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To cite this article: Alexander B. Michaud & Spencer Apollonio (2022) Overwinter oxygen and silicate dynamics in a high Arctic lake (Immerk Lake, Devon Island, Canada), Inland Waters, 12:3, 418-426, DOI: [10.1080/20442041.2022.2063623](https://doi.org/10.1080/20442041.2022.2063623)

To link to this article: <https://doi.org/10.1080/20442041.2022.2063623>



Published online: 25 Jul 2022.



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RESEARCH BRIEF



Overwinter oxygen and silicate dynamics in a high Arctic lake (Immerk Lake, Devon Island, Canada)

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ABSTRACT

Arctic lakes are ice covered for 8–12 months of the year, but the duration and thickness of ice cover is decreasing with increased warming. There is a paucity of baseline data documenting the geochemical dynamics of nutrients and oxygen beneath ice cover of high Arctic lakes, a gap that presents a challenge when attempting to understand the impacts of a rapidly changing Arctic on lake ecosystems. We present an annual cycle of temperature, oxygen, and silicate data from Immerk Lake on Truelove Lowland, Devon Island, Canada. Water column oxygen concentrations decreased while silicate concentrations increased during the ice-covered season. Ice cover melting during spring–summer is associated with rapid net decreases of the silicate standing stock at almost 3 times the rate of its net increase over winter. These data show the importance of the extended winter season for regeneration of silicate, an essential nutrient for diatom populations, which are important members of the phytoplankton community and carbon cycle of Arctic lakes. These data collected 60 years ago serve as a benchmark and document the water column oxygen and silicate dynamics in an Arctic lake during ice formation, winter darkness, and ice-cover melting periods.

ARTICLE HISTORY

Received 7 October 2021

Accepted 3 April 2022

KEYWORDS

Arctic; lake; oxygen; silica; under-ice; winter limnology

Introduction

Lakes occur at the highest density in boreal and Arctic latitudes (45–75°N) and are significant sites of carbon (C) cycling (Tranvik et al. 2009, Verpoorter et al. 2014). Lake ice cover is a physical barrier between the water column and atmosphere that prevents wind-driven mixing and controls gas exchange (Leppäranta 2015). Ice cover for most shallow (5 m) lakes above the Arctic Circle (66°N) may persist for >250 days (Walsh et al. 1998). Thus, under-ice chemical dynamics in Arctic and high latitude lakes dominate most of the year. Ice cover on Arctic lakes is decreasing in extent and duration because of climatic warming (Surdu et al. 2014, Sharma et al. 2019). These decreases in Arctic lake ice cover will lead to changes in lake ecosystem structure and function, such as the C cycle (Šmejkalová et al. 2016). There is a dearth of information on chemical and biological changes to lakes during the shoulder seasons and especially the winter season of Arctic lakes (Hampton et al. 2017). Data collected throughout the ice-formation, ice-covered, and ice-melting seasons will clarify the annual cycles of nutrients and gases critical to primary productivity, which underpins the lake food web (Anderson 2000, Hampton et al. 2017).

Oxygen and silicon (Si) are important geochemical components of freshwater lakes. Oxygen is especially important in Arctic lakes because a cessation of oxygen inputs after winter darkness limits photosynthesis, and ice cover restricts atmospheric exchange. Winter oxygen consumption rates contribute to whether higher trophic levels can survive overwintering in a lake. Si is a required nutrient for several types of phytoplankton, including members of the Bacillariophyta (diatoms) and Chrysophyceae. These phytoplankton are important members of the lake ecosystem because they connect the C and Si cycles (Falkowski and Raven 2007) and produce oxygen within the water column during sunlit months. Given the role of phytoplankton as the primary productivity base of the lake food web, the dynamics of nutrient cycles that impact their growth are important for understanding how lake ice cover phenology changes in a warming Arctic.

