Winter Limnology as a New Frontier

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No one seeks the most improved award. But if Limnology were to recognize a most improved topic, our vote in 2016 would go to winter limnology. While much work still remains, we are cautiously optimistic about recent progress in winter limnology research, especially for seasonally ice-covered lakes. How did we arrive here, and where are we headed?

Winter Research Historically Left Out in the Cold

Winter research in inland waters has long been neglected. For a variety of reasons, periods of ice cover have often been dismissed as ecologically unimportant relative to the summer open-water period, when most limnological field work has occurred. Consider the conceptual underpinnings of the term "growing season," which has been frequently used to describe the open-water, summer season in lakes. Similarly, what proportion of limnology articles include the words "winter" or "ice" in the title or abstract? How numerous and diverse are the lakes that have been sampled during ice cover, compared to those sampled during the open water phase? How many researchers have received winter-inclusive training? In general, the answers to these kinds of questions emphasize glaring scarcities of information about winter.

At the same time, a relatively small and scattered library of foundational limnological studies has indicated that under-ice ecology is dynamic and potentially important in ecosystems. Photosynthesis can occur under ice and under snow cover, sometimes yielding high biomass of under-ice algae, even when compared to summer (Kozhova 1961; Maeda and Ichimura 1973). Similarly, zooplankton can be diverse and abundant, with some populations peaking in winter rather than summer (Rigler et al. 1974). Such activity under ice also has been shown to influence plankton dynamics that occur in the spring and summer (Gerten and Adrian 2000). Studies involving under-ice nutrients (Knowles and Lean 1987; Wehenmeyer 2004), heterotrophic processes (reviewed in McKnight et al. 2000) and greenhouse gas production (Striegl et al. 2001) have been provocative. These are not the only examples, and below we highlight several recent developments in winter-focused limnology that indicate the rise of the topic, including articles published in *Limnology and Oceanography*, as well as contributions to a newly synthesized under-ice data set involving more than 100 lakes around the world. Despite these contributions, it appears that only a minority of the limnology community has absorbed and actively moved forward on existing winter knowledge, even as worldwide shortening in ice duration has become widely recognized (Magnuson et al. 2000; Benson et al. 2012; Sharma et al. 2016).

Multiple recent literature reviews, workshops, and conference activities illustrate rapidly increasing interest in winter limnology, and together they have revealed a variety of specific knowledge gaps (Salonen et al. 2009; Bertilsson et al. 2013; Hampton et al. 2015). In contrast to sea-ice ecosystems (Arrigo and Thomas 2004; Post et al. 2013), quantitative analyses of winter-summer differences in lakes are still lacking for primary productivity, nutritional quality of phytoplankton, respiration, and energy flow through food webs. There are cross-seasonal connections still to explore, such as carry-over of energy and nutrients between the seasons (Salonen et al. 2009; Bertilsson et al. 2013; Hampton et al. 2015). The role of ice in greenhouse gas production and dynamics is not sufficiently understood, especially given societal need for this information. Hydrodynamics and the coupling of physical and biological processes under ice have not been frequently studied, despite the profound implications for lake organisms and biogeochemistry (Salonen et al. 2009; Bertilsson et al. 2013). Similar winter knowledge gaps are present for many other structural and functional features in both lakes and reservoirs.

This past June at the ASLO Summer Meeting in Santa Fe, we convened a special session titled *Ecology under ice*. In the session, we addressed questions involving under-ice primary productivity, food webs, and biogeochemistry, and we explored how the effects of winter processes may carry-over throughout the year. Participants contributed oral and poster presentations that focused on topics such as winter productivity and metabolism, biogeochemistry including nutrients and iron, zooplankton community composition, and under-ice thermal structure. The session consistently drew approximately 100 or more of the approximately 600 ASLO attendees throughout the morning, demonstrating enthusiasm and a growing community of winter-curious colleagues.

The *Ecology under ice* session in Santa Fe was just one manifestation of the upsurge in winter limnology that has been occurring. Several ice-focused articles have been published in *Limnology and Oceanography* over the past few years (Table 1). For example, a review on the

TABLE 1. Recent publications on under-ice limnology in *Limnology and Oceanography* since January 2013. All publications had derivations of the words "ice" or "winter" in the title or abstract, and are focused on inland waters.

