similarly to DOC, dissolved forms of inorganic nitrogen, NH_4^+ and NO_3^-, also accumulated under ice. Their concentrations approximately doubled relative to open-water conditions in Lake SS901. In Lake SS2, the concentration of NO_3^- was 3x higher under ice, and concentration of NH_4^+ was about 5x higher. Dissolved inorganic nitrogen (DIN) became rapidly depleted upon ice-out, with NO_3^- concentrations falling below quantification level (<3 µg.L^{-1}) (Figures 4b and 4c), while total phosphorus (TP) concentration increased (Figure 4d). Simultaneous increase in TP and decrease in DIN led to a substantially lower DIN:TP ratio during the open-water season (Figure 4e). Dissolved Si concentration was two-fold higher in Lake SS901 relative to Lake SS2 and progressively decreased over the course of the season in both lakes (Figure S2a).

3.2. Seasonal and Vertical Changes in Biological Metrics

Under ice, extracted chlorophyll-*a* in Lake SS2 was low, with the highest concentrations in upper layers of the water column (0.42 µg.L^{-1}), and mean phytoplankton cell density also low (20.7 ± 16 cells L^{-1}), only about 3% of mean open-water cell density (Figure 4f; Table S1). At ice-out, chlorophyll-*a* reached its maximum in the metalimnion (3.7 µg.L^{-1}), also evidenced by vertical profiles of chlorophyll fluorescence that show pronounced peaks in the metalimnion (Figures 3b and 4f). High fluorescence and measured chlorophyll-*a* were consistent with the highest values of phytoplankton cell density and biovolume (Figures 5a and 5b) in the metalimnion and hypolimnion. The phytoplankton bloom had a short duration and all metrics of phytoplankton biomass declined by midsummer. In Lake SS901, extracted chlorophyll-*a* reached relatively high concentrations under ice (1.4 µg.L^{-1}), matching the highest values measured during the open-water period in the hypolimnion (Figure 4a). Also, under-ice phytoplankton cell density in Lake SS901 (79.8 ± 43 cells L^{-1}) was comparable to open-water values and was four-fold higher than under-ice cell density in Lake SS2. Phytoplankton cell density was relatively even over the whole monitoring period