Historical studies of aquatic systems are useful benchmarks for contemporary or future studies to help determine the magnitude, trajectory, and consequences of change (Tippa 2013). The historical data presented here are from an area of the Arctic (the Canadian Arctic Archipelago) where few published studies have occurred (Metcalf et al. 2018). Further, Arctic

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freshwater ecosystems are among the most sensitive to warming and simultaneously lack long-term monitoring data, which poses a challenge to understanding how these northern lake ecosystems are changing (Schindler and Smol 2006, Williamson et al. 2009). We report the silicate (SiO_4^{2-}) and dissolved oxygen concentrations collected by one of the authors (SA) from September 1961 to August 1962, including the ice-formation, winter darkness, and spring–summer ice cover melting period from an Arctic lake located on Devon Island within the Canadian Arctic Archipelago. These data document an element cycle (Si) that has rarely been studied in Arctic lakes, serve as a benchmark from 60 years ago, and provide a valuable comparison for future under-ice limnological studies.

Methods

Immerk Lake (75°40'N, 84°33'W) is located on Truelove Lowland on the northern shore of Devon Island, Nunavut, Canada. Immerk Lake is shallow with a mean depth of 3.24 m, a maximum depth of 8 m (Minns 1977), and a relatively large littoral area (~66%). The lake is separated into a northern and southern basin by a sill that sits 1 m beneath the water level in summer. The northern basin is much shallower and smaller than the southern basin. Given the shallow sill, the northern basin is likely cut off from the larger southern basin during winter (Minns 1977). The sun set on 23 October 1961 and did not rise again until 8 February 1962. Immerk Lake was covered by a complete, thin layer of ice on 11 September 1961. Water column sampling was conducted from a small sampling hut through a hole in the ice cover, when permitted, or from a rowboat when ice was off the lake. Water column profiling was completed every ~7 d in 1961, then every ~14 d in winter, spring, and summer 1962 (black dots in Fig. 1a–b). Ice thickness measurements were made using standard measuring equipment at each time point. Water samples for silicate, dissolved oxygen, and temperature were collected at each depth with a single Van Dorn bottle. Dissolved oxygen concentrations were measured using the Winkler titration method (Barnes 1959). Silicate measurements were made using the standard molybdenum blue colorimetric assay (Mullin and Riley 1955). The samples for silicate were not filtered to avoid contamination with glass fiber filters. Linear interpolations of oxygen and silicate data were conducted in R (RStudio 3.6.3; R Core Team 2020) using the *approx* function within the stats package and calculating a point every 25 cm of depth and every 3 d (see code and data availability statement). Depth-integrated oxygen and silicate contents of the entire water column were calculated at

each timepoint from the air–water interface during ice-free periods or the ice–water interface during ice-covered periods to the deepest sample depth of 6 m and summed. Depth-integrated oxygen and silicate contents were calculated using linear interpolations between collected depths to compare the 2–3 m (epilimnion) and 5–6 (hypolimnion) m depth intervals. The 2–3 m depth interval was chosen for the epilimnion because it was the uppermost temperature-stratified depth interval not impacted by ice cover, with ice reaching only 1.97 m at its thickest. The integrated quantities of oxygen and silicate were plotted over time, and a linear regression was used to calculate the net rates of change over time. We present the epilimnion and hypolimnion rates before and after 5 March 1962 because on this day the sampling hole was enlarged to deploy a zooplankton net (Apollonio and Saros 2013). Enlarging the sampling hole introduced oxygen to the water column (before and after arrow in Fig. 1a–b).

Results and discussion

Dissolved oxygen dynamics

Immerk Lake was well mixed with respect to temperature and oxygen during the open water period before ice cover formation (Fig. 1a, 2c). Ice cover after 11 September 1961 led to the loss of wind-driven mixing and the development of thermal inverse stratification and oxygen stratification (Fig. 1a, 2c). After ice-cover formation, oxygen concentrations in the water column began decreasing (Fig. 2a). A net oxygen loss rate of $0.20 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ was calculated for the water column throughout the ice-covered period (10 Sept 1961 to 5 Jun 1962; 269 d; Table 1). Net oxygen loss in Immerk Lake over winter may be partially attributed to *Limnocalanus macrurus*, the only copepod present in Immerk Lake, which had measurable respiration throughout winter and represented about 6.5% of the net oxygen loss (Apollonio and Saros 2013). Arctic char (*Salvelinus alpinus*) was the only fish present in Immerk Lake, but its contribution to net oxygen loss throughout the winter is unknown (Apollonio and Saros 2013). Heterotrophic bacterioplankton may also contribute to net oxygen loss; they were identified as respiring most of the oxygen within the water column during the ice-covered season from high mountain ice-covered lakes of Colorado, USA (Pennak 1968). Minns (1977) sampled Immerk Lake during spring 1973 and calculated a net oxygen loss rate of $0.19 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ using samples collected only in early May 1973, assuming a fully saturated water column before ice cover development (autumn 1972) and a linear decrease over the 1972–