Year	Citation	System and region
2016	Kouraev et al.	Lakes Baikal and Hovsgol, Siberia and Mongolia
	Ma et al.	Lake Taihu, Jiangsu province, China
	Morgan-Kiss et al.	Lake Bonney, McMurdo Dry Valleys, Antarctica
	Salmi and Salonen	Lake Vesijärvi, southern Finland
2015	Beyene and Jain	Eight lakes in Maine, U.S.A.
	Bruesewitz et al.	Lake Sunapee, New Hampshire, U.S.A.
	Katz et al.	Lake Baikal, Siberia
	Steel et al.	Lake Untersee, Antarctica
	Dolhi et al.	Four lakes in McMurdo Dry Valleys, Antarctica
2014	Hawes et al.	Lake Hoare, Antarctica
	Rizk et al.	Lake Pääjärvi, Finland
	Salonen et al.	Lake Pääjärvi, Finland
	Titze and Austin	Lake Superior, Laurentian Great Lakes, U.S.A. and Canada
	Van Cleave et al.	Lake Superior, Laurentian Great Lakes, U.S.A. and Canada
2013	Arp et al.	55 lakes in Alaska, U.S.A.
	Bertilsson et al.	Review article, > 20 lakes were specifically referenced, including lakes in Germany, USA, Canada, Siberia, Antarctica, Hungary, Estonia
	Forrest et al.	Pavilion Lake, British Columbia, Canada
	Kleeberg et al.	Lake Langer See, Germany

under-ice microbiome by Bertilsson et al. (2013) has been cited 25 times according to Google Scholar. Other recent examples include research on ice phenology (Arp et al. 2013; Van Cleave et al. 2014; Beyene and Jain 2015), under-ice physical limnology (Forrest and Jain 2013; Rizk et al. 2014; Salonen et al. 2014; Titze and Austin 2014; Bruesewitz et al. 2015; Steel et al. 2015; Kouraev et al. 2016), and under-ice primary production (Hawes et al. 2014; Katz and Austin 2015). In addition, there has been a clear surge of research on biogenic gas production and carbon cycling under ice (e.g., Ducharme-Riel et al. 2015; Denfeld et al. 2016), likely built upon the work of Striegl et al. (2001) on potential gas emissions measured during ice cover, Karlsson et al. (2008) on under-ice respiration, and Cole et al. (2007) on lakes within the global carbon cycle, among others.

Progress in winter-inclusive research has been associated with a sense of urgency and societal need. Long-term declines in lake ice duration provide some of the clearest evidence of climate change yet observed (Magnuson et al. 2000; Sharma et al. 2016). Improved understanding is needed on how ecology in lakes and rivers may respond to shifting winter severity (Özkundacki et al. 2016) and ice duration (Bertilsson et al. 2013), and how these trajectories can be managed intentionally. We need to better understand the ecology of under-ice processes before they are lost.

Under-Ice Data Already in Hand

Using a recently compiled data set (Hampton et al. 2016) generated through a National Science Foundation supported workshop (NSF DEB #1431428), we are now able to ask a variety of questions about winter limnology, including the extent to which specific regions, lake types, and topical areas have been explored. *So, where has prior winter limnology research occurred? And for how many years and variables?* Perhaps unsurprisingly, Fig. 1 illustrates the geography of prior winter sampling in lakes is highly clustered, with much winter effort occurring in regions around the Laurentian Great Lakes and the Baltic Sea, in addition to the permanently frozen lakes of Antarctica (not shown).

The under-ice data set contains seasonally aggregated information from contributed data sets at 135 sampling sites on frozen lakes around the world. The data include under-ice values for more than 40 variables including biological (e.g., chlorophyll *a* (Chl *a*), zooplankton density), chemical (e.g., total phosphorus, dissolved organic carbon), and physical (e.g., water temperature, ice depth) variables. The data set is certainly not a complete representation of all winter limnology research, especially given very recent research that has happened since the call for participation and data in 2014, but it does offer lessons about prior winter research efforts.

One of the most frequently sampled variables in the data set was Chl *a* ($n = 94$ sites, Fig. 1). Chl *a* was also often measured at the same site in many winters, with 34 sites having time series across 10 or more winters, and 12 sites having time series across 30 or more winters. Other frequently sampled variables included total phosphorus ($n = 107$ sites), total nitrogen ($n = 76$), and zooplankton density ($n = 36$). Our 136 respondents indicated high interest in measures of fish, periphyton, macrophytes, and benthic invertebrates under ice, but had little or no data to provide for these variables.

