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### Special Section:

Winter limnology in a changing world

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### Key Points:

- Many lakes experience ice cover, yet there are no general frameworks for understanding responses to differing ice and snow conditions
- The Lake Ice Continuum Concept is a framework representing how lake ecosystems vary along a continuum of energy inputs mediated by winter
- We present a new approach for characterizing lakes within a landscape context and for testing our knowledge of changing winter climates

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## The Lake Ice Continuum Concept: Influence of Winter Conditions on Energy and Ecosystem Dynamics

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**Abstract** Millions of lakes worldwide are distributed at latitudes or elevations resulting in the formation of lake ice during winter. Lake ice affects the transfer of energy, heat, light, and material between lakes and their surroundings creating an environment dramatically different from open-water conditions. While this fundamental restructuring leads to distinct gradients in ions, dissolved gases, and nutrients throughout the water column, surprisingly little is known about the resulting effects on ecosystem processes and food webs, highlighting the lack of a general limnological framework that characterizes the structure and function of lakes under a gradient of ice cover. Drawing from the literature and three novel case studies, we present the Lake Ice Continuum Concept (LICC) as a model for understanding how key aspects of the physical, chemical, and ecological structure and function of lakes vary along a continuum of winter climate conditions mediated by ice and snow cover. We examine key differences in energy, redox, and ecological community structure and describe how they vary in response to shifts in physical mixing dynamics and light availability for lakes with ice and snow cover, lakes with clear ice alone, and lakes lacking winter ice altogether. Global change is driving ice covered lakes toward not only warmer annual average temperatures but also reduced, intermittent or no ice cover. The LICC highlights the wide range of responses of lakes to ongoing climate-driven changes in ice cover and serves as a reminder of the need to understand the role of winter in the annual aquatic cycle.

**Plain Language Summary** Millions of lakes worldwide freeze during winter. The formation of lake ice dramatically alters lakes by isolating them from their surrounding landscape and atmosphere. The thickness and optical qualities of ice and snow regulate the amount of solar radiation entering lakes, while shielding them from wind energy. Consequently, lake ice is an important factor regulating physical mixing dynamics within lakes, and structuring vertical thermal and chemical gradients. Although organisms from bacteria to fish have adapted to the winter environment, we lack a comprehensive understanding of how variation in lake ice cover conditions affects fundamental ecosystem processes or food web structure. Here, we combine a synthesis of the current literature with three novel case studies to develop the Lake Ice Continuum Concept as a framework for understanding how key aspects of the physical, chemical, and ecological structure and function of lakes vary along a continuum of energy inputs mediated by winter climate. This framework is useful for understanding changes associated with seasonal ice dynamics and for predicting how lakes may respond to climate change.

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## 1. Introduction

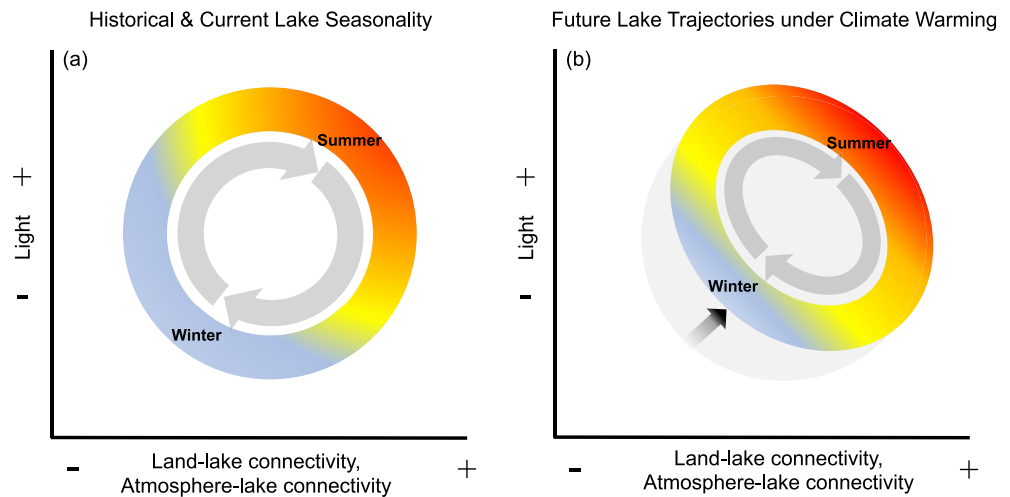
Lake ice has profound ecological and societal consequences (Denfeld et al., 2018; Knoll et al., 2019; Özkundakci et al., 2016; Sharma et al., 2019). There are an estimated 117 million lakes worldwide, most of which are located above 45° North (Verpoorter et al., 2014) and typically freeze over during winter. Although our understanding remains limited in comparison to studies conducted during ice-free seasons, numerous studies have documented the physical, chemical, and biological processes that occur under ice (e.g., Bižić-Ionescu et al., 2014; Denfeld et al., 2018; Hampton et al., 2017; McMeans et al., 2020; Powers, Labou, et al., 2017; Rue et al., 2019). Despite often being considered a period of relative quiescence, ecosystem functions during the winter are often dynamic (Bertilsson et al., 2013; Denfeld et al., 2018; Grosbois et al., 2017; Jansen et al., 2021). Moreover, there is growing evidence that winter conditions set the stage for those of summer, and vice versa (Hampton et al., 2017), and that lakes must be viewed across a full seasonal continuum (Salonen et al., 2009).

A comprehensive understanding of winter ecosystem structure and function must include the full range of interannual and long-term variation experienced by a lake. While some lakes experience little or no snow cover (Schindler & Smol, 2006) or interannual variability in snow cover, warmer winters are likely to cause increasing ablation of the snowpack and precipitation falling as rain rather than snow in the future (Dumanski et al., 2015; Fernandez et al., 2020; Sadro et al., 2018; Sickman et al., 2003). Many lakes with extended records of ice history show declines in ice duration over the last century (Benson et al., 2012; Magnuson, 2000), a trend that is expected to continue with climate warming (Caldwell, Chandra, Albright, et al., 2020; Filazzola et al., 2020). The number of lakes periodically experiencing an ice-free winter is expected to increase by hundreds of thousands depending upon the intensity of warming (Sharma et al., 2019). Climate warming is also impacting lakes in polar regions, where thinning margins of perennially ice covered lakes are creating new hotspots for littoral productivity (Bégin et al., 2021; Castendyk et al., 2016). Although changes in lake ice conditions appear to be accelerating (Imrit & Sharma, 2021) and may have a myriad of cascading effects (Preston et al., 2016), we lack a conceptual framework to understand and predict the effect of such changes on ecosystem structure and function.

Many of the effects of ice cover arise from the constraints it places on energy fluxes associated with transmission of solar radiation, mixing dynamics, and heat exchange. Depending on the lake and year, the duration of seasonal ice cover can range from as short as a few days to the entire year, and ice thickness from less than a centimeter to multiple meters. The formation of lake ice severs or mutes linkages with the landscape and atmosphere, creating an aquatic environment that strongly contrasts with open-water conditions. Viewed in terms of light inputs and connectivity to the atmosphere/landscape (Figure 1a), the response of ice-covered lakes to seasonal changes in light and energy inputs resemble hysteresis loops. Light and energetic inputs in the winter are low, increasing during spring and summer until lakes become ice-free, with the shape and lag of these trajectories modulated by ice cover dynamics. Changes in climate that reduce the duration of ice cover, cause intermittency, or result in its complete loss have the potential to dramatically alter winter light and thermal regimes within lakes; effects that can also carry over to subsequent seasons (Figure 1b). Consequently, developing a general framework is imperative for characterizing how the ecological structure and function of lakes may shift under future climate scenarios. Such a framework is equally important for understanding differences among lakes that span large gradients in winter ice dynamics. Drawing from a synthesis of the literature, we present a conceptual model (Figure 2) that explores these conditions as a continuum of lake ice duration and condition (e.g., thickness and snow depth), which regulate energy inputs and subsequent physical, chemical, and biological structure. In support, we offer winter case study examples from three lakes (Simoncouche, Mendota, and Stechlin; Boxes 1–3) to demonstrate key processes and patterns relevant to the conceptual model, exceptions thereto, and associated hypotheses in a changing world.

