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Winter limnology in a changing world

The Changing Face of Winter: Lessons and Questions From the Laurentian Great Lakes

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Abstract Among its many impacts, climate warming is leading to increasing winter air temperatures, decreasing ice cover extent, and changing winter precipitation patterns over the Laurentian Great Lakes and their watershed. Understanding and predicting the consequences of these changes is impeded by a shortage of winter-period studies on most aspects of Great Lake limnology. In this review, we summarize what is known about the Great Lakes during their 3–6 months of winter and identify key open questions about the physics, chemistry, and biology of the Laurentian Great Lakes and other large, seasonally frozen lakes. Existing studies show that winter conditions have important effects on physical, biogeochemical, and biological processes, not only during winter but in subsequent seasons as well. Ice cover, the extent of which fluctuates dramatically among years and the five lakes, emerges as a key variable that controls many aspects of the functioning of the Great Lakes ecosystem. Studies on the properties and formation of Great Lakes ice, its effect on vertical and horizontal mixing, light conditions, and biota, along with winter measurements of fundamental state and rate parameters in the lakes and their watersheds are needed to close the winter knowledge gap. Overcoming the formidable logistical challenges of winter research on these large and dynamic ecosystems may require investment in new, specialized research infrastructure. Perhaps more importantly, it will demand broader recognition of the value of such work and collaboration between physicists, geochemists, and biologists working on the world's seasonally freezing lakes and seas.

Plain Language Summary The Laurentian Great Lakes are the world's largest freshwater ecosystem and provide diverse ecosystem services to millions of people. Affected by multiple interacting stressors, this system is the target of extensive restoration and management efforts that demand robust scientific knowledge. Winter limnology represents a key knowledge gap that limits understanding and prediction of the function of the Great Lakes and other large temperate lakes. Here, we summarize what is known about the Great Lakes during their 3–6 months of winter, identify key questions that must be addressed to improve understanding of the physical, chemical, and biological functioning of large lakes in winter, and suggest ways to address these questions. We show that ice cover is a "master variable" that

Key Points:

- Winter limnology is a key knowledge gap that limits understanding and management of the Great Lakes and other large, seasonally frozen lakes
- We review the winter physics, chemistry, and biology of the Great Lakes and identify priority questions for winter research on large lakes
- Ice cover is a "master variable" for many large lake limnological processes, making a better understanding of its role a research priority

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controls numerous aspects of large temperate lake ecology and that the effects of the ongoing reduction in ice cover extent and duration cannot be predicted without improved knowledge of winter limnology.

1. Introduction and Background

The five Laurentian Great Lakes (Superior, Michigan, Huron, Erie, and Ontario) comprise the largest freshwater ecosystem on the planet and provide valuable ecosystem services to millions of people in Canada and the US. A defining feature of the Great Lakes region is a long and sometimes harsh winter that can last for more than 1/3 of the year (see Box 1 for several Great Lakes-specific definitions of winter). Winter in the Great Lakes region is, however, rapidly changing. Over the past four decades, the Great Lakes suffered a significant decrease in the extent and duration of ice cover (Wang et al., 2018), and projections suggest that ice cover may become a rare occurrence by the end of the 21st century (Filazzola et al., 2020). In addition to changes to ice patterns, climate change has impacted the amounts, timing, and form of winter precipitation, soil freeze and thaw cycles, and the timing of the spring freshet (Baijnath-Rodino et al., 2018; Byun & Hamlet, 2018; Contosta et al., 2019).

Predicting the consequences of ice loss and other winter-period changes for the Great Lakes is difficult because of a large knowledge gap about their winter limnology. Few *in situ* Great Lakes studies have examined processes that occur during winter or the connections between winter and other seasons. Two reasons help explain the scarcity of winter research on the Great Lakes. The first is the logistical difficulty and danger of winter field work on the Great Lakes (Block et al., 2019; Bolsenga et al., 1988). Between November and March, gale force winds and unstable ice keep most of the relatively small Great Lakes research vessels (none of which have ice breaking capabilities) in port, and instrumented surface buoys on shore. In addition, the size of the Great Lakes and their unpredictable ice cover makes over-ice travel difficult beyond nearshore areas, further restricting access to the lakes. The second reason for the lack of Great Lakes winter research is the historical belief among many limnologists that little of importance happens in lakes during winter, which is thought to be mainly a time of dormancy and senescence (Hampton et al., 2015, 2017; Salonen et al., 2009).

Studies on the Great Lakes and other freshwater systems have begun to challenge the assumption that the winter ice cover period is characterized by negligible biological activity and that winter conditions have no bearing on subsequent seasons (e.g., Beall et al., 2016; Hampton et al., 2017; Katz et al., 2015; Powers et al., 2017; Reavie et al., 2016; Straškrábová et al., 2005; Twiss et al., 2012; Vanderploeg, Bolsenga, et al., 1992; Vanderploeg et al., 2010; Yang et al., 2020). The findings of these studies provide a strong impetus to improve understanding of the functioning of the Great Lakes during their 3–6-month period of winter. The rapid pace of change in winter conditions additionally motivates increased attention to winter limnology in the Great Lakes and other large temperate lakes. After all, how can we predict and manage the future of an ecosystem if we do not understand how it functions for significant portions of the year?

Box 1. What is "winter" on the Great Lakes?

Researchers working on small north temperate lakes often define "winter" as the period when lakes are ice-covered. Defining winter for the Great Lakes is more difficult. The five Great Lakes experience different ice cover extent, from 80% to 100% on Lake Erie to <50% on Lake Ontario (Figure 1). The Great Lakes also experience dramatic interannual fluctuations in ice cover extent. For example, the maximum areal ice cover on Lake Superior was 96% in the winter of 2014; in 2012 it was only 8% (Figure 2). This variability makes it difficult to identify a single definition of winter for the Great Lakes. We offer a few potential definitions of "winter" for the Great Lakes:

Calendar winter: in the Northern Hemisphere, the period between the winter solstice and spring equinox, or December 21 to March 20.

Meteorological winter: the period when long-term average daily air temperatures are below freezing. This period varies widely in different parts of the Great Lakes, from 79 days in Toledo, OH to 139 in Duluth, MN (1981–2010 data).

Ice cover period winter: the typical period when appreciable ice cover is present. This period typically extends from mid-December to early-May on the Great Lakes but varies widely among lakes and years.
Stratification winter: the period of inverse stratification which occurs when surface temperatures are below 4°C, the maximum density of freshwater. This period can last as long as 5–6 months on Lake Superior, but may not occur at all in Lakes Michigan and Ontario, which mix continuously through the winter during all but the coldest winters.
Logistical winter: the period when the lakes become difficult to access due to dangerous weather conditions, insurance rules or the presence of ice cover that presents a "hard stop" to most Great Lakes research vessels.
Ignorance winter: the cold-weather period for which the least limnological information is available. This period generally extends from November to April for all five Great Lakes and their connecting waters.

Of course, none of these definitions are fully comprehensive and all overlap in some respects. The choice of the definition should depend on the context and questions of interest, and this is how we use "winter" in this study.

The winter "blind spot" has recently been recognized as one of the most important knowledge gaps in understanding the functioning of seasonally frozen lakes, spurring increasing interest in winter limnology (Hampton et al., 2015; Powers & Hampton, 2016; Salonen et al., 2009; Sommer et al., 2012). However, much of this new work has focused on relatively small lakes. The large size, spatial heterogeneity in environmental conditions, intermittent ice cover, and sensitivity to winter conditions make the winter dynamics of the Great Lakes distinct in many ways from more intensively studied small lakes. We believe that studies from the Great Lakes and other large lakes are necessary to expand and bridge our knowledge of the winter behavior of lakes of diverse sizes and climatic settings as well as coastal marine environments.

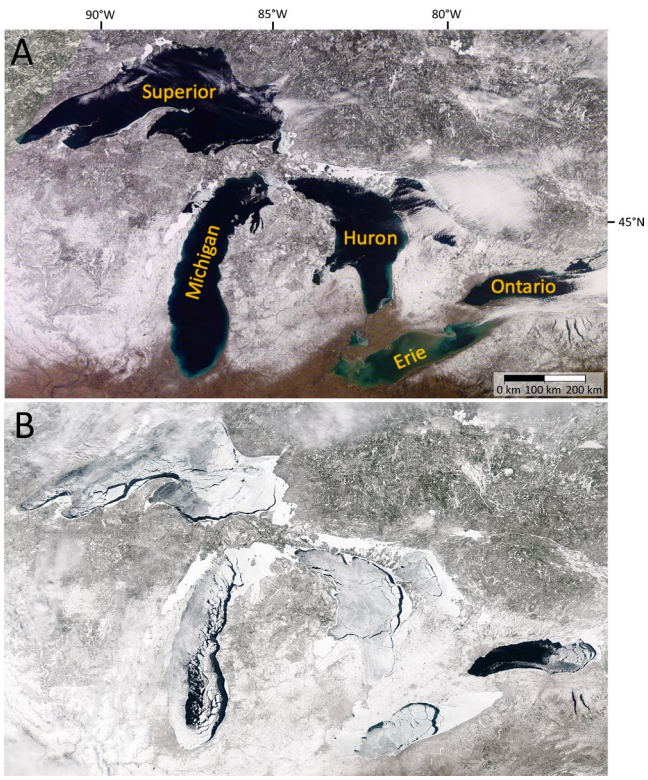

Figure 1. Maximum ice cover extent on the Great Lakes during a low ice year (2020, February 22; (a) and high ice year (2014, March 6; (b). Image credit: NOAA CoastWatch/OceanWatch.

In this review, we summarize the current state of knowledge on Great Lakes winter limnology, identify the most important knowledge gaps and associated questions, and suggest pathways to addressing these information gaps. This discussion is organized along three disciplinary topics: physics, biogeochemistry, and biology. We hope this contribution will stimulate more interest in large lake winter research in the limnological community and recognition of the urgent need for this work among members of the public, resource managers, and funding agencies. While we focus on the Laurentian Great Lakes, the lessons and questions we highlight here are of broad relevance to other northern large lakes (e.g., Baikal, Onega, Ladoga, Winnipeg, Peipus, Vänern, Constance, and many others), as well as to smaller lakes and coastal marine ecosystems such as the Baltic Sea, the Gulf of St. Lawrence, and Hudson Bay, among others.