For most variables, the temporal extent of winter sampling has been relatively limited, and a relatively small proportion of the lakes had sustained winter research occurring over 10+ yr. Comprehensive winter sampling, here defined as 20+ variables measured in at least 1 yr, was also relatively rare, but examples where this has occurred include northern Wisconsin U.S.A. (site of the North Temperate Lakes Long-term Ecological Research (LTER) project), the Experimental Lakes Area of southwest Ontario, and multiple lakes in Saskatchewan, Estonia, Finland, and Germany. These are just a few of the highlights from the compiled data set, anticipated to be released for unrestricted use in 2017.

Research Opportunities in Winter Limnology

Our incomplete understanding about winter processes in lakes, and the prospect of changing winter duration and severity, are being recognized more than ever within the limnology community. It is important to follow through on the winter research momentum that has been built. Below, we highlight examples of emerging winter research opportunities in lakes, inspired not only by previous reviews (Bertilsson et al. 2013; Hampton et al. 2015), but also by the workshops, symposia, and database explorations in which we engaged with dozens of colleagues over the past 2 yr. A subset of the players and processes involved in these winter research opportunities (e.g., microbes, phytoplankton, gross primary production (GPP)), is shown in Fig. 2.

Further research is needed to understand the rates and dynamics of winter productivity across a wider sample of lakes. Only a small collection of scientific articles have focused on primary producers under lake ice, with examples provided by Bashenkhaeva et al. (2015), Catalan et al. (2002), Katz et al. (2015), Tulonen et al. (1994), and Twiss et al. (2012). By comparison, the role of under ice productivity has been demonstrated more clearly in marine systems, where studies in both the Arctic and Antarctic illustrate primary productivity can be important to consumers (Lizotte 2001; Grebmeier 2012), including algae that use ice as a substratum (Arrigo and Thomas 2004). In some areas under Antarctic sea ice, algae contribute 25–30% of total annual productivity (Arrigo and Thomas 2004). Far less is known of the role of winter primary producers in lakes (Hampton et al. 2015).

The presence of a winter "ice lid" for air-water gas exchange provides a window to understanding biogenic gas production in lakes. Once ice cover has solidified over the surface of a lake, air-water gas exchange is essentially cut off, a few exceptions being leakage that occurs through ice cracks, pockets of open water near tributaries and inlets, and indirect exchange through streams and lakes that receive water from frozen lakes. Dissolved gases and bubbles containing methane, nitrous oxide, and carbon dioxide often accumulate underneath the ice (Bertilsson et al. 2013). During this time, exogenous inputs from direct atmospheric fixation and nutrient deposition are negligible, offering opportunities to more closely understand things such as biogenic gas production, internal nutrient cycling, aerobic respiration, anaerobic processes, and the functional roles of benthic microbes. In contrast, during the open water