## 2. The Lake Ice Continuum Concept

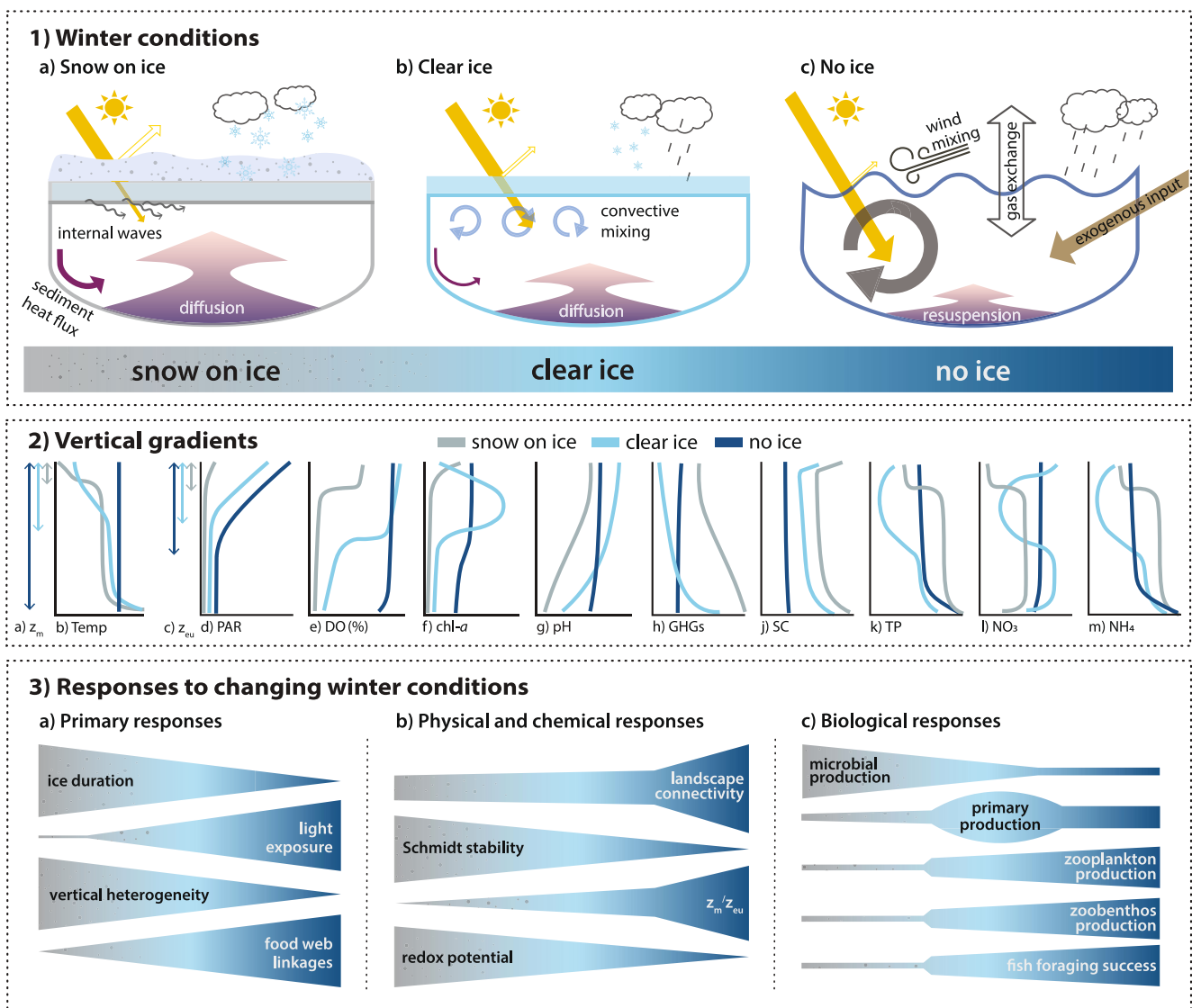
The Lake Ice Continuum Concept (LICC) provides a framework for understanding how lake ecosystems vary along a continuum of energy inputs mediated by winter climate, ice, and snow. The LICC is not intended to represent a continuum of successive states through which an individual lake will necessarily transition in association with changes in climate. In lakes that experience seasonally freezing conditions, the ice and snow regime a given



**Figure 1.** Hysteresis patterns of average annual light and connectivity conditions in a given lake under (a) Historical & Current Lake Seasonality and (b) Future Lake Trajectories under Climate Warming as lakes experience a loss of snow and ice cover with reductions in the duration of winter. The shifts in seasonality further alters the lake temperature regime, reducing the period of colder temperatures (blue) and prolonging warmer conditions (yellow-orange-red). Lake thermal regimes and the responses of individual lakes to climate warming will in part depend on factors such as lake depth, morphometry, and water clarity.

lake experiences will be regulated by a combination of large and small scale factors. Climate variability along latitudinal and elevational gradients interacts with local scale factors such as aspect, land cover, lake morphometry, and lake trophic state to drive the energetics affecting seasonal and interannual variability in ice and snow. These properties may also mediate the lake ecosystem response to changing winter conditions. Variation in ice thickness, ice structure or optical quality, depth of snow cover, and overall duration of ice cover together regulate exposure to wind, incoming solar radiation, and other atmospheric/landscape processes, and establish the dominant mixing regimes within lakes (Figure 2.1). The presence of ice and the climatic conditions that cause precipitation to fall as snow reduce the connectivity between lakes and their air- and watersheds (Figures 2.1a and 2.1b). Periods without winter ice cover have the potential for higher energetic fluxes through wind exposure, and higher or altered input rates of allochthonous material when precipitation falls as rain (Figure 2.1c). As a result of the increased connectivity to the atmosphere and landscape, lakes that lose ice cover will respond more directly to variation in winter or early spring weather patterns (Smits et al., 2020), leading to profound differences in the early spring lake condition.

By regulating energetic fluxes, lake ice determines the dominant physical mixing regimes within lakes (Lewis, 1983), influences time scales of mixing, controls the distribution of matter and energy throughout the water column, and establishes the template for biological structure and ecosystem function (Figure 2.2). Thus, the duration of ice cover also factors in the development and strength of redox and biogeochemical gradients in the water column. Differences in phytoplankton biomass and rates of primary productivity along the continuum of light availability in ice-covered lakes will drive differences in the oxycline and variation in redox potential with depth. Such vertical gradients will in turn affect biochemical reactions and, together with differences in rates of biological uptake, the distribution of nutrients (Figures 2.2 and 2.3b). Variation in some aspects of ecosystem structure along the LICC may be approximately linear, such as with water column stability or redox potential. Others may involve step changes, as with the change in mixing depth ( $z_m$ ) and euphotic depth ( $z_{eu}$ ) among lakes with or without ice (Figure 2.3b), or changes in secondary production fueled by increased phytoplankton biomass in lakes with clear ice compared to lakes with ice and snow (Figure 2.3c). Although heterotrophic microbial processes will continue across the entire lake ice continuum, there will be fundamental differences in microbial metabolism and community composition under aerobic versus anaerobic conditions, as a function of complex interactions among water temperature, organic substrate, nutrient, and light availability (Dillon et al., 2020; Tran et al., 2018; Vigneron et al., 2019). We predict that the importance of microbial production for sustaining food webs will be highest under conditions where ice and snow persist and decline with increasing energy inputs and mixing along the LICC (Figure 2.3c),



**Figure 2.** Lake Ice Continuum Concept: framework for understanding how conditions vary along a continuum of energy inputs mediated by winter climate, conditions mediated by ice, and snow in a representative mesotrophic temperate lake of moderate size and depth, with at least one annual full mixing. (1) We highlight how lake ecosystem dynamics change when winter ice cover is (a) snow-covered (dotted gray), (b) clear (light blue), or (c) absent (dark blue). Moving across a continuum of winter energetic constraints imposed by variation in ice and snow, lakes will experience increased inputs of energy and allochthonous material from the atmosphere and the surrounding landscape. Increasing energy inputs into the lakes will destabilize the water column (arrows and swirls) and affect the distribution of gases, particles, and heat. Also, light penetration will deepen as lake ice becomes clearer or completely disappears (yellow arrows). (2) Across the continuum, we show vertical shifts in the following variables: (a) mixing depth ( $z_m$ ), (b) temperature (Temp), (c) depth of the photic zone ( $z_{eu}$ ), (d) photosynthetically active radiation (PAR), (e) dissolved oxygen saturation (DO), (f) chlorophyll- $\alpha$  (chl- $\alpha$ ), (g) pH, (h) greenhouse gases (GHGs), (j) specific conductance (SC), (k) total phosphorus (TP), (l) nitrate ( $NO_3$ ), and (m) ammonium ( $NH_4$ ). (3) We show (a) primary, (b) physical and chemical, and (c) biological responses along the continuum of winter conditions. Increasing width of wedges suggests an increase in response variable and wedge color corresponds to the shift along the continuum of winter conditions.

