Oxygen Depletion in Arctic Lakes
Circumpolar Trends, Biogeochemical Processes, and Implications of Climate Change
Klanten, Y.; Couture, R. M.; Christoffersen, K. S.; Vincent, W. F.; Antoniades, D.

Published in:
Global Biogeochemical Cycles

DOI:
10.1029/2022GB007616

Publication date:
2023

Document version
Publisher's PDF, also known as Version of record

Document license:
CC BY-NC-ND

Citation for published version (APA):
Oxygen Depletion in Arctic Lakes: Circumpolar Trends, Biogeochemical Processes, and Implications of Climate Change

Y. Klanten1,2,3, R.-M. Couture1,2,4, K. S. Christoffersen5,6, W. F. Vincent1,3,7, and D. Antoniades1,2,3

1Centre for Northern Studies (CEN), Université Laval, Québec City, QC, Canada, 2Département de géographie, Université Laval, Québec City, QC, Canada, 3Takuvik International Research Laboratory, Université Laval, Québec City, QC, Canada, 4Département de chimie, Université Laval, Québec City, QC, Canada, 5Département de biologie, Université Laval, Québec City, QC, Canada, 6Arctic Biology, University Centre in Svalbard, Longyearbyen, Norway, 7Département de biologie, Université Laval, Québec City, QC, Canada

Abstract  Polar amplification of climate change has the potential to cause large-scale shifts in the dissolved oxygen (DO) dynamics of Arctic lakes, with implications for fish survival, greenhouse gas production, and drinking water quality. While DO is also a sentinel of environmental changes of physical, chemical, and biological nature (e.g., ice cover, temperature, dissolved organic carbon, photosynthesis, and respiration), no synthesis exists of current knowledge of DO dynamics across the diverse freshwater systems of the Arctic. We thus conducted a systematic review of the literature that yielded DO data from 167 sites north of the Subarctic limit (based on vegetation zones), spanning 76 years and including 40 sites with time series. The compilation revealed insufficient observations for adequate representativeness of oxygen dynamics over Arctic ecosystem gradients. We described the main processes controlling DO budgets of Arctic lakes and tested relationships of summer oxygen depletion with maximum depth and latitude. The meta-analysis showed that most sites with low O2 concentrations were shallow (<10 m) and situated toward the southern end of the latitudinal gradient. Permanently stratified lakes with deep, perennially anoxic basins were located toward the northern end of the gradient. By way of a conceptual model, we identified the direct and indirect drivers and mechanisms that lead to changes in oxygen budgets in the context of the warming Arctic. This comprehensive update on available data allowed us to suggest future research directions and recommend the use of moored instruments for continuous all-season observations, combined with modeling, remote sensing, and paleo-reconstructions.

Plain Language Summary  Lakes are dominant features of the Arctic landscape, and they have great cultural and environmental significance. The amplified effects of global warming observed in the Arctic represent a threat to the integrity of these systems. Levels of dissolved oxygen (DO) in lake water have implications for fish survival, greenhouse gas production, and drinking water quality. To summarize the state of knowledge about DO in Arctic lakes, we reviewed literature and extracted data from 167 sites. We describe the main processes known to control the oxygen balance and classified the lakes according to their bottom oxygen concentrations during summer. Most lakes that had low oxygen were shallow and situated toward the southern part of our study region. Lakes that never mix, and thus preserve permanent oxygen depletion in their deep waters, were located toward the northern end of the gradient. With a conceptual model, we illustrate how climate change is likely to influence oxygen balance by the way of direct and indirect drivers. We suggest future research directions including the collection of continuous data throughout all seasons, modeling, remote sensing, and studies of sediment cores to reconstruct past conditions.

1. Introduction  Surface freshwaters are pervasive across the Arctic, and the polar amplification of climate warming implies that numerous characteristics of these highly sensitive ecosystems are susceptible to change due to environmental forcings (Culp et al., 2022; Saros et al., 2022). Oxygen dynamics respond strongly to ongoing physical, chemical, and biological changes, and oxygen may therefore be considered an integrator of climate-mediated alterations in aquatic environments (Hanson et al., 2006). Oxygen regime transitions in aquatic ecosystems are commonly rapid, unidirectional shifts that have strong repercussions for biological communities and biogeochemical processes (Bush et al., 2017; Preece et al., 2019). Shifts toward anoxia in high-latitude lakes are of major importance for the global carbon cycle because they promote methanogenesis, which could create a positive
feedback by contributing to greenhouse gas emissions, and climate-driven oxygen changes have been shown to drive greenhouse gas emissions in Arctic lakes (Cadieux et al., 2017).

A wide variety of mixing regimes has been documented in lakes across the Arctic, implying a diversity of oxygen dynamics. Mixing regimes range from amictic and meromictic ice-capped lakes in the extreme North to cold monomictic lakes at many High Arctic sites, and polymictic and dimictic lakes in Subarctic regions (W. M. Lewis, 1983; Vincent et al., 2008). However, any geographic generalization about the distribution of mixing regimes—and by extension of their influence on oxygen dynamics—is difficult because sites vary concurrently along climatic gradients from south to north, east to west, and from coastal to continental sites. At the southern limits of the Arctic, some dimictic lakes become oxygen depleted during summer (Deshpande et al., 2015; Paquette-Struger et al., 2018), but more northerly systems are particularly vulnerable to winter oxygen depletion due to prolonged periods of ice cover and darkness. It has been hypothesized that oxygen availability will become enhanced as ice cover duration diminishes (Couture et al., 2015). The consequences are of major ecological and societal importance since there are impacts on water quality and the survival of fish stocks (Lienesch et al., 2005; Preece et al., 2019; Ruggerone, 2000).

While initiatives such as the Circumpolar Biodiversity Monitoring Program provide assessments of the current status and trends in Arctic freshwaters (Lento et al., 2019), there is still an existing knowledge gap about Arctic limnology in many regions due to logistical challenges in accessing sites, particularly with respect to data from outside the short summer period. Recent developments and cost reductions of instrumentation that allow for the continuous monitoring of oxygen and other variables such as temperature, specific conductivity, and solar radiation have opened opportunities for studies of annual dynamics.

