REVIEW SUMMARY

CLIMATE CHANGE

Environmental and societal consequences of winter ice loss from lakes

Stephanie E. Hampton*, Stephen M. Powers, Hilary A. Dugan, Lesley B. Knoll, Bailey C. McMeans, Michael F. Meyer, Catherine M. O'Reilly, Ted Ozersky, Sapna Sharma, David C. Barrett, Sudeep Chandra, Joachim Jansen, Ryan P. McClure, Milla Rautio, Gesa A. Weyhenmeyer, Xiao Yang

BACKGROUND: Lakes are rapidly losing ice in response to climate change. Most of the world's lakes freeze, with a median ice duration of 218 days. The rate of lake ice loss has markedly accelerated over the past 25 years, with ice melt in some regions across the Northern Hemisphere arriving 45 days per century earlier and with many lakes experiencing increased intermittency of ice cover during winter in addition to ice-free winters. Lake ice loss is expected to affect a substantial proportion of the world's population, who rely on these lakes for diverse needs, including drinking water, fisheries, transportation, and more. Until recently, both logistical challenges as well as misconceptions of winter as a time of quiescence resulted in limited winter research. Conspicuous decreases in ice cover and advances in technology have spurred rapid growth in winter research on seasonally ice-covered lakes. This Review is structured around a central question that winter researchers are frequently asked: Why does it matter that lakes are losing winter ice?

ADVANCES: Changes in ice cover have critical consequences for water quality, fisheries and biodiversity, weather and climate, as well as important cultural and socioeconomic activities. Socioeconomic benefits of freshwater ice include recreation, cultural identity, ice fishing, and ice roads for winter transportation. Ice roads across lakes and rivers are extensively used in oil and gas exploration, and they offer connectedness for remote communities during winter. Although the full socioeconomic importance of lake ice has not been accounted, illustrative examples exist. For Sweden's population of about 10.5 million people, ~$880 million US dollars are spent annually on ice fishing. Less easy to quantify is the extent to which interacting with lake ice contributes to cultural identity while shaping social cohesion and cultural heritage for the millions of people who live near a lake that seasonally freezes. Global data syntheses and models reveal further change. Shifts in ice quality, toward thinner and less stable white ice, have also contributed to increased fatal drowning events in areas of the world where ice was once safer for humans to traverse. Shorter ice duration has allowed lakes to warm faster, accelerating evaporative water loss globally and contributing to summer water quality issues, such as cyanobacteria blooms. Warmer water can favor invasive species and negatively affect cold-water fish and other organisms that are well adapted to ice-covered aquatic conditions. Ice seasonally creates a distinctive ecological niche space. Clear ice allows for high transmission of light that can fuel substantial algal growth, providing highly nutritious food for zooplankton grazers and their predators and generating food web effects that extend beyond winter. Ice provides a stable structure that effectively isolates lakes from the atmosphere and surrounding land, with several important implications: Ice cover can prevent shoreline erosion from wave action during the winter and reduce greenhouse gas emissions as well as evaporative water loss to the atmosphere. For lakes prone to creating lake-effect snow, ice cover prevents these extreme events from occurring in downwind communities.

OUTLOOK: Recent model projections predict complete loss of ice on thousands of lakes that historically experienced seasonal ice cover. Synthesis of historical ice records combined with global climate models suggests that up to 230,400 of the world's 1.4 million lakes larger than 0.1 km^2 will experience some years with no ice cover by 2080. Lakes at lower latitudes are vulnerable to losing 80% of ice days that are safe for humans to traverse. Anticipating the environmental and societal consequences of freshwater ice loss requires updated theory and models that consider the role of winter conditions and that incorporate data across the full annual cycle. Greater scientific and public understanding of the importance of lake ice for ecosystem health is key to supporting breakthrough science that informs sound stewardship of freshwater resources. ■

Baikal seal pup on the ice of Lake Baikal. The Baikal seal (*Pusa sibirica*) is the world's only exclusively freshwater pinniped, and it is well adapted to a lake that freezes for half the year. It gives birth and raises pups on lake ice and maintains open holes in the ice to fish under ice through the winter.

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Environmental and societal consequences of winter ice loss from lakes

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Climate change is reducing winter ice cover on lakes; yet, the full societal and environmental consequences of this ice loss are poorly understood. The socioeconomic implications of declining ice include diminished access to ice-based cultural activities, safety concerns in traversing ice, changes in fisheries, increases in shoreline erosion, and declines in water storage. Longer ice-free seasons allow more time and capacity for water to warm, threatening water quality and biodiversity. Food webs likely will reorganize, with constrained availability of ice-associated and cold-water niches, and ice loss will affect the nature, magnitude, and timing of greenhouse gas emissions. Examining these rapidly emerging changes will generate more-complete models of lake dynamics, and transdisciplinary collaborations will facilitate translation to effective management and sustainability.

Winter research represents both a scientific frontier and a moving target as climate change alters ecosystems worldwide (*1*). Although the impact of climate change on the loss of winter lake ice has been clearly established, the full societal and environmental consequences of this loss remain unclear. Most of the world's known lakes freeze, with a median ice duration of 218 days over recent decades (*2*). Over the past 165 years, ice duration decreased by 31 days, and thousands of lakes that historically froze every winter now experience ice-free years (*3*, *4*). These changes have broad socioeconomic consequences. Seasonally frozen lakes occur near densely populated areas (Fig. 1), and human societies depend on these lakes for diverse uses, including drinking water, recreation, fisheries, and transport (Fig. 2). Future scenarios anticipate an acceleration of lake ice loss as well as increased intermittency and thinning of ice cover (*3*, *5*). In addition to providing important socioeconomic benefits, ice quality and duration control key physical, chemical, and biological processes within freshwater ecosystems (Fig. 2) through both direct and indirect pathways. Yet, the pace of ice loss may exceed our capacity to understand and predict the full extent of environmental and socioeconomic consequences.