but recognize other factors, such as increased lability of dissolved organic matter (DOM) from microbial or phytoplankton production, could mediate this general pattern. Likewise, we predict an increase in heterotrophic, chemolithotrophic, phagotrophic, or mixotrophic strategies among algae and microbes along a gradient of decreasing light (Özkundakci et al., 2016; Rautio et al., 2011). Among higher trophic levels, we expect increased light under clear ice or no ice conditions to benefit zooplankton, benthic organisms, and fish due to increased primary production and visual prey detection (Varpe et al., 2015). Higher rates of secondary production and foraging success are expected to increase the number and strength of trophic linkages within food webs (Figures 2.3a and 2.3c; Perga et al., 2020).

**Box 1: Responses to intra-annual variation in snow cover in Lake Simoncouche**

Lake Simoncouche (48°13'52"N 71°15'3"W) is a dimictic, mesotrophic lake in Québec (Canada) with a surface area of 0.83 km<sup>2</sup>, 8 m maximum depth, and 2.5 m mean depth. The lake is usually ice-covered from mid-November to early May, with ice thickness reaching up to 1.2 m in some years. Measurements of ice and snow coverage were collected manually during the winter of 2017-2018, with a nearly complete loss of snow in January caused by a rain-on-snow event. A sensor system installed at 1.4 m continuously measured temperature, specific conductance, and dissolved oxygen saturation. Data available from Rautio et al., 2021.

The variability in snow and ice thickness during winter caused shifts in photosynthetically active radiation (PAR), temperature, specific conductance (SC), and dissolved oxygen saturation (DO). The onset of ice cover in late-November attenuated PAR; however, greater reductions were linked to the presence of snow cover on ice. A snow thickness of less than 15 cm was enough to virtually block PAR transmission. In spring, PAR was not detectable until after the loss of snow, and then increased substantially after ice-off and as solar radiation increased in May. After ice-on, water temperature at 1.4 m was stable and appeared insensitive to variability in ice and snow conditions. In May, when ice began to melt, temperature initially dropped as cold meltwater mixed with lake water, but later increased responding to higher radiant heat flux. SC rose steadily throughout the winter, likely as a result of cryo-concentration under the increasing ice thickness and potentially diffusive processes, suggesting minimal mixing. In April, as the ice thickness decreased, meltwater diluted the ions, decreasing SC. When ice coverage began to disappear and the lake began to mix, SC increased again. Draw-down of DO that lasted until late April was possibly the result of respiration and decomposition of organic matter. In Lake Simoncouche, macrophytes cover more than 25% of the lake surface area; hence, they can be a major source of particulate and dissolved organic matter, fueling respiratory processes under ice. In late April, increasing PAR enhanced primary productivity, and together with lateral flows of oxygenated water, increased DO.

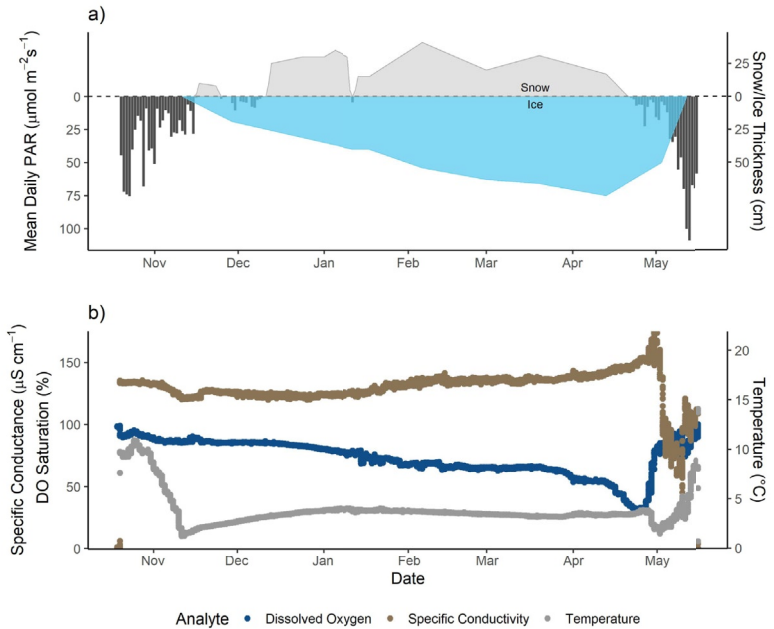


Fig. 1: Lake Simoncouche time-series data of (a) mean in-situ daily photosynthetically active radiation (PAR) values, biweekly snow (grey), and ice thickness (light blue) measurements, (b) high-frequency temperature (grey), specific conductance (brown), and dissolved oxygen saturation (blue) collected during the winter of 2017-2018.

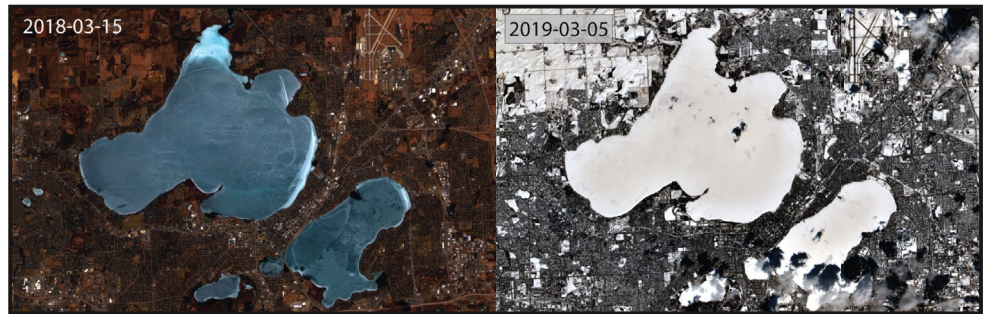
**3. Ecosystem Dynamics Along the Lake Ice Continuum**

To illustrate the LICC, we examine three possible winter conditions along the lake ice continuum, which differ in energetic constraints: (a) lake ice with snow cover (constraints to solar radiation penetration, wind-mixing and atmospheric/landscape exchanges), (b) clear ice with no snow (more solar radiation inputs, but constraints to wind-mixing and atmospheric/landscape exchanges), and (c) no ice (all constraints lifted, Figure 2). For each of these scenarios, we characterize the dominant physical processes and synthesize what is known about how differences in energetics affect chemical and biological dynamics. While our discussion is categorical, individual lake winter conditions along the continuum may vary intra- and inter-annually (Beall et al., 2015; Prowse & Stephenson, 1986). For example, ice can form and melt multiple times, snowfall can accumulate or be swept clear of lake ice by winds, ice quality can change throughout the winter, and the duration of snow-covered ice versus clear ice may vary among lakes and years—all affecting surface albedo and ecosystem energetics. Consequently, conditions of individual lakes will depend on where they fall along the continuum in ice cover and snow cover through time within any given winter, or through multiple winters across years (Beall et al., 2015; Bruesewitz et al., 2015).