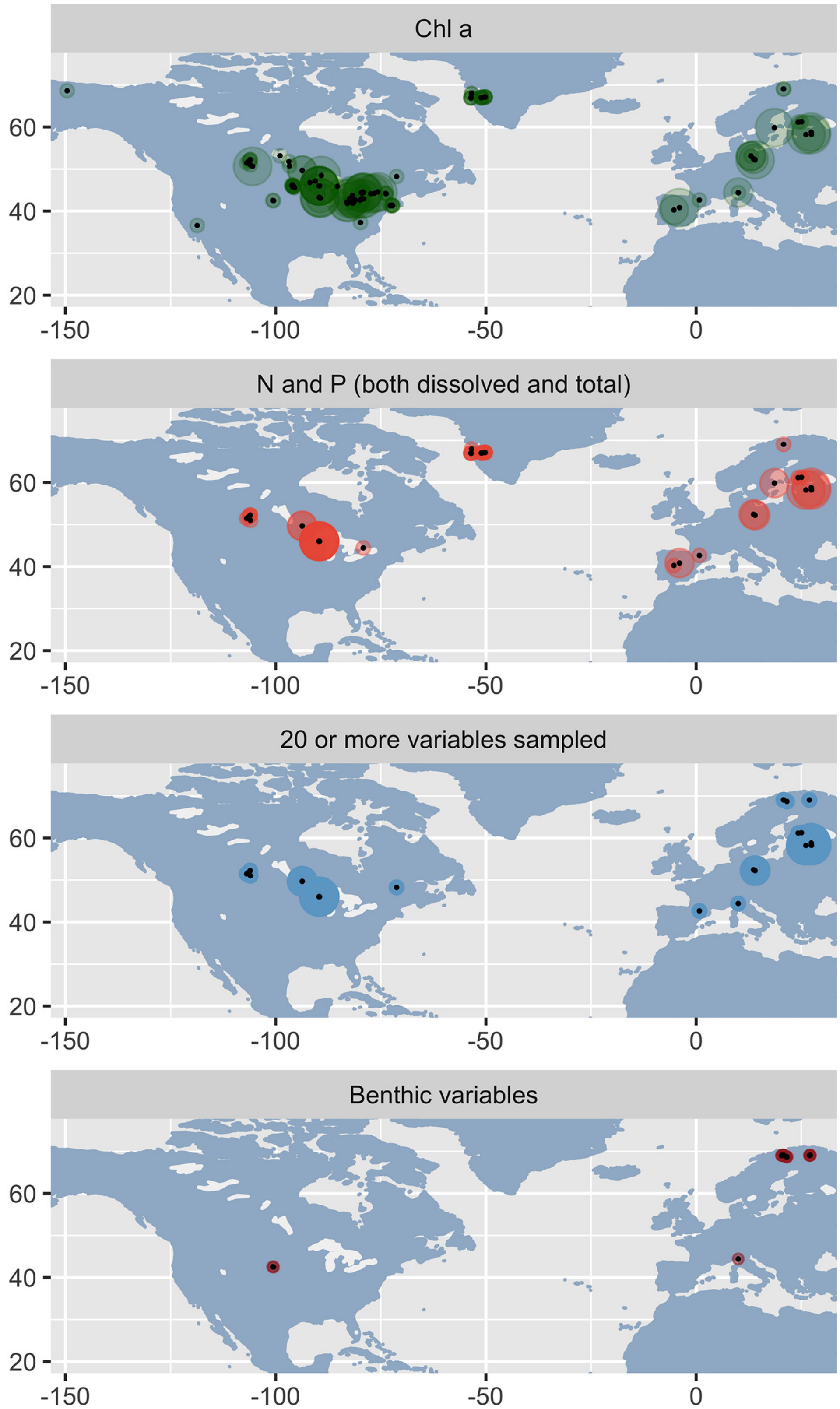

FIG. 1. Sites of prior research under lake ice, from the contributed data sets presented in Hampton et al. (In press). Large circles indicate under ice sampling has taken place during 10 or more years. Medium circles indicate sampling in 3–9 yr, and small circles in 1 or 2 yr. Sample sizes are as follows: 94 sites with Chl *a* data; 40 sites with water N and P (both dissolved and total) sampled during the same winter; 28 sites with 20 or more variables sampled during the same winter; 11 sites with benthic variables sampled.

