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### Special Section:

Winter limnology in a changing world

### Key Points:

- Ecosystems of seasonally ice-covered lakes are governed by poorly understood interactions between abiotic and biotic processes
- Density-driven currents enable gradients in redox potential, create niche habitats and redistribute substrates and organisms under ice
- Winter limnology has tended to progress within disciplines; an interdisciplinary approach is necessary to resolve extant knowledge gaps

### Supporting Information:

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

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## Winter Limnology: How do Hydrodynamics and Biogeochemistry Shape Ecosystems Under Ice?

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**Abstract** The ice-cover period in lakes is increasingly recognized for its distinct combination of physical and biological phenomena and ecological relevance. Knowledge gaps exist where research areas of hydrodynamics, biogeochemistry and biology intersect. For example, density-driven circulation under ice coincides with an expansion of the anoxic zone, but abiotic and biotic controls on oxygen depletion have not been disentangled, and while heterotrophic microorganisms and migrating phytoplankton often thrive at the oxycline, the extent to which physical processes induce fluxes of heat and substrates that support under-ice food webs is uncertain. Similarly, increased irradiance in spring can promote growth of motile phytoplankton or, if radiatively driven convection occurs, more nutritious diatoms, but links between functional trait selection, trophic transfer to zooplankton and fish, and the prevalence of microbial versus classical food webs in seasonally ice-covered lakes remain unclear. Under-ice processes cascade into and from the ice-free season, and are relevant to annual cycling of energy and carbon through aquatic food webs. Understanding the coupling between state transitions and the reorganization of trophic hierarchies is essential for predicting complex ecosystem responses to climate change. In this interdisciplinary review we describe existing knowledge of physical processes in lakes in winter and the parallel developments in under-ice biogeochemistry and ecology. We then illustrate interactions between these processes, identify extant knowledge gaps and present (novel) methods to address outstanding questions.

**Plain Language Summary** Winter is an important but poorly understood period for lake ecosystems at high latitudes. Incoming solar radiation is diminished by ice and (often) snow, flows of oxygen and substrates such as organic matter or nutrients from outside the lake are limited, and wind no longer causes turbulent mixing of the water column. The sediments become a source of heat as well as of solutes which drive denser water toward the bottom. The resulting density stratification creates a template for the development of winter ecosystems. Distinct oxygenated and oxygen-depleted zones will affect microbial community structure and the habitat and behavior of zooplankton and fish. Conditions can rapidly change in spring with increased irradiance and incoming snowmelt. This paper reviews how physical, biogeochemical and biological processes act together to shape aquatic ecosystems in winter and in spring. In addition, we present an overview of the unknowns regarding the interactions between the different processes, which can now be posed due to improved understanding of under-ice hydrodynamics and the nature of lake ice, of biogeochemistry, and of ecology. However, work to date has largely been conducted within distinct disciplines. We therefore outline interdisciplinary approaches that can bridge current knowledge gaps in winter limnology.

## 1. Introduction

Lakes in cold regions of the world can be ice-covered perennially or for periods of weeks. The ice-cover period remains poorly studied compared to the ice-free season, yet a complex suite of linked hydrodynamic, biogeochemical, and biological processes is important at this time (Salonen et al., 2009). The appreciable production of biogenic climate forcing trace gases in the sediment and subsequent accumulation in the water column under the ice (Huttunen et al., 2003; Jansen et al., 2019; Michmerhuizen et al., 1996) attest to considerable microbial activity despite the cold as well as redistribution of solutes by currents (MacIntyre et al., 2018). Under-ice processes cascade into and from the ice-free season, so understanding their controls is relevant to the annual cycling of energy and carbon through aquatic food webs (Hampton et al., 2015).

Winter limnology is a rapidly expanding field (Powers & Hampton, 2016). Significant progress is being made along disciplinary lines such that many under-ice physical processes and biological phenomena are now better quantified and understood (Bertilsson et al., 2013; Kirillin et al., 2012). While some of the earliest studies have linked hydrodynamics and biogeochemistry (Mortimer & Mackereth, 1958), impacts on biology were not included. As understanding of hydrodynamic processes under the ice increased, links were established with phytoplankton ecology (Farmer, 1975; Kelley, 1997). With the advent of new microbial techniques, diverse and active communities of viruses, Bacteria and Archaea have been identified in ice-covered lakes (Bertilsson et al., 2013; Comeau et al., 2012; Tran et al., 2018), as well as of more complex assemblages of phytoplankton (Hampton et al., 2017; Özkundakci et al., 2016; Vincent, 1981). Enhanced sensitivity of chemical detection techniques has helped reveal a strong coupling between redox chemistry in the sediments and the development of chemical gradients in overlying waters (Gammons et al., 2014; Joung et al., 2017) that could enable these communities and drive the microbial food web. Studies of higher organisms in ice-covered lakes are less comprehensive. Only a few papers link the richness and vitality of under-ice biological communities with the abiotic (i.e., physical and chemical) processes (Comeau et al., 2012; Forsström et al., 2007; Rue et al., 2020; Ventelä et al., 1997). Major progress can be achieved by linking changes in circulation, availability of resources, and communities of plankton, invertebrates and fish, with a further step identifying impacts on food webs. Such interdisciplinary studies that synthesize existing knowledge and utilize novel methodologies offer the potential for significant advances in the field of winter limnology.

Our goal in writing this paper is to review our current understanding of abiotic-biotic interactions in seasonally ice-covered freshwater lakes and to highlight potential linkages between disciplines. We constrain our review to lakes with a complete cover of land-fast ice. First, we detail the current level of knowledge of hydrodynamic processes under ice and the nature of the surface cover itself, followed by a brief overview of recent developments in under-ice ecology and biogeochemistry. In so doing, we will develop likely scenarios of community interaction, from the microbial food web to the classical food web, and how they are enabled and driven by chemical gradients and hydrodynamics. We present extant **knowledge gaps** made evident by this analysis of ecological, biogeochemical and hydrodynamic processes (Table 1). Finally, we review emerging methods including new sensor technologies that will help address these questions.

## 2. Hydrodynamics Under Lake Ice

From a hydrodynamic point of view, we can distinguish three key time periods (Figure 1): (a) **early winter**, that is, approximately the month after ice-on when sediment heat flux and sediment respiration set up convective circulation; (b) **mid-winter** when the convective circulation continues but flows are slower; and, (c) **spring** when radiatively driven, penetrative (vertical) and horizontal convection increase flows (Kirillin et al., 2012).

In early winter, with water temperatures typically less than the maximum density of freshwater (4°C), **inverse thermal stratification** develops (e.g., Bengtsson & Svensson, 1996). Temperature profiles in lake sediments indicate that considerable heat can be stored there (Birge et al., 1927; Likens & Johnson, 1969). Heat built up during summer transfers from the sediment to the overlying water over winter, as well as from the water through the ice, keeping the ice-water interface at near freezing temperatures (Golosov & Kirillin, 2010; Huttula et al., 2010; Jakkila et al., 2009). This vertical thermal gradient helps maintain stable

stratification. Solutes produced by organic carbon mineralization often contribute to strong near-bottom density gradients (Malm et al., 1997; Mironov et al., 2002). Although the ice prevents direct action by wind, a variety of water movements occur under the ice. These are largely driven by changes in water density associated with heating or solute production which cause local instabilities. Hence, they are called density-driven or convective flows.

Sediment heating of the overlying water generates **density currents** which flow downslope to deep locations, and respiration at the sediment-water interface contributes to the flow by producing solutes which also increase density (MacIntyre et al., 2018; Mortimer & Mackereth, 1958). These flows can be detected as soon as ice cover forms (Figure 1a) and can last for extended periods of time (e.g., Rizk et al., 2014). Density currents form in large lakes, such as 330 km<sup>2</sup> Torneträsk (Mortimer & Mackereth, 1958), and their formation in lakes smaller than 0.1 km<sup>2</sup> has been inferred from the rapid near-bottom accumulation of heat and solutes immediately after ice on (Deshpande et al., 2015; Jansen et al., 2019; MacIntyre et al., 2018). The density stratification in the lower water column increases with the ongoing accumulation of the somewhat warmer and solute-enriched water. Consequently, later intrusions flow at progressively shallower depths (Figure 1b). The downslope flow velocities are on the order of 10<sup>-3</sup> m s<sup>-1</sup> (Malm, 1998). It is not known whether they transport any particulate matter and create intermediate or benthic **nepheloid layers** with high concentrations of suspended solids, as in stratified lakes in ice-free conditions (Chambers & Eadie, 1981; Hawley, 2004; Hawley & Lee, 1999). Upward flows balance the downslope gravity currents resulting in an overturning convective circulation (Malm, 1998; Rizk et al., 2014) which sometimes becomes two-layered (Welch & Bergmann, 1985). Upward velocities in early winter are of order 10<sup>-5</sup> m s<sup>-1</sup> (MacIntyre et al., 2018), but decrease mid-winter to order 10<sup>-6</sup> m s<sup>-1</sup> and those nearer the sediments are an order of magnitude lower (Malm, 1998). These slow near-bottom flows may increase the volume of water in contact with sediment oxygen sinks and, in this way, contribute to the expansion of anoxic zones (Terzhevik et al., 2009).

**Cryoconcentration** is the exclusion of solutes when ice freezes. These include salts as well as substrates such as colored dissolved organic matter (CDOM) (Belzile et al., 2001) and sparingly soluble carbon trace gases (Boereboom et al., 2012). Modeling (Olsthoorn et al., 2020) and laboratory studies (Bluteau et al., 2017) demonstrate that sinking plumes of solutes can take the form of salt fingers, which do not contribute to mixing but may hasten the development of density gradients, or induce penetrative convection which does cause mixing. Which process dominates depends on the near-surface stratification and on the solute concentrations. Granin et al. (2000) illustrate that shortly after ice on in Lake Baikal, the solutes can induce an increase in density sufficient to cause penetrative convection down to about 1 m below the ice. Pieters and Lawrence (2009), working in a 12 m deep lake about 10 times saltier than most freshwater lakes, observed the solutes to gradually mix down to the bottom. The fate of the solutes may vary over time. Tracer experiments conducted in mid-winter indicate that the solutes become part of the horizontal convective circulation (Welch & Bergmann, 1985), but they may also be retained in place. An increase in specific conductance (SC) from 252 to 258 μS cm<sup>-1</sup> between January and April in the upper 4 m of a small arctic lake near Toolik Field Station (MacIntyre & Cortés, 2017) matching the SC value expected from ~80% exclusion of dissolved solids out of the 9 cm thick ice layer (Kirillin et al., 2012) is indicative of retention. Furthermore, increased near-surface SC under ice in spring (Cortés et al., 2017; Forrest et al., 2013) implies that the stable temperature stratification of the water directly under the ice (Figures 1c and 1d) could compensate for the destabilizing force of the increased solute load. To what extent organisms at the ice-water interface can utilize enhanced solute concentrations remains unclear (Table 1; Q7).