The LICC may be applied to any lake that experiences annual to seasonal periods of ice-cover. Although we describe the LICC as it applies to a representative lake (i.e., mesotrophic lake of moderate size and depth that is ice-free for some period of the year, mixing at least once; Figure 2), individual lake responses to changing winter conditions may be further affected by lake-specific characteristics such as trophic state or morphometry. For example, lake trophic state or lake size may interact with the lake ice continuum to mediate energy fluxes into lakes, affecting sediment heat fluxes and mixing, differentially fueling pelagic or benthic production, and subsequently influencing biotic responses and the fate of winter production within lake food webs. For this reason, in addition to our discussion of these three scenarios along the lake ice continuum, we present case studies from lakes that vary in size and trophic state, and explore how they deviate from expectations based on the LICC framework. Such empirical tests will be an important aspect of evaluating the applicability of the concepts underlying the LICC and predicting how individual lakes may respond to climate change. Ultimately, we hope that this concep-



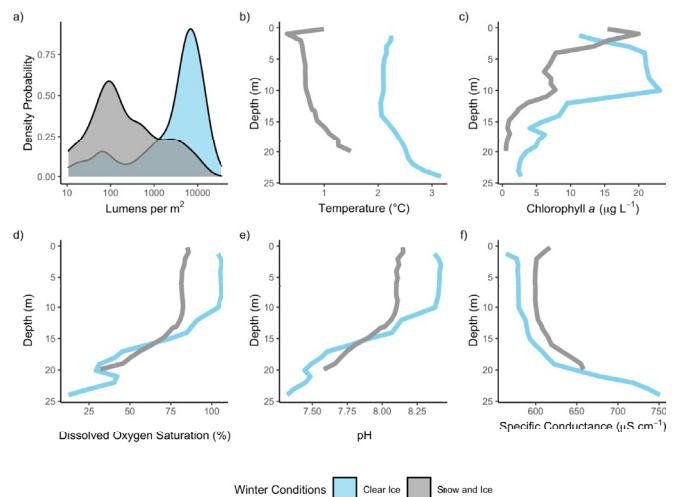
**Box 2: Responses to clear ice and ice with snow in Lake Mendota**



*Fig. 1: Satellite imagery of ice covered Lake Mendota, Wisconsin shows stark differences between the condition of ice cover on March 15th, 2018 when the lake ice was almost entirely snow-free and on March 5th, 2019 when a layer of snow covered the ice. Both images have been processed to true color composites using RGB bands. While the dates of imagery do not overlap with the dates of manual sampling, the conditions represented in the satellite images reflect the conditions during which the vertical profiles presented in Fig. 2 were taken. Sentinel-2 multispectral imagery obtained courtesy of the European Space Agency.*

Lake Mendota (43°06'24"N 89°25'29"W) is a dimictic, eutrophic lake in Madison, Wisconsin (USA) with a surface area of 39.6 km<sup>2</sup>, 25 m maximum depth, and 12.5 m mean depth. Lake ice coverage usually lasts from mid-December to early-April. Under-ice light intensity was collected from a moored buoy approximately 1 m below the lake surface during Feb 26-28 in 2018 and throughout the month of February in 2019. Vertical water column profiles were taken on February 26th, 2018 and February 22nd, 2019 with a YSI EXO multiprobe. Although the total duration of ice cover was similar between the two years, total snow accumulation differed—in 2019 it was 137 cm, compared to 79 cm in 2018, as measured at a meteorological station northeast of Madison. Data available from Dugan, 2021b.

The effect of snow on radiative inputs can have a cascading influence on the lake ecosystem. The absence of snow dramatically increased the intensity of light transmitted, leading to water temperatures that were warmer by ~2°C throughout the entire water column. Antecedent conditions are important in setting up under-ice conditions, and while the water column of Lake Mendota is typically isothermal near 0.5°C prior to ice-on in December or January (Yang et al. 2021), in 2018 it was <1°C warmer soon after ice formation compared to 2019. Overall chlorophyll-*a* concentration was higher under clear ice, and the chlorophyll peak occurred deeper in the water column, likely as a result of greater light penetration and radiative conductive mixing. This was associated with supersaturated oxygen conditions from the surface down to 10 m. The high DO saturation, along with higher pH under clear ice suggest that the increase in chlorophyll *a* led to higher primary production. In contrast, with snow on ice, chlorophyll-*a* maximum was right under the ice because of light-limitation and oxygen saturation was only about 75% in the upper 10 m. Specific conductance was generally lower with clear ice, reflecting potential differences in antecedent conditions.



*Fig. 2: Comparison of (a) light intensity at 1 m beneath the ice cover (lm.m<sup>-2</sup>), from Feb 26-28 2018 (clear ice, blue) and Feb 1-28, 2019 (snow-covered ice, gray), and under-ice water column profiles in Lake Mendota from Feb 26, 2018 (blue) and Feb 22, 2019 (gray) of (b) water temperature, (c) chlorophyll-*a*, (d) dissolved oxygen saturation, (e) pH, (f) specific conductance.*

tual model will be used to generate predictions and testable hypotheses to advance our understanding of winter limnology, and we encourage researchers to apply this framework across a spectrum of lakes.

**3.1. Lake Ice With Snow Cover**

When snow is present on ice, the lake environment has limited light availability and a stable water column. Snow on ice both increases albedo and limits transmission of solar radiation into the water column (Figure 2.1a). Mixing is limited to convective processes from sediment heat flux and minor turbulence at the surface due to internal waves from ice deformation by strain or wind stress. Inverse stratification persists (Figures 2.2b and 2.3b), with upward solute distribution by diffusion. Low light availability restricts the chlorophyll maximum to near the ice-water interface, further contributing to strong oxygen, redox, pH, and other biogeochemical gradients (Fig-

**Box 3: Cross-seasonal linkages in years with cold, ice-covered winter, and warmer winter with no ice cover in Lake Stechlin**

Lake Stechlin (53°09'20"N 13°01'52"E) is a deep, dimictic, oligo-mesotrophic, hardwater lake in the Baltic Lake District located in Northeast Germany. It has a surface area of 4.25 km<sup>2</sup>, 69.5 m maximum depth, and 23.3 m mean depth. Lake ice coverage usually lasts from January to March, but in recent years, warm winters have led to shorter ice cover duration and even ice-free conditions throughout the winter. To demonstrate the effect of warmer, ice-free winters on cross-seasonal linkages, we selected two sets of profiles representing winter (February) and spring (April) conditions in two years with differing winters. Profiles were taken in 2012, the last year on record with a cold winter and full ice cover on the lake (February 15 when ice thickness = 15 cm and April 12, when the lake was ice-free), and in 2020, when winter conditions were warm and the lake was ice-free (February 5 and April 8, with the lake ice-free on both dates). A YSI 6000 multiprobe was used for vertical profiling in 2012 and YSI EXO in 2020 (intercalibrations of the instruments were performed). Water samples for nutrient analyses were collected at discrete depths and water clarity was measured with a Secchi disk (through a hole in the ice when the lake was ice-covered). Euphotic depth ( $Z_{eu}$ ) was then approximated using the following equation:  $Z_{eu} = 3x Z_{secchi}$ , assuming that a thin layer of clear ice does not substantially reduce light penetration. Data are available from Berger et al., 2021.

During the cold winter with clear ice cover in 2012, the water column was inversely stratified and temperature was approximately 2°C cooler relative to the warmer winter with no ice cover in 2020. The cooler water temperatures in 2012 persisted into spring, likely as a result of the buffering effect of lake ice cover on spring warming. While Lake Stechlin was dimictic in the year with ice cover (2012), it switched to monomixis when ice cover was absent (2020). As a result of warmer air temperatures during an ice-free winter, the lake did not lose enough heat throughout the fall and winter to mix completely, and full mixing was delayed until March 2020. The incomplete mixing during the ice-free winter illustrates the importance of lake depth in mediating LICC predictions, with deeper lakes likely to remain stratified throughout the winter due to their greater thermal inertia, despite the increased exposure to wind. Incomplete mixing during the ice-free winter subsequently had important implications for the distribution of solutes throughout the water column, resulting in the persistence of a large anoxic region below a depth of 40 m. Sustained anoxia in the hypolimnion fostered and prolonged the period of phosphorus loading from the sediments, leading to higher TP concentration in the spring following the warmer winter without ice cover as well as lower pH and higher hypolimnetic specific conductance. Weak gradients in the upper water column reflected deepening of the mixed layer and erosion of remaining stratification during winter with no ice cover. For example, chlorophyll-*a* was uniformly distributed throughout the mixed layer in the absence of ice cover; however, oxygen subsaturation (~70%) suggests active mineralization of sinking, senescent organic matter. In contrast, during the cold winter when the lake was ice-covered, chlorophyll-*a* peaked at 1 m depth, corresponding to oxygen saturated conditions and indicating primary production just below the ice. While winter differences in oxygen saturation disappeared in the spring as the lake equilibrated with the atmosphere, chlorophyll-*a* remained higher (~3x) in spring following the cold winter with ice cover, possibly as a result of favorable light conditions in the upper water column after the onset of stratification ( $Z_{eu} = 20.1$  m in spring 2012). In contrast, water clarity was lower in spring following the warm winter without ice, shrinking the extent of the photic zone by more than 50% ( $Z_{eu} = 8.7$  m in spring 2020). In both years, these differences in water clarity carried over from winter to spring ( $Z_{eu} = 15.9$  m in 2012, and  $Z_{eu} = 10.5$  m in 2020). During the year with warmer winter, the formation of an extensive surface-layer bloom of cyanobacterium *Planktothrix rubescens* (S. A. Berger, pers. obs., Berger et al., 2021) likely contributed to the decreased water clarity, creating light-limiting conditions for the phytoplankton distributed throughout the water column. Moreover, increased connectivity to the landscape and winter precipitation that fell as rain may have led to higher inputs of allochthonous material, further reducing light availability during the warm year.