To date, there has been no synthesis of the state of knowledge concerning lake oxygen dynamics in the Arctic. Earlier work includes overviews of general Arctic limnology that underlined oxygen as a key variable (e.g., Rautio et al., 2011; Vincent et al., 2008), while other reviews focused on lake oxygen with regards to phosphorus release (Hupfer & Lewandowski, 2008), effects on stable isotopes (Mader et al., 2017), and hypolimnetic oxygenation (Preece et al., 2019). A recent meta-analysis of temperate lakes suggested a widespread deoxygenation trend in the past decades (Jane et al., 2021), but there was insufficient data from Arctic sites to make such an assessment for the North.

The Arctic is at the frontline of climate change, and sea ice loss, together with warming temperatures, is predicted to have wide-ranging consequences for the ice cover, hydrology, and biogeochemical functioning of lakes (Kopec et al., 2016; Post et al., 2013; Woelders et al., 2018). While little is known about dissolved oxygen (DO) in northern high latitude freshwaters at broad spatial scales, the amplification of climate change in the region implies that their dynamics are also more likely to change in response to future warming (Vincent et al., 2013). Models of a high greenhouse gas emission scenario (SSP5-8.5) predict the first ice-free summers in the Arctic Ocean as early as 2035 (Docquier & Koenigk, 2021), and sea ice declines have been shown to influence lake ice dynamics in northern Alaska (Alexeev et al., 2016).

Lake ice cover phenology and thickness have changed with warming climates, causing changes in oxygen regimes (Brown & Duguay, 2010; Dauginis & Brown, 2021; Smejkalova et al., 2016). For example, previously perennially ice-covered Ward Hunt Lake (83°N) is now experiencing occasional ice-free summers, which has resulted in oxygen loss during summer and slower decreases in oxygen concentrations at the onset of winter (Bégin et al., 2021). Climate-driven permafrost disturbances causing increased carbon mobilization into aquatic systems have also disrupted oxygen gradients (Deshpande et al., 2017; L. Guo et al., 2007; Reyes & Lougheed, 2015). For example, in West Lake, on Melville Island in the Canadian Arctic Archipelago, anoxic waters were preserved throughout summer as a result of density stratification following local active-layer detachments (Dugan et al., 2012). Warmer temperatures also have direct impacts on stratification and biological processes (Kraemer et al., 2015; Pace & Prairie, 2005; Williamson et al., 2009), which may lead to shifts in oxygen balance. Given the high diversity of freshwater systems and the many climatic factors at play, the expected response of oxygen dynamics across Arctic freshwaters is still poorly constrained.

Our primary objective in this review was to assess the state of current knowledge regarding oxygen dynamics in Arctic freshwaters. This synthesis of previously published research is intended to guide future investigation of the functioning and trends of oxygen dynamics. We first analyze the temporal and geographical distribution of available oxygen data in the Arctic. We then summarize the main processes involved in the oxygen balance. We
also investigate the evidence of seasonal oxygen depletion in Arctic lakes by exploring trends with regard to lake depth and latitude. We additionally depict the consequences of changes in oxygen regimes and present the main changes in the oxygen balance of Arctic lakes that are observed or predicted in the context of rapid and amplified climate changes. Finally, we suggest perspectives for a better understanding of oxygen dynamics at northern high latitudes.

2. Methods (Data Collection)

To collect publications presenting oxygen data in the Arctic, defined for the purposes of this review as sites that were north of the southern boundary of the Subarctic, we used the Web of Knowledge database (http://apps.webofknowledge.com). Our search terms included [oxygen* OR anoxic OR anoxia] AND [lake OR limnology OR pond OR freshwater OR “water column”] AND [arctic OR “polar lake” OR subarctic] NOT [isotop*]. We searched the database for studies published up to 6 June 2022, which resulted in a total of 612 publications. We then individually checked the publications to eliminate any irrelevant studies. We only selected articles with either water column profiles or time series of DO. We defined profiles as a minimum of 3 depths and time series as data presented with time on an axis in the paper. We thus excluded articles that were restricted to point sampling, mean DO values, oxycline depths, redox potential, oxygen production or consumption rates, sediment pore water profiles, paleo-reconstructions of oxygen, oxygen stable isotopes, and other non-comparable data. We also made specific additions of any encountered or priorly known papers that presented data that fit our constraints but were either not found by our search terms or not included in the Web of Knowledge database.

With the goal of including the maximum number of publications possible, we included both Arctic and Subarctic studies, and thus included in the data acquisition all sites that were north of the Subarctic southern limit (based on vegetation zones; Figure 1) as defined by the Arctic Biodiversity Assessment and provided by the Conservation of Arctic Flora and Fauna (CAFF, 2001). One exception was made for a site that was below but near this geographical limit in Russia, a region that is poorly represented in our data set. This selection process retained 90 publications, presenting data from 167 distinct field sites. Duplicate sites were excluded from the data for the map and are identified in the repository database (Klanten et al., 2023). The depths, geographical coordinates, and years of data measurements were extracted from the papers or supplementary materials. Data sets included in multiple publications were counted only once for the assessment of the temporal distribution of oxygen measurements. For the investigation of seasonal oxygen depletion, we classified oxygen saturation values into three categories: low (DO < 30%), moderate (30% > DO < 70%), and high (DO > 70%), following the classification of Leppi et al. (2016). When oxygen concentrations were presented in mg L−1, we extracted the temperatures from figures or tables to convert concentrations to percent saturation based on solubility due to temperature following oxygen solubility tables (YSI a Xylem brand, 2019). Pressure and conductivity were not considered in the conversion. Sites were classified according to the lowest concentrations observed in the summer in the bottom of their water column. However, because the time and depths of measurements varied between sites, the classification of certain lakes may have differed if data had been collected later during summer or deeper in the water column. Sites were excluded when data did not seem reasonably representative of the summer conditions in the bottom of the water column (e.g., the probe was at an intermediate depth in the water column). The full list of references, data and data sources for our database can be found in the Nordicana D online repository (Klanten et al., 2023).