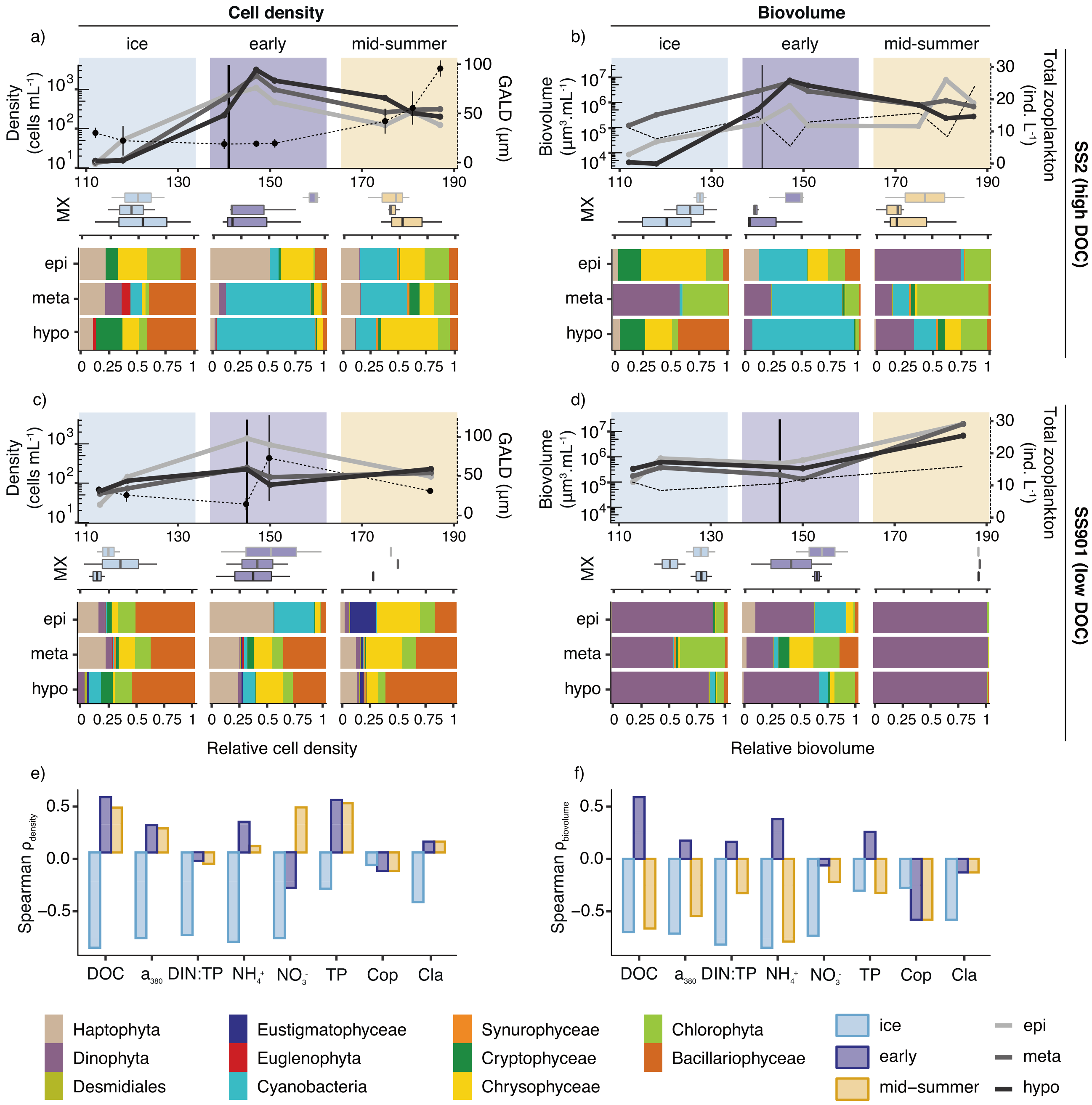


Figure 5. Seasonal changes in phytoplankton cell density (panels on the left side; [a, c]), biovolume (panels on the right side; [b, d]), and their drivers (e, f). Upper left panels (a, c) show changes in total phytoplankton cell density (thick lines), mean greatest linear axial dimension (GALD, dotted line), proportion of cell density contributed by mixotrophic taxa (MX, box and whisker plots, scale corresponds to the scale with relative proportions below), and shifts in relative abundance of higher taxonomic groups in epilimnion, metalimnion, and hypolimnion over the course of the season in lakes SS2 and SS901. Upper right panels (b, d) show changes in phytoplankton biovolume (thick lines), zooplankton density (dotted line), proportion of biovolume contributed by mixotrophic taxa (MX, box, and whisker plots), and shifts of higher taxonomic groups based on biovolume in epilimnion, metalimnion, and hypolimnion over the course of the season in each lake. Bar graphs represent how the relationships (based on Spearman correlation combining data from both lakes) between environmental variables and phytoplankton cell density (e) or biovolume (f) change over time.

with a pronounced peak shortly after ice-out in the epilimnion (Figure 5c); however, chlorophyll-*a* as well as other pigments increased with depth (Figures 3e and 4a; Figure S3).

Similar to chlorophyll-*a*, concentrations of photosynthetic accessory pigments were low under ice in Lake SS2 (0.24 nmol.L^{-1}, 0.11 nmol.L^{-1} when excluding chlorophyll-*a* and phaeophytin) relative to Lake SS901, where mean under-ice concentration was more than six-fold higher (1.52 nmol.L^{-1}, 0.74 nmol.L^{-1} when excluding chlorophyll-*a* and phaeophytin) (Figure S3). Pigment concentrations rapidly increased after ice-out in Lake SS2 (8x higher), but did not change substantially in Lake SS901. Pigments suggesting the presence of mixotrophic algae, such as peridinin in dinoflagellates and alloxanthin in cryptophytes, were detected in both lakes accompanied by chlorophyll-c_2 (various brown algae) throughout the season, together comprising on average ~60% of all accessory pigments. After ice-out, concentration of zeaxanthin (indicating the presence of cyanobacteria) was detected in both lakes, increasing and reaching the highest concentrations during the mid-summer period (9x higher in Lake SS2, and 3x higher in Lake SS901 relative to early period). Overall, the composition of pigments was comparable between lakes, largely composed of chlorophyll-c_2, peridinin, fucoxanthin, and alloxanthin, pointing to the presence of brown, siliceous algae, dinoflagellates, haptophytes, and cryptophytes (Figure S3). These pigments comprised approximately 50% of accessory pigments in Lake SS2 and 80% in Lake SS901. On average, accessory pigments comprised 47 ± 20% in each sample relative to the sum of chlorophyll-*a* and phaeophytin-*a*.