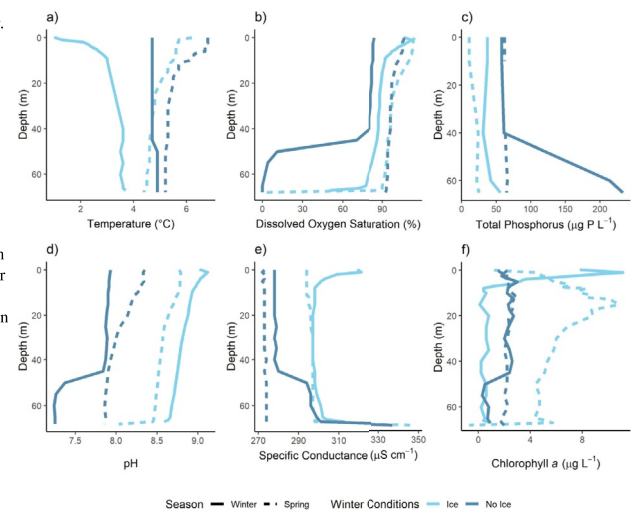


Fig. 1. Lake Stechlin winter (February, solid lines) and spring (April, dashed lines) profiles of (a) temperature, (b) dissolved oxygen saturation, (c) total phosphorus, (d) pH, (e) specific conductance, and (f) chlorophyll-*a* from two years with different winter conditions. In 2012 the lake had a 15 cm thick, snow-free ice cover (light blue solid line), and in 2020 the lake was ice-free (dark blue solid line).

ure 2.2). Rates of both primary and secondary production are low, and microbial activity is expected to dominate, including feedback through the microbial loop (Figure 2.3c). However, there remain open questions regarding the role of the basal food web in subsidizing higher trophic levels during winter and across seasons.

Snow on ice reduces transmission of solar radiation, contributing to a stable inverse stratification (Figure 2.2b). The extent to which ice and snow reduce solar radiation depends in large part on the thickness of the snow and, to a lesser extent, the quality of the ice. Snow can reduce the transmissivity of light into lakes by over an order of magnitude (Box 1). Albedo can reach 80%–90% with just 5 cm of snow depth (Jakkila et al., 2009), and attenuation of remaining light by snow leads to higher transmissivity in the low-energy 500–600 nm range (Leppäranta, 2015; Perovich, 2007). In areas with heavy snowfall, the weight of snow can push lake ice into surface waters where it freezes as a slushy snow-ice matrix, further decreasing light penetration (Leppäranta, 2015; Melack et al., 2020). Because radiatively driven convective mixing near the surface is low, the majority of heat flux would come from heat stored in the sediments (Figure 2.1a). Such sediment heat fluxes can reach up to 5 W m<sup>-2</sup> (Lik-

ens & Ragotzkie, 1965; Malm, 1998), and can initiate density currents that flow downslope to the deepest part of the lake or reach neutral buoyancy (MacIntyre et al., 2018; Mortimer & Mackereth, 1958). Downslope flows can establish central upwelling and circulation cells with rates up to  $10^{-5}$  mm s<sup>-1</sup> that persist until the sediment temperatures equilibrate with the water column (Kirillin et al., 2012). During the earlier phases of winter, sediment heat fluxes can be the main driver of mixing, depending upon lake depth and volume (Figure 2.1a; Jansen et al., 2021; MacIntyre et al., 2018).

Reduced light availability also depresses primary production and algal biomass, and respiration and decomposition are dominant (Figures 2.2f and 2.3c). In general, primary production is constrained to just below lake ice or shallow littoral zones (Marchand, 1987). However, depending upon light availability, chlorophyll-*a* maxima may not be immediately at the surface (e.g., Box 2). Considering that photosynthesis reaches saturation at lower irradiance at low temperatures, biochemical reactions may not be able to keep up with higher light intensity near the ice surface (Davison, 1991; Falkowski & Raven, 2007). While adaptations (e.g., increased concentration of enzymes, changing pigment composition and quantity) help phytoplankton cope with low-light and low-temperature conditions, we expect that snow-covered lakes will generally be net heterotrophic, as confirmed by oxygen depletion throughout the water column in many lakes (e.g., Brentrup et al., 2020; Catalan, 1992). The magnitude of heterotrophy is influenced by lake trophic status and catchment characteristics that regulate external carbon loads (Brentrup et al., 2020; Roiha et al., 2015). With primary production limited, the role of the microbial loop in transferring resources to higher trophic levels will be more prominent (Stockner & Porter, 1988). Mineralization may be an important process, particularly in smaller and more productive lakes where organic matter accumulates in the summer (Rabaey et al., 2021). However, there can be large differences in overwinter oxygen demand and extent of anoxia depending on water clarity and the relative contribution from pelagic and benthic production (Rabaey et al., 2021).

Together, stratification and limited oxygen production influence biogeochemical gradients. Snow covered lakes have strong gradients in dissolved oxygen (Figure 2.2e; Catalan, 1992), as well as vertical changes in pH (Figure 2.2g) and the concentrations and composition of DOM (Gonsior et al., 2013; Rue et al., 2019), greenhouse gases (GHGs; Figure 2.2h; Denfeld et al., 2018), nutrients, and other solutes (Figures 2.2j–2.2m; Cavaliere & Baulch, 2018, 2020; Joung et al., 2017; Rue et al., 2019). Oxygen consumption under ice is strongly influenced by transparency of the ice and snow (Granados et al., 2020), and these redox gradients facilitate microbial-driven redox reactions (Figure 2.3c), such as ammonification, nitrification (Cavaliere & Baulch, 2019; Powers, Baulch, et al., 2017), denitrification (Cavaliere & Baulch, 2018), sulfate reduction (Urban et al., 1994) and sulfide oxidation, organo-sulfogenesis (Rue et al., 2019), ferrotrophy, methanogenesis, and methanotrophy (Vigneron et al., 2019). Under-ice supersaturation of nitrogen gas and N<sub>2</sub>O, both the products of denitrification and anammox (anaerobic ammonium [NH<sub>4</sub>] oxidation), suggest that concentrations of N (both NO<sub>3</sub> and NH<sub>4</sub>) could be constrained by these microbial processes (Cavaliere & Baulch, 2018; Loeks-Johnson & Cotner, 2020). Low light and the persistence of stable stratification might together explain why phytoplankton communities are dominated by mixotrophic and motile forms under ice (Bertilsson et al., 2013; McKnight et al., 2000; Özkundakci et al., 2016; Pennak, 1968), which facilitates the acquisition of resources in a spatially or temporally heterogeneous environment. Mixotrophs can have a two-fold advantage in ice covered lakes—first, they are usually motile, hence, they can actively adjust their position within the water column and access to light, and second, they can supplement phototrophy with organic carbon sources (bacteria, DOM) under resource limitation (McKnight et al., 1993; Rue et al., 2019; Stoecker, 1998). By consuming and exuding organic material, heterotrophic organisms contribute to the internal loading of nutrient and carbon pools, subsidizing the under-ice food web (Fitch et al., 2018; Rue et al., 2019; Stockner & Porter, 1988; Thompson & Cotner, 2018, 2020).