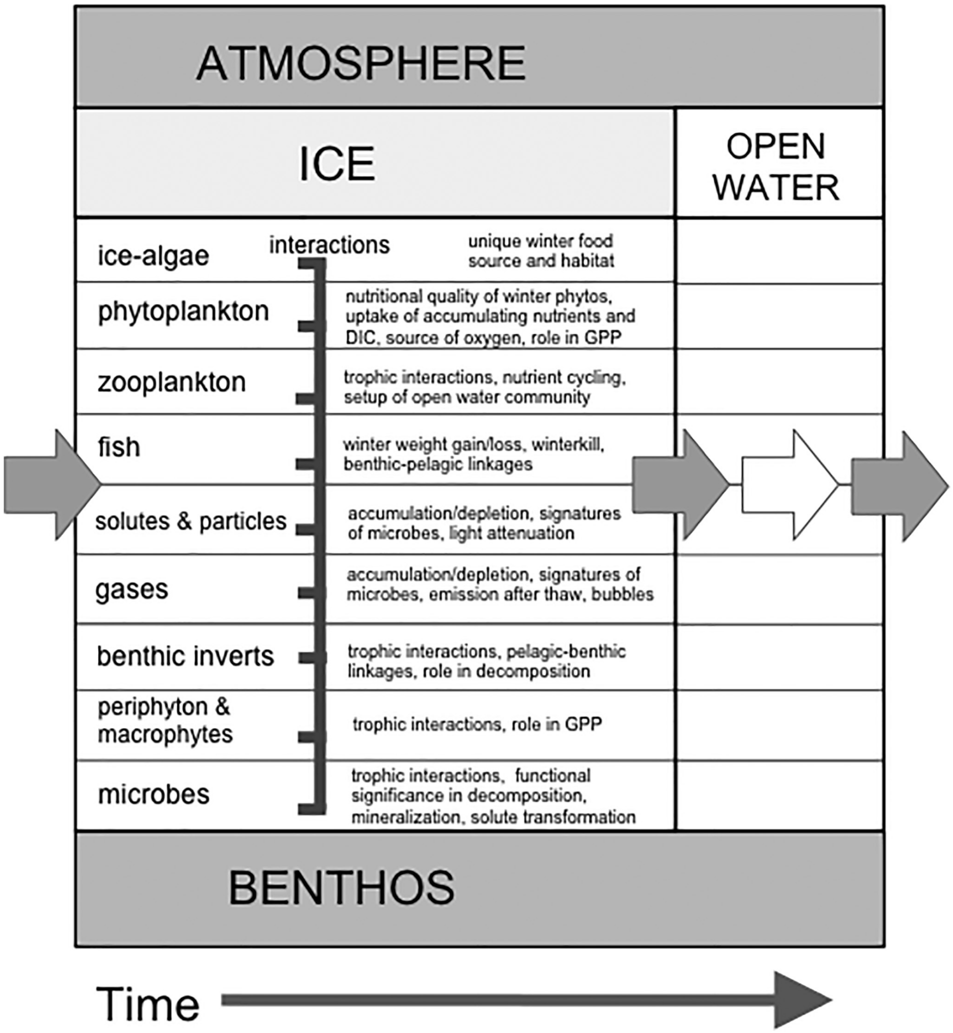

FIG. 2. Examples of under ice players, processes, interactions, and dynamics including cross-seasonal connections (dark arrows) between the under ice phase and open water phase.

period our ability to understand rates and controls on biogenic gas production in lakes is complicated greatly by the large and dynamic air-water exchange that occurs, and by the additional exogenous inputs that we cannot assume to be zero.

Oxygen depletion during winter is another research area, perhaps especially in nitrogen (N)-saturated lakes. In extreme cases, oxygen depletion under ice can result in "winterkill." While winterkill has been a well-recognized phenomenon in limnology for decades, there is incomplete understanding of how winter oxygen depletion, and associated ammonium accumulation or nitrite accumulation, could be changing across lakes. More specifically, because nitrification is an oxygen-consumptive process, high N loading and N cycling in water bodies that freeze has the potential to increase winter oxygen depletion rates. In principle, changes in these processes could alter the frequency or severity of winterkill. These issues may point to a need for research on winterkill frequency and severity, as well as nitrogen-oxygen coupling, under changing ice phenology and land use.

Molecular methods now enable taxonomic and functional characterizations of the microbes that participate in or drive under-ice processes (Bertilsson et al. 2013), as well as the identity of macroorganisms that are active under ice (e.g., environmental DNA, Goldberg et al. 2015). These molecular techniques can provide direct evidence of the mechanisms involved in elemental cycling, pathogen transmission, presence/absence of impactful species, and functional responses to pollutants at the ecosystem level (Rosi-Marshall and Royer 2012). Clearly, there are many possibilities where molecular techniques could be applied in concert with the winter opportunities we address in this article.

The presence of ice and snow on lakes can regulate local weather, including air temperature, precipitation, and wind, especially around large lakes. How will lake-atmosphere-land linkages affect local climate during winter under shifting snow-ice regimes? This is a rich area for research with important societal implications (Brown and Duguay 2010), perhaps especially for those communities affected by extreme lake-effect snow events. Shifts in lake-effect snow could also alter stream and groundwater flows seasonally or annually, potentially affecting large numbers of lakes simultaneously.

Remote sensing approaches may allow characterizations of under-ice algal biomass and patterns of productivity, facilitating a broad geographic perspective on under-ice lake ecology. Remote sensing may be most promising for lakes that are large and only partially covered with snow, such as Lake Baikal and Lake Hovsgol, or those where substantial blooms occur inside ice and at its edges. While such constraints may limit the number of lakes where remote sensing studies are feasible, these opportunities are intriguing, partly because the clarity of some lake ice can greatly exceed that of sea-ice systems.

The reduced turbulence under ice relative to summer could allow more detailed in situ sensor-based and image-based surveys of the benthos, pelagic zone, and organisms. While not frequently used within limnology to date, there is optimism that use of moored sensors (Baehr and DeGrandpre 2002) and autonomous underwater vehicles (Forrest et al. 2008) will expand in the future. In addition, although not often demonstrated, there are likely opportunities to deploy sensors and probes from the ice surface, perhaps to explore linkages between ecology and hydrodynamics. These approaches could allow us to revisit familiar limnology research questions in new spatially and temporally explicit ways, or reveal completely new questions about under ice processes and lake structure and functions generally.

