

Whither winter: The altered role of winter for freshwaters as the climate changes

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Abstract:

Our changing climate is having effects on freshwater ecosystems in all seasons, especially winter. High latitude lakes, wetlands, and rivers are experiencing shorter periods of ice cover, and lower latitudes systems that used to freeze are experiencing open water conditions throughout the winter. An 2019 AGU Chapman conference convened aquatic scientists to examine these changes and address the implications of changing winters to aquatic life, chemistry and physics. Several studies demonstrate decreased ice cover duration than in the past. The removal of an ice 'lid' from lakes and rivers impacts the exchange of gases with the atmosphere and the predominant types of metabolism occurring in the waters below, with the potential for more photosynthesis and an increase in oxic vs. anoxic metabolism when the 'lid' is removed. Multiple studies indicated an increase in the inter-annual variability of winters, especially in terms of ice-cover duration and ice quality. Increased variability may simply be an outcome of a more variable winter climate or small differences in environmental conditions such as temperature that can have strong effects on gas exchange, light transmission and turbulence when ice forms. A question that merits further consideration is whether and how winter, especially those of shorter duration and severity, will change the dynamics of freshwater systems. Are there memory or legacy effects that carry over to the next season or year? There is much work to be done to understand how changing winters will impact the biogeochemical behavior of lakes and rivers in the coming decades.

key points:

1. Several of the papers point to interannual variability in winter and seasonal ice cover along with decreased ice cover duration
2. Available winter datasets have grown supporting conceptual developments, but increased efforts focused on ecological responses are needed
3. Future research should examine connections between seasons, deploy submersed sensors year-round, and use remote sensing approaches

Plain language summary

Winters at mid-high latitudes are changing rapidly with important implications for freshwater ecosystems. An AGU Chapman conference, convened in 2019, brought together scientists to outline what we know about the changes that are occurring and what questions need further study. This special issue is a collection of the papers that developed from that workshop. These

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studies demonstrate that lakes and rivers at mid-high latitudes are experiencing less ice cover duration and greater variability in year-to-year ice cover. Changing ice and snow cover impacts processes occurring under ice in winter by altering the light regime, mixing, biota present, and the availability of oxygen. There are many important research questions regarding winter dynamics that still need to be addressed but one of the most important ones has to do with how changing winters might influence the biota in other seasons.

The Earth is warming due to increased greenhouse gas concentrations in the atmosphere, but warming is not uniform. Specifically, ecosystems at high latitudes and elevations are warming faster than the global average over the past 150 years (IPCC 2021). As temperatures increase and precipitation patterns shift globally (Harris et al. 2020, O'Reilly et al. 2015), ecological and biogeochemical processes are responding to a changing winter where there is more precipitation as rainfall and the winter season is of shorter duration. Lakes and rivers occupy center stage in this dynamic environment because they are sentinels of human influence on landscapes and climate (Adrian et al., 2009; Williamson et al., 2009). Most of the world's naturally formed freshwater lakes are located above 45° north (Verpoorter et al. 2014), typically freeze during winter, and are expected to continue losing ice coverage in coming decades (Magnuson et al. 2000, Sharma et al. 2019).

As seasonal lake ice-cover duration declines or even disappears in some regions, these freshwater systems are losing one of the most important features of the winter season in temperate and polar regions. Yet, mostly due to the difficulties of sampling during periods of ice-cover, we actually know little about what happens in lakes under ice and what the significance of under-ice processes are following ice-breakup. How much of annual production occurs under ice? In the past, it was presumed to be very little, but recent estimates are challenging those assumptions (Hampton et al. 2017; Song et al. 2019; Yoshida et al. 2003). Do winter and under-ice biogeochemical conditions have implications for spring and summer dynamics and if so, how are those implications changing with rapidly changing winters?

To address these questions and many others, a group of investigators held a Chapman Conference in October 2019 at Flathead Lake Biological Station ('Winter Limnology in a Changing World'). Organizing topics included climate and ice dynamics, biological and biogeochemical connections across seasons, temperature dependency of biotic processes and habitat, and trophic interactions under ice. There were more than 50 participants from 8 countries and more than 25% of the attendees were students. An "unconference" format was emphasized and working groups included many collaborators who had never met before. This conference was the last many would attend for some time because of the Covid-19 pandemic that erupted shortly after. We are fortunate that we were able to push forward on winter work and the relationships cultivated by the conference may prove to have lasting impact in aquatic science. The papers presented in this volume are likely to be an important part of that legacy. Here, we provide an overview of the key findings of articles contained in this special issue.