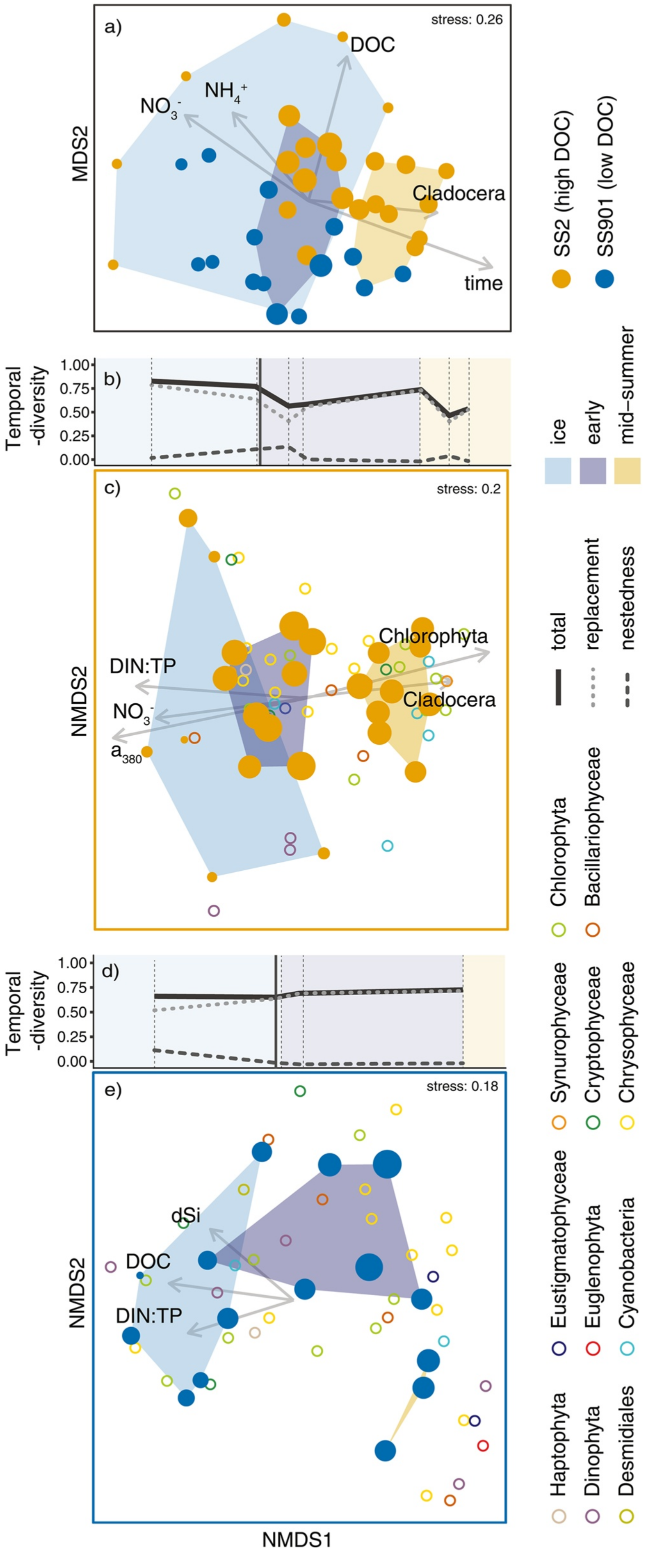
3.3. Seasonal Changes in Zooplankton Community Structure

Under ice, Copepoda (mostly members of Diaptomidae and nauplii of Cyclopoida) were present under ice in both lakes at densities comparable to the open-water period, on average 10 ind.L^{-1} in SS2 and 14 ind.L^{-1} in Lake SS901(Figure 6; Table S1), while cladocerans were notably missing. Rotifers (e.g., *Keratella earlinae*, *K. hiemalis*, *Filinia terminalis*) were also observed in under-ice samples (Table S2). After ice-out, cladocerans (*Daphnia* spp.) begun to appear in Lake SS2, gradually increasing in density until midsummer (on average, ~6 ind.L^{-1}). In Lake SS901, density of copepods remained stable throughout the season, and cladocerans only appeared during midsummer but in low numbers (on average, ~2 ind.L^{-1}, Table S1 and S2; Figure 6).

3.4. Seasonal and Vertical Changes in Phytoplankton Community Structure

PERMANOVA results show that phytoplankton communities were distinct between lakes ($R^2 = 0.13$, $F = 7.4$, $p = 0.001$) and also across time periods ($R^2 = 0.31$, $F = 4.54$, $p = 0.001$) while within-group variability was homogeneous. Clearly, midsummer communities in both lakes diverged strongly from those under ice and shortly after ice-out (Figures 5a, 5c and 5e). Many species found under ice persisted in the water column until after ice-out, especially the haptophyte *Chrysochromulina parva* was able to take advantage of the changing conditions after ice-out and bloomed in the epilimnion of both lakes (Figure S4). While dissimilarity between under ice and early communities was high and mostly due to species turnover, contributions of nestedness were almost 17% in Lake SS2 (Figures 5b and 5d). Dissimilarity between samples in Lake SS901 was even over time and on average higher compared to Lake SS2 where dissimilarity between communities fluctuated over the course of the monitoring season.

