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# Sentinel responses of Arctic freshwater systems to climate: linkages, evidence, and a roadmap for future research

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## Abstract

While the sentinel nature of freshwater systems is now well recognized, widespread integration of freshwater processes and patterns into our understanding of broader climate-driven Arctic terrestrial ecosystem change has been slow. We review the current understanding across Arctic freshwater systems of key sentinel responses to climate, which are attributes of these systems with demonstrated and sensitive responses to climate forcing. These include ice regimes, temperature and thermal structure, river baseflow, lake area and water level, permafrost-derived dissolved ions and nutrients, carbon mobilization (dissolved organic carbon, greenhouse gases, and radiocarbon), dissolved oxygen concentrations, lake trophic state, various aquatic organisms and their traits, and invasive species. For each sentinel, our objectives are to clarify linkages to climate, describe key insights already gained, and provide suggestions for future research based on current knowledge gaps. We suggest that tracking key responses in Arctic freshwater systems will expand understanding of the breadth and depth of climate-driven Arctic ecosystem changes, provide early indicators of looming, broader changes across the landscape, and improve protection of freshwater biodiversity and resources.

**Key words:** Climate change, climate indicators, Arctic lakes, Arctic rivers, polar limnology

## Introduction

Inland freshwaters continuously exchange with the overlying atmosphere and the surrounding landscape (Forel 1891) and are sentinels of broader environmental change, meaning that we can often detect and quantify climate-driven ecosystem changes in lakes and rivers prior to those occurring in adjacent terrestrial systems (Jassby 1998; Vincent and Smol 2009; Williamson et al. 2009; Camacho et al. 2012; Castendyk et al. 2016; Zhang and Duan 2021). For this review, we define a sentinel response of Arctic freshwater systems to climate as a physical, chemical, and (or) biological attribute or set of attributes of these systems with a demonstrated and sensitive response to climate forcing. These responses include measurable changes in lake level as a consequence of shifting water balance and hydrology (reviewed by Fritz 2008); the extent and timing of ice off as a consequence of air temperature anomalies (e.g., Beyene and Jain 2015; Bégin et al. 2021*a*); deoxygenation in response to lake warming and stratification (Jane et al. 2021); changes in river discharge and timing of spring freshet (Peterson et al. 2002; Feng et al. 2021); solute changes as a consequence of extreme precipitation events (e.g., Warner and Saros 2019) and changing flowpaths (Toohey et al. 2016); changes in species diversity of algae as a consequence of climate-driven changes in physical habitat structure (e.g., Saros et al. 2016), and more. The heightened sensitivity of freshwater systems to climate underscores the utility of routine tracking of key responses in freshwaters across multiple spatial and temporal scales.

Sentinel responses of freshwater systems to other regional-scale drivers have become centrally integrated into policy and management aimed at broadly protecting ecosystems. For example, many of the first detectable ecosystem responses to changing atmospheric deposition across a landscape are found in freshwaters, including measurable changes in dissolved organic carbon concentrations with reductions in sulfur deposition (e.g., Monteith et al. 2007) and shifts in algal community structure with increases in nitrogen deposition (e.g., Wolfe et al. 2001). Recognizing this high sensitivity, many management agencies in the USA and Europe focus on critical deposition loads that are based on responses in freshwater systems, relying on the principle that using the most sensitive indicators across a landscape to develop policy and management approaches will be broadly protective across ecosystems (Pardo et al. 2011). This same principle can be applied to climate-driven ecosystem changes; recently proposed frameworks call for expanded integration of freshwater indicators into climate impact assessments (Kenney et al. 2016).

Understanding climate-driven changes in Arctic ecosystems similarly requires utilizing inland waters as sentinels. Widespread integration of freshwater processes and patterns into our understanding of broader climate-driven Arctic terrestrial ecosystem change has been slow. Freshwater systems are a dominant feature of the Arctic terrestrial landscape (Vincent and Hobbie 2000); 24% of the global lake area falls between latitudes of 60–69° N (Downing et al. 2006) and 82% of Arctic lakes are situated on continuous permafrost (Paltan et al. 2015), and Arctic rivers drain approximately 15% of the global land surface (Feng et al. 2021). Changes in Arctic freshwater systems highlight how rapidly these systems reflect shifting climate, ranging from shifts in water balance in response to warming (Smol and Douglas 2007; Lehnherr et al. 2018); altered dissolved organic and inorganic carbon dynamics (Striegl et al. 2005; Wauthy et al. 2018) and higher methane emissions (Walter Anthony et al. 2016) that are likely consequences of permafrost thaw (Vonk et al. 2015), and higher rates of algal community turnover that are likely consequences of warming air temperatures (Smol et al. 2005) and altered water column structures (Saros et al. 2019; Bégin et al. 2021*b*). These changes highlight that Arctic freshwater systems provide early warning signals of change. When coupled with the spatial biases that result from overrepresentation by some Arctic field sites (Metcalfe et al. 2018), even with the progress to date, we are likely missing many rapid, potentially fundamental responses in Arctic freshwater systems that signal looming, broader terrestrial changes.

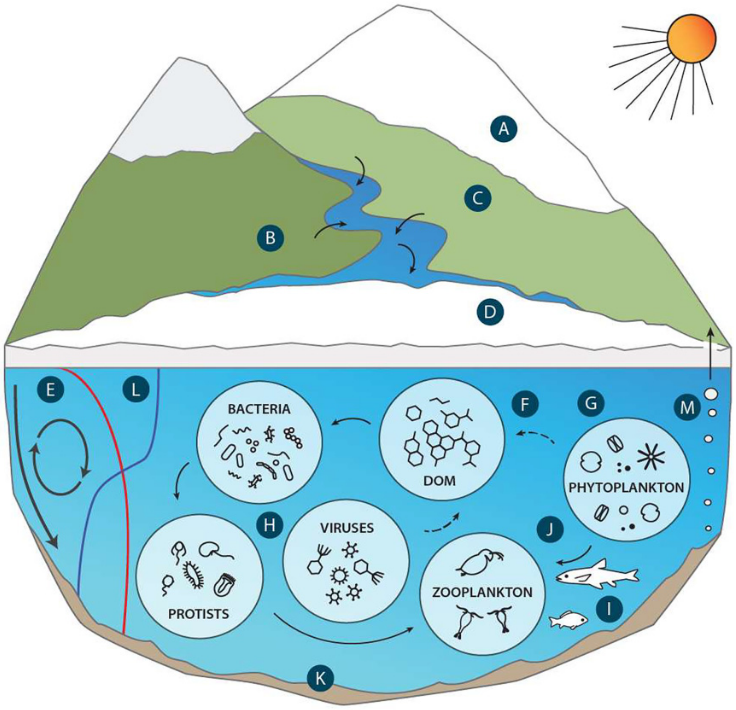
The importance of freshwater ecosystems in the Arctic has been highlighted in several recent reviews. The Snow, Water, Ice and Permafrost in the Arctic report (AMAP 2017) provides a systems framework to assess the changing Arctic cryosphere and its effects on ecosystems, including terrestrial freshwater systems. Several recent reviews of Arctic freshwater biodiversity (Heino et al. 2020; Goedkoop et al. 2022) underscore the need for more coordinated monitoring programs at greater spatial and temporal resolution, and have suggested that Arctic countries develop more extensive programs to track biodiversity, water quality and ecosystem services of Arctic freshwaters. These needs align with priorities defined in a global agenda to advance freshwater biodiversity research (Maasri et al. 2022). Broadly, the Arctic Monitoring and Assessment Programme (AMAP 2021) has emphasized the need to better understand the consequences of future warming for the Arctic, specifically underscoring the need to expand monitoring of Arctic change, address information gaps, and improve relevance and availabilty of scientific information for decision making.

To inform and support the expansion of freshwater monitoring efforts in the Arctic, we review the current understanding across Arctic freshwater systems of key sentinel responses to climate. Our overall aims in this review are to: (1) describe key sentinel responses of Arctic freshwater systems (overview in Fig. 1), (2) clarify the various linkages between these sentinels and climate to contextualize these responses and inform parameter selection, (3) describe key insights gained from these sentinels, and (4) provide a roadmap for future research by identifying current knowledge gaps (summarized in Table 1). This review is a contribution to the International Arctic Science Committee project "Terrestrial Multidisciplinary distributed Observatories for the Study of Arctic Connections", which examines Arctic system-level responses to climate change (Vincent et al. 2019).

## Arctic freshwater sentinels

We describe 13 Arctic freshwater sentinels below, with their key components and knowledge gaps also summarized in Table 1.

**Fig. 1.** Climate responsive components of Arctic freshwater ecosystems: (A) snow and ice fields; (B) catchment soils and vegetation; (C) water and chemical inputs; (D) snow and ice cover; (E) stratification, mixing, and currents; (F) dissolved organic carbon (and other solutes); (G) primary producers; (H) microbial processes; (I) invasive species; (J) food webs; (K) phytobenthos and zoobenthos; (L) oxygen concentrations; and (M) greenhouse gas dynamics. Modified and extended from Vincent (2018).



## Ice regimes of lakes and rivers

Ice formation, growth, and decay are sequences of the natural cycle or regime of Arctic lakes and rivers in response to the rapidly changing seasons that define Arctic climate. Ice regimes vary from perennial ice cover on a few high latitude lakes, to seasonal ice cover on the majority of northern water bodies, and intermittent ice cover on an increasing number of lakes and rivers where ice forms in some years and not others or even breaks up and refreezes multiple times during winter (Prowse et al. 2011). Another type of ice regime is determined by water depth relative to maximum seasonal ice thickness, which causes lakes and rivers to either freeze solid with bedfast (grounded) ice or maintain liquid water below floating ice (Jeffries et al. 1996; Engram et al. 2018). These regimes of perennial to intermittent ice cover and bedfast- to floating-ice are strongly influenced by climate, and thus regime shifts are indicative of where and how rapidly climate is changing. For example, at Ward Hunt Lake in the Canadian High Arctic, perennial ice cover rapidly thinned at the beginning of the 21st century, culminating in complete ice-cover disappearance during some years because of coupled warmer summers, warming of the water column beneath the ice, and warm water inflows from the surrounding catchment (Paquette et al. 2015). A surprising, counter-intuitive impact of such complete loss of ice cover during warmer years is full wind exposure of the lake surface and complete mixing of the water column, resulting in heat ventilation from lake waters to the atmosphere and water temperatures several degrees lower than under ice-covered conditions (Bégin et al. 2021*a*). These observations underscore the complex interplay between "external" (increasing temperatures) and "internal" (local landscape properties) driving factors, as well as the vulnerability of thick perennial ice cover to nonlinear climate change.

The sentinel value of ice regimes is most apparent at broad spatial scales (i.e., satellite remote sensing) and long temporal scales (i.e., phenology records from river and lake-shore communities or research stations). Satellite inventories of lake (Smejkalova et al. 2017; Sharma et al. 2019) and river (Cooley and Pavelsky 2016; Yang et al. 2020) ice regimes coupled with model-based forecasts suggest important shifts in freshwater ice cover regimes primarily driven by air temperature. In coastal permafrost regions where lakes are shallow and abundant, slight reductions in ice thickness can lead to threshold reductions in bedfast ice extents (Arp et al. 2012; Surdu et al. 2014), partly in response to sea ice dynamics (Alexeev et al. 2016). Records of progressively later lake ice freeze-up and earlier break-up provide some of the best direct long-term evidence linked to air temperature warming dating back to the 1850's in the northern hemisphere (Benson et al. 2012). Ice phenology records provide important information to local communities given the critical role rivers and lakes play in human transportation and subsistence, for example as key wildlife habitats and vital hunting-fishing-trapping grounds for Indigenous communities (Brown et al. 2018; Knoll et al. 2019). The role of ice regimes in many ecosystem processes is also largely evident, yet the varying complexities of how this sentinel driver is manifested in physical, chemical, and

**Table 1.** Summary of the major sentinel responses of Arctic freshwater systems, with applicable system (s) indicated (L = lake, R = river), specific components listed, and knowledge gaps briefly summarized. See text for fuller description of each. Each component is listed in simple terms; note that many of them can be further refined by defining specific spatial or temporal scales (e.g., surface or deep water temperatures, winter or summer water temperatures, and length of period or frequency of anoxia in hypolimnion).

| Major sentinel response | System | Components | Knowledge gaps and research recommendations |
|---|---|---|---|
| Ice regimes | L, R | Ice freeze-up date<br>Ice break-up date<br>Ice thickness | -Quantifying variation in ice thickness and rates of decay over varying spatial and temporal scales<br>-Quantifying sequence of freeze-up and break-up processes relative to ecosystem processes and human uses of rivers and lakes<br>-Investigating ice quality of Arctic lakes and rivers, including white ice, black ice and snow cover |
| Thermal regimes | L, R | Water temperature<br>Thermal structure | -Obtaining high frequency records of temperature, conductivity and oxygen from moorings across a broad range of Arctic lakes, throughout all season<br>-Integrating in situ time series measurements with remote sensing and coupled biogeochemical and hydrodynamic modeling to facilitate scaling up and prediction |
| Baseflow | R | Discharge | -Investigating setting-specific baseflow response to permafrost thaw<br>-Identifying new talik formation<br>-Integrating discharge with biogeochemistry sentinels and landscape factors |
| Water balance | L | Surface area<br>Water levelLake distribution | -Integrating lake area change with lake bathymetry and water level fluctuation<br>-Characterizing ground ice content, temperature, and distribution near and below lakes<br>-Identifying drivers of changes in lake water sources, flow paths, and residence times |
| Permafrost-derived inorganic chemical concentrations | L, R | Dissolved ions<br>Nutrients | -Identifying linkages between nutrient and ion inflow<br>-Characterizing soluble ion loads across permafrost gradients and boundaries<br>-Measuring ions across pre-post fire events in different settings to constrain wildfire effects |
| Carbon mobilization | L, R | Dissolved organic matter (DOM) concentration | -Elucidating DOM source through radiocarbon and molecular structure work |
| | | DOM composition | -Quantifying rapid cycling of novel dissolved organic C inputs to freshwaters<br>-Quantifying regional and cross-system variability in response to warming and permafrost thaw |
| | | $CO_2$<br>$CH_4$ | -Conducting more long-term studies of greenhouse gas (GHG) fluxes<br>-Investigating processes to quantify effects of climate on GHG emissions<br>-Identifying key times, systems, and (or) variables in GHG dynamics<br>-Linking GHG fluxes, processes and (or) variables to remotely sensed data<br>-Developing process-based and statistical models of GHG dynamics and fluxes |
| | | $^{14}C$ of organic C<br>$^{14}C$ of $CO_2$<br>$^{14}C$ of $CH_4$ | -Developing long-term baseline records of freshwater $^{14}C$<br>-Standardizing expression (i.e., units) of loss rates of permafrost-derived organic carbon<br>-Targeting research in transition zones between continuous and discontinuous permafrost, and in regions severely impacted by thermokarst processes |
| Dissolved oxygen (DO) | L | DO concentration<br>Anoxia | -Measuring high temporal resolution oxygen, temperature, and conductivity data across diverse Arctic lakes<br>-Collecting key complementary data to enable modeling, including light and DOM, as well as lake bathymetry and hydrology |
| Trophic status | L | Total phosphorus<br>Algal pigment concentration | -Investigating the magnitude and extent of eutrophication across Arctic lakes to decipher lake and catchment features that promote resilience<br>-Standardizing methods to quantify trophic state and production across studies to better enable comparisons |
| Prokaryotic communities | L | Indicator taxa<br>Indicator traits | -Employing the numerous new molecular tools to investigate microbial ecology of Arctic lakes<br>-Identifying new sentinels focused on traits, processes, and ecological thresholds revealed by molecular tools |

**Table 1** (*concluded*).

| Major sentinel response | System | Components | Knowledge gaps and research recommendations |
|---|---|---|---|
| Algal communities | L, R | Community turnover<br>Diversity<br>Habitat classification<br>Trait classification<br>Indicator taxa | -Improving understanding of climate-lake-algal linkages across lakes by employing mechanistic frameworks<br>-Increasing focus on benthic algal ecology studies given prevalence of this habitat in Arctic lakes<br>-Coupling pigment biomarkers, DNA techniques, and experiments with taxonomic work in both contemporary and paleolimnological approaches |
| Invertebrates | L, R | Abundance<br>Diversity | -Increasing monitoring of invertebrate abundance and distribution in Arctic freshwaters<br>-Integrating invertebrate data with environmental data and paleolimnological reconstructions to improve mechanistic understanding of controls on invertebrate communities across spatio-temporal scales |
| Fish | L, R | Physiology<br>Productivity<br>Population structure<br>Diversity | -Increasing attention to fish community structure, traits and processes, as described in Rolls et al. (2017)<br>-Increasing involvement of Indigenous partners in monitoring populations and habitats for key species that are important to northern communities, as described in Knopp et al. (2020) |
| Invasive species | L, R | Microorganisms<br>Aquatic plants<br>Invertebrates<br>Fish<br>Waterfowl | -Quantifying distributions of invasive species in Arctic freshwaters<br>-Increasing cooperation with Indigenous partners and northern communities to integrate local knowledge of invasive species presence and distribution |

biological systems (Mueller et al. 2009) require further exploration.

Some of the knowledge gaps in the understanding of sea ice dynamics and its consequences also present challenges in the study of freshwater ice in Arctic lakes and rivers. Observations of Arctic sea ice focus heavily on changing extents and ice concentrations (Stroeve et al. 2012; Stroeve and Notz 2018), whereas freshwater ice studies focus largely on ice cover duration relative to exact periods of freeze-up and break-up—both of which are enhanced (i.e., continually improving spatial and temporal resolution of satellite imagery) and limited (i.e., increasing clould cover in some regions and barriers to observation as freeze-up becomes later in the season and thus more obscured by darkness and shadows) by satellite remote sensing (Brown et al. 2018). Ice growth and thickness reflect winter temperature (air and water) and snow cover dynamics, as well as mechanical surface processes (i.e., currents, wind-shear, thermal dynamics, etc.). Rates of ice decay also reflect temperature, intensity of solar radiation, and mechanical processes that vary greatly by water body or watershed size (Ashton 2011; Prowse et al. 2011). Observations of both freshwater and sea ice thickness are often lacking and much less is known about how thickness and rates of growth and decay vary in time and space. Coupling observations of ice thickness with modeling of ice growth and decay is helping to fill this gap in the ice cycle between freeze-up and break-up timing. Such advancements will help link the intricacies of the ice cycle with other complex lake processes such as sediment temperatures, light penetration and primary productivity, methane ebullition, and under-ice dissolved oxygen and photosensitive chemical reactions (Hampton et al. 2017). In rivers, understanding the often increasingly protracted sequence of freeze-up and beak-up that impact winter travel (Brown et al. 2018) and ice jam flooding (Beltaos and Prowse 2009) may be advanced by closer examination of winter water temperature and groundwater dynamics (Jones et al. 2015). The quality of ice in terms of its crystalline structure, strength, transparency, and chemical composition is another topic where general knowledge is lacking across the range of ice regimes in Arctic environments. Ice quality directly impacts safe travel conditions on lakes and rivers (Ashton 2011; Herman-Mercer et al. 2011), but also may have un-realized effects on a range of in- and under-ice ecosystem processes, such as the storage and transformations of organic carbon (Imbeau et al. 2021) and development of diverse benthic biomes (Mohit et al. 2017). Sea ice quality is a topic where Arctic physicists and chemists have made important advancements in recent years (Petrich and Eicken 2017) and Arctic freshwater scientists may be poised to make progress as well through integrative research.