**Gyres** are rotational structures made possible by the deflection of density-driven flows by Earth's rotation. Rotation can influence flow in water bodies larger than the internal Rossby radius, the length scale at which rotational forces are balanced by buoyancy forces. While typically such flows have been characterized in large water bodies (i.e., at length scales greater than the internal Rossby radius), they can potentially form in ice-covered lakes as small as a few hectares when density stratification—and therefore the internal Rossby radius—is reduced relative to that in summer. Consequently, Coriolis forcing increases in significance in winter, enabling rotational flows. Initially modeled (Huttula et al., 2010), under-ice gyres have since been observed in detailed field campaigns in ice-covered systems at mid- (Forrest et al., 2013; Kouraev et al., 2016) to high latitudes (Kirillin et al., 2015; Salonen et al., 2014). These gyres are typically at the scale

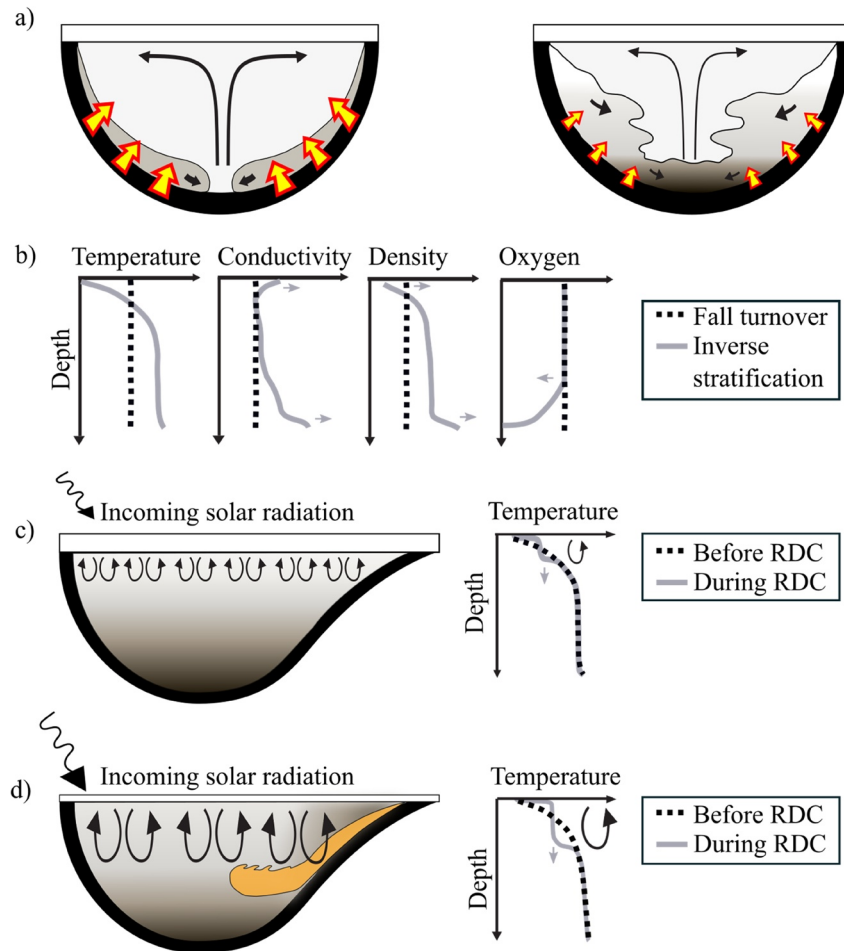
of the internal Rossby radius of the lake (e.g., 500–1000 m during typical inverse thermal stratification), are generally stationary and slow-moving ( $10^{-2} \text{ m s}^{-1}$ ; Forrest et al., 2013; Kirillin et al., 2015) and also translate underneath the ice (Kouraev et al., 2016). Remote sensing tools can capture gyres as their presence tends to thin the ice via horizontal motion, which in turn drives vertical upwelling of warmer water (Kouraev et al., 2019). This upwelling could contribute to fluxes of solutes which have accumulated in near-bottom waters and could also disrupt layered communities under the ice.

**Internal waves** are ubiquitous in stratified waters (Imboden & Wüest, 1995) and are also found beneath lake ice (Cortés & MacIntyre, 2020; Malm et al., 1998; Petrov et al., 2006). Driven primarily by wind-induced oscillations of the ice, the oscillatory flows are so slow,  $\sim 10^{-3} \text{ m s}^{-1}$ , that detecting them has required highly sensitive instrumentation (Bengtsson, 1996; Malm, 1999). They are also energized by penetrative convection (Bouffard et al., 2016) or by the release of potential energy from readjustment of a sloping thermocline immediately after ice-on (Kirillin et al., 2009). In small as well as in larger lakes, internal waves can take the form of basin-scale **standing waves** or **seiches**. The extent to which oscillating water movement contributes to horizontal dispersion and transport offshore is unknown. Additionally, more effort is required to determine when they become non-linear and thus induce turbulence, particularly near boundaries (Kirillin et al., 2018). Non-linear waves can form quickly at ice-off and induce considerable mixing (Cortés & MacIntyre, 2020). Rotational or **Kelvin waves** exist in lakes larger than the internal Rossby radius (Kirillin et al., 2009), and can generate strong currents along shore in the ice-free season (Flood et al., 2020), but whether such waves induce mixing or turbulence near the benthic boundary layer under ice remains unknown.

In spring, hydrodynamic processes can become more energetic and dynamic if the increased solar radiation penetrates through the ice (Matthews & Heaney, 1987). **Radiatively driven convection** (RDC) causes vertical convective circulation which penetrates from the surface boundary layer into the stratified water column below (Farmer, 1975; Mironov et al., 2002) (Figure 1c). Velocities are of order  $10^{-3} \text{ m s}^{-1}$  (Bouffard et al., 2019; Jonas et al., 2003; Kelley, 1997). However, in lakes that are snow-covered or in which snowmelt or rapid ice-melt cause a pronounced near-surface density gradient or where density stratification has been enhanced by solutes, the development of penetrative convection can be delayed or may not occur at all (Cortés et al., 2017; Cortés & MacIntyre, 2020; Pieters & Lawrence, 2009). RDC decays after the forcing stops (Nieuwstadt & Brost, 1986), and the observed median breakdown time of convective mixing in Lake Onego, Russia was 3.5 h after sunset (Bouffard et al., 2019). The upper water column remains near-isothermal for some time afterward, and it is uncertain if lakes typically restratify during night. Because RDC can extend to depths above or below the euphotic zone, its properties have important implications for rates of primary productivity (Jewson et al., 2009) and functional traits of phytoplankton under ice (Section 5.2).

**Horizontal convection** is another form of RDC analogous to flows driven by sediment heating. Horizontal density gradients can result from rapid warming of littoral zones or from meltwater runoff, and can similarly generate downslope density currents and lateral intrusions that flow away from the shore ( $10^{-2} \text{ m s}^{-1}$ ; Cortés & MacIntyre, 2020; Forrest et al., 2008; Kirillin et al., 2015; Salonen et al., 2014; Ulloa et al., 2019). These currents transport oxygen offshore to deeper waters and increase viable habitat for fish (Stefanovic & Stefan, 2002). Warming of nearshore waters above  $4^{\circ}\text{C}$  creates a convergence zone, called the **thermal bar**, with two distinct circulation cells that limit exchange between littoral and pelagic waters (e.g., Salonen et al., 2014; Zilitinkevich et al., 1992). These are typically seen after (partial) ice off and the formation of moats along the shore (Nolan et al., 2002). Phytoplankton whose growth rates had been increasing due to greater illumination of shallow waters could seed the development of chlorophyll maxima offshore (Salmi & Salonen, 2016) or be retained in the near-shore convective cell when the thermal bar sets up (Suarez et al., 2019). In addition, horizontal motions could promote previously uncharacterized lateral transfer of solutes.

The pathway and magnitude of the density-driven currents may vary over time, with lake morphometry and by latitude. The proportion of lake volume affected by density-driven circulation is expected to scale inversely with lake size, due to a smaller sediment-area relative to water volume in larger lakes as well as a decrease of the under-ice sediment heat flux with increasing water depth (Fang & Stefan, 1996). As the upwelling flow occurs by continuity, upward velocities may also be less in larger lakes. Insolation and precipitation



**Figure 1.** Circulation under ice in winter and spring. (a) Gravity currents, driven by heat and solute fluxes from the sediment, begin to flow downslope immediately after ice on (red and yellow arrows). Subsequent gravity currents may flow at shallower depths. Upward flows occur to balance the downward ones (black arrows). (b) Depth profiles of temperature, specific conductivity (SC), density and oxygen during inverse thermal stratification in early to mid-winter. Small arrows mark the direction of change over time. Note how solutes (as SC) modulate density stratification at the interfaces. (c) In spring, increased solar radiation through the ice begins radiatively driven convection (RDC), which initially creates a thin convective mixing layer. (d) The vertical extent of the mixing layer increases with increased solar radiation. Density stratification below the ice (gradient shading), potentially enhanced by flows of dense water from the littoral zone (orange plume), may limit the mixing depth.

vary along latitudinal gradients which affect ice quality and the lake's annual heat budget (Section 3). The horizontal exchange of solutes and heat from near-shore waters will also depend on latitude, as well as lake size. When the internal Rossby radius is large, and thus rotation not significant, the warmer and denser waters can flow offshore. For lakes whose dimensions exceed the Rossby radius, density currents can be deflected along-shore, although modeling results indicate that pulses of heat and solutes may intermittently flow offshore (Ramón et al., 2021). Thus, the effect of lake morphometry and latitude on under-ice circulation remains a question to pursue.

In spring, while lakes are still ice-covered, **snowmelt** from streams or thawed shores flows into the lakes. Snowmelt may transport the largest quantity of suspended particles and solutes from terrestrial systems to rivers and streams on a yearly basis (Olefeldt & Roulet, 2012; Townsend-Small et al., 2011), though budgets for downstream lakes are lacking. Meltwater flows also have the potential to supply oxygen (Jansen et al., 2019; Stefanovic & Stefan, 2002). However, retention of meltwater inputs (**loading**) requires that the incoming water be mixed downward. Snowmelt typically enters as a buoyant plume being colder and fresh-

er than the ambient lake water. Mixing requires sufficient momentum from the plume itself or sufficient solar heating of the introduced water such that RDC weakens the density gradients (Cortés et al., 2017). Tracer studies show that loading can range from negligible to 10%–15% (Bergmann & Welch, 1985; Cortés et al., 2017). Through-flow velocities of river and stream water are of order  $10^{-4}$ – $10^{-2}$  m s<sup>-1</sup> and depend in part on the surface roughness of the ice-water interface (Bengtsson et al., 1996; Hamblin & Carmack, 1990), which in turn is modified by ice-trapped gas bubbles emitted from the sediment (Engram et al., 2020). The depth of intrusion and extent of mixing are also a function of temperature, as warming can result in negatively buoyant plumes (Forrest et al., 2012), and of the volume of snowmelt in relation to the volume of the lake (Cortés et al., 2017; Jansen et al., 2019; Melack et al., 2021).

Depending on discharge and lake volume, as well as density stratification, lake water can be partially or entirely **displaced by meltwater** within days (Cortés et al., 2017; Cortés & MacIntyre, 2020; Jansen et al., 2019). This process flushes out greenhouse gases or cryoconcentrated salts at the ice-water interface (Cortés et al., 2017; MacIntyre et al., 2018). However, in shallow lakes where the flow path of incoming water is constrained by ice cover, heat and solutes accumulated at depth may also be displaced or flushed out. **Lateral exchange flows** in lakes with complex morphometry can similarly displace water (Figure 2). They can be generated when denser water overflows the boundaries of shallow basins into deeper ones, by snowmelt displacing lake water, or via tilting of pycnoclines as a result of variable wind action on the ice (Cortés & MacIntyre, 2020).

**Turbulence** is expected under lake ice prior to the onset of penetrative convection in spring, but has only been measured in a few cases (Kirillin et al., 2018, 2020). It is expected from cryoconcentration (Bluteau et al., 2017; Granin et al., 2000; Olsthoorn et al., 2020) and from the interaction of Kelvin waves with the benthic boundary layer (Kirillin et al., 2009, 2012). Recent observations in Lake Baikal show that large scale circulation can generate a turbulent boundary layer at the ice-water interface (Kirillin et al., 2020). While measurements in summer indicate that a turbulent boundary layer can also form at the sediment-water interface even at low flow rates (Lorke et al., 2003; Schwefel et al., 2017), sensitive velocity measurements are required to determine its properties in winter (Table 1; Q3). Thinning of the diffusive boundary layer by turbulent motions could lead to enhanced fluxes of heat and solutes (e.g., dissolved oxygen) at the sediment-water interface, as has been documented in summer (Bryant et al., 2010; Colman & Armstrong, 1987; Schwefel et al., 2017).

### 3. Ice Quality

Properties of lake ice determine the amount and wavelength of irradiance entering the water column. The incoming light moderates the heat budget and determines whether mixing will occur via radiatively driven convection, and regulates rates of photosynthesis throughout the ice-covered period. In this way, ice quality is directly coupled to under-ice primary production and respiration rates (Jewson & Granin, 2015; Prowse & Stephenson, 1986). Light **transmission**, or the converse, **attenuation**, through the ice is moderated by the presence or absence of **snow cover** and the **type of ice** (Jewson et al., 2009; Leppäranta, 2015). Lake ice can be generally classified into three types; two without snow cover and one with (Figure 3): (a) black ice; highly transparent, (b) white ice which combines ice and snow; highly opaque, and (c) snow-on-ice. Light transmission is reduced with the second and third types due to high albedo and internal light scattering. The light climate under ice changes substantially throughout winter and spring due to metamorphosis of the ice layer and varying snow cover (Leppäranta, 2015). Generally, the direction of change is from transparent to opaque, unless dry weather and stable sub-zero temperatures persist throughout winter.