Generally, under-ice communities included small-celled, mixotrophic flagellates such as chrysophytes and haptophytes, larger cryptophytes and dinoflagellates (e.g., *Peridiniopsis elpatiewski)*, but also nonmotile small cells of centric diatoms and coccoid chlorophytes (Figures 5a–5d). Mixotrophic species contributed to 43% and 24% of total under-ice abundance in Lake SS2 and Lake SS901, respectively; however, they comprised the majority of under-ice phytoplankton biovolume in both lakes, 64% and 68% (Figures 6b and 6d; Table S1). While the contribution of mixotrophic algae to cell density in both lakes remains relatively stable (on average ~40%) over the course of the season, the variability is high (Figures 6a and 6c; Table S1). With regards to biovolume, mixotrophs comprise on average almost 60% in Lake SS2 and 75% in Lake SS901, but again, the variability is high (±32% and 25%, respectively) (Figures 6b and 6d; Table S1). The highest cell density of phytoplankton was observed shortly after ice-out; mostly due to the presence of small blooming haptophyte *Chrysochromulina parva*, flagellated chrysophytes (*Chrysococcus* spp., *Kephyrion* spp.), and coccoid cyanobacteria (Figures 6a and 6c). In Lake SS2, cyanobacteria *Gloeocapsa siderochlamys* dominated the plankton in meta- and hypolimnion along with *Woloszynskia* sp.—a small dinoflagellate. In Lake SS901, *Chrysochromulina parva*, as in Lake SS2, reached high densities in the epilimnion, accompanied by colonies of coccoid cyanobacteria *Chroococcus aphanocapsoides,* and *Aphanocapsa* sp. which increased the average cell size (Figures 6a–6d; Figure S4). During the midsummer period, cell density of phytoplankton declined but biovolume stayed high. In Lake SS2, average cell size increased substantially (up to 100 μm) in comparison to the previous period; assemblages were dominated by *Aphanocapsa* sp., *Dinobryon divergens*,


a)
stress: 0.26
DOC
NH_4^+
NO_3^-
Cladocera
time
MDS2
b)
Temporal
-diversity
1.00
0.75
0.50
0.25
0.00
c)
stress: 0.2
Chlorophyta
DIN:TP
Cladocera
NO_3^-
a_{380}
NMDS2
d)
Temporal
-diversity
1.00
0.75
0.50
0.25
0.00
e)
stress: 0.18
dSi
DOC
DIN:TP
NMDS2
NMDS1
SS2 (high DOC)
SS901 (low DOC)
ice
early
mid−summer
total
replacement
nestedness
Chlorophyta
Bacillariophyceae
Synurophyceae
Cryptophyceae
Chrysophyceae
Eustigmatophyceae
Euglenophyta
Cyanobacteria
Haptophyta
Dinophyta
Desmidiales

cryptophytes *Cryptomonas marssonii* and *Plagioselmis nannoplactonica*, and relative abundance of coccoid green algae substantially increased (e.g., *Oocystis submarina, Willea irregularis*) (Figures 6a and 6b). In Lake SS901, neither cell density nor average cell size changed, but biovolume increased by an order of magnitude, mostly due to the presence of large dinoflagellate *Ceratium hirundinella* (Figure 5d). The community was dominated by centric diatoms and *Asterionella formosa* in the hypolimnion, while chrysophytes (*Dinobryon bavaricum, D. pediforme, D. divergens*) persisted in the upper layers of the water column (Figures 6c and Figure S4).

Spearman rank correlations suggest that both phytoplankton cell density and biovolume under ice are negatively related to variables affecting light, such as higher concentration of DOC ($\rho_{\text{density}} = -0.83$, $\rho_{\text{biovolume}} = -0.7$), and absorbance at 380 nm (a_{380}; $\rho_{\text{density}} = -0.75, -0.73$) (Figures 6e and 6f, Table S3). The relationship is negative also with DIN ($\rho_{\text{density}} = -0.78$, $\rho_{\text{biovolume}} = -0.84$), and DIN:TP ($\rho_{\text{density}} = -0.72$, $\rho_{\text{biovolume}} = -0.82$). During the early period after ice-out, the relationship with DOC and NH_4^+ is the opposite—higher DOC ($\rho_{\text{density}} = 0.48$, $\rho_{\text{biovolume}} = 0.59$), and ammonium ($\rho_{\text{density}} = 0.27$, $\rho_{\text{biovolume}} = 0.38$) are positively related to cell density and biovolume. Cell density is negatively related to nitrate concentration ($\rho_{\text{density}} = -0.31$) and positively to TP ($\rho_{\text{density}} = 0.46$); biovolume is negatively correlated with the abundance of copepods ($\rho_{\text{biovolume}} = -0.58$). At the end of the sampling season, correlations with cell density and biovolume uncouple further, higher cell density is positively related to DOC ($\rho_{\text{density}} = 0.4$), TP ($\rho_{\text{density}} = 0.43$), and NO_3^- ($\rho_{\text{density}} = 0.4$), but biovolume is negatively related to all variables explored with the strongest relationship to NH_4^+ ($\rho_{\text{biovolume}} = -0.79$), DOC ($\rho_{\text{biovolume}} = -0.67$), and the abundance of copepods ($\rho_{\text{biovolume}} = -0.58$). While the coefficients are likely inflated given that the number of samples used for this exploratory analysis is limited, these results provide a more quantitative basis for assessing the relationships between variables and phytoplankton metrics for remote Arctic lakes for which seasonally resolved data are scarce.