The compiled under ice data set from Hampton et al. (In press) includes data from both the under-ice period and ice-free period, so there remain opportunities to address broad questions about cross-seasonal connections, including seasonal carry-over, and negative feedbacks. In addition, analyses at finer temporal resolutions may be possible by contacting the contributing researchers who provided data. We specifically point to future research opportunities that involve (1) the subset of long-term time series contained in the under ice data set, (2) interactions among the limnological variables, (3) analyses that integrate the compiled data set with independent limnological data, and (4) analyses that integrate the compiled data set with non-limnological data sets, for example land use, meteorology, or management data. Above all, we look forward to witnessing and contributing to the continued progress that is underway in winter limnology, and we extend a special thanks to the many participants who have generously provided winter data to the limnology community.

References

Arp, C. D., B. M. Jones, and G. Grosse. 2013. Recent lake ice-out phenology within and among lake districts of Alaska, USA. Limnol. Oceanogr. 58: 2013–2028. doi:10.4319/lo.2013.58.6.2013

Arrigo, K. R., and D. N. Thomas. 2004. Large scale importance of sea ice biology in the Southern Ocean. Antarct. Sci. 16: 471–486. doi:10.1017/S0954102004002263

Baehr, M. M., and M. D. DeGrandpre. 2002. Under-ice CO2 and O2 variability in a freshwater lake. Biogeochemistry 61: 95–113. doi:10.1023/A:1020265315833

Bashenkhaeva, M. V., Y. R. Zakharova, D. P. Petrova, I. V. Khanaev, Y. P. Galachyants, and Y. V. Likhoshway. 2015. Sub-ice microalgal and bacterial communities in freshwater Lake Baikal. Russia. Microb. Ecol. 70: 751–765. doi:10.1007/s00248-015-0619-2

Benson, B. J., J. J. Magnuson, O. P. Jensen, V. M. Card, G. Hodgkins, J. Korhonen, and D. Livingston. 2012. Extreme events, trends, and variability in Northern Hemisphere lake-ice phenology (1855–2005). Clim. Change 112: 299–323. doi:10.1007/s10584-011-0212-8

Bertilsson, S., and others. 2013. The under-ice microbiome of seasonally frozen lakes. Limnol. Oceanogr. 58: 1998–2012. doi:10.4319/lo.2013.58.6.1998

Beyene, M. T., and S. Jain. 2015. Wintertime weather-climate variability and its links to early spring ice-out in Maine lakes. Limnol. Oceanogr. 60: 1890–1905. doi: 10.1002/lno.10148.

Brown, L. C., and C. R. Duguay. 2010. The response and role of ice cover in lake-climate interactions. Prog. Phys. Geogr. 34: 671–704. doi:10.1177/0309133310375653

Bruesewitz, D. A., C. C. Carey, D. C. Richardson, and K. C. Weathers. 2015. Under-ice thermal stratification dynamics of a large, deep lake revealed by high-frequency data. Limnol. Oceanogr. 60: 347–359. doi:10.1002/lno.10014

Catalan, J., and others. 2002. Seasonal ecosystem variability in remote mountain lakes: Implications for detecting climatic signals in sediment records. J. Paleolimnol. 28: 25–46. doi:10.1023/A:1020315817235

Cole, J. J., and others. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems 10: 171–184.

Denfeld, B. A., P. Kortelainen, M. Rantakari, S. Sobek, and G. Weyhenmeyer. 2016. Regional variability and drivers of below ice CO2 in Boreal and Subarctic Lakes. Limnol. Oceanogr. 19: 461–476.

Dolhi, J. M., A. G. Teufel, W. Kong, and R. Morgan-Kiss. 2015. Diversity and spatial distribution of autotrophic communities within and between ice-covered Antarctic lakes (McMurdo Dry Valleys). Limnol. Oceanogr. 60: 977–991. doi:10.1002/lno.10071

Ducharme-Riel, V., D. Vachon, P. A. del Giorgio, and Y. T. Prairie. 2015. The relative contribution of winter under-ice and summer hypolimnetic CO2 accumulation to the annual CO2 emissions from Northern Lakes. Ecosystems 18: 547–559. doi:10.1007/s10021-015-9846-0

Forrest, A. L., B. E. Laval, R. Pieters, and D. S. S. Lim. 2008. Convectively driven transport in temperate lakes. Limnol. Oceanogr. 53: 2321–2332. doi:10.4319/lo.2008.53.5_part_2.2321