## Thermal regimes of lakes and rivers

Water temperatures and thermal structure of lakes and flowing waters are components of this sentinel response to climate. Melting degree days (MDD; annual sum of mean daily air temperatures in excess of freezing) and the extent of snow cover in spring are critical variables moderating changes in temperature in Arctic streams and lakes. In the High Arctic, an increase in MDD has led to intermittent ice cover in formerly amictic Ward Hunt Lake, Canada's northernmost lake (Bégin et al. 2021*a*). As a result, the lake is now intermittently cold monomictic, that is, it has fully circulated in summer in some years with a concomitant decrease in water temperature in summer to less than 2 °C, whereas when amixis is maintained, temperatures under the ice in summer can reach 8 °C and the lake stratifies (Bégin et al. 2021*b*). An increase in MDD elsewhere has led to earlier melt of glaciers. In High Arctic Lake Hazen (Ellesmere Island, Nunavut, Canada), the mean daily ice-free area from early May to early September ranged from 45% to 65% from 2000 to 2012 with an overall increase in open water and increased water temperatures (Lehnherr et al. 2018). This change results in part from an earlier onset of ice melting on the lake, but the higher discharge from the glaciers combined with a higher load of suspended sediments due to concomitant soil warming has had a larger impact on the extent of ice-cover. Lake ice off is on average 6 days earlier in West Greenland now than in the 1990s with consequences for temperature dependent upon the quantity of heat stored under the ice prior to the melt and the extent to which it is mixed downwards (Saros et al. 2019), similar to observations in Cortés and MacIntyre (2020) in the Alaskan Arctic. Temperatures also depend on the quantity of incoming cooler glacier meltwater. River temperatures depend on the timing of their melt in spring, which is in part regulated by MDD and snowcover (Docherty et al. 2019). In summer, stream temperatures are highly dependent on solar radiation and air temperatures. The same is true for small dimictic lakes. Temperatures during the ice-free period in larger lakes ($>1$ km$^2$) have a greater dependency on wind induced mixing and the volume of stream inflows (MacIntyre et al. 2009). Large scale differences in warming over the Arctic moderate the extent to which lakes in different regions are warming. Hence, greater warming is occurring in some regions of Greenland due to the influence of the North Atlantic Oscillation (Ding et al. 2014), and northern Finland and Russia are warming more rapidly than Arctic Alaska. Comparative, high resolution studies are required to assess the consequences for temperatures and thermal structure within the lakes and streams.

Controls on temperatures under the ice depend on the extent to which salinity (as measured by specific conductance) contributes to their density structure, ice and snow cover, and the extent of heating and wind mixing in the preceding summer and fall. Temperatures under the ice in salinity-stratified meromictic lakes depend on whether the ice is black ice (clear) or white ice (highly scattering), and whether phytoplankton or other particulates are layered in the water column and absorb incoming radiation (Vincent et al. 2008). Such layering can create depth dependent changes in temperature stratification. In many dimictic lakes, temperatures are inversely stratified with the warmer near bottom temperatures dependent upon the amount of heat absorbed by the sediments over the summer, thus showing a link between summer and winter conditions. Lake size and the magnitude of winds prior to ice-on also moderate temperatures under the ice. Wind-induced mixing effectively strips heat from the lakes prior to ice-on. Few time series measurements exist to quantify the changes in temperature and thermal structure under the ice. However, modeling studies indicate that wind induced mixing in summer in meromictic lakes will lead to changes in winter stratification (Vincent et al. 2008). That is, over time, the depth of the near-isothermal layer will increase and the temperature maximum will decrease. Delays in ice on, as observed in Lehnherr et al. (2018), can also lead to greater heat loss from the sediments and thus cooler temperatures under the ice. The extent of near-bottom density is a critical determinant of ecosystem function under the ice. It moderates the extent of anoxia and structure of aquatic communities (MacIntyre et al. 2018*a*; Jansen et al. 2021). Density stratification in the winter depends on heat stored in sediments, quantity of organic matter, and flow in the water column (MacIntyre et al. 2018*a*). Thus, conditions in the preceding summer, particularly the extent of warming, stratification, and loading of organic matter either from within lake productivity or the landscape, will moderate ecosystem processes including metabolic activity under the ice.

Ecosystem responses under the ice depend on latitude and the extent of snow cover, as they influence the amount of sunlight, including damaging ultraviolet radiation, and whether mixing will be induced in autumn and spring by radiatively driven convection (RDC) (Farmer 1975; Belzile et al. 2001; Bouffard et al. 2019; Cortés and MacIntyre 2020). Limited snowcover enables growth of autotrophs immediately under the ice. The mixing from RDC determines the productivity of diatoms versus flagellates (Jansen et al. 2021). Similarly, the growth of heterotrophs is moderated by depth dependent variations in anoxia and redox. These depend on the horizontal convective circulation driven by heat flux from the sediments and sediment respiration. The extent to which altered mixing regimes will change gradients in key elements is unknown, with more frequent mixing events likely to induce microbially mediated processes such as methanotrophy. While controls on the density structure under the ice have been identified, more effort is required to establish links to ecosystem function.

Knowing temperatures and thermal structure within lakes and flowing waters at present, and predicting their changes in the future, is critical for understanding how aquatic ecosystems will undergo future change. A combination of time series measurements of temperature, specific conductivity, ice thickness and snow cover, meteorology, optical properties, discharge and the use of paleo-indicators enabled the changes described above to be quantified in the lakes in far northern Canada, Greenland, and Alaska. Expansion of time series measurements at other sites is critical. While profile data are available at a number of sites, only a few sites have year-round time series measurements of temperature, specific conductivity, oxygen, snow and ice thickness, optical properties, and meteorology. The first annual data sets for temperature, conductivity, oxygen and other limnological variables were obtained at 2-weekly intervals from 1969 to 1972 in Char Lake in High Arctic Canada (Schindler et al. 1974). Year-round measurements at Toolik Lake, Alaska, began in 2001, while those in the Kuparuk River, Alaska, began by 2012, and those in western Greenland began in 2018. Studies in northern Sweden began in 2009 and with concurrent biogeochemical measurements enabled quantification of emissions of climate forcing trace gases (Jansen et al. 2019; 2021). Measurements of ice thickness in Ward Hunt Lake, Canada, began in the 1950 s (Paquette et al. 2015), and continuous mooring data from the lake have been recorded since 2016 (Bégin et al. 2021*a*). Calculations of stream metabolism in the Kuparuk River contributed to understanding how net ecosystem productivity changes with temperature (Song et al. 2018). The availability of high quality sensors which can be deployed for one or multiple years has facilitated such measurements as has access to remote field stations for longer periods. Software has been developed for processing time series data and quantifying surface energy budgets, temperature and density structure, and the extent of mixing in summer and winter which moderates the persistence of anoxia and the light climate of phytoplankton. Combining the physical measurements with biological ones is critical (e.g., Hazuková et al. 2021). The addition of oxygen sensors enables metabolism to be quantified as well as the gradients in oxygen which favor different microbial communities, while chlorophyll *a* fluorescence sensors allow the continuous tracking of phytoplankton populations. The time series measurements in lakes and streams at different latitudes and of different sizes enables basic understanding. Scaling up to assess changes on an ecosystem level requires combining this work with remote sensing (Gardner et al. 2021; Kuhn and Butman 2021) and with coupled biogeochemical and hydrodynamic modeling. The combination of approaches will enable predictions with respect to how changes in the Arctic Ocean and elsewhere modify meteorology and precipitation over the terrestrial landscape such that the combined influence of MDD, air temperature, wind speed, and precipitation on thermal structure and ecosystem structure and function within lakes and streams can be assessed.

## Baseflow of rivers

Arctic streams reflect strong seasonality with often brief warm periods of snowmelt and rainfall runoff and longer dry and cold periods where flow is supported by groundwater discharge as baseflow, or rivers run dry (Lewis et al. 2012). The spatially integrative nature of rivers makes long-term stream discharge records in northern regions valuable for detecting multi-scale hydrologic change where weather stations and monitoring wells are sparse. Yet because multiple, interacting processes control streamflow, challenges arise in parsing causal relationships of detected change, particularly between those directly attributable to surface processes (i.e., hydroclimatological shifts) and those attributable to subsurface processes (i.e., permafrost thaw). Positive trends in annual streamflow discharge in the Arctic over the past several decades (McClelland et al. 2006; Feng et al. 2021) have been ascribed to intensification of the hydrologic cycle (Rawlins et al. 2010; Rawlins et al. 2021) and increased contribution of glacial meltwater in glacier-influenced regions (Liljedahl et al. 2017). Seasonal shifts in streamflow have been linked to a combination of processes that reflect changes in precipitation amount, timing, and phase (Zhang et al. 2013; Stuefer et al. 2017; Arp et al. 2020) as well as changes in seasonally frozen ground and permafrost that affect groundwater fluxes (Yang et al. 2002; Walvoord and Kurylyk 2016; Hiyama et al. 2021). Here, we highlight the baseflow component of streamflow for its sentinel response in detecting changing hydrogeologic (physical and hydrologic subsurface) conditions, conditions that are not directly or easily observable, especially across large scales.

Historical streamflow records for large Arctic rivers show consistent multi-decadal positive trends in baseflow, observed in winter and low discharge periods, across permafrost-covered regions of Europe (Smith et al. 2007; Evans et al. 2020), North America (Walvoord and Striegl 2007; St Jacques and Sauchyn 2009), and Asia (Duan et al. 2017). Though changes in precipitation can contribute to variations in groundwater recharge, and thus baseflow, a primary factor responsible for pervasive, unidirectional trajectories in baseflow in the Arctic is permafrost thaw (Bring et al. 2016). In hydrogeologic settings with relatively permeable substrate, permafrost thaw opens and deepens pathways for flow, promoting groundwater recharge, circulation, storage, and release to streams. Physics-based modeling studies provide theoretical support for thaw-induced baseflow enhancement as a direct result of active-layer deepening (Bense et al. 2009), supra-permafrost talik development (Walvoord et al. 2019), and wholesale permafrost loss (Walvoord et al. 2012). Stream chemistry provides additional support for temporal increases in the proportion of groundwater in streamflow (O'Donnell et al. 2012; Vonk et al. 2015).

Spatiotemporal trends in baseflow can help fill critical scaling gaps in permafrost thaw detection and trajectories. Indirect methods to map, monitor, and model permafrost across large scales show good progress, but limitations in depth of investigation and spatial resolution remain (Jorgenson and Grosse 2016). Direct observations of permafrost loss are sparse and where available yield non-uniformity and heterogeneity that is currently unrealistic to capture in large-scale modeling approaches (Streletskiy et al. 2015; O'Neill et al. 2020; Rey et al. 2020). In the absence of flow regulation, a positive baseflow trend offers a key signal that a watershed or basin underlain by permafrost may be undergoing progressive thaw. Improved permafrost thaw detection via ongoing baseflow monitoring has broad implications for Arctic infrastructure, water resources, critical habitat, and rural community subsistence practices. Increased baseflow introduces its own set of ecosystem and social consequences. Changes in baseflow impact (1) stream biogeochemistry and riverine export of dissolved constituents (Vonk et al. 2015), (2) stream temperatures and habitat suitability for aquatic species (Winfree et al. 2018), (3) river ice thickness and related safety concerns for winter transportation (Jones et al. 2015), and (4) riverbank erosion (Brown et al. 2020).

Understanding setting-specific mechanisms influencing streamflow magnitude and seasonality is critical for fully utilizing baseflow records as an indicator and predictor of Arctic change. For example, in certain settings, lateral talik development can be an important mechanism for enhancing shoulder season baseflow (Walvoord et al. 2019). Due to the characteristic nature of taliks as a precursor to accelerated thaw (Rey et al. 2020), identification of new talik formation through monitoring (Farquharson et al. 2022) may be useful in predicting future stream conditions. Also, baseflow recessional analysis can be a useful means of distinguishing between active layer deepening that enhances supra-permafrost groundwater discharge to streams and widespread permafrost loss that enhances deep subsurface groundwater circulation and discharge to streams as the primary mechanism responsible for observed baseflow trends (Evans et al. 2020). Advancements in developing the use of baseflow information as a sentinel for permafrost thaw requires coordinated multi-disciplinary studies in various hydrogeologic and climatic settings. Intensive subsurface characterization and streamflow chemistry analysis with a plan for long-term monitoring in targeted areas with baseflow change are required to provide extensible quantification and parameterization of permafrost changes reflected in baseflow magnitude and recession characteristics. Taking advantage of the tight coupling between water source and chemistry, a comprehensive approach should incorporate the aquatic biogeochemical response and landscape factors (Tank et al. 2020). Geophysical investigations provide useful hydrogeologic baseline characterization and serve as a means of measuring and monitoring thaw response (i.e., Briggs et al. 2017) coupled to observed baseflow change. Supported by this collection of region-specific data, coupled land surface and cryohydrogeological models can then be constructed to simulate expected streamflow response to various modes of permafrost loss spanning a spectrum of thaw rates and patterns. Ultimately, the development of knowledge in setting-specific baseflow response to permafrost thaw can be broadly applied to enhance risk assessment and improve predictive model capacity.

## Water balance of lakes

Lake distribution, surface area, and water level are strongly affected by climatic factors that influence lake water balance both directly (e.g., precipitation/temperature/ evapotranspiration) and indirectly via permafrost processes that affect thermokarst activity (Grosse et al. 2013; Kokelj and Jorgenson 2013), vegetation change (Turner et al. 2014), subsurface connectivity and drainage (Yoshikawa and Hinzman 2003; Jepsen et al. 2013), and flooding (Jepsen et al. 2016). This climate sensitivity, combined with advances in remote sensing tools, renders lake change a key sentinel response of Arctic freshwater systems. Yet due to the multiple and interconnected factors influencing lake water balance at different spatial and temporal scales, attributing observed change to specific hydroclimatic and thaw mechanisms across diverse Arctic landscapes is challenging.

Key observational findings regarding lake area, distribution, and water level changes across the Arctic have been gathered through two main approaches: spatial analysis, based on remote sensing, documenting recent (i.e., years to decades) hydrological, geomorphological and ecological changes, and paleoenvironmental reconstructions (from sediment archives) providing a long-term temporal perspective (centuries to several millennia). More rarely, such investigations combine both recent and paleoenvironmental change perspectives (MacDonald et al. 2012; Medeiros et al. 2014; Coleman et al. 2015).

The complexity in lake area response to climate change is well illustrated by studies in Siberia and northern Canada reporting on decadal-scale net expansion of lakes and wetlands in the continuous permafrost zone with concurrent net contraction and lake water level decline mostly in the discontinuous zone (Smith et al. 2005; Carroll et al. 2011). This divergence can be explained by a "continuum" concept: climate-induced permafrost thawing and erosion initially leads to thermokarst lake development and expansion, especially in the continuous zone where subsurface flows are limited, but is then followed by declining area and water level as surface and subsurface drainage events become more frequent and widespread, especially in the discontinuous/sporadic zone (Smith et al. 2005).

Thermokarst lake shrinkage and ultimate disappearance, although primarily driven by climate factors, can be strongly modulated by local landscape properties, and typically involves one or more of the following, as summarized by Bouchard et al. (2017): a) rapid drainage (partial or complete) resulting from shoreline breaching after higher-than-average precipitation (Turner et al. 2010; Lantz and Turner 2015); b) lake-level drawdown due to factors that lead to increased evaporation and sometimes complete desiccation (Riordan et al. 2006; Bouchard et al. 2013); c) subsurface drainage through an open "talik" to the deeper groundwater system (Yoshikawa and Hinzman 2003); and d) terrestrialization via rapid peat accumulation and lake infilling (Payette et al. 2004; Roach et al. 2011). The Arctic lake continuum concept has strong physical support and broad merit, but is challenged by a growing number of studies that document heterogeneous patterns of lake area change that deviate from generalized expectations in continuous and discontinuous permafrost, thereby requiring nuanced analyses that account for localized hydroclimatic and landscape variables in addition to permafrost conditions (Karlsson et al. 2012; Pastick et al. 2019; Rey et al. 2019).

Numerous remote sensing studies have examined changes in the areal extent of lakes across permafrost regions over the past few decades, often as a means to determine hydrological consequences of climate change, mainly increasing temperatures and (or) decreasing precipitation (although with strong spatial heterogeneity), especially during the winter (e.g., Smith et al. 2005; Riordan et al. 2006; Labrecque et al. 2009; Jones et al. 2011; Lantz and Turner 2015; Nitze et al. 2018; Nitze et al. 2020). Some investigations have focused, for example, on the increasing activity and areal extent of terrain disturbances such as "retrogressive thaw slumps," which can strongly modify downstream lake hydrochemistry and biological communities (Lantz and Kokelj 2008; Segal et al. 2016). The abundance of these landscape features, as well as their geomorphological activity, have notably increased during the last decades, suggesting that "downstream effects" of climate-induced permafrost degradation on lake dynamics will be significant in the future (see Sections 5&6), although strongly modulated by local topography and ground-ice conditions (Vonk et al. 2015; Tank et al. 2020).

Freshwater ecosystems across the circumpolar Arctic, especially lacustrine basins in permafrost regions, are unique "sediment sinks" that can collect useful environmental archives over their life span (Bouchard et al. 2017, and references therein). Past hydrological changes within lake basins and their surrounding catchments can thus be reconstructed based on "multi-proxy" analyses of sediment archives, and include for instance: past limnological conditions and associated sedimentological processes (Bouchard et al. 2011; 2014; Coulombe et al. 2016), inputs of organic matter and nutrient balance (Coleman et al. 2015; Korosi et al. 2015; MacDonald et al. 2015), abrupt catchment disturbances and associated downstream limnological impacts (Thienpont et al. 2013; Kivilä et al. 2022), and extreme hydroclimatic events such as floods and lake drainage/desiccation (Smol and Douglas 2007; Bouchard et al. 2013; Tondu et al. 2017).

Lagging behind major advances in lake area change detection are complementary applications for characterizing: (1) lake bathymetry (static) and water level elevation (dynamic), required components for translating large-scale lake area change to lake water volume/storage, and (2) ground ice content, temperature, and distribution near and below lakes, required information for estimating thaw rate, thermokarst (subsidence) potential, and hydrologic impact (Grosse et al. 2013; Wellman et al. 2013; Vonk et al. 2019). In addition, integrating water isotope tracers ($^2$H, $^{18}$O) and geospatial analysis at the catchment scale may provide promising avenues for deciphering drivers of change in lake water sources (surface runoff vs. groundwater), flow paths and residence/storage times (Turner et al. 2014; Remmer et al. 2020), as well as temporal hydrological "trajectories" of lakes in response to climate change at the decadal scale (MacDonald et al. 2021). These are key observational pieces that should be prioritized in future Arctic research.

