A synthesis of carbon dioxide and methane dynamics during the ice-covered period of northern lakes

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Abstract

The ice-covered period on lakes in the northern hemisphere has often been neglected or assumed to have less importance relative to the open water season. However, recent studies challenge this convention, suggesting that the winter period is more dynamic than previously thought. In this review, we synthesize the current understanding of under-ice carbon dioxide (CO2) and methane (CH4) dynamics, highlighting the annual importance of CO2 and CH4 emissions from lakes at ice-melt. We compiled data from 25 studies that showed that the ice-melt period represents 17% and 27% of the annual CO2 and CH4 emissions, respectively. We also found evidence that the magnitude and type of emission (i.e., CO2 and CH4) varies with characteristics of lakes including geographic location, lake morphometry, and physicochemical conditions. The scarcity of under ice data from ice-covered lakes calls for future research to better understand CO2 and CH4 emissions from northern lakes in a changing climate.

Scientific Significance Statement

Seasonally ice-covered northern lakes are globally abundant and play an important role in the global carbon (C) cycle. The ice-covered period is a time of altered C cycling—with reduced catchment inputs, limited light and low temperatures influencing metabolism under lake ice—but C processing continues over winter. This period has traditionally been excluded from annual C budgets. In this paper, we review the C cycling during the winter period and its importance to annual CO2 and CH4 emission budgets of northern lakes. The scarcity of under ice data from ice-covered lakes calls for future research to better understand CO2 and CH4 emissions from northern lakes in a changing climate.

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

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The majority of the world’s lakes are at higher latitudes in the northern hemisphere (Verpoorter et al. 2014), where seasonal ice cover is a common phenomenon (Fig. 1). The presence of snow and ice on lakes alters hydrodynamics and the coupling of physical and biological processes, with important implications for lake organisms and biogeochemistry that have year-round repercussions (Bertilsson et al. 2013). However, despite its importance, the ice-covered period on lakes has received limited attention compared to studies conducted during the open water season (Hampton et al. 2015). Current climate observations and projections of future scenarios converge to suggest a more pronounced increase in air temperature over the northern hemisphere compared to global means, with an even greater temperature increase during the winter and spring period (Zhang et al. 2008), with predicted consequences on the length of ice cover and on the properties of the ice cover itself (Magnuson et al. 2000). Thus, knowledge of the ecological and biogeochemical role of the winter period is not only important for the present day understanding of seasonally ice-covered lakes but also for predicting the implications of changing winter conditions. Recent reviews on under ice physics (Kirillin et al. 2012), plankton dynamics (Hampton et al. 2017), and microbiology (Bertilsson et al. 2013) in lakes have furthered our understanding of winter limnology while highlighting areas that warrant further investigation. One such topic, carbon (C) cycling in ice-covered lakes, has seen a recent surge in individual studies, yet a comprehensive understanding of under-ice carbon dioxide (CO₂) and methane (CH₄) dynamics is lacking (Powers and Hampton 2016).

There is increasing evidence that northern lakes can emit a substantial amount of radiatively important trace gases, CO₂ and CH₄, into the atmosphere, and part of these emissions are directly linked to under ice processes (Tranvik et al. 2009; Bastviken et al. 2011; Raymond et al. 2013). Although the winter period has traditionally been excluded from annual C and nutrient budgets, it is now becoming clear that under-ice processes and subsequent ice-melt emissions play an important role in determining the amount and type (i.e., CO₂ and CH₄) of greenhouse gases (GHG) emitted from northern lakes on an annual cycle (Striegl et al. 2001; Karlsson et al. 2013; Ducharme-Riel et al. 2015; Denfeld et al. 2016; Wik et al. 2016). In this paper, we review the current knowledge on under-ice CO₂ and CH₄ dynamics and subsequent emissions into the atmosphere at ice-melt. Further, we synthesize data on the magnitude of CO₂ and CH₄ emissions at ice-melt and their potential contribution to annual emissions across lakes in the northern hemisphere. We conclude

Fig. 1. Latitudinal distribution of northern hemisphere lakes greater than 1 ha (gray + blue) of which a large proportion are seasonally ice-covered (blue). Ice-covered northern hemisphere lakes in the GLOWABO database (Verpoorter et al. 2014) were determined by applying an air temperature function and solar radiation adjusted model (Weyhenmeyer et al. 2011). Climate data (1960–1990) was obtained from the world climate data interpolated at 0.5 km² resolution (WORLDCLIM; www.worldclim.org; Hijmans et al. 2005). Less than 1% of all lakes >60°N had to be removed from the ice model because climate data was unavailable.
by highlighting knowledge gaps and recommending future research needs.