3. Oxygen Data in the Arctic and Subarctic

Most studies presenting profiles used probes from brands such as Hydrolab, RBR®, or YSI to measure DO. Other methods included the use of an oxygen meter or Winkler titration on sampled water (e.g., Strickland & Parsons, 1972). Some time series resulted from repeated measurements with these same methods, but more recent time series were mostly recorded remotely at higher time resolution using moored instruments (e.g., Bégin et al., 2021; Cortés & MacIntyre, 2020) equipped with optode-based sensors such as the PME MiniDOT®.

In total, there were 40 sites with time series and 127 sites with profiles but no time series. Despite the vast territorial expanse and ecological importance, limnological studies that consider oxygen remain few and sparse (Figure 1). Some regions, such as northern Greenland, Svalbard, and northern Asia are particularly under-represented, which may partly be due to a selection bias resulting from our systematic search being carried out in English. Given the underrepresentation of countries where English is not the language of use, it could be relevant to include
publications in other languages in future literature reviews. Lakes cover 6% of the Arctic land on average, but this proportion rises to 12% in some regions characterized by the presence of permafrost and tundra vegetation (south of the Canadian northern territories, northern Alaska, north-west Russia [Murman Sikh Oblast], and northern Russia in the Laptev Sea vicinity) (Paltan et al., 2015). When comparing the geographical distribution of studies presenting DO data with the density of lakes, regions such as the Russian Arctic and the Canadian region south of the Arctic Archipelago (between approximately 65° and 75°N) are proportionally underrepresented. Studied sites in the literature were often selected because of their proximity to communities or research stations, for their value as sentinels or for their unique characteristics that provide opportunities to expand the frontiers of knowledge. In some cases, this may raise questions about the representativeness over the key ecosystem gradients of the Arctic.

While sites that had only profiles outnumbered sites with time series, when the available data are compared through time, as presented in Figure 2, both types of data were proportionate. This is the result of time series over a few years giving more weight to a single study. As expected, Figure 2 shows a growing interest in DO measurements, and although it may appear to decrease recently, this is most likely an artifact of delays in the publication of collected data (data are presented by year of data measurement rather than year of publication).

Figure 1. Location of lakes with profiles or time series of dissolved oxygen north of the southern boundary of the Subarctic. Mean annual air temperatures are long-term (1981–2010) GHCN Gridded V2 data provided by NOAA/OAR/ESRL PSL, Boulder, Colorado, USA. The southern boundary of the Subarctic is defined by the Arctic Biodiversity Assessment and provided by the Conservation of Arctic Flora and Fauna (CAFF, 2001).
4. The Oxygen Balance in Arctic Lakes

Dissolved oxygen dynamics in lakes are the result of a delicate balance between oxygen sources and sinks (see overview in Figure 3), where the main oxygen sources are photosynthesis and water-atmosphere exchanges (Golosov et al., 2012), although in some cases a large proportion of oxygen may come from meltwater inputs or tributaries (Figure 3a) (e.g., Craig et al., 1992). Respiration in water and sediment is the main oxygen sink (Pace & Prairie, 2005), but groundwater discharge could also deliver oxygen-depleted water (Vachon et al., 2020). The oxidation of reduced species transported across the sediment-water interface (MacIntyre et al., 2018) as well as of compounds reduced by photochemical processes can also be a significant oxygen sink (Miles & Brezonik, 1981) (Figure 3f).

The processes controlling oxygen in Arctic lakes are distinctive in several ways. Extreme annual photoperiod cycles in the polar regions exert a strong influence on oxygen dynamics via their effects on photosynthesis (Figure 3b). During polar summers, the amplitude of diurnal light cycles is much less pronounced than in other regions, and therefore, less variation in O₂ production is expected at this scale. By contrast, the prolonged absence of light during long polar nights strongly limits or eliminates oxygen production by photoautotrophs for several months of the year (e.g., McKnight et al., 2000; Schindler, Kalff, et al., 1974; Schindler, Welch, et al., 1974). Even after the return of the sun, and despite increased photoperiods, light can remain limiting in spring due to low penetration through lake ice and snow covers (Hazuková et al., 2021; McKnight et al., 2000; Salonen et al., 2009). In cases where light can penetrate well through the ice, primary productivity increases may be initiated under ice cover (Bégin et al., 2021; Christoffersen et al., 2008).

Figure 3. Principal sources and sinks of oxygen in lakes (gray boxes) and the main variables controlling these flux processes (blue boxes) that are discussed in the text. Oxygen sinks are represented by orange arrows and oxygen sources by black arrows. The letters identifying the boxes are referred to throughout Section 4, and interactions between the variables are described in the main text.
Water-atmosphere exchanges are critical for oxygen dynamics, and the prolonged, and in some cases the perennial duration of ice cover has a prevailing effect in Arctic lakes (Figure 3d). The presence of ice cover reduces or even prevents the effect of other variables that can control water-atmosphere exchanges (e.g., wind, air temperature, oxygen concentration). Lake water is usually oxygen saturated at the start of freeze-up and the exclusion of gases during ice formation increases DO concentrations (e.g., Huang et al., 2021). Without further supply of oxygen, and with reduced photosynthetically available radiation at the onset of ice cover, O₂ sinks typically become proportionately more important, inducing oxygen depletion that progresses upward in the water column from the sediment-water interface (Golosov et al., 2007). In spring, the physical properties of snow and ice influence radiatively driven convection and thus the transport of oxygen to deeper layers (Mironov et al., 2002; Yang et al., 2017). With the melting and loss of lake ice, further mixing processes supply and distribute oxygen in the water columns of Arctic lakes (Cortés & MacIntyre, 2020). For instance, during once rare but increasingly frequent summers when it loses its ice cover, Canada's northernmost lake has oxygen concentrations in equilibrium with the atmosphere (100%) (Bégin et al., 2021). However, when its ice cover persists during the period of high photosynthetic activity, its water becomes supersaturated with oxygen and equilibration with the atmosphere is prevented by the ice. An analogous situation exists in perennally ice-covered lakes from Antarctica that are supersaturated with O₂ as a result of high photosynthesis and lack of mixing, along with the delivery of oxygen from meltwater streams (Spaulding et al., 1994; Wharton et al., 1986). Hydrological connectivity has also been shown to influence the interannual variability of under-ice oxygenation in northern lakes (Palmer et al., 2021).