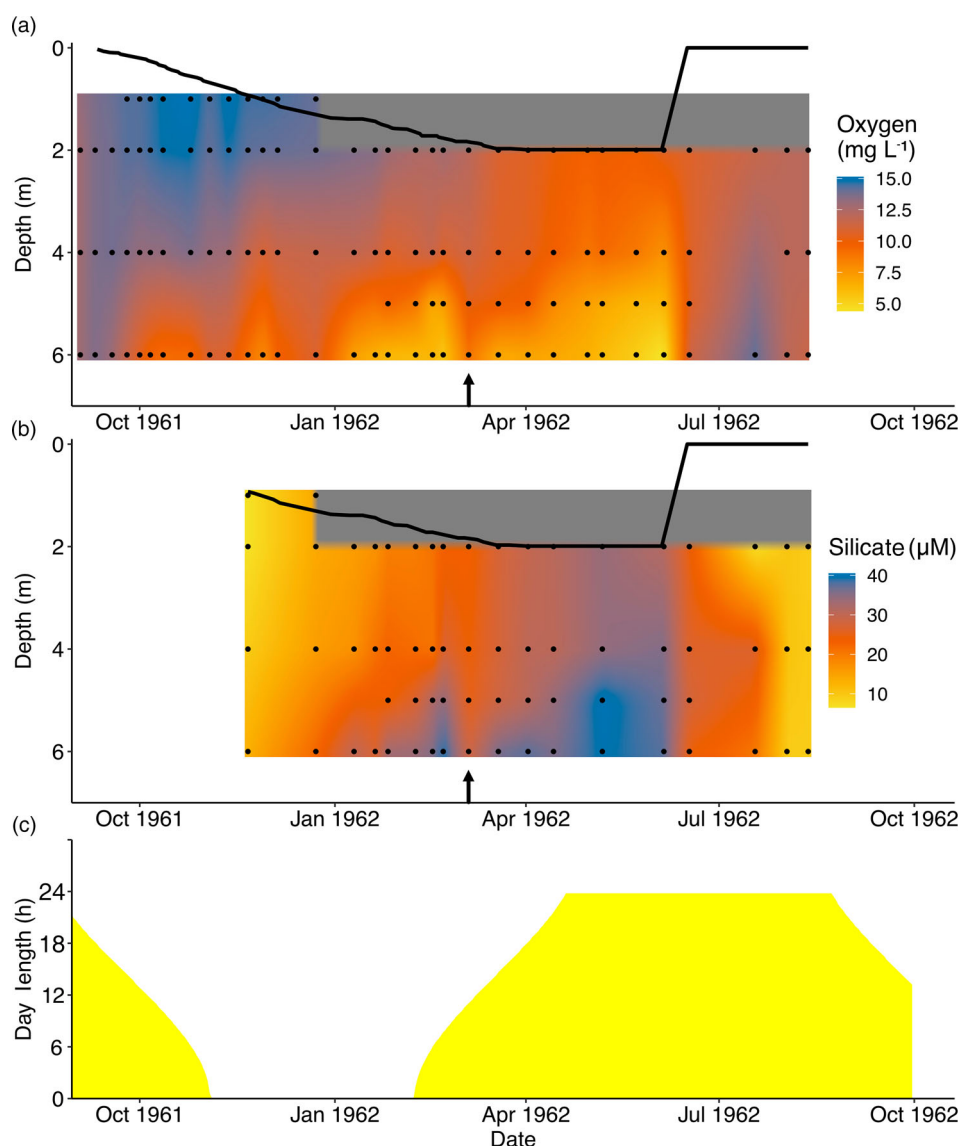


Figure 1. (a) Dissolved oxygen and (b) silicate concentrations from Immerk Lake, and (c) day length during the sampling period. The oxygen and silicate profile data were linear interpolated to produce a semicontinuous visualization of the concentration changes with depth and time. The grey box in panels a and b represents no data at the sampling station. The black line is a linear interpolation of the ice thickness data until 5 June 1962, when it represents a loss of ice from the edges of the lake and a connection with the water column. Black dots within the contour plot represent the actual sample points in depth and time. The vertical black arrow denotes timing of a sampling event that introduced oxygen to the water column (see text for details). Colour version available online.