Until recently, methodological challenges and pervasive misconceptions (*6*–*8*) resulted in limited incorporation of winter conditions into the annual cycle of lake ecosystem dynamics. This winter knowledge gap means that applied and theoretical freshwater science focused primarily on ice-free conditions, creating great uncertainty in predicting the effects of warming winters on lake ecosystems. Recent work has shown that under-ice processes can be dynamic and varied and that winter conditions affect ecosystems across seasons (*9*). These findings are spurring rapid growth in winter research through a combination of increasing availability of in situ sensors, process-based models, and remote sensing data. This growing knowledge has led to widespread acknowledgement that the imminent loss of seasonal ice cover across many thousands of lakes (Fig. 1) (*3*) is likely to be among the most important climate change impacts on the world's inland waters, particularly for those at northern latitudes.

The accelerating loss of lake ice as well as the need for, and surge of interest in, winter limnology necessitates a broad review. Our review is structured around a central question that winter lake researchers are frequently asked: Why does it matter that lakes are losing ice? Understanding the importance of the loss of ice cover for human and environmental systems frequently returns to the critical role of lake ice in providing strong physical structure that stabilizes and isolates underlying water and controls water temperature, which in turn influences a wide range of ecological dynamics and biogeochemical processes. Our goal is to inform nonspecialists and freshwater scientists alike about the multifaceted ways that ice structures environmental processes and supports socioeconomic benefits.

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Lake ice allows human uses of lakes that provide socioeconomic value

Winter lake ice supports a variety of important human activities tied to recreation, spiritual connections, aesthetic appreciation, cultural identity, ice fishing, and ice roads for winter transportation (*10*). These ice-associated activities contribute to local economies during a time of year that typically supports fewer visitors than the summer (*11*). Loss of seasonal ice challenges high-latitude and alpine communities, altering the environmental conditions that have shaped their cultural identity, social traditions, and economies during the cold and dark winter season (*12*, *13*). The overall socioeconomic importance of winter ice is still unknown, but studies have examined components of this question. For example, in 2011 it was estimated that ice anglers spent ~$240 million US dollars (USD) on ice fishing equipment across the US (*14*). In Sweden, as much as 0.027% of the gross national product (roughly $880 million USD) relates to ice fishing, and more than 2 million fishing days are dedicated to ice fishing in a country of about 10.5 million people (*15*).

In addition to fishing access, ice also offers an inexpensive way to create road networks for isolated northern communities and commercial enterprises (*16*). In some cases, roads are developed across networks of natural lake and river ice, and in other cases, water from lakes is used to construct roads made of ice across tundra (*17*–*19*). Construction of seasonal ice roads is estimated to be less than 1% of the cost of building permanent roads (*20*). These roads are extensively used in oil and gas exploration in remote northern areas (*18*), and they also represent a cost-effective option for remote communities to access social, cultural, and economic benefits (*21*, *22*). Climate change threatens the critical transportation infrastructure that winter ice roads provide (*23*).

Declining ice cover also threatens distinct cultural identities. Many of the world's most populous areas are colocated with some of the largest extent of lake ice (Fig. 1). Living in a northern climate and interacting with lake ice can contribute to one's identity and sense of place while shaping the social capital, cohesion, and cultural heritage of a community (*13*).

