The under-ice microbiome of seasonally frozen lakes

Stefan Bertilsson,[1,*] Amy Burgin,[2] Cayelan C. Carey,[3] Samuel B. Fey,[4] Hans-Peter Grossart,[5,6] Lorena M. Grubisic,[1] Ian D. Jones,[7] Georgiy Kirillin,[5] Jay T. Lennon,[8] Ashley Shade,[9] and Robyn L. Smyth [10]

[1] Department of Ecology & Genetics, Limnology, Uppsala University, Uppsala, Sweden
[2] School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska
[3] Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia
[4] Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire
[5] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
[6] Institute for Biochemistry and Biology, Potsdam University, Germany
[7] Centre for Ecology and Hydrology, Lancaster, United Kingdom
[8] Department of Biology, Indiana University, Bloomington, Indiana
[9] Department of Molecular, Cellular, and Developmental Biology, Yale University, New Haven, Connecticut
[10] Center for Environmental Policy, Bard College, Annandale-on-Hudson, New York

Abstract

Compared to the well-studied open water of the "growing" season, under-ice conditions in lakes are characterized by low and rather constant temperature, slow water movements, limited light availability, and reduced exchange with the surrounding landscape. These conditions interact with ice-cover duration to shape microbial processes in temperate lakes and ultimately influence the phenology of community and ecosystem processes. We review the current knowledge on microorganisms in seasonally frozen lakes. Specifically, we highlight how under-ice conditions alter lake physics and the ways that this can affect the distribution and metabolism of auto- and heterotrophic microorganisms. We identify functional traits that we hypothesize are important for understanding under-ice dynamics and discuss how these traits influence species interactions. As ice coverage duration has already been seen to reduce as air temperatures have warmed, the dynamics of the under-ice microbiome are important for understanding and predicting the dynamics and functioning of seasonally frozen lakes in the near future.

The quality of freshwater, which is tightly tied to many essential ecosystem services, is influenced in large part by the activities of microbial communities. In inland waters, as in other ecosystems, microorganisms are at the hub of most biogeochemical processes and largely control ecosystem functioning via their metabolic activities. However, attempts to describe the taxonomy and ecology of the freshwater microbiome mainly involve samples collected during the ice-free season and, hence, largely neglect microbial communities and their activities during the ice-covered period. Knowledge about the year-round ecological and biogeochemical traits of typical freshwater microorganisms is required to understand when and where certain microorganisms will appear and how they will influence other organisms or biogeochemical processes and, hence, water quality. Together, this information will improve our ability to predict and model freshwater ecosystem and biogeochemical dynamics and to determine their role in the landscapes in the face of environmental change.

A large number of lakes, particularly those situated at high altitude and the numerous high-latitude lakes in the temperate and boreal climate zones, are seasonally covered by ice for more than 40% of the year (Walsh et al. 1998). Despite this, surprisingly little is known about the ecology, diversity, and metabolism of microorganisms that reside under the ice cover in such lakes (Salonen et al. 2009). The traditional view is that ecosystems subjected to low temperatures are "on hold" and that cellular adaptations for survival at low temperatures control the composition of the winter microbial community, which awaits environmental conditions more conducive for growth. This traditional concept fails to recognize that the winter season affects the ecology and metabolic features of freshwater microorganisms, as well as their involvement in food webs and global biogeochemical cycles throughout the year. Moreover, the shortage of empirical data on winter microbial growth and related biogeochemical processes likely biases our estimates of annual elemental budgets and models at local, regional, and global scales. As ice coverage duration has already been reduced on many lakes as air temperatures have increased (Weyhenmeyer et al. 2011), dynamics of the under-ice microbiome are important for understanding and predicting the dynamics and functioning of seasonally frozen lakes. In addition, the number of seasonally frozen lakes will likely increase, as permanently frozen systems experience warmer temperatures and exhibit open-water conditions for at least some periods of the year (Solomon et al. 2007). Changes in the duration of such seasonal ice-cover patterns influence phytoplankton succession and other well-characterized lake features (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Kirillin et al. 2012); however, the effects of such climate-driven changes in ice phenology on microbial communities are not well understood.

In this review, we synthesize the available information on freshwater microbial communities under ice. Our use of

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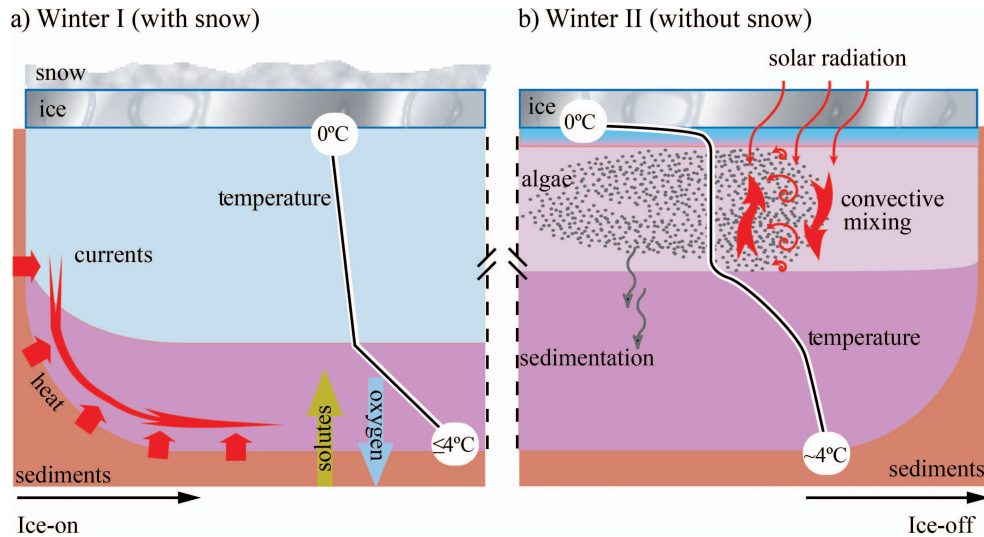* Corresponding author: stebe@ebc.uu.se

Fig. 1. Physical structure of ice-covered lakes and processes important for microorganisms and other taxa. Physical pattern of Winter I (panel a) typically develops shortly after ice-on and transforms into Winter II (panel b) before ice-off. Colors mark the vertical density structure, which is two-layered in Winter I and three-layered in Winter II. The layered structure is mostly determined by water temperature, with the exception of the bottom water, which is affected by solutes from the sediment.

the word "'microbial'' is inclusive. When and where it is appropriate, we discuss processes that are carried out by bacteria, archaea, and eukaryotic phytoplankton. Most microbial under-ice work to date has focused on eukaryotic communities, providing an excellent starting point for future examination of the changing linkages between under-ice prokaryote and eukaryote ecology. Due to their global importance, our emphasis will be on seasonally frozen lakes. We discuss how the distribution and activity of microorganisms in such lakes are controlled by a combination of abiotic and biotic processes during the ice-covered period. We begin our review with the abiotic processes, including the physical and chemical structure of ice-covered systems, about which extensive knowledge is available. We then discuss their associated effects on microorganisms and their resources. Combined with an overview of the principal factors of microbial mortality and adaptations to life under ice, we use this information to address temporal and spatial dynamics of microbes and their metabolic activities and biogeochemical roles in ice-covered lakes. Because of the shortage of biological data from lakes during winter conditions, we combine this with a more extensive treatise on the abiotic environment under the ice and established microbial concepts.

