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HORIZONS

Heating up a cold subject: prospects for under-ice plankton research in lakes

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Long-term patterns and drivers of ecosystem structure may be misunderstood if knowledge of an ecosystem is derived primarily from a single season, a situation common in many temperate lakes where the role of winter has been less studied. In lakes, avoidance of winter research has been especially pronounced for those that experience winter ice, but critical ecological processes can take place under ice. Even when obscured by snow, ice transmitting as little as 2% incident light can allow relatively high rates of photosynthesis, and winter trophic interactions may have year-round repercussions. Here, we offer a suite of research questions that require attention, in order to build a mature understanding of seasonal plankton dynamics in lakes. Specifically, we ask freshwater ecologists to consider the extent to which abundance and nutrition of winter primary productivity supports consumers under the ice, reorganizes food webs, and how long the effects of winter trophic dynamics extend throughout the year. In addition, we recognize some critical gaps in knowledge about physical and biogeochemical conditions at the time of ice-off. Worldwide shortening in ice duration lends imperative to under-ice studies, in order to more fully understand changes in ecosystem structure and function that may already be underway.

KEYWORDS: winter; ice; plankton; trophic interactions; nutritional quality; state transitions

INTRODUCTION

Temporally dynamic aspects of ecology are attracting increasing attention as ecologists attempt to unravel and predict the complexity of ecosystem response to climate change. In lakes, long-term warming trends can alter ecosystem metabolism (Baulch *et al.*, 2005) and essential properties of the physical environment such as ice duration and area of bottom-fast ice (Sturm and Liston, 2003; Surdu *et al.*, 2014), while also shifting the phenology of important processes such as spring turnover and the onset of the spring bloom (Adrian *et al.*, 2006; Thackeray *et al.*, 2013). These changes may reorganize food webs and fundamentally change carbon flow in ecosystems (O'Connor *et al.*, 2009). Empirical and theoretical frameworks exist to model temporal regime changes and state transitions (Klausmeier, 2010; Dakos *et al.*, 2012), but as models become more complex, they require more information to drive them. In contemplating the mechanisms and consequences of the longer term (e.g. multidecadal) ecosystem shifts now unfolding with climate change, ecologists are faced with admitting that we lack basic knowledge about ecosystem state transitions in a large number of ecosystems, even at the intra-annual scale. Most prior research focuses on non-winter months (Salonen *et al.*, 2009), particularly in temperate regions, such that the drivers and consequences of state transitions are poorly understood.

WINTER LIMNOLOGY AS A NEW FRONTIER

Limnologists' historical aversion to winter has both logistical and theoretical underpinnings. Academic schedules, extreme conditions and a prevailing view that winter is the "dormant season" have inhibited winter work. This neglect of winter has been especially strong in ice-covered lakes. In a Web of Science search of the 14 418 papers on lake algae since 1964, 4% of abstracts included ice, and only one of 50 randomly selected papers from this list included winter research on an ice-covered lake. This view of winter as a season of negligible activity has started to appreciably change (Salonen *et al.*, 2009); we now better understand that mortality, decomposition and dormancy are not the only processes occurring under lake ice.

Even when blanketed with snow and ice, aquatic ecosystems may have high productivity, and winter trophic interactions can have year-round repercussions. These principles have been demonstrated in marine ecosystems, where polar research has dramatically advanced under-ice ecology. In both Arctic and Antarctic systems, under-ice primary productivity can be high and significant for consumers (Lizotte, 2001; Grebmeier, 2012); for

example, in some areas Antarctic ice-associated algae contributes 25–30% of total annual productivity (Arrigo and Thomas, 2004). Far less is known of the role of winter processes in lakes.

One of freshwater ecology's most influential papers was the Plankton Ecology Group's (PEG) model that described seasonal development of plankton in temperate lakes (Sommer *et al.*, 1986). In the original PEG model, winter was a time of physical suppression and essentially a "reset" button; community assembly began anew each spring. In 2012, the model was comprehensively revised (Sommer *et al.*, 2012), reflecting (among other things) an explicit appreciation for the importance of winter states and transitions, with a call for winter work. The winter studies that have been conducted in ice-covered lakes suggest that some of the most critical ecological processes are playing out under the ice, highlighted by the recognition of greenhouse gas release at ice-out and high-profile fish kills that can occur in oxygen-depleted lakes under ice (Bertilsson *et al.*, 2013). Worldwide shortening in ice and seasonal snow cover duration (Magnuson *et al.*, 2000) lends imperative to under-ice studies, in order to understand how ecosystems are responding to these changes.