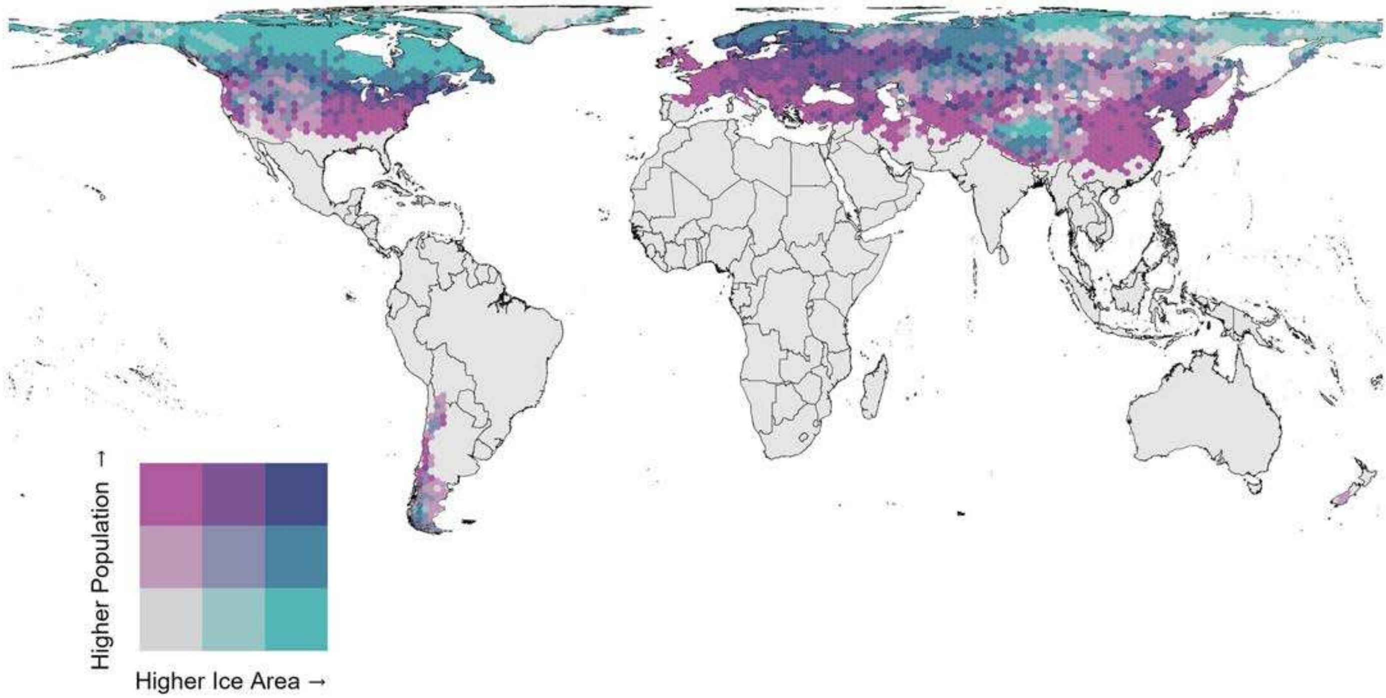

Fig. 1. Human populations adjacent to seasonally ice-covered lakes. At least 1.1 billion people live in the watersheds of ~1 million lakes that experience ice cover, as evaluated by daily imagery of lake ice [see materials and methods and (*138*) for reference]. Lakes are binned spatially, colored by the corresponding tertile of the bin's cumulative human population and lake ice area. Lake ice area was estimated using the HydroLAKES dataset (*139*) as a stencil for location and shape and daily observations from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellites from 2001 through 2022. Human population was estimated using the Gridded Population of the World dataset (*140*). A bright turquoise hexagon indicates an area in the highest tertile of lake ice area globally but the lowest tertile of human population. A bright magenta hexagon indicates an area with the highest tertile of human population but the lowest tertile of lake ice area. A bright purple hexagon indicates an area with the highest tertile of both lake ice area and human population. Lakes with no detectable lake ice area (e.g., lakes on the African continent, in Australia, and within the tropics) were removed from tertile calculations. The materials and methods section of the supplementary materials describes the development of Fig. 1 from public data, including R code.

For instance, several religious groups incorporate ice-covered water bodies into their ceremonies and traditions [e.g., Shintoism in Japan, Orthodox Christianity in Eastern Europe, and Catholicism in Germany and Switzerland (*10*, *24*)]. Additionally, subsistence activities in Indigenous communities offer important economic and nutritional benefits that cannot be separated from social and cultural identities (*25*). For many cultures and communities, projected ice losses (*3*, *26*) may mark a substantial shift in their way of life and interaction with nature. Although the impacts will vary distinctly by region and community (*10*), interviews conducted with Indigenous communities in Alaska have indicated that the loss of lake ice is a serious concern and will result in drastically changed ways of life (*27*).

Recent model projections forecast changes that will reduce the reliability of ice cover for human uses. Lakes that historically froze for the entire winter are beginning to experience intermittent ice cover—transient ice that does not persist every winter—with up to 18.4% of the 1.4 million lakes larger than 0.1 km^2 predicted to become intermittently ice covered by 2080 if global air temperatures continue to rise, affecting 656 million people who live near those lakes (*3*). Ice thickness will also markedly decline in response to climate change (*28*, *29*), making ice unsafe for humans to traverse (*23*, *30*). For example, in some regions of the world, the minimum ice thickness safe for human use is considered to be 10 cm of strong, black ice. Historically, across the Northern Hemisphere, lakes averaged 152 days of safe ice cover, with considerable latitudinal and altitudinal variation. However, if global air temperatures were to rise by 1.5° to 3°C, there would be, on average, 13 to 24 fewer days of safe ice (*23*). The number of safe ice days per year in lower-latitude lakes could decrease by 80% (*23*). In addition to changes in ice duration and thickness, lake ice quality is also shifting toward white ice, which is mechanically weaker than black ice, contributing to increased fatal drowning events in warmer winters (*30*, *31*).

On the other hand, ice loss may contribute to economic benefits through extended open-water seasons; reduced infrastructure costs, such as maintenance of docks; or other activities that are currently limited by periods of unsafe ice conditions. Areas that currently experience intermittent (transient) ice cover in the winter are predicted to transition to open water as air temperatures increase (*3*, *4*). This ice loss may extend to increased open-water fishing or other recreational activities that are limited by ice and to improved hydroelectric operations with fewer ice jams (*12*). Additionally, reduced ice cover is predicted to expand the shipping season for areas such as the Laurentian Great Lakes and thereby increase shipping activity (*32*), and it also may create greater potential for developing wind energy generation on large lakes (*33*).

Lake ice moderates water quality

Ice loss allows water to warm more quickly as it is exposed to warm air and solar radiation, which leads to a longer ice-free season with warmer water and stronger summer stratification (*29*) as well as associated water quality concerns. Importantly, cyanobacteria blooms are widely linked to warmer temperatures (*34*), longer summers, nutrient loading (*35*), and the interactions among these factors