Physical structure of ice-covered lakes

The hydrodynamical structure under the ice exerts a strong control on nutrient availability and other factors critical for microbial growth. Furthermore, the physical environment under the ice is considerably different from the open-water period. Ice cover acts as a shield over the lake surface, preventing atmospheric inputs of particulate matter and gas exchange. The solar radiation available for photosynthesis is furthermore reduced, especially when

snow covers the ice (Fig. 1). With the water column isolated from two major drivers of open-water mixing, wind shear and heat loss, under-ice mixing and circulation are substantially reduced. Under the ice, hydrodynamics are, instead, largely density-driven processes that result from differences in temperature and salinity (we do not consider here the partially ice-covered lakes, where hydrodynamic processes are still wind-driven, at least in marginal areas between ice and open water). Combined with slow, diffusion-driven transport of solutes (Ellis et al. 1991; Bengtsson et al. 1996), physio-chemical gradients and distinct microbial niches can, thus, develop and persist in ice-covered lakes. In this section, we briefly describe the physical mechanisms that influence microbial dynamics under the ice.

The nonlinear effect of temperature on density, with minimal temperature effects and maximum density occurring around 3.94°C, plays a fundamental role in under-ice circulation. Weak but stable stratification occurs under the ice, with temperature increasing with depth (i.e., opposite of the vertical temperature gradient in summer). During the ice-covered season, two of the most important drivers of circulation and mixing are heat flux from sediments and penetration of solar radiation below the ice (Kirillin et al. 2012). In many seasonally frozen shallow lakes, the role of these two drivers in lake dynamics changes over time, dividing the ice-covered period into two phases (Fig. 1).

For small shallow lakes in early winter (Fig. 1a, Winter I), heat stored in epilimnetic sediments during summer continues to warm the overlying water and drives a down-slope flow that reinforces winter stratification (Malm et al. 1997; Terzhevik et al. 2009). Such water movements can transport bioactive constituents to deep, offshore waters and contribute to the formation of physical and chemical gradients. The second phase of the ice-covered season

(Fig. 1b, Winter II) is characterized by gradually increasing inputs of solar radiation that melt the snow cover, penetrate the ice, and warm the upper part of the water column. Water heated by solar radiation convectively mixes downward under conditions that are also favorable for photosynthesis (Farmer 1975; Mironov et al. 2002). In these ways, convective mixing circulates microorganisms below the ice and improves their access to nutrients (Jewson et al. 2011).

By contrast, in larger and deeper lakes, sediment heat storage is less important for driving lake-wide circulation. Furthermore, larger lakes typically receive greater wind forcing than smaller ones, and greater wind forcing increases the likelihood of snow being cleared from the ice. For such systems, circulation driven by the solar radiation (Winter II, Fig. 1b) dominates during the entire ice-covered period (Farmer 1975; Shimaraev and Granin 1991). Lakes in milder climates, with only intermittent ice cover, do not possess a well-defined ice season (Bernhardt et al. 2012), and their under-ice circulation is typically governed by both sediment heat and solar radiation, superimposed on residual effects of wind-driven circulation (Kirillin et al. 2009).

Nevertheless, most seasonally ice-covered lakes reveal this two-stage temporal pattern, determined by the interplay of several physical factors: heat accumulation by the lake sediment during the open-water season, strong convective loss of heat from the water column during the autumn cooling, low radiation level in the early winter, and high albedo of snow, which makes even a thin first snow layer a shield from solar heating (Fig. 1; Kirillin et al. 2012). From a biological perspective, the concentration of heat and mixing energy near the sediment–water interface would favor microbial activity in the bottom boundary layer. In contrast, the availability of solar radiation just beneath the ice would promote microbial growth in the upper water column.

Apart from the heat input at the water–sediment and ice–water interfaces, other physical drivers may contribute to the transport of energy and substances in specific areas of lakes. Among them are the groundwater and subsurface inflows (Bengtsson 1996), standing waves (seiches) produced by oscillations of the ice sheet (Petrov et al. 2007; Kirillin et al. 2009), and fluxes of dissolved salts. Ice formation causes an increase in the salt concentration in the upper water column (cryo-concentration), whereas melting has the opposite "freshening" effect. The former may cause convective mixing, which is typically much weaker than mixing generated by solar heating (Granin et al. 1999). The latter effect (i.e., freshening) increases the stability of the upper water column (Kirillin and Terzhevik 2011) and may delay or even inhibit spring overturn (Pieters and Lawrence 2009). To conclude, the physical structure under the ice is dynamic and controls the distribution of planktonic microorganisms. Hydrodynamic processes also influence the availability of energy sources, nutrients, and electron acceptors needed for microbial processes described in the subsequent sections.

Microbial growth and resources under the ice

Ice cover has far-reaching consequences for microbial resource availability. Ice cover dramatically reduces the input of dissolved and particulate nutrients from the atmosphere and nearby terrestrial surroundings. The distribution of available organic and inorganic nutrients is also diminished by reduced mixing; thus, chemical gradients can persist for extended periods of time. Ice cover accumulates nutrients deposited from the atmosphere and may serve as a nutrient source during melting. Under windy conditions during the surface freezing, Langmuir circulation may drive the down- and up-welling of frazil ice to the lake bottom and back, allowing entrainment of sediment into ice as it forms, and, thereby, potentially seeding sub-ice water when the ice melts (Dethleff and Kempema 2007). Similarly, buoyant up-welling of sediment-rich anchor-ice is another potential mechanism for transporting particulate matter to the upper part of the water column. It is currently unknown how these effects influence elemental stoichiometry and associated microbial growth.

Pelagic microbial biomass is typically lower during ice cover compared to the ice-free period (Personnic et al. 2009; but *see* Twiss et al. 2012). In addition, bacterial productivity is normally lower in winter compared to summer, which has been attributed to factors such as low temperature, reduced nutrient remineralization due to lower protozoan grazing, and qualitative differences in organic substrates with limited inputs of labile and terrestrial organic matter (Tulonen 1993; Tulonen et al. 1994; Bergström and Jansson 2000). For example, seasonal studies of bacterial abundance, biomass, and production in the shallow Lake Vortsjärv, Estonia, revealed low bacterial abundances, biomass (< 75 mg C m^{-2}), and growth ($<$ 150 mg C m^{-2} d^{-1}) from November to February (Tammert and Kisand 2004). Low bacterial biomass and production during the cold winter months have also been found in other temperate lakes (Scavia and Laird 1987; Simon 1987), suggesting that low temperature and low primary production negatively affect bacterial biomass and productivity under the ice. However, it is clear that winter microbial communities are actively growing, as the turnover of biomass for the combined bacterial communities estimated from these studies ranges between 4 and 10 d. Hence, there is a great potential for succession and rapid community change under the ice in response to both episodic and more gradual changes in environmental drivers.