Progress in lake change process-based research will involve integrated data and modeling approaches for investigating climate response across varied landscapes at multiple spatial and temporal scales. For example, using a set of many lakes spanning eco-climatic gradients (e.g., from the boreal forest to the shrub tundra), it should be possible to gain knowledge about past environmental changes related to local geomorphological and hydrological processes, in addition to regional climate (e.g., Dallimore et al. 2000; Wolfe et al. 2011). Ascribing hydrologic and geomorphic mechanisms responsible for lake area change is critical for understanding Arctic lake distribution and lake water balance under continued air temperature increase and permafrost thaw, a necessary underpinning to advance predictive modeling capability.

## Permafrost-derived dissolved ion and nutrient concentrations in lakes and rivers

Dissolved inorganic ions in freshwaters are primarily derived from the chemical weathering of minerals within soils (e.g., Lacelle et al. 2019) and also during fluvial transport (Striegl et al. 2007; Graly et al. 2016; Tipper et al. 2021). The ionic strength, total dissolved solids (TDS) concentration, and electrical conductivity of freshwater are all proportional to the total dissolved ion content of a solution. Major ions include chloride ($Cl^-$), sulfate ($SO_4{}^{2-}$), bicarbonate ($HCO_3{}^-$), sodium ($Na^+$), calcium ($Ca^{2+}$), and magnesium ($Mg^{2+}$). While nitrate ($NO_3{}^-$), bromide ($Br^-$), phosphate ($PO_4{}^{3-}$), ammonium ($NH_4{}^+$), and potassium ($K^+$) often comprise a relatively small proportion of overall ionic strength, these constituents represent important nutrients or markers of specific sources of water or weathering environments (Louiseize et al. 2014). Trace metals are not considered under this review as they typically account for a small proportion of the total dissolved ion load, and the fate and transport of these redox sensitive elements can be very different from those of major ions (Barker et al. 2014). Previous reviews detail permafrost thaw effects on freshwater inorganic chemistry (Colombo et al. 2018). Here, we summarize primary linkages between climate change and dissolved ion loading to freshwaters within the northern permafrost zone.

Rising air temperatures (Serreze and Barry 2011) and increased and (or) intensifying precipitation are among the primary climatic drivers of increasing dissolved ion loading to freshwaters across the circumpolar north (Kokelj et al. 2005; Tank et al. 2016; Toohey et al. 2016; Drake et al. 2018*b*; Beel et al. 2021). Rising air temperatures lead to active layer warming and deepening (Luo et al. 2016), terrain consolidation following thaw (thermokarst) (Kokelj and Jorgenson 2013), and (or) physical slope disturbances (e.g., thaw slumps and active layer detachment slides). These thermally controlled processes are increasing freshwater ion loads primarily by enhancing the supply of dissolved ions (Egli et al. 2008; Gislason et al. 2009; Romero-Mujalli et al. 2019). Increasing thaw depths increases the residence time of water in the subsurface (e.g., Hindshaw et al. 2018), which enhances the pool of dissolved ions derived from chemical weathering reactions. In addition, the availability of soluble ions increases substantially near the top of the permafrost, or in the transition zone in many continuous permafrost regions (Kokelj and Burn 2005; Lamhonwah et al. 2017), as a result of vertical transport with percolation during the thaw season, and translocation of ions towards the freezing front when soils freeze (two-way freeze back can amplify the ion enrichment). There is also evidence to support that permafrost has higher inorganic N loads than the active layer soils, and that this feature is relatively consistent across the Arctic (Wickland et al. 2018; Fouché et al. 2020).

Thus, thawing and permafrost disturbances enhance the supply of soluble ions by exposing soluble ions and weatherable sediments that were immobilized for millennia within permafrost (Keller et al. 2010; Lafrenière and Lamoureux 2013; Tank et al. 2016; Drake et al. 2018*b*; Zolkos and Tank 2020). Thawing also indirectly affects the transport of the enhanced ion pool by activating new groundwater flow pathways across broad scales and opening new taliks (Walvoord and Kurylyk 2016; Paquette et al. 2020*a*). This is evidenced by studies that report on increasing ion concentrations in large lakes (Roberts et al. 2017) and rivers across the circumpolar Arctic (Keller et al. 2010; Drake et al. 2018*b*; Song et al. 2020). Increasing and (or) intensifying precipitation drives increases in ion loading to freshwaters by mobilizing the ions supplied by thaw, weathering, or disturbance, to fluvial networks. Thus deeper thaw combined with rainfall driven flushing of solute rich soils in the transition zone and exposed permafrost (as a result of enhanced groundwater flow, or leaching as a result of rainfall runoff) can yield higher solute (e.g., Lamhonwah et al. 2017) and nutrient loads (e.g., Harms and Jones 2012; Louiseize et al. 2014). In areas affected by physical disturbances (e.g., mass wasting/slope failures and thermokarst), increases in rainfall runoff enhance fluvial ion concentrations by mobilizing solutes supplied by the exposure and weathering of material within disturbed areas, which is often on a more localized basis than observed for thermal perturbations (Lewis et al. 2012; Abbott et al. 2015).

The magnitude and nature of fluvial ion loading varies regionally depending on landscape factors (Tank et al. 2020) including permafrost extent (Petrone et al. 2007)), soil substrate composition and its modification due to prior thaw (Lacelle et al. 2019; Zolkos and Tank 2020), potential for physical perturbation associated with ground ice content (Kokelj et al. 2013), and glacial coverage (Tank et al. 2012; Hawkings et al. 2016; Graly et al. 2017). Relatively ice-rich glacial margins across the circumpolar north may become loci of hillslope thermokarst development (Kokelj et al. 2017) and point-sources of ion loading to freshwaters. For example, on the formerly glaciated Peel Plateau in northwestern Canada where accelerating hillslope thermokarst activity is exposing previously unmodified glacial tills to chemical weathering (Malone et al. 2013; Zolkos et al. 2018), increases in summertime fluvial ion loads propagate through local fluvial networks (Zolkos et al. 2020), and are likely detectable at regional to continental scales (Tank et al. 2016). Studies from disturbed and undisturbed permafrost settings highlight that both thaw depth and the timing and intensity of rainfall events are important in controlling the fluvial ion flux response. Depending on the extent of thaw and nature of rainfall events, the flux response can exhibit a threshold response to warming (i.e., thaw must reach the transition zone) and also nonlinear response to rainfall intensities due to the importance of the controls of thaw depth and antecedent moisture (Roberts et al. 2017; Beel et al. 2020; Beel et al. 2021).

The implications for changes in ionic loads to surface waters depends largely on the nature of the local permafrost (e.g., existence of brine, or saline waters at depth) and the downstream environments and end use (Rogers 2018). Elevated concentrations of major ions in the form of significant increase in salinity ($Cl^-$ and $Na^+$) or changes in nutrient ions or metal contaminants (e.g., Hg and As) can have important implication for ecosystems. Also, because solute concentrations are conservative, easily monitored, and are good indicators of enhanced subsurface flows, or the exposure of permafrost soils through disturbance, dissolved ion loads can be important tracers of these geomorphological and hydrological changes that may have direct ecological effects (Chin et al. 2016; Levenstein et al. 2021). Electrical conductivity (EC) is an easily measured proxy of total ion concentration, that could be easily monitored in nearly any fluvial setting at very low cost with long-term stability (Gillman et al. 2017). Thus, EC may represent a very good sentinel of changes in thaw (groundwater flow) and permafrost stability (physical disturbance) (e.g., Roberts et al. 2017). Some biological proxies, such as fish and diatoms, may be suitable for tracking ionic changes in surface waters. Paleolimnological techniques (e.g., Gregory-Eaves et al. 1999) can reveal past (decadal to centuries) changes where direct measurements are absent. Similarly, novel techniques such as otolith (ear stones from fish that possess annular growth rings from which changes in ionic content can be measured to generate a long-term record) chemistry may reveal ionic trends over timescales of years to several decades (e.g., Roberts et al. 2017).

Important knowledge gaps include the extent to which, and where, nutrient concentrations (e.g., $PO_4^{3-}$, $NO_3^-$ and $NH_4^+$) follow those of major ions. It would be helpful to establish whether there are conditions, environments, or permafrost settings where electrical conductivity is a proxy for inorganic P and N loads. We also still have a limited understanding of the landscape, permafrost and hydrological conditions that regulate how and where ion concentrations are enhanced in the transition zone (e.g., Lamhonwah 2020; Paquette et al. 2020*b*), hence a key focus area for future work would be to characterize soluble ion loads and nutrients especially across the active layer-transition zone boundary and through the permafrost across permafrost types (e.g., syngenetic, epigenetic) and landscape/moisture gradients. In addition, pre- and post-fire (near immediate and longer-term) measurements of ions among terrains with varying ecosystems or parent material could help to constrain wildfire effects on permafrost thaw and more broadly disturbance to aquatic ecosystems.

## Carbon mobilization through lakes and rivers

One of the biggest concerns as the Arctic warms and permafrost thaws is the release of carbon (C) that was previously sequestered through plant uptake and subsequent build-up in permafrost soils (Schuur et al. 2015). Permafrost soils are estimated to contain ∼1300 Pg C, equivalent to about 1.5 times the C currently in the atmosphere (Hugelius et al. 2014). The release of permafrost organic C to the atmosphere in the form of greenhouse gases (GHG) carbon dioxide ($CO_2$) and methane ($CH_4$) can lead to further warming and thus form a positive feedback loop whereby Arctic warming and permafrost thaw is exacerbated—the permafrost carbon feedback (Schuur et al. 2015). However, there are several processes that are still not accounted for in existing models simulating this feedback loop. These include: (1) abrupt and localized landscape disturbances (thaw slumps), which may amplify and disproportionally contribute to organic C release through progressive thaw (Turetsky et al. 2020); (2) lateral transport of organic C by streams and rivers which can enhance or attenuate C fluxes (Vonk et al. 2019); (3) interactions between organic and mineral matter, specifically abiotic interactions between mineral surfaces (e.g., clays and Fe-oxides) and sorbed organic C aggregates which can stabilize thawed organic C (Opfergelt 2020); and (4) the seasonal patterns of carbon emissions across permafrost regions, especially the winter season which is rarely studied but is likely characterized by non-negligible C emissions, both from soils (Natali et al. 2019) and freshwater ecosystems (Hughes-Allen et al. 2021).

As permafrost soils thaw, previously frozen organic C complexes are mobilised into pore water which, depending on local relief, can be transported via hydrologic pathways to freshwater ecosystems (Guo et al. 2007; Raymond et al. 2007; Vonk et al. 2015). This organic C release is generally classified into two size classes: dissolved (generally <0.7 μm nominal pore size) and particulate (generally >0.7 μm) organic C (DOC and POC, respectively). DOC is commonly considered more bioavailable, although there is some exchange between DOC and POC pools (Battin et al. 2009). During its time in the soil zone and eventual release into freshwater ecosystems, organic C can be converted by microbial processes to the GHG $CO_2$ and $CH_4$ (Vonk et al. 2015; Voigt et al. 2020). At the same time, POC release—more common in abrupt thaw scenarios—may enable re-burial of thawed permafrost carbon in sedimentary reservoirs (Shakil et al. 2020). Although the mobilization and fate of organic C and GHG are dependent on numerous factors, they are important components of the permafrost carbon feedback and thus their release into and emission from freshwater ecosystems can be valuable sentinels of permafrost thaw.

## Dissolved organic matter

Dissolved organic matter (DOM) in northern freshwaters can be sourced from active layer or non-permafrost soils, thawed permafrost soils, deep (i.e., sub-permafrost) groundwater, leaching of terrestrial leaf litter, or from within-system (autochthonous) productivity. Given this diversity, DOM composition and concentration (i.e., as dissolved organic carbon; DOC) can be expected to change as a result of climate forcing via a variety of mechanisms, including, but not limited to: permafrost thaw and declining permafrost integrity (e.g., Vonk et al. 2015; Fouche et al. 2020), changing catchment primary production (Pienitz and Vincent 2000), changes in catchment soils and vegetation related to wildfire (Kicklighter et al. 2014; Larouche et al. 2015), changes in land-water connection or within-catchment water residence times (Striegl et al. 2005), increased groundwater inputs due to permafrost degradation (Walvoord and Striegl 2007), changing residence times and possible evaporative concentration in lakes (Johnston et al. 2020), and changing length of ice-free season (Wrona et al. 2016) and associated modified stratification regimes in lakes (e.g., Lau and del Giorgio 2020). Thus, while permafrost thaw has often been a focus for investigations of altered DOM in northern freshwaters, there are multiple climate-related mechanisms that may act concurrently to drive changing DOM. One particular example of climate-driven effects on DOM comes from open-basin lakes, where within-lake retention of the substantial inflows of freshet-origin DOM is largely dependent on penetrative convection. In lakes where near-surface conductance declines with snowmelt inflows, only 10%–15% of DOM may be retained, with the rest flowing downstream (Cortés et al. 2017; Cortés and MacIntyre 2020). A transition to increased precipitation during summer relative to winter (e.g., Beel et al. 2021) would decrease snowmelt inflows and could lead to greater retention of DOM during a season when stream inflows are able to penetrate deeper within the lake (see, for example, Rueda and MacIntyre 2009).

Permafrost thaw can affect DOM concentration and composition directly when it enables laterally-flowing water to access soils that vary in their carbon content, alters the duration of soil-water interaction (Frey and McClelland 2009; Wickland et al. 2018), enables the collapse of permafrost and (or) active layer soils into freshwaters (i.e., via thermokarst; Kokelj et al. 2005; Wauthy et al. 2018), or enables DOM interactions with newly-exposed mineral soils (Opfergelt 2020). In many regions, permafrost-origin DOM can be more aliphatic than DOM sourced from seasonally-thawed soils, as indicated by higher slope ratios, lower specific UV absorbances, and H/C ratios $>$ 1.5 (Littlefair et al. 2017; Wang et al. 2018; Fouché et al. 2020). However, because these aliphatic molecules are also more labile (Mann et al. 2015; Spencer et al. 2015), they can be rapidly mineralized (Drake et al. 2015), which may limit our ability to use compositional differences at the source of thaw to trace permafrost carbon within aquatic networks (Drake et al. 2018*a*). In addition, evidence is emerging that the composition of permafrost-origin DOM can vary across permafrost soils of different origins (MacDonald et al. 2021), and that lability may vary by geographic location and season (Wickland et al. 2018; Burd et al. 2020). As well as degradation by microbes, photodegradation may also rapidly consume DOM liberated by permafrost thaw within aquatic networks (Cory et al. 2013). Regardless of the source, alterations in the flow of DOC to freshwater systems are likely to perturb a “fast cycling” component of the carbon cycle (e.g., Dean et al. 2020), so understanding climate drivers of change in DOM is of broad interest. In addition to C-cycle effects, changing DOM can provoke pronounced physical, chemical, and ecological change within aquatic ecosystems (Creed et al. 2018). Examples include strengthening lake stratification with consequent effects on bottom water oxygen concentrations (Bartosiewicz et al. 2019), fish habitats (Couture et al. 2015), and carbon mineralization (Bartosiewicz et al. 2019); and changes to primary production and food webs (Karlsson et al. 2009; Karlsson et al. 2015; Wauthy and Rautio 2020)

Across aquatic systems generally, rates of change will differ based on whether press (e.g., gradual permafrost thaw, changing catchment vegetation, effects of temperature on primary production and respiration) or pulse (e.g., thermokarst, wildfire, and flood) disturbances dominate. Whether permafrost thaw engenders an increase or decrease in DOM will also depend on the depth of organic soils relative to the thaw front (i.e., for active layer deepening) or nature of soils unearthed (i.e., for thermokarst). While DOM has been shown to increase with thaw, or across permafrost gradients in some regions (Frey and Smith 2005; Wauthy et al. 2018), increasing contributions from mineral soils have caused DOM declines in others (Kokelj et al. 2005; Littlefair et al. 2017; Beel et al. 2021). In many cases drivers of change will be similar across lacustrine and fluvial systems: for example, increasing precipitation (Fowler et al. 2020) and terrestrial primary production (Finstad et al. 2016) have both been linked to increasing DOM. However, drivers may also be system specific, with changing DOM related to changing stratification, and factors such as evaporative concentration (Anderson and Stedmon 2007; Johnston et al. 2020) specific to lakes. Changing hydrologic connectivity can affect DOM in both lakes (Tank et al. 2011; Bogard et al. 2019*b*) and fluvial systems (Walvoord and Striegl 2007), but the geographic scale of consideration is often necessarily larger for fluvial networks.

The fact that changes in DOM can be forced by a variety of processes (see above) and are often “ephemeral” within aquatic networks (Drake et al. 2018*a*) makes this sentinel a complex one that should be interpreted with caution. However, because changing DOM is of such broad interest to the aquatic community, we suggest here some important next steps to help elucidate the mechanisms behind changes observed. First, a continued (and expanded) focus on the use of radiocarbon measurements and detailed work to assess molecular structure, such as via Fourier-transform ion cyclotron resonance mass spectrometry (e.g., McCallister et al. 2018; Wang et al. 2018) will help determine DOM source when concentration or compositional changes occur. Developing relationships between compound-specific measurements and more readily measured optical properties will be helpful in this regard. Second, work to assess the origin of DOC most readily mineralized to $CO_2$ and $CH_4$ using tools such as radiocarbon and coupled in situ measurements of DOC and carbon gases will help to better understand rapid cycling of novel DOC inputs to freshwaters (e.g., Bogard et al. 2019*a*), and gauge the global importance of these changes to generate climate feedbacks (Drake et al. 2018*a*; Dean et al. 2020). Finally, more attention to regional and cross-system variability is necessary for upscaling via geospatial techniques. Specific to lakes, this includes a better understanding of how different lake types (i.e., via varying modes of formation and subject to different types of thaw) may differ in their response to permafrost thaw and warming-driven changes in stratification and primary production (e.g., Prėskienis et al. 2021). Across all aquatic systems, a focus on understanding how broad-scale variation in landscape factors (including organic carbon contained within permafrost, the mineral composition of soils, and geomorphic change) regulate the yield and fate of aquatic DOM (e.g., Tank et al. 2020) will be critical for understanding change at the pan-Arctic scale.

## Greenhouse gases—carbon dioxide and methane

The GHG carbon dioxide ($CO_2$) and methane ($CH_4$) are produced and consumed by biological and chemical processes in sediments and water columns of lakes and rivers (Tranvik et al. 2009; Ward et al. 2017). Freshwater systems also receive dissolved $CO_2$ and $CH_4$ from inflowing surface waters and groundwater in their watersheds (Paytan et al. 2015; Street et al. 2016; Rasilo et al. 2017), thus integrating terrestrially derived and aquatic-derived GHGs. Depending on whether dissolved $CO_2$ and $CH_4$ concentrations are undersaturated or supersaturated in near-surface waters with respect to the atmosphere, freshwater systems absorb (from the atmosphere) or emit (to the atmosphere) GHG across surface-layer boundaries. Studies have shown that many Arctic freshwater ecosystems are sources of carbon GHGs to the atmosphere (Kling et al. 1991; Abnizova et al. 2012; Striegl et al. 2012; Crawford et al. 2013; Negandhi et al. 2013; Sepulveda-Jauregui et al. 2015; Spawn et al. 2015; Wik et al. 2016; Stackpoole et al. 2017; Denfeld et al. 2013, 2018; Zolkos et al. 2018, 2019; Matveev et al. 2019), although lakes can be sinks of $CO_2$ (Tank et al. 2009; Laurion et al. 2010; Bogard et al. 2019b; Lougheed et al. 2020). In addition to regional variabilities, there are considerable local spatial (Bouchard et al. 2015) and temporal (Hughes-Allen et al. 2021; Prėskienis et al. 2021) variabilities in freshwater GHG exchange with the atmosphere, and quantifying patterns and drivers of GHG exchange is an area of active research.