1973 winter (212 d). Immerk Lake possessed similar winter net oxygen loss rates when sampled a decade apart. Minns (1977) assumed a linear decrease of oxygen throughout winter, which we show here to be reasonable when measurements throughout the winter are integrated over the water column (Fig. 1a, 2a). Other studies have suggested that winter net oxygen loss rates of temperate lakes are nonlinear (Babin and Prepas 1985), with a faster net oxygen loss rate during the first half of the winter; however, we find that a linear model fits the data and explains most of the variability ($R^2 = 0.97$, p -value < 0.001; Table 1) for the ice-covered season.

Immerk Lake net oxygen loss rates from the 1961–1962 and 1972–1973 winters are at the low end, but within one standard deviation (SD) of the mean (range 0.04–0.85, mean 0.28 [0.16] $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) compared to under-ice net oxygen loss rates measured in a range of temperate, seasonally ice-covered Canadian lakes (Babin and Prepas 1985). A strong correlation exists between winter net oxygen loss rates and mean depth and summer areal chlorophyll *a* (Chl-*a*) concentration (Babin and Prepas 1985). Winter net oxygen loss rates and summer Chl-*a* concentration are linked because more summer productivity, as measured

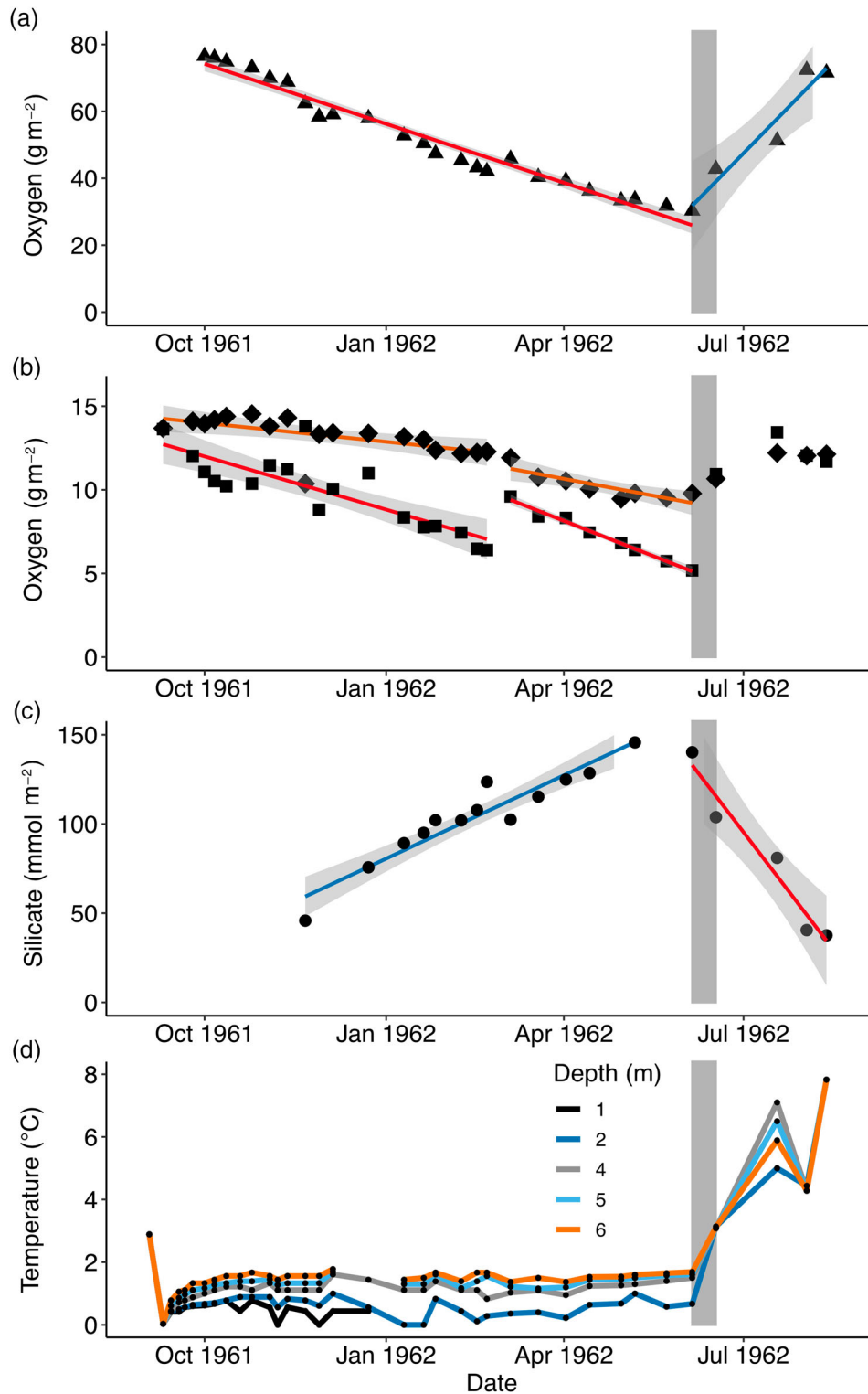


Figure 2. (a) Total integrated unfrozen water column dissolved oxygen; (b) integrated oxygen by epilimnion (2–3 m) and hypolimnion (5–6 m); (c) total integrated unfrozen water column silicate throughout the 1961–1962 winter; and (d) temperature data measured at discrete depths. Warm and cold colors indicate negative and positive slopes, respectively, of the linear models (details of linear models shown in Table 1) with their respective 95% confidence bands shown in grey shading. The orange lines are the linear model for the epilimnion, and the red lines are the linear models for the hypolimnion before and after the 5 March 1962 oxygen introduction event depicted in Fig. 1b. The vertical grey rectangle indicates the time period between temperature measurements and when the lake was connected with the moat and caused water column mixing, as indicated by the transition to a uniform temperature at all measured depths. Field observations indicate a continuous moat of open water surrounding the remaining ice pack indicated by the right limit of the grey box (16 Jun 1962). Colour version available online.