**Under-ice CO₂ and CH₄ dynamics**

CO₂ and CH₄ dynamics in lakes are influenced by the balance between external C inputs and internal (biotic and abiotic) processes that produce or consume C gases. External CO₂ and CH₄ imported from land directly contributes to internal lake GHGs, and this applies to the ice cover period as well. Although lakes also fix carbon internally via photosynthesis, lake metabolism is generally net heterotrophic and a net source of CO₂, because a portion of the allochthonous organic C that enters the systems is respired (del Giorgio and Peters 1993). While respiration is an important process for mineralization of terrestrial organic matter (OM), photochemical mineralization of terrestrially-derived OM can also be significant (Bertilsson and Tranvik 1998). Further, CO₂ and other C compounds can be used by Archaea spp. under anoxic conditions to produce CH₄, which can then be consumed by methane-oxidizing bacteria with CO₂ as a typical byproduct. Consequently, respiration and photosynthesis are processes that contribute a large proportion of the internal CO₂ flux, while methanogenesis (CH₄ production) and CH₄ oxidation dominate internal CH₄ flux.

During winter, ice-covered lakes experience reduced hydrological inputs, low water temperatures, impeded air-water gas exchange, and highly heterogeneous light availability, which alter under-ice CO₂ and CH₄ fluxes through changes to the timing and magnitude of external inputs and to the rates of internal processes (Fig. 2A). There is evidence of vigorous microbial activity in both the water column and sediments of ice-covered lakes (Maurice et al. 2010; Bertrilsson et al. 2013; MacIntyre et al. 2018), which undoubtedly results in OM degradation. Several studies have concluded that the decomposition of allochthonous OM is the primary source of under-ice respiration (Striegl et al. 2001; Kortelainen et al. 2006). This is likely the case for small, colored lakes, where external terrestrial-derived OM via streams, groundwater and subsurface flow plays a larger role in under-ice CO₂ and CH₄ dynamics (Fig. 3A,C). Hydrological inputs of allochthonous OM in early winter and especially during late winter and spring melt can be large (Cortés et al. 2017), and in some cases, represent the period of peak allochthonous input (Rautio et al. 2011).

While the most common winter scenario is one characterized by relatively low photosynthetic C fixation (e.g., Porcal et al. 2004; Roiha et al. 2016), this is not true of all ice-covered lakes. Photosynthesis can be substantial below ice, particularly in large, oligotrophic, clear-water lakes (Fig. 3B,D) where under-ice phytoplankton blooms have been found to generate significant amounts of allochthonous OM that subsequently fuels under ice metabolism (Bizić-Ionescu et al. 2014). Further, in subarctic lakes in Sweden, winter respiration was partly driven by decomposition of detrital carbon originating in local benthic algal production from the previous summer (Karlsson et al. 2008; Karlsson and Säwström 2009). This temporal decoupling, between the period of net C fixation and its subsequent decomposition under ice, complicates estimates of the net C balance of these lakes, and necessarily requires an integrated, annual perspective. Altogether, the current evidence indicates that both allochthonous and autochthonous OM fuels wintertime microbial activity under ice, yet major uncertainties still exist concerning the relative importance of these sources in various types of lakes. Further,
these sources, and therefore the composition of under-ice pools of C, are likely temporally dynamic across and within lakes, although few studies have addressed the change in the OM pool through winter.

There is indeed evidence that the OM pool is dynamic over winter, partly driven by solute exclusion from ice (Rautio et al. 2011; Roiha et al. 2016), which is restricted to the winter period, and OM release from lake sediments, especially upon the development of anoxic conditions (Mortimer 1942; Gonsior et al. 2013) (Fig. 2B). Solute exclusion from ice results in a localized increase in dissolved organic C concentration and in the colored dissolved OM fraction at the water–ice interface (Belzile et al. 2002), which can suppress photosynthesis and influence mixing dynamics under the ice, in addition to locally enhancing heterotrophic respiration. Concurrently, release of OM from lake sediments further enhances bottom water mineralization (Peter et al. 2016), potentially enhancing anoxia and subsequent methanogenesis in bottom waters. Observations of solute exclusion from the ice and OM release from the sediment during winter highlight the importance of the ice-water interface and sediment–water interface, respectively, as zones of active C cycling during winter.

**Spatial patterns in under-ice CO2 and CH4**

The contribution of sediment vs. water column metabolism to under-ice CO2 build up varies systematically as a function of both lake area and mean depth, with winter CO2 build-up driven mostly by sediment metabolism in smaller, shallower lakes, and water column processes playing a more prominent role in larger, deeper lakes (Ducharme-Riel et al. 2015; Denfeld et al. 2016a; MacIntyre et al. 2018). In small, shallow and/or organic rich ice-covered lakes (Fig. 3A,C), ongoing sediment metabolism and subsequent diffusion of CO2 into the overlying water leads to highest CO2 concentrations found in bottom waters (Kortelainen et al. 2006; Ducharme-Riel et al. 2015). Large, deep lakes can also accumulate CO2 in stratified bottom waters (Fig. 3B,D), although the resulting under ice CO2 concentrations may be lower compared to those in small, shallow lakes. For example, in a small, humic lake, sampled at the end of the ice-covered period in Sweden (Surface Area: 0.04 km², Max. Depth: 7 m), the under-ice profile of CO2 shows a build-up in bottom waters (Fig. 4A); whereas the under-ice profile of CO2 in a large, deep lake in Sweden (Surface Area: 24 km², Max. Depth: 21 m) shows comparatively less bottom water CO2 build-up (Fig. 4B). Moreover, in surface waters, wind-exposure on large lakes often causes an uneven distribution of snow cover on the ice surface, leading to patchy under ice light and temperature conditions (Fig. 3B). Typically, this physical patchiness drives convection under the ice, maintaining algae and nutrients in suspension within the photic zone (Kelley 1997), and possibly altering surface water CO2 concentrations. Furthermore, in clear-water lakes, surface waters below ice are exposed to deeper light penetration and oxic conditions (Fig. 3D), with the potential for photosynthesis, and a subsequent drawdown in CO2 (e.g., Baehr and DeGrandpre 2004). Thus, in large and/or clearwater lakes, under ice surface water CO2 concentrations can be interannually variable due to changes in snow and ice conditions as well as under ice plankton development (Domysheva et al. 2017).