UNDER-ICE ECOLOGY

Much of the pioneering under-ice limnology to date has been done in polar lakes, where darkness associated with winter and heavy snow can favor heterotrophic processes as the conditions suitable for autotrophy decline. Accordingly, polar limnology has focused on heterotrophic activity and mixotrophic strategies that allow biota to persist through darkness (McKnight *et al.*, 2000; Vincent *et al.*, 2008).

However, in many ice-covered lakes, light can continue to fuel substantial primary productivity in winter. When free of snow, clear lake ice can allow as much as 95% PAR transmission (Bolsenga and Vanderploeg, 1992), and when obscured by snow, ice transmitting as little as 2% incident light can allow relatively high rates of photosynthesis (Cota, 1985). Further, light transmission can promote complex convection patterns under the ice, sometimes but not always (e.g. Vehmaa and Salonen, 2009) keeping small celled organisms and nutrients in suspension in the photic zone (Granin *et al.*, 2000; Bertilsson *et al.*, 2013). As ice grows vertically downwards, solutes are frozen out of lake ice with their concentration increasing in the water immediately below (Canfield *et al.*, 1983). Although effects of such enhanced solute concentrations on freshwater plankton are largely unknown, it is possible that nutrient concentration under the ice could benefit growth of phytoplankton. In the marine environment, the rejected brine exported from growing ice crystals can prohibit rapid algal

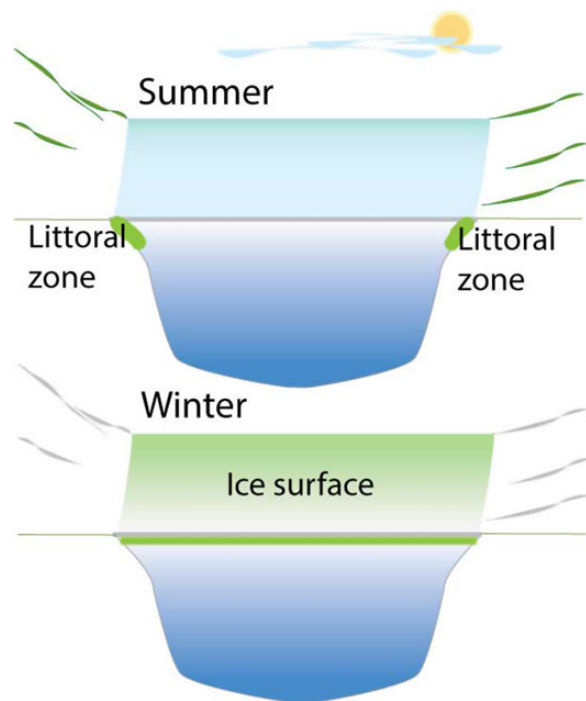


Fig. 1. Timoshkin's (Timoshkin, 2001) concept of ice as a "second bottom," based on experiences at Lake Baikal. In lakes, conditions where both attached and planktonic algae can exploit numerous habitats with relatively consistent access to light and nutrients (represented by green color), and habitat complexity can shelter diverse consumers, are typically thought to occur almost exclusively in the littoral zone. In winter, if light penetrates ice, the real estate for such productivity potentially spans the full lake surface, essentially providing a "second bottom."

growth by inducing full water-column convection that carries phytoplankton cells in and out of the photic zone (Shcherbina *et al.*, 2003). Such a phenomenon may also occur in ice-covered saline lakes.

Importantly, ice can provide a potentially vast, seasonally available habitat on which algae can grow (Figs 1 and 2). Ice-attached algae provide habitat and resource complexity for a community of associated microscopic consumers, which pass on energy to larger consumers (Melnik *et al.*, 2008). Although the extent of its importance in lakes is currently unknown, we know from some marine and lake studies that under-ice primary productivity can profoundly reorganize energy flow, providing temporal and spatial energy subsidies to consumers in energy deprived time periods or habitats. For example, mobile consumers move energy from the ice-associated community to other areas of the ecosystem (Nicol *et al.*, 2008), and dead algae sink to benthic consumers (Bondarenko *et al.*, 2006; Grebmeier, 2012; Boetius *et al.*, 2013).