Table 1. Rates of oxygen and silicate change over selected time intervals for the surface (2–3 m), deep (5–6 m), and the unfrozen water column. First line of each cell is the rate, and the numbers in parentheses are the R^2 and p -value for the rate, respectively. NA = not available.

	Start End	Time Interval			
		10 Sept 1961 5 Jun 1962	10 Sept 1961 5 Mar 1962	5 Mar 1962 5 Jun 1962	5 Jun 1962 12 Aug 1962
Oxygen ($\text{g m}^{-2} \text{d}^{-1}$)	2–3 m	NA	−0.012 (0.38, 0.006)	−0.022 (0.74, 0.006)	NA
	5–6 m	NA	−0.035 (0.69, <0.001)	−0.046 (0.99, <0.001)	NA
	0–6 m	−0.20 (0.97, <0.001)	NA	NA	0.604 (0.93, 0.008)
Silicate ($\text{mmol m}^{-2} \text{d}^{-1}$)	0–6 m	0.52 (0.90, <0.001)	NA	NA	−1.4 (0.95, 0.005)

through Chl-*a* concentration, drives more respiration in the water column and sediments over winter (Babin and Prepas 1985). Using the winter net oxygen loss rates calculated here and the model from Babin and Prepas 1985, we estimated that Immerk Lake contains a summer Chl-*a* content of $\sim 3 \mu\text{g L}^{-1}$. This summer Chl-*a* concentration estimate is 2–6 times higher than other oligotrophic, high Arctic lakes (Mathias and Barica 1980) and 3 times higher than measured during summer 1973 (Minns 1977). Higher production is needed to drive the winter net oxygen decrease measured in Immerk Lake, but summer Chl-*a* measurements ($0.75 \mu\text{g L}^{-1}$; Minns 1977) are too low to account for the high winter net oxygen decrease measured here. Thus, excess production in Immerk Lake is likely benthic and not captured by water column measurements of Chl-*a*. This situation is not uncommon in clear, oligotrophic Arctic lakes; in fact, benthic production can account for 60–80% of primary productivity (Kalff and Welch 1974). Active benthic primary productivity in Immerk Lake would lead to an accumulation of C at the sediment surface over summer and more benthic respiration during the ice-covered season.