The energy required for cell maintenance and growth can be supplied from either light (phototrophs), oxidation of reduced organic compounds (organotrophs), or inorganic reduced compounds (lithotrophs) coupled to the reduction of various electron acceptors (oxygen [O_2], nitrate, sulfate, etc.). Ice cover and seasonal shifts in temperature, as well as the physical structure of the water column and irradiance, control the relative importance of these metabolic modes and, hence, also determine the composition of the indigenous microflora that can rapidly respond to such changes in available resources.

Phototrophy: Compared to summer conditions, when light is in ample supply and photoautotrophic growth (bacterial and eukaryotic) often dominates microbial biomass production, winter photoautotrophic activity, particularly under the ice, is often limited by the availability

of photosynthetically available radiation (PAR). PAR is limiting because incoming solar radiation levels are lower in winter, and the incoming radiation that does reach the water column is affected by scattering and absorption through the water and ice (Lundberg et al. 2007). In addition, natural ice is optically heterogeneous because of depth-dependent variations in temperature, pressure, and concentration of air bubbles as well as insoluble dust, which increases light scattering and absorption. Snow may also limit PAR to 10% or less of the incident light (Bolsenga and Vanderploeg 1992). Despite low light, ultraviolet radiation levels just below the ice may still be sufficient to inhibit microorganisms (Vincent et al. 1998).

Oxygenic phytoplankton may nevertheless persist and even form transient blooms under the ice, particularly in the absence of snow. For example, blooms of low-light adapted photoautotrophs (*Fragilaria crotonensis* and *Cryptomonas erosa*) develop under ice in Lake Michigan (Vanderploeg et al. 1992). The physical stability of the lake was identified as the key factor behind the initiation of such blooms. Similarly, very large blooms, especially of the diatom *Aulacoseira islandica*, can occur under the ice in Lake Erie (Twiss et al. 2012). These blooms typically occur directly below the ice or embedded in the ice and can exhibit chlorophyll *a* (Chl *a*) concentrations exceeding 73 μg L^{-1} (Twiss et al. 2012). Some phytoplankton, including cyanobacteria, may also be directly adapted to the lower light conditions prevailing under the ice (Vincent and Vincent 1982). For example, *Aphanizomenon flos-aquae* bloomed in Lake Stechlin, Germany, during the winter of 2009–2010 and showed unique photosynthetic behavior adapted to under-ice conditions (Uveges et al. 2012). The maximum photosynthetic rate of *A. flos-aquae* featured a strong interaction with temperature: at high light levels, the cyanobacterium's photosynthetic optimum occurred above 20°C, whereas it varied between 2°C and 5°C at low light levels (Uveges et al. 2012). This suggests that this particular strain is well adapted to winter temperature and low light conditions. Studies in Antarctic lakes have also shown that changes in light availability, by as little as 3 μmol photons m^{-2} s^{-1}, can result in large variations in the primary productivity of cyanobacterial assemblages (Fritsen and Priscu 1998).

Additional traits may be involved in phototrophic adaptation to under-ice conditions. Photosynthetic parameters measured in shallow Lake Balaton, Hungary, indicate a pronounced acclimation to shading in winter: high cellular Chl *a* content and low light saturation suggest that phytoplankton can adapt to the annual variation in PAR (Somogyi et al. 2009). In Balaton, picoeukaryotes and other small algae (< 100 μm³ biovolume per cell) dominate the plankton in winter; whereas, in summer, larger cells (> 100 μm³) are more prominent (Somogyi et al. 2009). In winter, algae with a high surface-to-volume ratio (e.g., *Monoraphidium* sp.) or small- and medium-sized spherical or ovoid flagellates (*Cryptomonas* sp. and *Rhodomonas minuta*) are common. Active movement or high surface-to-volume ratios are other important physiological traits that compensate for increased sinking in winter when vertical mixing of the water column is reduced. Therefore,

phototrophic life under ice in the absence of wind-driven mixing is often mediated by phytoplankton assemblages dominated by flagellates and other motile taxa that are able to regulate their position in the water column (Henshaw and Laybourn-Parry 2002). Consequently, the diversity of the winter phytoplankton is often lower than in other periods of the year (Vörös et al. 2009). Overall, these examples illustrate how physical conditions in ice-covered lakes can create niches for specific groups of phototrophic microorganisms, in addition to oxygenic photoautotrophs under the ice (Wright 1964), which have been well studied (Sverdrup 1953).

In addition to phytoplankton, certain anoxygenic phototrophs may be abundant under the ice. One example of this comes from the permanently ice-covered Lake Fryxell, Antarctica, where photoautotrophic purple non-sulfur bacteria make up a significant part of the microbial community at redoxclines (Priscu et al. 1987). Photosynthetic sulfur bacteria can be present in high local densities at the redoxcline of ice-covered lakes characterized by high hydrogen sulfide concentrations (Takahashi and Ichimura 1970; Burke and Burton 1988a,b). In addition to photoautotrophs, aerobic anoxygenic phototrophs (AAP) can represent the dominant portion of microbial communities in low-productivity lakes (up to 80% of the total bacteria biomass; Masin et al. 2008). The limited data available so far (only for a single lake) suggest that AAP undergo strong seasonal changes in abundance that are strongly coupled to temperature, resulting in lower abundances in winter (Masin et al. 2008).

Organotrophy: Overall, organotrophic microbial growth seems to be lower under the ice compared to the ice-free period, at least in the upper pelagic zone (Morris and Lewis 1992). Because of the light constraints and, as a result, lower photoautotrophy, the release of biologically labile organic substrates from primary producers will be low or at least patchy (Bertilsson and Jones 2003). Instead, organotrophs in the upper water column rely largely on volatile metabolites from anoxic bottom waters or sediments, humic substances, and/or allochthonous organics from the watershed (Biddanda and Cotner 2002; Karlsson et al. 2009). Organic energy sources imported from sediments would include gases such as methane (CH_4), but also hydrophilic volatile fatty acids such as acetate and other degradation intermediates could be of importance.

Several studies have shown that CH_4-oxidizing bacteria are highly active in ice-covered lake water, within the range of rates measured for ice-free conditions (Sundh et al. 2005; Kankaala et al. 2006; Wand et al. 2006). The psychrophilic type I CH_4-oxidizing bacteria represented by *Methylomonas*, *Methylomicrobium*, and *Methylosarcina* are particularly abundant and can contribute almost 40% of the total bacterial biomass (Sundh et al. 2005). Their relative contribution appears to be highest near the sediments in which CH_4 oxidation activity in winter is highest (Sundh et al. 2005; Kankaala et al. 2006). As a consequence, CH_4 concentrations in the upper water column are often low. Thus, methanotrophs can efficiently control the CH_4 released from the underlying anoxic strata. Notably, CH_4 oxidation seems to occur even in anoxic conditions

(Kankaala et al. 2006), suggesting that CH_4 oxidation is coupled to sulfate reduction (Panganiban et al. 1979), denitrification (Raghoebarsing et al. 2006), or some other anaerobic respiratory process. For example, denitrification is thermodynamically favorable but depends critically on supply of nitrate via nitrification or inputs from the surrounding landscape. Nitrification, however, seems to be negatively influenced by anoxia and low temperatures (Pauer and Auer 2000). These microbially mediated biogeochemical dynamics during winter, coupled with spring mixing conditions, are central for understanding nutrient availability at the start of the growing season and greenhouse gas (GHG) release after ice-off.