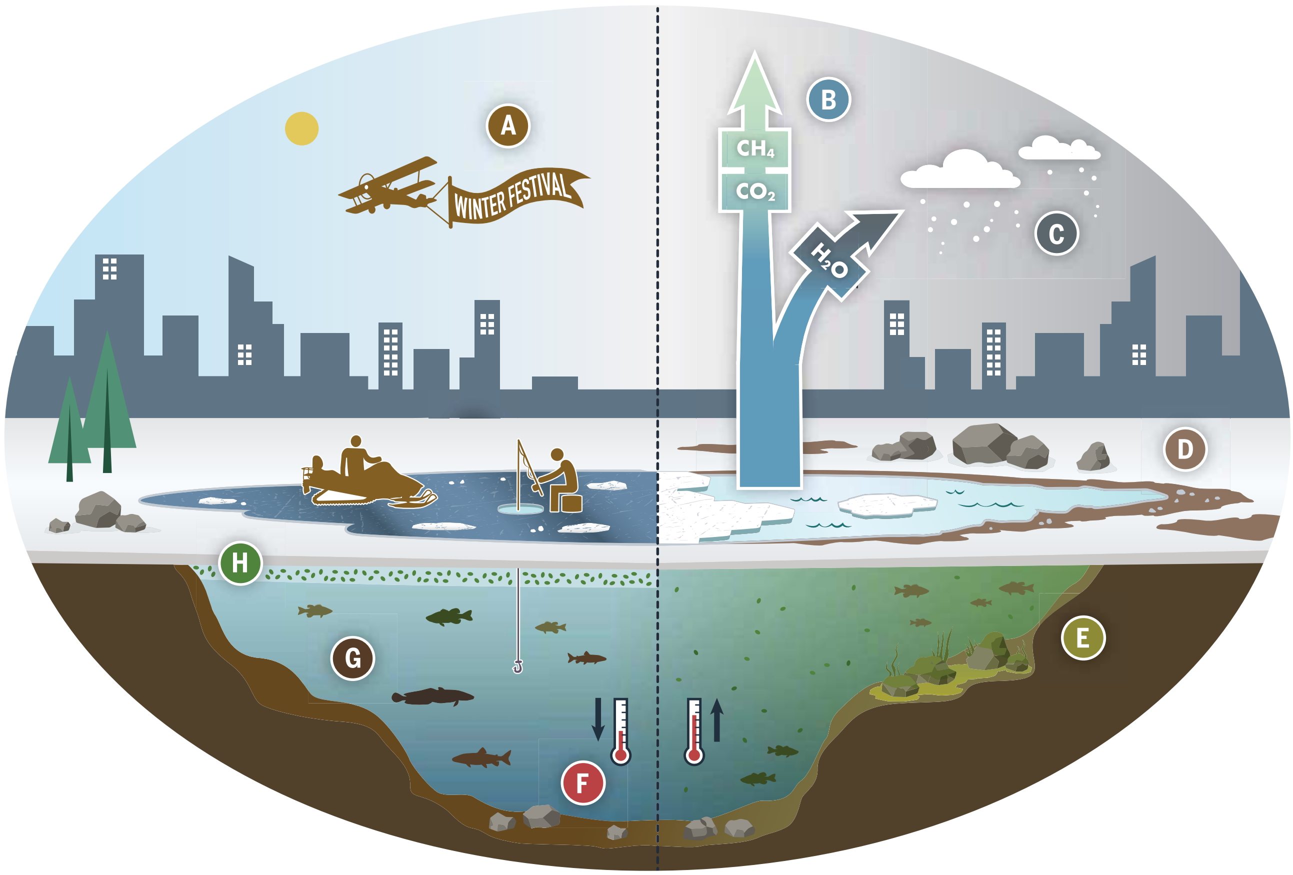

Fig. 2. Environmental and societal importance of seasonal ice cover on lakes. (**A**) Lake ice supports culturally and economically relevant activities, such as recreation, fishing, and transportation. (**B** and **C**) Ice cover reduces carbon emissions as well as evaporative water losses (B) that can contribute to lake-effect precipitation (C). (**D**) Ice cover can limit shoreline erosion associated with wave action of open-water periods. (**E** and **F**) Water quality can degrade with ice loss (E) as increasing water temperature (F) promotes nuisance algal blooms and liberates pollutants from sediments. (**G** and **H**) Ice cover can contribute to preserving native biodiversity by providing distinctive ecological niches for cold-water fish (G) and other organisms that thrive in cold, icy conditions, such as winter algae associated with the underside of ice (H).

(*36*). Cyanobacteria can produce cyanotoxins that negatively affect human and wildlife health, and cyanotoxin production may increase in a warming world (*37*, *38*). In addition to the potential production of toxins harmful to humans and wildlife, cyanobacteria blooms complicate water treatment by clogging intakes and producing dissolved organic matter that creates harmful by-products during treatment, and these blooms create unpleasant conditions for water recreation.

Ice cover can have complex or even opposing effects on the internal dynamics of nutrients and pollutants that are relevant for water quality through its control of dissolved oxygen. Nutrients that fuel algal growth and some pollutants, such as metals, are commonly sequestered in lake sediments as long as the water column stays oxygenated. When the water at the sediment-water interface goes anoxic, nutrients are liberated, and some metals become more bioavailable (*39*–*44*). Liberated nutrients may drive algal blooms that can become nuisances (*43*). Metals may directly threaten drinking water, especially if an intake is in or near an anoxic zone. Metals can also bioaccumulate or biomagnify within the food web (*45*), endangering wildlife and people who eat fish from these lakes. On one hand, prolonged ice cover commonly creates anoxia during the winter, particularly in small, shallow lakes, because the lake is cut off from the atmosphere, and microbial respiration consumes a great deal of the retained oxygen. On the other hand, prolonged open water that leads to warmer temperatures and stronger stratification can also create summertime anoxic conditions in the bottom layer of the lake (*46*). In either case, ice cover strongly affects oxygen dynamics, with important implications for the biogeochemistry most relevant for water quality. Essentially, fewer winter problems with shorter ice duration may be offset by more extensive problems with summer water quality.