Lower primary production under ice with snow cover has a range of implications for higher trophic levels. Zooplankton and zoobenthos have lower production rates at lower temperatures (Figure 2.3c; Shuter & Ing, 1997; Sutcliffe et al., 1981; Strayer, 2009), and may be supported primarily by mixotrophs (Perga et al., 2020) and microbial production (Bastviken et al., 2003). Zooplankton secondary or tertiary winter production peaks are restricted to early winter (Beaver et al., 2018; Grosbois et al., 2020). Most cladocerans and some copepods produce resting eggs and disappear from the water column, while other copepods are inactive through the winter and others stay active with the help of accumulated fat reserves (Schneider et al., 2017). Fat reserves can also be allocated to egg production in late winter immediately prior to the increasing light levels and the return of phytoplankton production (Schneider et al., 2017). The profundal zoobenthos has been shown to experience a mid-winter pro-



ductivity minimum (Dermott et al., 1977; Jónasson, 1975), which is attributed to reduced inputs of sedimenting pelagic production more than to low temperatures, since annual temperature variation in profundal sediments is usually low in stratified lakes. Since profundal organisms exhibit diverse feeding strategies, they are differentially affected by the reduced winter supply of sedimenting organic matter. Littoral zoobenthos show a larger seasonal drop in production compared to profundal zoobenthos, since they experience both a sharper reduction in temperature and a decrease in their food base due to suppression of benthic primary production (Jónasson, 1996).

Fish have a diversity of winter coping strategies to survive cold, dark, and limited prey conditions (Shuter et al., 2012). Winter-inactive fish experience dramatic energy savings from reduced swimming and foraging, and can survive winter with little to no feeding (Speers-Roesch et al., 2018). Winter-active fish possess the physiological capacity to sustain foraging when it is cold and dark (Blanchfield et al., 2009; Helland et al., 2011), although activity rates can decline in winter in some species (Watson et al., 2019). Variation in winter activity also exists among individuals of the same species (Auer et al., 2016). For example, smaller-bodied individuals are thought to be more susceptible to overwinter mortality (Byström et al., 2006; Hurst, 2007). The local environment also plays a role for fish activity and survival over winter. Widespread and persistent hypoxic and anoxic conditions in some snow and ice-covered lakes can result in a higher probability of fish-kills (Barica & Mathias, 1979; Greenbank, 1945). In other lakes, fish can behaviorally cope with and survive winter by moving to available habitats with more suitable temperature, oxygen, and light conditions (Blanchfield et al., 2009; Magnuson et al., 1985).

### 3.2. Clear Ice Cover With No Snow

Clear ice cover without any snow allows for increased transmittance of solar radiation in the water column. The extent of the differences between clear ice and snow + ice conditions will depend on the optical properties and thickness of the ice. Overall higher input of solar radiation under clear ice generates convective mixing, which leads to relatively deeper mixing and euphotic zones (Figures 2.1b, 2.2a, and 2.2c). These conditions allow for the formation of chlorophyll-*a* maxima in the euphotic zone (Figures 2.2f, 4 and 5), leading to higher primary production and phytoplankton biomass (Figure 2.3c). Higher resource availability will also stimulate secondary production (Figure 2.3c). While conditions in the upper water column will likely be oxygen-saturated, anoxia can develop in the bottom waters, exacerbating gradients of redox and solutes (Figure 2.2). Lakes that experience little or no snow may be expected to have either shorter or longer ice duration than lakes that remain snow-covered, depending on variation in ice-structure and thickness—a pattern that could be explored across climate gradients.

The absence of snow cover increases the transmittance of solar radiation to the water column (Figures 3 and 4), but the extent and intensity of the heat flux depends on the quality and thickness of the ice. Ice that has undergone freeze-thaw cycles, includes debris, snow, or gas bubbles will reflect or scatter more downwelling radiation and have lower transmission than clear, congelation ice, which can be extremely transparent to many wavelengths (Leppäranta, 2015; Warren, 2019). It is common for large lakes with long fetches to be snow free at many points during the winter due to blowing snow (Agbeti & Smon, 1995). Without the insulating effect of snow, ice thickness is more dependent on local climate forcing (Gould & Jeffries, 2005), potentially affecting light penetration. The overall lower albedo of ice compared to snow increases convective mixing through radiative gain (Figure 2.1b), decreasing water column stability with measured mixing rates of up to  $7 \text{ mm s}^{-1}$  (Bouffard et al., 2016; Kirillin et al., 2012).

Radiative inputs through clear ice allow for higher primary production than when there is snow on the ice (Figure 2.3c). The primary production peak will extend deeper (Figures 2.2f, 4, and 5) due to higher light intensity and convective mixing. Under clear-ice conditions, phytoplankton biomass may be comparable to or exceed summer concentrations (Paształeniec & Lenard, 2008; Twiss et al., 2012; Vörös et al., 2009). Compared to winters when lake ice is covered with snow, non-motile algae are often abundant under clear ice and massive blooms of large diatoms have been frequently reported from large lakes experiencing such conditions (Beall et al., 2015; Bondarenko et al., 2006; Kerfoot et al., 2010). Moreover, clear ice itself can be a productive habitat for algae and bacteria (Bondarenko et al., 2012). While radiatively driven convective mixing can help non-motile algae to remain in suspension and increase their access to deeper nutrients (Katz et al., 2015; Kelley, 1997), it can also compromise their access to light if the mixing depth is too deep (Diehl et al., 2002a, 2000b). Small phytoplankton taxa with traits such as motility and mixotrophy appear to be successful under clear ice or ice and snow (Butts & Carrick, 2017; Callieri et al., 2006; Özkundakci et al., 2016). Small cell size allows for efficient

resource uptake, fast growth, and minimizes sinking rates, but these species generally have low grazing resistance (Chisholm, 1992; Litchman & Klausmeier, 2008).

Differences between surface and deeper water biogeochemistry will be accentuated under clear ice compared to ice with snow. Greater primary production and convective mixing would result in higher dissolved oxygen in the upper water column (Yang et al., 2017, 2020), while the hypolimnion may be more oxygen-depleted (Figures 2.2e and 4), possibly as a result of sinking autochthonous carbon produced during the winter, in addition to legacy or refractory sources of organic matter. Accordingly, we expect that there would be strong differences in net metabolism between the surface and deep waters. However, in more shallow lakes where the photic zone could extend to the bottom, these gradients would likely shift toward the sediment-water interface. The more oxic environment found under clear ice will enhance nitrification—with  $\text{NH}_4$  oxidation being a substantial sink for oxygen where  $\text{NH}_4$  is abundant (Figure 2.2i; Cavaliere & Baulch, 2019; Massé et al., 2019; Powers, Baulch, et al., 2017). As a consequence of nitrification and phytoplankton uptake,  $\text{NH}_4$  concentrations may be lower within the euphotic zone (Figure 2.2m). Denitrifying bacteria may take advantage of accumulated organic matter and nitrate ( $\text{NO}_3$ ) (Cavaliere & Baulch, 2018; Palacin-Lizarbe et al., 2018). Increased nitrification rates and nitrate accumulation could also affect phytoplankton community structure. While some phytoplankton preferentially take up  $\text{NH}_4$ —competing with nitrifiers for that substrate—diatoms have preferential uptake of  $\text{NO}_3$  (Lomas & Glibert, 1999). Uptake and assimilation rates of  $\text{NO}_3$  are high at low temperatures (Glibert et al., 2016); therefore, diatom growth could be enhanced if light conditions are favorable.

Given the higher rates of biogenic oxygen production in clear ice lakes, mineralization of organic matter may be more rapid, affecting nutrient availability, DOM lability (Rue et al., 2019), and GHG production (Jansen et al., 2019) during the winter and into spring (Tönno et al., 2005). Subsequent mineralization of both settled particulate organic matter (POM) and DOM in bottom anoxic waters during winter may regenerate nutrient pools, as well as replenish reduced nitrogen species (Figure 2.2m) and phosphorus (Figure 2.2k; Cavaliere & Baulch, 2020; Rue et al., 2019). The flux of P to the upper water column is also influenced by redox conditions at the sediment-water interface (Nürnberg et al., 2013), so if the convectively mixed layer extends to lake sediments and keeps them oxygenated, sediment P fluxes may remain low (Markelov et al., 2019).