Lithotrophy: Microbial growth fueled by energy acquired from chemolithotrophic processes is traditionally believed to be confined to the sediment or the sediment–water interface, where there is an ample supply of reduced inorganic compounds for metabolic use. Therefore, chemolithoautotrophic energy acquisition is not necessarily hampered by the presence of ice cover, at least not to the same extent as phototrophy and organotrophy. However, the physical stability of the water column in winter will stabilize gradients of potential electron acceptors and donors in the water column above the sediment, possibly leading to the formation of zones in which different chemolithotrophic energy acquisition modes would be favored. Apart from methanogens, which are typically confined to the anaerobic sediments in which more thermodynamically favorable electron acceptors are absent (Redox potential < 300 mV; Wolfe 1971), a number of chemolithotrophic metabolisms can take place in the water column when environmental conditions become favorable. For example, sulfur-oxidizing bacteria usually appear in zones in which hydrogen sulfide and O_2 overlap (Sattley and Madigan 2006). In permanently ice-covered Lake Fryxell, this usually occurs at around 10 m depth. To our knowledge, there is no comparable study for temperate, seasonally mixing lakes, but a similar interface could be expected to develop in these lakes, provided that the thermal stratification lasts long enough for such fine-scale chemical gradients to form. Analogously, ammonia-oxidizing bacteria appear to be confined to stable overlapping gradients of ammonium and O_2 in the water column (Voytek et al. 1999) or the sediment–water interface (Pauer and Auer 2000). In addition, reduced manganese is a feasible energy source for bacteria during winter (Gregory and Staley 1982). Iron oxidation, however, is believed to be restricted to acidic waters and to interfaces such as groundwater-fed creeks, where iron(II)-rich water rapidly comes in contact with O_2 and where a biofilm of iron-oxidizing bacteria can develop (Duckworth et al. 2009).

O_2: Among all gases in lakes, O_2 is the most energetically favorable electron acceptor and consequently has been studied the longest, particularly because of its importance in regulating winter fish kills in eutrophic lakes with extended ice cover (Mathias and Barica 1980). In lakes, molecular O_2 is supplied via oxygenic photosynthesis or diffusion from the atmosphere. Both of these processes are negatively influenced by the ice cover. Concurrently, O_2 is consumed by aerobic respiration, lithotrophic metabolisms

(e.g., nitrification and CH_4 oxidation), and abiotic oxidation processes (e.g., iron oxidation). Biological O_2 consumption is caused by respiratory processes in which O_2 acts as the terminal electron acceptor; this process is largely controlled by the availability of labile organic matter as an electron donor. The risk for depletion of O_2 under ice varies by lake and is greatly controlled by the ratio between lake volume, area of exposed sediment, and concentrations of allochthonous inputs, especially dissolved organic carbon. O_2 is more rapidly depleted in shallow lakes because of the proportionately larger influence of the sediment by volume. Other factors, such as trophic state and rates of internal mixing, will also influence the supply and demand for O_2 in the water column (Mathias and Barica 1980; Babin and Prepas 1985). However, the first-order O_2 depletion rate (the ratio of the instantaneous depletion rate to the available amount of O_2) can often be assumed to remain nearly constant during the ice-covered season and varies in the typical range 10^{-8}–10^{-6} s^{-1} (Terzhevik et al. 2009). O_2 depletion rates are nonlinear over the season and decay most rapidly after ice-on, when changes in the ratio of photosynthesis to respiration cause massive changes in the dynamics and distribution of both O_2 and carbon dioxide (CO_2; Babin and Prepas 1985). Whereas light absorption and scatter by ice and snow restrict O_2 production by photosynthesis to the near-surface, respiratory processes take place throughout most of the water column. Hence, it can be hypothesized that O_2 concentrations decrease over depth throughout the water column as seen in Lake Grosse Fuchskuhle, Germany (Fig. 2), whereas partial pressure of CO_2 will increase.

Bacterial–phytoplankton coupling

Although data are limited, some studies have reported "bloom-like" development of heterotrophic bacteria beneath the ice in frozen lakes. One example is the shallow Siberian Rybinsk reservoir, where such a heterotrophic under-ice bloom was fueled by the accumulation of detritus from *Melosira islandica* at the ice–water interface (Kopylov et al. 2010). This shows that bacteria can, in some instances, reach high standing stocks and presumably high growth rates under the ice, despite the low prevailing water temperature (< 4°C). Phytoplankton blooms frequently occur under the ice of lakes when ice- and snow-cover conditions allow for enhanced light availability near the surface (Kelley 1997). Similar observations have been made for Lake Baikal, Russia, where ice establishes abiotic conditions (convective mixing and dim light) conducive for rapid growth of Baikal's endemic diatoms (Jewson et al. 2011). For this system, shorter duration of the ice cover could even curtail or prevent the diatom bloom (Moore et al. 2009). An early spring increase in phytoplankton biomass under the ice in Lake Baikal also led to increased bacterial abundance, biomass, and production, such that heterotrophic bacteria processed roughly 20–40% of the daily primary production in the top 20 m (Straškrabova et al. 2005). A third example is from shallow and eutrophic Lake Balaton, where an under-ice bloom of picoeukaryotes was significantly coupled to decreasing water temperature (Vörös et al. 2009). This also resulted in increased bacterial
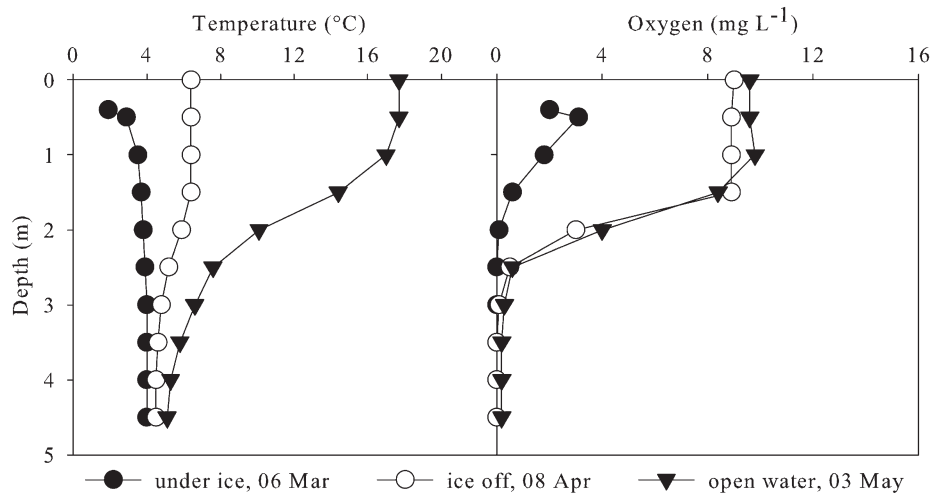
Fig. 2. Temperature and O$_2$ profiles in the northeast basin of Lake Grosse Fuchskuhle during under-ice, ice-off, and open water in 2010 (H. P. Grossart unpubl. data).

abundance and growth, but at a much lower level than in summer, when phytoplankton biomass and production is typically much higher (Vörös et al. 1996). A fourth example for high bacterial abundance and biomass under the ice of a temperate, deep, and oligotrophic lake (Lake Stechlin) is provided below. These examples clearly demonstrate that bacteria are not necessarily limited by low temperatures and inorganic nutrient availability during winter and, instead, seem to be limited by low availability of organic carbon substrates due to limited phytoplankton growth (Hall et al. 2010).