Whereas the accumulation of CO2 under ice is a ubiquitous feature of northern lakes, under-ice CH4 dynamics
appear to be much more heterogeneous among lakes. However, there are fewer data available on under-ice CH\(_4\) compared to CO\(_2\). CH\(_4\) diffusion and ebullition (bubble-mediated transport) from the anoxic sediments (Fig. 2A) may be significant during winter (Juutinen et al. 2009; Sepulveda-Jauregui et al. 2015), although these two pathways result in very different spatial patterns of under-ice CH\(_4\), the former leading to CH\(_4\) accumulation in bottom waters (Fig. 4A) and the latter leading to an increase in CH\(_4\) at the water–ice interface (Walter et al. 2006; Ricão Canelhas et al. 2016). While a strong depth-dependence of CH\(_4\) ebullition has been reported for the open water season, with highest ebullition recorded in littoral zones and < 3 m depth (Bastviken et al. 2004; DeSontro et al. 2016), the depth-dependence of wintertime CH\(_4\) ebullition remains uncertain (Wik et al. 2011). In addition, the positive temperature dependence of CH\(_4\) ebullition has been shown to be stronger than that of both CH\(_4\) diffusion and oxidation (DeSontro et al. 2016), and therefore the patterns of sediment cooling and warming during the winter-spring transition will play a major role in shaping under-ice CH\(_4\) dynamics.

Contrasting patterns in under-ice CH\(_4\) dynamics have been observed throughout several boreal and subarctic lakes (Karlsson et al. 2013; Sepulveda-Jauregui et al. 2015), with some lakes accumulating significant amounts of CH\(_4\) under the ice (Fig. 4A), and others showing little or no build-up (Fig. 4B). The limited data available on under-ice CH\(_4\) do not allow us to identify the mechanisms linked to these contrasting under-ice CH\(_4\) accumulation patterns. Nevertheless, it likely reflects the complexity of CH\(_4\) regulation with possible explanations that include differences in ice dynamics, lake morphometry, hydrological input of CH\(_4\), CH\(_4\) ebullition and the magnitude of CH\(_4\) oxidation. CH\(_4\) can escape ice-covered lakes via openings in the ice, caused by ice cracks due to increased pressure and/or warm waters from inflows and frequent CH\(_4\) bubbling (Phelps et al. 1998; Greene et al. 2014), as well as from emergent vegetation through ice (Larmola et al. 2004). In most cases, however, atmospheric
exchange is limited, and gases are trapped in the ice and underlying water. Although CH$_4$ accumulation under ice is typically high in shallow lakes (Juutinen et al. 2009), if a complete freezing to the sediments occurs, a build-up of CH$_4$ (and CO$_2$) under ice is less likely (Jammet et al. 2015; Manasypov et al. 2015). Input of CH$_4$ from the catchment can differ between lakes as a function of water residence time, land cover and water body type. For example, snow-covered wetlands are known to emit and export CH$_4$ throughout winter (e.g., Melloloh and Crill 1996), thus lakes draining wetlands have the potential to be sourced with a continuous CH$_4$ supply over winter (Karlsson et al. 2013). Additionally, for northern lakes and ponds above 50°N, wintertime CH$_4$ differed by lake type, with higher concentrations in thermokarst lakes compared to glacial and post-glacial lakes (Wik et al. 2016b).