Effects of warming on pathogens and parasites under lake ice provide a rich area for research. Relatively few studies address this topic, although some interesting patterns suggest differential effects of ice-covered conditions on viral, bacterial, and fungal pathogens as well as eukaryotic parasites. There is evidence that ecologically important viruses are robust to cold temperatures of ice cover but sensitive to ultraviolet light exposure and warming after ice melts (*47*). Norovirus, which affects humans, is thought to persist longer at low temperatures (*48*), and the same appears to be true for other human and bovine viruses (*49*, *50*). By contrast, some studies show that bacterial infections, such as *Escherichia coli*—presumably waterborne—can be higher with higher temperatures (*51*). Thus, common knowledge of gastroenteritis is that viral forms tend to occur in the winter and bacterial forms in the summer. Fungal (*52*, *53*) and oomycete (*54*) infections of aquatic organisms also appear to be positively related to temperature, but links between human fungal pathogens and temperature in surface waters have not been established.

These preceding water quality issues are associated with warming and thus are generalizable to most of the world's lakes, whether or not they seasonally freeze, but several additional water quality issues are specific to seasonally ice-covered lakes. First, ice cover during the winter maintains relatively stable temperatures that protect drinking water intake pipes from large fluctuations. In the Laurentian Great Lakes, during open-water winters, supercooling can lead to frazil and anchor ice that blocks intake pipes (*55*). Second, atmospheric deposition of pollutants (e.g., nutrients, hydrocarbons, and metals) tends to accumulate in ice and snow in the watershed. The timing and nature of their entry to the lake depends on precipitation and melt dynamics on both land and water. A longer open-water period presumably creates a longer period of exposure to relatively low levels of atmospheric pollutants, although a spring pulse of cumulative pollutants will remain likely if snow and ice persist in the watershed. Whether these materials are flushed downstream during spring melt or suddenly melt into lake water during spring breakup appears to be highly system specific, but spring thaw typically does bring a pulse of pollutants into water bodies (*56*).

Lake ice promotes cold-water fisheries

Fish residing in seasonally ice-covered lakes can be important culturally, economically, and as a food source for many people, with harvest rates of some species, such as northern pike, being higher during the winter compared with ice-free periods (*57*). Correspondingly, the loss of winter ice cover threatens winter fisheries in a variety of ways. First, access to fish during winter hinges on the quality of ice cover. Thinner and weaker ice is dangerous and can result in loss of equipment or loss of human life (*31*). Second, the nutritional quality of fish as a source of omega-3 and -6 fatty acids could decrease with warmer temperatures (*58*). Particularly for sustenance fishing, the nutritional value of fish depends on the availability of high-quality prey, which can change seasonally with variability in environmental conditions and algal assemblages. For example, the storage fats accumulated by zooplankton (Fig. 3) and other primary consumers in the previous season constitute an important resource to fish in winter (*59*, *60*). Taipale *et al.* (*61*) found that lower-quality prey consumption decreased tissue quality and growth in rainbow trout (*Oncorhynchus mykiss*) fry, whereas Keva *et al.* (*62*) found that decreased nutritional value of prey in warmer subarctic lakes, relative to cooler lakes, was not reflected in fish. These conflicting results suggest that some fish may be capable of offsetting increasing temperatures and declining prey quality by increasing prey intake or lipid biosynthesis (*63*). The ultimate effects of ice loss on the nutritional value of fish likely

Fig. 3. Zooplankton with winter fat reserves. Copepods and other zooplankton under ice build lipid reserves that have been found to make up as much as 76% of their body mass (*141*), a critical resource for surviving winter months when algal resources become variable. The fatty acids that they accumulate are highly nutritious for fish that consume copepods and for humans who consume fish. [Photo: Guillaume Grosbois]

Box 1. Key knowledge gaps for understanding, predicting, and addressing the societal and environmental impacts of changing freshwater ice conditions.

Social, cultural, and economic relationships with lake ice

- Understanding and communicating the rapidly increasing risks of ice conditions
- Development of early warning systems for the safe use of ice
- Assessing current and future cultural and social adjustments to changing human use of ice
- Global economic and environmental implications of reduced capacity for transport, recreation, and other human uses of freshwater ice
- Opportunities to offset social, cultural, and economic losses associated with reduced human uses of ice

Biogeochemistry associated with seasonal lake ice

- Altered lake oxygen dynamics that control nutrient, pollutant, and carbon cycles under ice and through changing mixing patterns the rest of the year
- Shifts in "press" and "pulse" influxes of material (e.g., nutrients, pollutants, and carbon) from the atmosphere, ice and snow cover, and the watershed during winter and advancing spring melt
- Biological effects of changing winter light conditions under altered ice and snow characteristics
- Interactions of seasonally frozen lakes with the global carbon cycle
- Shifts in magnitude and form of greenhouse gas emissions, not only gross annual carbon emissions (both CO_2 and CH_4) but also nitrogen emissions (both N_2O and N_2)

Biodiversity associated with seasonal lake ice

- Speed of biological adaptation relative to speed of ice loss
- Ecosystem-wide effects of shifting dominance between cold-water and warmwater species
- Food web effects of ice-associated biota and their loss
- Changes in migration patterns and ranges of fish and wildlife
- Spread of invasive species and their ecological impacts
- Pathogens and parasite dynamics

Physical implications of shifting lake ice conditions

- Major changes in internal mixing patterns within lakes (e.g., from dimictic to monomictic)
- Winter storm effects on shoreline erosion, sediment transport, and resuspension under more-open winter conditions
- Effects of winter evaporative water loss and water level change on the global water cycle
- Patterns of altered regional weather patterns associated with ice loss, particularly for water-dominated regions