The linkage between climate and Arctic freshwater GHG exchange with the atmosphere is complicated, as many processes play a role in $CO_2$ and $CH_4$ production, consumption, and flux across water surfaces. The complex suite of physical, chemical, and biological processes, autotrophic versus heterotrophic sources, and dual location of processes within freshwater systems (sediments, water column) precludes a singular definitive response of GHG production and exchange to changing climate. For example, it is well known that $CO_2$ and $CH_4$ production rates in freshwater systems generally increase with water and sediment temperature (Gudasz et al. 2010; Yvon-Durocher et al. 2011), and this has been documented in incubation studies of high-latitude ponds (Negandhi et al. 2016) and rivers (Wickland et al. 2012). However, processes that consume $CO_2$ (primary production, Lauridsen et al. 2020) and $CH_4$ ($CH_4$ oxidation, Thottathil et al. 2019) also increase with temperature. Furthermore, temperature has effects on physical processes that influence GHG dynamics and flux in freshwater systems including water column mixing and stratification (MacIntyre et al. 2009; Matveev et al. 2019; McIntosh Marcek et al. 2021) and gas transfer velocities (Wanninkhof 2014; MacIntyre et al. 2018*b*, 2021*a*, 2021*b*). Increased discharge will also moderate gas transfer velocities in rivers (Ulseth et al. 2019). These examples illustrate the complex nature of linkages between climate and freshwater GHG dynamics. Therefore, while it may not be appropriate to consider Arctic freshwater GHG production or exchange as a sentinel response to climate, the numerous linkages identified between GHG processes and better-defined climate sentinels (including several discussed in this paper) serve to inform the varying and sometimes opposing effects of climate on GHG emissions. That said, studies that identify regional increases in emissions in permafrost-derived carbon and $CH_4$ emissions are directly relevant to modeling increased atmospheric warming.

Despite the complex relationships between climate and carbon GHG, insights into changing climate and freshwater GHG dynamics have been achieved in the Arctic in a range of systems using a variety of approaches. Long-term data on GHG in these systems are rare, but at least four studies have documented changes in dissolved inorganic carbon constituents over multidecadal periods across the Arctic using sporadic or continuous long-term data. These studies collectively show that bicarbonate ($HCO_3^-$, a constituent of total dissolved inorganic C and a product of respiration) or alkalinity (comprised primarily of bicarbonate) exports has increased over recent 20 to 40-year periods in the Yukon River, Alaska (Striegl et al. 2005), the Mackenzie River, Canada (Tank et al. 2016), and the Ob and Yenisey Rivers, Russia (Drake et al. 2018*c*), and alkalinity has increased in three Russian tundra lakes over 43 years (Drake et al. 2018*c*). The increases are attributed, at least in part, to increased weathering and respiration and longer water residence in deepening active layer soils due to permafrost thaw, and they reveal how freshwater systems integrate carbon cycle processes relevant to GHG across their watersheds.

Another approach that has given insights into changing freshwater GHG dynamics is conducting studies over gradients or chronosequences in "space for time" substitutions. A study of riverine $CO_2$ emissions along a north-south transect in the Western Siberian Lowlands showed that emissions were lowest in rivers draining continuous permafrost and they increased moving south into discontinuous and sporadic permafrost zones, suggesting emissions may increase when continuous permafrost areas thaw (Serikova et al. 2018). A chronosequence study in Arctic polygonal tundra in Alaska investigated $CO_2$ and $CH_4$ fluxes of ponds formed from ice wedge degradation and found fluxes varied significantly with pond evolution, which occurs on decadal to century timescales (Wickland et al. 2020). In the first approximately ten years of formation, ponds were net $CO_2$ sinks and moderate $CH_4$ emitters; as ponds deepened and widened with time (~20 years after formation) they switched to $CO_2$ sources with no change in $CH_4$ emissions; and as emergent aquatic vegetation and organic matter accumulated the ponds became strong net $CO_2$ sinks and strong $CH_4$ emitters about 30–100 years after formation (Wickland et al. 2020). While several studies have investigated GHG fluxes of polygon tundra ponds (Prėskienis et al. 2021; Rehder et al. 2021), the study by Wickland et al. (2020) is the first to put fluxes into the context of pond formation and evolution. Insights have also been gained by investigating links between freshwater GHG and other sentinels or impacts of climate change such as thermokarst formation. For example, a study of the effects of stream GHG fluxes in western Arctic Canada found that $CO_2$ efflux was significantly greater, but $CH_4$ efflux was generally similar or smaller from thermokarst-impacted streams compared to non-thermokarst streams (Zolkos et al. 2019).

While much understanding has been gained on freshwater GHG in the Arctic in recent decades, future work needs to focus on key knowledge gaps and enact a variety of approaches not only to detect changes in GHG, but also to predict them as climate change continues. First, more long-term data from freshwater systems are needed. Long-term studies of GHG fluxes in ecosystems representative of important lake, pond, and river types, regions, and disturbance regime are of utmost importance. The recovery of historic data sets, and (or) adding to them with new efforts, will also increase the pool of long-term data. Second, in addition to quantifying emissions over time, studies that investigate relevant processes are of utmost importance to understand why emissions may be changing in response to climate. Third, studies that focus on identifying key times, systems, and (or) variables to detect change in response to climate are needed. For example, under-ice GHG dynamics and effects of shorter ice-cover seasons, or the impact of flood events and shifting hydrological regimes that drive terrestrial-aquatic linkages are gaps in our current knowledge. Fourth, linking GHG fluxes, processes, or key variables to remotely sensed data will vastly improve our ability to assess systems over larger areas and with greater frequency (e.g., Kuhn et al. 2020). Finally, development of process-based and statistical models of GHG dynamics and fluxes in aquatic systems, with an eye to how processes may vary regionally and seasonally across system types, will provide platforms to evaluate past and future change.

## Radiocarbon ($^{14}C$)

Organic C has been building up in permafrost soils and Arctic peatlands since at least the Holocene or even older (MacDonald et al. 2006; Hugelius et al. 2020). In some parts of the Arctic, particularly east Siberia, Alaska, and the Yukon territory in the western Canadian Arctic, substantial deposits of Pleistocene-aged organic C is frozen in permafrost as well (Strauss et al. 2017). Because permafrost has potentially been sequestering C since $>$50 000 years ago, radiocarbon ($^{14}C$) is a powerful tool for identifying whether C found in Arctic freshwater ecosystems has come from recent biological turnover or from the thawing of long frozen permafrost. In some regions, the age of thawed permafrost organic C has been linked to its biolability (how readily it is broken down by microbial activity), and thus its conversion to GHG. Vonk et al. (2013) and Drake et al. (2015) found that very old, permafrost-derived DOC (20 000–30 000 years old) could be rapidly converted to $CO_2$ upon thaw. This high biolability of aged permafrost C may limit the potential of $^{14}C$ of organic C as a sentinel within systems with high residence times. Nevertheless, measurements that are less affected by residence-time, such as those of $CH_4$ bubbles released in thermokarst (thaw) lakes in Alaska and east Siberia (Walter Anthony et al. 2016), have found C ages up to 42 900 years. Radiocarbon of freshwater C therefore has the potential to be a powerful sentinel for the thawing of very old permafrost soils, and by extension, the processes driving the Permafrost Carbon Feedback.

Radiocarbon dating of the GHGs emitted by Arctic freshwater ecosystems can show whether thaw of very old permafrost material is directly contributing to ongoing climate forcing. Walter Anthony et al. (2016) showed that the age and amount of $CH_4$ released from Arctic and boreal lakes were directly related to the input of organic matter from adjacent permafrost soils. This study focused mainly on thermokarst lakes which, by definition, are impacted by permafrost thaw, and measured only ebullition $CH_4$, which is generated in lake sediments and released in stochastic events leading to highly heterogeneous fluxes and locally specific C sources (isolated ebullition "seeps"). In a study of lakes across the Alaskan north slope more broadly, Elder et al. (2018) focused on dissolved $CH_4$, an "integrated" $CH_4$ pool more representative of whole lake processes. This study found that $CH_4$ emissions tended to be driven by younger permafrost C, with a maximum age of 3300 years compared to the maximum age of 42, 900 years found in $CH_4$ ebullition from thermokarst lakes (Walter Anthony et al. 2016; Elder et al. 2018). The oldest $CH_4$ ages observed by Elder et al. (2018) were in lakes developed in fine-grained, ice-rich sediments that thawed rapidly to expose older C beneath the lakes.

There are far fewer studies of the $^{14}C$ composition of $CO_2$ emissions from Arctic freshwater ecosystems. In general, freshwater $CO_2$ emissions tend to be younger than $CH_4$ (Bouchard et al. 2015; Elder et al. 2018, 2019; Dean et al. 2018, 2020). $CO_2$ emissions from Alaskan lakes were found to contain anything from 0% to 50% carbon $>$ 5000 years

(Elder et al. 2018), while in headwater streams and lakes in the NW Canadian Arctic, $CO_2$ older than 1000 years likely contributed only 0%–1% of emissions (Dean et al. 2018). It is harder to detect contributions of old permafrost C within younger bulk $^{14}CO_2$ ages due to the potential for contemporary biological turnover to overwhelm relatively small old permafrost C signatures (Drake et al. 2018*a*; Wild et al. 2019). However, incubation studies of freshwater DOC have demonstrated that organic C released from thawing ancient Yedoma soils (>20 000 years old) is not only biolabile (Vonk et al. 2013; Drake et al. 2015), but this older organic C may be preferentially respired by heterotrophic microorganisms (Mann et al. 2015). Recent in situ studies comparing the age of freshwater organic C and dissolved $CO_2$ have shown that contemporary C will generally dominate freshwater C emissions overall (Campeau et al. 2019), even in the presence of ancient organic C sources (Dean et al. 2020). This suggests that the detection of old organic C in freshwater ecosystems may not necessarily be a good indicator for substantial release of old C to the atmosphere.

Despite these limitations, the age of freshwater organic C is a good sentinel for the release of old permafrost OC in general. Wild et al. (2019) analysed the $^{14}C$ content of organic C across the major Siberian Arctic Rivers, finding that while DOC was dominated by C fixed by contemporary biological turnover, POC was dominated (63 ± 10%) by thawed permafrost C, potentially because POC is less labile than DOC. These findings should be couched by the total flux data, which show that POC represented only 5%–35% of the total organic C transported by these rivers, and thus total organic C in these large rivers is mostly dominated by contemporary DOC (Holmes et al. 2012; McClelland et al. 2016). Regions dominated by abrupt thaw processes, such as the Peel Plateau in NW Canada, can be overwhelmed by particulate fluxes, where $PO^{14}C$ reflects the primary release of permafrost C into watersheds (Shakil et al. 2020). To summarize, DOC in headwaters can show clear evidence of permafrost thaw (Vonk et al. 2013; Dean et al. 2020). However, in larger rivers, or in regions where abrupt thaw is the norm, POC is a better indicator of the mobilization of permafrost organic C. This is because the DOC pool can be quickly overwhelmed by contemporary organic C inputs downstream, which is exacerbated by the potential for rapid decomposition of biolabile old organic C (Drake et al. 2015; Wild et al. 2019).

To improve our understanding of permafrost thaw contributions to Arctic freshwater carbon export, we suggest some considerations and net steps. First, future studies looking to employ $^{14}C$ analyses of permafrost-derived freshwater carbon should consider which are the most appropriate forms (s) of carbon to sample based on the research question, region and measurement scale. POC and $CH_4$ are more likely to be sensitive to the mobilisation of old organic C from permafrost thaw while DOC and $CO_2$ are more likely to be the largest components of lateral and vertical freshwater C fluxes, respectively. Both compound-specific and ramped-pyrolysis oxidation radiocarbon analyses hold promise to overcome the biolability and low-sensitivity constraints of riverine organic C pools (e.g., Zhang et al. 2017). Second, severe permafrost destabilization is generally clear in freshwater $^{14}C$ signatures at the site of thaw (Vonk et al. 2013; Walter Anthony et al. 2016), but gradual permafrost thaw, such as increasing active layer depths over several years, are much harder to detect (Dean et al. 2018; Schwab et al. 2020). Long-term baseline records of freshwater $^{14}C$ for comparison are only available for the major Arctic Rivers (Raymond et al. 2007), and expansion of these records would be very beneficial. In addition, work that can provide independent estimates of expected range of freshwater C ages in a river or lake based on catchment characteristics, such as net primary production and soil organic C turnover times derived from vegetation distribution and soil C content, or inputs of glacier-meltwater or groundwater, would also help contextualise individual or sets of freshwater $^{14}C$ observations (Dean et al. 2018; Estop-Aragonés et al. 2020). Third, expressing loss rates of previously frozen organic C sources per unit of soil organic C stocks thawed, e.g., mass of permafrost C released to the atmosphere as $CO_2$ or $CH_4$ per mass of thawed soil organic C per unit area and time, would help compare loss rates of old permafrost carbon between sites (Estop-Aragonés et al. 2020). Finally, the Arctic is a vast and diverse space. Research efforts to understand how the age of freshwater C may be expected to change in the future should consider targeting transition zones between continuous and discontinuous permafrost, and regions severely impacted by thermokarst processes (Vonk et al. 2019).

## Dissolved oxygen concentrations in lakes

Oxygen is a master variable that controls numerous ecological and biochemical processes in the aquatic environment. The threshold response of dissolved oxygen (DO) as a sentinel can be broken down into six discrete states that might be considered in Arctic lakes and across which we can expect a reversible "regime shift" to a new set of conditions, with major implications for aquatic biota and ecosystem functioning. Those states range from frozen solid without DO (state 1) to oxygen supersaturation (state 6). State 1 refers to the case of shallow lakes that freeze to the bottom, which are common in the Arctic, and therefore have no liquid water to contain DO. Conversely, at the other end of the spectrum, DO supersaturation is a feature of productive lakes in the spring, even under ice, and in the summer. Some organisms may then experience high oxidative stress. The potential for the formation of light-mediated reactive oxygen species (Rose 2016) occurs within this state, although such conditions would be mostly optimal for net phototrophy.

In between the two end members (states 6 and 1), DO levels range from saturation with respect to atmospheric oxygen (state 5) that is conducive to diverse aquatic life dominated by aerobes, to successive levels of oxygen depletion, from below saturation but above hypoxia (state 4) to hypoxia (state 3). Definitions of hypoxia depend on the field of study or taxa of interest, and can be considered as DO levels that fall below thresholds that affect organisms such as salmonids (2 mg/L; Leppi et al. 2016), mesozooplankton (1–3 mg/L; Vanderploeg et al. 2009*a*), cladocerans (0.3–2 mg/L; Wright and Shapiro 1990; Vanderploeg et al. 2009*a*; Vanderploeg et al. 2009*b*) and copepods (0.6–1.2 mg/L; Stalder and Marcus 1997; Vanderploeg et al. 2009*b*).

Under conditions of extreme depletion, the water becomes anoxic (state 2), which can be operationally defined as levels below 0.03 mg/L (1 μmol/L). Zooplankton taxa that are tolerant to anoxia include taxa such as *Chaoborus* (Doubek et al. 2018). Anoxia may also be defined as a chemically-relevant threshold below which anaerobes respire electron acceptors other than DO, such as nitrate, metal oxides, sulfates and ultimately $CO_2$, leading to methanogenesis (e.g., Vigneron et al. 2019). This is a key threshold for sediment release of P and reduced chemical species (Orihel et al. 2017). The accumulation of reduced species such as sulfidic compounds results in a strong DO deficit (oxygen demand).

Shifts between the discrete states listed here have major implications for aquatic ecosystem structure and functioning. These thresholds are likely to be highly responsive to climate, in particular via changes in the physical barriers to DO and mixing (ice cover and thermocline), and changes in rates of microbial metabolism (organic carbon supply and direct temperature effects). While the pathways linking climate to oxygen dynamics are increasingly understood in aquatic systems (e.g., Jane et al. 2021), high latitudes are poorly represented in this area of research.

Many recent changes in water column stratification and the resulting seasonality of DO concentrations in freshwater systems are climate-driven (e.g., Fang and Stefan 2009;Palmer et al. 2014; Couture et al. 2015; Schwefel et al. 2016; Nelligan et al. 2019). Environments with seasonal bedfast ice are transitioning to floating ice (Engram et al. 2018), which now provides habitat during winter darkness, conducive to anoxia and methane production (Mohit et al. 2017). The disappearance of bedfast and perennial ice is particularly striking as a sentinel response to increasing air temperature (see Section 1). Permafrost thaw at the base of lakes (and talik formation; Arp et al. 2016) opens up new anoxic habitats for anaerobic microbes (see Section 9). Further transition implies shorter ice cover periods, generally associated with shortened winter anoxia period and thinner oxygen-depleted zones (Fang and Stefan 2009; Terzhevik et al. 2009; Couture et al. 2015). An increasing number of systems previously covered by perennial ice might thus experience seasonally alternating oxic-anoxic regimes (Mohit et al. 2017; Bégin et al. 2021*a*).

A longer ice-free season and elevated air temperatures can also cause summer stratification that may result in the establishment of an oxygen depleted hypolimnion (e.g., Palmer et al. 2014) or prolong the near-bottom anoxia which develops under the ice in winter (Cortés and MacIntyre 2020) and, if either the loading of chromophoric dissolved organic matter or primary production increases, reduced transparency, which leads to stronger thermal stratification (e.g., Bartosiewicz et al. 2019). This is especially important in systems where organic matter and nutrients are sustaining the respiratory oxygen demand (Golosov et al. 2007; Fang and Stefan 2009). While recent evidence from temperate systems suggests that fixed morphometry does not play as broad of a role in controlling thermal structure of lakes relative to other local to regional drivers such as climate and browning (Bartosiewicz et al. 2019; Pilla et al. 2020), the extent to which this applies to the Arctic remains unclear. DO depletion is more important in basins which have a small volume of water in relation to the surface area of sediments (Mathias and Barica 1980; Leppi et al. 2016), and such conditions are typical of the permafrost thaw (thermokarst) lakes and ponds that occur throughout the Arctic landscape (Laurion et al. 2010; Deshpande et al. 2017).