Black ice forms under calm conditions that allow for formation of aligned, relatively uniform crystals that transmit the largest amount of light (Kirillin et al., 2012; Leppäranta, 2015). Generally, the dimensions of initial ice crystal formations range from 1 mm to 10 cm, with the larger crystals forming more slowly and under calmer conditions (Leppäranta, 2015). Black ice forms from the bottom of the initial ice layers downwards, which allows for cryoconcentration as well as inclusion of impurities present in the water column. In addition to turbulence and temperature affecting ice properties and crystal structure, gas content also influences ice clarity. The quantity of semi-transparent gas bubbles is directly coupled to the lake's biogeochemical characteristics. Large, clustered bubble plumes (1–100 cm diameter) consist mostly of ice-

trapped methane bubbles originating from the sediment (Walter Anthony et al., 2010), while smaller bubbles (0.1–1 cm diameter) form via exsolution and encapsulation of sparingly soluble gases at the downward freezing front (Boereboom et al., 2012). The volumetric ice bubble content is generally of order 1% in black ice (Kirillin et al., 2012).

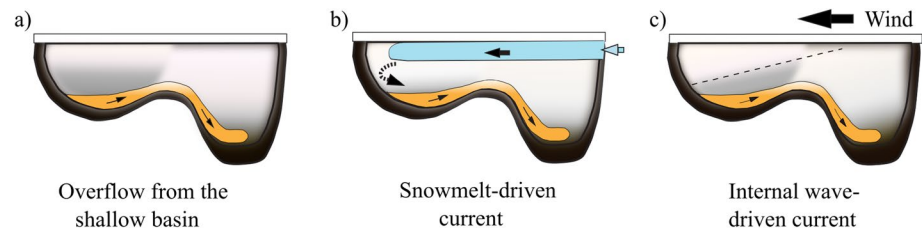
In contrast to black ice, white- or snow-ice formation is driven by variable weather conditions that enable thaw and re-freezing (Ashton, 2011). White ice can form on a preexisting ice cover via a number of different physical processes. Precipitation on top of the primary ice often contributes. When precipitation is liquid, the temperature difference can drive localized freeze-thaw events which result in the formation of white ice. A similar process occurs during rain-on-snow events and the subsequent refreezing of slush layers (Brown & Duguay, 2010). Furthermore, white ice can form due to the weight of slush and snow pressing down on the ice, resulting in the upwelling of liquid water through cracks in the ice and/or the submersion of the ice surface (Leppäranta, 2015; Saloranta, 2000). High concentrations of impurities, including gas bubbles inherited from the snowpack, contribute to the opacity of white ice.

The presence of snow on ice greatly reduces the transmission of light through the surface cover. Only a small fraction of solar radiation reaches the water column, and transmission is typically less than 5% (Huang et al., 2021; Prowse & Stephenson, 1986). Generally speaking, when substantial snow is present on top of ice, the euphotic depth of the system will be less than the thickness of the snow and ice layer (Kirillin et al., 2012). Light transmission varies depending on the properties of the snow, including albedo, snow crystal structure, and snow age, with fresh snow having the greatest limiting effect due to its high albedo and larger crystal sizes (Leppäranta, 2015). Additionally, the insulative properties of snow mediate heat transfer from the upper water column and limit ice growth (Caine, 2002). Rain on snow reduces both the albedo and insulation of the surface cover, and can either increase solar heating of the water column or, if followed by a cold period, increase cooling (Rogers et al., 1995). When the ice cover is thin, snow-on-ice can exert a strong and highly variable influence on both the under-ice light climate and water temperature, and significantly impact lake metabolism on interannual, seasonal and diel timescales (Huang et al., 2021).

While there is a growing body of literature about how the timing of ice formation and the duration of ice cover influences under-ice ecology (Hampton et al., 2017; Özkundakci et al., 2016; Sommer et al., 2012; Vincent, 1981), there is a paucity of data on the optical properties of lake ice which enable these communities (Bégin et al., 2020; Pernica et al., 2017). Quantitative relations between ice quality and **photosynthetically active radiation** (PAR) under ice have been obtained in perennially ice-covered Antarctic lakes (Fritsen & Priscu, 1999; Howard-Williams et al., 1998), but similar studies in the northern hemisphere are relatively sparse (Belzile et al., 2001; Bolsenga et al., 1996; Huang et al., 2021). Controlled experiments are required to distinguish the effects of PAR and temperature changes by snow-on-ice on lake metabolism (Huang et al., 2021). In addition, more work is required to assess the extent to which autotrophic community structure and distribution under the ice in northern regions depends on adaptation to specific light levels or wavelengths.

Geographic setting and local meteorology, which control the type and amount of precipitation as well as the (re)distribution of snow (e.g., lake size, prevailing winds and proximity to mountains), play a decisive role in regulating the light regime under ice (Bégin et al., 2020; Duguay et al., 2003; Huang et al., 2021). As northern regions undergo rapid climatic change, expected shifts in ice cover duration and surface cover composition will depend on this local context (Sharma et al., 2019). For example, the prevalence of white ice is predicted to increase in many areas of North America but decrease in parts of Canada and Eastern Siberia, corresponding to projected variations in snow depth (Dibike et al., 2012). In warmer winters, meltwater intrusions could become more important for the light climate under ice if the loading of terrestrial CDOM differs from that in the lake (Section 4).

Changes in the optical properties of winter surface cover on lakes will, through altering the under-ice light climate, ultimately lead to changes in food web structure and function under the ice. Under-ice algal blooms which directly depend on the optical properties of the surface cover will have cascading effects upon the open-water period via modification of the lake oxygen content and the biochemical conversion of inorganic carbon and nutrients to organic resources for higher organisms (Hampton et al., 2017; Reavie et al., 2016; Vachon et al., 2019; Yang et al., 2020). Changes in the amount, type and timing of winter precipitation and



**Figure 2.** Redistribution of heat and solutes in lakes with complex bathymetry. Flow from a smaller basin to a large basin as heat fluxes and solute production create density gradients that drive gravity currents across basin boundaries (a), via displacement of lake water by a buoyant meltwater plume (b) or thermocline tilting induced by internal waves (c).

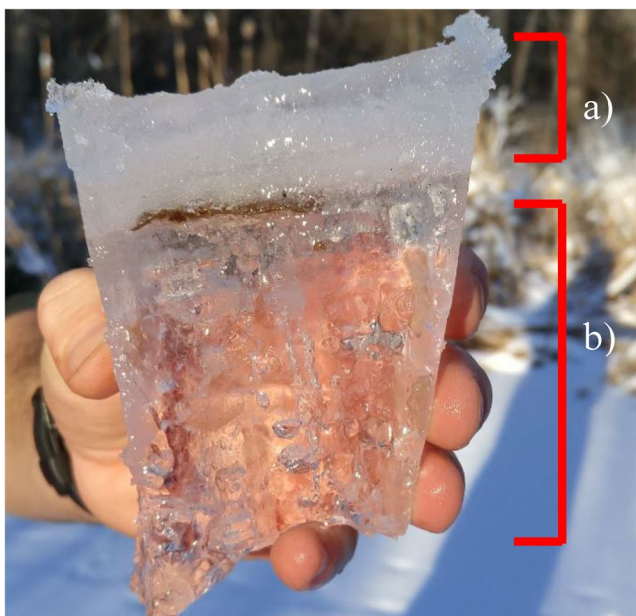
associated white ice formation could introduce a timing mismatch between the break of winter dormancy, which is dependent on temperature and photoperiod, and the availability of key food sources (Bokhorst et al., 2016). A quantitative assessment of the relation between resource availability, primary production and ice quality is currently lacking, but is essential for the understanding of ecosystems in seasonally ice-covered lakes (Table 1; Q7–9, Q15–16).

#### 4. Biogeochemistry

Under-ice biogeochemistry depends in part on the physical redistribution of heat and solutes, the associated chemical conversion processes and resulting changes in the spatial distribution of **oxygen**. Oxygen is consumed at the sediment surface (Hondzo, 1998; Mathias & Barica, 1980) via microbial degradation of organic matter (Maerki et al., 2009; Santschi et al., 1990; Welch et al., 1976) as well as via nitrification (Cavaliere & Baulch, 2019; Powers et al., 2017a). In small lakes with organic sediments, the entire water column can become anoxic within weeks after ice-on (e.g., Deshpande et al., 2015, 2017; Jansen et al., 2019) although in deeper lakes and/or lakes with mineral sediments, only a shallow layer near

the bottom will become anoxic (Sepulveda-Jauregui et al., 2015; MacIntyre et al., 2018). After oxygen, **alternative terminal electron acceptors**, such as inorganic oxides, are consumed (Santschi et al., 1990; Sundby et al., 1986). Benthic porewaters are subject to a myriad of biogeochemical and physical processes that control the flux of redox active species across the sediment-water interface (Giles et al., 2016; Smith et al., 2011). Under ice, these fluxes are governed primarily by chemical conversion rates, which determine concentration gradients and rates of transport via molecular diffusion, as well as the extent of turbulence in the diffusive boundary layer (Bryant et al., 2010; DiToro, 2001; Schwefel et al., 2017). Whether turbulence occurs at the benthic boundary layer under the ice is an area of active research (Kirillin et al., 2012) (Table 1; Q3). To establish biogeochemical linkages, a dynamic perspective is required. Studies which quantify turbulence need to have a biogeochemical component which assesses if the more rapid exchanges allow greater fluxes at the sediment or upper boundary of the anoxic layer.

With the down-slope transport of heat and solutes emitted from the sediment following ice-on and the establishment of stratification (Figures 1 and 4), reduced chemical species can accumulate in the water column below the chemocline and form **redox fronts**. Accumulating chemicals can include metals (Fe, Mn) (Joung et al., 2017; Schroth et al., 2015) in their soluble and reduced forms, nutrients ( $\text{NH}_4$ ,  $\text{PO}_4$ ) (Hampton et al., 2017; North et al., 2015; Powers et al., 2017b) and carbon substrates ( $\text{CH}_4$ ) (e.g., Jansen et al., 2019). Redox-active substances may be harmful to life, as in certain oxidation states of contaminants such as chromium and arsenic



**Figure 3.** An example of highly transparent black ice (a) formed from rapid, undisturbed freezing or from continued ice growth, below a thinner layer of opaque white ice (b) from a small seasonally ice-covered lake system. Photography by D. Barrett, 2015.

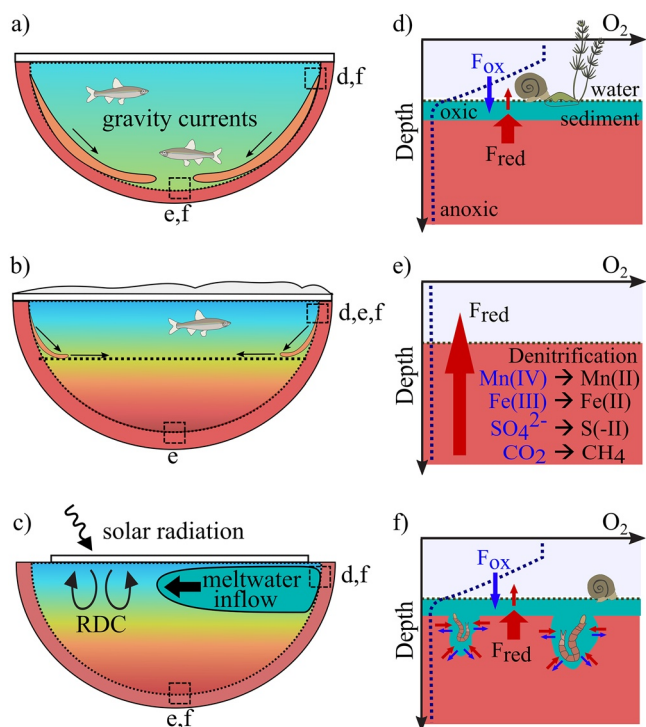
(Baker & Eisenreich, 1989; Jackson et al., 2004; Palmer et al., 2020; Tseng et al., 2004), and biogenic toxins ( $H_2S$ ) (Gammons et al., 2014; McKnight et al., 2000); the last may potentially contribute to winterkill of bottom-feeding fish (Magnuson & Karlen, 1970).