The hypolimnion (5–6 m) of Immerk Lake sustained net oxygen loss first and to the greatest degree compared with the rest of the water column (Fig. 1a, 2b). The rate of net oxygen loss from the hypolimnion ($0.035 \text{ g O}_2 \text{ m}^{-2} \text{d}^{-1}$; 5–6 m; Fig. 2b, Table 1) was almost 3-fold greater than from the epilimnion ($0.012 \text{ g O}_2 \text{ m}^{-2} \text{d}^{-1}$; 2–3 m; Fig. 2b); however, oxygen at the ice–water interface may be slightly elevated by disturbance while sampling and the open hole in the ice. The sustained decrease of oxygen and resulting low oxygen content during the ice-covered period of Immerk Lake follows predictions that a shallow lake with a large littoral area is a strong predictor of net oxygen loss during winter (Leppi et al. 2016) because of a high sediment area to lake volume ratio that promotes more sediment–water interactions (Mathias and Barica 1980, Leppi et al. 2016). Lake sediments are strong sinks for oxygen, which can produce steep oxygen gradients at the sediment–water interface and lead to oxygen losses from the shallower depths (Baxa et al. 2021). We suggest

that the higher net oxygen loss rates in deeper water are driven by sedimentary oxygen consumption, a finding consistent with other lakes (Matzinger et al. 2010). Sedimentary oxygen consumption is the result of both heterotrophic and chemoautotrophic microbial activity and abiotic reactions of oxygen with reduced substances (Matzinger et al. 2010). Given the elevated net oxygen decrease within the hypolimnion, Immerk Lake sediment is the site of active respiration and microbial activity over winter.

The final stratified water column samples were collected on 5 June 1962, when oxygen values in the deep water (6 m) reached a minimum (Fig. 1a). Correspondingly, the temperature profile of the water column on 5 June 1962 ranged from 0.67°C at 2 m to 1.7°C at 6 m depth, indicating the water column was still cold and inversely stratified. The oxygen increased rapidly throughout the Immerk Lake water column as the ice began to ablate; however, the sampling frequency does not allow us to determine the exact day the water column was mixed. The ice cover was first lost from the edges of the lake as a shallow moat formed. The moat water temperature was recorded at 3.3 – 5.5°C on 17 June 1962 and was likely well aerated from wind action, based on field observations. This moat water was warm, dense, and oxygen saturated (data not shown) relative to the water column at the regular sampling station and would have sunk to the bottom of the lake once ice had thinned sufficiently for the moat to connect to the main basin; thus, it would have introduced oxygen at depth and induced convective mixing (Salonen et al. 2014), thereby likely disrupting the winter stratification. In fact, the 17 June 1962 sampling shows the water column was uniformly mixed, well oxygenated (7.6 – 8.0 mL L^{-1} ; Fig. 1a), and 3.1°C throughout. The relatively uniform, warm, and oxic water column on 17 June 1962 provides evidence that the moat water was connected to the main basin of the lake that contained the sampling site. The timing of ice loss from Immerk Lake during summer 1962 is similar to the ice loss during summer 1973, which began on ~ 20 June 1973, as indicated by a decrease in the surface area of ice cover and warming of the water column (Minns 1977). We

know Immerk Lake began mixing sometime within a 12 d period between 5 and 17 June 1962. The reoxygenation and mixing of the water column was rapid (<12 d) compared to the development of stratification and overwinter net oxygen loss (269 d). July 1962 was a slightly warmer month on average across the Canadian Arctic, but the 1961 and 1962 annual temperatures are now exceeded on an annual basis after 1995 (van Wijngaarden 2015). These data imply Immerk Lake is a polar monomictic lake where ice cover melting during June to July quickly resets the oxygen content of the water column and alleviates the hypoxia that developed in the hypolimnion over the long ice-covered season.