Concepts and syntheses

One of the goals of the conference was to develop conceptual perspectives on how winter is responding to a changing climate and how wintertime processes interact with processes during

other seasons. The significance of winter to freshwater processes has long been recognized (Wetzel 2001) but the underpinnings of the relationships between the physical drivers and biogeochemical dynamics have lacked a conceptual model. In the Lake Ice Continuum Concept (LICC), Cavaliere et al. (2021) identify key drivers of variation in winter processes in lakes focusing particularly on the myriad aspects of ice itself and the subsequent role of ice in mediating ecosystem energetics. Ice can be present or absent, it can cover a lake for a long time or a short time, and it can vary from optically transparent columnar ice ('black ice') to more opaque ('white ice'), all with important implications for biological, chemical and physical processes. The review and synthesis by Jansen et al. (2021) focused on developing an integrative understanding of how physical processes in lakes in winter are linked to biogeochemical and ecological dynamics. Primary drivers such as light availability and distribution of heat within the water column have cascading effects on critical chemical parameters such as redox state, which impacts both nutrients and predominant metabolic processes including aerobic respiration, nitrification-denitrification coupling, methane oxidation (Sawakuchi et al. 2021), and other anaerobic metabolisms such as methanogenesis, sulfate reduction, anoxygenic photosynthesis and anammox. These metabolic differences at the bottom of the food web impact higher trophic levels but our understanding of these connections are understudied. Cavaliere et al. (2021) present important hypotheses about the within lake differences under various types of winter regimes, and the significance of these within lake dynamics to ecosystem scale processes in winter and subsequent seasons needs further exploration.

Changes in lake and river ice

In lakes, the phenomenon of a decreasing period of winter ice in the northern hemisphere has been recognized for quite some time (Anderson et al. 1996; Magnuson et al. 2000; Magnuson et al. 1997). The rich dataset available at the Experimental Lakes Area in Canada adds an important nuance to this general trend by clearly demonstrating that not only is the duration of ice cover decreasing with time, but the interannual variability is actually increasing (Higgins et al. 2021). This work shows that ice-on dates in these lakes are trending later with a high degree of variation and a mean decrease of about 25 days for all of the lakes in the past 50 years. Interannual variation in ice cover duration has doubled over that same time-period.

Evidence continues to grow that many lakes worldwide are experiencing declines in the number of ice-covered days. Focusing on the Laurentian Great Lakes, Ozersky et al. (2021) reviewed available information about winter processes. Similar to the ELA lakes, there can be dramatic interannual variability in the maximum spatial extent of ice on in-lake physics, biology, and biogeochemistry. Of particular importance for communities in the extensive Great Lakes region of North America, winters achieving 25% or less ice coverage have become more frequent in the last two decades in Lake Superior, Michigan, Huron, Erie, and Ontario. The Great Lakes present unique logistical challenges for studying winter-time processes, such as safely accessing sampling sites located far from shore. But they also can behave very differently than small lakes due to greater patchiness and transitory nature of ice cover along with very different stratification patterns. Additional research infrastructure would greatly enhance our ability to understand winter processes in large lakes, and their role in shaping broader seasonal cycles (Figure 1), in advance of potentially unprecedented changes that could occur in association with continued ice loss.

The special issue includes two other new analyses of long-term trends in lake ice using well over a century of records for lakes around the world. Imrit and Sharma (2021) found that ice-on dates have shifted 11 days later per century based on linear regression in 18 lakes, while ice-off dates have shifted 9 days earlier per century. Sharma et al. (2021) explored questions involving lake ice trends, with attention to the warmer winters of record, for 60 lakes mostly in North America and Northern Europe that had more than 100 years of ice records. They found that in addition to shifts in mean ice cover duration, the more extreme years of latest ice-on, earliest ice-off, and shortest ice cover duration have also become more frequent in the last few decades. Perhaps most importantly, they found the rate at which lakes are becoming ice-free has increased with respect to historic analyses. The most recent years in the analysis (1992-2016) had the most rapid change in ice cover. These analyses of lake ice trends contribute to an important and very active research area that builds on earlier ice work (Magnuson et al. 2000, Benson et al. 2012). Will these trends continue? Undoubtedly that question is in the forefront of many researchers' minds. Decreases in uncertainty of long range global and regional climate models lead many researchers to expect that weather conditions required for longer seasonal ice duration, thicker ice, and larger spatial extent of ice coverage will generally continue shifting northward and to higher elevations in coming decades.