In permafrost landscapes, soil warming triggers dramatic loss of water by drainage, percolation, thawing and erosion. Increased evaporation, combined with warmer temperature, results in the drying out of aquatic habitats (Bouchard et al. 2013). Furthermore, extensive dissolved organic matter inputs from increased precipitation, temperature, permafrost thaw and terrestrial vegetation are likely to induce greater oxygen depletion (Deshpande et al. 2017; Wauthy et al. 2018; Knoll et al. 2018). DOC provides electron donors for oxic organic matter degradation (Couture et al. 2015), whose rates depend on both DOC concentrations and temperature. Colored DOC favors shallow heat absorption, leading to more stable and persistent stratification (Houser 2006; Read and Rose 2013; Pilla et al. 2018). While the isolation of bottom waters impedes atmospheric DO recharge, it also allows the deeper waters to remain cool, which slows down metabolism (Bartosiewicz et al. 2019). Increasing DOC is likely to have greater repercussions on the oxygen balance in clear, oligotrophic waters (Knoll et al. 2018). Fertilization brought about by DOC-bound nutrients (Creed et al. 2018) are likely drivers of enhanced metabolism and thus DO depletion. In contrast to temperate lakes hosting aquatic vascular macrophytes that die off in the winter and draw down oxygen, Arctic lakes host perennial microbial mats and mosses. We hypothesize that Arctic lakes covered by perennial microbial mats and mosses would respond to a transition to seasonal macrophyte dominance under a warming climate by more frequent anoxia.

Similar to many ecosystem responses to climate change (Burkett et al. 2005), DO changes are largely nonlinear. Nonlinearity is associated with the coupled second order kinetic reactions involving redox processes (e.g., the oxidation of sulfides) and microbial respiration, which themselves respond to oxy-thermal and optical parameters in a nonlinear unimodal fashion to changing DOC. DO concentrations can also experience threshold responses as a result of drainage or ice-off events. This is particularly relevant for the coldest regions of the High Arctic, where extreme warming events may cause loss of multi-year ice and shift to a regime of higher year-to-year variability (Bégin et al. 2021*a*).

Models are being developed to better understand oxygen dynamics and the linkages with climatic drivers (Couture et al. 2015; Golosov et al. 2012; Koue et al. 2020). Because of logistical difficulties, what little aquatic biogeochemical data exist from remote areas of the Arctic comes mostly from midsummer sampling during the short, ice-free period. Moorings equipped with oxygen and temperature probes provide high temporal resolution data, allowing analysis of the seasonal and interannual variability (e.g., Deshpande et al. 2017; MacIntyre et al. 2018*b*; Paquette-Struger et al. 2018; Begin et al. 2021*a*) that is important for interpreting long-term trends. Further studies of this type are needed across diverse freshwater systems of the Arctic to evaluate the drivers of variability, and as a baseline to evaluate future changes.

Digitized information on bathymetry and local weather time-series are essential starting points for modeling these DO fluctuations, along with high frequency measurements of temperature and conductivity. The latter is especially important give that small changes in solute concentrations can have large effects on density structure, and therefore on stratification and mixing regimes in cold polar waters (Cortés and MacIntyre 2020; Bégin et al. 2021*b*). These measurements should be augmented with light data, either with high-frequency sensors or from profiles with high vertical resolution, allowing resolution of temporal changes in light attenuation and its effect on primary productivity, thermal stratification, and photooxidation. Complementary data on DOM and dissolved sulfide concentrations would also help better constrain the modelling of biogeochemical oxygen fluxes and their sentinel responses to environmental change.

## Trophic status of lakes

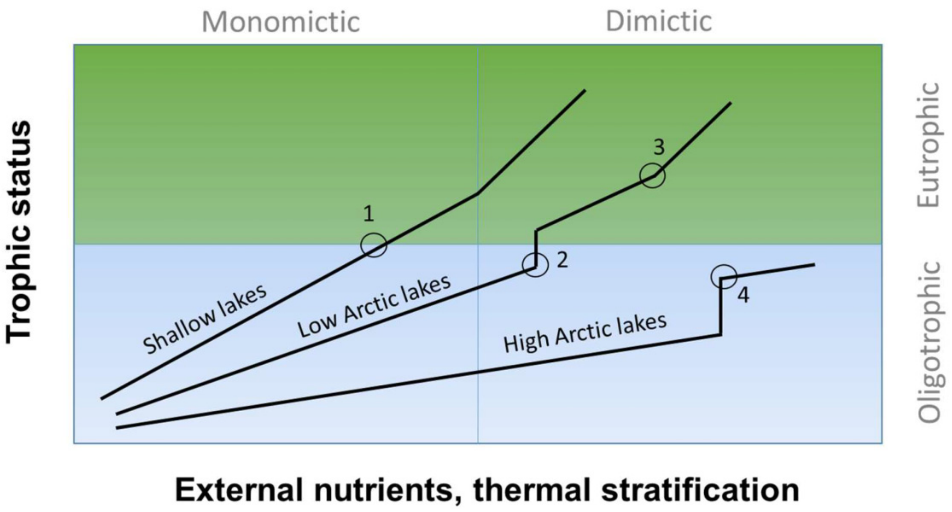
Lakes can be classified in different trophic status categories according to their total phosphorus concentrations: oligotrophic (0–12 μg/L), mesotrophic (12–24 μg/L), eutrophic (24–96 μg/L) and hypereutrophic (>96 μg/L) (Carlson and Simpson 1996). Arctic lakes have typically been considered oligotrophic, including at the lower, ultraoligotrophic end of this range (Hamilton et al. 2001; Michelutti et al. 2002), with low P concentrations and low content in chlorophyll *a* (Chl-*a*). The data from about 1200 Canadian Arctic lakes and ponds from 1970s onward showed the mean TP concentration was 12 μg/L and only 8% were classified as eutrophic based on their phosphorus content > 30 μg/L (Dranga et al. 2018). However, in the warmer climate, the P concentrations are increasing. In a study that included 254 circumpolar ponds from more recent measures, the mean TP concentration was about 50 μg/L for sites that were affected by climate-induced permafrost thaw but < 15 μg/L for nonimpacted sites (Wauthy et al. 2018). Region-specific studies have also indicated that the eutrophication of Arctic waterways is now more common and (or) has increased in recent years (Ayala-Borda et al. 2021; Dranga et al. 2018; Wauthy and Rautio 2020), and it is the shallow lakes that are first becoming eutrophic (Fig. 2). They are naturally more eutrophic due the water column—sediment interaction and the release of P from the high concentration of TP in the sediment (Rautio and Vincent 2006). In the long-term, changes in the trophic characteristics of Arctic lakes have been traced using sediment archives. Concentration and composition of algal pigments and subfossil community assemblages have shown large shifts in trophic status over the last 150 years, in tandem with climate change (Antoniades et al. 2007; Larocque et al. 2001; Smol et al. 2005; Michelutti et al. 2005; Kivilä et al. 2022).

The main climate drivers influencing the trophic status of lakes are the increase in temperature due to Arctic amplification and changes in precipitation regimes. The effects of temperature can be direct; for example, certain algal and cyanobacterial species are indicators of increasing maximum temperatures in high latitude lakes, associated with a concomitant change in trophic status (Freeman et al. 2020). More commonly, temperature effects are indirect. Increasing cumulative temperatures promote higher annual productivity in aquatic ecosystems as the growing season becomes longer, with greater light exposure. With an earlier ice break-up, light availability in the water column potentially increases, allowing higher production rates of photosynthetic organisms and affecting community structure (Bégin et al. 2021*b*; Lehnherr et al. 2018). Indirect temperature effects are further driven by changes in the landscape through permafrost thaw (Vonk et al. 2015; Tank et al. 2020), Arctic greening (Campbell et al. 2020), and shifts in migratory bird and anadromous fish movement and reproductive patterns (Hines et al. 2000; Reist et al. 2021), all of which potentially affect external nutrient loading. For example, abundant goose populations modify the terrestrial landscape through intensive grazing and by bringing high quantities of nutrients into inland waters through feces accumulation (Buij et al. 2017; Cadieux et al. 2005; Luoto et al. 2014), which in addition to increasing T and N concentrations, alter carbon cycling due to increased C demand by primary producers (Macdonald et al. 2015). Similarly, temperature together with dispersal barriers (Jeppesen et al. 2021) determine the northernmost limit of many fish in Arctic lakes. Fish communities have a cascading effect on the lower food web (e.g., Jeppesen et al. 2001), including via nutrient excretion that causes algal biomass to be higher in water bodies with fish (Rautio and Vincent 2006).

Large increases in precipitation are expected over the Arctic landscape (especially rainfall; McCrystall et al. 2021) and these work in tandem with higher temperatures through their additive impact on nutrient and other external inputs. A wetter and warmer climate intensifies the transfer of nutrients and organic matter into aquatic ecosystems (Schaeffer et al. 2013), with consequences for trophic status via changing production and species composition. The increase of temperature leads to higher evaporation rates (Lewis et al. 2016) and may reduce water volume and hence increase the concentration of solutes that promote primary production (Andresen and Lougheed 2015), although in a reduced habitat that may even evaporate to dryness and disappear (Smol and Douglas 2007). Without increasing temperatures, lakes with high N and P concentrations are suggested to remain low in productivity (Dranga et al. 2018), while increasing temperatures and concurrent intensification of thermal stratification would likely promote a trophic state shift in such lakes (Hobbie et al. 1999; Taranu et al. 2015) (Fig. 2). However, early studies at polluted but cold (maximum temperatures <10 °C) Meretta Lake in the Canadian High Arctic (Kalff and Welch 1974) found that Chl-*a* concentrations were 20 times higher than in nearby unenriched lakes, clearly pointing to nutrients as a more important control than temperature on lake trophic status.

Changes in trophic status have an impact on ecosystem services from Arctic lakes, including reduction in drinking water quality if cyanobacteria become more abundant, and declining food web health through shifts in producer community composition. A gradual loss of benthic algae has been well documented when lakes become more eutrophic (Vadeboncouer et al. 2003). Concurrently, food webs that were dominantly benthic driven have been documented to change to dominantly pelagic as a response to increasing

**Fig. 2.** Linked climate vectors (external nutrients, thermal stratification) and trophic status for Arctic lakes. The response of trophic status to climate vectors is close to linear but the rate of increase is different for different lakes and changes when crossing certain thresholds. Shallow lakes with a large watershed-lake ratio may respond strongly to external nutrient load and rapidly become eutrophic (Mariash et al. 2019; Ayala Borda et al. 2021) (1). Low Arctic lakes can be monomictic if clear-watered and not very deep but in the current climate are often thermally stratified without being eutrophic (Forsström et al. 2005). When exposed to thawing permafrost or other nutrient sources, these lakes may experience an abrupt increase in trophic status (Wauthy and Rautio 2020) (2). Another rate change in these lakes occurs when summer hypolimnion anoxia triggers internal nutrient load from the sediments (3). High-Arctic lakes are currently mostly oligotrophic and monomictic and may stay resilient to changes in trophic status because they are cold and fishless. An increase in trophic status may however abruptly occur if the lake is exposed to a rapid impulse of nutrients, e.g., from anthropogenic pollution (Kalff and Welch 1974) (4).



trophic status (Korhola et al. 2002; Lehnherr 2018) with consequences on macroinvertebrate (Kivilä et al. 2019) and fish communities (Lehnherr 2018) that are supported by habitat and resource variability in Arctic lakes (Grosbois et al. 2022). Increasing temperature and productivity appear to shift subarctic lake communities toward increasing dominance of cyanobacteria and cyprinid fish, associated with decreasing quality in terms of essential fatty acids content in phytoplankton, zooplankton and deep-water macroinvertebrates (Keva et al. 2021).

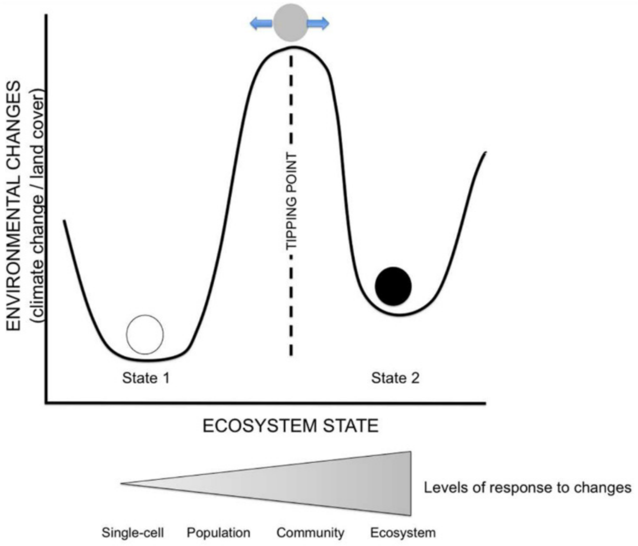
While climate drivers and the pathways and processes affecting trophic shifts are rather well known, the knowledge gaps remain when it comes to estimating the magnitude and geographical extent of eutrophication in the Arctic. The key climate vector, permafrost thaw, is intensifying across the circumpolar Arctic but the trophic response in water bodies depends on lake morphology, hydrological connectivity, thermal stratification, water retention time and watershed size. Shallow lakes and hydrologically isolated systems may be less resilient because they lack volume and have a long residence time that would dilute the impact of external nutrients. Shallow and deep lakes as well as lakes at different latitudes have a different thermal stratification, with stratified lakes being more prone to steep increases in trophic status as they are subject to internal loading if hypolimnetic waters become anoxic. However, the northernmost lakes, even when deep, are monomictic in the present climate and may not become stratified for decades, making latitude an important element in defining how a given lake reacts to the warming climate and associated change in trophic status. Lakes in the High Arctic, although influenced by the highest relative temperature increase, are therefore likely more resilient and respond slower to the initial increase in nutrients than lakes in the Low Arctic (Bonilla et al. 2005) (Fig. 2).

Coordinated increased baseline measures, long-term monitoring and accompanying experiments should be a focus of future studies of Arctic freshwater ecosystems (Culp et al. 2012). Although trophic status is a climate sentinel with direct climate feedback effects and consequences on ecosystem services, sporadic spot measures and different sampling methods and analyses do not allow for adequate assessment of the rates, places and conditions of change. Nutrients, Chl-*a* samples, and measurements of primary production are collected from different depths and at different times in different studies, and are rarely accompanied by microscopic and pigment analyses that would quantitatively measure phytoplankton species composition and biomass and allow for the detection of, for example, the geographical expansion of bloom-forming cyanobacteria. At present, the greatest limitation is the poor geographical coverage of limnological studies across the Arctic.

## Prokaryotic communities of lakes

Within lakes, prokaryotic communities (Bacteria and Archaea) are key players in many ecological and biogeochemical processes, including primary production, pathogenesis, food web transfers, degradation of DOM, cycling of nitrogen and other elements, oxygen regulation and GHG emissions. This pervasive influence on lake functioning makes prokary-

**Fig. 3.** Alternative stable states of northern lakes in transition. The white and black balls at the bottom of the two troughs represent alternative stable states of the lake environment and its associated microbiome, while the grey ball at the top indicates that the lake ecosystem is at a tipping point for abrupt change between states. States 1 and 2 represent different environmental conditions and microbial assemblages; for example, low and high DOM, nutrient, temperature or light exposure regimes, and their respective communities. As the climate continues to warm, Arctic lake ecosystems and their microbiomes are exposed to increasing pressure on their structure and integrity. These changes will push lake ecosystems to microbial tipping points that depend on intrinsic properties of the communities (e.g., taxonomic composition; functional redundancy; resistance to change), populations (e.g., metabolic flexibility; intraspecific variations in environmental responses), and cells (e.g., gene expression; microbial lipid and protein acclimation to warming).



otes an important set of indicators to detect and track climate impacts on lake ecosystems. In this respect, microbial sentinels can be identified at two levels: indicator taxa that respond to threshold changes in the lake environment, and indicator traits that describe the status of a lake ecosystem along its climate-driven environmental trajectory. The relative importance of these two components and their interplay in the overall response of lake ecosystems to global warming remain poorly known, but an improved understanding is urgently needed to determine the direction and speed at which Arctic lakes are pushed closer to tipping points for the shift between microbial states (Fig. 3), with potentially largescale changes in ecosystem functioning and services. The sensitivity of Arctic lakes is determined by an ensemble of microbial properties that operate at different temporal and biological scales (from genes to communities; Fig. 3) that collectively affect the resistance and resilience of Arctic lakes to environmental change. We present below some examples of these state changes that operate within Arctic lake ecosystems in response to warming.

As described in previous sections, climate change has direct effects on lakes through changes in snow cover, ice duration and thickness, the amount and spectral composition of underwater solar radiation, and the stratification, mixing and oxygenation regimes. Changes in these factors are likely to cause threshold effects on the microbial communities, with appearance or disappearance of certain taxa. For example, psychrophiles such as *Polaromonas* currently thrive in Arctic snow, rivers and lakes (Comte et al. 2018), and warming effects may push these cold-water taxa towards extinction. Conversely, warm-water taxa such as the colonial, bloom-forming cyanobacteria *Microcystis, Dolichospermum* and *Aphanizomenon* are conspicuously absent from the phytoplankton of most northern lakes, but may be favored by warming temperatures and increased stratification (Pick 2016;Przytulska et al. 2017; Ayala-Borda et al. 2021; Sivarajah et al. 2021), as well as by changing nutrient and DOM regimes. Warming may indirectly favor the success of bacterial and other pathogens of northern animals, including cold-dwelling aquatic species like Arctic char, by weakening their physiological performance and immune systems (Bradley et al. 2005).

The development of anoxia in bottom waters is a major environmental pressure on aquatic microbiota, and is favored in northern lakes by prolonged ice cover that cuts off re-oxygenation from the overlying atmosphere (see Section 7). This has a decisive influence on microbial species composition by selecting for obligate anaerobic taxa. A notable example is methanogenic Archaea. These are known to thrive in many ice-covered waterbodies, including thermokarst lakes and ponds that are considered to be biogeochemical hotspots of methane production and emission in the tundra landscape (Matheus Carnevali et al. 2018; Vigneron et al. 2019).

The shift of many shallow Arctic lakes from bedfast ice conditions to liquid water environments over winter is allowing an expansion of anoxic habitats and the development of methanogenic populations in benthic biofilms that were previously frozen and inactive during winter (Mohit et al. 2017). Cyanobacterial constituents of these biofilms may also have longer periods of photosynthesis under these liquid water conditions, shifting to an increased importance of photosynthetic sulfur bacteria once anoxia is established and light is available in fall and spring (McGowan et al. 2016).

The subsequent summer loss of ice and water column circulation leads to a lake environment favouring methanotrophic bacteria (Crevecoeur et al. 2015), which affects the net emission of methane. Recent studies have identified diverse Verrucomicrobia in water columns under ice as well as abundant bacteria from the Candidate Phylum Radiation group. These taxa are poorly understood and may play key roles in the methane cycles of northern lakes (Vigneron et al. 2020), with indicator value as microbial sentinels.

Under future climate scenarios (IPCC 2022), the projected warming and increased precipitation will not only cause changes within lakes, but also across the terrestrial landscape in which they are embedded (Wrona et al. 2016). For example, higher precipitation will result in increased run-off, which in turn will translate into greater terrestrial inputs of DOM into lakes, thereby changing the quantity and composition of organic carbon available for microbial degradation

(Williamson et al. 2015). This effect has already been observed in northern lakes (Wrona et al. 2016; Wauthy et al. 2018), and may accelerate with the increasing shift from snow to rain dominance for Arctic precipitation (McCrystall et al. 2021). In addition, climate change has also caused increases in vegetation cover ("greening"), and this terrestrial biomass and leaf litter represents another potential source for export of organic carbon to lakes, in particular in northern regions (Finstad et al. 2016). This mobilization of carbon derived from climate change may affect Arctic microbial community composition and metabolism (e.g., Colatriano et al. 2018; Comte et al. 2016) in ways that can be used as indicators of change.