Silicate dynamics

Silicate shows an opposite pattern to oxygen throughout the annual cycle of Immerk Lake (Fig. 1b). Silicate concentrations were low (6–13 μM) throughout the water column on the first day silicate samples were collected (21 Nov 1961) and slightly increased with depth on that date (Fig. 1b). The silicate content of the Immerk Lake water column increased throughout the ice-covered season until 7 May 1962, when the bottom water reached a maximum silicate concentration (40 μM ; Fig. 1b). The net silicate increase rate within the unfrozen water column was $0.52 \text{ mM m}^{-2} \text{ d}^{-1}$ (Fig. 2c). Water just below the ice cover on Immerk Lake reached silicate concentrations of >30 μM , well above the concentration (7 μM) that relieved silica limitation on phytoplankton communities in ice-covered Lake St. Clair during experimental manipulations (Wallen 1979). Silicate concentrations >20 μM supported phytoplankton growth in Toolik Lake, an Arctic, deep (~20 m), oligotrophic, kettle lake (Cornwell and Banahan 1992). Note that both Immerk Lake and Toolik Lake bottom waters reached similar silicate concentrations (30–38 μM) at the end of the ice-covered season (Cornwell and Banahan 1992). Two lakes from Western Greenland show similar patterns of increased silica concentrations in their hypolimnetic water during early spring ice-covered periods, decreasing as ice melted and phytoplankton populations increased in abundance (Hazuková et al. 2021). Thus, the silicate concentrations in Immerk Lake were conducive to supporting a diatom-dominated phytoplankton community. Taken together, these data suggest that the resupply of silicate to the water column during the ice-covered season was sufficient to promote diatom growth during the spring and summer.

The most conspicuous aspect of silicate dynamics in Immerk Lake is that the sediments are an apparent source of silicate to the water column (Fig. 1, 2). While we do not have in situ data to confirm the sediments as a source, sediments are a well-described source

of silicate to the water column (Johnson and Eisenreich 1979, Conley et al. 1988, Ryves et al. 2006, 2013). After diatoms die and sink to lake sediments, frustules of biogenic Si are degraded and the silica is recycled to the water column (Nriagu 1978, Bidle and Azam 1999). Dissolution of biogenic Si is promoted by bacteria in freshwater (Patrick and Holding 1985) and sediments (Bidle and Azam 1999). Lake sediments dissolve diatom frustules to varying degrees, with numerous physicochemical factors influencing the degree of dissolution (Ryves et al. 2006). Lake sediments typically have higher microbial activity and thus would produce a relatively consistent dissolution of biogenic Si throughout the year in Immerk Lake, independent of ice cover. However, ice cover on Immerk Lake induces hypoxia in the bottom waters (Fig. 1a), which has been suggested as a mechanism that increases the rate of biogenic Si dissolution (Ryves et al. 2013). Ryves et al. 2013 suggested that anaerobic microbial activity may contribute to the dissolution of diatom frustules in freshwater lake sediments. Microbial iron (Fe) reduction is an anerobic metabolism that may contribute to both the Si flux to the water column and dissolution of diatom frustules. The increased release rate of silica from sediments during hypoxia was related to the release of anions of Si from Fe(III)-oxides due to microbial iron reduction (Lehtimäki et al. 2016). Fe cycling has been implicated in the control of silica dynamics across numerous aquatic habitats with fluctuating redox conditions (Tuominen et al. 1998, Sommer et al. 2006, Tallberg et al. 2008, Cornelis et al. 2011). Additionally, the metabolic process of microbial Fe reduction produces alkalinity and can shift the pH of an environment to more alkaline conditions (Adams et al. 2007), which is also conducive to a greater rate of biogenic Si dissolution (Loucaides et al. 2008). Our data suggest that ice cover enables hypoxic hypolimnetic waters that promote net silicate increases in the water column over the long Arctic winter.