CH$_4$ oxidation has also been found to differ between lake types (Martinez-Cruz et al. 2015; Denfeld et al. 2016b), although very few comparative studies exist. In this regard, the role that aerobic CH$_4$ oxidation plays in shaping under ice CH$_4$ dynamics is still unclear. Some studies have suggested that methanotrophic activity is strongly suppressed at cold temperatures (e.g., Phelps et al. 1998), whereas other studies have shown that rates of wintertime CH$_4$ oxidation are at par with those observed during the open water period (e.g., Kankaala et al. 2006). CH$_4$ oxidation is under dual control by temperature and CH$_4$ concentration (Duc et al. 2010), such that the effect of low temperatures may be to some extent offset by the relatively high CH$_4$ concentrations that are found in some northern ice-covered lakes (Juutinen et al. 2009). A recent study by Samad and Bertilsson (2017) found that the relative abundance of methanotrophs was higher during winter compared to the summer in five Swedish lakes. This is in line with previous incubation studies that have found large methanotroph biomass and activity at low temperatures (Sundh et al. 2005; Ricão Canelhas et al. 2016). In lakes that accumulate CH$_4$ in bottom waters over winter, CH$_4$ oxidation at the aerobic–anaerobic interface, where CH$_4$ concentrations are high and oxygen is still available, has been found to be high (Bastviken et al. 2002). In addition, CH$_4$ oxidation at the ice–water interface has been reported, as CH$_4$ bubbles released from lake sediments become encapsulated into a growing mass of ice or diffuse into surface waters (Greene et al. 2014; Ricão Canelhas et al. 2016). These observations imply that the winter period is not only a suitable environment for methanotrophic activity but, for some types of methanotrophs, winter may be competitively advantageous.

**CO$_2$ and CH$_4$ variation in relation to ice-cover dynamics**

The length of the ice-cover period and the timing of ice-on and ice-off varies across northern lakes, and, also, for a given lake between years (Prowse et al. 2011; Weyhenmeyer et al. 2011; Šmejkalová et al. 2016). Lake morphometry in part determines the intensity and length of the autumn overturn period, and therefore, influences the background gas concentrations at the time of ice-on. A complete autumn overturn prior to ice-on will tend to vent CO$_2$ and CH$_4$ from the lake and replenish the O$_2$ pool, whereas an incomplete overturn will result in elevated CO$_2$ and CH$_4$ as well as O$_2$-depleted waters at ice-on (López Bellido et al. 2009; Huotari et al. 2011). Small lakes are often well sheltered from the wind and cool quickly (Kirillin et al. 2012), leading to incomplete autumn mixing and faster ice development, which may in part explain why under-ice CO$_2$ and CH$_4$ concentrations tend to be high in small lakes.

As ice forms, a weak, yet often stable, thermo- and oxygencline develop, with cool, oxygenated surface waters and warmer (4°C), O$_2$-depleted bottom waters (Fig. 4A,B). The under-ice water column structure has been found to vary between lakes and over the winter, ranging from stable surface layers to solar- or inflow-induced convective mixed surface layers (Kirillin et al. 2012; Cortés et al. 2017; Pernica et al. 2017). Little research has been done on how the development of convectively mixed layers below the ice alters surface water CO$_2$ and CH$_4$ dynamics, despite the potential implications for primary production, heterotrophic respiration, and methanogenesis. Recent work suggests that sediment metabolism may drive not only under ice CO$_2$ dynamics, but also water column convective mixing (MacIntyre et al. 2018). Comparatively more is known about under-ice O$_2$ dynamics, since for many decades it was a matter of significant concern and study, mostly because many eutrophic and mesotrophic lakes tended to develop anoxia toward the end of the ice cover period, which resulted in massive winter fish kills and loss of benthic organisms (Barica and Mathias 1979; Stefan et al. 2001). Oxygen is a master variable in key ecosystem dynamics throughout the year, and strongly affected by duration and characteristics of the ice cover that prevents or reduces gas exchange throughout the water column and with the atmosphere.

A net decline in water column O$_2$ concentrations throughout the ice-cover period is a widespread feature of northern lakes, although there are exceptions. The extent of O$_2$ depletion has been shown to be related to initial O$_2$ concentration and water temperature at ice-on, dissolved OM quantity, heat flux from the sediment and ice cover length (Terzhevik et al. 2009), in addition to mean depth and nutrient levels (Mathias and Barica 1980). Unfortunately, large-scale studies that link under-ice O$_2$ and C gas dynamics are rare (Kortelainen et al. 2006; Juutinen et al. 2009), yet these are critical in determining the balance between wintertime CH$_4$ production and CH$_4$ oxidation and the balance between CO$_2$ and CH$_4$ accumulation. Winter O$_2$ dynamics have strong effects on OM processing, metabolic pathways, and the resulting CO$_2$ and CH$_4$ dynamics, which in turn influence under ice pH, affecting organic matter conformation
and solubility. For example, Finlay et al. (2015) showed that in hard-water lakes, the length of ice cover is a major determinant of the end of winter pH, which in turn shapes the carbonate equilibrium, such that shortening of ice cover results in chemically induced decreases in CO₂ emissions. [Correction made here after initial online publication.]

The breakdown in stratification during ice cover, resulting in a complete mixing of gases and nutrients across the water column, has been observed in some lakes (e.g., Hohmann et al. 1997), but complete mixing is more commonly observed only at the time of ice-off (Fig. 2C). The timing of this mixing has important implications for CO₂ and CH₄ emissions at ice-melt. If water column mixing occurs prior to the ice-melt, low O₂ and accumulated C gas in bottom waters converge with surface waters, resulting in a homogenous gas distribution across the water column (Baehr and DeGrandpre 2004) and an increased potential for CH₄ oxidation prior to ice-melt. On the other hand, water column mixing upon ice-melt tends to release C gases accumulated in bottom waters directly into the atmosphere (e.g., Striegl et al. 2001). The depth and duration of mixing at ice-melt has been shown to vary within and across lakes and between years (Huotari et al. 2011; Jammet et al. 2015; Miettinnen et al. 2015), yet the impact of this variation on CO₂ and CH₄ emissions at ice-melt is not well understood.