2. Physics, Ice, and Water Movement

Physical processes set the stage for, and control, many aspects of the biogeochemistry and biology of large lakes (Tilzer, 1990). Vertical and horizontal mixing, the presence and properties of ice, and water temperature affect the distribution of matter and organisms, the underwater light environment, and temperature-dependent biological rates. Physical processes also have important socioeconomic implications, since water and ice motion can damage coastal infrastructure, impact shipping activity, transport pollutants, and affect regional weather patterns (Gronewold et al., 2013; Millerd, 2011; Wright et al., 2013). Thus, the study of full-year physical dynamics in lakes is crucial for understanding their annual biogeochemical and biological cycles and for predicting how ecosystem structure, functioning, and services will change in the future.

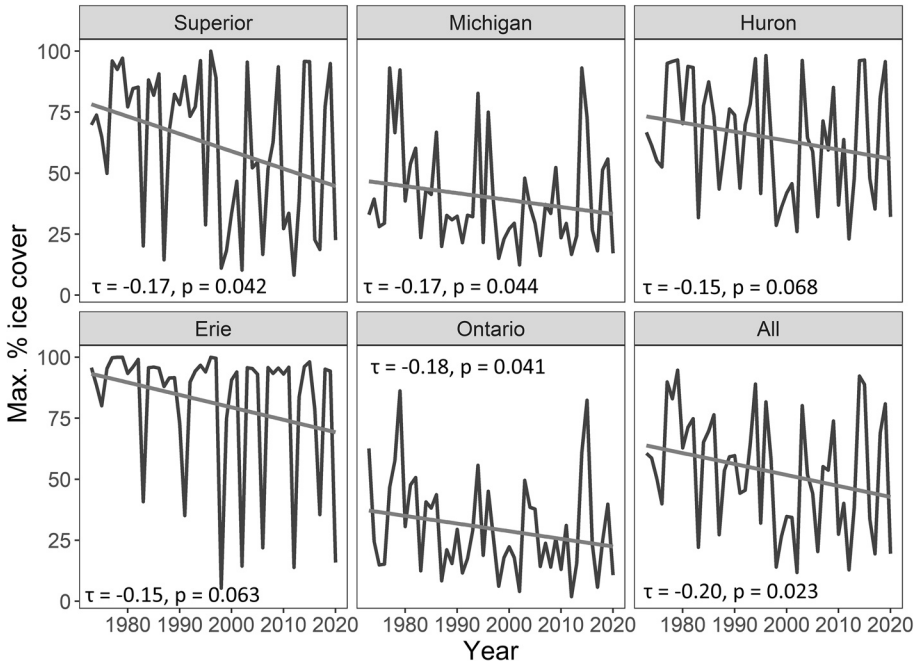

Figure 2. Annual maximum ice cover (AMIC) extent for individual Great Lakes and across all five lakes ("All") for the period between 1973 and 2020, with simple linear regression lines and tau and *p*-values for one-tailed Mann-Kendall trend tests. AMIC is defined as the maximum value of the daily ice extent over the entire ice season.

Knowledge of winter physical limnology in the Great Lakes is remarkably limited. This stands in contrast to the growing body of literature on the winter physical limnology of smaller lakes (e.g., Bengtsson, 2011; Bouffard & Wüest, 2019; Kirillin et al., 2012; Leppäranta, 2015; Yang et al., 2020). The Great Lakes, however, are not simply scaled-up versions of small lakes. By virtue of their size, the physical processes that are important in the Great Lakes are not necessarily those that dominate in smaller lakes. For instance, rotationally controlled processes such as Ekman transport and near-inertial oscillations play a more important role in the winter circulation of larger lakes (Austin, 2013; Bootsma, 2018; Choi et al., 2012). The large fetch of the Great Lakes causes large surface waves and vigorous surface mixing in the fall and winter, which results in a different pathway to ice formation than in smaller lakes and to reduced snow accumulation over the ice (Bolsenga & Vanderploeg, 1992). The large heat capacity of the deep Great Lakes results in water temperatures much higher than air in the fall and winter. The resulting convection in the atmospheric boundary layer enhances surface winds over water, evaporation and lake effect snow, and transfer of momentum to the water in the form of waves and currents (Croley, 1989). The size of the Great Lakes also results in larger spatial variation and complexity in meteorological forcing and resulting physical conditions than in smaller lakes. Below we review the state of knowledge on winter physical processes in the Great Lakes and identify key research questions that relate to ice and water-column physics.

2.1. Ice Cover Processes and Properties

Ice cover moderates the transfer of heat, light, wind energy, and gases between water and the atmosphere and is, therefore, a key variable in aquatic ecosystems (Post et al., 2013; Sharma et al., 2019). The regional climate, importance of teleconnections, and size of the Great Lakes results in large interannual and among-lake variations in ice cover duration and extent. A key finding from remote sensing studies (Assel, 2003, 2005; Bolsenga, 1992) is that the extent and duration of Great Lakes ice have been decreasing since the 1970s (Figure 2), with a possible regime shift to a lower-ice state in Lake Superior the late 1990s (Austin & Colman, 2007; Wang et al., 2012; Van Cleave et al., 2014).

Studies of relationships between ice cover extent and environmental conditions have shown that Great Lakes ice cover extent is sensitive to even small variations in air temperature and is affected by large-scale

climate teleconnections such as the North Atlantic and El Niño–Southern Oscillations, Pacific Decadal Oscillation, and Atlantic Multi-decadal Oscillation (Bai et al., 2012; Wang et al., 2018). These observations have been used to inform and ground-truth coupled ice-hydrodynamics models (e.g., Anderson et al., 2018; Croley & Assel, 1994; Fujisaki-Manome et al., 2020; Fujisaki et al., 2013), and to explore interactions between climatic forcing, ice cover and vertical and horizontal water circulation.

Despite progress in modeling ice cover extent, important questions about mechanisms of ice formation and ice dynamics remain. The formation of ice on large lakes is distinct from ice formation on smaller lakes and is not well understood (Fujisaki et al., 2012). On smaller lakes, ice formation typically occurs soon after most of the water mass reaches 4°C (the temperature of maximum density) and a thin layer of colder (near 0°C), lighter water forms above the dense 4°C water. In contrast, due to the large size and energetic fall/winter meteorological forcing of the Great Lakes, mixing can prevent the formation of ice cover until a much deeper upper layer of the water column is close to 0°C (Fujisaki et al., 2012; D. J. Titze & Austin, 2014). In addition, ice is not laterally monolithic on the Great Lakes. Ice formation is spatially and temporally variable (Figure 2) and likely a function of not just wind forcing but precipitation patterns and the thermal structure of the water column below (Fujisaki-Manome et al., 2020), factors that have been examined mostly through modeling rather than empirical approaches. Important questions also remain about ice—surface wave interactions. As in Arctic seas, surface waves in the Great Lakes play important roles in ice dynamics (Bai et al., 2020; Ruest et al., 2016), and questions about how surface waves affect ice formation, how ice cover attenuates wave energy and how waves break ice cover into smaller pieces, leading to increased melting, remain open.

Patterns of ice drift are also poorly characterized in the Great Lakes with few direct observations. Campbell et al. (1987) used four satellite-tracked on-ice buoys on Lake Erie during the winter of 1984 to measure drift speeds. More recently, Titze & Austin (2016) used an upward looking Acoustic Doppler Current Profiler (ADCP) to generate a time series of ice drift from Lake Superior during the cold winter of 2013–2014 and showed a strong relationship between the wind velocity and the ice drift velocity, as well as periodic locking up of the ice sheet (i.e., absence of ice movement in the presence of strong winds). Knowledge gaps concerning ice cover formation and its interactions with wave motion must be addressed to enable forecasting the long-term future of Great Lakes ice cover and its response to changing climate conditions.

Another important knowledge gap concerns the physical properties of Great Lakes ice, including its thickness and clarity. Measurements of ice thickness are important for modeling lake heat budgets, understanding ice-wave interactions, engineering shoreline infrastructure, and the Great Lakes shipping industry. The few papers that address Great Lakes ice thickness tend to focus on nearshore areas (e.g., Assel, 1976; Bolsenga et al., 1988; Gilbert, 1991; Sleator, 1995) rather than the open lake. Two recent studies of open lake ice thickness in Lake Erie (Hawley et al., 2018) and Lake Superior (Titze & Austin, 2016) have shown that ice thickness is highly heterogeneous in space, and that ice movement and ridging can result in the formation of ice keels over 10 m deep. Additional studies are needed to produce better estimates of offshore ice thickness and determine how Great Lakes ice thickness responds to climate variation.

Like ice thickness, the optical properties of Great Lakes ice have received minimal attention. Together with solar-driven convective mixing, the attenuation of light by ice and snow controls the availability of light to primary producers and hence their ability to support winter food webs (Katz et al., 2015; Kelley, 1997). In smaller lakes, snow accumulation over the ice often results in low transmittance of light to the water column below (Leppäranta, 2015; Pernica et al., 2017; Yang et al., 2020). Due to their large fetch, snow accumulation on Great Lakes ice is usually less than on smaller lakes, and snow tends to get blown into windrows, creating patches of clear and snow-covered ice. Bolsenga and Vanderploeg (1992) and Vanderploeg, Bolsenga, et al. (1992) presented some of the only published estimates of light transmission through Great Lakes ice and showed that almost half of the light reaching the ice surface can be transmitted to the water below. The optical properties of Great Lakes ice and their spatial and temporal variation must be much better characterized to understand how ice cover and its characteristics affect light availability and light-dependent processes, such as primary production and photochemical reactions.