4. Discussion

4.1. Seasonal Changes in Drivers of Phytoplankton Biomass

Substantial phytoplankton biomass was observed in a low DOC lake with deeper light penetration under ice, while in a high DOC lake with greater light attenuation, biomass relative to the open-water period was negligible—suggesting the importance of the ice-covered period for the annual phytoplankton cycle, especially in clearer Arctic lakes. Our findings support our first hypothesis and provide further evidence that light is the main limiting factor of phytoplankton production under ice. While light limitation under ice due to the presence of snow cover or white ice is generally acknowledged (Hampton et al., 2017), our results draw attention to lake internal conditions that further modulate the availability of light transmitted through the ice cover. While both lakes receive similar radiation in the upper layers of the water column, lower concentration of DOC and lower quantity of chromophoric compounds (reflected by low a_{380}) allow light to penetrate deeper in Lake SS901, creating more suitable conditions under ice for phytoplankton growth. Under-ice accumulation of DOC has been observed across a larger set of Greenland lakes (Whiteford et al., 2016), alpine lakes (Miller & McKnight, 2010), and there is some evidence that it more commonly occurs in smaller lakes (Hampton et al., 2017). The lack of sunlight during polar night, senescence of autochthonous organic matter (phytoplankton and substantial biomass of macrophytes; Osburn et al., 2019), and its under-ice microbial degradation lead to accumulation of DOC with chromophoric properties (Gonsior et al., 2013). Moreover, in the case of Arctic lakes located in semi-arid, open landscapes,

Figure 6. Visualization of shifts in phytoplankton species composition using nonmetric multidimensional scaling with Morisita-Horn similarity on phytoplankton cell density matrix. Between lakes, (a) phytoplankton structure is distinct during the open-water period, less so when lakes are ice-covered. In Lake SS2, (b) the largest shifts in species composition occurred during under ice/beginning of the early period, and at the end of early period/beginning of the midsummer period as indicated by binary Jaccard index comparing community structure between two adjacent sampling periods designated by dotted lines (e.g., similarity between first and second, and second and third, etc.), (c) phytoplankton community structure during the midsummer period was clearly less similar to the earlier ones, associated with more chlorophytes and increasing density of cladocerans. In Lake SS901, (d) changes in β-diversity were relatively high and stable throughout the monitoring season, dominated by species turnover; however, (e) there were differences between phytoplankton communities during different time periods. The length of fitted vectors of environmental variables is proportional to their correlation with the nonmetric multidimensional scaling (nMDS) scores and they are oriented in the direction of the greatest change in the ordination space. Size of the points in each ordination is proportional to phytoplankton cell density in each sample.

limited belowground connectivity and high lake water residence time further contribute to the overall high concentrations of DOC (Osburn et al., 2017).

Intensified exposure to natural sunlight upon ice-out degrades the chromophoric compounds associated with DOC (Gonsior et al., 2013; Moran et al., 2000; Reche et al., 2000), contributing to the loss of quantity and shifts in quality of DOC (Bertilsson & Tranvik, 2000; Cory et al., 2014; Fowler et al., 2018; Morris & Hargreaves, 1997). Photobleached, less colored, DOC allows for deeper light penetration favorable to the growth of phytoplankton. Different rates of DOC loss upon ice breakup in our lakes provide an indirect piece of evidence for the role of photolytic processes in the degradation of DOC. In Lake SS2, where high DOC increases light attenuation, the largest losses of DOC occur in the epilimnion (-37.5% [-12 mg. L^{-1}]), and get smaller with increasing depth. On the other hand, in Lake SS901, where light penetration is deeper, DOC declines proportionally by about 10% in each thermal layer. However, while we observed substantial decline in DOC quantity, quality metrics ($SUVA_{254}$, a_{380}) slightly increased following ice-out. This suggests that photobleaching occurs simultaneously with inputs of fresh allochthonous organic matter from melting ice and seepage from the thawing permafrost (Kellerman et al., 2019; Osburn et al., 2017). At the same time, inputs of meltwater can also contribute to decline in DOC via dilution (in both lakes, conductivity decreases by -13% upon ice-out). All DOC metrics reach their low by midsummer, indicating intensive processing and transformation of organic matter during the short open-water period (Osburn et al., 2017).

Assuming that under-ice phytoplankton biomass is only limited by the availability of light, more biomass would be expected in the upper layers of Lake SS2 where irradiation is similar to Lake SS901. That is, however, not the case; instead, phytoplankton biomass is accumulated deeper in both lakes. One possible explanation is that convective mixing induced by stronger radiation toward the end of the ice-covered period has been turning over the upper layers of the water column, potentially exposing phytoplankton cells that would otherwise accumulate closer to the ice to less overall irradiation (Pernica et al., 2017; Salmi & Salonen, 2016; Salonen et al., 2014). Also, low under-ice phytoplankton stock was related to high concentration of inorganic nitrogen (NO_3^-, NH_4^+) and high DIN:TP—all characteristic of the conditions in Lake SS2. High NH_4^+, a reduced form of inorganic N, is a signature of anoxic decomposition of organic matter and is accumulated in anoxic environments as NO_3^- can be utilized as an terminal electron acceptor for microbial respiration. Accumulation of NH_4^+, and NO_3^- to a lesser degree is also reflective of the low phytoplankton uptake rate. High ratio of NH_4^+ to NO_3^- can affect N uptake ability of phytoplankton, possibly leading to inhibition (Glibert et al., 2016; Syrett & Morris, 1963). Under low temperature conditions, NO_3^- is the preferential source of N, particularly for diatoms (Lomas & Glibert, 1999) that in both lakes constitute about 50% of abundance. Prevailing oxic conditions under ice in Lake SS901 might have led to more active nitrification, providing a preferred source of N for diatoms. Although light availability under ice is crucial, favorable nutrient ratios might further stimulate phytoplankton production.