The influence of climate on the mixing regimes of Arctic lakes controls DO in multiple ways (Figure 3c). The duration of lake ice cover is closely linked with mixing depth and the development of stratification (Cortés & MacIntyre, 2020; Dibike et al., 2011; Mueller et al., 2009). This is further supported by paleolimnological records showing changes in stratification resulting from climate-induced changes in lake ice cover (Rühland et al., 2015). In dimictic lakes, warming waters are predicted to induce the earlier onset of summer stratification as well as its longer duration (Dibike et al., 2011), and weaker mixing and increased thermal stability in longer summers represent favorable conditions for oxygen depletion. Rapid thermal stratification, resulting in poor mixing after ice-out, can also contribute to low summer oxygen concentrations (O’Brien et al., 2005). In Arctic monomictic lakes, the duration of the ice-free period and summer temperatures is likely to influence the efficiency of the mixing, and thus the oxygenation process. Changes in snowmelt and glacial meltwater may also modify mixing dynamics with implications for oxygenation processes (Cortés et al., 2017; St. Pierre et al., 2019). Moreover, changes in mixing depth have been shown to mediate phytoplankton biomass (Northington et al., 2019), which could further influence oxygen concentrations via photosynthesis.

The low temperature of Arctic waters influences biological processes in the water column and sediment, and thus the equilibrium between photosynthesis and respiration (Figures 3b and 3c). In cold water, very small increases in temperature have been shown to strongly stimulate respiration and can therefore eventually lead to anoxic conditions in the hypolimnion (Pace & Prairie, 2005). This is supported by the results of Golosov et al. (2007), who showed O₂ depletion resulting from thermal regime changes in ice-covered lakes. Because respiration supplies reduced compounds for oxidation, feedback can trigger further decreases in DO. However, recent evidence suggests that other factors, such as microbial community composition, may be more important than temperature in cold environments (Gudasz et al., 2021). Sediment respiration also stimulates heat and solute fluxes at the sediment-water interface, creating density currents involved in overturn at the onset of ice cover, which promotes DO depletion (MacIntyre et al., 2018; Terzhevik et al., 2009). Although increases in water temperature also stimulate photosynthesis (Rae & Vincent, 1998), the overall effect of warmer waters is to decrease the ratio of photosynthesis to respiration and therefore promote oxygen depletion (Staehr & Sand-Jensen, 2006). For instance, the loss of ice cover on Ward Hunt Lake induced cooling of the water and sediment, which slowed the decrease in oxygen concentrations at the onset of winter (Bégin et al., 2021). However, this is a feature of the most northern lakes, whereas most Arctic and especially sub-Arctic lakes would be expected to have warmer waters in response to increasing air temperatures (Prowse et al., 2011) and therefore faster oxygen depletion as ice covers are established.

The most abundant aquatic ecosystems in Arctic landscapes result from permafrost thaw and are thus typically shallow and rich in colored organic matter (Pienitz et al., 2008). These high concentrations of organic matter promote bacterial decomposition, a major sink for O₂ (Deshpande et al., 2017). High inputs of colored humic compounds also lead to less available light in the water column, which can become limiting for photosynthesis and thus promote further oxygen depletion (Golosov et al., 2007; Kirillin et al., 2012; Modenutti et al., 2001;
O2 depletion due to warming that stimulates respiration; (d) organic rich sediment; and (e) high concentrations of dissolved organic matter attenuating the light available for photosynthesis and providing more substrates for respiration (Rautio et al., 2011). On the other hand, some have large biomass stocks of mosses, benthic algae or cyanobacterial mats that produce oxygen when light is available at the sediment surface (Bonilla et al., 2005; Rautio & Vincent, 2006; Riis et al., 2016).

5. Evidence of Seasonal Oxygen Depletion in Arctic Lakes

The period during which lakes are vulnerable to oxygen depletion is dependent on their mixing regimes. A large variety of mixing regimes coexist at high latitudes (amictic, meromictic, monomictic, dimictic, polymictic; W. M. Lewis, 1983; Vincent et al., 2008), and assessing the oxygen dynamics of these systems is complex. A wide range of oxygen concentrations in Arctic lakes was pointed out early by pioneers such as Røen (1962), Reed (1962), Kalff (1965), and Watson et al. (1966). While oxygen depletion has been studied at sites around the circumpolar North (Figure 1), these results have never been compiled, resulting in a lack of perspective at the pan-Arctic scale. To explore the geographic distribution of seasonal oxygen depletion in the Arctic, we classified the lakes in our database according to their oxygen level in the bottom of their water column in summer. A total of 138 lakes had data that were considered sufficient to determine the state of oxygen concentrations in summer. Among those, 21 lakes were permanently stratified and were thus considered as a separate group, given that their oxygen-depleted state is independent of seasonal cycles. Forty-two lakes were categorized as having low summer oxygen concentrations, 16 were categorized as having moderate DO, while 62 lakes were categorized as having high DO availability (further details are given in Klanten et al., 2023).