Arctic lakes are mostly clear, oligotrophic waterbodies and may therefore be more sensitive to increasing DOC than lakes with naturally higher DOM concentrations, due in part to the limited metabolic potential of oligotrophic bacteria to utilize refractory terrestrial carbon (Kirchman 2018). Given that climate will alter the connectivity between arctic lakes and their terrestrial surroundings (Comte et al. 2018; Wauthy et al. 2018), aquatic microbiomes may shift from a dominance of psychrophiles to cold-tolerant generalists that can outcompete psychrophiles in carbon utilization under warmer temperatures. This transition to a new regime may be abrupt beyond a certain threshold of DOM and temperature (Fig. 3), or may occur more gradually.

Recent advances in next generation sequencing have allowed the widespread and cost-effective applications of metabarcoding and meta-"omics" in microbial ecology (Knight et al. 2018), which is opening up new opportunities to detect and monitor microbial sentinels in high latitude environments (Edwards et al. 2020). These techniques now allow the specific characterization of microbial traits such as the genes they carry (genomics) and whether those genes are being transcribed and translated into functional proteins and enzymes (transcriptomics). The use of these molecular tools paves the way to investigate more deeply northern lake features such as anoxia, including previously overlooked biogeochemical cycles such as those for sulphur and metals, and newly discovered microbial processes (e.g., the archaeal shunt; Vigneron et al. 2022). The large-scale characterization of proteins (proteomics; e.g., Reyes-González et al. 2022) and lipids (lipidomics; e.g., Holm et al. 2022) is also opening up new perspectives on microbial community interactions and responses to environmental change. These –omic approaches offer the possibility to identify new sentinels that are more focused on microbial traits and processes (e.g., expression of methanogenesis and denitrification genes; microbial lipid and protein reponses to warming) than taxonomic composition, which in turn could lead to new definitions of sentinel thresholds and shifts in Arctic lake function.

## Algal communities of lakes and rivers

Research on aquatic eukaryotic phototrophs has been dominated by the study of diatoms and other siliceous taxa in the Arctic. Siliceous diatom frustules and chrysophyte cysts preserve in lake sediments and can be identified to species level allowing algal investigations over timescales spanning decades to millenia. Such records have proven valuable in the Arctic where routine monitoring is scarce (Kahlert et al. 2022; Goedkoop et al. 2022). However, interpreting causal linkages between climate and algal community shifts is not straightforward because climate effects on lake biota are indirect and mediated by limnological conditions (Leavitt et al. 2009). Here, we explore three main ways that algae can be used as sentinels by (1) summarising community or assemblage changes; (2) using habitat- or trait-based classifications; and (3) using indicator taxa.

### Summarizing community or assemblage changes

Diatoms in lake sediment cores provided some of the first indications of major shifts in High Arctic lake biota over recent centuries which were inferred to be associated with warming (Douglas et al. 1994). Compositional turnover ($\beta$-diversity) of diatom and chrysophyte cyst sediment records assessed using detrended correspondence analysis in $>$ 40 Arctic lakes showed pan-Arctic regime shifts over the past 200 years (Smol et al. 2005). Greater turnover in the Canadian High Arctic and Hudson Bay Lowlands was interpreted as evidence for more pronounced warming in these regions in comparison to the eastern Canadian Arctic (Kahlert et al. 2022). However, linkages of community shifts to climate rely on inference. Due to the scarcity of systematic Arctic monitoring programmes, diversity metrics have been rarely used; but the Circumpolar Biodiversity Monitoring Programme recently collated data sets of phytoplankton and benthic algae in Arctic lakes and rivers. These spatial analyses illustrate that diatom species richness is lower in the High Arctic in comparison to Low Arctic and sub-Arctic regions, providing baseline data against which to assess future shifts in biota as the Arctic warms (Kahlert et al. 2022). $\alpha$-diversity of diatoms in North American Arctic river sites is correlated with bedrock geology and temperature (Lento et al. 2019), suggesting that river diatom assemblages may hold promise as sentinels for assessing temperature change in the Arctic.

### Habitat or trait-based classifications

Categorizing lake diatoms by the habitats in which they live can help to detect climate-driven lake ecosystem responses. Paleolimnology records integrate algal remains from across different lake habitats (Law et al. 2015) and categorizing diatoms as planktonic (P, living in the water column) or benthic (B, living in the sediments) to create a P:B ratio can indicate changes in lake habitat apportionment. Habitat availability for benthic diatoms is more commonly limited by light than nutrients (Bonilla et al. 2009; Vadeboncoeur et al. 2014). Declines in P:B ratios may indicate increasing water clarity as seen, for example, in West Greenland lakes between the 1990s and 2013 (Fowler et al. 2020; Saros et al. 2019) and in thermokarst slump-affected lakes in Northwest Canada (Thienpont et al. 2013). In contrast, P:B ratios may increase when exogenous inputs of DOM (Rosén et al. 2009) or glacial meltwater (Burpee et al. 2018; St. Pierre et al. 2019) reduce water clarity and restrict benthic habitat. Higher P:B ratios have been linked to reduced ice cover, longer open-water periods, and enhanced stratification in Arctic lakes (Sorvari et al. 2002; Smol et al. 2005; Lehnherr et al. 2018; Michelluti et al. 2020). High planktonic biomass can lead to shading and decline in transparency, reducing the surface area of habitat available to benthic algae (Vasconcelos et al. 2018). On the other hand, "benthification" can lead to higher retention of nutrients in the benthic zone, supporting clear-water conditions in the waters above (Vander Zanden and Vadeboncoeur 2020) and possibly enhancing the coverage of aquatic macrophytes and so the diversity of benthic algae (Mesquita et al. 2008; Thienpont et al. 2013). While it is difficult to definitively link community-level shifts with changing climate, P:B allows sheds some light on how changes in habitat might link to physical lake structure and, ultimately, climate. Proper contextualization of this sentinel response also requires consideration of lake basin morphometry and water level shifts (Stone and Fritz 2004; 2019).

Trait-based classifications of Arctic algae hold promise for understanding climate-related changes in aquatic systems. Early Arctic paleolimnology work interpreted that shifts away from smaller adnate (low-growing) towards larger (*Pinnularia* spp.) diatoms that grow on mosses reflected increasing habitat complexity associated with High Arctic warming over the last century (summarized in Douglas and Smol 1999). The complexity of benthic diatom assemblages in lakes around Kangerlussuaq (West Greenland) has increased since the late 1990 s to encompass a broader range of cell sizes and growth forms (Saros et al. 2019). In the latter case, limnological measurements were able to link this biological change with a possible climate-driven reduction in lakewater DOC and TP in this region and an associated increase in water clarity. Assignation of functional traits to phytoplankton taxa classifies them in terms of how they reproduce, acquire resources and avoid predators (Litchman and Klausmeier 2008). There are obvious applications in Arctic systems for tracking shifts in biogeochemical processes. Shifting terrestrial-aquatic DOC fluxes are likely to have impacts on the "microbial loop" of Arctic water bodies (see Sections 6, 9; Kling 1995). Mixotrophy (the acquisition of carbon by both autotrophic and heterotrophic pathways) is a common strategy for Arctic phytoplankton when inorganic nutrient availability is limited (Laybourn-Parry and Marshall 2003; Brutemark et al. 2006; Charvet et al. 2012). Widespread shifts in chrysophyte cysts in Arctic lakes (Betts-Piper et al. 2004) might suggest a change in this mixotrophic group, but cyst taxonomy is not yet well correlated with functional traits. However, climate-driven "greening" of vegetation around Arctic lakes increases the dominance of potentially mixotrophic cryptophye taxa (assessed using bioindicator carotenoid pigments) over millennial timescales, suggesting that aquatic organisms are responding to the increasing fluxes of terrestrial carbon (McGowan et al. 2018*a*). Nitrogen fixation is a common trait of cyanobacteria in Arctic benthic biofilms (Bonilla et al. 2009). Some diatoms including *Epithemia* and *Rhopalodia* may host symbiotic $N_2$-fixing cyanobacteria and their relative abundance in epilithic diatom assemblages increases in Greenlandic lakes with low nitrogen availability (McGowan et al. 2018*b*). Over millennial timescales, increases in sedimentary *Epithemia* are observed during periods of low precipitation when soil development and nitrogen delivery to lakes is lower (McGowan et al. 2018*b*), suggesting a link between hydroclimate and the prevalence of $N_2$-fixing taxa.

## Indicator taxa

"Indicator taxa" defines a taxon or group of taxa that demonstrate a strong affinity with an environmental condition of interest; ideally, some mechanistic information about the basis of that environmental association is determined through observations or experiments. In Arctic lakes, one of the most well quantified algal sentinels of climate is the *Cyclotella sensu lato* complex of diatoms, particularly the small, planktonic *Cyclotella sensu lato* taxa such as *Discostella stelligera* (Saros et al. 2014; Malik and Saros 2016; Saros et al. 2016; Malik et al. 2017). In many lakes, relative abundances of *D. stelligera* are higher during periods of strong thermal stratification and relatively shallow surface mixed layer depths (Saros et al. 2012; Saros et al. 2016). Lake thermal structure is shaped by both climate-driven energy and mass inputs, with the strength of each depending largely on lake surface area. In smaller lakes (<500 ha), mass inputs of dissolved organic matter and nutrients dominate the link between climate and lake thermal structure because water clarity is the primary control on thermal structure. In larger lakes (>500 ha), energy inputs form wind dominate this link. While the response of *D. stelligera* to changing thermal structure is documented through experiments and observations in some Arctic lakes, we note that additional drivers that alter lake resource availability (e.g., lake ontogeny, permafrost thaw) can also influence the success of *D. stelligera,* an opportunistic, fast-growing taxon. Increased nitrogen influx to Lone Spruce Pond (Alaska, USA) as a consequence of alder development on the watershed likely drove increased relative abundances of *D. stelligera* in the early Holocene (Perren et al. 2017).

Indicator taxa have been used in Arctic lakes to pinpoint climate-driven shifts in lake ecosystems. The pan-Arctic synthesis of Smol et al. (2005) found increases in the relative abundances of small *C. sensu lato* taxa in many lake sediment records after 1850, suggesting widespread limnological change as a consequence of warming. Recent warming over the past few decades in West Greenland has also driven changes in the relative abundances of *D. stelligera* across 18 lakes, but in this case, these relative abundances have declined (Saros et al. 2019). Since the early 1990 s, as June and July mean air temperatures increased, water clarity of these lakes increased as DOC concentrations declined, and ice-out dates became earlier; both of these changes would elicit deeper mixing depths in these small Arctic lakes, creating less favorable conditions for *D. stelligera*. In Arctic rivers, the use of indicator taxa is less well established, but the mucous-rich and sometimes invasive diatom *Didymosphaenia geminata* is associated with nutrient-scarce riverine environments, with a circum-Arctic distribution (Lindstrøm and Skulberg 2008), suggesting that it could be a useful indicator taxon of changing nutrient status.

Diatoms are very well-established sentinels for tracking changes and regime shifts in Arctic lakes, particularly in lake sediment records. However, each of the examples above underscore the importance of understanding algal ecology and the limnological context when using diatoms and other algae as climate sentinels (Saros and Anderson 2015). Aquatic phototroph responses to climate are indirect because meteorological drivers (e.g., temperature, solar radiation, and precipitation) influence diverse lakes and catchments in different ways. The unifying concept of energy and mass fluxes (Leavitt et al. 2009) can help to better understand climate-lake-phototroph linkages, providing a way forward for interpreting sentinels. This integration will enable clearer insights into patterns (e.g., why opposite trends in relative abundances of an indicator taxon can happen in different lakes experiencing the same climate forcing). Because benthic taxa are frequently dominant in Arctic lakes, a better understanding of their ecology could be an important avenue for future research (Vadeboncoeur et al. 2003; Karlsson and Säwström 2009; Mariash et al. 2014). Broader detection of eukaryotic algae beyond diatoms can be achieved through microscopic approaches, pigment biomarkers and DNA techniques which, in combination with experimental approaches, can facilitate a better understanding of Arctic phycology (Brutemark et al. 2006; Whiteford et al. 2016). Analysis of DNA in sediments (sed DNA) from the aquatic environment (eDNA), and from individual organisms will facilitate taxonomic advances and allow a more complete assessment of spatial and temporal patterns of Arctic aquatic phototrophs (e.g., Capo et al. 2016).

## Invertebrate abundance and diversity in lakes and rivers

Occupying the middle or top (fishless systems) of aquatic food webs, variation in the abundance and diversity of invertebrate assemblages represents an integrated signal of climate change in Arctic freshwaters. As ectotherms, extreme temperatures directly constrain invertebrate metabolic and life-history rates, which are typically optimized under intermediate conditions (Huey and Stevenson 1979). These constraints are invoked to explain larger-scale patterns of greater invertebrate abundance and species richness at lower altitudes (Gillooly and Dodson 2000; Danks 2007; Schartau et al. 2022) and unimodal changes in invertebrate diversity with warmer temperatures at both local and pan-Arctic scales (Woodward et al. 2010; Novichkova and Azovsky 2017). Temperature interacts with precipitation to establish hydrological regimes of aquatic ecosystems (Bring et al. 2016), directly controlling habitat availability. Larger and deeper water bodies often support more diverse assemblages of zooplankton and macroinvertebrates (Friberg et al. 2001; O'Brien et al. 2004; Hessen et al. 2007) in accordance with classic ecological area-richness relationships. In the short-term, predicted increases in Arctic warming and precipitation could promote higher invertebrate abundance and species richness (Lento et al. 2022*a*); however, this will likely result in loss of endemic species as ranges shift northward (Wrona et al. 2006). Despite these general trends, the predictive power of climate drivers on their own is often limited (Hessen et al. 2007; Pinel-Alloul et al. 2013) due to complex changes in ecosystem structure and function (O'Gorman et al. 2012; Wrona et al. 2013).

Climate change indirectly affects invertebrate communities by altering cryospheric processes. For lentic water bodies, the clearest signal of these effects is the timing and duration of winter ice cover (see Section 1). Earlier ice-out leads to advanced zooplankton phenology, linked to differential hatching rates associated with changes in photoperiod/temperature, ultimately resulting in higher abundances of large-bodied *Daphnia* and calanoid copepods and declines in *Holopedium*, cyclopoid copepods, and rotifers (Carter and Schindler 2012; Jones and Gilbert 2016; Beaver et al. 2019). Bedfast ice also plays a prominent role in structuring riverine invertebrate assemblages, as higher abundances and more diverse communities are found in spring-fed systems with perennial flow (Huryn et al. 2005). Winter precipitation and summer thermokarst activity further influence these communities by elevating spring runoff and suspended sediment loads, which can result in catastrophic declines in invertebrate abundance and diversity (Chin et al. 2016; Docherty et al. 2018). These effects are most profound in glaciated catchments where declines in both macroinvertebrate and zooplankton richness are associated with the delivery of tremendous amounts of runoff and sediments into aquatic systems (Cauvy-Fraunié and Dangles 2019).

Cryospheric changes also influence invertebrate assemblages by altering food-web dynamics. Higher annual temperatures and precipitation are likely to elevate nutrient inputs into aquatic ecosystems through increased permafrost melting and overland flow (see Section 5). Nutrient enrichment of Arctic rivers can stimulate primary production (see Section 8) leading to increased invertebrate production and abundance, most commonly favoring chironomid and tricopteran taxa (Deegan et al. 1997; Slavik et al. 2004). Enrichment responses in ponds and lakes have received less attention, but nutrient concentrations have been linked to greater abundances of *Daphnia* (O'Brien et al. 1992; Van Geest et al. 2007) and diversity of macroinvertebrates (Lento et al. 2022*b*). Climate change can also strongly affect invertebrate assemblages by altering connectivity between water bodies (Bennike et al. 2008). Increased connectivity could lead to higher colonization by fish predators, which are a primary control on invertebrate community composition through size selective predation on larger-bodied zooplankton and macroinvertebrates (Jeppesen et al. 2017). In contrast, greater visitation by migratory birds could enhance zooplankton abundance and richness by stimulating primary production through nutrient excretion and serving as vectors of transport for new species (Jensen et al. 2019). Together, indirect and direct climate effects will considerably alter Arctic invertebrate community structure resulting in significant changes in aquatic ecosystem function and food web dynamics.

Teasing apart these different drivers to predict future changes in invertebrate communities will require a wholistic ecosystem-level approach. To begin, this effort will require an increase in monitoring, as basic data on aquatic invertebrate abundance and distribution lags well behind that for aquatic primary producers and vertebrate consumers. Recent progress in this area has been made by the Circumpolar Biodiversity Monitoring Program of the Conservation of Arctic Flora and Fauna Working Group of the Arctic Council (Culp et al. 2022). Initial results from these efforts confirm geographic patterns described above and highlight the importance of including in situ physiochemical measurements in long-term monitoring programs. These data, combined with remote sensing (ice-out dates, primary production, and sediment delivery) and paleolimnological approaches, should allow for a better mechanistic understanding of local, regional, and pan-Arctic controls on invertebrate communities. Increased use of experimental methods is also critical for isolating and investigating the effects of specific climate drivers on invertebrate assemblages and, when combined with long-term monitoring data, this approach can be a powerful tool for understanding past and predicting future dynamics of whole foodwebs under a changing climate (Klobucar et al. 2018).

## Fish in lakes and rivers

Fish are excellent integrators of limnological change, and therefore provide a wide range of sentinel responses as indicators of climate-induced changes in lake ecosystems. These include changes in physiological condition, productivity, population structure of fish communities, including the extirpation of native taxa and the arrival and expansion of invasive species, and diversity. The Arctic fish fauna has a limited number of species, and many of these are potentially sensitive to climate impacts on their habitats (Laske et al. 2022).

Salmonids are commonly found in northern waters, and these generally have a requirement for cold, highly oxygenated, oligotrophic lakes. Arctic char (*Savelinus alpinus)* is an iconic species of northern salmonids that plays an important role in the diet of Inuit and other northern cultures, and there is an urgent need to identify habitat features that may lead to the impairment of these populations. Moderate warming may increase overall lake productivity, and thereby stimulate Arctic char production (Reist et al. 2006), however shifts to warmer, lower oxygen conditions are likely to have negative effects. Observations from the southern end of the Arctic char range, in the north temperate zone, are helpful in this regard. For example, at Lake Windermere in northwest England, Arctic char appear to have changed their migration patterns to avoid hypoxic oxygen levels (Jones et al. 2008). Modeling of water temperatures suggests that European populations of Arctic char are highly vulnerable to climate warming (Kelly et al. 2020).

We refer the reader to Rolls et al. (2017), which provides an extensive review of insights and knowledge gaps on the topic of fish as sentinels of climate change in subarctic freshwaters, as well as Knopp et al. (2020) for a review of documented Indigenous knowledge of historical fish diversity in the Arctic.

## Invasive species in lakes and rivers

There has been considerable discussion about the northward movement of invasive species into the Arctic Ocean due to climate change (Chan et al. 2019) and increased human activities (Sardain et al. 2019), but little attention to the risk and potential impacts of similar invasions into Arctic lakes and rivers. In other parts of the world, invasive species have had wide-ranging effects on freshwater ecosystems, including displacement and extirpation of native species, perturbation of food webs, and disruptions of ecosystem services such as drinking water and fisheries (Pyšek et al. 2020).