While the relationship between DOC and phytoplankton metrics was negative under ice, the opposite was observed during the open-water period, demonstrating the dual effects of DOM on phytoplankton growth via light attenuation and nutrient subsidization (Bergström & Karlsson, 2019). Under ice, when light availability is limited due to the presence of ice cover, DOC absorption further exacerbates light limitation experienced by phytoplankton. Once ice melts, light penetration through the water column increases substantially and the photic zone extends to the bottom of these lakes (Saros et al., 2016; Whiteford et al., 2016; Table S1). Upon ice breakup, complex organic matter compounds exposed to direct sunlight are photolytically broken down into smaller, less aromatic organic molecules that are more readily available for processing via biological pathways, promoting bacterial and primary production through increased nutrient availability (Sanders et al., 2015; Seekell et al., 2015; Wetzel et al., 1995). In both lakes, but especially in Lake SS2 where DOC concentration is higher, phytoplankton biomass increased rapidly after ice-out, likely as a result of increased light penetration and increased nutrient availability from degradation of organic matter, mixing, and inputs of allochthonous subsidies from ice melt and permafrost thaw.

Decline of phytoplankton cell density during midsummer period (end of June/early July) is likely attributable to increasing zooplankton grazing pressure. While populations of copepods remain relatively stable throughout the season, density of cladocerans progressively increases throughout the open-water period. The impact of grazing is particularly marked in Lake SS2 where phytoplankton cell density declines but mean GALD increases over time—in sync with increasing density of cladocerans. Only a small number of cladocerans was observed in Lake SS901, possibly due to presence of *Lepidurus arcticus* (pers. obs.), a known predator of *Daphnia* (Christoffersen, 2001). Phytoplankton cell density in Lake SS901 is relatively stable but biovolume increases by an order of magnitude at the end of the monitoring season due to the presence of a large dinoflagellate *Ceratium hirundinella*. While increasing size of algal cells is often considered a predation defense, it was suggested that the key mechanism of predation avoidance is the unfavorable nutrient ratio of large algae rather than a large size per se (Branco et al., 2018). Another factor contributing to decreasing cell density is also continuing nutrient depletion. While our data indicate N-limitation and colimitation in most of the open-water samples (DIN:TP < 3.4; Bergström, 2010), concentrations of dissolved nutrients are extremely low. Previous experiments in these lakes have shown that phytoplankton and microbial communities invest more heavily in P acquisition, suggesting they are strongly P-limited during the open-water period (Brutemark et al., 2006; Burpee et al., 2016). Effects of grazing and nutrient availability are, however, intertwined as zooplankton grazing contributes to recycling of nutrients (Carpenter & Kitchell, 1984). Especially in oligotrophic lakes, the positive effect of increasing availability of nutrients through excretion can exceed the negative effect of grazing as a loss process (Rogers et al., 2020).

4.2. Seasonal Changes in Phytoplankton Community Structure

Phytoplankton community structure changed rapidly throughout the season with species replacement contributing the most to observed dissimilarities, reflecting dynamic changes in lake conditions. However, our data are not in line with our hypothesis that the largest shifts in phytoplankton community structure would occur upon ice melt as a result of changing environmental conditions. Instead, our results support the notion of seeding communities; a “priority effect” for phytoplankton already growing under ice as suggested elsewhere (De Meester et al., 2002; see e.g., Feuchtmayr et al., 2012; McKnight et al., 2000; Vehmaa & Salonen, 2009). Taxa that dominated during the early open-water period (i.e., *Chrysochromulina parva*, and picocyanobacteria) were already present under ice, suggesting that species able to establish under ice can readily bloom once the conditions become more favorable—pre-empting niches for later arriving species (Fukami et al., 2015). However, whether under-ice establishment of phytoplankton species is deterministic or contingent and how do winter phytoplankton populations affect spring blooms is not clear. Considering that varying structure of phytoplankton communities and changing trajectory of seasonal succession could affect energy transfer through the food web, it should be a focus of future studies, particularly with respect to changing ice phenology.