Bacterial community composition

With active growth of bacterioplankton fueled by phytoplankton-derived carbon or other energy sources, different bacterial populations will compete for limited resources. Since the quality and availability of such substrates are dynamic in space and time, shifts in microbial community structure are likely to occur. It is only within the past 10 yr that access to more efficient and powerful molecular tools has enabled systematic exploration of the diverse and largely uncultivable bacterioplankton communities that typically populate lakes (Newton et al. 2011). Within this time, only a handful of studies have paid any attention to microbial communities during the ice-covered period of the year. Although limited, the data from these few studies suggest that under-ice microbial communities differ significantly from the ice-free period (Shade et al. 2008). Furthermore, a recent study based on 7 yr of monthly sampling in a temporary ice-covered lake (Lake Tiefwaren, Germany) indicates that the community composition of particle-associated bacteria (> 5 μm) is more variable among seasons than that of free-living bacteria ($<$ 5.0 μm; Rösel et al. 2012). These findings highlight that winter and, specifically, under-ice conditions greatly affect bacterial communities via shifts in the availability and quality of organic matter and particulates.

Temporal surveys reveal that microbial communities change over the course of the ice-covered period. For example, in two Siberian lakes, photosynthetic purple sulfur bacteria had a peak in abundance at ice-on, and their abundances then varied greatly over the course of the ice-covered season, likely as a result of variations in light availability and redox conditions (Rogozin et al. 2009). Several studies of specific functional groups of bacteria point to significant community changes taking place under ice. Particularly, in perennially ice-covered Antarctic lakes, shifts in bacterial community composition appear to be coupled with environmental factors other than temperature; e.g., stratification pattern, nutrient availability, and overall productivity (Villaescusa et al. 2010; Bielewicz et al. 2012). Analogously, Toolik Lake in arctic Alaska also exhibited seasonal changes in bacterial community composition coupled to shifts in organic matter sources (Crump et al. 2003). In the Toolik Lake study, it was proposed that planktonic bacteria under the ice were composed of both persistent and transient populations, with the latter triggered either by advection of meltwater into the upper water column of the lake or the development of the under-ice phytoplankton community with a coupled release of organic substrates. The *Polynucleobacter necessarius* clade, Actinobacteria, and freshwater SAR11 clade (LD12) were typically persistent over time, whereas distinct freshwater groups such as LD2 and FukuN47 within the Bacteroidetes were classified as either persistent or transients (Crump et al. 2003).

Bacterioplankton dynamics were also tracked during the winter to spring transition in a high mountain lake in the Pyrenees (Lake Redon, Spain; Llorens-Marès et al. 2012). During this transition period, bacterial production increased by a factor of 50 or more, coincident with significant increases in bacterial abundance (3–4 times more bacterial cells). This enhanced growth was mainly associated with three groups of bacteria (Bacteroidetes, Betaproteobacteria, Actinobacteria) that were each about 10-fold more abundant in spring than winter. During this transition period, enhanced light availability promoted a massive growth of phytoplankton that presumably fueled bacterial growth. In contrast to the dynamic temperature-independent changes observed in the open-water column,
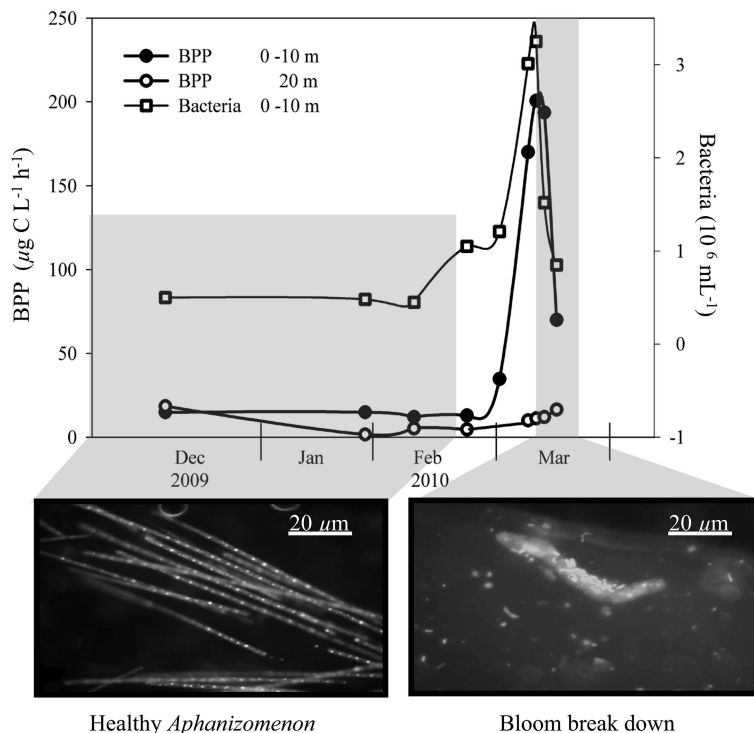
Fig. 3. Bacterial protein production (BPP) and bacterial abundance during the breakdown of a cyanobacterial bloom (*Aphanizomenon flos-aquae*) in Lake Stechlin under ice cover in 2010 (H. P. Grossart unpubl. data).

the sediment microflora composition seems to be more consistent and insensitive to such large temporal changes (Tsertova et al. 2011).

Phylogenetic identifications of under-ice bacteria are also reported from permanently ice-covered, chemically stratified lakes in Antarctica. Glatz et al. (2006) characterized bacterial communities along vertical profiles in both lobes of Lake Bonney and described quite diverse communities with multiple representatives from Alpha-, Beta-, Gamma-, and Deltaproteobacteria, Actinobacteria, Bacteroidetes, and Planctomycetes in the less saline surface water. Similar results have been obtained from a detailed and extensive survey of bacterioplankton communities in multiple lakes within the Vestfold Hills, Antarctica (Logares et al. 2013).