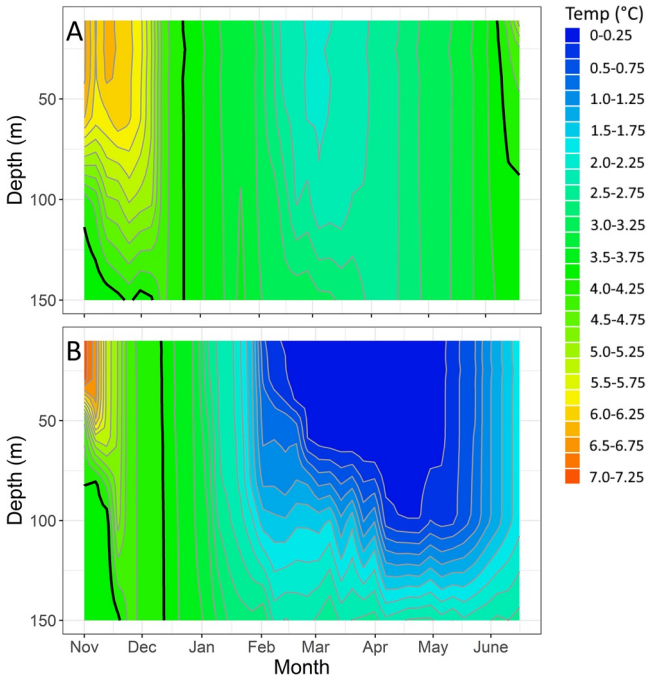

Figure 3. Winter thermal structure in eastern Lake Superior in a warm winter (2009–2010, 27.3% maximum areal ice cover; (a) and cold winter (2013–2014, 95.8% maximum areal ice cover ice cover; (b) Black contour represents 4°C (temperature of maximum density).

We identify four broad questions regarding Great Lakes ice which must be addressed to enable a predictive understanding of ecosystem dynamics, local and regional weather patterns, as well as transportation and infrastructure safety:

Q1.1: How do atmospheric and climatic conditions influence Great Lakes ice cover on interannual and decadal time scales?

Q1.2: How does ice cover attenuate surface waves and in return how do waves mechanically break ice cover, leading to thermal melting?

Q1.3: How thick is Great Lakes ice, what factors govern ice thickness, and what role do ice ridges and keels play in water column mixing and disturbance of benthic habitats?

Q1.4: How much light is transmitted through Great Lakes ice and snow cover and what factors control the optical properties of Great Lakes ice?

2.2. Thermal Structure and Circulation

Vertical and horizontal mixing of water masses critically affects the function of aquatic ecosystems, controlling the distribution of nutrients, oxygen, and organisms. In freshwaters, vertical and horizontal mixing is strongly affected by thermally driven density gradients and wind forcing. Thus, seasonal changes in air temperature and wind patterns lead to large variations in water movements and density stratification. In the Great Lakes, thermal structure and circulation of the water column are often considered together and are addressed in two principal ways: *in situ* observations and numerical modeling. Numerical models which are configured to run over an interannual time span simulate water column winter thermal structure and circulation and are relatively common in the Great Lakes literature (e.g., Anderson et al., 2018; Bai et al., 2020; Beletsky & Schwab, 2001; Beletsky et al., 2012;Fujisaki-Manome et al., 2020). *In situ* observations of wintertime horizontal and vertical water movement on the Great Lakes are much more limited, resulting in difficulties in model calibration and validation.

Year-round, depth-resolved temperature observations are available only for Lake Michigan and Lake Superior. An NOAA buoy in south-central Lake Michigan provides a continuous temperature record from 1990 (Anderson et al., 2021; GLERL, 2019), making it the longest time series of full-year thermal structure in the Great Lakes. Moorings in Lake Superior (Austin, 2013; Titze & Austin 2014) provide information on thermal structure and circulation at several locations starting in 2005. The other Great Lakes have no continuous long-term observations of wintertime thermal structure, making it a high-priority information gap. Results from observations in Lake Michigan and Lake Superior show that winter-period stratification patterns are highly sensitive to winter air temperatures and ice cover conditions (Anderson et al., 2021). In Lake Superior, cold, high-ice winters are associated with strong inverse stratification that lasts well into spring; stratification is much weaker in warm winters, resulting in deeper mixing of the water column and earlier warming in spring (Figure 3). The ongoing increase in winter air temperatures and decrease in ice cover extent may be leading a large-scale restructuring of the mixing regime of the Great Lakes, with a transition from a dimictic mixing pattern (with inverse stratification in winter and mixing during spring and fall) to a warm monomictic pattern (with continuous deep mixing from fall to spring). The scarcity of wintertime temperature observations makes it difficult to determine whether such a shift is occurring or to forecast when a shift might occur. Because mixing depth and stratification critically affect the light climate for planktonic primary producers (Kelley, 1997; Rowe et al., 2017), improved characterization of winter-period vertical mixing (along with measurements of light levels in ice-covered and ice-free regions) is vital for modeling winter-period productivity and its response to changes in winter climate.

Winter period horizontal water movement is also poorly studied. Understanding of winter currents is based on a handful of observational studies (e.g., Austin, 2013; Beletsky et al., 1999; Beletsky & Schwab, 2001; Bennington et al., 2010; Pickett, 1980; Saylor & Miller, 1983). Many of these studies represent "snapshots" of winter circulation rather than "mean" circulation patterns and have a low spatial resolution (Beletsky et al., 1999; Bennington et al., 2010). Despite their limitations, results of these studies reveal that, due to stronger winter winds, year-round horizontal circulation is dominated by winter-period processes (Beletsky et al., 1999; Rao & Schwab, 2007). Because vertical stratification is weaker or nonexistent in winter, wind-driven horizontal currents penetrate deeper into the water column than in summer, moving larger quantities of water. Horizontal winter currents have been shown to redistribute large quantities of sediment, nutrients, and pollutants between nearshore and offshore areas (Eadie et al., 1996). Given the importance of winter currents in moving solutes and particles, additional observations are sorely needed to better characterize current patterns and how climatic and meteorological factors, including ice presence, influence winter lake currents (Fujisaki et al., 2012).

Thermal structure and water movement affect the heat balance of the Great Lakes, the light environment, and the distribution of solutes, particles, and organisms. We identify four priority questions about winter water movement and vertical mixing in the Great Lakes:

Q1.5: What are the processes that determine the development of thermal structure and stratification through the full annual cycle?

Q1.6: What are the long-term trends for thermal structure in the five lakes and what governs interannual variability in stratification patterns? Will the Great Lakes transition to a different mixing regime (e.g., dimictic to monomictic) as the climate continues to warm?

Q1.7: How does vertical mixing interact with ice conditions to affect the underwater light environment and distribution of material and organisms?

Q1.8: What are the main horizontal circulation patterns during winter, and how do winter climate and weather affect the horizontal movement of water and material in the Great Lakes?

3. Winter Biogeochemistry

The concentrations and cycling of carbon (C), nitrogen (N), phosphorus (P), and silica (Si), along with some ions and metals (e.g., iron [Fe], manganese [Mn], mercury [Hg]), have important implications for lake ecosystem function. Nutrient availability determines rates of pelagic and benthic primary productivity and supports lake food webs, including fisheries. On the other hand, excess nutrients can cause harmful algal blooms, degradation of water quality, and increased sediment oxygen demand (Katsev, 2017; Miller et al., 2017; Orihel et al., 2017; Small et al., 2014). Biogeochemical processes also affect the role of freshwater ecosystems in the global C cycle, including C burial and emissions of greenhouse gases such as carbon dioxide and methane (Cole et al., 2007; Fernandez et al., 2020; Townsend-Small et al., 2016).

To better predict the consequences of environmental change on the Great Lakes, a thorough understanding of the sources, distribution, and transformations of biologically important elements is needed. In smaller temperate lakes, the physical conditions of winter–low temperatures, ice cover, inverse stratification, and reduced solar radiation–have been shown to affect rates of chemical reactions and biological activity, resulting in large differences between winter-time biogeochemical processes and the rest of the year (Cavaliere & Baulch, 2018; Greenbank, 1945; MacIntyre et al., 2018; Powers et al., 2017). The Great Lakes have distinct (and more temporally and spatially variable) winter conditions compared to better studied small temperate lakes, which can lead to important differences in their winter biogeochemistry. Unfortunately, too few studies have been conducted in the Great Lakes to form a synoptic view of their winter biogeochemistry or enable comparisons of their behavior to that of smaller lakes. Below we review the existing information on winter biogeochemistry in the Great Lakes and identify key open questions relating to concentrations and transformations of elements and temporal and spatial linkages of biogeochemical cycles in the Great Lakes ecosystem.

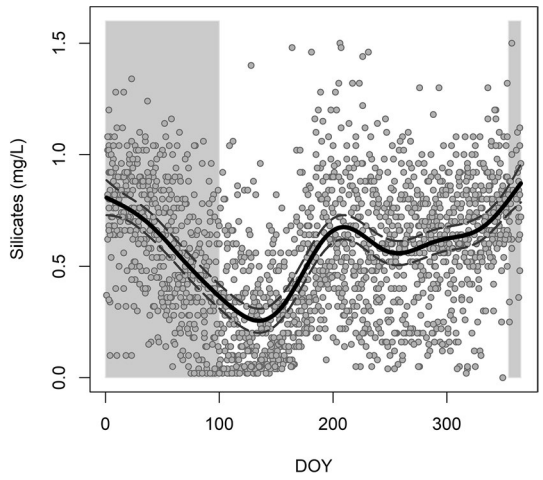

Figure 4. Seasonality of dissolved silicates in samples collected from the Union Water Treatment Plant on Lake Erie versus day of the year (DOY) for the period 1976–2013. The typical ice cover period is shown as a light gray polygon. The solid black line shows a generalized additive mixed effects model fit, with DOY as a fixed factor and year as a random factor; dashed lines represent the 95% CI ($F_{8.45} = 83.2$, $R^2_{adj} = 0.24$, $p < 0.0001$). These data are part of the Ontario Lake Water Quality at Drinking Water Intakes program, which reports biweekly water quality data from 18 drinking water intake treatment plants along the Ontario shore of lakes Superior, Huron, Erie, and Ontario (Ontario Open Data Team, 2020). These data are the most comprehensive record of winter-period water quality in the Great Lakes but are representative only of nearshore conditions.