We examined geographical and morphometric influences on summer DO by plotting the distribution of the lakes as a function of depth and latitude (Figure 4). Although the figure appears to show increasing lake depth with latitude, it is possible that this is the result of sampling bias, and that deep subarctic lakes and shallow high Arctic lakes may have been under-sampled. Within the data set, there were no lakes south of 60°N with a maximum depth over 4 m, consistent with the thermokarst lakes that dominate subarctic landscapes (Pienitz et al., 2008). However, there are also deeper lakes in these regions (e.g., Lac Wiyâshâkimî, formerly known as Clearwater Lake/Lac à l’Eau Claire; 56.2°N, maximum depth of 178 m; Vincent et al., 2013), and the lack of oxygen data from such sites means that it is not yet possible to assess their vulnerability to depletion. On the other hand, oxygen conditions in the numerous shallow lakes of the High Arctic seem to have attracted less interest so far, perhaps because it is assumed that they are well-mixed during the summer. Because of this suspected sampling bias, Figure 4 is intended as an exploratory illustration of the state of knowledge about summer oxygen depletion. Other morphological variables, such as lake surface area, water volume, or surface area to volume ratio are highly relevant, but were not systematically available in the published literature such that they could be considered in this synthesis. It is important to note that the observations presented in Figure 4 range from 1954 to 2019, and may not be directly comparable due to interannual differences in weather and/or climate change over this period. The published data were also obtained at different times during the summer and at different depths from one site to another. Interpretations based on this classification must therefore be made with caution.

Oxygen dynamics are known to be closely linked to local climate and thus dependent on geographical location (Fang & Stefan, 2009). In our meta-analysis, the farthest north lakes that experienced summer DO depletion during ice-free conditions were situated on Bylot Island at about 73°N (Figure 4), where BYL27 (depth: 1.2 m) and BYL 36 (depth: 12 m) had bottom-water DO concentrations of ~20% and ~0%, respectively (Bouchard et al., 2015). In the High Arctic, the ice-free period is sufficiently short (i.e., one or 2 months) that the establishment of thermal stratification is not expected in summer. The classic work by Schindler, Kalfi et al. (1974) and Schindler, Welch et al. (1974) on Char and Meretta lakes, at 75°N in the Canadian High Arctic, showed the pronounced physical and chemical cycles during the year, and the prevalence of homogeneous, well-oxygenated conditions during the few weeks of summer.

The large majority of the sites showing low summer O2 concentrations were shallow (<10 m) Subarctic sites toward the southern end of the latitudinal gradient. By contrast, lakes with high O2 availability were present...
throughout the latitudinal and depth gradients, and no clear trends were evident in their distribution. It is well understood that depth has a direct impact on under-ice oxygen depletion, since as a general proxy for volume, it represents the overall availability of DO relative to the area of the sediment surface where high respiratory oxygen demand occurs (Clilverd et al., 2009). However, in the absence of ice, DO depletion is dependent on density structure (either salinity or thermal stratification; Hanson et al., 2006) that prevents DO supply from mixing throughout the water column (Deshpande et al., 2015). The establishment of summer thermal stratification depends strongly on basin morphology (Butcher et al., 2015), the duration of the ice-free period (Dibike et al., 2011), and air temperatures and wind (MacIntyre et al., 2009). Further investigation of the prevalence of summer stratification in Arctic lakes is thus fundamental for a better assessment of their susceptibility to oxygen depletion.

Dissolved oxygen data are available during both under-ice and ice-free conditions at a few sites, which deserve closer examination. Ward Hunt Lake was the only Arctic site with published data available at high temporal and
spatial DO in the two basins of Lower Martin Lake, which provides another rare opportunity to understand seasonal dynamics while considering interannual variability (Palmer et al., 2021). A total of 33 lakes had DO data that was recorded both under ice and during ice-free conditions. Lake Hazen (z\text{max} = 250 m) is the deepest lake for which comparable oxygen concentrations between the two seasons exist, and these data reveal under-ice oxygen depletion (reaching 1 mg L\text{−1}) in the bottom ~5 m of the water column in spring (Lehnherr et al., 2018). Lake Vasikkaselan (z\text{max} = 95 m, Puro-Tahvanainen et al., 2011) has also undergone spring oxygen depletion in its bottom, which has intensified over the last few decades and reached ~30% saturation in 2009. However, these two deep lakes both had well-oxygenated waters during summer. The other 31 lakes also all experienced under-ice depletion, but the occurrence of depletion during the ice-free period varied among sites (see Klanten et al. (2023) for more details). Lakes West, East, Char and Mellemsø are the next deepest lakes (34, 30, 27.5, and 27 m, respectively) with measurements under ice and in ice-free conditions. While West and East lakes were shown to develop an under-ice anoxic layer extending for 10 months (Dugan et al., 2012), Char and Mellemsø lakes experienced less pronounced winter depletion, with oxygen concentrations falling to around 5 mg L\text{−1} (Røen, 1962; Schindler, Welch, et al., 1974). The much shallower (<3 m) permafrost thaw lakes at lower latitudes all developed anoxia after freeze-up, consistent with high bacterial respiration resulting from high organic matter availability (Deshpande et al., 2015, 2017; Hughes-Allen et al., 2021). During the ice-free period, there were mixing events that oxygenated these peatland thaw lakes, with the exception of one site where bottom waters remained anoxic throughout the winter and summer as a result of incomplete spring mixing due to density stratification (Deshpande et al., 2017).

The general lack of data about under-ice oxygen concentrations makes it difficult to establish the prevalence of oxygen depletion around the Arctic during the ice-covered period. Despite the winter DO depletion in 31 sites described above, other publications with under-ice profiles or time series have shown well-oxygenated waters in Arctic lakes. Leppi et al. (2016) presented oxygen time series throughout the winter from the bottom of three lakes in northern Alaska but did not include data from the summer open-water period. The deepest lake (20 m), located near Toolik Field Station, had oxygen concentrations over 8 mg L\text{−1} throughout the ice cover period, while the 16 and 2 m deep lakes reached 0 mg L\text{−1} at some point. Profiles of DO under early spring ice cover in four lakes on northern Ellesmere Island indicated that two deeper lakes (28 and 49 m) were well-oxygenated, as opposed to two shallower lakes (9 and 7 m) that had pronounced hypoxia throughout much of their water columns (Klanten et al., 2021).