Lake Stechlin as an under-ice microbial observatory

The launch of microbial observatories that build on well-characterized lake ecosystems is a feasible strategy for a better understanding of under-ice microbiology. Temperate Lake Stechlin is an oligotrophic dimictic lake in northeastern Germany. It has been studied intensively for > 50 yr, with microbiology as a more recent addition (Allgaier and Grossart 2006; Rösel and Grossart 2012). Recently there has been an increased focus on under-ice conditions, which has revealed pronounced shifts in the microbial community. One example is the winter of 2009–2010, when the collapse of a massive under-ice cyanobacterial bloom (*A. flos-aquae*; Uveges et al. 2012) triggered growth of heterotrophic bacteria, with an increase in bacterial production up to 100 μg protein L^{-1} d^{-1} and cell concentrations close to 3×10^9 L^{-1} (Fig. 3).

During the winter of 2009–2010, the cyanobacterial population bloomed under clear ice in January until the beginning of March, when 20 cm of snow had covered the ice. Cyanobacteria then became increasingly colonized by heterotrophic bacteria, leading to high total abundances despite low ($< 4^{\circ}$C) temperatures. At the same time, bacterial community composition changed dramatically, indicating that inputs of cyanobacteria-derived substrates, rather than ice cover, caused these changes. Sequencing of 16S ribonucleic acid genes revealed communities containing phyla typical for freshwaters, but with some unique phylotypes increasing during the bloom collapse (M. Bizic and H. P. Grossart unpubl.). This included some members of the freshwater Actinobacteria, which were almost exclusively recovered in the free-living portion of the community. Alphaproteobacteria were also abundant in the under-ice community, but some typical freshwater groups, such as freshwater representatives of the ubiquitous aquatic SAR11 clade, declined during the collapse of the phytoplankton bloom. Betaproteobacteria also featured considerable under-ice dynamics, and several populations emerged and increased in abundance during the collapse of the cyanobacterial bloom, particularly in the particle-associated fraction. Interestingly, Flavobacteria formed a bloom in late winter in parallel to the breakdown of the cyanobacterial bloom. Most of the bacterial cells were attached to cyanobacterial cells, indicating that they benefit from cyanobacterial cell lysis (H. P. Grossart unpubl. data). It has previously been shown that such associated bacteria can also facilitate ice nucleation and, hence, promote diatom localization just beneath the ice cover (D'Souza et al. 2013).

Mortality factors

Grazing and viral lysis are two important processes that control bacterial growth during the summer months (Nixdorf and Arndt 1993). Here, we review evidence for how predation and viral-induced lysis influence microbial communities of seasonally ice-covered lakes, based on existing knowledge of aquatic microbial food webs and the physical structure of lakes during winter.

Bacterivores: Predation, whether by microeukaryote or mesozooplankton bacterivores, is an important driver of bacterial community composition and size structure (Pernthaler et al. 2001; Pernthaler and Amann 2005). Some phytoplankton and bacterial taxa are capable of mixotrophy for organotrophic energy and nutrient acquisition, thereby removing bacterial cells (Roberts and Laybourn-Parry 1999; Laybourn-Parry et al. 2005). Cryptophytes, chrysophytes, and dinoflagellates, all eukaryotic phytoplankton groups capable of mixotrophy, often dominate under-ice phytoplankton assemblages (Laybourn-Parry et al. 2000; Laybourn-Parry 2009). Additionally, such mixotrophic phytoplankton appear to be predominantly heterotrophic in the winter, as light is in short supply (Pålsson and Granéli 2003; Thurman et al. 2012). The scarce data available for mixotrophy in freshwater lakes suggest that this process can account for removal of up to 11% of the standing stock of bacterial cells d^{-1} in some lakes (Berninger et al. 1992).

Whereas bacterial production tends to be the lowest in winter months (Laybourn-Parry et al. 1995), the abundance of bacterivorous ciliates (Macek et al. 2001; Thurman et al. 2012) and heterotrophic nanoflagellates (Thurman et al. 2012) is stable throughout the year. This has led to the hypothesis that bacterial loss via microeukaryote predation may be most significant during winter months (Nixdorf and Arndt 1993; Starink et al. 1996), despite apparently low consumption rates at cold (2–4°C) temperatures (Laybourn-Parry et al. 1995). In fact, bacterivory can occasionally exceed bacterial production during the winter months (Nixdorf and Arndt 1993).

However, as predation pressure on bacteria by microeukaryotes increases during the winter months, losses due to mesozooplankton tend to decrease. This may be due in part to the physical factors that influence zooplankton life-history strategies, physiological constraints, the availability of alternative food sources, and top-down biotic forces. Winter conditions (e.g., reduced temperature, light, and food availability) often serve as a cue that initiates zooplankton diapause (Larsson and Wathne 2006), which reduces the total amount of mesozooplankton present during the winter months. Similar to microeukaryotes, cold water temperatures will slow down metabolic processes and will reduce zooplankton feeding and filtering rates (Loiterton et al. 2004). The higher viscosity of cold water decreases zooplankton feeding rates (Bertilsson et al. 2003; Loiterton et al. 2004), and experiments have demonstrated that viscosity alone can account for more than 60% of the decrease in the phytoplankton filtering rates of the herbivorous cladoceran zooplankton *Daphnia galeata* and *Chydorus sphaericus* (Loiterton et al. 2004).

Finally, the spatial distribution of zooplankton may change during winter. Many zooplankton shift in winter from a primarily pelagic to a benthic life stage (Karlsson and Säwström 2009). Due to the reduced availability of photoautotrophic algae during winter periods, zooplankton may become increasingly dependent on microorganisms as their primary food source (Rellstab and Spaak 2009). For example, winter and summer isotope analyses indicate that methanotrophic bacteria may constitute an important food source for zooplankton in the winter (Bastviken et al. 2003). Additionally, the breakdown of organic matter from benthic algae by microbes in the winter may provide an important zooplankton food source (Karlsson and Säwström 2009).

Viruses: Viruses are the most abundant biological entities in lake ecosystems. As obligate parasites, viruses have the potential to structure host communities directly through selective lysis-induced mortality (Bouvier and del Giorgio 2007) or indirectly by altering the concentration of growth-limiting resources via host lysis (Lennon and Martiny 2008). Although most studies of viruses in aquatic ecosystems have been conducted during the ice-free season, viruses remain abundant and infectious during winter months, when they are thought to play an important role in recycling carbon and nutrients in ice-covered lakes (Säwström et al. 2007; Matteson et al. 2011).

A number of studies have documented the dynamics of virus-like particles in temperate lakes across multiple seasons (Bettarel et al. 2003; Goddard et al. 2005; Filippini et al. 2008). Virus densities are typically lower under ice and during the winter months (Liu et al. 2006) but in some cases are equivalent to virus densities reported in warmer seasons (Filippini et al. 2008; Lymer et al. 2008; Wilhelm and Matteson 2008). Some studies have found that the virus to bacteria ratio can even be higher in winter than in summer (Filippini et al. 2008). This pattern may be influenced in part by lower viral decay rates under ice due to colder temperatures and reduced ultraviolet radiation (Madan et al. 2005). However, viruses are not merely persisting through the winter months as inert particles. Virus burst sizes and the frequency of infected cells can be high in ice-covered lakes (Bettarel et al. 2003), contributing to viral production rates that are comparable to those reported under warmer conditions (Weinbauer 2004; Laybourn-Parry et al. 2007). In addition to the seasonality of viral abundances, there is growing evidence that viral communities are dynamic through time (Tijdens et al. 2008; Short and Short 2009). For example, based on the distribution of genome sizes, temperature was a strong predictor of viral community composition in a seasonal survey of Lake Erken, Sweden (Lymer et al. 2008).