It has conventionally been assumed that the release of wintertime accumulated CO₂ and CH₄ into the atmosphere at ice-melt occurs as a large, single pulse (e.g., Striegl and Michmerhuizen 1998). Recent studies, however, indicate that CO₂ and CH₄ emissions at ice-melt are more dynamic than once believed; multiple emission outbursts can occur (Denfeld et al. 2015), spring overturn is not always complete (Huotari et al. 2011; Ducharme-Riel et al. 2015), and stream and catchment melt-water (Denfeld et al. 2015; Miettinnen et al. 2015; Vachon et al. 2017), in addition to internal processes (Crump et al. 2003; Vachon et al. 2016), substantially contribute to ice-melt CO₂ and CH₄ emissions. The processes governing GHG dynamics at ice-melt are therefore complex, and it is often difficult to apportion the contribution of winter under ice dynamics from spring hydrologic inputs (Vachon et al. 2017), but it is clear that the former plays a key role in virtually all cases.

**Quantitative importance of CO₂ and CH₄ emissions at ice-melt**

The release of CO₂ and CH₄ into the atmosphere at the time of ice melt has seldom been considered in annual GHG budgets of northern lakes. To quantify the potential contribution of late winter and early spring emissions following ice-melt to the annual C gas budget of northern lakes, we compiled the extant published data on lake CO₂ or CH₄ air-water fluxes for both the ice-melt (E_{CO₂, Ice} and E_{CH₄, Ice}) and the corresponding open water (E_{CO₂, Open} and E_{CH₄, Open}) period. Ice-melt emission refers to the late winter and early spring period where the lake transitions from ice-covered to ice-free. We obtained data for 271 (258 data points) and 447 (689 data points) individual lakes, for CH₄ and CO₂, respectively (Table 1; Supporting Information Table S1; Denfeld et al. 2018). The method used to estimate CO₂ and CH₄ concentration and emission varied between studies, and a detailed method description for each study can be found in the Supporting Information (Supporting Information Table S1). Moreover, there is a clear geographical structure in the available data, as most lakes sampled are in the boreal region of Fenno-Scandinavia and North America (Fig. 5). Nevertheless, for the available data, the average E_{CH₄, Ice} was 106 mmol m⁻² (median = 10 mmol m⁻²) and E_{CO₂, Ice} was 1165 mmol m⁻² (median = 488 mmol m⁻²). We acknowledge that different methods may result in potential bias in CO₂ and CH₄ emissions, especially those utilizing calculated CO₂ concentrations (e.g., Abril et al. 2015; Golub et al. 2017), and as such, we have attempted to reduce the uncertainty between methods by expressing all estimates in terms of the percent contribution of ice-melt fluxes to annual lake C emissions (%CO₂, Ice and %CH₄, Ice see Supporting Information Material for details). This synthesis of published data suggests that ice-melt emissions on average account for 17% (median = 13%) and 27% (median = 17%) of the annual emission for CO₂ and CH₄, respectively. At ice-melt, lakes ranged from acting as a net CO₂ sink (i.e., %CO₂, Ice < 0) to fully offsetting open water net CO₂ uptake (i.e., %CO₂, Ice > 100), although these cases were rare in our dataset (2.2% and 2.2%, respectively). For CH₄, lakes ranged from no CH₄ emission at ice-melt (%CH₄, Ice = 0, representing 6.6% of the dataset) to an ice-melt CH₄ emission that accounted for the whole annual period (%CH₄, Ice = 100, representing <1% of the dataset). Only a few of these studies included CH₄ ebullition (9% of lakes), the dominant pathway of CH₄ emission in many lakes (Bastviken et al. 2011). Whereas ice-melt and annual CH₄ emissions were higher for measurements that included ebullition, the %CH₄, Ice for estimates that included ebullition was similar to the %CH₄, Ice for estimates that did not include ebullition (Fig. 5; Supporting Information Table S2).

Since the available data lack spatial and temporal resolution, interpretation of ice-melt emission patterns should be made with caution. Only a few studies include GHG emission estimates at ice-melt for the same lake over multiple years. Ice-melt emissions appear to vary inter-annually (Table 1; Study # 9,10,14,15,25), but the magnitude and drivers of this variation require further attention. Our analysis also reveals biome-specific differences in the contribution of ice-melt emissions to annual lake emissions, with the highest average %CO₂, Ice and %CH₄, Ice found in the arctic and sub-arctic regions, and lower and roughly similar %CO₂, Ice and %CH₄, Ice across boreal and temperate regions (Fig. 5; Supporting Information Table S2). The ice-cover period may play a larger role in annual GHG emissions in arctic lakes for several reasons, including a longer...
ice cover (Prowse et al. 2011), high wintertime CH$_4$ ebullition in thermokarst lakes (Zimov et al. 1997; Walter et al. 2006; Wik et al. 2016b) and high wintertime CO$_2$ respiration in lakes with high benthic photosynthesis in summer (as discussed in Karlsson et al. 2008, 2013). It is interesting to note that whereas length of ice cover varies substantially along a