3.1. Concentrations and Transformations

As with other Great Lakes winter data, most available information on C, nutrients, and other elements in the winter are from lakes Erie and Michigan, with some additional data from drinking water treatment facilities along the Canadian shorelines of lakes Erie, Ontario, Huron, and Superior (Winter et al., 2015). Ontario's Lake Water Quality at Drinking Water Intakes program provides a long-term (starting in 1964 at some locations) and temporally resolved (bi-weekly sampling throughout the year) record of nutrients and phytoplankton (Ontario Open Data Team, 2020). However, these data are representative of only nearshore conditions, leaving a large knowledge gap about biogeochemical dynamics offshore. From the limited existing data, we can infer that concentrations of nutrients are dynamic during winter and are affected by various biotic and abiotic processes.

In Lake Erie, internal and external loading, and uptake by phytoplankton leads to winter-period spatial and temporal variation in phosphorus concentrations (Burns et al., 1978). Prater et al., (2017) found that particulate C:P ratios in the lake were lower in fall and winter than in spring and summer, possibly due to increased assimilation of P relative to C into phytoplankton biomass under low light winter conditions. Dissolved Si concentrations in Lake Erie also decrease during winter due to rapid uptake by growing diatoms, and Si concentrations are typically at their annual minimum in late winter and early spring (Beall et al., 2016; Burns et al., 1978; Hartig & Wallen, 1984; Twiss et al., 2012; Figure 4). Ice cover extent has been shown to play an important role in the winter biogeochemistry of Si in Lake Erie. Higher ice cover promotes the growth of large diatoms, while ice-free conditions favor the production of smaller phytoplankton (Beall et al., 2016), which are not associated with large winter-time nutrient drawdowns.

Ice cover extent affects concentrations of important elements in other ways. Winter storms cause large nearshore resuspension events in lakes Michigan, Huron, and Superior (Biddanda & Cotner, 2002; Cotner et al., 2000; Eadie et al., 1990; Eadie et al., 2008). Ice cover has been shown to reduce resuspension, with a strong inverse relationship between ice cover extent and resuspension (Eadie et al., 2008; Nicholls, 1998; Scavia et al., 2019). While sediment resuspension is limited to nearshore areas in the deeper Great Lakes, strong winds can resuspend sediment throughout the shallow central and western basins of Lake Erie (Valipour et al., 2017), potentially resulting in lake-scale effects of ice cover reductions. Winter sediment plumes contain elevated concentrations of particulate and dissolved P, N, and C compared to nonplume water (Cotner et al., 2000; Vanderploeg et al., 2007). The increased nutrients and turbidity associated with these resuspension events impact water column primary and microbial production, biomass, and taxonomic composition (Millie et al., 2002, 2003). Winter resuspension events also deliver sediment to the profundal regions of the Great Lakes, with much higher sediment fluxes in winter than during the summer stratified season (Eadie et al., 1990; Eadie et al., 2008). The significance of winter storm resuspension events for biogeochemical cycling, productivity, and movement of material in the Great Lakes is still unclear (Vanderploeg et al., 2007), making it difficult to predict the consequences of reduced ice cover and the resultant increased frequency of winter resuspension events.

To our knowledge, there are no studies that document winter water column elemental uptake, transformation, and processing rates in the Great Lakes. The exception is measurements of primary and bacterial production (Beall et al., 2016; Cotner et al., 2000; Depew et al., 2006; Fahnenstiel & Carrick, 1992; Glooschenko et al., 1974; Wilhelm et al., 2014). Average rates of biological activity are generally lower in winter than in summer for most lakes (Hampton et al., 2017); nonetheless, significant productivity and associated nutrient turnover can occur in the Great Lakes in winter, which has important implications for the food web (see biology section below). Unfortunately, the paucity of observations makes it difficult to constrain the rates of

these transformations and model how they will change in response to changing winter conditions including water temperatures, vertical and horizontal mixing, and ice cover.

Winter nutrient cycling in sediments has received even less attention than water column processes. Sediments in the Great Lakes are an important biogeochemical reactor and, depending on water column conditions, can serve as either long-term sinks or sources for C, N, and P (Katsev & Crowe, 2015; Matisoff et al., 2016). In a rare study of Great Lakes winter sediment biogeochemistry, Doan et al., (2018) examined the seasonality of sediment dissolved P efflux rates in Lake Ontario's eutrophic Bay of Quinte. P efflux was about 50% lower during winter than summer but still contributed significantly to total annual internal P loading. Open-water season studies of Lake Superior sediments revealed significant seasonal variation in sediment processes, with some of the lowest sediment oxygen penetration and highest rates of N and P efflux into the water occurring in early spring (Li et al., 2012, 2018; Li & Katsev, 2014). These results suggest that sediment biogeochemistry is seasonally dynamic and that winter-period sediment processes may make important contributions to annual elemental dynamics, as has been demonstrated in smaller lake systems (Orihel et al., 2017).

Water column and sediment geochemical processes do not occur in isolation and are coupled through time. One hypothesized example of seasonal carry-over between winter and summer water column and sediment processes concerns seasonal hypoxia in Lake Erie. Winter blooms of diatoms in high ice years have high sedimentation rates, resulting in efficient export of organic matter to the sediments (Wilhelm et al., 2014). This organic matter may play an important role in the summer geochemistry of Lake Erie by driving hypolimnetic microbial respiration, hypolimnetic hypoxia, internal P loading, and redox-sensitive N transformations (Reavie et al., 2016; Wilhelm et al., 2014). Seasonally resolved measurements of sediment characteristics and carbon and nutrient flux between the water column and sediment are necessary to begin integrating these processes into full-year models and to determine how changing winter conditions will affect the geochemistry of the Great Lakes.

We propose four key questions that need to be addressed to advance understanding of biogeochemical cycles and their effects on biological productivity and water quality in the Great Lakes.

Q2.1: How do concentrations and forms of biologically important elements (e.g., C, N, P, Si, Fe, and Hg) vary in the pelagic and littoral zones of the Great Lakes through the full annual cycle?

Q2.2: How do transformation rates (e.g., uptake and remineralization by biota) and the relative importance of different processes (autotrophic vs. heterotrophic) vary seasonally in the water column and the sediments? And how do these processes respond to changes in winter conditions?

Q2.3: How do nutrients and other material moves between nearshore and offshore regions of the Great Lakes and how are these processes affected by winter climate over the Great Lakes and their watershed?

Q2.4: How are biogeochemical cycles of P and other biologically important elements coupled through time and what are their legacy effects? How will changing winter conditions affect these temporal connections?

3.2. Lake–Watershed Connections

Human activities in Great Lakes watersheds have large impacts on the health and function of the lakes (Chapra & Dolan, 2012; Prater et al., 2017; Williams et al., 2016). Upstream activities such as urbanization and the associated stormwater runoff, and increased water and fertilizer use for agriculture affect water quality and elemental cycling both in tributaries and the Great Lakes themselves (Larson et al., 2014; Williams et al., 2016). Historically, the major period of water and material export from catchments to the Great Lakes has been associated with the spring snowmelt period, which is characterized by high flows of water and often large fluxes of nutrients and other material to the lakes (Long et al., 2014). These spring nutrient inputs have been linked to severe late summer algal blooms in western Lake Erie (Stow et al., 2015). Except for a few tributaries (e.g., Maumee River, Stow et al., 2015), data on winter-time nutrient export to the Great Lakes is sparse, in part because of logistical challenges, assumptions about low biological activity in receiving waters, and a historical preoccupation with point source inputs such as wastewater treatment plants. Ongoing changes in climate (e.g., rain-on-snow events) and land use may alter the timing, quantity, and

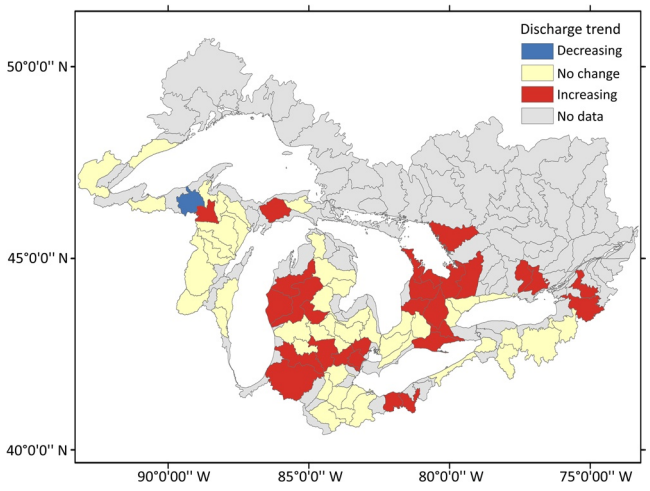

Figure 5. Trends in January-March water discharge in Great Lakes watersheds between 1960 and 2015 for stations with adequate data. Watersheds are color coded based on the predominant temporal trends as assessed by a modified Mann-Kendall test to account for short term persistence (see Norton et al., 2019 for data and methods). *Note*. Watershed level trends displayed here are aggregate measures for all gauges within the watershed.

composition of tributary inputs, making it crucial to incorporate the winter period into studies of land-lake connections in the Great Lakes region.