Many of the physical and biological processes that contribute to the formation and migration of redox fronts under ice have not been disentangled (Table 1; Q1). The thickness of the anoxic layer above the sediments will depend on the extent of mixing prior to ice on, trophic state, the organic matter content of the sediments and their surface to water volume ratio, and hence on the overall respiration rates (Mathias & Barica, 1980). Oxygen depletion rates also depend on sediment structure (e.g., porosity; Berner, 1980) and any preconditioning of the sediments over the summer and fall. For example, enhanced oxygen uptake from sediments may be associated with burrowing by invertebrates via increases in exposed sediment surface area (Figure 4f and Section 5.4) or with internal wave motions that cause exchange of sediment porewater with overlying lake water prior to freeze up (Olsthoorn et al., 2012; Olsthoorn & Stastna, 2014). Additionally, gravity currents which intrude above the bottom layer may become anoxic and contribute to the overall anoxia of the water column (Figure 4).

In spring, the strength of stratification can influence whether radiatively driven convection aerates deeper waters prior to ice-off (Pernica et al., 2017; Yang et al., 2017) or enables persistence of hypoxia and reduced solutes (Deshpande et al., 2015, 2017, 2017; Pieters & Lawrence, 2009; Vachon et al., 2019). Radiatively driven convection may increase or deplete oxygen concentrations in shallow littoral zones by bringing oxygenated surface water in contact with the sediment (Bengtsson & Ali-Maher, 2020). The extent of mixing from RDC and that at ice-off induced by wind and internal waves will determine whether solutes produced over the winter or introduced at snowmelt will be retained in concentrated zones or diluted and perhaps swept out of the lake (Cortés & MacIntyre, 2020; Jansen et al., 2019). The extent to which these processes redistribute heat, solutes and organisms near ice-off is a likely determinant of how winter conditions moderate ecosystem function in the ice-free period. Specifically, the fraction of accumulated  $CH_4$  which is oxidized versus emitted at ice-out in spring ultimately determines the radiative forcing impact of many seasonally ice-covered lakes (Jansen et al., 2019; Michmerhuizen et al., 1996; McIntosh Marcek et al., 2021), but is poorly quantified (Table 1; Q8).

Snowmelt can oxygenate part of water column and reduce the extent and duration of anoxia prior to spring mixing (Jansen et al., 2019; Stefanovic & Stefan, 2002). Meltwater can also contribute to dissolved organic matter (DOM) and nutrient loading (Sadro et al., 2018), but this depends in part on the hydrologic pathway prior to reaching the lake (surface or subsurface flow), the catchment landscape (e.g., wetland or forest) (Denfeld et al., 2018), and timing of meltwater inflows (Joung et al., 2017; Schroth et al., 2015). For example, nitrate inputs may originate from near-surface soils when their temperature is above freezing, or from atmospheric deposition (i.e., the snowpack) (Sickman et al., 2003). Meltwater can also introduce terrestrial bacteria (Hobbie et al., 1983; Crump et al., 2003). Inputs of terrestrial DOM may increase microbial productivity under ice, especially in floodplain lakes of Arctic river deltas, where prolonged riverine transport allows for photodegradation and increased bioavailability of DOM (Gareis & Lesack, 2018). While “browning” of boreal lakes has been attributed to increases in terrestrial organic carbon loading over the past decades (Solomon et al., 2015), the contribution of snowmelt to this long-term trend has not been quantified.

The impact of snowmelt is expected to vary along latitudinal and altitudinal gradients, as well as between years. For example, in the high-altitude lakes of the Sierra Nevada (California), a considerable fraction of lake water is replaced by snowmelt each year (Melack et al., 2021). Long-term records from these lakes show that the volume of snowmelt determines the loading of nitrate, dilution of base cations, and acid neutralizing capacity which builds up prior to winter, and so regulates primary production in summer (Jassby et al., 1990; Melack et al., 2021; Sadro et al., 2018). Conversely, inputs of CDOM can, if retained, reduce water transparency in summer (Cortés et al., 2017), which may limit annual primary production (Table 1; Q9). Such **seasonal carry-over effects** increase uncertainty about the effect of meltwater intrusions on ecosystem productivity of seasonally ice-covered lakes. Comparative and long-term studies enable predictions about the relation between climate variability, melt phenology (e.g., winter warming events; Graham et al., 2017) and ecology under lake ice.



**Figure 4.** Linked hydrodynamics and biogeochemistry under ice. Colors represent a redox gradient from anoxic (red) to oxygen saturated (blue). **Left (a)–(c):** Dynamics in the water column. (a) In early winter, gravity currents transport water depleted in oxygen but enriched in reduced solutes downslope. Stratification develops quickly in the lower water column, followed by anoxia; subsequent intrusions occur at shallower depths (Figure 1). (b) Anoxia can increase over winter but controls on its vertical extent are not fully known. (c) In spring, solar radiation penetrating the ice causes radiatively driven convection (RDC). Downward mixing of oxygenated water below the ice from meltwater inflows, and from photosynthesis may once again establish oxygenated conditions at the sediment-water interface, but the depth to which oxygenation occurs will depend on density gradients established in winter. Letter labels indicate characteristic profiles at different times and depths (right panels). **Right (d)–(f):** Dynamics at the sediment-water interface. Idealized oxygen profiles (dotted blue lines) and fluxes of oxygen ( $F_{ox}$ ; blue arrows) and chemically reduced substances  $F_{red}$  ( $NH_4^+$ ,  $Mn^{2+}$ ,  $Fe^{2+}$ ,  $S^{2-}$ ,  $CH_4$ ; red arrows). (d) Aerobic respiration in the upper sediments is maintained by transport through a diffusive boundary layer. Reduced substances produced in anoxic deeper sediments may be oxidized at the sediment-water interface. (e) Under anoxic conditions, reduced solutes diffuse out of the sediment and accumulate in the water column. (f) Bioturbation increases the exchange of solutes across the sediment-water interface.

## 5. Biology

### 5.1. The Under-Ice Microbiome

The richness and vitality of microbial communities under ice changes along geochemical gradients (Comeau et al., 2012; Rogozin et al., 2009; Schütte et al., 2016) (Figure 5). Elevated metabolic rates are expected to occur at the chemocline, where the supply of electron donors ( $CH_4$ ,  $NH_4$ ) meets that of electron acceptors ( $O_2$ ,  $NO_3$ ) (Cavaliere & Baulch, 2019; Martinez-Cruz et al., 2015; Rudd & Hamilton, 1978). Rates will vary with fluxes, yet such have rarely been documented. Hence, more is currently known about distributions. The abundance and activity of methanotrophs has been observed to peak at the chemocline in winter (Dalcin Martins et al., 2017; Kankaala et al., 2006; Sundh et al., 2005; Wand et al., 2006). Similarly, in the perennially ice-covered Antarctic Dry Valley lakes, the chemocline is populated by chemolithotrophs, such as sulfur-oxidizing (Sattley & Madigan, 2006) and ammonia-oxidizing bacteria (Voytek et al., 1999). Seasonal changes in geochemical gradients can drive concurrent shifts in communities and trophic pathways (Bertilsson et al., 2013). For example, in the water column of a Canadian thermokarst lake, the microbiome consisted primarily of phototrophs and aerobic heterotrophs in summer, while in mid-winter, when the lake was covered with ice and snow, lineages were characterized by reductive metabolic pathways, such as fermentation and methanogenesis (Vigneron et al., 2019). Similarly, the close correlation between nitrification rates and ammonium concentrations under ice (Cavaliere & Baulch, 2019; Powers et al., 2017b) implies that winter blooms of nitrifying bacteria (Butler et al., 2019) are enabled by the accumulation of reduced nitrogen species. An increased reliance on reduced substrates is therefore expected in winter.

Overall, microbial life under ice is thought to be characterized by high diversity but low biomass and productivity, a strategy that enables rapid adaptation and filling of ecological niches in response to geochemical changes induced by, for example, advection, snowmelt or mixing (Bertilsson et al., 2013; Vigneron et al., 2019). In an oxygen-stratified boreal lake in summer, methanotroph communities with diverging tolerance of anoxia have been observed to form vertical layers across the oxic/anoxic interface and some have genes for cell motility (Rissanen et al., 2021). This is indicative of genetic adaptation of Bacteria and Archaea to fluctuating chemical gradients that typically occur under ice, and which enables bloom-like behavior when a food source becomes suddenly abundant (Bižić-Ionescu et al., 2014). Heterotrophs benefit from algal growth at or below the ice-water interface during periods of limited snow cover or RDC (Arvola & Kankaala, 1989; Straškrábová et al., 2005), and also utilize terrestrial inputs of organic carbon and nutrients associated with snowmelt events (Roiha et al., 2016; Karlsson et al., 2008). It has been hypothesized that the upward movement of the redox front via gravity

currents provides (anaerobic) communities with access to labile organic matter from senesced macrophytes (Jansen et al., 2019). Some geochemical shifts in spring may be too rapid for microbial response; during mixing and reoxygenation at ice-out, a large part of the accumulated methane can escape to the atmosphere instead of being oxidized (Jansen et al., 2019; McIntosh Marcek et al., 2021; Michmerhuizen et al., 1996). The fate of reduced chemicals and associated microbes after winter thus requires further exploration (Table 1; Q4, Q14, Q25).

Though apparently abundant, the contribution of microbes as food sources to grazers in winter (i.e., the microbial loop, Figure 5) remains unknown. In the ice-free season, methanotrophs can constitute an im-

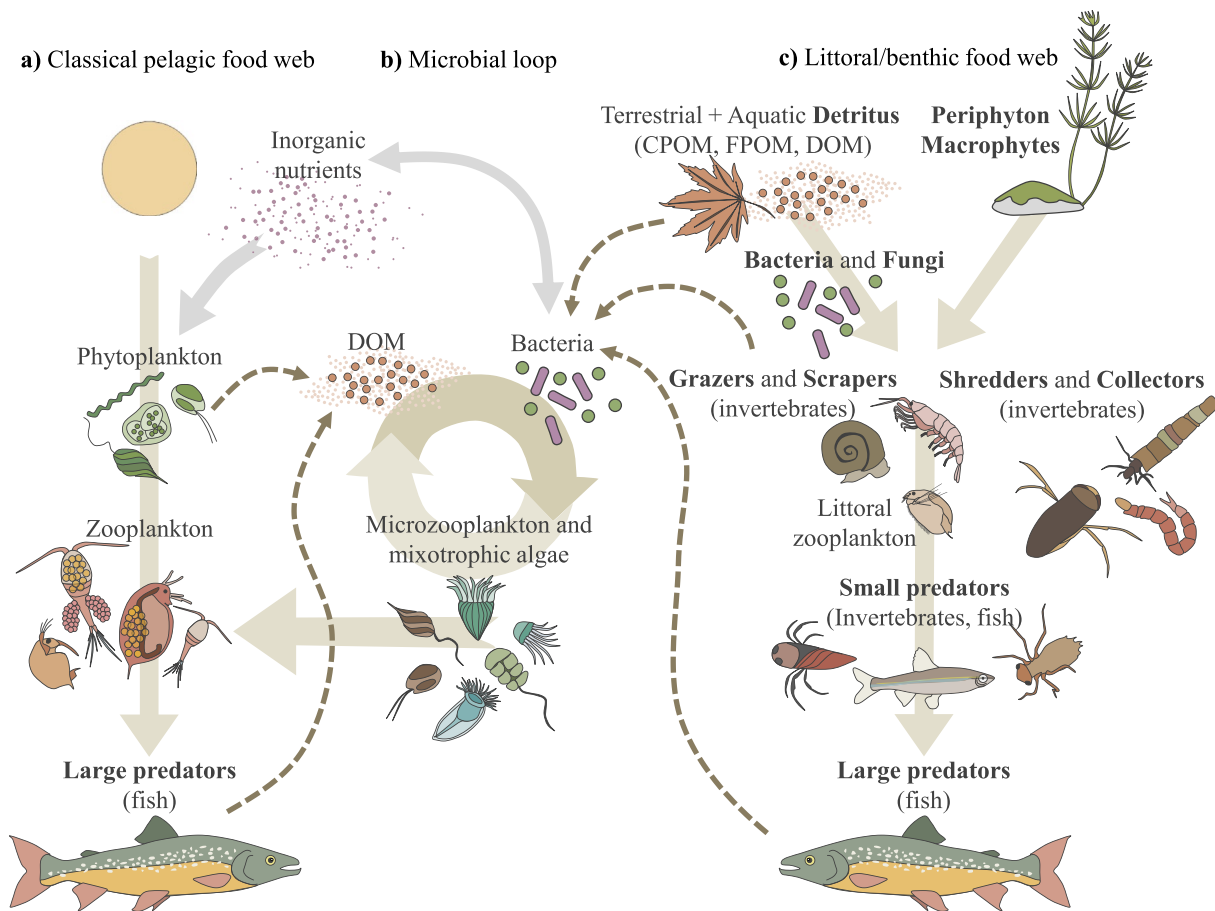
portant food source to zooplankton in humic lakes with anoxic hypolimnia (Bastviken et al., 2003; Kankaala et al., 2006), and have been isotopically traced to higher species (Jones & Grey, 2011), including fish (Sanseverino et al., 2012). Under ice, zooplankton abundance can coincide with regions of high bacterial biomass (Rivier, 2005) while other studies indicate bacteria make up only a small part of the diet of zooplankton in winter (Grosbois et al., 2017) (Section 5.3). The increasing abundance of highly reactive reduced chemicals (Gammons et al., 2014; Joung et al., 2017) as well as methanotrophs (Samad & Bertilsson, 2017) with depth in winter implies either that ciliates and other microzooplankton cannot make immediate use of food sources at or below the chemocline, or that the rate increase of methanotrophs outpaces grazing rates.