Evidence suggests that viral life-history strategies may be affected by under-ice conditions. In general, there are two strategies that viruses use when infecting their microbial hosts (for an extensive review, *see* Wommack and Colwell 2000). A lytic strategy involves the rapid production and release of viruses, resulting in host lysis. This strategy should be favored in more productive environments, when hosts are abundant and of high nutritional quality. In contrast, lysogeny is a strategy that involves the integration and

"silent" replication of a virus in a host's genome. Thus, lysogeny may be advantageous in low-productivity environments, when a virus particle is less likely to encounter an active and sensitive host. Growing evidence suggests that there is a seasonal shift in the relative importance of these contrasting viral life-history strategies in aquatic ecosystems. For example, lysogeny was more prevalent in coastal populations of *Synechococcus* during winter months when there was reduced primary productivity (McDaniel et al. 2002). Similarly, a high occurrence of lysogeny was reported in an ice-covered eutrophic lake in Quebec, Canada (Maurice et al. 2010), suggesting that bacterial hosts serve as a refuge for viruses during winter conditions. Interestingly, however, lysogeny was much less common under ice in a nearby oligotrophic lake (Maurice et al. 2010). The authors hypothesized that the poor physiological status of the cells in an oligotrophic under-ice environment may induce an "abandon the sinking ship" response by pelagic viruses. Such interactions between lake trophic status, thermal properties, and viral infection should have important implications for the effects that viruses have on microbial structure and function in lake ecosystems.

Resting stages, dormancy, and other adaptations

Many microorganisms are capable of entering a reversible state of reduced metabolic activity (Lennon and Jones 2011), and certain resting stage characteristics indicate that dormancy is an adaptation to low temperature conditions (Fryxell 1983). For example, some phytoplankton taxa that form resting spores only occur in temperate or boreal areas where lakes freeze in winter (Hargraves and French 1983). Spore formation is triggered by decreasing temperatures and light, with germination upon increasing light levels (Hargraves and French 1983; McQuoid and Hobson 1996). For cyanobacteria, several taxa (including *Anabaena*, *Cylindrospermopsis*, and *Nodularia*) can produce akinetes, or thick-walled dormant cells (Nichols and Adams 1982). Most akinetes are able to survive in lake sediments for decades: metabolic levels are low and the akinetes withstand both low O_2 levels and freezing (Karlsson-Elfgren and Brunberg 2004; Carey et al. 2012).

Some cyanobacterial taxa, such as *Microcystis*, produce resting vegetative cells (not akinetes) that can survive for several months on anoxic lake sediments under the ice in a state of lowered metabolic activity (Fallon and Brock 1981; Brunberg 1995). In temperate lakes, overwintering on the sediments is a crucial stage in the *Microcystis* life cycle, and it has been shown that decreasing ice cover reduces the benthic populations of *Microcystis* cells (Brunberg and Blomqvist 2002). Overwintering *Microcystis* cells are able to begin photosynthesizing immediately after an increase in light and temperature in spring (Fallon and Brock 1981), and these cells in the sediments provide an important inoculum for water column populations (Verspagen et al. 2005). Heterotrophic bacterial taxa can also undergo stages of dormancy in the water column under the ice and embedded in the ice layer (Paerl and Priscu 1998; Priscu et al. 1998; Christner et al. 2000) and remain viable, although the importance of diapause in their life cycle is unknown.

It is important to note that many microorganisms are capable of down-regulating metabolism in ways that are not morphologically obvious, and dormancy does not always involve a conspicuous stage of cell differentiation (e.g., spore or cyst; Lennon and Jones 2011). Additionally, there is evidence that the plasticity of microbial membranes is an important bacterial response to cold temperatures that has implications for their metabolism. Microbial membranes are more fluid at high temperatures so that nutrient uptake is more efficient, but the fitness cost to this fluidity is increased respiration. At cold temperatures, microbial membranes are more rigid, which restricts nutrient uptake but increases respiration efficiency (Hall et al. 2010). Though some microbial taxa may be more cold- or warm-adapted, the ability of some community members to change their membrane fluidity (by replacing lipids) may be one way to control metabolism during transitional periods at ice-on and ice-off.

Traits and adaptations to under-ice conditions

Increasingly, traits-based approaches are being used to explain the distribution and abundance of microbial taxa along environmental gradients (Litchman and Klausmeier 2008; Wallenstein and Hall 2011). Traits refer to the morphological, physiological, or genetic attributes of organisms that influence their performance under a given set of conditions. Here, we provide a list of functional traits that we hypothesize to be critical for aquatic microorganisms experiencing under-ice conditions.

Light-use efficiency: Owing to the physical properties of ice, selection should act to favor phototrophic organisms that can maintain a positive energy balance under reduced or altered light conditions (Vanderploeg et al. 1992). Light-use efficiency may be increased via genetic or phenotypic changes in light-harvesting capacity or through augmentation of accessory pigments (Schwaderer et al. 2011).

Oligotrophy: Under-ice conditions may select for microorganisms that have low resource requirements. These "gleaner" or k-strategist taxa may have low half-saturation constants (K_m) and low maximum uptake rates (V_{max}; Litchman and Klausmeier 2008).

Recalcitrant carbon utilization: In instances in which ice and snow cover can lead to reduced rates of primary production, under-ice conditions should select for heterotrophic bacteria that have the ability to use carbon substrates derived from the sediments or terrestrial landscape (Biddanda and Cotner 2002).

Fermentation product utilization: Small, shallow, and eutrophic lakes will experience O_2 limitation during under-ice conditions, which may lead to the accumulation of fermentation products (e.g., acetate, propionate, butyrate). Therefore, there may be selection under ice for microorganisms that have active fermentative metabolic pathways.

Dormancy: Growing evidence suggests that microorganisms may survive stressful environmental conditions by entering a reversible state of reduced metabolic activity

(Lennon and Jones 2011). Therefore, dormancy may be a bet-hedging strategy that allows microorganisms to persist through cold, low-resource conditions that are typical of under-ice lakes.

Motility: Resource availability is often patchy under ice (e.g., phytoplankton blooms are restricted to thin layers). Chemotactic behavior (*see* above) may be a useful bacterial adaptation to efficiently exploit hotspots of organic matter and inorganic nutrients (Kiørboe et al. 2002).

Mixotrophy: Because the relative abundance of different resources changes over the course of the year, it may be advantageous for some microorganisms to have the capacity to switch between different types of metabolism (e.g., heterotrophic and phototrophic).