Forrest, A. L., B. E. Laval, R. Pieters, and D. S. S. Lim. 2013. A cyclonic gyre in an ice-covered lake. Limnol. Oceanogr. 58: 363–375. doi:10.4319/lo.2013.58.1.0363

Gerten, D., and R. Adrian. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. Limnol. Oceanogr. 45: 1058–1066. doi:10.4319/lo.2000.45.5.1058

Goldberg, C. S., K. M. Strickler, and D. S. Pilliod. 2015. Moving environmental DNA methods from concept to practice for monitoring aquatic macroorganisms. Biol. Cons. 183: 1–3. doi:10.1016/j.biocon.2014.11.040

Grebmeier, J. M. 2012. Shifting patterns of life in the Pacific Arctic and Sub-Arctic Seas. Annu. Rev. Mar. Sci. 4: 63–78. doi:10.1146/annurev-marine-120710-100926

Hampton, S. E., A. W. E. Galloway, S. M. Powers, and others. In press. Ecology under lake ice. Ecology Letters.

Hampton, S. E., S. G. Labou, K. H. Woo, and others. 2016. Winter and summer comparison of biological, chemical, and physical conditions in seasonally ice-covered lakes. Knowledge Network for Biocomplexity. doi:10.5063/F12V2D1V.

Hampton, S. E., M. V. Moore, T. Ozersky, E. H. Stanley, C. M. Polashenski, and A. W. E. Galloway. 2015. Heating up a cold subject: prospects for under-ice plankton research in lakes. J. Plankton Res. 37: 277-284. doi: 10.1093/plankt/fbv002.

Hawes, I., H. Giles, and P. T. Doran. 2014. Estimating photosynthetic activity in microbial mats in an ice-covered Antarctic lake using automated oxygen microelectrode profiling and variable chlorophyll fluorescence. Limnol. Oceanogr. 59: 674–688. doi:10.4319/lo.2014.59.3.0674

Karlsson, J., J. Ask, and M. Jansson. 2008. Winter respiration of allochthonous and autochthonous organic carbon in a subarctic clear-water lake. Limnol. Oceanogr. 53: 948-954. doi: 10.4319/lo.2008.53.3.0948.

Katz, S. L., L. R. Izmest'eva, S. E. Hampton, T. Ozersky, K. Shchapov, M. V. Moore, S. V. Shimaraeva, and E. A. Silow. 2015. The "Melosira years" of Lake Baikal: Winter environmental conditions at ice onset predict under-ice algal blooms in spring. Limnol. Oceanogr. 60: 1950–1964. doi:10.1002/lno.10143

Kleeberg, A., A. Freidank, and K. Joehnk. 2013. Effects of ice cover on sediment resuspension and phosphorus entrainment in shallow lakes: Combining in situ experiments and wind-wave modeling. Limnol. Oceanogr. 58: 1819–1833. doi:10.4319/lo.2013.58.5.1819

Knowles, R., and D. R. S. Lean. 1987. Nitrification: A significant cause of oxygen depletion under winter ice. Can. J. Fish. Aquat. Sci. 44: 743–749. doi:10.1139/f87-090

Kouraev, A. V., E. A. Zakharova, F. Remy, A. G. Kostianoy, M. N. Shimaraev, N. M. J. Hall, and A. Y. Suknev. 2016. Giant ice rings on lakes Baikal and Hovsgol: Inventory, associated water structure and potential formation mechanism. Limnol. Oceanogr. 61: 1001–1014. doi:10.1002/lno.10268

Kozhova, O. M. 1961. On the periodical changes in the development of phytoplankton in Lake Baikal. Proc. All-Soviet Hydrobiol. Soc. 1: 28–43.

Lizotte, M. P. 2001. The contributions of sea ice algae to Antarctic marine primary production. Am. Zool. 41: 57–73.

Ma, J., and others. 2016. The persistence of cyanobacterial (Microcystis spp.) blooms throughout winter in Lake Taihu, China. Limnol. Oceanogr. 61: 711–722. doi:10.1002/lno.10246

Maeda, O., and S. E. Ichimura. 1973. On the high density of a phytoplankton population found in a lake under ice. Int. Revue ges. Hydrobiol. Hydrogr. 58: 673–689. doi:10.1002/iroh.19730580507

Magnuson, J. J., and others. 2000. Historical trends in lake and river ice cover in the northern hemisphere. Science 289: 1743–1746. doi:10.1126/science.289.5485.1743

McKnight, D. M., B. L. Howes, C. D. Taylor, and D. D. Goehringer. 2000. Phytoplankton dynamics in a stably stratified Antarctic lake during winter darkness. J. Phycol.: 36: 852–861.