## 5.2. Phytoplankton Under Lake Ice

Species assemblages and strategies for growth of phytoplankton under the ice vary with respect to summer conditions. Light limitation by ice and snow may be a stronger determinant of phytoplankton abundance than zooplankton grazing (Hryciuk & Stockwell, 2021). Adaptations to be viable and competitive under the ice include acclimatization to low irradiance (Neale & Priscu, 1995) and motility to maintain access to light (Forsström et al., 2007; Pithart, 1997; Vehmaa & Salonen, 2009), increase food encounters, and to avoid predation (Franks, 1992; Özkundakci et al., 2016). Strategies may vary with morphological stages of the life cycle (Jewson & Granin, 2015; Perga et al., 2020b). Motile taxa can dominate phytoplankton communities in weakly stratified water columns (Özkundakci et al., 2016; Rue et al., 2020), form vertical layers under ice (Kiili et al., 2009; Vehmaa & Salonen, 2009; Vincent, 1981), or perform (daily) vertical migrations between the photic zone and a nutrient-rich refuge layer (Pithart, 1997; Pettersson, 1985) (Figure 6). Negatively buoyant taxa, such as many diatoms, are at a disadvantage until convective mixing in spring allows them to remain suspended in the photic zone of the water column (Bouffard et al., 2019; Kelley, 1997; Salmi & Salonen, 2016; Pernica et al., 2017). Some species are mixotrophic, that is, they can utilize both heterotrophic and autotrophic metabolic pathways (Jones et al., 1997, 2000; Laybourn-Parry & Marshall, 2003). Although mixotrophic phytoplankton taxa are common in winter (Charvet et al., 2014; Kalinowska & Grabowska, 2016; McKnight et al., 2000), we have little knowledge about the overall degree of mixotrophy in ice-covered lakes, in part because mixotrophy is difficult to measure (Anderson et al., 2017; Rautio et al., 2011) (Table 1; Q10).

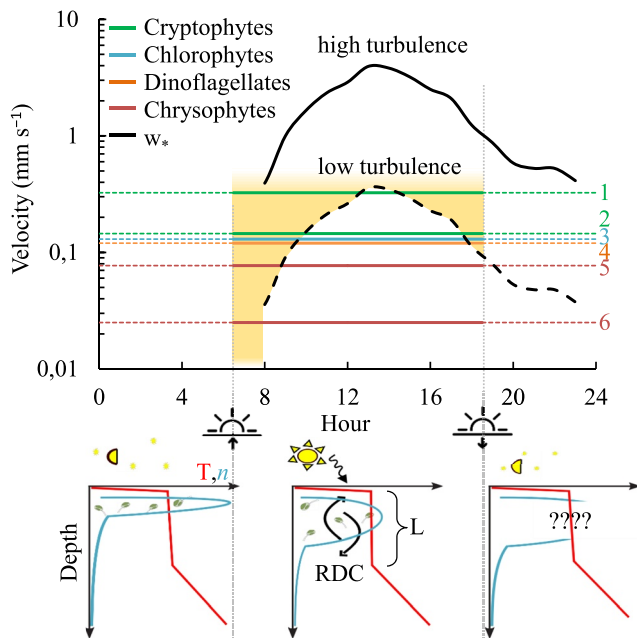
While phytoplankton growth under ice may be limited by low light conditions, internal nutrient supply, especially of phosphorus, may increase in winter (Joung et al., 2017). Soluble reactive phosphorus accumulates in anoxic regions, where it may be available to slow-growing, migratory dinoflagellates (Pettersson, 1985) as well as to other motile species. Its availability to fast-growing non-motile taxa, such as diatoms, depends on redistribution and mixing via convective circulation or gyres (Figures 1 and 4). Snowmelt could supply nutrients in spring, but their availability depends on the extent to which meltwater mixes with ambient water (Section 2). Despite these caveats, phytoplankton production can be substantial under ice, and winter blooms are well-documented (Katz et al., 2015; Rue et al., 2020; Twiss et al., 2012). In clear lakes with minimal light attenuation by snow-on-ice or CDOM, phytoplankton biomass under ice can be as high as in the ice-free season (Hazuková et al., 2021; Jewson et al., 2009). In a quantitative analysis of data from 101 temperate lakes, concentrations of chlorophyll-*a* in winter averaged 43% of values in summer (Hampton et al., 2017), indicating the potential for substantial accumulation of algal biomass in many ice-covered lakes.

In order to understand and predict under-ice algal blooms, a modeling framework is required that quantifies how the velocity of convective flows and mixing determine the proliferation of motile versus non-motile phytoplankton species. Successful growth of diatoms under ice during RDC in spring has been attributed to their sinking rates being less than the velocity scale of thermals from penetrative convection (Bouffard et al., 2019; Jewson et al., 2009; Kelley, 1997). Building upon these findings, improved models should account for day-to-day variations in solar insolation and intermittent snowfall which affects light penetration (Figure 6). Moreover, they must address the light limitation or photoinhibition which vary with mixing depths (Jewson et al., 2009). It is also essential to consider whether the duration of RDC is sufficient for the abundance of diatoms to increase. Given ongoing losses of negatively buoyant cells even with convection, modeling must incorporate the processes moderating the timing and vertical extent of mixing and the depth dependent growth rates essential to maintain populations (Bouffard et al., 2019; O'Brien et al., 2003).



**Figure 5.** Food webs in lakes and links between them. (a) Classical pelagic food web is based on solar radiation and nutrients that activate photosynthesis and the buildup of phytoplankton biomass that in turn supports the growth and reproduction of higher organisms. Zooplankton that feed on autotrophic phytoplankton can have fast growth rates and are able to build extensive fat reserves making them a preferred diet for some pelagic fish. (b) The microbial food web operates alongside the classical food web. It is fueled by dissolved organic matter (DOM) released by living organisms and decomposing aquatic and terrestrial material (dashed arrows); the DOM is repackaged in increased biomass of heterotrophic bacteria, mixotrophic algae and microzooplankton (solid arrows) making it trophically available to higher organisms. With no autotrophic algae involved, the organic resources from the microbial loop lack many growth-supporting essential compounds and hence zooplankton feeding on this source grow slowly and are unable to accumulate fats. (c) The littoral/benthic food web is driven by the combination of autotrophic periphytic algae and macrophytes and terrestrial and aquatic detritus. Detritus is divided into coarse (CPOM) and fine (FPOM) particulate organic material and DOM, which fuel different invertebrates and the microbial loop. Mobile, generalist fish can feed in both classical and microbial pathways. The different food webs occur concurrently but their relative importance is depth- and season-dependent. The microbial food web dominates in mid-winter and often deeper in the water column and the solar radiation-driven pelagic and littoral food webs may increase in importance toward spring and/or closer to the surface depending on the quality of the ice.

Links between convective velocities, growth of and grazing on motile phytoplankton also are required (Table 1; Q13). Convective velocity scales measured at the peak of RDC in spring ( $0.4\text{--}3.1\text{ mm s}^{-1}$ ) (Bouffard et al., 2019) exceed the swimming speeds of flagellated phytoplankton (median  $0.1\text{ mm s}^{-1}$ ) as well as phototactic grazers such as ciliates (median  $0.7\text{ mm s}^{-1}$ ) (Lisicki et al., 2019) and rotifers ( $0.1\text{--}1.0\text{ mm s}^{-1}$ ) (Perga et al., 2020a). These comparisons suggest that layered populations would be disrupted and diatoms favored under RDC (Figure 7) (Salmi & Salonen, 2016). However, motile phytoplankton can take advantage of low turbulence niches. Long-term phytoplankton surveys in the Müggelsee, Germany, indicate motility is more prevalent when ice is thicker (Kalinowska & Grabowska, 2016; Özkundakci et al., 2016) and clustering of motile phytoplankton at the ice-water interface tends to be associated with weak stratification which provides resistance to mixing (Vehmaa & Salonen, 2009; Kiili et al., 2009; Ventelä et al., 1997). The extent to which layering will persist when conditions are turbulent is unclear. Dispersion modeling based on eddy diffusivity (Fisher et al., 1979) implies that population densities remain elevated at the depths of the initial patches over timescales of mixing ( $\tau_{mix} = L / w_*$ , where  $L$  is the mixed layer depth and  $w_*$  is the convec-



**Figure 6.** Can flagellated plankton layer under penetrative convection to optimize access to light or nutrients or to facilitate grazing? Here we compare the swimming speeds ( $w_s$  - horizontal lines) of phototactic autotrophs with  $w_*$  (black solid and dashed lines), the convective velocity scale from RDC-induced turbulence which will lead to their being mixed.  $w_* = \sqrt[3]{L\beta}$  (Deardorff, 1970), where  $\beta$  is buoyancy flux which induces RDC and  $L$  the depth of the mixing layer. A high turbulence scenario as on a sunny day (solid black line) corresponds to under-ice measurements of  $w_*$  (ADCP, Bouffard et al., 2019) and calculated using diurnal variability of  $\beta$  ( $10^{-9}$ – $10^{-11}$   $m^2 s^{-3}$ ) (Jonas et al., 2003) and  $L$  of 30 m.  $w_*$  varies over the day from 0.4 to 3.1  $mm s^{-1}$ . Would  $L$  decrease to 2 m,  $w_*$  decreases but continues to exceed  $w_s$  for many hours. During cloudy conditions with lower  $\beta$  (Jonas et al., 2003), calculated velocities have a diurnal maximum of 0.4  $mm s^{-1}$  for  $L = 2$  m (dashed black line) and increase with  $L$  such that for  $L = 30$  m,  $w_*$  again would be appreciably larger than  $w_s$ . Colored lines mark swimming speeds of phytoplankton that are known to occur under lake ice: (a). *Hemiselmis simplex*, (b). *Cryptomonas phaseolus*, (c). *Chlamydomonas reinhardtii*, (d). *Peridinium cinctum*, (e). *Ochromonas danica* and 6. *Spumella sp.* (Lisicki et al., 2019 and references therein). RDC does not occur at night. Yellow shading indicates opportunities for layering between sunrise and sunset under the low turbulence scenario. Additionally, horizontal convection occurring at night can increase stratification, transport organisms from other locations, and may increase stratification enough to reduce the depth of penetrative convection.

population densities of copepods peak in mid-winter (Grosbois et al., 2017; Larsson & Wathne, 2006; Rautio et al., 2000; Rigler et al., 1974) implying that mechanisms exist to supply resources to active zooplankton under the ice.