Temperature acclimation or adaptation: Microorganisms need to contend with reduced temperatures. This does not necessarily mean that they are psychrophiles (optimal growth in the cold), but many are merely able to cope and survive in such conditions (psychrotrophs; Vincent 2007). This can be achieved in various ways. For example, some bacteria have the ability to alter the composition of their membranes in response to temperature in ways that facilitate resource uptake (high temperatures) or increase respiratory efficiency (low temperatures; Hall et al. 2010).

Ice cover, GHGs, and climate change

The greenhouse warming potential (GWP) of CO_2 is 1; i.e., all GHGs are, in this regard, standardized to CO_2. CO_2 is mainly produced via anaerobic and aerobic mineralization of organic carbon compounds and is consumed during autotrophic carbon fixation. As much as 60% of the CO_2 in lake profundal zones originates from anaerobic microbial processes (Jones and Simon 1980). The CO_2 levels encountered under the ice often exceed those recorded in summer, when mineralization is offset by photosynthesis-driven CO_2 fixation and equilibration with the atmosphere (Kling et al. 1992). In essence, the ice acts as a gas barrier, allowing CO_2 accumulation during winter that may be rapidly released to the atmosphere upon ice-off.

CH_4, with a GWP of 20, is produced anaerobically by archaea via methanogenesis and is consumed by microbial methanotrophs. Lake water is often supersaturated with CH_4 during winter (Juutinen et al. 2009). This can lead to a massive CH_4 release to the atmosphere upon ice-off, a process that may contribute up to 40% of the CH_4 emitted annually (Michmerhuizen et al. 1996; Phelps et al. 1998). However, for some lakes an extended ice cover can also lower the total release of CH_4 by greatly extending the transit time to the atmosphere and, thereby, causing a more efficient microbial oxidation of this potent GHG (Sundh et al. 2005; Kankaala et al. 2006). This may be particularly important for CH_4 ebullition, since CH_4 gas will accumulate under the ice. If a suitable electron acceptor such as O_2 is available, CH_4 would be subject to oxidation (Walter et al. 2008), thereby potentially decreasing O_2 concentrations just below the ice.

Incomplete denitrification results in the accumulation of nitrous oxide (N_2O), which has a GWP of ~ 300. The sink for N_2O in the water column is biological reduction via N_2O reductase. The dynamics of N_2O in aquatic ecosystems is poorly understood, and we know very little about N_2O emissions in summer and even less in winter (Knowles et al. 1981; Mengis 1997).

Both produced and consumed by microbial processes, the concentrations of these three GHGs are likely to build up and be trapped or transformed (e.g., CH_4 to CO_2, N_2O to dinitrogen gas) in ice-covered lakes. Microbial processes under the ice will largely determine what is released to the atmosphere upon ice-off, and such processes will vary temporally and spatially within and across lakes. Without additional knowledge about under-ice microbial dynamics, it is difficult to predict the net effect of lakes on GHG emissions to the atmosphere (Michmerhuizen et al. 1996; Huttunen et al. 2001; Kankaala et al. 2006).

Future research directions

The paucity of under-ice data for seasonally frozen freshwater lakes calls for future research to better understand under-ice processes and their consequences for biogeochemical fluxes, water quality, and seasonality of microbiota. Some promising and pressing research needs are listed here:

Density-driven vertical and horizontal mixing processes are important for defining the transport and distribution of solutes and organisms (Kirillin et al. 2012). Such processes are partly controlled by differential heating of the water, resulting from heat stored in sediments and variability in ice and snow cover (Bengtsson 2011). Measuring sediment temperatures in shallow, sloping, and deep regions would enable both the characterization of heat storage during the summer and the calculation of the density-driven lateral water movements resulting from winter sediment heat flux. As temperature effects on density are minimal at winter temperatures, cryo-concentration upon freezing with concomitant shifts in salinity could play an important role in vertical mixing below the ice sheet (Pieters and Lawrence 2009). Despite the significance of these processes, there are few direct measurements of spatial variation in under-ice solar radiation, temperature, salinity, and water movements. Such measurements of the physical environment could be important for explaining microbial dynamics.

Dissolved oxygen (DO) has a central role for microbial processes in lakes. When ice cover prevents atmospheric inputs of DO to the lake water, spatial and temporal O_2 dynamics will be controlled by microbial activity (Golosov et al. 2007). Interpretation of DO data can be complicated by lateral transport and vertical mixing (Terzhevik et al. 2009). O_2 concentration at the end of the ice-covered period, the vertical distribution of this gas, and possible near-bottom anoxia are some of the more crucial factors determining the nutrient dynamics, food web structure, and overall functioning of the ecosystem. Until recently, the measurement of DO during the entire ice-covered period with sufficient spatial and temporal resolution was practically impossible due to low stability of DO sensors,

limited data storage capacity, and poor battery lifetime at low temperatures. Recent methodological advances now offer new possibilities for a better understanding of DO dynamics under ice.

Variability in microbial metabolic processes compromises our ability to accurately model the role of lakes in biogeochemical cycles during winter. Hence, the spatial and temporal distribution of metabolic processes under ice deserves further scrutiny. Besides temperature and nutrient availability, ice quality and the coupled penetration of solar radiation are critical for phototrophic processes. In addition, it is imperative to measure where reduced organic or inorganic energy sources and suitable electron acceptors for respiration (preferably O_2) exist, as these factors influence metabolism and elemental cycling at the ecosystem level. To understand the causes and consequences of such variability, we need in-depth knowledge of the internal and external supply and redistribution of labile organic substrates, as well as the availability and internal production of alternative electron acceptors for organic matter respiration.

The buildup of CO_2 and CH_4 under ice not only affects the quantity and timing of GHG release: CO_2 accumulation from organic matter mineralization might also affect pH at certain strata, which may affect both biota and metal speciation. So far, these consequences have not been taken into account in lake ecology. Enhanced levels of biogenic CH_4 under the ice will further foster localized methanotroph communities and are, thus, intimately linked to the composition of microbial communities and their combined metabolic features. Hence, spatial and temporal surveys of CO_2, CH_4, N_2O, and other volatile lake constituents are certainly needed and can be mapped against the resident transcriptome to better understand the under-ice microbiome.

At the core of the under-ice microbiome are the microbial communities. The identities of the under-ice microbial community members, their metabolic strategies, and their abundances are critical for understanding microbial responses to changes in ice phenology. Progress in molecular methods now enables us to map the taxonomic and metabolic features of microbial communities at high spatial and temporal frequency, and, for seasonally frozen lakes, it is time to turn our attention to the winter period. We know that ice coverage greatly affects solar irradiance and physical processes: this may result in the formation of steep physical and chemical gradients over time and the emergence of functionally and taxonomically distinct local microbial communities. The microbial community structure will not only affect microbially mediated processes and dynamics under the ice, but the resident community at ice-off will also serve as an ''inoculum'' for the ice-free season and likely influence successional shifts in the microbiota during spring and possibly the rest of the year. By studying these processes, we will learn how frozen lakes interact with the rest of the biosphere and how seasonal lake dynamics may change in the future with significantly altered freezing and stratification patterns due to climate change.

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