Table 1. The percent contribution of CO$_2$ and CH$_4$ emission at ice-melt to annual emission (%CO$_2$$_{Ice}$ and %CH$_4$$_{Ice}$) for northern lakes with available data reported as the median (min-max). For each study, we also provide the median CO$_2$ and CH$_4$ emission (E$_{CO_2,Ice}$ and E$_{CH_4,Ice}$). $n$ refers to the number of individual lakes sampled in each study, unless denoted otherwise.

| Study # | $n$ | Region          | %CO$_2$$_{Ice}$ (%) | E$_{CO_2,Ice}$ (mmol m$^{-2}$) | %CH$_4$$_{Ice}$ (%) | E$_{CH_4,Ice}$ (mmol m$^{-2}$) | References |
|---------|-----|-----------------|---------------------|-------------------------------|---------------------|-------------------------------|------------|
| 1       | 1   | Boreal          | 20                  | 684                           |                     |                               | Denfeld et al. (2015), Chmiel et al. (2016) |
| 2       | 2*  | Boreal          | 15 (12–17)          | 775                           | 5 (4–5)             | 0.9                           | López Bellido et al. (2009), Ojala et al. (2011) |
| 3       | 1   | Boreal          |                     |                               | (22–48)¶            | 359#                          | Huttunen et al. (2003) |
| 4       | 1   | Boreal          |                     |                               |                     | 112                           | Phelps et al. (1998) |
| 5       | 1   | Boreal          |                     |                               | 19                 | 69#                           | Weyhenmeyer (1999) |
| 6       | 1   | Boreal          |                     |                               | 6                  | 6#                            | Kuhlbusch and Zepp (1999) |
| 7       | 1   | Arctic          |                     |                               | 53                 | 191#                          | Jammert et al. (2015) |
| 8       | 2   | Arctic          |                     |                               | 43¶               | 675#                          | Walter et al. (2006) |
| 9       | 2†/**| Boreal         | 12 (7–16)           | 384                           | 4 (3–5)            | 4                             | Huotari et al. (2011), Kankaala et al. (2006) |
| 10      | 2†  | Boreal          | 28 (24–31)          | 7000                          | 15 (13–18)         | 9                             | Miettinen et al. (2015) |
| 11      | 2   | Temperate       | 55 (10–100)         | 865                           | 14 (13–14)         | 230                           | Striegl and Michmerhuizen (1998) |
| 12      | 2   | Boreal          |                     |                               | 11 (10–13)         | 35#                           | Larmola et al. (2004) |
| 13      | 4/1 | Temperate       | 12 (–31 to 15)      | 301                           | 26                 | 7                             | Riera et al. (1999), Michmerhuizen et al. (1996) |
| 14      | 5‡  | Boreal          | 31 (23–52)          | 1658                          | 12 (5–18)          | 0.7                           | Demarty et al. (2011) |
| 15      | 6†  | Boreal          | 13 (10–16)          | 248                           |                     |                               | Rantakari and Kortelainen (2005) |
| 16      | 12  | Subarctic       | 25 (11–100)         | 259                           | 25 (3–80)          | 27                            | Karlsson et al. (2013) |
| 17      | 15  | Boreal/Temperate| 15 (3–80)           | 500                           |                     |                               | Ducharme-Riel et al. (2015) |
| 18      | 15  | Arctic/Boreal   | 20 (0–56)           | 75#                           |                     |                               | Sepulveda-Jauregui et al. (2015) |
| 19      | 19  | Arctic          |                     | 74¶                           | 312#              |                               | Zimov et al. (1997) |
| 20      | 46  | Boreal          | 13 (3–100)          | 264                           |                     |                               | Rantakari and Kortelainen (2005) (Rantakari pers. comm.) |
| 21      | 29  | Boreal          | 14 (7–33)           | 178                           |                     |                               | Sobek et al. 2003 (Sobek pers. comm.) |
| 22      | 146§ | Boreal/Subarctic| 13 (2–64)           | 248                           |                     |                               | www.slu.se/vatten-miljo; Denfeld et al. (2015) |
| 23      | 176 | Boreal          | 10 (–3 to 100)      | 1936                          |                     |                               | Kortelainen et al. (2006) (Kortelainen pers. comm.) |
| 24      | 207 | Boreal          | 13 (0–100)          | 7                             |                     |                               | Juutinen et al. (2009) (Juutinen pers. comm.) |
| 25      | 241∥ | Temperate      | 13 (–20 to 100)     | 181                           |                     |                               | www.lter.limnology.wisc.edu (Golub pers. comm.) |