Conditions prior to ice-on may be a critical factor for maintaining active zooplankton in winter. At this time, if algal biomass and quality is sufficient, zooplankton accumulate lipids that can be used when the availability of other food resources in the water column is low (Grosbois et al., 2017; Grosbois & Rautio, 2018; Mariash et al., 2017). These zooplankton, many of which are copepods, do not need to seek depths where food is most abundant but may instead look for optimum temperatures. The detailed vertical structure of zooplankton communities under ice is not known, but we could expect increased copepod abundance directly above the chemocline where oxygen levels and temperatures are sufficient to sustain heterotroph-

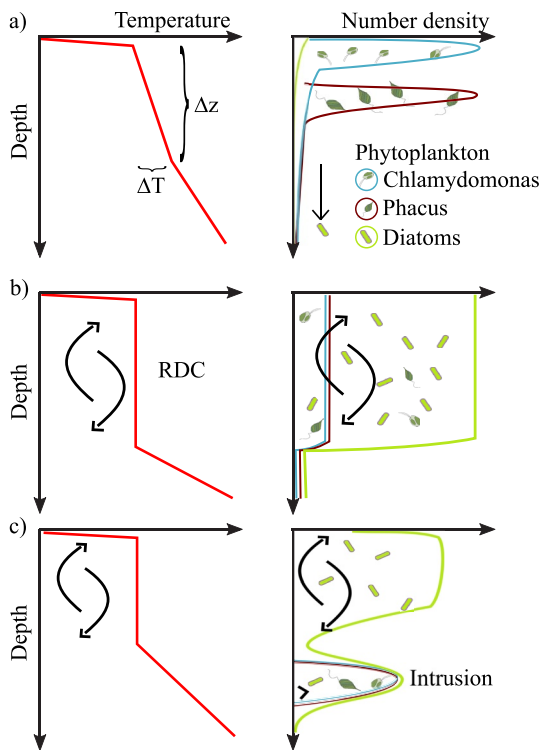
active velocity scale), even for high turbulence scenarios. Diurnal patterns in convective velocities, particularly time lags between radiative forcing and the onset and decay of convection, as well as heterogeneity in near surface density gradients (Bouffard et al., 2019; Cortés et al., 2017; Perga et al., 2020a) provide additional opportunities for layering.

Whether diatoms prevail, or patches of flagellates persist will influence the transfer of energy within and between food webs. Persistent layering would provide concentrated food sources for higher trophic levels under the ice. Because many cryptophytes and chrysophytes are small and mixotrophic, the energy would likely be retained in the microbial food web. In contrast, dominance of autotrophic diatoms during penetrative convection may increase the availability of high-quality food for zooplankton either under the ice or at ice off as algal productivity increases with more light (Section 5.3). Thus, RDC and increasing diatom productivity may lead to considerable energy entering the classical food web or, as in Lake Baikal, the benthic food web (Moore et al., 2009). Computer models that take into account the vertical extent of eddies, their velocities, and swimming/sinking speeds in combination with metabolic costs and opportunities of migration will form a basis for predicting such trophic transfers (Table 1; Q11).

For regional assessments of winter primary production, spatial and temporal variability of stratification and its effects on mixing by RDC need to be considered (Table 1; Q32). Even a weak chemical density gradient can resist vertical mixing, which implies that phytoplankton community structure depends not only on ice quality but also on landscape setting, lake morphometry and sediment type. For example, in two relatively nearby locations in the Alaskan Arctic, increased solar radiation in spring only led to horizontal convection in two 1 ha size lakes with specific conductance over 100  $\mu S cm^{-1}$ , penetrative convection for only a week in a more dilute 10 ha, 10 m deep lake (Cortés & MacIntyre, 2020), spatially variable depths of penetrative convection in 150 ha, 24 m deep Toolik Lake with considerable inflows from snowmelt (Cortés et al., 2017), and penetrative convection for over a month in mountain Lake Peters (640 ha, 150 m deep) (Barnes & Hobbie, 1960).

### 5.3. Zooplankton Under Lake Ice

Maintaining active zooplankton under the ice requires resources. Predominantly phytoplankton grazers, many zooplankton become dormant and disappear from the water column into sediments during winter when algae become scarce in the absence of light (Larsson & Wathne, 2006; Nilssen & Elgmork, 1977). In some boreal and arctic lakes, however, pop-



**Figure 7.** Temperature (left) and phytoplankton concentration (right) in weakly stratified systems. (a) Motile phytoplankton (maroon and blue lines) are able to form layers in zones with favorable light or nutrient conditions while diatoms (green line) sink. (b) Temperature and phytoplankton abundance during RDC. Convective velocities exceed swimming speeds, disrupting layers. Diatoms are maintained in suspension and proliferate if growth rates are high enough. (c) Phytoplankton maxima at depth can be caused by diel migration or lateral transport from horizontal convection (e.g., Vehmaa & Salonen, 2009).

ic metabolism (Figure 8). Small crustacean zooplankton that store less resources and need more frequent foraging, such as cladocerans or copepod nauplii (Grosbois et al., 2017; Larsson & Wathne, 2006) could, on the other hand, be expected to exhibit a vertical migration pattern following the depth distribution of their phytoplankton prey (Perga et al., 2020b) (Table 1; Q19).

When primary productivity is limited by low irradiance in winter, the role of organisms in the classical food web is expected to decline (Hampton et al., 2017) (Table 1; Q15). Alternative food sources, such as mixotrophic microorganisms and allochthonous organic material can sustain active zooplankton when phytoplankton are scarce (Forsström et al., 2007; Grey et al., 2001; Grosbois et al., 2020; Rautio et al., 2011; Sävström et al., 2009). This diet, however, is deficient in polyunsaturated fatty acids (PUFA) required for growth and reproduction (Taipale et al., 2012), which may mean that the abundant microbial biomass at the chemocline is only sufficient to maintain baseline metabolism in active zooplankton. In shallow clear-water lakes, organic matter generated and released by benthic algae can provide food to zooplankton in winter (Karlsson & Sävström, 2009). Although this DOM resource is transferred to zooplankton via the microbial loop (Figure 5), it is not known if the transfer takes place in the anoxic zone usually avoided by zooplankton, or at the chemocline, and whether zooplankton migration behavior is directed by this potential food source. Phytoplankton becomes a direct food source again in late winter when light returns and RDC creates conditions favorable for negatively buoyant diatoms and other cells of high nutritional value. Thus, the duration of winter and the extent of snow cover will moderate the availability of phytoplankton for grazing and the migratory behavior of zooplankton throughout the ice-cover period (Figures 7 and 8).

The contribution of different food sources to zooplankton diets may change through the winter as light penetration and the stability of the water column vary. In late winter and spring, even under low light conditions, zooplankton activity may be facilitated by layered phytoplankton near the ice-water interface. However, sustaining both communities re-

quires that zooplankton grazing rates be less than phytoplankton growth rates. As discussed in the previous section, mixing can disrupt layered assemblages of motile phytoplankton but can support diatom growth - both of which would influence zooplankton survival. Therefore, observed shifts in zooplankton abundance in late winter or early spring may result from penetrative convection (Perga et al., 2020a). Swimming speeds of zooplankton are often size-dependent. Thus, dispersion via penetrative convection may make it difficult for mixotrophs, micro-zooplankton, and larval zooplankton to graze, but macrozooplankton are likely to outswim the turbulent eddies. Hence, whether conditions are quiescent or turbulent under ice would favor different groups of zooplankton and different life-stages of macrozooplankton (Table 1; Q29).

#### 5.4. Macroinvertebrates Under Lake Ice

Macroinvertebrates are critical links in aquatic food webs. They recycle nutrients and energy by breaking down living periphyton and macrophytes as well as terrestrial and aquatic detrital biomass (Merritt et al., 2008) (Figure 5). They can also be an important food source for fish in winter (Section 5.5). The greatest abundance and diversity of macroinvertebrates is generally found in the benthos of vegetated littoral regions (Merritt et al., 2008). This increases vulnerability to predation in winter, when vegetated habitat diminishes (Burks et al., 2001; Crowder & Cooper, 1982) (Figure 8) due to the autumnal die-off of littoral macrophytes, drought-induced decreases in water level prior to freeze-up, or bottom-freezing of shallow waters. Many benthic macroinvertebrates therefore exhibit both physiological and behavioral adaptations to under-ice con-

ditions. Some species enter diapause, a state of dormancy with reduced metabolic demand for energy and oxygen (Danks, 2007; Lencioni, 2004) which is common for invertebrates that overwinter in the egg stage (e.g., some species of dragonfly). Other taxa enter torpor, a state of reduced metabolic demand more quickly reversible than diapause (Lencioni, 2004). Organisms lacking freeze tolerance or supercooling abilities that become dormant will first move to microhabitats that do not freeze - either in hypoxic deeper water or buried into the anoxic sediment (Moore & Lee, 1991). Although dormancy is in itself a response to limited oxygen availability, some species including mayflies (Brittain et al., 1981) and chironomids (Gingras et al., 2007; Hamburger et al., 1998) have developed further adaptations to anoxic conditions. In contrast, winter-active taxa may retreat and re-colonize littoral areas in response to changes in ice cover and oxygen levels.

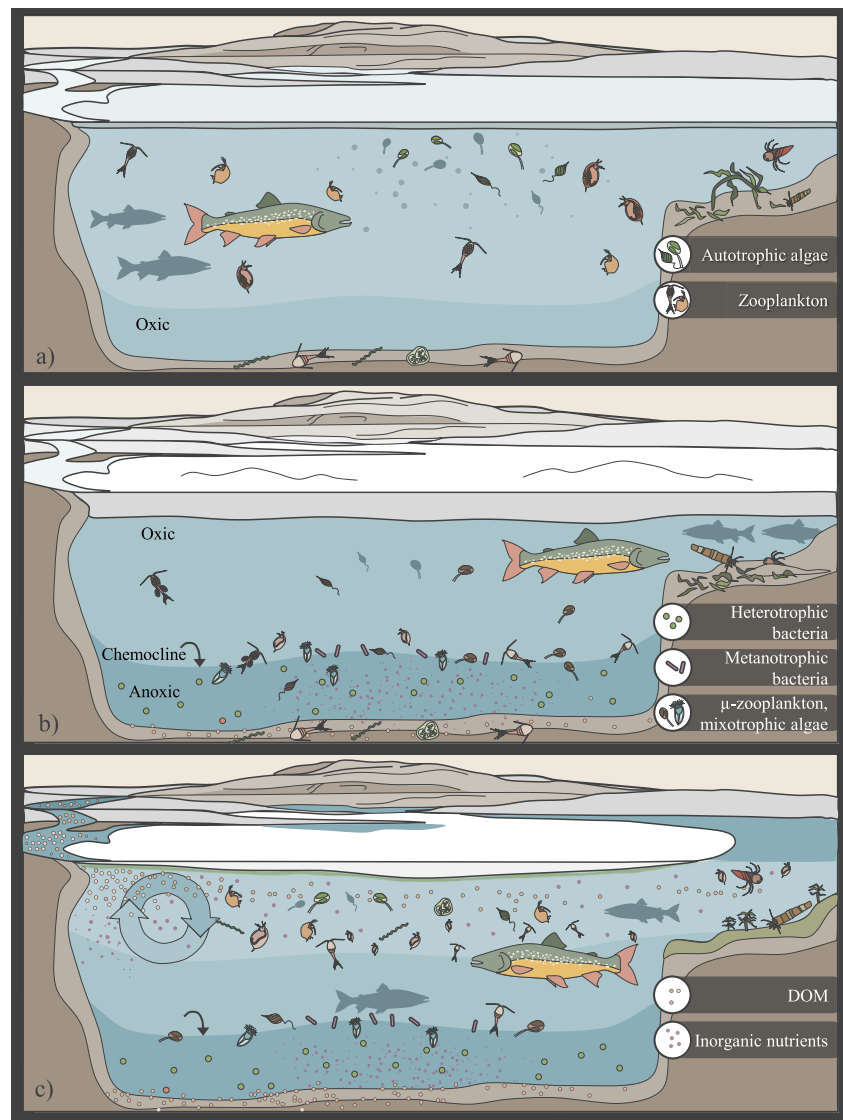
Winter activity in benthic macroinvertebrates may be more common than assumed, though it likely depends on the physical and chemical properties of their habitat as well as the likelihood of predation. Entrance into dormancy is probably facultative rather than obligate for many aquatic taxa, but the abiotic thresholds for such behavior have yet to be determined (Danks, 2007; Hungerford, 1919). For example, backswimmers, which collect air bubbles from the surface to breathe, are documented as overwintering buried in sediment (Clark, 1928). Yet they can also be seen actively swimming under ice for at least as long as ice remains transparent (Hungerford, 1919) and can be collected from the water column under ice 12 cm thick throughout the winter in ponds supersaturated with oxygen (R. Martin pers. obs.). Senescence of terrestrial and aquatic vegetation in autumn can provide organic substrate during the ice-cover period. Some species, particularly detritivores, can therefore achieve active growth over winter (e.g., caddisflies, Bjelke et al., 2005; Bohman & Herrmann, 2006; mayflies and blackflies, Bengtsson, 1981; Merritt et al., 1982; glassworms, Schröder, 2013). Like zooplankton, macroinvertebrate species that do not feed during winter but remain active, for example to avoid predation, rely on internal energy reserves which must be recouped in later seasons (Danks, 2007).