Organisms that feed on the ice-associated algae may receive more than basic winter sustenance; ice-algae likely provide a unique nutritional cocktail. Algae growing in colder conditions are often richer in key polyunsaturated

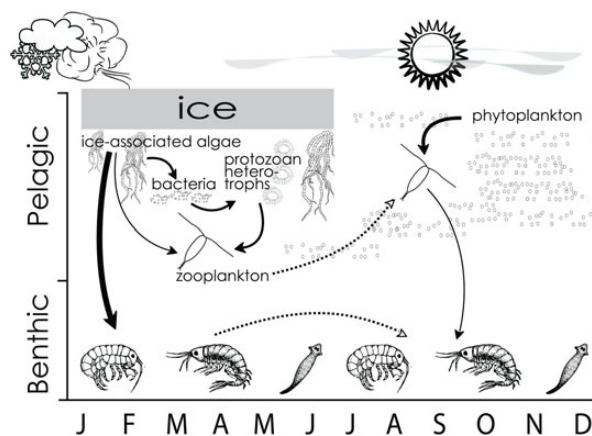


Fig. 2. A conceptualization of potential changes in food web organization that may occur seasonally in a large deep lake under conditions of relatively high light penetration through ice. Weather and water conditions at ice onset determine ice qualities that influence under-ice processes—e.g. light transmission that promotes photosynthesis and nutrient availability. Dominant under-ice algae may be too big to be readily eaten by many pelagic consumers (zooplankton), but blooms foster microbes and bacterivores on which zooplankton feed, lengthening the pelagic food chain relative to summer. Large under-ice algae directly provide a vital food resource to benthic consumers as filaments die and settle, strengthening benthic-pelagic coupling with a shorter food chain in winter relative to summer when smaller phytoplankton do not reach the benthos. Both benthic and pelagic consumers carry forward energetic and nutritional benefits of the under-ice algal bloom (dotted lines).

fatty acids (PUFAs) (Guschina and Harwood, 2006). These PUFAs are an essential dietary component for zooplankton and fish (Dalsgaard *et al.*, 2003), and may impose limitations on zooplankton biomass and thus food web relationships (Brett and Müller-Navarra, 1997). It has also been noted that under low light conditions, such as may be encountered under lake ice, algae tend to contain higher cellular N:C and P:C ratios (Sterner *et al.*, 1997; Hessen *et al.*, 2008), and may have higher PUFA content (Guschina and Harwood, 2006), and nutritional quality. Moreover, in Antarctic sea-ice, algal production of mycosporine-like amino acids (MAAs) helps to protect both the algae and their consumers from damaging ultraviolet (UV) radiation (Arrigo and Thomas, 2004). In lakes, zooplankton similarly acquire UV protection from consuming MAAs in algae (Hansson *et al.*, 2007) but the role of winter algae in providing these compounds is not as well understood. The magnitude and quality of ice-associated algae as food has been demonstrated to be fundamental to maintaining Arctic and Antarctic inter-seasonal ecosystem functioning, and while many mysteries remain in these systems, polar marine research is years ahead of freshwater science in closing the loop between ice-covered and ice-free ecosystem functioning.

Lake Baikal in Siberia is one of the more well-studied systems in winter, illustrating important under-ice lake dynamics. For example, a large winter-time bloom in primary production under the ice frequently exceeds production

in the ice-free period (Kozhova and Izmet'eva, 1998; Hampton *et al.*, 2008), a phenomenon not exclusive to Baikal (e.g. Lake Haruna) (Maeda and Ichimura, 1973). Strong winter winds at Lake Baikal can sweep snow off the ice, increasing light penetration (Moore *et al.*, 2009). Baikal's under-ice blooms often include a large, endemic diatom *Aulacoseira baicalensis* (Popovskaya, 2000), and algal density can range from several hundred to tens of thousands of cells per liter (Kozhova, 1961). Extensive research has focused on determining the drivers of these remarkable blooms (Kozhova, 1961; Shimaraev, 1971; Verkhozina *et al.*, 2000; Bondarenko *et al.*, 2006) and while specific mechanisms remain unknown, it is increasingly clear that ice characteristics play an important role in driving algal growth (Mackay *et al.*, 2006; Jewson *et al.*, 2009). Whatever the underlying causes for these *Aulacoseira* blooms, the manifestation is dramatic, with under-ice video showing a productive and complex community developing around blooms, likely supporting high microbial biomass in addition to fueling grazers (Bondarenko *et al.*, 2006).

A recent review (Bertilsson *et al.*, 2013) focusing on microbial activity under the ice highlighted some of the differences that have been observed or that might be expected from winter to summer in seasonally ice-covered lakes. Overall growth and biomass of bacteria appear to be lower under the ice, although several groups (e.g. CH₄-oxidizing bacteria) maintain activity that parallels that of summer or may go through at least brief periods of high activity under ice. Bertilsson *et al.* (2013) make the case that understanding such strong differential responses to winter conditions among functionally diverse bacterial groups is critical in order to anticipate nutrient conditions at the beginning of the growing season as well as the release of greenhouse gases after ice-off.