Multiple articles highlight differences in ice phenology within and among regions. As discussed above, Higgins et al. (2021) found that winter ice-cover duration varied by more than one month among 30 lakes in Northwestern Ontario. Cross-lake variation in the ice-off date involved relationships between lake size, snow thickness, and ice thickness. Smits et al. (2021) used a set of 15 lakes spanning a large elevation gradient in the Sierra Nevada of California to highlight the considerable among-year variability in duration of ice cover, with about a 40 day difference in duration of ice-cover resulting from variation in winter snowpack and temperature. Very high snowpack on high elevation mountain lakes was identified as a more important driver of ice-off and ice-phenology than in low elevation lakes. In Antarctic lakes that experience year-round ice cover, new insights about seasonal dynamics and long-term trends in phytoplankton (Patriarche et al. 2021) provide an important juxtaposition for the community of researchers who have worked primarily in the northern hemisphere.

Similar to lakes, the winter conditions experienced by rivers at high latitude are changing due to the impacts of climate change (Thellman et al. 2021). Due to the tremendous variability in river size, steepness, flow, shape and watershed characteristics, the local manifestations can be incredibly variable. Nonetheless, many rivers and streams experience some degree of winter ice conditions and we know very little about how ice influences aquatic ecology and biogeochemistry in these systems, particularly in headwater systems. It is critical to observe these dynamics to predict and manage them in the future. Changing phenology is one of the well-studied components of changing climate in terrestrial systems, but it is far less understood in lotic systems. The timing of leaf-fall, ice formation, and ice break-up are not often considered in rivers but could have far-ranging effects on food webs and biogeochemistry.

Physical and biogeochemical dynamics

Physical dynamics are a fundamental abiotic control on ecosystem processes during the winter. Jansen et al. (2021) provide a thorough review of physical mechanisms occurring during the winter, and importantly synthesize their implications for geochemical and biological processes.

They address such questions as: How much mixing is occurring under ice, what are the most important drivers and what does it mean for biological processes like primary production and decomposition? What are the implications for nitrification/denitrification and other redox-coupled processes? During ice cover, organisms are exposed to complex hydrodynamics involving density currents, gyres, internal waves, and horizontal convection (Jansen et al. 2021). For example, density currents associated with slight warming or cooling of water near its maximum density of 4°C, and solute production, can be detected as soon as ice cover forms. These density currents have been observed to circulate water both downslope and upslope within lakes, with velocities on the order of 10^{-3} m s⁻¹ on the downslope and 10^{-6} m s⁻¹ to 10^{-5} m s⁻¹ on the upslope.

A key component discussed in the LICC (Cavaliere et al. 2021) are the effects of ice, and snow and ice, on redox conditions. Redox is a master variable (Wetzel 2001) that strongly influences the types of metabolism that occur in aquatic ecosystems. McAdams et al. (2021) observed the migration of reduced sulfur species from several centimeters below the sediment-water interface when no ice was present in shallow Prairie Pothole lakes to at or above the sediment-water interface under the ice. Another study found a relationship between methane oxidation and P content among different lakes (Sawuchi et al. 2021), which could also be a redox-related relationship given that phosphate is released from sediments at higher rates under lowered redox states (Mortimer 1942).

The tools available for studying winter biogeochemical processes are improving rapidly, enabling high frequency measurements even under ice of important parameters such as temperature, pH and dissolved oxygen (DO). Using temperature and DO probes in lakes of the Sierra Nevada and the Klamath mountains, Smits et al. (2021) concluded that air temperature and precipitation (snowfall) were the most important drivers of the timing of ice formation and ice-off, while lake morphometry was the most important factor determining DO depletion rates under ice. They found that seasonal and interannual variability were higher in small, shallow lakes than larger, deeper lakes. New research describes the particulate organic matter, fatty acid, and inorganic nutrient content within Arctic lake ice (Imbeau et al. 2021), under-represented components of lake biogeochemical budgets that become available to planktonic microbes upon ice-out in spring or summer.

Another factor affecting DO depletion rates under ice in shallow lakes is the dominant plant types. A considerable literature has examined differences in shallow lakes where the dominant plants are macrophytes ('clear' lakes) vs. phytoplankton ('turbid' lakes). Rabaey et al. (2021) observed similar DO dynamics in these systems in the open water seasons (spring, summer and fall), while in winter under ice, there were greater oxygen depletion rates in the clear lakes, likely a consequence of degradation of the accumulated plant biomass without ingress from the atmosphere. Coupled with observations that clear lakes have lower N:P ratios than turbid lakes, likely due to increased denitrification (Ginger et al. 2017), it may be that winter provides some 'memory' that is manifest throughout the year in these shallow lakes.

In deep lakes, winter may also induce memory effects that remain throughout the open water period. Dugan (2021) examined ice-on and ice-off dates at different latitudes and observed that ice-off dates are changing more than ice-on dates but that the effects are different in northern vs.

southern Wisconsin lakes. Earlier ice-off in the northern lakes led to warmer hypolimnia but not necessarily increased dissolved oxygen depletion due to incomplete mixing at late ice-off. Nonetheless, changes in stratification due to a warming climate are likely going to be most severe in higher latitude lakes due to the fact that those systems are warming fastest. The findings raise the possibility that the strength of linkages between winter and summer may decrease as lake ice is lost.