Benthic macroinvertebrates can directly affect biogeochemical cycles and physical processes under ice. For example, in summer, bioturbation by dipteran larvae, chironomids and glassworms (*Chaoborus larvae*) facilitates the rapid exchange of solutes including oxygen across the sediment-water interface (Svensson & Leonardsson, 1996; Mermillod-Blondin & Rosenberg, 2006). If continued in early winter, this process would enhance respiration rates and fluxes of heat and carbon dioxide to the water column (Figures 1 and 4), and in turn contribute to the initial gravity currents (Section 2). In one study, chironomid larvae were observed to move up and down in their burrows to harvest the small amount of oxygen generated at the sediment-water interface by photosynthetic periphyton even under anoxic ice-covered conditions (Gingras et al., 2007). While most glassworms remain active in the water column through the ice-cover season, a fraction has been observed to burrow into the sediment in early winter (Sardella & Carter, 1983). Winter burrowing behavior in dipteran larvae is likely species specific, as well as dependent on water depth, food availability, and benthic substrate type (Danks, 1971; Sardella & Carter, 1983).

Winter phenology and activity remain unexplored for many invertebrate species. A major uncertainty is the link between different biogeochemical and physical states and behavioral responses including survival strategies (Table 1; Q20, Q28). The impact of winter warming events on the activity of littoral macroinvertebrates is likely underappreciated. When moat formation or meltwater plumes reoxygenate littoral regions (Figures 1 and 2), organisms such as mayflies can actively migrate to the margins (Brittain et al., 1981). Indeed, on warm February days in southern Ontario, Canada, leeches, caddisflies, damselflies, dragonflies and beetles can be observed moving around in littoral habitat still covered by 27 cm of ice (Supplementary Movie S1). If such activity is facilitated by snowmelt, then the increasing frequency and duration of winter warming events (Graham et al., 2017) may have a profound effect on the macroinvertebrate community.

### 5.5. Fish Under Lake Ice

The activity of fish under lake ice will vary with physiological and morphological traits combined with the extent of ice and snow cover which moderates irradiance. Fish that are physiologically adapted to perform best at low temperatures should have a higher capacity for activity during the cold of winter (McMeans et al., 2020; Shuter et al., 2012). Smaller fish, which have lower energy storage capacity and a higher risk of overwinter starvation, should also be more likely to forage during winter compared to larger individuals (Bystrom et al., 2006; Hurst, 2007). However, the decision to forage might also be informed by the abiotic



**Figure 8.** Linked hydrodynamics, biogeochemistry and biology under ice. (a) **Early winter.** With downward gravity currents along the sides and slow upward flow in the center of the lake, negatively buoyant non-motile cells settle to the bottom, autotrophic and heterotrophic flagellated algae persist under thin and transparent ice and provide resources to winter-active micro- and macro-zooplankton. With decreasing food supply and littoral habitat structure, some macroinvertebrates and zooplankton slow their metabolism or become dormant. Some fish species begin to slow down and cease feeding, while others continue to feed on available resources. (b) **Mid-winter.** The lower water column becomes anoxic and chemically reduced solutes increase in concentration and sustain microbial communities. Energy is provided to the microbial loop as Bacteria, motile phytoplankton and microzooplankton accumulate at the rising chemocline. The extent to which the microbiome contributes to growth of species in higher trophic levels is unknown. Some macroinvertebrates remain active while others retreat to the sediments or other safe habitats and enter a state of dormancy. Fish have either ceased feeding or continue to feed on available resources. Foraging habitats may shift to include littoral prey. (c) **Spring.** Layered communities of flagellates can form once solar radiation increases and the water column remains stratified, whereas diatoms can be sustained by penetrative convection (Figure 7). Snowmelt introduced by streams, rivers or via the shoreline moat transport DOM and nutrients to the surface layers. These incoming waters may push the accumulated phytoplankton out of the lake, or if they mix with the underlying water, provide heterotrophs and autotrophs with key subsidies. With rapid autotrophic growth, as hypothesized here, the biomass of zooplankton in the upper water column would increase. Depending on the extent of mixing in spring, the bottom layer enriched in microbes, CH<sub>4</sub> and other substrates may be mixed upwards further contributing to growth. With light returning, and temperatures and oxygen increasing, inactive macroinvertebrates exit dormancy and return to their summer habitats, and fish are free to move around the water column consuming pelagic, benthic or littoral prey depending on the species.

environment and the resultant resource landscape in any given lake or winter. For example, many fish are visual predators that need light to detect and successfully capture prey (Blanchfield et al., 2009). Higher light availability during early winter and spring, or in systems or years with less snow and ice cover, could increase not only resource density via increased primary production, but also the visual capacity of fish to find and detect prey. Less snow cover and more light penetration might therefore translate into more active and successful foraging by fish, with potentially cascading effects through the food web (Varpe et al., 2015). However more field data is needed to examine this idea in ice-covered lakes (Table 1; Q16).

Physical processes that influence mixing, temperature and oxygen levels throughout the water column could also influence fish behavior during winter. Some data suggest that fish select for specific depths under ice cover, which could be attributed to selecting for specific temperatures in order to minimize metabolic costs (Harrison et al., 2016; Suski & Ridgway, 2009). Even the small differences in temperature with depth of 0°C–4°C could therefore be relevant for overwintering fish. More work is required to explore how the location of fish within a lake should be expected to shift from early to mid-winter to spring, or vary from year to year in response to changes in thermal structure (Table 1; Q21). Oxygen gradients under ice can force fish to select for certain habitats during winter (Hasler et al., 2009), and anoxia is thought to act as a strong filter determining which fish species are able to survive the ice-cover season in different lakes (e.g., large predators can be excluded; Magnuson et al., 1985). In turn, winter fish kills can explain larger-sized zooplankton in summers following colder winters in shallow Danish lakes (Balayla et al., 2010). These examples highlight the cascading effects of winter conditions on the structure of whole communities and food webs.

Any change in the abiotic environment that influences primary production (e.g., mixing, ice quality, biogeochemistry) might also play a role in governing habitat and resource use by fish and in this way shape the structure of the winter food web. If declines in phytoplankton during winter lead to declines in zooplankton, and potentially declines in small planktivorous fish, predatory fish might seek out alternative resources. Benthic prey that are larger-bodied and slower-growing appear less sensitive to abundance declines in winter and can become an important resource for fish under ice (Hayden et al., 2014). Some evidence suggests that pelagic fishes move inshore and effectively become littoral predators during colder months of winter and spring (McMeans et al., 2020). Although not well studied, such seasonal habitat shifts could have widespread consequences for lake nutrient cycling because fish are vectors for nutrient transport (Vanni, 2002). Increased reliance on inshore prey during winter could also influence fish body burdens of biomagnifying contaminants like Hg and polychlorinated biphenyls (PCBs), especially if benthic and pelagic prey sources differ in their contaminant levels (Keva et al., 2017). However, many questions remain (Table 1). The possibility that gravity currents help sustain the microbial loop and the pelagic food web, and provide fish with sustained access to pelagic prey, remains completely unexplored (Table 1; Q22). More work is required to examine the availability and accessibility of pelagic versus littoral resources to fish in winter, and whether reliance on littoral resources varies predictably with the physical environment.

## 6. Knowledge Gaps

Key knowledge gaps emerge at the intersections of the different disciplines that span the field of winter limnology (Figure 9). Table 1 lists 33 open research questions, together with approaches to solutions based on interdisciplinary methodology.

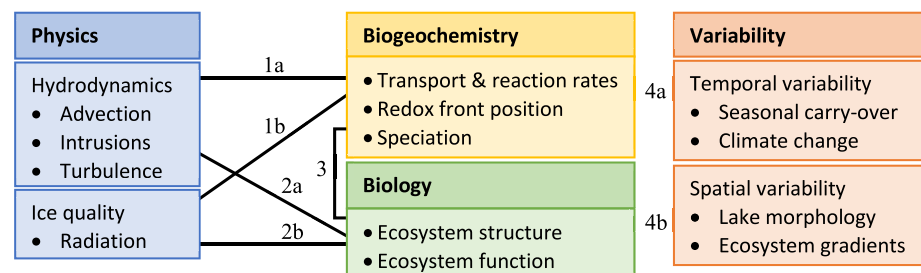


Figure 9. Overview of under-ice processes. Numbers mark categories in Table 1.

**Table 1**

*Interdisciplinary Knowledge Gaps, Methodological Recommendations and Complexity (C) of Methods Involved (---: Common, Limited Special Expertise Required, ++ Experimental, Collaborative Expertise Advised)*

Research Questions	Method Recommendations	C
<b>1a Physics, Hydrodynamics - Biogeochemistry</b>		
Q1 What is the contribution of advection (circulation, convection) versus in situ respiration in formation and expansion of anoxic zones under ice?	OW-TCO arrays plus CO <sub>2</sub> sensors, in situ incubations	+
Q2 Do internal waves cascade to turbulence enabling exchange of redox-active substances across the chemocline in winter? Does this exchange enhance microbial activity at the chemocline?	OW-TCO arrays and current meters, redox voltammetry, periodic microbial surveys	++
Q3 Can under-ice flows generate turbulent boundary layers and if so, do they enhance transport of heat and solutes (e.g., across the sediment-water interface)?	As above and including temperature microstructure profiling	++
Q4 What are links between dilution, advection and supply of terminal electron acceptors in spring, and emissions of climate forcing trace gases at ice-off?	As above, plus voltammetry along trajectory of current	++
Q5 To what extent are (sediment) respiration rates modified by heat from warmer gravity currents flowing from shallower regions?	OW-TCO, current meters, (automated) CO <sub>2</sub> monitoring	+
Q6 Does a benthic nepheloid layer develop during the winter in weakly stratified lakes?	Sediment traps. OW-TCO plus turbidity sensors	–
<b>1b Physics, ice quality - Biogeochemistry</b>		
Q7 How does cryoconcentration (salt exclusion) affect biogeochemical cycling at the ice-water interface?	OW-TCO arrays, chemistry/laboratory incubations	+
Q8 Does production of oxygen by photosynthesis under ice contribute significantly to breakdown of organic carbon and CH <sub>4</sub> prior to ice-out?	OW-TCO arrays. Stable isotopes of CH <sub>4</sub> , DOM. High resolution DO profiles	+
Q9 In humic lakes, how is light transmission in spring affected by changes in surface cover versus CDOM loading from snowmelt?	Sensors for snow depth and ice thickness. Pyranometers + fluorometers in the water	---
<b>2a Physics, hydrodynamics - Biology</b>		
Q10 What are the dominant metabolic pathways under ice (auto/hetero/mixotrophy)? How are speciation and distribution of organisms affected by hydrodynamics?	OW-TCO, fluorescence microscopy in winters with distinct hydrodynamics	+
Q11 How do under-ice flows contribute to seasonal shifts in trophic structure (classical food web/microbial loop)?	OW-TCO, stable isotope tracing and fatty acids	++
Q12 What are the relative contributions of decreasing light and temperature, lack of mixing, and zooplankton grazing in explaining the decline of phytoplankton in early winter?	Mesocosm experiments; Comparative limnology.	+
Q13 What is the quantitative relation between under-ice flow velocities and the vertical distribution (layering) of microbes, phyto- and zooplankton? Do flagellated phytoplankton diminish under RDC?	Phytoplankton; microscopy; flow cytometry. Flows: ADCP, OW-TCO plus irradiance	+
Q14 How do inflows from melting ice- and snowmelt contribute to the supply, relocation and/or flushing of microbes, phytoplankton, and higher organisms?	Spatiotemporally resolved community surveys in spring, distributed OW-TCO arrays	++
<b>2b Physics, ice quality - Biology</b>		
Q15 How does the quality of ice affect circulation patterns that influence biomass and functional trait composition of primary producers? What conditions allow for layered communities?	Phytoplankton surveys, OW-TCO plus PAR, ADCP, profiling with fluorometers	++
Q16 Do changes in light level directly affect higher species? (e.g., visual acuity in fish)	Light sensors, biotelemetry tagging of fish	–
<b>3 Biogeochemistry - Biology</b>		
Q17 Does anoxia constrain benthic activity by burrowers during winter and if so, does this limit diffusive transport of heat and solutes across the sediment-water interface to molecular rates?	Sensor-monitored sediment incubations with and without burrowers	++
Q18 Are algal blooms in spring enabled by nutrients, especially P, from (external) meltwater inputs or from the (internal) anoxic hypolimnion? If the latter, what are the pathways by which nutrients reach the photic zone?	OW-TCO plus PAR, stream discharge and loading, high resolution profiling of N and P. Nutrient stores in algae.	++
Q19 Does migration of zooplankton under ice contribute to the transfer of inorganic nutrients and organic matter from the chemocline to the surface (biological pump)?	Excretion experiments on vertically migrating zooplankton	++
Q20 How do oxygen levels through the winter affect the activity of benthic macroinvertebrates in the littoral zone?	Video footage (>10 min) paired with OW-TCO arrays	–