* Sample size represents different emission methods.
†Sample size represents years.
‡Three lakes, two of which were sampled two different years.
§Lakes in the Swedish National Lake Inventory Programme with calculated CO$_2$ for under ice and open water period.
∥Multiyear data from 10 lakes in the North Temperate Lake Long Term Ecological Research program with calculated CO$_2$ for under ice and open water period.
¶Only range or mean reported in the literature.
#Ebublition included in ice-melt CH$_4$ flux estimate.
The latitudinal boreal-temperate gradient in Québec, the end-of-winter CO$_2$ concentrations and the emissions associated with degassing of this CO$_2$ stock were similar across lakes, in part reflecting the fact that higher latitude lakes tend to be more oligotrophic, whereas in lower latitude lakes the shorter ice-cover period is offset by higher in lake metabolism and C processing (Ducharme-Riel et al. 2015). This observation highlights the complexity of the regulation of winter C dynamics, which are influenced by interactions between geographic location, lake morphology, trophic status, and watershed properties.

The available studies report a wide range in %CO$_2$$_{\text{ice}}$ and %CH$_4$$_{\text{ice}}$, not only across, but also within regions (Table 1; Study #16-25), suggesting that individual lake characteristics are important in determining ice-melt emissions. In general, $E_{\text{CH}_4,\text{ice}}$ and $E_{\text{CO}_2,\text{ice}}$ increased with decreasing lake size (Supporting Information Table S3), as small lakes tend to accumulate larger amounts of GHG under ice (Figs. 3A, 4A). Surprisingly, the average %CO$_2$$_{\text{ice}}$ and %CH$_4$$_{\text{ice}}$ were similar across lake size classes (Supporting Information Table S3). Although ice-melt fluxes appear to scale with lake size, their contribution to annual emissions does not follow a clear pattern, mostly due to the fact that open water fluxes also scale to roughly similar lake characteristics (e.g., Read et al. 2012). Further, the controls on ice-melt CO$_2$ and CH$_4$ emissions may not necessarily be the same. For example, $E_{\text{CO}_2,\text{ice}}$ tends to decrease with increasing mean lake depth, whereas $E_{\text{CH}_4,\text{ice}}$ is unrelated to maximum lake depth (Supporting Information Table S4).

Overall, the published data confirm that winter is a period of active C cycling, and that on average spring ice-melt emissions contribute to about a fifth and a fourth of the annual C budget of northern lakes, for CO$_2$ and CH$_4$, respectively. Our %CO$_2$$_{\text{ice}}$ and %CH$_4$$_{\text{ice}}$ estimates agree well with previous reports; ice-melt emissions have been found to contribute 22% of the annual CO$_2$ flux from Finnish lakes (Kortelainen et al. 2006) and 23–27% of the annual CH$_4$ flux from northern lakes and ponds above 50°N (Wik et al. 2016b). Although the net CO$_2$ production rates during winter tend to be lower than those reported for the open water season (Ducharme-Riel et al. 2015), the generally long ice cover period implies that the cumulative GHG accumulation during winter and associated spring ice-melt emissions are
still significant on an annual basis. Further, recent studies have shown that ice-melt emissions are significant in northern rivers as well, contributing on average 21% of the annual CO2 budget of boreal rivers (Campeau et al. 2014). It is clear that winter C dynamics of inland waters play a major role in the biogeochemical function at the whole network scale in northern landscapes and should be included in assessments of annual C processing and emission by Northern lakes; exclusion introduces serious biases in the estimated C budgets for seasonally ice-covered regions.

**Knowledge gaps and future research needs**

The extant evidence suggests that the winter and subsequent ice-melt period constitute a significant component of the annual C cycle in northern seasonally ice-covered lakes. Yet, we are far from being able to robustly incorporate under-ice dynamics to annual C budgets of northern lakes, and even further from being able to effectively predict how climate change trends will alter these dynamics. Our synthesis highlights significant C processing under ice in northern lakes, and further suggests that winter C dynamics in inland waters remains one of the largest uncertainties in the regional C balances of northern, water-rich landscapes. We conclude by identifying knowledge gaps and research needs that have evolved as part of this synthesis.

**Spatial representation**

Winter sampling has been to date extremely spatially patchy and temporally fragmented, and this is reflected in the scarcity of actual empirical estimates of winter processes (as synthesized in Fig. 5). Furthermore, direct measurements of CO2 below ice are recommended when possible, to minimize sampling bias (Abril et al. 2015; Golub et al. 2017). Systematic and robust winter sampling programs are needed, targeting representative ranges of northern lakes, and capturing the large temporal variability in C dynamics and lake metabolism that we now know exists under the ice. This need is particularly important for the vast, underrepresented regions where warming is occurring rapidly, such as Siberia and regions of North America, and for lakes that are most sensitive to changes in winter conditions, such as small and shallow lakes (Šmejkalová et al. 2016) and lakes located along the 0°C mean annual isotherm (Weyhenmeyer et al. 2011). In addition, more spatially and temporally extensive sampling within lakes is needed (e.g., Denfeld et al. 2015) to better understand the balance between external inputs and internal processes in determining under-ice CO2 and CH4 dynamics.