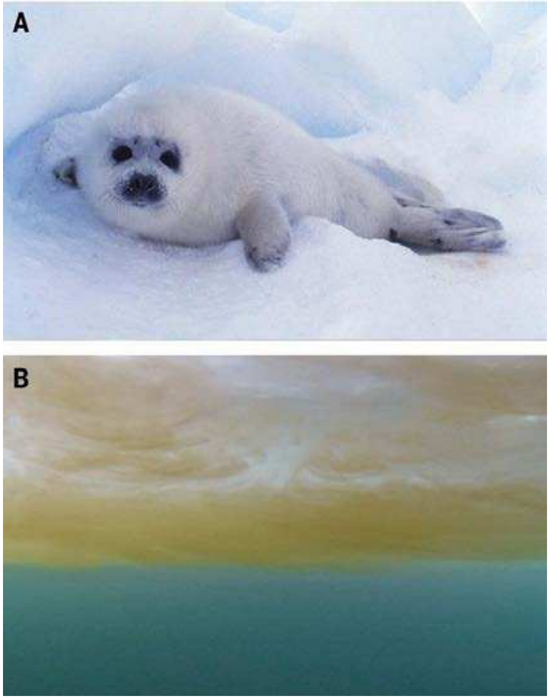

Fig. 4. Dependence of Lake Baikal's top predator and primary producers on seasonal ice cover. In ancient Lake Baikal, both the top and bottom of the food web directly depend on ice (*142*). (**A**) Endemic Baikal seals (*Pusa sibirica*), Baikal's top predators, give birth in ice caves where the pups are protected from predators and harsh weather. Adults also rely on long ice cover to complete molting, an energetically costly process. [Photo: CCY-BY-2.0 Pacific Environment] (**B**) The ice plays an important role in creating winter algal blooms, which dominate annual phytoplankton biomass in most years. [Photo: Kirill Shchapov]

vary with species and life stage and warrant further research given the importance of fish for human health (*64*).

Additionally, climate-driven changes to winter conditions could also affect the sustainability of fisheries through effects on fish growth and reproduction, although the impacts will be highly species and system specific. Increasing temperatures will increase fish metabolic rates (*65*) and could increase growth rates (*66*). Changes in ice and snow cover will alter light transmission (*30*) and thus primary production, oxygen, and fish habitat (*67*). How changes in winter conditions affect fish growth (through access to habitats and prey) will depend on attributes of the system (e.g., lake size and prey density) and species [e.g., thermal preference, light, and oxygen requirements (*68*–*72*)].

Altered ice conditions could also affect the timing and success of fish reproduction. Reduced ice cover and warmer winter temperatures have been linked with earlier spawning, reduced egg and larval survival, and smaller gonads (*66*, *73*–*75*). Fishes with colder thermal preferences that can thrive during winter periods, including the culturally relevant coldwater salmonids, are thought to be most at risk from warmer winters (*76*). It remains unknown whether these species will adapt quickly enough to changing winters to survive and whether warm-adapted invasive species (*77*) might provide cultural, nutritional, and commercial value similar to that provided by native, cold-adapted species. In addition to physiological constraints, additional pressures on native fish will be associated with overall changes in their food source availability, competitors, and predators.

Lake ice promotes native biodiversity and inhibits species invasions

Declines of native biodiversity and species invasions have reached crisis levels in freshwater ecosystems (*78*). Decreased ice cover and winter severity may facilitate range expansions and invasions of warm-adapted species, including fish, invertebrates, and plants (*77*, *79*, *80*).

Lake ice creates a distinctive ecological niche space. These conditions include low temperatures (<4°C), a stable water column, reduced light levels, protection from ultraviolet radiation, and the creation of sympagic (ice-associated) habitats at the ice-water interface and within the ice and snow. Clear and snow-free ice allows high transmission of light that can fuel substantial algal growth. Snow cover and cloudy ice can create near-total darkness in which rates of respiration far exceed those of photosynthesis. Although overall diversity can be lower during ice cover than the open-water season, many groups of microbes are well adapted to life under, and even inside, lake ice (*81*–*84*). Ice cover extent has been shown to strongly affect phytoplankton and bacterial community structure both during winter and in subsequent seasons (*83*–*85*), and sympagic habitats can host distinct microbial communities (*86*) such that biodiversity across the full annual cycle may be higher in seasonally ice-covered systems. These ice-associated organisms provide important food sources for higher–trophic level organisms, not only during the winter but also during spring ice melt when they drift in the water column and to the lake bottom (*87*). Cold-water and warmwater fish may coexist as a result of distinct niches provided by ice-covered winters and open-water seasons (*88*). The challenging conditions imposed by ice and snow cover create a bottleneck for survival of many species (*59*); species native to seasonally frozen lakes must have the necessary physiological and behavioral adaptations for surviving extended winter periods (*88*). Organisms native to warmer regions are less likely to have these adaptations and face a greater risk of overwinter mortality owing to inefficient winter foraging and starvation or failure of physiological systems under cold temperatures (*59*, *89*). Further, some wildlife preferentially use lake ice during critical life stages, such as reproduction (Fig. 4), or for migration (*90*). Therefore, the loss of ice and ice-associated niches may reduce seasonal variation in community composition and reduce diversity over annual or longer timescales.

The loss of lake ice will also affect biodiversity by allowing fish to establish in formerly fishless lakes. Seasonal freezing in shallow, productive lakes can lead to winter anoxia or freezing to the bottom, preventing fish establishment or eliminating preexisting communities (*91*, *92*). Fishless lakes host distinct communities of invertebrates and amphibians that become disrupted after fish introductions because of fish predation (*93*, *94*). In landscapes where fish-inhabited and fishless lakes co-occur, reductions in ice cover duration, reductions in ice thickness, or complete ice loss could eliminate fishless lakes, leading to reduced landscape-scale diversity. Although these biodiversity losses could be a concern, the establishment of new fish populations may also be valued by recreational fishing enthusiasts.