Climate warming is an important driver of species invasions in general, and water temperature is considered a key variable influencing the suitability of high latitude habitats for new species (Rolls et al. 2017). For example, thermal modelling predicted that numerous lakes in Canada, including some lakes in the Arctic, would have suitable temperature regimes for the invasion of smallmouth bass by the end of this century (Sharma et al. 2007). Subsequent modeling indicated a potential shift toward new fish community structures and species interactions, increasing the vulnerability of coldwater species (Van Zuiden et al. 2016). Slimy sculpin, a fish species until recently thought to be limited to the North American mainland, was recently found in lakes in the Canadian Arctic Archipelago (Power et al. 2022), increasing the number of fish species to nine in the Canadian Arctic. Subarctic species such as Atlantic salmon (*Salmo salar)* are likely shifting northwards, in the process competing with native species such as Arctic char (Bilous and Dunmall 2020).

Increased human activity is another important factor, acting in concert with climate change. The dispersion of the invasive macrophyte *Elodea* in Alaskan lakes has been tied to float plane activities (Larsen et al. 2020), which may be conduits for other freshwater species (Schwoerer et al. 2019) that are increasingly favored by warmer water temperatures and a longer ice-free season. Another example of human activity is increasing fish tourism in the Arctic. Infected fishing gear acts as a vector to carry parasites and pathogens to northern lakes and rivers. The ectoparasite *Gyrodactylus salaris* has invaded Arctic river systems, causing the total loss of Atlantic salmon populations in several freshwaters in Norway (Adolfsen et al. 2021). The optimum temperature for the growth and spread of this parasite is around 13 °C, and increasing summer temperatures heighten the risk of its northward expansion. These examples also highlight the need for Arctic limnologists to take special care in the cleaning and disinfection of sampling equipment that has been used in the South.

Bird species are also known to be moving northwards and may have a variety of impacts on northern lakes. For example, the arrival of certain species may add a new trophic level (e.g., the observed colonization by Red throated loons of high Arctic lakes that have lost their ice cover because of climate warming; Vincent et al. 2009), or may change the trophic status of lakes. Increasing populations of geese migrating from lower latitudes have the potential to cause changes in the nutrient regime of northern lakes; for example, in a goose-breeding site in the eastern Canadian Arctic, a decadal rise in populations of Lesser snow geese (*Chen caerulescens)* was accompanied by a doubling of total phosphorus concentrations in lakes of the area (Mariash et al. 2018) and an increase in planktonic cyanobacteria (Mariash et al. 2019).

**Table 2.** Approaches for the collection of freshwater sentinel data in Arctic regions categorized as well-established for high quality data (XXX), providing a medium quality or simplified overview of sentinel data (XX), and methods that have potential or are under development but not yet widely applied (X). Relative timescales covered by each approach indicated by circles.

| | Remote sensing | *In situ* sensors | Paleolimnology | Sampling/analysis | Indigenous knowledge |
|---|---|---|---|---|---|
| Timescales of approach | ●● | ● | ●●● | ● | ●● |
| Ice regimes | XXX | XX | | XXX | XXX |
| Thermal regimes | XX | XX | XX | XXX | X |
| Baseflow | XX | XXX | | XXX | XXX |
| Water balance | XXX | XXX | X | XXX | XXX |
| Nutrients and major ions | | XX | X | XXX | |
| Dissolved organic matter | X | XX | X | XXX | X |
| Greenhouse gases | X | | | XXX | |
| Radiocarbon | | | XXX | XXX | |
| Dissolved oxygen | | XXX | | XXX | |
| Trophic state | XX | XX | XX | XXX | X |
| Prokaryotes | | | X | XXX | X |
| Algae | | | XXX | XXX | X |
| Invertebrates | | | XX | XXX | X |
| Fish | | | X | XXX | XXX |
| Invasive species | | | X | XXX | XXX |

Perhaps the most numerous and potentially most harmful invasive organisms are various microorganisms. As the cryosphere changes, Arctic lakes become more susceptible to infection by opportunistic parasites which spread northward when the environment becomes more favorable for them or their hosts. For instance, specialized fungi (chytrids) and diverse protists are some key early warning indicators of ecosystem balance. These parasites destroy and decompose phytoplankton prior to their becoming food and available up the food chain (Frenken et al. 2017), and can also attack zooplankton, causing changes in species composition (Redfield and Vincent 1979). Cold winter temperatures in Arctic lakes have provided a cold-water refuge that has reduced the prevalence of certain parasites such as chytrids with their capacity for epidemic development (Bruning 1991). Warmer winters are expected to cause a gradual disappearance of this refuge for parasite-free development of phytoplankton early in the season.

The arrival of new species and changes in the populations of migratory species have the potential to substantially alter lake and river trophic status, food web structure and ecosystem functioning. In the extreme case, native (fish) species may be extirpated, as has happened in freshwaters infected by *G. salaris*. Less evident but perhaps more important changes include disruptions in carbon transfer along energy transfer pathways in food webs, which occur for example by fungal or viral attacks of specific phytoplankton or zooplankton.

Invasive species are increasingly present in the Arctic and the risks associated with them are recognized but information of their distribution is limited. Working with Indigenous partners and other people living in the North would be a key in recognizing lakes where locals have seen a change in fish taste or health, often associated with the prevalence of parasites and changes in the food web. Local and Indigenous knowledge is also critical when it comes to observing changes in the arrival of new bird species, shifts in population sizes or changes in dispersal regimes.

## Synthesis and future directions

Numerous climate sentinels have been identified and measured in Arctic freshwater systems, as summarized here. These sentinel responses span physical, chemical, and biological variables, and their links to climate vary in nature and strength. We have attempted to clarify these links to aid selection of sentinel responses used in future research and monitoring. Table 1 provides a guide to the major sentinel responses and their components, and summarizes the knowledge gaps and research recommendations that are described further in the text. It is important to realize that, as with all research, the selection of which sentinel responses to measure will depend on the research questions and objectives. Defining those questions and objectives early and clearly will aid in sentinel selection; the links, insights, and knowledge gaps identified in this review provide guidance to help inform that selection. We have distilled some of the information presented throughout as well as our collective experience to summarize the current state of approaches used to measure sentinel responses and the timescale typically possible with each approach (Table 2). In addition to aiding parameter selection, the information depicted in Table 2 underscores that our understanding of Arctic freshwater sentinel responses would be advanced by further development of some methods (e.g., new capabilities with sensors or remote sensing) as well as by continuing to use multiple approaches to quantify sentinel responses. We further note that when establishing any monitoring program, we encourage freshwater scientists to engage early in the study design (as well as throughout the research) with local communities in the Arctic to integrate their interests and co-produce knowledge.

It is important to recognize, as highlighted in many cases throughout this manuscript, the myriad linkages among various sentinel responses. There are too many to describe within the scope of this paper, so we simply provide some examples. Oxygen depletion induces nutrient and metal release from sediments which can influence trophic state, but also bioavailability and toxicity of numerous chemical species (Borch et al. 2010; Kirf et al. 2015). The quantity and seasonality of GHG emissions from Arctic lakes are responding to climate-driven changes in oxygen dynamics (Cadieux et al. 2017). It can stimulate methanogenesis, especially in sulfate-poor systems (Bastviken et al. 2004; Isidorova et al. 2019). The enhanced release of mineral ions or nutrients (N, P, Si) from permafrost thaw or increases in weathering can enhance biological productivity in downstream lakes and rivers (Frey et al. 2007; Hobbie et al. 1999). It is possible that over longer timescales, increasing alkalinity export (e.g., Tank et al. 2016) to coastal oceans may help to temper ecological effects of acidification (Terhaar et al. 2020). Increasing trophic status, which is accompanied by higher pelagic nutrients and DOC, and intensification of thermal stratification, further changes carbon sequestration in Arctic lakes and therefore their GHG emissions (Laurion et al. 2010). While the interconnected nature of sentinel responses may complicate our inferences from them, it also underscores the broadly integrative nature of these responses. Using the most sensitive indicators across a landscape to assess climate impacts will be broadly protective across ecosystems.

In closing, we provide three recommendations for future work to deepen insights that may be gained from the freshwater sentinels approach in the Arctic:

1) Coordinate the measurement of sentinel responses of freshwater systems across diverse Arctic landscapes. Adopting the same protocols when quantifying a sentinel response across regions will enable identification of large-scale effects as well as local-scale modifiers of signals. This goal could be accomplished through deeply collaborative efforts, and (or) standardized methods and protocols shared across independently operating groups, as developed for example by the permafrost thaw research community for landscape monitoring (Boike et al. 2022) and by CAFF for freshwater biodiversity monitoring (Culp et al. 2012). Several recent reviews of Arctic freshwater biodiversity (Heino et al. 2020; Goedkoop et al. 2022) underscore the need for more coordinated monitoring programs at greater spatial and temporal resolution.
2) Integrate Indigenous knowledge into the understanding of Arctic freshwater sentinels. Arctic Indigenous knowledge and subsistence systems are tightly connected to ancestral lands; responsible inclusion of Indigenous knowledge systems of the environment will deepen understanding of Arctic climate change and support environmental justice (David-Chavez and Gavin 2018; Vincent 2020; Hauser et al. 2021). Across Arctic freshwater systems, Knopp et al. (2020) identified local-scale loss or gain of fish species as well as changing water levels, length of ice cover, and ice thickness as frequent observations from Indigenous knowledge; greater integration of knowledge systems (as indicated in Sections 12 & 13) will advance our understanding of climate-driven ecosystem changes in the Arctic.
3) Employ a systems approach to quantify and integrate multiple linked sentinel responses. It is apparent that more work remains in investigating and quantifying the links among sentinel responses and how climate features affect them. As future studies are designed, employing integrative frameworks and systems approaches (with attention to linkages, feedbacks, thresholds and scale) will yield deeper insights into the mechanisms by which climate features drive changes in multiple sentinels (e.g., Anderson et al. 2017).

Freshwater systems are widespread and abundant across the circumpolar Arctic. They play vital roles as wildlife habitats, biogeochemical conduits (e.g., carbon and nitrogen cycles), and water resources and fishing-hunting grounds for local/Indigenous communities. The high sensitivity of freshwater systems to various climate features renders them particularly vulnerable to climate change, and quantifying their sentinel responses is key to understanding the scope of current change and predicting future conditions.

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## Competing interests

The authors declare there are no competing interests.

## References

Abbott, B.W., Jones, J.B., Godsey, S.E., Larouche, J., and Bowden, W.B. 2015. Patterns and persistence of hydrologic carbon and nutrient export from collapsing upland permafrost. Biogeosc. **12**: 3725–3740. doi:10.5194/bg-12-3725-2015.

Abnizova, A., Siemens, J., Langer, M., and Boike, J. 2012. Small ponds with major impact: the relevance of ponds and lakes in permafrost landscapes to carbon dioxide emissions. Glob. Biogeochem. Cycles **26**: GB20411. doi:10.1029/2011GB00423.

Adolfsen, P., Bardal, H., and Aune, S. 2021. Fighting an invasive fish parasite in subarctic norwegian rivers – the end of a long story? Man. Biol. Invas. **12**: 49–65. doi:10.3391/mbi.2021.12.1.04.

Alexeev, V.A., Arp, C.D., Jones, B.M., and Cai, L. 2016. Arctic sea ice decline contributes to thinning lake ice trend in northern Alaska. Environ. Res. Lett. **11**: 074022. doi:10.1088/1748-9326/11/7/074022.

AMAP. 2017. *Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017*. Arctic Monitoring and Assessment Programme (AMAP), Oslo, Norway. pp. xiv + 269.

AMAP. 2021. *Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers*. Arctic Monitoring and Assessment Programme (AMAP), Tromsø, Norway. p. 16.

Anderson, N.J., and Stedmon, C.A. 2007. The effect of evapocencentration on dissolved organic carbon concentration and quality in lakes of SW greenland. Freshw. Biol. **52**: 280–289. doi:10.1111/j.1365-2427.2006.01688.x.

Anderson, N.J., Saros, J.E., Bullard, J., Cahoon, S., McGowan, S. Bagshaw, E., et al. 2017. The Arctic in the 21st century: changing biogeochemical linkages across a paraglacial landscape of greenland. Bioscience **67**: 118–133. doi:10.1093/biosci/biw158. PMID: 28596614.

Andresen, C.G., and Lougheed, V.L. 2015. Disappearing arctic tundra ponds: fine-scale analysis of surface hydrology in drained thaw lake basins over a 65 year period (1948-2013). J. Geophys. Res. Biogeosci. **120**: 466–479. doi:10.1002/2014JG002778.

Antoniades, D., Crawley, C., Douglas, M.S.V., Pienitz, R., Andersen, D. Doran, P.T., et al. 2007. Abrupt environmental change in Canada's northernmost lake inferred from fossil diatom and pigment stratigraphy. Geophys. Res. Lett. **34**(18): 142–161. doi:10.1029/2007gl030947.

Arp, C.D., Jones, B.M., Grosse, G., Bondurant, A.C., Romanovsky, V.E., Hinkel, K.M., and Parsekian, A.D. 2016. Threshold sensitivity of shallow Arctic lakes and sublake permafrost to changing winter climate. Geophys. Res. Lett. **43**: 6358–6365. doi:10.1002/2016GL068506.

Arp, C.D., Jones, B.M., Lu, Z., and Whitman, M.S. 2012. Shifting balance of thermokarst lake ice regimes across the Arctic coastal plain of northern Alaska. Geophys. Res. Lett. **39**: L16503. doi:10.1029/2012GL052518.

Arp, C.D., Whitman, M.S., Kemnitz, R., and Stuefer, S.L. 2020. Evidence of hydrological intensification and regime change from northern Alaskan watershed runoff. Geophys. Res. Lett. **47**: e2020GL089186. doi:10.1029/2020GL089186.

Ashton, G.D. 2011. River and lake ice thickening, thinning, and snow ice formation. Cold Reg. Res. Tech. **68**: 3–19. doi:10.1016 /j.coldregions.2011.05.004.

Ayala-Borda, P., Lovejoy, C., Power, M., and Rautio, M. 2021. Evidence of eutrophication in Arctic lakes. Arct. Sci. **7**: 859–871. doi:10.1139/AS-2020-0033.

Barker, A.J., Douglas, T.A., Jacobson, A.D., McClelland, J.W., Ilgen, A.G. Khosh, M.S., et al. 2014. Late season mobilization of trace metals in two small Alaskan Arctic watersheds as a proxy for landscape scale permafrost active layer dynamics. Chem. Geol. **381**: 180–193. doi:10.1016/j.chemgeo.2014.05.012.

Bartosiewicz, M., Przytulska, A., Lapierre, J.-F., Laurion, I., Lehmann, M.F., and Maranger, R. 2019. Hot tops, cold bottoms: synergistic climate warming and shielding effects increase carbon burial in lakes. Limnol. Oceanogr. Lett. **4**: 132–144. doi:10.1002/lol2.10117.

Bastviken, D., Cole, J., Pace, M., and Tranvik, L. 2004. Methane emissions from lakes: dependence of lake characteristics, two regional assessments, and a global estimate. Global Biogeochem. Cycl. **18**: 4. doi:10.1029/2004gb002238.

Battin, T.J., Luyssaert, S., Kaplan, L.A., Aufdenkampe, A.K., Richter, A., and Tranvik, L.J. 2009. The boundless carbon cycle. Nat. Geosci. **2**: 598–600. doi:10.1038/ngeo618.

Beaver, J.R., Arp, C.D., Tausz, C.E., Jones, B.M., Whitman, M.S. Renicker, T.R., et al. 2019. Potential shifts in zooplankton community structure in response to changing ice regimes and hydrologic connectivity. Arct. Antarct. Alp. Res. **51**: 327–345. doi:10.1080/15230430.2019.1643210.

Beel, C.R., Heslop, J., Orwin, J.F., Pope, M.A., Schevers, A. Hung, J., et al. 2021. Emerging dominance of summer rainfall driving high arctic terrestrial-aquatic connectivity. Nat. Commun. **12**(1): 1448. doi:10.1038/s41467-021-21759-3.

Beel, C.R., Lamoureux, S.F., Orwin, J.F., Pope, M.A., Lafrenière, M.J., and Scott, N.A. 2020. Differential impact of thermal and physical permafrost disturbances on high Arctic dissolved and particulate fluvial fluxes. Sci. Rep. **10**(1): 11836. doi:10.1038/s41598-020-68824-3. PMID: 32678255.

Bégin, P.N., Tanabe, Y., Kumagai, M., Culley, A.I., Paquette, M. Sarrazin, D., et al. 2021a. Extreme warming and regime shift toward amplified variability in a far northern lake. Limnol. Oceanogr. **66**: S17–S29. doi:10.1002/lno.11546.

Bégin, P.N., Tanabe, Y., Rautio, M., Wauthy, M., Laurion, I. Uchida, M., et al. 2021b. Water column gradients beneath the summer ice of a high arctic freshwater lake as indicators of sensitivity to climate change. Sci. Rep. **11**: 2868. doi:10.1038/s41598-021-82234-z.

Beltaos, S., and Prowse, T. 2009. River-ice hydrology in a shrinking cryosphere. Hydrol. Process. **23**: 122–144. doi:10.1002/hyp.7165.

Belzile, C., Vincent, W.F., Gibson, J.A.E., and Van Hove, P. 2001. Bio-optical characteristics of the snow, ice, and water column of a perennially ice-covered lake in the high arctic. Can. J. Fish. Aquat. Sci. **58**: 2405–2418. doi:10.1139/cjfas-58-12-2405.

Bennike, O., Sørensen, M., Fredskild, B., Jacobsen, B.H., Bocher, J. Amsinck, S.J., et al. 2008. Late quaternary environmental and cultural changes in the wollaston forland region, north east Greenland. Adv. Ecol. Res. **40**: 45–79. doi:10.1016/S0065-2504(07)00003-7.

Bense, V.F., Ferguson, G., and Kooi, H. 2009. Evolution of shallow groundwater flow systems in areas of degrading permafrost. Geophys. Res. Lett. **36**(22): L22401. doi:10.1029/2009GL039225.

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

Betts-Piper, A.M., Zeeb, B.A., and Smol, J.P. 2004. Distribution and autecology of chrysophyte cysts from high Arctic Svalbard lakes: preliminary evidence of recent environmental change. J. Paleolimnol. **31**(4): 467–481. doi:10.1023/B:JOPL.0000022546.21996.41.

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

Bilous, M., and Dunmall, K. 2020. Atlantic salmon in the canadian arctic: potential dispersal, establishment, and interaction with Arctic char. Rev. Fish. Biol. Fish. **30**: 463–483. doi:10.1007/s11160-020-09610-2.

Bogard, M.J., Johnston, S.E., Dornblaser, M.M., Spencer, R.G.M., Striegl, R.G., and Butman, D.E. 2019a. Extreme rates and diel variability of planktonic respiration in a shallow sub-Arctic lake. Aquat. Sci. **81**: 60. doi:10.1007/s00027-019-0657-9.