EMERGING RESEARCH QUESTIONS

Sea-ice and freshwater literature points to many questions ripe for exploration in seasonally ice-covered lakes, some that may be addressed with data in hand while others necessitate further data collection. Below we suggest several key areas requiring future research.

What are the relative contributions of under-ice versus ice-free primary productivity?

A literature review suggests that algal biomass under ice is typically less than that of summer (Bertilsson *et al.*, 2013), with some dramatic exceptions such as Lake Baikal, but

even a ballpark estimate of the relative contribution of winter to overall annual productivity currently does not exist for most ecosystems. Many long-term lake sampling programs collect biotic and physical data periodically during ice cover (e.g. North Temperate Lakes Long Term Ecological Research; lter.limnology.wisc.edu/datacatalog/search), and syntheses could reveal general patterns in the relative contributions of winter and summer productivity as well as, potentially, the seasonal variation in environmental controls. Winter-time data gaps will likely necessitate interpolation and creative modeling of ice condition and extent to produce estimates of biological, physical and chemical dynamics under ice. As *in situ* sensor use increases, and particularly as the logistics of moored sensor (Baehr and DeGrandpre, 2002; Tanabe *et al.*, 2008) use or autonomous underwater vehicles (Forrest *et al.*, 2008) in harsh conditions become better understood, such data gaps will be radically reduced.

Further, inferences on under-ice phytoplankton biomass can be drawn from some remote-sensing products (Twiss *et al.*, 2012), although such results may be limited to lakes with largely snow-free ice or algal blooms forming at cracks or edges. Exploration of the potential for using such remote sensing techniques would likely yield highly influential results in this field, as it would facilitate field observation that is otherwise intractable in many ecosystems.

How does nutritional quality of winter and summer phytoplankton differ?

The increased content of PUFAs in phytoplankton growing in cold environments (Arrigo and Thomas, 2004) and the more favorable (higher) N:C and P:C ratios of phytoplankton from light-limited conditions (Hessen *et al.*, 2008) may mean that bulk under-ice primary production is of higher nutritional quality than summertime production. The virtual absence of wind-driven resuspension in ice-covered lakes could also mean that a greater proportion of suspended material under ice is of phytoplankton origin, rather than resuspended sediment, increasing the nutritional quality of suspended material. Thus, under-ice primary production may provide a more important contribution to higher trophic levels than would be apparent from rates of primary production alone. Because fatty acid profiles vary among phytoplankton groups (Dalsgaard *et al.*, 2003), changes in food quality between ice-on and ice-off periods may actually be driven primarily by community composition, and less so by temperature- or light-mediated effects on phytoplankton lipid synthesis. Characterizations of winter and summer algal and suspended material composition, and determination of nutrient stoichiometry, lipid content and lipid class analysis across different lakes will

help address the question of the relative quality of winter and summer production.

How does the flow of energy through the food web differ from winter to summer?

Previously many limnologists have presumed that the under-ice food web is similar to that of summer, albeit less active. However, as in sea-ice systems, grazer composition changes from winter to summer. In some cases, lake-ice algal communities can be strongly dominated by relatively large diatom filaments attached to ice and less readily consumed by pelagic grazers, and with faster sinking rates. This algae can be important to benthic consumers who access it when it sloughs off and sinks to the substrate (Bondarenko *et al.*, 2006). The complexity of hydrodynamics that can develop under ice (e.g. Kelley, 1997; Vehmaa and Salonen, 2009) may alter exchange among strata in numerous ways during winter, particularly as the light environment shifts throughout the season. Benthic–pelagic coupling thus may change substantially from winter to summer, as has been demonstrated in sea-ice systems (Grebmeier, 2012). For example, recent research in high-latitude lakes has demonstrated the importance of both lipid-rich zooplankton and littoral zoobenthos to Arctic char (Eloranta *et al.*, 2013) in winter during ice-cover.