Upon ice-out, deeper light penetration and higher nutrient availability resulting from mixing and inputs of allochthonous nutrient subsidies likely contributed to improved habitability of the whole water column. Vertical gradients of light, its spectral properties, and nutrient concentrations allow for niche differentiation across the water column, allowing many phytoplankton species to coexist (Brauer et al., 2012; Shimadzu et al., 2013). Using the two blooming species as an example, picocyanobacteria had higher abundance in metalimnion and hypolimnion, and *Chrysochromulina* was dominant in epilimnion, suggesting different responses along the light-nutrient gradient (Figure S3) that likely stem from differences in their pigment composition and modes of nutrition. Spectral properties of light change with depth but also with different concentrations of cDOM; hence, both changes in irradiance and light quality affect phytoplankton community composition and allow for fine-tuned niche partitioning among species (Burson et al., 2018, 2019; Holtrop et al., 2020; Stomp et al., 2007). For example, higher availability of blue light in low DOC lake can contribute to the observed prevalence of diatoms equipped with pigments such as fucoxanthin and chlorophyll-c_2 that have absorption peaks in the blue wavelengths. On the other hand, in high DOC lake, green algae can have an advantage because chlorophyll-*b* efficiently absorbs light in the orange spectrum.

Temporal heterogeneity likely contributed to the high rate of species replacement between samples. After ice-out, small and rapidly growing taxa were favored by improved light conditions, but their outburst was attenuated shortly, likely by density-dependent mechanisms, for example, resource draw-down, increased grazing, and in the case of *Chrysochromulina*, viral infections are also known to contribute to termination of blooms (Mirza et al., 2015; Stough et al., 2019). Later during the season under nutrient-depleted conditions and heightened grazing pressure, phytoplankton communities in both lakes were clearly distinct from the previous ones. In both lakes, less edible algae such as mucus-enveloped chlorophytes (e.g., *Botryococcus, Oocystis, Elakatothrix, Willea*) and colony-forming picocyanobacteria (*Aphanocapsa* spp.) were abundant along with larger chrysophytes and slow-growing dinoflagellates. Such variations in life-history strategies and associated trade-offs among species in this succession-like dynamics have consequences for species coexistence (Ehrlich et al., 2020; Kneitel & Chase, 2004; Tilman, 1990). Different environmental preferences and responses to temporal fluctuations may promote coexistence of species that share resources (Chesson, 2000; Li & Chesson, 2016).

4.3. Mixotrophy in Oligotrophic Arctic Lakes

As a consequence of lower light availability under ice, we hypothesized that mixotrophic algae will be more competitive during ice-covered period relative to strict phototrophs that will be dominant during the open-water period. However, the evidence for our third hypothesis is mixed. In our samples, mixotrophs did not reach higher abundance than autotrophs under ice; instead, they were present during the whole monitoring period and consistently made up about 40% of total phytoplankton cell density. While phototrophs under ice prevailed in terms of cell density, mixotrophs comprised on average 66% of total under-ice biovolume. Mixotrophs are able to combine autotrophic and heterotrophic strategies which can, under certain conditions, give them an advantage over phototrophs and heterotrophs. While rapidly growing, small-sized autotrophs (centric diatoms, coccoid chlorophytes, picocyanobacteria) tend to be highly efficient at resource uptake and light harvesting (Chisholm, 1992; Edwards et al., 2012; Litchman et al., 2007; Schwaderer et al., 2011), mixotrophs can support their larger size because they supplement limiting resources by consumption of organic matter, that is, bacteria and DOM (Bruggeman, 2011; Mitra et al., 2016). In our samples, high mixotrophic contribution to biovolume was negatively associated with high TP ($\rho = -0.48$) and DOC ($\rho = -0.36$), and positively with high DIN:TP ($\rho = 0.27$) suggesting mixotrophy is a successful strategy when P is very limited as demonstrated theoretically and empirically (Crane & Grover, 2010; Kamjunke et al., 2007).

Traditionally, the relative benefit of mixotrophy to strict autotrophy was thought to be higher under conditions of high light and low nutrient availability, while low prey abundance would provide advantage over strict heterotrophs (de Castro et al., 2009; Tittel et al., 2003). However, mixotrophs are also able to dominate when light is low, for example, due to high cDOM (e.g., Jansson et al., 1996). Mixotrophs, now regarded to be an important link between trophic levels across systems (Flynn et al., 2013; Mitra et al., 2016), are efficient intraguild predators as they can decimate bacterial populations (Bird & Kalff, 1986; Isaksson, 1999; Unrein et al., 2014) but also consume picophytoplankton (Callieri et al., 2006; Gerea et al., 2019; Wilken et al., 2014), reducing competition for resources while benefiting from the prey itself. Under nutrient deplete conditions, mixotrophs are considered to be a valuable prey for zooplankton because of their more favorable stoichiometry relative to autotrophs (Hansson et al., 2019; Katechakis et al., 2005). Diverse assemblages of both autotrophs and mixotrophs were able to coexist over the course of the season, suggesting their differential responses to resource availability and grazing pressure.