While oxygen dynamics seem to be related to depth and latitude, other characteristics of Arctic systems make this relationship more complex. Lake fertilization may affect both summer and winter DO conditions (Budy et al., 2022; Daniels et al., 2015; Schindler, Kalff, et al., 1974), and other characteristics such as distance to the ocean, elevation, area, geomorphology, and snow depth may also influence DO (Devlin & Finkelstein, 2011; Leppi et al., 2016; Whiteford et al., 2016). The apparent complexity of the interactions between lake characteristics that determine the susceptibility to oxygen depletion highlights the need for greatly improved observations that capture both complete annual cycles and the diversity of systems in this vast territory.

6. Consequences of Changes in Arctic Lake Oxygen Regimes

Oxygenated Arctic lakes are valuable resources as they represent drinking water supplies for northern communities. Anoxic conditions causing the release of redox-sensitive trace elements generate issues for drinking water quality (Gora et al., 2020; Preece et al., 2019), a growing concern for northern residents’ health in the context of climate change (Harper et al., 2020). Some elements released from sediments, such as arsenic, are contaminants that are threatening to human and ecosystem health (Palmer et al., 2021).

Aquatic organisms have different tolerances to oxygen depletion, and Arctic freshwaters that remain oxygenated through the winter are essential overwintering habitats for fish (Hagerman, 1998). Some small-bodied Arctic fish are tolerant to low oxygen concentrations (e.g., Alaska blackfish [Dallia pectoralis] and ninespine stickleback [Pungitius pungitius]; Haynes et al., 2014). However, Arctic char (Salvelinus arcticus), the most abundant and culturally important species in Arctic lakes, is among the species most sensitive to oxygen depletion (Anttila et al., 2015; Power et al., 2008). Hypoxia influences behavior, reproduction, growth and ultimately survival of Arctic char (Cassidy & Lamarre, 2019; I. D. Jones et al., 2008; Liensch et al., 2005), which further influences lake trophic structure as they are top predators (Jeppesen et al., 2017). In the many fishless Arctic
lakes, invertebrates are the top predators (e.g., Anderson et al., 2008; Calizza et al., 2022), and oxygen also influences their presence, abundance and species distribution (Namayandeh & Quinlan, 2011). Considering how oxygen availability determines the ecological niches of key species in Arctic food webs, hypoxia caused by direct anthropological impacts (e.g., nutrient inputs; Antoniades et al., 2011), water removal (Sibley et al., 2008), or by climate-induced shifts has the potential to substantially affect ecological functioning in Arctic lakes.

Oxygen has also been identified as an important driver of microbial community structure in Arctic lakes (Comeau et al., 2012; Schütte et al., 2016; Somers et al., 2020). Inshore-offshore oxygen gradients associated with distance from ice margins in Arctic lakes may influence microbial activities such as those observed in the biofilms of Ward Hunt Lake (Bégin et al., 2020; Mohit et al., 2017), while DO concentrations also seem to be associated with bacterial assemblages at the Arctic landscape scale (Somers et al., 2020).

Because they spend long periods under ice cover, many Arctic lakes have strongly reducing conditions during most of the year, which favors methanogenesis and thus the accumulation of CH₄, a potent greenhouse gas which is released into the atmosphere at ice out (e.g., Crevecoeur et al., 2015; McIntosh Marcek et al., 2021). Aerobic conditions in surface waters promote methanotrophy, which mitigates emissions of CH₄ (Bastviken et al., 2008; Deshpane et al., 2015). In complete anoxic conditions, particularly occurring in shallow ice-covered Arctic lakes, CH₄ oxidation is limited by reducing conditions, which can lead to methane oversaturation (Martinez-Cruz et al., 2015; Matveev et al., 2019; Phelps et al., 1998). However, it was recently shown that in some Siberian lakes, anaerobic oxidation of CH₄ can fully consume the produced methane (Cabrol et al., 2020; Thalasso et al., 2020).

Longer aerobic conditions imply the promotion of terrestrial OC mineralization rather than sequestration, which could increase CO₂ emissions, particularly in the context of observed and predicted increases in the delivery of terrestrial OC in Arctic lakes (Larsen et al., 2011; Tan et al., 2015; Tranvik et al., 2009; Wauthy et al., 2018). However, terrestrial OC processing in arid Arctic landscapes could be minor with respect to global C turnover, whereas aquatic OC, which is more easily degraded both aerobically and anaerobically, sustains mineralization (Bogard et al., 2019; Sobek et al., 2009, 2014). The fact that Arctic lakes are so abundant and reactive implies that changes in their oxygen dynamics will likely be of great importance for the global carbon cycle (Tan & Zhuang, 2015; Wik et al., 2016), underlining the need for a better assessment of the extent of these processes and potential feedback at the global scale.

Changes in the extent and duration of oxygen depletion could have important repercussions on nutrient cycling in Arctic lakes as oxidation states affect the speciation, reactivity and fate of many chemicals in water (Balistrieri et al., 1992; Hupfer & Lewandowski, 2008; Zhang et al., 2014). For example, persistent anoxia in the lower water column of meromictic Arctic lakes allows the build-up of ammonium, dissolved reactive phosphorus, silicate and reduced iron, manganese, and sulfur (Gibson et al., 2002). Because nitrogen (N) and phosphorus (P) may be limiting in numerous Arctic lakes, changes of nutrient fluxes caused by oxygen concentrations could play a regulatory role in phototrophic growth (Hogan et al., 2014; Levine & Whalen, 2001; Osaka et al., 2022; Whalen & Alexander, 1986). This was observed in an Alaskan lake (N-2, z_max = 10.3 m), where a fertilization experiment that stimulated oxygen depletion resulted in phosphorus release from sediments and concomitant increases in phytoplankton biomass (O’Brien et al., 2005). Hypoxia has also been suggested to increase the dissolution rates of silicates, an essential nutrient for diatoms, which are important components of the phytoplankton communities in many Arctic lakes (Michaud & Apollonio, 2022).