The Great Lakes region is projected to experience an increase of up to 30% in precipitation and annual average air temperature is projected to increase by 3.3°C–6.5°C (under RCP 4.5 and RCP 8.5, respectively) by the end of the 21st century (Byun & Hamlet, 2018). Several models predict that precipitation will increase most significantly in winter, with a greater proportion falling as rain rather than snow, leading to a decline in snowpack depth and earlier spring melts (Byun & Hamlet, 2018; Contosta et al., 2019). A recent assessment of winter (defined as January–March) streamflow in the Great Lakes basin suggests that such changes are already occurring, with significant increases in discharge volume over time (Norton et al., 2019, Figure 5), consistent with predictions of regional climate warming. In the future, the proportion of the total annual water inputs entering the Great Lakes in winter is projected to increase (Byun & Hamlet, 2018), likely with significant effects on material export from the watershed. Increased monitoring of winter stream flow (currently taking place in only a minority of Great Lakes watersheds; Figure 5) is needed to provide a better description of winter discharge trends and the consequences of these changes.

The southern half of the Great Lakes watershed supports most of the human population in the region, and in turn, is a more intensively managed landscape. Since nutrient exports are dominated by transport processes (Basu et al., 2010), changes in the timing, form, and intensity of precipitation events have strong potential to impact nutrient delivery into the Great Lakes from tributaries. In agricultural landscapes, rain-on-snow and snowmelt events have been identified as major contributors to the mass export of P (Macrae et al., 2007; Miles et al., 2013), N (Crossman et al., 2016), and dissolved organic C (Ruark et al., 2009). In urbanized watersheds, rain-on-snow events can enhance the export of P from disturbed soils (i.e., construction piles; Duval, 2018) as well as P and N derived from decomposing plant biomass and engineered infrastructure (Bratt et al., 2017; Fork et al., 2018).

Additional changes during the winter season that could affect material export may also include increased freeze-thaw cycles, decreased frost duration and frost depth, and the loss of winter snow cover (Contosta et al., 2019). Freeze-thaw cycles can lyse microorganisms and destroy fine root cells (Tierney et al., 2001), releasing their internal C and N and increasing the C and N content of the soil solution (Risk et al., 2013). Freeze-thaw cycles can also alter the structure of soil and/or streambank sediments, which can enhance nutrient availability (Risk et al., 2013) or increase susceptibility to erosion (Good et al., 2019). Additional changes may occur through the loss of snowpack and subsequent re-exposure to freezing temperatures, which has been shown to lead to increased leaching loss of N (Fitzhugh et al., 2001; Mitchell et al., 1996) and the development of impenetrable concrete frosts, which inhibit penetration of meltwaters into the soil (Shanley et al., 2002). Shifting dominance of flow paths could alter the particulate/dissolved ratios of exported nutrients (Liu et al., 2013). Enhanced "greening" (i.e., increased NPP) in terrestrial ecosystems under a warming climate may also affect the total pool of nutrients available for export or the ratios of exported N:P, Si, and/or organic N, particularly in regions that receive sufficient precipitation (Hessen et al., 2009).

We propose two questions that will help improve understanding of the connections between the Great Lakes and their watershed and predict how climate and land use change will affect inputs of nutrients and other material into the Great Lakes:

Q2.5: What proportion of material (water, nutrients, sediment, C) currently enters the Great Lakes during the winter period, and how do winter inputs vary with land use and precipitation amount, timing, and form?

Q2.6: How will the quantity, timing, and form of winter material delivery respond to changes in land use, management, and climate?

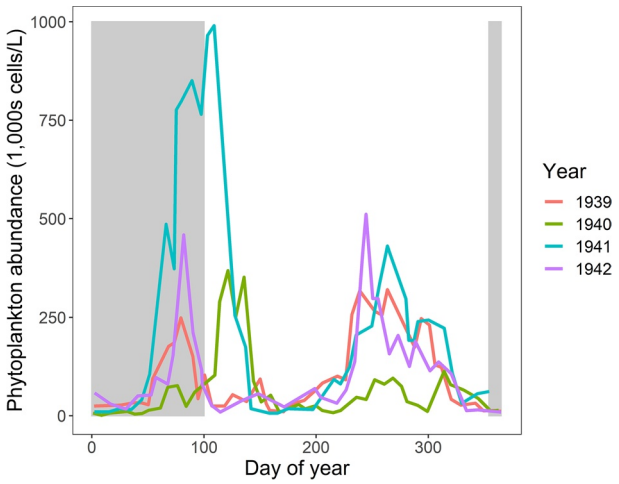

Figure 6. Annual variation in phytoplankton abundance in the Bass Islands region of western Lake Erie between 1939 and 1942, based on data from Chandler (1940, 1942, 1944), Chandler & Weeks (1945). Approximate period of ice cover during study years is shown in gray.

4. Winter Biology

The winter biology of lakes is still relatively poorly understood (Hampton et al., 2015, 2017), especially compared to marine systems (e.g., Arrigo et al., 2008; Grebmeier, 2012; Kaartokallio, 2004; Meier et al., 2014). While some studies find little biological activity under lake ice (Leppäranta, 2015; Sommer et al., 1986), others show diverse and productive winter communities, with few consistencies among systems (Bondarenko et al., 2006; Hampton et al., 2015, 2017; Salonen et al., 2009; Vanderploeg, Bolsenga, et al., 1992). Due to the logistical challenges of winter work and their size, the winter biology of the Great Lakes remains even less understood than that of smaller lakes. The relatively few existing studies show that biological processes in the Great Lakes remain active during winter and are highly heterogeneous in space and time. These studies also indicate that winter conditions, such as the extent and properties of ice cover, stratification and mixing, and availability of light, nutrients, and other resources structure biological systems in the Great Lakes.

Past studies of winter biology on the Great Lakes have been uneven in their geographic and taxonomic focus. Lakes Erie and Michigan have received the most attention while Superior and Huron have been studied very little. Phytoplankton and, to a lesser extent, zooplankton are the only groups that have been studied systematically across the full annual cycle in any of the Great Lakes. Information about the biology of viruses, bacteria, protists, benthos, and fish remains scarce. Improved understanding of winter populations, communities, and productivity across trophic levels is urgently needed to close the winter biology knowledge gap on the Great Lakes and improve prediction of what the future holds for their ecosystems.

4.1. Populations and Communities During Winter

Great Lakes populations and communities are strongly influenced by thermal stratification, currents, sediment resuspension, light penetration, nutrient concentrations, and the effects of watershed stressors, particularly in nearshore areas (e.g., Bramburger & Reavie, 2016; Paver et al., 2020; Pothoven & Vanderploeg, 2020; Vanderploeg et al., 2007; Zhao et al., 2009). Despite marked shifts in these forcing agents during winter, contrasts between summer and winter communities have not been systematically evaluated. One assumption is that winter communities comprise relicts of "dominant" summer populations representing dormant or senescent life cycle phases. This assumption appears false; rather, Great Lakes winter biological communities likely represent distinct assemblages adapted to winter conditions and characterized by active metabolism.

Few studies have examined the full-year seasonality of phytoplankton communities in the Great Lakes. Comprehensive surveys in western Lake Erie in the 1930s and 1940s showed two recurring seasonal peaks in phytoplankton abundance: a late winter-early spring bloom that typically started under the ice in mid-February (Figure 6) and reached peak densities around ice off in late March-early April; and one in late summer-early fall (Chandler, 1940, 1942, 1944; Chandler & Weeks, 1945). Spring blooms were composed almost entirely of diatoms including *Asterionella, Synedra, Stephanodiscus,* and *Cyclotella* spp. In Lake Ontario (which does not typically freeze over in winter), the same diatom genera attain their peak annual densities during the winter-spring transition, although the late winter diatom bloom is less pronounced than in Lake Erie (Munawar & Munawar, 1982; Stoermer et al., 1975). Smaller-scale surveys in Lake Michigan showed that mid-winter mixotrophic phytoflagellates, which prey on bacteria and picoplankton, can also be an important component of the offshore phytoplankton community (Butts & Carrick, 2017; Carrick, 2005). Detailed, large-scale, seasonal phytoplankton studies have not been conducted in all Great Lakes and recent survey data (e.g., Reavie et al., 2014) illustrate that spring phytoplankton communities in Lakes Erie and Ontario have changed markedly since the aforementioned decades-old studies, illustrating the need to revisit seasonal phytoplankton dynamics in all five Great Lakes.

Figure 7. Photograph showing brownish accumulations of diatoms and sediment entrained in slush (i.e., frazil ice) on the underside of ice left in the wake of US Coast Guard icebreaker NEAH BAY on Lake Erie. Gulls would follow the ice breaker and periodically dive into the slush to feed—likely not on microbes but further up the food chain—showing how important these sympagic communities are in this great lake. Photo by Lauren Jorgensen, U.S. Coast Guard.

The role of winter conditions in structuring Great Lakes phytoplankton communities is not well-studied, complicating our understanding of winter-spring phytoplankton community development and differences among lakes and years (Figure 6). This lack of mechanistic understanding undermines the ability to predict the effects of environmental change on Great Lakes phytoplankton. Existing evidence suggests that ice cover plays a key role in controlling phytoplankton community characteristics. Great Lakes ice is often blown clear of snow by the wind, resulting in relatively high light transmittance (Bolsenga & Vanderploeg, 1992). Ice cover curtails effective mixing and associated turbidity, potentially resulting in favorable light conditions for phytoplankton compared to those in ice-free waters (Bolsenga & Vanderploeg, 1992; D'souza et al., 2013; Twiss et al., 2012; Vanderploeg, Bolsenga, et al., 1992). When ice is absent, deep, storm-driven mixing results in uniform distributions of phytoplankton throughout the water column and sediment resuspension in shallow areas, leading to a poor light climate for phytoplankton (Beall et al., 2016; Stoermer et al., 1975; Vanderploeg, Bolsenga, et al., 1992; Vanderploeg et al., 2007). In Lake Erie, ice cover extent has been linked to changes in phytoplankton abundance and community structure: high ice cover has been correlated with high densities of large filamentous diatoms, whereas low phytoplankton biomass and smaller taxa characterized low-ice years (Beall et al., 2016).