4.4. Consequences of Under-Ice Phytoplankton Accumulation

We have shown that differing DOC concentration affects seasonal distribution of phytoplankton biomass. High concentration of DOC under ice diminished light penetration through the water column, negatively impacting phytoplankton growth and biomass accrual; however, during the open-water period, higher phytoplankton biomass was supported likely through nutrient subsidization associated with degradation of organic matter. Phytoplankton biomass in clearer Lake SS901 was distributed equally throughout the monitoring season while in Lake SS2, the bulk of biomass accumulated during the open-water period, suggesting the importance of the under-ice period for lake metabolism and annual carbon budget in clear lakes. Moreover, negligible phytoplankton biomass coupled with high concentration of organic matter under the ice cover in Lake SS2 was reflected by hypolimnetic anoxia which persisted until ice-out; in contrast, in clearer Lake SS901, the hypolimnion was oxic throughout the monitoring season. These findings, while only demonstrated in a pair of lakes, have ecosystem-wide consequences considering that anoxic conditions stimulate the accumulation of methane and carbon dioxide (Denfeld et al., 2018; Ducharme-Riel et al., 2015; Jansen et al., 2019), and underscore the importance of including under-ice processes in limnological studies given the ongoing changes in winter climate patterns (Saros et al., 2019) and shortening of the ice-covered season (Šmejkalová et al., 2016).

Both biomass and species composition of primary producers matter for the flow of energy within aquatic food-webs. Divergent species responses to seasonal variability allow for coexistence of diverse assemblages over time (Angert et al., 2009; Mellard et al., 2019). Despite variations in environmental conditions between our study lakes, low light, low temperatures, but also relaxed grazing pressure and relatively higher availability of nutrients were characteristic of the under-ice conditions in both lakes. Under ice, suboptimal light regime paired with low temperatures likely exerted a strong environmental control, promoting the growth of species able to handle these conditions while maximizing functional differences between them (i.e., mixotrophs and small, low-light adapted autotrophs; Vasseur et al., 2005; Weithoff et al., 2015). Taxa with higher growth rates that were already under ice took advantage of the sudden improvement in light conditions after ice-out and rapidly bloomed, priming zooplankton populations. "Seeding" of open-water blooms by under-ice phytoplankton implies that its quality (e.g., edibility, nutrient ratios) will have consequences for transfer of energy to higher trophic levels. Therefore, in order to understand how species interactions and aquatic food-webs will be affected by ongoing changes in winter duration and prolonged growing season, it will be necessary to consider multiyear time series of seasonal changes in species abundances, not just bulk biomass.

5. Conclusions

Under-ice phytoplankton biomass in a clear water, oligotrophic lake was comparable to open water, suggesting that the under ice period can be an important part of the annual phytoplankton dynamics. As hypothesized, our data indicate that a high concentration of dissolved organic matter inhibited phytoplankton biomass accrual under lake ice cover but stimulated growth during the open-water period. Lakes in semi-arid Arctic regions with low hydrologic connectivity and high residence time are fairly transparent during open-water period as a result of intense photobleaching despite often high concentrations of DOC (Cory et al., 2014; Fowler et al., 2018; Gonsior et al., 2013). However, photobleaching is very limited when lakes are ice-covered; therefore, dissolved organic compounds can accumulate, affecting light attenuation and exacerbating light-limitation experienced by phytoplankton. Once light regime in lakes improved, nutrient subsidization associated with processing of organic matter appeared to stimulate phytoplankton biomass. Rapid changes in environmental conditions were reflected by dynamic phytoplankton community composition. Marked shifts in composition occurred later during the season when nutrients became depleted and grazing pressure intensified, not immediately after ice-out, suggesting that under-ice assemblages acted as inocula for early phytoplankton bloom. Mixotrophs and strict autotrophs were codominant throughout the season; however, mixotrophs made up higher proportion of biovolume when phosphorus was likely to be limiting.

Early spring temperatures in West Greenland have risen rapidly by more than 2°C since the 1990s, triggering shifts in the timing of lake ice-out, onset and duration of stratification, and ultimately shifts in environmental conditions for aquatic biota (Saros et al., 2019). In order to understand changes associated with the impacts of changing climate and associated shifts in phenology in Arctic lakes (Sharma et al., 2019; Šmejkalová et al., 2016), we first need to have a grasp of the contemporary conditions and their seasonal patterns. Although remote Arctic lakes experience the most rapid changes in climate patterns, seasonal studies that would link shifts in biological assemblages to ecosystem process in these remote lakes are lacking. High-frequency sensors are promising tools to harness data from remote lakes during times when they are inaccessible (i.e., transition to ice-out; polar night), helping us connect understudied ice-covered period with open-water season and improve our understanding of cross-seasonal interactions. Our findings suggest that differences in winter conditions across lakes matter; therefore, further investigations focusing on seasonal changes and the implications of changing phenology for Arctic lake ecosystems should be a priority.

Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

Data are accessible from Arctic Data Center (Hazukova & Saros, 2021).

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