Diatom growth during ice-cover melting (5–17 June 1962) is likely responsible for the rapid decrease ($1.4 \text{ mmol m}^{-2} \text{ d}^{-1}$; Table 1) in silicate concentrations measured through late June and into August (Fig. 1b, 2c). The decrease in silicate was almost 3 times the rate of silicate increase during the ice-covered season, indicating mechanisms that resupply silicate to the water column were much slower than processes that consumed silicate from the water column (Fig. 2c). The consumption of silicate from the water column during spring is likely due to the biological uptake by planktonic and benthic diatom populations. The phytoplankton community composition of Immerk Lake has not been determined; however, sedimentary records document

biological silica deposition in the top 6 cm and *Fragilaria* species in the surficial sediments (Wolfe and King 1999). *Fragilaria* is a common diatom genus found in other temperate and Arctic lakes (Anderson 2000), and its occurrence in the surficial sediments indicates that benthic diatom communities also inhabit the large littoral areas of Immer Lake. These benthic diatom mat communities also likely contributed to the net loss of silicate from the water column. To estimate the growth that this silicate drawdown could support, we assumed (1) a cellular Si content of 2 pmol cell^{-1} as determined for *Fragilaria* within Lake Constance, and (2) that the entire decrease of silicate in the water column is due to pelagic *Fragilaria* (Sommer and Stabel 1983, Conley et al. 1989). The observed silicate drawdown in Immer Lake would therefore support growth of $7 \times 10^8 \text{ cells m}^{-2} \text{ d}^{-1}$, integrated over the entire water column (less if some growth is benthic), about 1 order of magnitude less than the growth reported for *Fragilaria* in Lake Constance (Sommer and Stabel 1983). Phytoplankton activity was not measured during summer 1961, but another expedition to Immer Lake during summer 1973 showed peak Chl-*a* content and ^{14}C -based primary productivity rates during early July and the early ice-melting period (Minns 1977), consistent with other studies that show diatom growth initiates under ice and is maximal around ice melting (Anderson 2000). We assumed that the phytoplankton growth occurred at a similar time during summer 1961, given the similarity in ice-loss timing and development of water temperature profiles between 1962 and 1973 (discussed earlier; Fig. 1; Minns 1977); thus, the timing of peak production and growth likely corresponds to the rapid drawdown of silicate (Fig. 2).

Conclusions

Lake ice is an important component of high-latitude lake ecosystems, and with rising temperatures, many Arctic lakes are at risk of having substantially reduced ice cover (Surdu et al. 2014, Sharma et al. 2019, Woolway et al. 2020). Our data show that net silicate increase in the water column during the ice-covered season was slow when compared to net silicate decreases during the spring–summer period. Despite the large accumulation of silicate over winter, the water column returned to autumn levels (Fig. 1b, 2c). The conditions beneath the ice cover and the duration of ice cover on Immer Lake were important for regenerating the large standing stock of silicate to the water column. Earlier lake-ice breakup may lead to earlier growth of planktonic and benthic photosynthetic organisms that require the nutrient Si (Anderson 2000, Weyhenmeyer 2008). The

earlier lake-ice breakup leads to shorter, stable, under-ice water columns that allow accumulation of a large standing stock of silicate. Thus, shorter ice-covered seasons may abbreviate seasonal nutrient cycles. The data presented here from 60 years ago provide the benchmark to test whether shorter ice covers do alter Arctic lake ecosystem function.

Acknowledgements

This work is a tribute to the legacy of Spencer Apollonio, and an indication of how forward thinking his scientific ideas were and remain. ABM would like to acknowledge and honor Spencer for his friendship, stories, and inspiring love of science, especially the Arctic, to the very end. The authors thank Paty Matrai, David Emerson, and Laura Sofen for comments on the manuscript. Thanks to Caroline Moseley at the Bowdoin College Library for scanning field notebooks. This work was part of the Devon Island Expedition (1960–1963) of the Arctic Institute of North America. SA led the Devon Island expedition and braved the Canadian Arctic winter to collect and analyze the Immer Lake samples and helped to write the manuscript. ABM analyzed the data and wrote the manuscript. Both authors approve the final submitted version.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The field sampling was supported by funds and supplies from the Arctic Institute, Defense Research Board of Canada, National Research Council of Canada, Royal Society, United States Steel Foundation, Hudson's Bay Company, Office of Naval Research (USA), Massey-Ferguson Ltd., United States Weather Bureau, Meteorological Branch of the Department of Transportation (Canada), and Quartermaster Corps of the United States Army. ABM was supported by a grant from National Science Foundation (USA) (#1754358 awarded to D. Emerson).

Availability of data and material

No sample material remains from this study. All data used in this manuscript are publicly available at <https://github.com/abmichaud/truelove>. R code used in this study is publicly available and explained at <https://github.com/abmichaud/truelove>.

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