The extensive spread of invasive dreissenid (zebra and quagga) mussels starting in the late 1980s has dramatically altered food web dynamics in all Great Lakes except Lake Superior (Bunnell et al., 2014), but the impacts of dreissenids on winter ecological dynamics have not been broadly examined. Dreissenid mussels are physiologically active throughout the year and filter feed even at 1°C (Vanderploeg et al., 2010). The impact of their filtering ability is evident in the disappearance of the winter-spring phytoplankton bloom in Lake Michigan, where *Dreissena* filtering rates can exceed phytoplankton growth rates (Rowe et al., 2015; Vanderploeg et al., 2010). Modeling and observations have shown that inverse stratification (surface water temperatures < 4°C) can limit quagga mussel filtration impacts on phytoplankton, while concurrently enhancing phytoplankton growth by limiting the mixed layer depth and associated light limitation (Rowe et al., 2015, 2017). In Lake Erie, dreissenid filtering has led to a post-invasion shift in the winter diatom community, where large, heavily silicified chain-forming diatoms (*Aulacoseira* spp. and *Stephanodiscus binderanus*) came to dominate the community at the expense of smaller taxa (Beall et al., 2016; Chandler, 1940; Sze & Stewart, 1974; Twiss et al., 2012). Additional research to determine the impacts of winter conditions on interactions between dreissenid mussels and phytoplankton is urgently needed to better predict what the future holds for the role of *Dreissena* in Great Lakes ecosystem function.

Another knowledge gap in the Great Lakes concerns sympagic communities–microbes associated with the underside of the ice and the water column immediately beneath it. In marine systems, productive microbial communities are found in brine channels in the ice and on the lower surface of the ice (Garrison et al., 1983; Horner et al., 1992; Kaartokallio, 2004; Post et al., 2013). Until recently, limnologists have paid very little attention to the sympagic environment. However, evidence from Lake Baikal (and more recently other lakes) suggests that diatom-dominated sympagic communities exist in and under freshwater ice, taking advantage of the relatively high light environment and stable substrate this environment affords (Bondarenko et al., 2006; Bullerjahn et al., 2020; Frenette et al., 2008; McKay, Prášil, et al., 2015; Melnik et al., 2008; Timoshkin, 2001).

Sympagic communities have been recently documented in Lake Erie, where very large accumulations of phytoplankton biomass (greatly exceeding water column concentrations) occurred in association with frazil ice (Figure 7; Twiss et al., 2012). These communities were dominated by diatoms along with bacteria, non-diatom phytoplankton, and heterotrophic protists. D'souza et al. (2013) showed that these accumulations occur due to trapping of phytoplankton cells in newly forming frazil ice and that diatoms and associated bacteria partition to overlying ice by catalyzing biological ice nucleation. At present, very little is known

about the taxonomic composition of these communities, their spatial and seasonal dynamics, and their ecological importance.

The zooplankton of the Great Lakes exhibits varying abundances and life history strategies during winter conditions. Winter zooplankton community studies have been conducted in Lakes Erie, Ontario, Superior, and Michigan (Chandler, 1940; Glooschenko et al., 1972; Selgeby, 1975; Vanderploeg et al., 2012). Overall crustacean zooplankton abundance and biomass are at their annual minimum from late fall to late spring, during which time native herbivorous cladocerans and the invasive, predatory cladoceran *Bythotrephes longimanus* are almost completely absent. On the other hand, many predatory and omnivorous calanoid copepods and the large opossum shrimp (*Mysis diluviana*) maintain high abundances and the calanoids have a major reproductive pulse during the winter in the deep Great Lakes (Pothoven & Vanderploeg, 2017; Selgeby, 1975; Twiss et al., 2012; Vanderploeg et al., 2012). Predacious and omnivorous calanoids have been shown to feed actively during winter in the upper water column under ice (Vanderploeg, Bolsenga, et al., 1992) and in open water (Bundy et al., 2005; Warren, 1983), with potentially important consequences to the structure of plankton communities during the rest of the year. The overwintering, univoltine calanoids represent taxa that have developed extreme lipid storage and lifecycle strategies that allow new offspring to be sufficiently developed by late winter to capitalize on under-ice production and ultimately recruit to adults in the summer (Vanderploeg, Gardener, et al., 1992; Vanderploeg et al., 1998).

Unlike crustacean zooplankton, microzooplankton (flagellated and ciliated protists) in the Great Lakes exhibit a winter/spring abundance peak (Carrick, 2005). These organisms are generally phagotrophs that feed on bacteria and picoplankton-sized prey. Studies in Lakes Michigan and Erie have shown that microzooplankton communities form a key food web linkage during winter, applying high grazing pressure on small phytoplankton cells while representing the main food source for winter-active omnivorous copepods (Bundy et al., 2005; Twiss et al., 2014). While zooplankton has received more attention than other components of the Great Lakes food web during winter, several important knowledge gaps remain. These include the magnitude of top-down effects of zooplankton on microbial communities, the nature of the relationships between phytoplankton, microzooplankton, and crustacean zooplankton, the effect of winter conditions in structuring zooplankton community composition and distribution, and the impacts of winter predation by fish (e.g., Link et al., 1995) on zooplankton. Beyond grazing pressure, recent studies point to microbial parasites (chytrid fungi and oomycetes) as additional contributors to structuring winter planktonic communities (Edgar et al., 2016).

Great Lakes fish communities are more compositionally stable across seasons than microbial, algal, and invertebrate communities because most fish species live for multiple years. Fish are thus subjected to climatic variability across a range of temporal scales during their lifetime, from short duration fluctuations in winter conditions (i.e., temporary presence of ice, altered water column mixing) to long-term trends (e.g., an ongoing decrease of ice extent). The range of environmental variation in winter conditions experienced by fishes results in important physiological and behavioral adaptations and trade-offs (Garvey et al., 2004). Great Lakes fishes are generally classified as warm, cool, or cold-water species (Elliott & Elliott, 2010; Fry, 1971; Shuter et al., 2012), exhibiting two common physiological coping strategies for over-winter survival. For obligate cold-water taxa, foraging is beneficial and individuals can sustain positive growth under winter conditions (Caldwell et al., 2020). Alternatively, for cool or warm-water species that are simply tolerant of winter conditions, foraging provides no benefit beyond starvation avoidance and winter growth is limited or not possible (Shuter et al., 2012).

Winter conditions can affect Great Lakes fish communities by imposing different pressures on population dynamics of cold, cool, and warm-water taxa, including influences on growth, survival, and reproduction. For example, increased ice cover in Lake Michigan protects lake whitefish (*Coregonus clupeaformis*, a cold-water species) eggs from wave action and abrasion during late winter (Brown et al., 1993; Freeberg et al., 1990), leading to higher recruitment. Similarly, yellow perch (*Perca flavescens*, a cool-water species) egg quality, larval survival, and recruitment in Lake Erie are reduced following warm, low-ice years compared to colder years (Farmer et al., 2015). In contrast, survival and recruitment of alewife (*Alosa pseudoharengus*), a warm-water invasive species, have been shown to be negatively affected by winter severity in Lake Ontario (O'Gorman et al., 2004).

While winter conditions have long been recognized as a key driver of fish community dynamics, many questions remain about the winter ecology of Great Lakes fishes (Marsden et al., 2021) including movement and

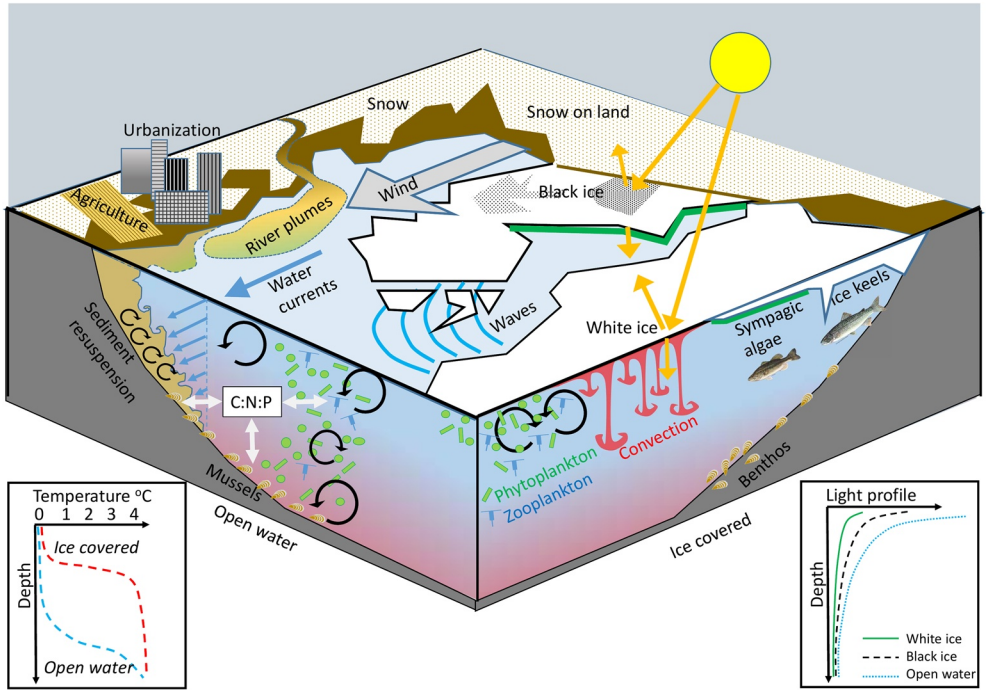

Figure 8. Conceptual diagram showing the effect of ice cover on the major physical, biogeochemical, and biological processes in the Great Lakes. The extent of ice cover is a major determinant of water temperature, with open water potentially cooling more than ice covered regions. In open water, the wind can drive waves and currents, which break and transport ice, potentially forming ice keels. Wind also drives the mixing of the water column and sediment resuspension. The magnitude of turbulence determines how deeply phytoplankton and zooplankton can be mixed, which differs between open water and ice-covered regions. The vertical light profile varies in winter depending upon whether there is open water, black ice, or white ice. Even under white ice, sufficient light can penetrate to support phytoplankton and sympagic algal communities. Solar radiation can drive convection under ice, which is an important source of mixing in absence of wind driven currents. During warmer winters, runoff from rivers, agriculture, and urban environments is an important source of nutrients for the food web. While it is not well known where fish overwinter, it is thought that representative species like Northern Pike, Lake Trout, and Largemouth Bass use shallower littoral regions of the Great Lakes.

habitat use (Figure 8). The ecosystem consequences of potential changes in fish community structure caused by changes in winter conditions (e.g., top-down effects on prey species, bottom-up effects of zooplankton, and competition between different fish taxa) require attention. For example, how abundances of different native and invasive taxa will change under projected changes to winter conditions remain poorly understood.