**Table 1**  
*Continued*

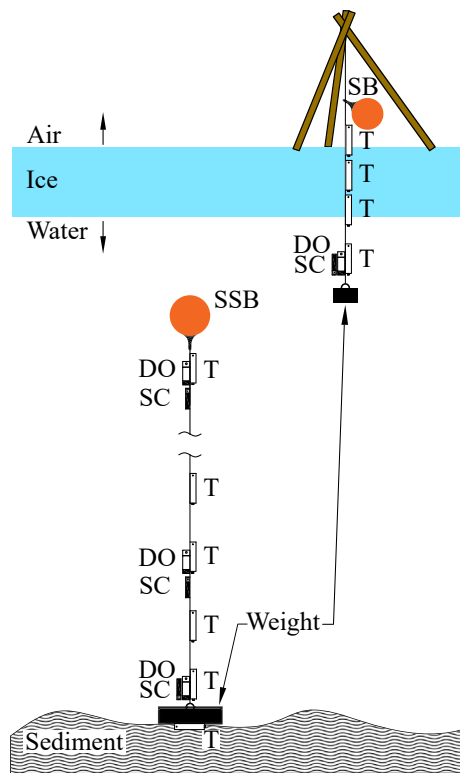
Research Questions	Method Recommendations	C
Q21 How does the extent of the hypoxic zone impact reliance on littoral habitats and prey for different species of fish and invertebrates?	High resolution OW-TCO + biotelemetry, scanning sonar	+
Q22 How do “classical,” including “benthic,” versus “detrital” energy pathways differentially support fish metabolism and biomass accrual during winter?	Stable isotopes, fatty acids and associated mixing models	+
<b>4a Temporal variability</b>		
Q23 Is interannual variability in lake biomass production in summer reflected in biogeochemical and physical states in winter?	Stable isotope tracing of C, multi-year OW-TCO	–
Q24 What are the main controls on retention of nutrients and DOM from snowmelt intrusions over the course of spring?	OW-TCO and profiling for same plus CDOM fluorescence.	++
Q25 Do reduced chemicals (e.g., P, CH <sub>4</sub> ) produced and accumulated over winter affect ecological functions under the ice and during the ice-free season?	OW-TCO, nutrients and CH <sub>4</sub> meas. Stable isotope tracing of N, P through trophic webs	+
Q26 How will (projected) changes in precipitation affect ice quality at geographic scales? How do these, in turn, modify the extent of RDC, both in the vertical and horizontal?	Remote sensing (e.g., MODIS) along a precipitation gradient. OW-TCO + PAR	+
Q27 How does year-round access to resources mediate winter behavior of zooplankton and fish? Do organisms in more productive lakes reduce foraging to save energy and reduce risks associated with movement in winter?	High-frequency spatial sampling (zooplankton), biotelemetry (fish)	+
Q28 How will shorter ice-cover seasons impact the duration and extent of anoxia? How will this change survival of benthic organisms?	DO + invertebrate surveys, respirometer experiments	--
Q29 Is the microbial loop important for sustaining zooplankton only when winter is long? What are the threshold conditions?	Stable isotopes, fatty acids from a range of lakes with different winter conditions	++
Q30 Will shorter ice-cover periods diminish charge-and-release phenomena, such as algal blooms and CH <sub>4</sub> emissions in spring?	Phytoplankton surveys and water sampling or eddy covariance in warm/cold years	+
<b>4b Spatial variability</b>		
Q31 What are the primary (climatic) factors that explain differences in abiotic-biotic interactions during winter in lakes at different latitudes and elevations?	Comparative limnology	++
Q32 In larger lakes, does spatial variability in ice quality and snow cover result in patchiness of under-ice processes (e.g., RDC, algal blooms)?	Remote sensing of snow cover distribution, OW_TCO and irradiance, ice core collection	–
Q33 How does lake size and the complexity of bathymetry influence the redistribution of heat, solutes and organisms by under-ice currents?	Multiple OW-TCO arrays, tracer studies	–

Many of the approaches will require time series of biogeochemical and physical variables under the ice via high resolution arrays, abbreviated as OW-TCO (over-winter temperature, conductivity and oxygen) (Figure 10) or acoustic doppler current profilers (ADCP). These methods are further detailed in Section 7.

## 7. Methods

Multi-disciplinary approaches, such as parallel winter measurement campaigns in the McMurdo Dry Valley lakes of Antarctica (Priscu, 1998) and in Lake Onego in Russia (Wüest et al., 2019) are invaluable and recommended. While there are methodological challenges associated with the ice-cover season (Block et al., 2018), below we describe well-tested approaches as well as new methods that are likely to lead to improved confluence of interdisciplinary observations.

Basic setups provide physical context to biogeochemical and biological observations. **Over-winter moorings** with **temperature, oxygen and conductivity loggers** can obtain continuous time series at multiple depths (Figure 10). Specific conductivity needs to be well-resolved in the vertical to quantify the density structure of the water column and the migration of the redox front. Multiple moorings - from the littoral zone to offshore - are recommended to study transport and circulation under the ice. **In-ice temperature, SC, and DO chains** can resolve the temporal and vertical variability of the ice-water boundary layer, assess ice thickness, and help trace incoming snowmelt and oxygenated waters (Figure 10). **Multi-parameter profilers** which measure conductivity, temperature and depth (CTD) (RBR, SeaBird, RINKO, YSI) provide a snapshot with greater vertical resolution than time series from anchored arrays and can be used to calibrate time series from moorings. Profilers may additionally obtain fluorescence, DOM, pH, turbidity, and



**Figure 10.** Sensor arrays for under-ice studies. The underwater mooring is deployed before ice-on and the in-ice profile is deployed once the ice can be safely walked on. Both include temperature (T), specific conductance (SC), and oxygen sensors (DO) (Cortés et al., 2017; Jansen et al., 2019). Sufficient SC sensors are required to accurately quantify density stratification given the considerable contribution of solutes to the small density gradients under ice (Kirillin et al., 2012; MacIntyre et al., 2018). Sensors for underwater irradiance or fluorescence could also be included. Thermistors embedded in dark plastic can be wrapped in reflective material to prevent direct solar heating of the sensor in clear ice. The depth of the subsurface buoy (SSB) is based on maximum expected ice-thickness, and the deepest sensor on the in-ice array should be shallower than the subsurface buoy to avoid tangling when ice becomes wind-driven near ice-off. The tripod shown here is only required when ice thickness rises over the winter. The surface buoy (SB) enables deployment throughout spring.

irradiance. Acoustic Doppler current profilers (ADCP) and point velocity measurements (ADV) can measure flows during part of the winter, although in mid-winter they may not be sufficiently sensitive. Turbulence can be measured with **microstructure profilers** (MacIntyre et al., 1999; Schwefel et al., 2017) but may be more successful if turbulence is greater in early to mid-winter and in spring when RDC begins.

Solutes and particles that cannot yet be accurately measured with self-contained sensors (particulate and dissolved nutrients, trace gases, alkalinity, chlorophyll-a, among others) can be quantified via laboratory analysis of water samples collected through the ice (Block et al., 2018) and sediment (porewater) samples obtained via grab sampling or membrane samplers (e.g., Hesslein, 1976). The low spatiotemporal resolution of manual sampling can make it difficult to establish linkages between biogeochemical state changes and hydrodynamics (“hot spots” and “hot moments”). However, **eddy covariance** stations on lake shores can capture rapid emissions of dissolved gases at ice-off (Jammet et al., 2015; Jansen et al., 2019). **Autonomous sensors for dissolved CH<sub>4</sub> and CO<sub>2</sub>** (e.g., Pro-Oceanus Mini CH<sub>4</sub>/CO<sub>2</sub> and Vaisala GMM220) will find applications in winter limnology. Recently, **voltammetric microelectrodes** have been applied to measure redox species in lacustrine benthic porewaters (e.g., Giles et al., 2016). Voltammetry offers the ability to identify and quantify multiple redox active species in a single scan and the ability to detect these substances in situ within the sediment matrix. Modern potentiostats are small and offer wireless communication. Long-term deployment of such electrodes enables monitoring of changes in redox speciation and establishing linkages with physical drivers. **OsmoSamplers** also provide continuous measurements of reduced species over winter (McIntosh Marcek et al., 2021). Sampling in littoral and pelagic zones as well as streams is essential to evaluate landscape interactions. A variety of water mass **tracers** (dye, specific conductance or fluorescence) can be used to track terrestrial inputs of (in)organic carbon and nutrients, as well as microorganisms.

Shifts in trophic interactions and increased reliance on prey sources that are ultimately supported by the classical food web or the microbial loop can be quantified via a combination of **dietary biomarkers** (stable isotopes, fatty acids) for zooplankton, (benthic) macroinvertebrates and fish. Dietary biomarkers can also quantify the potential for increased reliance on detrital energy sources during winter, which can include increased foraging on inshore or benthic prey by mobile predators like fish (Hayden et al., 2014). Connecting the abiotic environment (e.g., irradiance, T, DO) with responses in fish (e.g., changes in habitat use and movement rate) can be accomplished using a combination of sensors and biotelemetry technology. For example, **acoustic arrays** can be deployed year-round and help determine fish location and movement at high spatiotemporal resolution throughout the winter (Marsden et al., 2021). For phytoplankton, **fast-repetition rate fluorometry** can indicate adaptations to low light levels (Neale & Priscu, 1995). Large zooplankton and invertebrates can be identified on footage collected with a waterproof **digital camera** deployed under the ice (e.g., Supplementary Movie S1). Periodic collection of under ice footage would aid in the assessment of diversity and activity of these organisms associated with changes in the abiotic environment.

## 8. Summary

Advancing the emerging field of winter limnology requires an understanding of the links between hydrodynamics, biogeochemistry, and ecology. A rich literature exists illustrating hydrodynamic processes under the ice. This knowledge provides a basis for hypotheses about controls on the changes in biogeochemical

state and the dynamic response of organisms within the context of under ice flows. The knowledge gaps identified in this work illustrate dynamics that involve all three disciplines. However, these questions are based largely on a few key papers and require interdisciplinary studies at other sites to evaluate the larger scale effects of latitude, elevation, lake morphology and trophic state, as well as a shift in methodology from snapshots to high-resolution or continuous observations. Once confirmed and extended, these linkages allow predictions of energy and element flows through freshwater food webs with ongoing reductions in ice cover (Sharma et al., 2020), and further will provide the missing connection between ecosystem structure and function in the ice-cover and ice-free seasons. This understanding is essential for management and protection of lakes in future climates, and for advancing the overall science of limnology.

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### Data Availability Statement

Specific conductance measurements from lake N2 are available via the Arctic Data Center (<https://doi.org/10.18739/A2X54S>).

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