Overall, loss of ice cover is likely to cause the loss of sympagic communities, range expansions of warm-adapted species, and large-scale restructuring of biological communities, thereby furthering biodiversity change in fresh waters. However, because ice cover affects numerous water properties, the effects of ice loss on lake biodiversity could be system and species specific.

Lake ice protects against shoreline erosion

The physical presence of nearshore ice suppresses shoreline erosion by reducing wave action. On the Laurentian Great Lakes, ice shields shoreline bluffs from heavy waves, and freezing temperatures can help maintain the shear strength of shoreline sediments (*95*, *96*). Similarly, in the Arctic, erosion of shorelines of large lakes occurs mostly through mechanical wind energy, such that lake ice likely restricts lateral erosion (*97*). As ice conditions become incomplete across the lake or become intermittent, forming and breaking up multiple times, such conditions can magnify the erosion response to wave action (98–101).

The economic consequences of shoreline erosion are notable (102), and as lake ice coverage diminishes, there is more potential for wave activity and moving ice to scour shorelines. Aside from property damage, manifestations of erosion coincident with declining ice include elevated turbidity at municipal water intakes (103) and eutrophication of nearshore zones, as has been seen in the lower Laurentian Great Lakes (104, 105).

Lake ice can increase carbon retention

Ice cover effectively isolates lakes from the atmosphere and the atmosphere from lakes, preventing gas exchange during winter. Among the ideas that we highlight in this Review, the effects of ice loss on net greenhouse gas emissions from seasonally ice-covered lakes probably have the greatest uncertainty. Nonetheless, evidence exists that ice cover increases carbon retention. Most critically, lakes with longer ice duration tend to stay cooler year-round, slowing temperature-dependent biological processes with consequences for carbon cycling and greenhouse gas emissions. For example, in modeling lakes under global climate projections, cooler lakes had lower annual methane production (106). Ice cover also delays the emission of methane to the atmosphere, which, in the presence of oxygen, allows for its partial conversion to carbon dioxide through microbial oxidation (107). Carbon dioxide has lower global warming potential compared with methane at a 100-year timescale (108), and, unlike methane, carbon dioxide gets recycled back into phytoplankton biomass. Thus, ice cover is thought to be associated with a slower and more closed carbon cycle that keeps carbon in the lake longer. Further, a springtime carbon dioxide release may coincide with terrestrial "spring green-up," which allows for more carbon to become sequestered by plants relative to winter release from open water.

In what ways does ice duration affect the fluxes and pools of buried organic carbon? Because organic carbon burial efficiency depends on oxygen exposure time (109), indirect effects of ice duration on pools and fluxes of buried carbon may occur through direct effects of oxygen. For both methane and carbon dioxide, we emphasize a trade-off between ice-covered and ice-free production of greenhouse gases that is relevant in the context of climate warming and declining ice cover. This trade-off helps explain how lakes with longer ice duration may contain higher methane and carbon dioxide concentrations in late winter under ice, emit large pulses of greenhouse gas emissions during the spring breakup period for ice (110, 111), and yet exhibit overall lower annual emissions (112) associated with cooler temperatures during the ice-free period.

We posit that the above statements about carbon cycling are most relevant to small and intermediate-sized (e.g., <10-km^2) lakes that experience seasonal ice cover. For example, Hounshell *et al.* (113) have reported that full winter ice cover reduced overall carbon emissions from a small reservoir relative to intermittent ice cover. However, in very large and deep lakes, such as Lake Baikal, the proportion of water volume that interacts with seasonal ice cover is lower, and water-residence times are longer. Consequently, interannual variation in factors such as wind and intensity of spring mixing can be particularly important to the thermal regime in very large lakes (114) and, in turn, the oxygen dynamics and annual carbon budgets.

Lake gas emission is not only a story about carbon. It is possible that cooler lakes with longer ice cover have lower annual nitrous oxide emissions, another potent greenhouse gas, following the pattern shown by Jansen *et al.* (106) for methane production. This question has yet to be answered but could depend on interactions between nitrate concentration, water temperature, and ice cover. Kortelainen *et al.* (115) demonstrated not only that attention to greenhouse gas emissions from lakes should extend beyond carbon but also that winter measurements of nitrous oxide are required. They reported a positive relationship between lake nitrate concentration and nitrous oxide concentration across 87 Finnish lakes and that including winter data increased estimates of nitrous oxide emission fourfold compared with exclusively summer data.

Conditions beneath lake ice select for specialized microorganisms and metabolic processes that thrive in darker, colder conditions with lower oxygen, lower pH, and higher dissolved inorganic nutrients that accumulate as a result of organic matter breakdown and lower primary production (9, 82, 116). Without the exchange of carbon dioxide and oxygen with the atmosphere, lakes become a more closed system and, in smaller lakes, winter hypoxia can occur (117). But with ice loss, these underwater conditions will become less common, leading to fundamental shifts in stratification phenology, changes in greenhouse gas emissions, and faster biogeochemical cycles, underpinning many of the associated concerns for water quality and biodiversity (118).