**OM composition over winter**

This review highlights potential sources of under-ice OM (Fig. 2B), yet there is limited information on the relative contribution of these sources to under-ice mineralization and CO2 dynamics. Studies that address OM degradation in a diverse set of lakes, temporally sequenced throughout winter would be desirable. In addition to standard bioassays, techniques such as optical tools and stable isotopes offer an opportunity to investigate the role of OM composition and origin in regulating dissolved organic C degradation (e.g., McKnight et al. 2003; Karlsson et al. 2008; Mann et al. 2012).

**Under-ice CH4 dynamics**

The lack of empirical data on under-ice CH4 (Table 1; Wik et al. 2016b) limits our understanding of the current drivers of wintertime CH4, and our ability to determine the impacts of climate change on winter CH4 dynamics. We know very little about the contribution of external inputs to under ice CH4 dynamics or about the source of C (autochthonous vs. allochthonous) fueling internally produced CH4. Thus, under-ice CH4 studies between lakes with different catchment characteristics and lake morphometries would be of interest. The effect of a shift in ice cover might be even stronger on CH4, since the presence of ice prevents its escape to the atmosphere, therefore favoring aerobic CH4 oxidation in lakes that do not become completely anoxic over winter. In this regard, the net result of a change in the length of ice cover may cause not only a shift in the amount and timing of early spring CO2 and CH4 emissions, but also a shift in oxygen dynamics and the CO2 : CH4 ratio, with consequences on the regional GHG budget. Thus, under-ice CH4 measurements that cover a resolved temporal and spatial scale, both regionally and within lakes, are needed to gain insight on CH4 dynamics below ice, particularly CH4 ebullition (Wik et al. 2016a). Aerial photography and remote sensing offer opportunities to determine under ice bubble distribution and CH4 emissions at ice-melt (Walter et al. 2006; Walter Anthony et al. 2010; Wik et al. 2011) but should be supplemented with ambient measurements. For example, the newly developed infrared technique for mapping boundary layer CH4 (Gål Falk et al. 2015) could be deployed during ice-melt to pinpoint spatially resolved CH4 emission hotspots. Further, apparent from this review, wintertime CH4 oxidation could play a larger role than previously assumed, although additional lab experiments and field observations are needed to identify where and when wintertime CH4 oxidation is important.

**Ice-melt CO2 and CH4 emissions**

We found evidence that CO2 and CH4 emissions from northern lakes at ice-melt are significant within the context of the annual C budget. However, a more comprehensive understanding and quantification of these fluxes are needed, as few direct estimates of CO2 and CH4 emissions at ice-melt exist, partly due to logistic difficulties. The few studies that have directly estimated emissions at ice-melt, provide evidence that we can no longer assume that GHGs accumulate linearly below ice followed by a complete water column mixing and emission. And as such, methods that capture the
dynamic ice-melt period, including change in gas storage (Michmerhuizen et al. 1996; Karlsson et al. 2013), floating chambers (Kankaala et al. 2006; López Bellido et al. 2009), temporally resolved gas exchange gradient (Denfeld et al. 2015; Miettinen et al. 2015) and eddy covariance (Anderson et al. 1999; Jammet et al. 2015), should be used in estimating ice-melt emissions (see Supporting Information for details). Methods that require manual sampling during the ice-melt period (i.e., change in gas storage and floating chambers) rely on accurately capturing the timing of late winter and/or ice-melt conditions, which is difficult to predict, particularly for remote field sites. Cameras could be deployed in the lake catchment and connected to a web server to remotely monitor and capture ice-melt condition.

Further, advancements in sensor technology, including eddy flux towers and below ice aquatic sensors, offer an opportunity to directly measure CO2 and CH4 flux during periods when it is unsafe to sample. Currently, below ice CO2 aquatic sensors have mainly been deployed in surface waters at the deepest point in the lake (Denfeld et al. 2015; Miettinen et al. 2015), whereas future studies should make use of the new generation of aquatic CH4 sensors as well as expand sensor deployment location to include bottom waters and inflow shore zones. At the lake scale, a combination of empirical measurements and processes-based models, can be used to quantify the major processes contributing to emissions at ice-melt (e.g., Vachon et al. 2017).

Climate change
Climate change impacts on seasonally ice-covered northern lakes, including changes to winter hydrology and ice phenology, are likely to produce a range of effects on biogeochemical, hydrological, ecological, and societal systems. These changes may not necessarily co-occur in time and space, generating a wide range of scenarios of future winter conditions along latitudinal gradients and across major northern regions, greatly complicating the prediction of future changes in wintertime C dynamics in Northern lakes. In this regard, studies that assess different aspects of the impact of climate on winter C cycling in lakes are needed. Specifically, research should aim to address how changes in ice phenology, winter precipitation and warming will shift the extent of wintertime CO2 and CH4 accumulation and the temporal window of CO2 and CH4 emissions at ice-melt. Given the complexity of how changes in the winter period impact ice-covered lakes, improved understanding of winter C cycling in northern lakes requires research from a variety of disciplines, including biogeochemistry, hydrology, physical limnology, and microbiology.

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