In addition, an under-ice environment with attached algae creates a physically complex habitat in which a “microbial loop” can increase in prominence, with heterotrophic protists potentially lengthening the food chain for pelagic consumers (Hairton and Hairton, 1993; Moore *et al.*, 2004) in winter relative to summer, as is seen in marine ecosystems when zooplankton reliance on detritus increases during winter (El-Sabaawi *et al.*, 2010) and in some lakes where zooplankton living under ice may be subsidized by benthic algal production, which is channeled to consumers via heterotrophic bacteria (Karlsson and Sävström, 2009). Winter and summer trophic structure, from primary producers to apex predators, can be inferred from stable isotopes, fatty acid profiles or gut contents, synthesized across systems to reveal generalities (Karlsson and Sävström, 2009; Eloranta *et al.*, 2013; Galloway *et al.*, 2014).

How much does winter productivity affect growth of long-lived consumers through subsequent seasons?

Under-ice algal blooms, a high abundance of heterotrophs or mixotrophs, or a combination of these resources should provide nutritional benefits that manifest in the life history of the under-ice grazers and affect annual plankton

dynamics. For relatively longer lived animals that persist under ice, such as copepods or fish, the “fingerprints” of winter productivity may be apparent in the ice-free season (at varying time lags) by indicators such as body condition, stoichiometric ratios, lipid content, reproductive output or individual longevity. Quantitative analysis of biochemical tracer data (e.g. stable isotopes or fatty acids) can be used to tease apart which basal resources are primarily responsible for driving secondary production by zooplankton in lakes (Galloway *et al.*, 2014). Long-term data for some of these metrics may exist from some lakes and may be leveraged to test hypotheses about differences among seasons or years, by examining time-series models that utilize a variety of time lags (Hampton *et al.*, 2013) between under-ice drivers and grazer responses.

Do chemical and biological inputs from melting snow and ice influence ecological processes at the time of ice-off and beyond?

Algae, bacteria and viruses (Maranger *et al.*, 1994; Grebmeier 2012) as well as contaminants (Pfirman *et al.*, 1995; Tovar-Sanchez *et al.*, 2010) and organic carbon (Krembs *et al.*, 2002) are released from sea ice, and its surface, into the water column at the time of ice-off. Experiments in the Arctic Ocean show how inputs of organic carbon from melting sea ice increases the flux of carbon through the microbial food web, possibly leading to augmented productivity, in comparison to areas experiencing no organic carbon inputs from melting ice (Boras *et al.*, 2010).

In freshwater ecosystems, biological and chemical inputs from melting ice have received less attention, and while little is known about the effects these inputs on ecological processes, there have been relatively recent discoveries of biological communities living in lake ice (Felip *et al.*, 1995; Obolkina *et al.*, 2000; Bondarenko *et al.*, 2012). For example, in Lake Baikal, bacteria, diatoms, chrysophytes, ciliates and rotifers reside within the ice (Obolkina *et al.*, 2000; Bondarenko *et al.*, 2012), and these organisms are released into the water column upon ice-out, with some possibly seeding populations that develop during the early ice-free period. The ice of Lake Baikal accumulates heavy metals and other contaminants during the 4- to 6-month-long ice-cover period (Eugene Silow, personal communication) when air inversions develop over the lake, facilitating atmospheric transport and deposition of pollutants (Obolkin *et al.*, 2014), which may “shock” the ecosystem if a substantial amount of accumulated contaminants are released during ice-off. Of course, turnover is also occurring at the time of ice-off, mixing nutrients and resting stages up into the photic zone. In lakes, watershed inputs from melting snow and ice also will be important. Disentangling

ecological responses to the chemical and biological inputs from turnover and meltwater will require skillful field experimentation due to practical challenges associated with fieldwork at this time.

What long-term ecosystem changes can we expect to result from altered under-ice processes in seasonally ice-covered lakes as climate changes? Long-term changes in ice thickness, freeze and thaw dates and snow conditions are all being observed and predicted in the changing climate (Sturm and Liston, 2003). Studies of historical and contemporary interannual and spatial variability can indicate important physical and biological relationships that give us clues to how ecology will change under ice as climate changes. The prospect that changes in snow and ice will not be uniform across ecosystems certainly complicates global, regional or even lake scales of predicting ecosystem change that relate to ice. Linking these increasingly quantified changes in the physical system to biological changes and using this knowledge to predict future ecosystem shifts is a rich new frontier of interdisciplinary science.

We conclude with strong encouragement that such studies ideally should be undertaken as broad networks of collaboration, in order to speed the pace of our research relative to the change already occurring in seasonally ice-covered lakes. The production of synthetic analyses that facilitate prediction will require collaboration and knowledge sharing that moves beyond single lakes and regions and incorporates the critical physical, chemical and biological components that together shape the under-ice ecosystem and its contributions to annual processes.

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