Lake ice reduces evaporative water loss

Lake ice influences the global water cycle, seasonally closing off lakes from the atmosphere and effectively preventing evaporative loss. Evaporative water loss from the open water of lakes redistributes water from the hydro- and biosphere to the atmosphere, contributing to declines in water level and storage (118). From 1985 to 2018, global evaporative water loss from lakes increased at a rate of

Fig. 5. Loss of water by sublimation from ice. Taberlet and Plihon (143) recently described the importance of sublimation in creating "Zen stones" on ice-covered lakes. Found in nature as a stone sitting atop a thin ice pedestal on lake ice, Zen stones are thought to originate as a stone lying flat on the ice surface, and over the winter, sublimation reduces the ice around the stone while the shade of the stone protects the ice that becomes its pedestal. Although Zen stones are rare, they illustrate the potential for sublimation to be substantial under some circumstances and worthy of further study in the context of the global water cycle. [Photo: Mikhail Zykov/iStock]

3.12 km^3/year, with 23% of this increase attributed to an increase in open-water evaporation due to lake ice loss (*119*). The magnitude and timing of evaporative water loss for each lake depend on the area and duration of open water, both of which are currently changing (*118*–*120*). Evaporation rates generally increase with higher temperatures and changes in vapor pressure deficit (*119*, *120*). Although water loss also occurs above ice cover, through sublimation (Fig. 5), evaporative losses from open water are typically thought to be much greater (*121*); thus, the continuing trends of loss of ice cover are expected to increase evaporation rates at a global scale (*119*). This water returns to Earth's surface as precipitation (e.g., as lake-effect snow) to sites located far away from the lake (*122*) and thus may not be available to the human communities and ecosystems from which the water was lost.

Lake ice buffers regional communities from heavy precipitation events

Lake-effect snow is driven by a cold air mass moving across a warmer, open body of water. The cold air mass picks up moisture and heat from the water, causing the air to rise and subsequently condense into snow. Heavy snowfalls only develop in times of moderate wind speeds across a spatially extensive temperature gradient. The requirement of a large air-water temperature gradient [typically >13°C (*123*)] and a large lake width (fetch larger than 100 km) restricts lake-effect snow to the downwind side of only a handful of lakes on Earth, including the Laurentian Great Lakes, Lake Baikal, the Great Salt Lake, and the Caspian Sea (*124*). The large width, volume, and heat capacity of the Great Lakes often lead to autumn water temperatures that are higher than the air temperature (*125*). In November 2022, a 3-day snowstorm broke records for lake-effect snow in Buffalo, New York, dropping more than 53 cm of snow in a single day, with a total accumulation of more than 200 cm by the end of the storm. At the inception of this historic snowstorm, the temperature of Lake Erie was a relatively warm 11°C when the air temperature dropped to −9°C, with the difference between the water and air temperatures fueling the storm.

Lake-effect snow is only possible over open water. Once the lake freezes (*126*), evaporation is limited, and air-water temperature gradients are small. In simulations, Vavrus *et al.* (*127*) found that complete freezing of the Great Lakes reduced snowfall by 84% and decreased cloudiness, temperature, and near-surface wind speeds. With climate change, the forecasted loss of lake ice has the potential to substantially change winter climate downwind of the Great Lakes (*128*).

In the Great Lakes from 1973 to 2017, the maximum surface area covered by lake ice varied interannually, but there has been 5.1% of ice surface area lost per decade (*129*). Differences between lakes included a 6.2% decrease in ice area on Lake Superior compared with a 2.5% decrease on Lake Ontario (*129*). This loss of ice combined with warmer lake water temperatures is thought to have increased snowfall downwind of the Great Lakes from 1931 to 2001 (*130*), although a more recent reversal of this trend near Lake Michigan has been noted (*131*). During this period, no trend in precipitation was found at comparable non–lake-effect sites.

End-of-century climate projections in the Great Lakes region predict less lake ice, which may have cascading consequences on the magnitude, duration, and timing of snowfall. Notaro *et al.* (*132*) used a regional climate model to show that as ice cover declines, high wind fetch and lake evaporation result in higher precipitation. As air temperatures warm, much precipitation falls as rain instead of snow. This switch from snow to rain would reduce the snowpack available for drinking water supply in the Catskill Mountains, where watersheds provide 90% of New York City's drinking water (*133*). Only Lake Superior is predicted to generate consistent heavy lake-effect snow well into the 21st century (*132*). Given the economic and human health consequences of extreme snow and rain events, the relationship between climate warming, lake ice coverage, and extreme precipitation is tremendously important for communities surrounding the Great Lakes and other large northern lakes globally.

Conclusions

Lakes are losing ice rapidly. Long-term lake ice records reveal that lakes are freezing later, thawing earlier, or both (*5*, *26*, *28*, *134*–*136*). In the Northern Hemisphere alone, lake ice formation is delayed by an average of 11 days per century, and ice melt is hastened by 6.8 days per century (*4*). The rate of lake ice loss has markedly accelerated over the past 25 years, with ice melt occurring 45 days per century earlier in the Northern Hemisphere (*4*). Additionally, many lakes are transitioning from annual to intermittent ice cover, with periods of open water during winter as well as winters when the lakes do not freeze (*3*). The loss of ice cover is expected to accelerate under future scenarios of climate change (*5*, *28*, *137*), with substantial implications for physical, chemical, biological, and societal aspects of freshwater systems that are complex and often context dependent (*101*).

Although interest in winter research has rapidly increased in the past decade, critical knowledge gaps remain (Box 1). The loss of ice cover can contribute to both negative and positive feedback loops with trade-offs—e.g., between winter and summer water quality—that we are unable to predict with current knowledge. Essentially, reductions in lake ice will potentially cause massive shifts in our freshwater resources that are poorly understood at both local and macrosystem scales. Coproduction of knowledge as well as the archiving of cultural history associated with lake ice traditions, many of which will go extinct locally (*13*), can contribute to place-based management approaches and the identification of new opportunities for social, cultural, and economic benefits in an increasingly ice-free future.

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SUPPLEMENTARY MATERIALS

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