Biology

New tools are also becoming available to study how under low light conditions the amount of light available directly influences phytoplankton composition. Using an over winter deployment of a fluoroprobe to analyze shifts in phytoplankton pigments in a permanently ice-covered Antarctic lake, Patriarche et al (2021) were able to track the shifts from dominance by chlorophytes in summer to dominance by mixotrophic cryptophytes and haptophytes in winter, a condition of total darkness. This shift represents not only a change in phytoplankton composition, but also a change in overall ecosystem function during winter that may occur when snow cover greatly reduces the penetration of light through the ice and snow cover in Antarctic lakes. Coupling these *in situ* measurements with remote sensing tools that are being used to assess lake dynamics in winter (Engram et al., 2020; Moukomla & Blanken, 2016) and are likely to become increasingly important. Given that sampling in winter is inherently difficult and sometimes dangerous, these tools provide an avenue for dramatically expanding the scope of our understanding of winter dynamics in lakes. Moreover, the Covid-19 pandemic and associated disruption of travel globally has underscored the value of these sampling measures.

In another examination of winter-summer linkage, Hazuková et al. (2021) analyzed phytoplankton in two contrasting Arctic lakes that differed in dissolved organic carbon concentration, and by extension, light availability. Their data suggested that under-ice phytoplankton provide seed populations for early spring blooms, with largest shifts in species composition occurring in late summer associated with nutrient depletion and/or grazing. Even in situations where summer and winter conditions in the water column bear little resemblance to each other, it is still possible the seasons could be linked through unmeasured "carrier" variables- for example, if winter conditions favor secondary production of benthic invertebrates that then become an important summer food source to fish as they emerge.

Returning to rivers, Thellman et al. (2021) reviewed the literature on ecology under river ice and examined relationships between winter gross primary production (GPP) and river size. Based on a compiled stream dataset (Appling et al. 2018) that included 25 stream sites with mean winter air temperatures between 0 and 2°C., the fraction of annual GPP produced in winter was largest in small rivers. This finding is opposite of predictions from the river continuum concept and river observations taken during ice-free conditions, perhaps because small canopy-covered streams have high sensitivity to the gain in winter light availability associated with winter canopy loss. However, in the face of a warming winter, changes in the distribution of primary production and broader river ecology are possible. For example, Jankowski et al. (2021) found that in warmer winters, the Upper Mississippi River experienced higher chlorophyll and by extension, phytoplankton biomass. Chlorophyll concentration was highest in ice-free reaches and backwaters, and occasionally exceeded summer values.



Figure 1. Seasonal change at Lake Itasca, Minnesota, USA showing summer, autumn, winter, and early spring. Photos by Lesley Knoll.

Conclusions

This compendium represents state-of-the-art research on how freshwaters are changing in winter due to a changing climate and hydrology. Papers covered a wide range of aquatic system sizes, from small lakes to large and small rivers to the Laurentian Great Lakes, and a myriad of geographical regions from lowland to alpine systems, and Arctic to boreal to temperate to Antarctic systems. The tools and study foci exemplified in this collection of papers examining winter dynamics vary from physical processes to chemical dynamics to changes in organisms and communities to ecosystems.

Several avenues for future research emerged from collaborations presented in this special issue. In addition to long-term changes associated with ice and snow, interannual variability in air temperature and precipitation is significant and important for interpreting lake-climate and river-climate interactions. Interannual variability in temperature alone can change ice dynamics and increase variability, through numerous thermodynamically-controlled biological processes. As observations accumulate, interannual variability becomes increasingly useful for predicting the future. Prior event sequences can be classified and used to weigh predictions and forecasts if/when similar conditions return to the system. Long-term records can also be used to evaluate whether the current year deviates from other years that had similar patterns of air temperature, snowpack, or other climate variables. Time lags, memory, legacies— these concepts are relevant

for evaluating linkages to connections among seasons, and the degree to which summer follows winter conditions or vice versa. Collaborations represented in this special issue revealed considerable interest in seasonal connections, which could help us establish how patterns of ice loss interact with aquatic processes outside of winter. But there remains much work to be done in terms of identifying testable hypotheses about seasonal connections. Remote sensing of lake and river ice and color represents an important avenue that can help us understand the broader phenology of aquatic ecosystems, including potential connections among seasons, especially for sites where in situ approaches can be combined with satellite approaches. It is essential for researchers to continue expanding their capacity to collect observations across all seasons and deploy *in situ* sensors year-round.

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