Phytoplankton productivity under clear ice may stimulate production at other trophic levels, even if the strong temperature dependence of zooplankton, zoobenthos and fish production keeps their overall growth rates low (Figure 2.3c; Bramm et al., 2009; Bertilsson et al., 2013; Sommer et al., 2012). For example, some copepods and, less commonly, cladocerans are abundant during winter and have reproductive strategies that enable them to rapidly respond to increasing phytoplankton production (Beaver et al., 2018). Active zooplankton grazing may enhance nutrient recycling, and also interact with phytoplankton by reducing their biomass, and changing their community structure, since taxa such as small diatoms and cryptomonads are preferentially grazed (Hryciuk & Stockwell, 2020). Senescent phytoplankton biomass can stimulate production of microbes (Bižić-Ionescu et al., 2014) and profundal zoobenthos (Jónasson, 1975). Fish that remain active during the winter may experience increased predation rates or foraging efficiency because of higher light levels (Fullerton et al., 2000; Garvey et al., 2004; Varpe et al., 2015). Ice without snow could therefore support greater fish biomass compared to ice with snow conditions. Overall, increased light leads to greater biomass at the base of the food web, but further research is needed to understand how temperature regulated metabolic rates or shifts in phytoplankton community structure might restrict biomass to be transferred to the higher trophic levels (Figure 2.3a; Vad et al., 2020).

### 3.3. Loss of Winter Lake Ice Cover

In ice-free winters (Figure 2.1c), lakes experience constant interaction with the atmosphere and potentially greater exogenous inputs from the landscape due to precipitation falling mainly as rain (Figure 2.3b). Under these conditions, most of the incoming solar radiation is transmitted and absorbed by the water column, increasing  $z_{\text{eu}}$  (Figures 2.1c and 2.2d), which could contribute to higher primary production. However, this increase could be offset by greater wind-driven mixing (Figure 2.1c), which may deepen the mixing zone ( $z_{\text{m}}$ , Figure 2.2a) and could limit light availability depending on  $z_{\text{m}}/z_{\text{eu}}$  (Figure 2.3b). The increased mixing would also lead to a more uniform distribution of gases, ions, and nutrients throughout the water column (Figures 2.2 and 2.3a). Understanding how the frequency of ice-free winters shifts with regional and global climate change represents an important future research goal.

The loss of winter ice cover has profound implications for lake ecosystems through exposure to the atmosphere and wind energy. In general, wind-driven turbulence is expected to lead to greater mixing (Figures 2.1c and 2.2a), and the consequences of this mixing for thermal regimes will depend on regional and local factors affecting the energy budget (Box 3; Woolway & Merchant, 2019). Shallower lakes may mix continuously, but in deeper lakes, full mixing of the water column may be either substantially delayed (Box 3), or lakes may not fully turnover as a result of insufficient winter cooling and/or high solute concentrations (Box 3; Woolway et al., 2020). If full turnover during winter is completely halted, redistribution of gases and nutrients will be limited, resulting in persistent anoxia in bottom waters and resource-limitation in the upper water column (Lau et al., 2020; Yankova et al., 2017). Mixing will reduce the strength of vertical physio-chemical gradients (Figure 2.3a) and increase the supply of dissolved oxygen to the bottom waters (Figure 2.2e). Coupled with higher lakewater temperatures (Figures 2.2b and 5; Flicker et al., 2017), higher oxygen availability may lead to reduced carbon burial efficiency, and enhanced mineralization rates of more readily degradable organic matter, potentially increasing refractive carbon pools (Gudas et al., 2010, 2015; Sobek et al., 2009). A well-mixed water column also has the potential to redistribute sediments through the water column, with implications for turbidity, nutrients, and trace metals (Evans, 1994). Enhanced resuspension of sediments could also affect community structure and quality of prey by lifting plankton resting cysts from the sediments, inoculating the water column (e.g., akinetes of cyanobacteria and zooplankton eggs; Cirés et al., 2013; Özkundakci et al., 2016). Loss of ice and increased exposure to the atmosphere could also contribute to increased evaporation, gas exchange, and atmospheric deposition (Arp et al., 2015; Xiao et al., 2018).

Increased connectivity of lakes with their watersheds during ice-free winters (Figure 2.1c) will likely result in a change in the timing and/or magnitude of exogenous inputs of carbon and nutrients. The amount and composition of the input will depend on the local climate, precipitation patterns, hydrology, watershed size, and the type of land cover surrounding the lakes (Casson et al., 2019; Solomon et al., 2015). Similar terrestrial loading may also occur in ice-covered lakes if soils do not freeze during the winter (Melack et al., 2020). We expect that delivery of terrestrial inputs into ice-free lakes during winter will be primarily mediated by the frequency of rain and freeze-thaw events. While there is a scarcity of evidence of lake responses to open-water winters, warmer winters with more frequent rain events are associated with higher riverine dissolved organic carbon and nutrient exports (Huntington et al., 2016; Rattan et al., 2017). Increased runoff and loading of sediments, dissolved nutrients, and organic matter during ice-free winters could alter redox potential (Jansen et al., 2019) and exacerbate increasing turbidity, nutrient enrichment and/or browning of lakes (Cade-Menun et al., 2013; Box 3). Thus, net lake metabolism in winter under open water conditions may be more strongly influenced by landscape features. While decreasing water clarity with associated effects for stratification patterns, lake metabolism, and food webs has been documented during the summer (Hayden et al., 2019; Leech et al., 2018; Staehr et al., 2010), how enhanced connectivity to the landscape during winter will affect lake responses requires further exploration.

It is tempting to conclude that lower albedo and increased radiative inputs (Figure 2.2d) in winter ice-free lakes would result in the highest rates of primary production along the LICC. However, increased mixing will likely reduce residence time of phytoplankton within the euphotic zone, leading to light limitation and lower photosynthetic activity (higher  $z_m/z_{eu}$ , Figures 2.2a, 2.2c, 2.3b, 2.3c, and 3; Diehl et al., 2002b; Vincent, 1983). Moreover, increased mixing might also result in higher turbidity (Beall et al., 2015), reducing light availability and depth of the photic zone (Box 3). In Lake Erie, a shift from near complete ice coverage to largely open-water winter conditions led to a >70% decline in mid-February chlorophyll-*a* (Beall et al., 2015). These stark differences in chlorophyll-*a* under differing winter conditions persisted into spring (Beall et al., 2015). Similarly, spring diatom production in Tiefer See, Germany, was low after winters with low ice cover and prolonged mixing periods (Kienel et al., 2017). During ice-free winters, the phytoplankton community may shift toward one dominated by non-motile forms capable of withstanding fluctuating light in the mixed water column (e.g., diatoms and some cyanobacteria; Litchman, 1998; Shatwell et al., 2008); however, the distribution of their biomass will depend on the frequency, intensity, and depth of the mixing (Box 3; Huisman et al., 1999). Consequently, lake metabolic balance will also depend on mixing dynamics and factors controlling the depth of the euphotic zone, such as lake morphometry, water clarity, and rates of watershed loading (Obrador et al., 2014; Olson et al., 2020; Kelly et al., 2018).

Secondary production of invertebrates is expected to increase during winter under ice-free conditions as a result of the relatively higher temperatures, especially in the upper water column, and resulting increased food availa-

bility (Figure 2.3c); while primary production may be lower compared to clear ice conditions, it will be higher relative to snow-covered winters (Figure 2.3c). Massive swarms of reproducing cladocerans have been observed at water temperatures below 10 °C in Lake Mead (Beaver et al., 2018). Similarly, cladocerans can be abundant in Lake Washington, which remains ice-free during winters, with water temperatures typically ranging between 6.7 and 9.4 °C (Hampton et al., 2006). This suggests that an increase in water temperature by even a few degrees could lead to substantial changes in zooplankton production. Profundal benthic organisms could also benefit from ice loss due to a combination of increased temperatures and increased supply of food to filter feeders and surface-dwelling detritivores by deeper mixing (Rowe et al., 2017; Vanderploeg et al., 2010). Similarly, littoral zoobenthos production will likely be stimulated by littoral primary production that is expected to increase in response to higher light availability. Although rates of fish foraging and production could increase (Figure 2.3c; Varpe et al., 2015), foraging success and fish survival may decline if visibility is reduced as a result of wind driven wave action and shoreline erosion, resuspension of sediments, or increased turbidity (Hedström et al., 2016). Warmer spring temperatures might inhibit successful foraging of cold-water fish in productive, littoral zones (Caldwell, Chandra, Feher, et al., 2020; Guzzo & Blanchfield, 2017; Guzzo et al., 2017; Jansen & Hesslein, 2004) and decrease juvenile abundance (Farmer et al., 2015). While these examples show responses to earlier spring warming, not the lack of ice per se, these studies stress the importance of considering how fish behavior and foraging success during winters with no ice carries over, affecting growth and reproduction in subsequent seasons.