Four broad questions need to be addressed to improve understanding of the winter population and community dynamics in the Great Lakes.

Q3.1: How are abundance, community composition, and distribution of viruses, bacteria, archaea, fungi, phytoplankton, zooplankton, benthos, and fish affected by winter conditions, especially the extent and duration of winter stratification with and without ice cover?

Q3.2: How common are sympagic communities in the Great Lakes during winter, what determines their presence and structure, and what role do they play in the winter ecology of the Great Lakes?

Q3.3: What is the role of winter-time community interactions such as competition, grazing, predation, disease, mutualism, and parasitism in determining the abundance of different organisms during winter and subsequent seasons?

Q3.4: Which fish species (i.e., cold, cool, and warm-water species) are likely to be most resilient to predicted changes in winter climate (e.g., reduced ice cover, monomictic conditions, increased coastal sediment resuspension)?

Table 1
Summary of Great Lakes Winter-Summer Phytoplankton and Bacterioplankton Primary Production Rate Comparison Studies

Study	Study location and period	Method	Winter ice conditions	Winter rates	Summer rates	Winter: Summer ratio
Planktonic primary production						
Glooschenko et al. (1974)	L. Ontario. 32 locations throughout lake	^{14}C light/dark incubations	Ice-free	0.27 g C/m2/ day (average December- March)	0.69 g C/m^2/ day (average April- October)	0.39
Biddanda & Cotner, (2002)	L. Michigan. 4 winter and 4 summer locations in southern basin, nearshore to offshore.	^{14}C light/dark incubations	Ice-free	0.36 g C/m^2/day (regional average, March 1999)	0.33 g C/m^2/day (regional average, June 1999)	1.09
Depew et al. (2006)	L. Erie. 1–12 locations in east basin	^{14}C light/dark incubations	Ice-free	0.18 g C/m^2/ day (average December–March)	0.58 g C/m^2/ day (average April–October)	0.31
Saxton et al. (2012)	L. Erie. 5 winter and 4 summer locations	Oxygen evolution method	Ice-covered	0.18 g C/mg chl./day (average February)[a]	0.33 g C/mg chl./day (average June-July)[a]	0.55
Planktonic bacterial production						
Cotner et al. (2000)	L. Michigan,	[^{3}H]-leucine	Ice-free	2.62 µg C/L/day	1.38 µg C/L/day	1.90
	11 locations in the southern basin, nearshore to offshore	incorporation		(March 1998 nearshore) 0.60 µg C/L/ day (March 1998 offshore)	(August 1998 nearshore) 1.27 µg C/L/day (August 1998 offshore)	0.47
Biddanda and Cotner (2002)	L. Michigan. 3–4 locations in the southern basin, nearshore to offshore	[^{3}H]-leucine incorporation	Ice-free	2.10 µg C/L/day (average from March 1999 March 2000)	2.75 µg C/L/day (average from June 1999 May 2000)	0.76
Wilhelm et al. (2014)	L. Erie. 3–5 locations spanning all basins	[^{3}H]-leucine incorporation	Ice-covered	0.02 µg C/L/hr (average from February 2008 and 2009)	1.7 µg C/L/day (average from July 2002)	0.01
Xenopoulos et al., unpublished data	L. Erie, 3 pelagic locations (east, central, western basins).	[^{3}H]-leucine incorporation	Ice-covered (46–76 cm thick)	0.67 µg C/L/day (February 2014)	5.46 µg C/L/day (August 2014)	0.12

Note that different units are reported across the studies, but all are based on carbon.
[a]Rates were collected directly from the text or estimated via table values or by digitizing figures and the ratio was calculated from winter to summer. Rates reported in units of oxygen were converted to units of C using the assumed photosynthetic quotient of 1.2.

4.2. Winter Productivity

While freezing air temperatures render winter a time of minimal productivity in terrestrial ecosystems of the Great Lakes region (e.g., McCaughey et al., 2006; Studd et al., 2021), the unique physical properties of water create under-ice refugia from freezing, allowing primary production and its utilization to continue at higher rates than in terrestrial habitats. The magnitude and fate of winter production vary widely among lakes depending on winter conditions such as ice and snow cover, under-ice stratification and mixing patterns, and nutrient availability (Katz et al., 2015; Pernica et al., 2017; Straškrábová et al., 2005). Very few systematic measurements of winter primary and microbial productivity have been made in the Great Lakes, resulting in a critical knowledge gap on the contribution of winter productivity to total annual production and prediction of how the Great Lakes will respond to future environmental change.

Although lower than in summer, measured winter primary productivity rates in the Great Lakes are substantial. Glooschenko et al. (1974) and Depew et al., (2006) presented comprehensive year-round planktonic primary production estimates for Lakes Ontario and Erie, respectively (Table 1). Both studies were conducted during low-ice years and revealed that primary productivity rates were at their annual minimum during

winter, at 20%–30% of peak open water season rates. In contrast, a smaller-scale study in southern Lake Michigan found slightly higher gross primary productivity rates during ice-free winter sampling than during summer (mean 0.36 vs. 0.33 g C m^{-2} day^{-1}; Biddanda & Cotner, 2002). Lohrenz et al. (2008) measured a large range of winter primary productivity rates (0.18–0.48 g C m^{-2} day^{-1}) along nearshore to offshore transect in southeastern Lake Michigan, with rates increasing nearshore where nutrient concentrations were higher.

Very few Great Lakes winter productivity datasets include under-ice measurements. We are aware of only four studies from Lake Erie that report any primary production values for under-ice phytoplankton. Saxton et al. (2012) used lab incubations to compare primary productivity rates of phytoplankton collected in summer and under the ice. On average, winter primary productivity rates were ∼55% of summer rates (Table 1). Beall et al. (2016), Collier (2016), and D'souza (2012) compared primary productivity in open-water and ice-covered conditions, finding a wide range of primary productivity rates among phytoplankton communities under and within the ice. However, all these studies report chlorophyll-normalized maximum photosynthetic rates, making it difficult to compare results to those from studies reporting depth-integrated C fixation values. Overall, the diversity of methodological approaches and the limited spatial or temporal extent of most existing studies make robust generalizations about winter primary production difficult.

Winter bacterioplankton biomass and rate processes remain even less well-quantified than for phytoplankton. Wilhelm et al. (2014) estimated that winter bacterial productivity rates in Lake Erie were ∼1% of summer rates, attributing the large seasonal difference to temperature (Table 1). Additional data collected by co-author Xenopoulos' lab and reported here (Table 1) also showed lower rates of bacterial production in Lake Erie in winter (12% of summer rates). In contrast, Biddanda and Cotner (2002) and Cotner et al., (2000) found relatively high winter bacterial production rates (∼47%–190% of summer, with higher rates found in the nearshore) and biomass similar to summer in a late winter sediment plume in Lake Michigan. The dearth of seasonal studies on Great Lakes bacterioplankton makes it difficult to reconcile the divergent results from Lakes Erie and Michigan and to make generalizations on rates and controls on Great Lakes bacterioplankton abundance and production during winter.

While the above studies show that production is typically lower in winter than in summer, seasonal and spatial variation in primary and bacterial productivity remain poorly quantified across the Great Lakes during winter. The influences of drivers such as mixing, ice cover extent and clarity, sediment resuspension and nutrient availability on pelagic productivity rates during winter, and the balance between heterotrophy and autotrophy are important outstanding questions. Addressing these questions will help contextualize past findings (Biddanda & Cotner, 2002; Depew et al., 2006; Glooschenko et al., 1974; Kerfoot et al., 2008; Wilhelm et al., 2014) and parameterize predictive models of winter-period productivity under changing environmental conditions. To date, no studies have examined primary production by benthic algae or macrophytes during winter, which may respond very differently to changing winter conditions than phytoplankton.

The role of winter production in the Great Lakes food web is not well-known. Several researchers (Bundy et al., 2005; Kerfoot et al., 2008; Vanderploeg, Bolsenga, et al., 1992) demonstrated active feeding of micro- and meso-zooplankton on winter algae and suggested that this feeding may be important for the overwinter survival and spring reproduction of Great Lakes calanoid copepods. Phytoplankton growth and grazing rates measured in mid-winter in Lake Erie (Twiss et al., 2014) are similar to those measured in summer (Twiss & Campbell, 1998). Wilhelm et al. (2014) reported low bacterial degradation of a winter phytoplankton bloom in Lake Erie and efficient export of phytoplankton C to the benthos, where it may contribute to bacterial oxygen consumption and hypoxia during summer when temperature increases. The role of winter productivity in supporting benthic consumers has not been studied in detail. Vanderploeg et al. (2009) showed an increase in dreissenid mussel body condition in Lake Erie and Lake Huron's Saginaw Bay sometime between autumn and early spring, suggesting that winter feeding may be important to sustaining these (and potentially other) benthic consumers. Winter feeding has been demonstrated for some Great Lakes fish (Bailey, 1972; Link et al., 1995), but its importance to sustaining fish populations is unclear.