7. Arctic Lake Oxygen Dynamics in a Changing Climate

The majority of studies to date have focused on single ecosystem components, resulting in a lack of perspective about the interconnections between the principal mechanisms by which climate drives oxygen dynamics. In part, this may reflect the challenges of interdisciplinary collaboration, especially for the acquisition of long-term data. Specific sites or regions may also be intentionally studied because they are known to be influenced by a dominant variable of interest. For a general perspective at the circum-Arctic scale, a visual framework that identifies the principal variables and their interactions is currently lacking. To address this need, we developed a conceptual model that includes the six main climate forcings identified from our literature review (Figure 5). The model summarizes how climate drives oxygen dynamics in the circumpolar North by way of direct (warming waters, shorter lake ice cover duration) and indirect (glacier melt, precipitation, vegetation growth, permafrost thaw) linkages. It provides a conceptual framework that can be used to investigate and communicate the complexity of interacting processes regulating the DO regime of lakes in the warming Arctic.
Limnological studies in the circumpolar North have made some progress toward understanding the expected consequences of climate change on DO dynamics, but there are many uncertainties. The outcomes of climate warming may diverge among lakes, depending on site-specific characteristics. Ice-dominated lakes have sometimes been considered to be more influenced by climate through its direct impact on ice cover duration and water temperature, rather than indirectly through its influence on watersheds (e.g., Griffiths et al., 2017; Michelutti et al., 2007).

Increasing temperatures are expected to reduce the duration of lake ice (Dibike et al., 2011; Smejkalova et al., 2016) and shorten under-ice oxygen depletion periods (Terzhevik et al., 2009), but the effect of shorter ice cover duration on summer oxygen conditions is not as clear. Warmer air in summer will induce earlier and stronger thermal stratification which could possibly hinder spring oxygen supply in the hypolimnion and create permanent anoxic layers (Golosov et al., 2012). Higher temperatures could also cause stratification to occur in lakes that did not previously stratify, and this shift from cold monomixis to dimixis would induce a new risk of summer depletion (Lead et al., 2011; Prowse et al., 2011). However, more wind-driven mixing due to reduced ice duration may also prevent thermocline development in shallow lakes (Prowse et al., 2011). In other scenarios, increased oxygenation could result from warming-induced higher primary productivity or stronger mixing, at least on short time scales. Warmer water also decreases the solubility of oxygen, which can play an important role in oxygen depletion in oligotrophic Arctic lakes (Cremer et al., 2005). In short, the response of summer DO to ice cover changes and warmer temperatures remains uncertain, and Arctic lakes could respond via multiple pathways that will depend on their individual characteristics (Figure 5).

Climate change may have contrasting impacts on permafrost thaw lakes, ranging from drainage and evaporation to increases in size and abundance (M. C. Jones et al., 2012; Smol & Douglas, 2007; Zandt et al., 2020) (Figure 5). Thawing permafrost releases carbon and nutrients into lakes, but also to surrounding soils, stimulating terrestrial vegetation growth (Hobbie et al., 1999; Rydberg et al., 2010). Such landscape changes increase the
delivery of organic matter and nutrients to lakes, thus promoting microbial decomposition and oxygen demand (Budy et al., 2022; Zandt et al., 2020). Methane produced by anaerobic microbes is eventually released into the atmosphere and represents a positive feedback to climate warming (Walter, 2006). However, some scenarios predict extensive drainage of thermokarst systems following the loss of permafrost, ultimately resulting in a decline in their total area (Bouchard et al., 2014; Van Huissteden et al., 2011).

Changes in precipitation as a result of climate change have the potential to influence oxygen dynamics in various ways (Figure 5). Snow cover is for the most part expected to decrease in the Canadian Arctic, with longer snow-free seasons, but overall precipitation is expected to increase (Box et al., 2019; Brutel-Vuilmet et al., 2013; Mudryk et al., 2018). However, there is uncertainty about the timing of these precipitation changes as well as significant variability between different regions of the Arctic (McCrystall et al., 2021). Increased precipitation as snow decreases the availability of light for photosynthesis, causing a negative shift in oxygen balance (Huang et al., 2021). Changes in precipitation also contribute to streamflow regime shifts (Spence et al., 2011), which have a direct influence on under-ice oxygen concentrations (Palmer et al., 2021). Predicted increases in liquid precipitation will induce increased weathering in catchments (Hobbie et al., 2017; Kendrick et al., 2018), supplying more nutrients to aquatic systems, which in turn will promote decomposition, microbial respiration and concomitant loss of oxygen. The resulting greater organic matter inputs may further influence oxygen demand by decreasing water transparency, and reductions in thermocline depths (resulting from light attenuation) would cause thicker oxygen-depleted hypolimnia (Fortino et al., 2014). On the other hand, some regions predicted to become dryer will undergo opposite effects on terrestrial inputs, water clarity, and stratification (Schnell, 2009). Changes in precipitation could additionally modulate water levels, and thus basin volumes, further influencing the development of anoxic conditions (Mathias & Barica, 1980; Prowse et al., 2006). Finally, lakes with glazedier catchments will likely receive increased meltwater supply in response to warmer Arctic summers (Mueller et al., 2009) (Figure 5). This can modify oxygen dynamics by increasing the discharge of oxygen-rich glacial meltwater and delivery of nutrients or by altering the lake volume. The presence of large glaciers may also influence lake sensitivity to the direct effects of the warming by influencing local climate (Doran et al., 1996; Michelutti et al., 2006).

Alteration of light conditions resulting from changes in ice cover thickness and duration, from precipitation as snow or from suspended particle concentrations would also have repercussions for oxygen depletion (Figure 5). Radiation penetrating through ice and snow influences convective mixing (Ulloa et al., 2019) and thus the distribution of oxygen (Huang et al., 2021; Kirillin et al., 2012). Light also strongly influences oxygen distribution in summer as it regulates oxygen production by primary producers (Deshpande et al., 2015). To assess how annual oxygen production will respond to climate changes, a better understanding of under-ice photosynthetic processes is needed, including bacterial primary production (Salonen et al., 2009). Sunlight can also account for a major portion of carbon processing in the surface layer by regulating photochemical oxidation, and thus deoxygenation, in Arctic lakes (Cory et al., 2014).