Considering the substantial impact of ice cover on lake ecosystems, a shift toward year-round open-water conditions will affect habitat availability and likely alter the structure of biological communities. Differential responses among longer-lived organisms to cold, harsh conditions during winter contribute to stabilization of food webs and maintenance of diversity (Humphries et al., 2017; McMeans et al., 2015). For example, coexistence among fish with different thermal preferences is likely mediated by seasonal differences in habitat use, behavior, and fitness (Farmer et al., 2015; McMeans et al., 2020). Therefore, the loss of cold winters and resulting seasonal homogenization can affect population dynamics (e.g., lower winter mortality), resource use, and species interactions—having cascading effects on ecosystem function. Similarly, we could expect that homogenization of vertical gradients under full winter mixing may affect the structure of microbial communities taking advantage of spatial variability, for example in redox conditions (Figure 2.3a; Schütte et al., 2016). Finally, Timoshkin (2001) has called winter ice the “second bottom,” referring to the idea that ice creates a stable surface where growth can occur in the photic zone. Therefore, the disappearance of ice cover itself represents a loss of habitat for cold-adapted microorganisms living attached to (e.g., diatoms; Bondarenko et al., 2006), inside (e.g., bacteria; Santibáñez et al., 2019), or on top of the ice cover (e.g., flagellates and ciliates; Felip et al., 1999). Taken together, we expect that the loss of ice cover and cold conditions during winter will have consequences for coexistence of species and annual patterns of biodiversity.

#### 4. Implications of Declining Ice Duration

Our conceptual framework highlights the wide range of lake responses to ongoing climate-driven changes in winter lake ice cover. The shorter ice duration observed throughout the world has manifested as both later freeze and earlier ice breakup dates, strongly affected by temperatures in the months preceding these events (Magnuson, 2000; Shatwell et al., 2019). Such temporal connections serve as a reminder of the need to “close the loop” and understand the role of winter in the aquatic annual cycle (Salonen et al., 2009). For example, earlier ice-out will affect available light levels in the water, even though both day length and angle of incidence are lower earlier in the year (Preston et al., 2016), and autocorrelation of water temperatures means that warmer winter temperatures will often beget warmer spring temperatures (Box 3; Adrian et al., 1999; Caldwell, Chandra, Albright, et al., 2020). The accumulation, depletion or transformation of nutrient and carbon pools under ice (e.g., Cavaliere & Baulch, 2020; Powers, Labou, et al., 2017; Rue et al., 2019) will set the stage for early spring primary producers. For example, high concentrations of chlorophyll-*a* during winter were associated with low concentration of chlorophyll-*a* during the following summer, possibly due to the reduction of the pelagic nutrient pool as a result of higher winter productivity (North et al., 2014).

In years with shorter winters, the phenology of important events can be altered. For example, lakes that typically receive large influxes of spring melt water will likely receive that water, often rich in nutrients, earlier in the year (Sadro et al., 2018). Also, linkages to the landscape may persist for a longer portion of the year, delivering



allochthonous inputs (Haei et al., 2013) and potentially releasing GHGs (Denfeld et al., 2018) more consistently than as a pulse (Lake, 2000). The degree to which increased landscape connectivity influences lake processes both during winter and across seasons will depend upon lake (e.g., residence time), local (e.g., land use and watershed:lake area), and regional (e.g., climate) attributes. These interacting processes may also increase or buffer susceptibility of lakes to changes in trophic status, as well as the effects of eutrophication and humification on nutrient cycles and energy transfer efficiency of food webs therein (Karpowicz et al., 2020). However, the impact on biogeochemical processes and biological communities through the annual cycle (Missaghi et al., 2017; Orihel et al., 2017) will also largely depend on how shorter winters affect the duration and intensity of spring mixing given their connection with hypolimnetic temperatures and oxygen depletion (Dugan, 2021a; North et al., 2014).

As more lakes move toward ice-free winters, radical changes in ecosystem processes will undoubtedly be observed for many lakes (Figures 2 and 5). The complexity of nutrient influx, accumulation, and processing under changing winter conditions has uncertain implications for phytoplankton composition and biomass both under ice and at spring melt, as highly varied relationships of nutrients and ice duration have now been observed across systems. In turn, conditions that favor either high winter algal biomass or high spring algal biomass are expected to fuel zooplankton growth that can be transferred to fish and benthos, particularly under warming conditions. However, shifts in winter phenology may also result in mismatches among trophic levels (Thackeray et al., 2010; Weyhenmeyer et al., 2008) and systems susceptible to harmful algal blooms could experience further water quality problems associated with enhanced growth of cyanobacteria (Anneville et al., 2015; Ho & Michalak, 2019). “Winners” and “losers” will emerge across all trophic levels (Dornelas et al., 2019) given that annual patterns of biodiversity are, in part, maintained by the specialized niches created by contrasts between winter and summer (McMeans et al., 2020; Shatwell et al., 2008). Loss of winter habitat will reduce diversity and abundance of cold stenotherms or organisms otherwise specialized for growing under ice, such as those attached to ice (e.g., Bondarenko et al., 2006). This phenomenon is already evident among fish, such that major changes in winter duration would be expected to alter community composition throughout the year (McMeans et al., 2020; Shuter et al., 2016), with the potential for cascading ecological effects.

## 5. Conclusions

Global change is driving ice-covered lakes toward not only warmer annual average temperatures, but also reduced, intermittent or no winter ice cover. Concurrently, these lakes are experiencing shifts in the timing and intensity of precipitation, as well as the proportion arriving to lakes as rain or snow. For lakes that experience ice cover, it is well understood that ice duration, thickness, clarity, and snow cover together influence physical, chemical, and biological processes. The open questions concern the exact nature of these complex, interacting effects in any lake ecosystem and the repercussions of winter changes throughout the year. We expect seasonal linkages resulting from changing winter conditions to vary within individual lakes, affected by an assortment of factors including the timing and magnitude of inflowing melt waters, lake size and morphometry, and landscape variation from the continental to the local scale. At this stage in the development of winter limnology, we see an essential need to better articulate the elements of winter that appear generalizable enough to provide a useful research paradigm, both to advance fundamental knowledge and to anticipate future ecosystem changes. Accordingly, we propose the LICC as an organizing framework for future research. Conceptual frameworks have been vital for advancing our understanding of ecosystem processes and how they change across scales (Raymond et al., 2016; Seastedt et al., 2004; Vannote et al., 1980; Ward & Stanford, 1982). As such, the LICC contributes a new approach for characterizing lakes under a continuum of winter conditions that mediate energy fluxes into lakes in a landscape context, which can be used as a tool to test our knowledge of mechanistic linkages and ecosystem responses to globally changing winters. The pace of worldwide lake warming, decreasing ice duration, and altered precipitation patterns lends imperative to the establishment of this framework for addressing key questions in winter limnology and advancing discovery while ice still dominates the world's lakes.

## Data Availability Statement

Lake Mendota monitoring data and figure code are available in the Zenodo open-access data repository supported by the Conseil Européen pour la Recherche Nucléaire (<https://doi.org/10.5281/zenodo.4812868>). Lake Stechlin monitoring data, figure code, and photo are available from the Freshwater Research and Environmental Database

(FRED) operated by the Leibniz Institute of Freshwater Ecology and Inland Fisheries (<https://doi.org/10.18728/igb-fred-576.0>). The Lake Simoncouche data monitoring data are available from the Centre for Northern Studies data repository Nordicana D (<https://doi.org/10.5885/45717CE-5A9BFDF1C9064936>).

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