Morgan-Kiss, R. M., M. P. Lizotte, W. Kong, and J. C. Priscu. 2016. Photoadaptation to the polar night by phytoplankton in a permanently ice-covered Antarctic lake. Limnol. Oceanogr. 61: 3–13. doi:10.1002/lno.10107

Özkundakci, D., A. S. Gsell, T. Hintze, H. Täuscher, and R. Adrian. 2016. Winter severity determines functional trait composition of phytoplankton in seasonally ice-covered lakes. Glob. Change Biol. 22: 284–298. doi:10.1111/gcb.13085

Post, E., and others. 2013. Ecological consequences of sea-ice decline. Science 341: 519–524. doi:10.1126/science.1235225

Rigler, F. H., M. E. MacCallum, and J. C. Roff. 1974. Production of zooplankton in Char Lake. J. Fish. Res. Bd. Can. 31: 637–646. doi:10.1139/f74-095

Rizk, W., G. Kirillin, and M. Lepparanta. 2014. Basin-scale circulation and heat fluxes in ice-covered lakes. Limnol. Oceanogr. 59: 445–464. doi:10.4319/lo.2014.59.2.0445

Rosi-Marshall, E. J., and T. V. Royer. 2012. Pharmaceutical compounds and ecosystem function: An emerging research challenge for aquatic ecologists. Ecosystems 15: 867-880. doi:10.1007/s10021-012-9553-z

Salmi, P., and K. Salonen. 2016. Regular build-up of the spring phytoplankton maximum before ice-break in a boreal lake. Limnol. Oceanogr. 61: 240–253. doi:10.1002/lno.10214

Salonen, K., M. Leppäranta, M. Viljanen, and R. D. Gulati. 2009. Perspectives in winter limnology: closing the annual cycle of freezing lakes. Aquat. Ecol. 43: 609–616.

Salonen, K., M. Pulkkanen, P. Salmi, and R. W. Griffiths. 2014. Interannual variability of circulation under spring ice in a boreal lake. Limnol. Oceanogr. 59: 2121–2132. doi:10.4319/lo.2014.59.6.2121

Sharma, S., J. J. Magnuson, R. D. Batt, L. A. Winslow, J. Korhonen, and Y. Aono. 2016. Direct observations of ice seasonality reveal changes in climate over the past 320-570 years. Sci. Rep. 6: 25061. doi:10.1038/srep25061

Steel, H. C. B., C. P. McKay, and D. T. Andersen. 2015. Modeling circulation and seasonal fluctuations in perennially ice-covered and ice-walled Lake Untersee, Antarctica. Limnol. Oceanogr. 60: 1139–1155. doi:10.1002/lno.10086

Striegl, R. G., P. Kortelainen, J. P. Chanton, K. P. Wickland, G. C. Bugna, and M. Rantakari. 2001. Carbon dioxide partial pressure and 13C content of north temperate and boreal lakes at spring ice melt. Limnol. Oceanogr. 46: 941–945. doi:10.4319/lo.2001.46.4.0941

Titze, D. J., and J. A. Austin. 2014. Winter thermal structure of Lake Superior. Limnol. Oceanogr. 59: 1336–1348. doi:10.4319/lo.2014.59.4.1336

Tulonen, T., P. Kankaala, A. Ojala, and L. Arvola. 1994. Factors controlling production of phytoplankton and bacteria under ice in a humic, boreal lake. J. Plankton Res. 16: 1411–1432. doi:10.1093/plankt/16.10.1411

Twiss, M. R., and others. 2012. Diatoms abound in ice-covered Lake Erie: An investigation of offshore winter limnology in Lake Erie over the period 2007 to 2010. J. Great Lakes Res. 38:18–30. doi:10.1016/j.jglr.2011.12.008

Van Cleave, K., J. D. Lenters, J. Wang, and E. M. Verhamme. 2014. A regime shift in Lake Superior ice cover, evaporation, and water temperature following the warm El Nino winter of 1997-1998. Limnol. Oceanogr. 59: 1889–1898. doi:10.4319/lo.2014.59.6.1889

Wehenmeyer, G. A. 2004. Synchrony in relationships between the North Atlantic Oscillation and water chemistry among Sweden's largest lakes. Limnol. Oceanogr. 49: 1191–1201. doi:10.4319/lo.2004.49.4.1191

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