Variations in Arctic precipitation and air temperatures have driven shifts in terrestrial vegetation, with effects on plant distribution, biomass, and functional types (Kaplan & New, 2006; Pearson et al., 2013). Such changes are predicted to have a large influence on the geochemistry of lake tributaries, with higher supplies of detrital material contributing to oxygen depletion in downstream lakes (Klaus et al., 2021; Prowse et al., 2006) (Figure 5). Moreover, the northward advance of treeline is predicted to decrease oxygen concentrations not only as a result of increased dissolved organic carbon delivery but also as a result of decreased mixing through wind sheltering (Klaus et al., 2021). Furthermore, climate-induced changes in Arctic vegetation are likely to influence hydrology (Krogh & Pomeroy, 2019; Naito & Cairns, 2011), and increased hydrological connectivity in Arctic lakes enhances OC delivery (Bogard et al., 2019). Such changes could further influence lake oxygen dynamics (Klaus et al., 2021; Tan et al., 2018).

8. Perspectives

This review compiles current knowledge on oxygen dynamics in Arctic lakes, thus providing a baseline to establish future priorities in this area of research, both with respect to field locations and key research questions. Our recommendations for future investigations of oxygen dynamics include the development of more year-round time series, the modeling of oxygen dynamics, and the use of remote-sensing and paleolimnological tools.

One of the first priorities for an improved understanding of lake dynamics is to fill the gap in winter limnology (Jansen et al., 2021; Powers & Hampton, 2016; Salonen et al., 2009), despite the additional challenge for data.
collection during winter due to extreme conditions at high latitudes. While under-ice limnology has a long history (e.g., Schindler, Kalff, et al., 1974; Schindler, Welch, et al., 1974) and has recently gained increasing interest, the most ice-dominated systems remain vastly underrepresented (Hampton et al., 2017; Powers & Hampton, 2016). The deployment of instruments continuously measuring oxygen at high frequency has contributed to rapid progress regarding our understanding of annual oxygen dynamics in northern lakes (e.g., Bégin et al., 2021; Cortés & MacIntyre, 2020; Huang et al., 2021). Measures over multiple years are especially valuable for the identification of the linkages between climate and interannual variability in oxygen-related processes (Bégin et al., 2021; Koue et al., 2020). As temperatures continue to increase with concomitant effects on the duration of winter limnological conditions and stratification regimes during summer, many questions remain unanswered regarding the rates and controls of under-ice biogeochemical processes.

Several models have been developed to study oxygen dynamics (e.g., Couture et al., 2015; Golosov et al., 2007; Guseva et al., 2020; Stepanenko et al., 2016). Modeling approaches can be used to identify dominant factors controlling oxygen regimes in specific sites, predict anoxia events in lakes of interest, and estimate the response of DO to changes in precipitation patterns, air temperatures, nutrient loadings, and other climate-related variables (Fang & Stefan, 1997, 2009). Such models have already been used to show how morphometric and landscape characteristics can be used to predict oxygen concentrations in some Arctic lakes (Leppi et al., 2016). However, with the Arctic having such a heterogeneous landscape, an accurate assessment of ecosystem response to climate changes relies on improved knowledge of the coupling of climatic and site-specific factors. Future work should investigate how oxygen depletion varies along other key gradients in addition to the effects of latitude and maximum depth, as evaluated here.

Arctic and Subarctic regions are difficult to access, thus leaving huge regions with no oxygen data. Advances in remote sensing represent a further opportunity for the monitoring of DO variability at improved spatial and temporal scales (H. Guo et al., 2021). However, the long periods during which lakes are covered with snow and ice may justify why this approach has not been frequently applied at high latitudes. Remotely sensed lake properties, including water transparency, primary productivity, bathymetry, surface temperature, and ice phenology (Dörnhöfer & Oppelt, 2016), have strong effects on oxygen dynamics in Arctic lakes, as highlighted throughout this review. Studies have combined in situ data and satellite imagery for the monitoring of thermal structure, primary productivity, and ice phenology in Arctic lakes (e.g., Arp et al., 2010; Kuhn et al., 2020), but more oxygen-focused applications at high latitudes remain to be explored. The use of remote sensing could enable the upscaling of observations of summer oxygen dynamics from Arctic lakes for the development of regional and global models.

Direct, long-term observations of oxygen dynamics are mostly lacking for northern lakes, and therefore paleo-olimnological studies represent an important opportunity for improving our comprehension of the response of oxygen trends to climate. Studies in the Arctic analyzing chironomids (Brodersen & Quinlan, 2006; Luoto & Ojala, 2018), sedimentary pigments, or geochemistry (e.g., Antoniades et al., 2011) have provided insights about past transitions in redox processes. Other promising indicators for the tracking of anoxia in sediments include amino acids (Meckler et al., 2004; Menzel et al., 2013), hydrocarbons produced by cyanobacteria (7 and 8-methylheptadecane) (Filley et al., 2001), and lipid biomarkers (Petrisic et al., 2017). Paleolimnological studies thus represent a valuable opportunity to better understand long-term trends in oxygen depletion, which could provide complementary tools for future predictions.

**Data Availability Statement**

Data used for the literature review and for creating Figure 1, Figures 2 and 4 are published in the Nordicana D online repository [https://nordicana.cen.ulaval.ca/dpage.aspx?doi=45825CE-48781F291C0542CD](https://nordicana.cen.ulaval.ca/dpage.aspx?doi=45825CE-48781F291C0542CD) (Klanten et al., 2023). The map was created using ArcGIS pro version 2.9 (ESRI, 2021). Figures 2 and 4 were created using R (R Core Team, 2021), RStudio (RStudio Team, 2022), and the ggplot2 package (Wickham, 2016). Figures 3 and 5 were created using Lucidchart ([www.lucidchart.com](http://www.lucidchart.com)).
Acknowledgments
This research was carried out with funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Fonds de recherche du Québec—Nature et technologies (FRQNT). This research was supported in part by the Sentinel North program of Université Laval, made possible thanks to funding from the Canada First Research Excellence Fund.

References

KLANTEN ET AL.

14 of 20