Additional studies are also needed to constrain seasonal metabolism (i.e., productivity vs. respiration) in the Great Lakes, determine the way winter conditions affect this balance, and predict how climate change will affect the role of the Great Lakes in the global C cycle. Existing studies show that Lakes Ontario (Eadie & Robertson, 1976), Superior (Urban et al., 2005), Michigan (Lohrenz et al., 2008), and Erie (Depew

et al., 2006) have a distinct seasonal pattern of ecosystem metabolism, with increased net heterotrophy during winter months. However, these studies are insufficient for the construction of mechanistic models linking environmental conditions to whole-system metabolism. Thus, in addition to constraining microbial and phytoplankton process rates, studies of whole ecosystem metabolism linking allochthonous and autochthonous C to primary and microbial production are needed.

The below set of questions need to be addressed to integrate winter-period primary and microbial production into the understanding of whole year productivity, ecosystem metabolism, and food web dynamics of the Great Lakes.

Q3.5. What are rates of winter pelagic and benthic primary and microbial heterotrophic productivity in the Great Lakes and how do they vary temporally and spatially?

Q3.6. How are winter primary and microbial productivity influenced by ice cover, light, temperature, nutrients, organic carbon, and currents, turbulence, and sediment resuspension?

Q3.7. What is the role of winter production in supporting the food webs of the Great Lakes?

5. Lessons and Conclusions

The paucity of winter limnology studies in general—and on large lakes in particular—combined with rapid change in a winter climate, make winter research an urgent priority for Great Lakes science. As reviewed above, current knowledge gaps for the Great Lakes range from the physics of water column mixing and ice formation to community ecology and ecophysiology. These knowledge gaps are not unique to the Laurentian Great Lakes and extend across the spectrum of temperate and boreal lake sizes and winter conditions (Bouffard & Wüest, 2019; Grosbois et al., 2017; Hampton et al., 2017; Kirillin et al., 2012; Kouraev et al., 2016; Perga et al., 2020; Powers & Hampton, 2016). Addressing these gaps will require extensive state and process studies and collaboration of researchers working across the range of aquatic science subdisciplines and study systems.

Box 2. Existing and future approaches to the study of the Great Lakes in winter

Improved understanding of the Great Lakes in winter can be achieved by making better use of existing infrastructure and investment in new, specialized research platforms (Figure 9). Some winter-time work can be performed using existing research vessels during low ice years, as has been done on Lake Ontario during the International Field Year for the Great Lakes (1972–1973; e.g., Glooschenko et al., 1974) or as part of the Episodic Events - Great Lakes Experiment (EEGLE; e.g., Green & Eadie, 2004) cruises on Lake Michigan (1998–2000). Some nearshore areas of the Great Lakes (e.g., Apostle Islands in Lake Superior, Grand Traverse Bay and Green Bay in Lake Michigan, Saginaw Bay in Lake Huron, and Bay of Quinte in Lake Ontario) have regular and stable ice cover, permitting winter access to researchers on foot or snowmobile. Collaboration with U.S. and Canadian Coast Guard icebreakers has allowed unprecedented insights into winter limnology on the Great Lakes (Depew et al., 2006; McKay et al., 2011; Oyserman et al., 2012; Twiss et al., 2012). Such collaborations should continue to be nurtured and leveraged by researchers as one of the few available mechanisms for directly accessing the pelagic areas of the Great Lakes during periods of ice cover. Deployment of dedicated ice-strengthened or even ice-breaking research vessels would be an important advance in observational capabilities in the medium to the long-term timeframe. Progress in remote sensing and surface and subsurface autonomous sensor platforms has been rapid and now allows not only high-frequency recording of physical and bio-optical data but also collection and preservation of water samples for chemical and biological analyses. Increased use of such platforms holds great promise in studying the physics and biology of the Great Lakes in winter. Most importantly, a collaborative network of researchers interested in conducting winter research and securing investments in such research is crucial for closing the winter gap of Great Lakes limnology.

While much remains to be learned, our review of the Great Lakes literature has identified several important themes and lessons about the winter limnology of large lakes. One important conclusion pertains to the role of ice cover as a "master variable" that controls physical, biogeochemical, and biological processes during

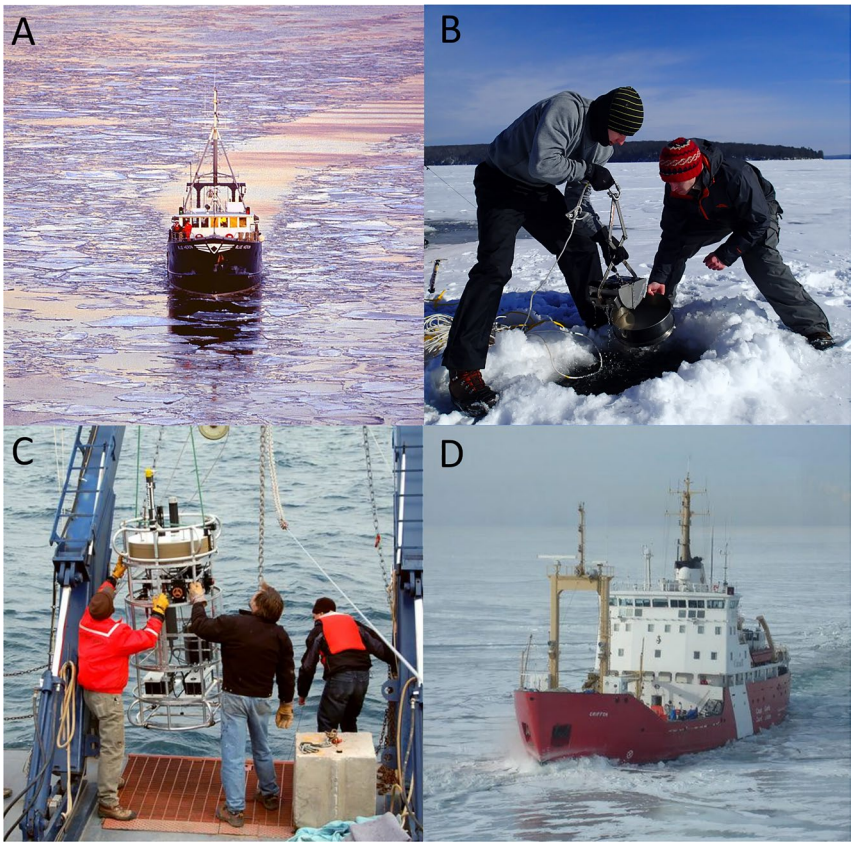

Figure 9. Several existing approaches to winter sampling in the Great Lakes. (a) The University of Minnesota's R/V Blue Heron traveling through early spring ice on Lake Superior (photo by University of Minnesota Duluth); (b) Researchers sampling benthos in the Apostle Island area of Lake Superior (photo by Ted Ozersky); (c) A WetLabs AMP100 autonomous profiler being deployed in Lake Superior. The instrument travels up and down its mooring tether, recording water column parameters including temperature, oxygen concentrations, and chlorophyll fluorescence (photo by Jay Austin); (d) The Canadian Coast Guard icebreaker Griffon, which has supported winter limnology research on Lake Erie (photo by Paul Miller from Canada Steamship Lines).

winter (Figure 8). Among its effects, ice cover can impact vertical and horizontal water column mixing and thermal regimes, sediment resuspension, and nutrient availability, directly and indirectly control light availability to primary producers, provide physical habitat for microbes, and affect the distribution of primary producers and their consumers. Similar conclusions have been reached for smaller lakes, making continued studies on the ecosystem-structuring role of ice cover a high priority for research.

Another important conclusion from our review is that winter conditions can impact physical, biogeochemical, and biological processes in subsequent seasons. For example, water temperatures remain colder for longer and stratification sets in later in the deep and large Great Lakes following cold winters than after warm winters (e.g., Figure 3; Anderson et al., 2021). Winter conditions can also affect spring phytoplankton community structure, the export of carbon to deep waters, and, consequently, summer hypoxia (Beall et al., 2016; Wilhelm et al., 2014). Winter severity has also been shown to impact the recruitment and survival of fish in the Great Lakes (Farmer et al., 2015; Freeberg et al., 1990; O'Gorman et al., 2004), which likely has cross-seasonal repercussions not just for the populations of these fish but also the parts of the food web these species interact with.

Finally, our literature review showed that winter conditions in large lakes can be highly variable spatially and temporally. Ice cover on the Great Lakes is very dynamic, with ice forming, moving many kilometers, and getting destroyed over the time span of days (Hawley et al., 2018; Titze & Austin, 2016). Resuspension of nearshore sediments by winter storms in ice-free regions can lead to large spatial heterogeneity in water clarity, nutrient concentrations, and biological activity (Eadie et al., 1996; Kerfoot et al., 2008; Vanderploeg

et al., 2007). Winter productivity may also be highly variable on interannual time scales. It is well-known that in Russia's Lake Baikal under-ice diatom blooms vary in intensity by more than an order of magnitude from year to year (Katz et al., 2015). Results from Lake Erie (Figure 6; Beall et al., 2016) suggest potentially similar variability. Winter research programs on large lakes must consider this variability and use sampling designs that span relevant spatial and temporal gradients.

How can progress in understanding the winter limnology of the Great Lakes to be made given the formidable challenges of winter research on these large and dynamic systems? We believe that an important step forward is wider recognition of the value of such work. Such recognition should lead to increased use of existing infrastructure for the study of winter limnology and to invest in new, specialized research platforms (Box 2). Equally important will be increased collaboration and exchange of ideas among researchers studying the winter physics, chemistry, and biology of diverse freshwater, marine, and terrestrial ecosystems.

Conflict of Interest

The authors declare no conflict of interest relevant to this study.

Data Availability Statement

All data presented in this manuscript is from the published literature or referenced, publicly available online sources. The exception is bacterial production data provided by co-author Xenopoulos, which are unpublished, but available in Table 1. Data used in figures and tables are available from Ontario Open Data Team (2020), Norton et al., (2019), Chandler (1940, 1942, 1944), Chandler and Weeks (1945), Glooschenko et al. (1974), Biddanda and Cotner (2002), Cotner et al., (2000), Depew et al., (2006), Saxton et al., (2012), and Wilhelm et al., (2014). This is NOAA GLERL Contribution No. 1982 and CIGLR Contribution No. 1179.

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