Bogard, M.J., Kuhn, C.D., Johnston, S.E., Striegl, R.G., Holtgrieve, G.W. Dornblaser, M.M., et al. 2019b. Negligible cycling of terrestrial carbon in many lakes of the arid circumpolar landscape. Nat. Geosci. **12**: 180–185. doi:10.1038/s41561-019-0299-5.

Boike, J., Chadburn, S., Martin, J., Zwieback, S., Althuizen, I.H. Anselm, N., et al. 2022. Standardized monitoring of permafrost thaw: a user-friendly, multiparameter protocol. Arct. Sci. **8**: 153–182. doi:10.1139/AS-2021-0007.

Bonilla, S., Rautio, M., and Vincent, W.F. 2009. Phytoplankton and phytobenthos pigment strategies: implications for algal survival in the changing Arctic. Polar Biol. **28**: 846–861. doi:10.1007/s00300-009-0626-1.

Bonilla, S., Villeneuve, V., and Vincent, W.F. 2005. Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. J. Phycol. **41**(6): 1120–1130. doi:10.1111/j.1529-8817.2005.00154.x.

Borch, T., Kretzschmar, R., Kappler, A., Van Cappellen, P., Ginder-Vogel, M., Voegelin, A., and Campbell, K. 2010. Biogeochemical redox processes and their impact on contaminant dynamics. Environ. Sci. Technol. **44**: 15–23. doi:10.1021/es9026248. PMID: 20000681.

Bouchard, F., Laurion, I., Prėskienis, V., Fortier, D., Xu, X., and Whiticar, M.J. 2015. Modern to millennium-old greenhouse gases emitted from ponds and lakes of the Eastern Canadian Arctic (Bylot Island, Nunavut). Biogeosciences, **12**: 7279–7298. doi:10.5194/bg-12-7279-2015.

Bouchard, F., Francus, P., Pienitz, R., and Laurion, I. 2011. Sedimentology and geochemistry of thermokarst ponds in discontinuous permafrost, sub-Arctic Quebec, Canada. J. Geophys. Res. Biogeosci. **116**: G00M04. doi:10.1029/2011JG001675.

Bouchard, F., Francus, P., Pienitz, R., Laurion, I., and Feyte, S. 2014. Subarctic thermokarst ponds: investigating recent landscape evolution and sediment dynamics in thawed permafrost of northern Québec (Canada). Arct. Antarct. Alp. Res. **46**: 251–271. doi:10.1657/1938-4246-46.1.251.

Bouchard, F., MacDonald, L.A., Turner, K.W., Thienpont, J.R., Medeiros, A.S. Biskaborn, B.K., et al. 2017. Paleolimnology of thermokarst lakes: a window into permafrost landscape evolution. Arct. Sci. **3**: 91–117. doi:10.1139/as-2016-0022.

Bouchard, F., Turner, K.W., MacDonald, L.A., Deakin, C., White, H. Farquharson, N., et al. 2013. Vulnerability of shallow subarctic lakes to evaporate and desiccate when snowmelt runoff is low. Geophys. Res. Lett. **40**: 6112–6117. doi:10.1002/2013GL058635.

Bouffard, D., Zdorovennova, G., Bogdanov, S., Efremova, T., Lavanchy, S. Palshin, N., et al. 2019. Under-ice convection dynamics in a boreal lake. Inland Waters **9**: 142–161. doi:10.1080/20442041.2018.1533356.

Bradley, M.J., Kutz, S.J., Jenkins, E., and O'Hara, T.M. 2005. The potential impact of climate change on infectious diseases of Arctic fauna. Int. J. Circum. Health **64**: 468–477. doi:10.3402/ijch.v64i5.18028.

Briggs, M.A., Campbell, S., Nolan, J., Walvoord, M.A., Ntarlagiannis, D., Day-Lewis, F.D., and Lane, J.W. 2017. Surface geophysical methods for characterizing frozen ground in transitional permafrost landscapes. Permafr. Periglac. Process. **28**: 52–65. doi:10.1002/ppp.1893.

Bring, A., Fedorova, I., Dibike, Y., Hinzman, L., Mård, J. Mernild, S.H., et al. 2016. Arctic terrestrial hydrology: a synthesis of processes, regional effects, and research challenges. J. Geophys. Res. Biogeosci. **121**: 621–649. doi:10.1002/2015JG003131.

Brown, D., Brinkman, T.J., Bolton, W.R., Brown, C.L., Cold, H.S., Hollingsworth, T.N., and Verbyla, D.L. 2020. Implications of climate variability and changing seasonal hydrology for subarctic riverbank erosion. Clim. Change **162**: 1–20. doi:10.1007/s10584-020-02748-9.

Brown, D.R.N., Brinkman, T.J., Verbyla, D.L., Brown, C.L., Cold, H.S., and Hollingsworth, T.N. 2018. Changing river ice seasonality and impacts on interior alaskan communities. Weather Clim. Soc. **10**: 625–640. doi:10.1175/WCAS-D-17-0101.1.

Bruning, K. 1991. Effects of temperature and light on the population dynamics of the *asterionella-rhizophydium* association. J. Plankton Res. **13**: 707–719. doi:10.1093 /PLANKT%2F13.4.707.

Brutemark, A., Rengefors, K., and Anderson, N.J. 2006. An experimental investigation of phytoplankton nutrient limitation in two contrasting low Arctic lakes. Polar Biol. **29**(6): 487–494. doi:10.1007/s00300-005-0079-0.

Buij, R., Melman, T.C.P., Loonen, M.J.J.E., and Fox, A.D. 2017. Balancing ecosystem function, services and disservices resulting from expanding goose populations. Ambio **46**: S301–S318. doi:10.1007/s13280-017-0902-1.

Burd, K., Estop-Aragonés, C., Tank, S.E., and Olefeldt, D. 2020. Lability of dissolved organic carbon from boreal peatlands: interactions between permafrost thaw, wildfire, and season. Can. J. Soil Sci. 503–515. doi:10.1139/CJSS-2019-0154.

Burkett, V.R., Wilcox, D.A., Stottlemyer, R., Barrow, W., Fagre, D. Baron, J., et al. 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. Ecol. Complex. **2**: 357–394. doi:10.1016/j.ecocom.2005.04.010.

Burpee, B.T., Anderson, D., and Saros, J.E. 2018. Assessing ecological effects of glacial meltwater on lakes fed by the greenland ice sheet: the role of nutrient subsidies and turbidity. Arct. Antarct. Alp. Res. **50**(1): S100019. doi:10.1080/15230430.2017.1420953.

Cadieux, M.-C., Gauthier, G., and Hughes, R.J. 2005. Feeding ecology of Canada geese (Branta canadensis interior) in sub-arctic inland tundra during brood-rearing. Auk **122**(1): 144. doi:10.1642/0004-8038 (2005) 122[0144:feocgb]2.0.co;2.

Cadieux, S.B., White, J.R., and Pratt, L.M. 2017. Exceptional summer warming leads to contrasting outcomes for methane cycling in small arctic lakes of greenland. Biogeosciences **14**: 559–574. doi:10.5194/bg-14-559-2017.

Camacho, A., Rochera, C., Villaescusa, J.A., Velázquez, D., Toro, M. Rico, E., et al. 2012. Maritime antarctic lakes as sentinels of climate change. Int. J. Des. Nat. Ecodyn. **7**(3): 239–250. doi:10.2495/DNE-V7-N3-239-250.

Campbell, T.K.F., Lantz, T.C., Fraser, R.H., and Hogan, D. 2020. High arctic vegetation change mediated by hydrological conditions. Ecosystems **24**: 106–121. doi:10.1007/s10021-020-00506-7.

Campeau, A., Bishop, K., Amvrosiadi, N., Billett, M.F., Garnett, M.H. Laudon, H., et al. 2019. Current forest carbon fixation fuels stream CO2 emissions. Nat. Commun. **10**: 1876. doi:10.1038/s41467-019-09922-3. PMID: 31015439.

Capo, E., Debroas, D., Arnaud, F., Guillemot, T., Bichet, V. Millet, L., et al. 2016. Long-term dynamics in microbial eukaryotes communities: a palaeolimnological view based on sedimentary DNA. Mol. Ecol. **25**(23): 5925–5943. doi:10.1111/mec.13893. PMID: 27761959.

Carlson, R.E., and Simpson, J. 1996. *A Coordinator's Guide to Volunteer Lake Monitoring Methods*. North American Lake Management Society, Madison, WI.

Carroll, M.L., Townshend, J.R.G., DiMiceli, C.M., Loboda, T., and Sohlberg, R.A. 2011. Shrinking lakes of the arctic: spatial relationships and trajectory of change. Geophys. Res. Lett. **38**: L20406. doi:10.1029/2011gl049427.

Carter, J.L., and Schindler, D.E. 2012. Responses of zooplankton populations to four decades of climate warming in lakes of southwestern alaska. Ecosystems **15**: 1010–1026. doi:10.1007/s10021-012-9560-0.

Castendyk, D.N., Obryk, M.K., Leidman, S.Z., Gooseff, M., and Hawes, I. 2016. Lake vanda: a sentinel for climate change in the mcmurdo sound region of antarctica. Glob. Planet. Change **144**: 213–227. doi:10.1016/j.gloplacha.2016.06.007.

Cauvy-Fraunié, S., and Dangles, O. 2019. A global synthesis of biodiversity responses to glacier retreat. Nat. Ecol. Evol. **3**: 1675–1685. doi:10.1038/s41559-019-1042-8. PMID: 31740846.

Chan, F.T., Stanislawczyk, K., Sneekes, A.C., Dvoretsky, A., Gollasch, S. Minchin, D., et al. 2019. Climate change opens new frontiers for marine species in the arctic: current trends and future invasion risks. Glob. Change Biol. **25**: 25–38. doi:10.1111/gcb.14469.

Charvet, S., Vincent, W.F., and Lovejoy, C. 2012. Chrysophytes and other protists in high arctic lakes: molecular gene surveys, pigment signatures and microscopy. Polar Biol. **35**(5): 733–748. doi:10.1007/s00300-011-1118-7.

Chin, K.S., Lento, J., Culp, J.M., Lacelle, D., and Kokelj, S.V. 2016. Permafrost thaw and intense thermokarst activity decreases abundance of stream benthic macroinvertebrates. Glob. Change Biol. **22**(8): 2715–2728. doi:10.1111/gcb.13225.

Colatriano, D., Tran, P.Q., Guéguen, C., Williams, W.J., Lovejoy, C., and Walsh, D.A. 2018. Genomic evidence for the degradation of terrestrial organic matter by pelagic arctic ocean chloroflexi bacteria. Commun. Biol. **1**: 90. doi:10.1038/s42003-018-0086-7. PMID: 30271971.

Coleman, K.A., Palmer, M.J., Korosi, J.B., Kokelj, S.V., Jackson, K. Hargan, K.E., et al. 2015. Tracking the impacts of recent warming and thaw of permafrost peatlands on aquatic ecosystems: a multi-proxy approach using remote sensing and lake sediments. Boreal Environ. Res. **20**: 363–377. ISSN: 1797-2469.

Colombo, N., Salerno, F., Gruber, S., Freppaz, M., Williams, M., Fratianni, S., and Giardino, M. 2018. Review: impacts of permafrost degradation on inorganic chemistry of surface fresh water. Glob. Planet. Change **162**: 69–83. doi:10.1016/j.gloplacha.2017.11.017.

Comte, J., Culley, A.I., Lovejoy, C., and Vincent, W.F. 2018. Microbial connectivity and sorting in a high Arctic watershed. ISME J. **12**: 2988–3000. doi:10.1038/s41396-018-0236-4. PMID: 30087410.

Comte, J., Monier, A., Crevecoeur, S.M., Lovejoy, C., and Vincent, W.F. 2016. Bacterial biogeography of permafrost thaw lakes in the changing northern landscape. Ecography **38**: 609–618. doi:10.1111/ecog.01667.

Cooley, S.W., and Pavelsky, T.M. 2016. Spatial and temporal patterns in arctic river ice breakup revealed by automated ice detection from MODIS imagery. Rem. Sens. Environ. **175**: 310–322. doi:10.1016/j.rse.2016.01.004.

Cortés, A., and MacIntyre, S. 2020. Mixing processes in small Arctic lakes during spring. Limnol. Oceanogr. **65**: 260–288. doi:10.1002/lno.11296.

Cortés, A., MacIntyre, S., and Sadro, S. 2017. Flowpath and retention of snowmelt in an ice-covered Arctic lake. Limnol. Oceanogr. **62**: 2023–2044. doi:10.1002/lno.10549.

Cory, R.M., Crump, B.C., Dobkowski, J.A., and Kling, G.W. 2013. Surface exposure to sunlight stimulates CO2 release from permafrost soil carbon in the arctic. Proc. Natl. Acad. Sci. U. S. A. **110**: 3429–3434. doi:10.1073/pnas.1214104110. PMID: 23401500.

Coulombe, O., Bouchard, F., and Pienitz, R. 2016. Coupling of sedimentological and limnological dynamics in subarctic thermokarst ponds in northern Québec (Canada) on an interannual basis. Sediment. Geol. **340**: 15–24. doi:10.1016/j.sedgeo.2016.01.012.

Couture, R.-M., de Wit, H.A., Tominaga, K., Kiuru, P., and Markelov, I. 2015. Oxygen dynamics in a boreal lake responds to long-term changes in climate, ice phenology, and DOC inputs. J. Geophys. Res. Biogeosci. **120**: 2441–2456. doi:10.1002/2015JG003065.

Crawford, J.T., Striegl, R.G., Wickland, K.P., Dornblaser, M.M., and Stanley, E.H. 2013. Emissions of carbon dioxide and methane from a headwater stream network of interior alaska. J. Geophys. Res. Biogeosci. **118**: 482–494. doi:10.1002/jgrg.20034.

Creed, I.F., Bergström, A.K., Trick, C.G., Grimm, N.B., Hessen, D.O. Karlsson, J., et al. 2018. Global change-driven effects on dissolved organic matter composition: implications for food webs of northern lakes. Glob. Change Biol. **24**: 3692–3714. doi:10.1111/gcb.14129.

Crevecoeur, S.M., Vincent, W.F., Comte, J., and Lovejoy, C. 2015. Bacterial community structure across environmental gradients in permafrost thaw ponds: methanotroph-rich ecosystems. Front. Microbiol. **6**: 192. doi:10.3389/fmicb.2015.00192. PMID: 25926816.

Culp, J.M., Goedkoop, W., Christensen, T., Christoffersen, K.S., Fefilova, E. Liljaniemi, P., et al. 2022. Arctic freshwater biodiversity: establishing baselines, trends, and drivers of ecological change. Freshw. Biol. **67**: 1–13. doi:10.1111/fwb.13831.

Culp, J.M., Goedkoop, W., Lento, J., Christoffersen, K.S., Frenzel, S. Gudbergsson, G., et al. 2012. The arctic freshwater biodiversity monitoring plan. CAFF International Secretariat, CAFF Monitoring Series Report Nr. 7. CAFF International Secretariat. Akureyri, Iceland. ISBN 978-9935-431-19-6.

Dallimore, A., Schröder-Adams, C.J., and Dallimore, S.R. 2000. Holocene environmental history of thermokarst lakes on richards island, northwest territories, Canada: theocamoebians as paleolimnological indicators. J. Paleolimnol. **23**: 261–283. doi:10.1023/A:1008184522637.

Danks, H.V. 2007. How aquatic insects live in cold climates. Can. Entomol. **139**: 443–471. doi:10.4039/n06-100.

David-Chavez, D.M., and Gavin, M. 2018. A global assessment of indigenous community engagement in climate research. Environ. Res. Lett. **13**: 123005. doi:10.1088/1748-9326/aaf300.

Dean, J.F., Meisel, O.H., Martyn Rosco, M., Marchesini, L.B., Garnett, M.H. Lenderink, H., et al. 2020. East siberian arctic inland waters emit mostly contemporary carbon. Nat. Commun. **11**: 1627. doi:10.1038/s41467-020-15511-6. PMID: 32242076.

Dean, J.F., van der Velde, Y., Garnett, M.H., Dinsmore, K.J., Baxter, R. Lessels, J.S., et al. 2018. Abundant pre-industrial carbon detected in canadian arctic headwaters: implications for the permafrost carbon feedback. Environ. Res. Lett. **13**: 034024. doi:10.1088/1748-9326/aaa1fe.

Deegan, L.A., Peterson, B.J., Golden, H., McIvor, C.C., and Miller, M.C. 1997. Effects of fish density and river fertilization on algal standing stocks, invertebrate communities, and fish production in an Arctic river. Can. J. Fish. Aquat. Sci. **54**: 269–283. doi:10.1139/f96-268.

Denfeld, B.A., Baulch, H.M., del Giorgio, P.A., Hampton, S.E., and Karlsson, J. 2018. A synthesis of carbon dioxide and methane dynamics during the ice-covered period of northern lakes. Limnol. Oceanogr. Lett. **3**: 117–131. doi:10.1002/lol2.10079.

Denfeld, B.A., Frey, K.E., Sobczak, W.V., Mann, P.J., and Holmes, R.M. 2013. Summer c$O_2$ evasion from streams and rivers in the Kolyma river basin, northeast Siberia. Polar Res. **32**: 19703–19718. doi:10.3402/polar.v32i0.19704.

Deshpande, B.N., Maps, F., Matveev, A., and Vincent, W.F. 2017. Oxygen depletion in subarctic peatland thaw lakes. Arct. Sci. **3**: 406–428. doi:10.1139/as-2016-0048.

Ding, Q., Wallace, J.M., Battisti, D.S., Steig, E.J., Gallant, A.J.E., Kim, H.-J., and Geng, L. 2014. Tropical forcing of the recent rapid Arctic warming in northeastern Canada and greenland. Nature **509**: 209–212. doi:10.1038/nature13260. PMID: 24805345.

Docherty, C.L., Dugdale, S.J., Milner, A.M., Abermann, J., Lund, M., and Hannah, D.M. 2019. Arctic river temperature dynamics in a changing climate. River Res. Appl. **35**: 1212–1227. doi:10.1002/rra.3537.

Docherty, C.L., Hannah, D.M., Riis, T., Leth, S.R., and Milner, A.M. 2018. Longitudinal distribution of macroinvertebrates in snowmelt streams in northeast greenland: understanding biophysical controls. Polar Biol. **41**: 1567–1580. doi:10.1007/s00300-017-2212-2. PMID: 30956389.

Doubek, J.P., Campbell, K.L., Doubek, K.M., Hamre, K.D., Lofton, M.E. McClure, R.P., et al. 2018. The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. Ecosphere **9**: e02332. doi:10.1002/ecs2.2332.

Douglas, M.S., and Smol, J.P. 1999. Freshwater diatoms as indicators of environmental change in the high arctic. Diatoms Appl. Environ. Earth Sci. **249**, 60–69.

Douglas, M.S.V., Smol, J.P., and Blake, W., Jr. 1994. Marked post-18th century environmental change in high-Arctic ecosystems. Science **266**: 416–419. doi:10.1126/science.266.5184.416. PMID: 17816685.

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J. Striegl, R.G., et al. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. **51**: 2388–2397. doi:10.4319/lo.2006.51.5.2388.

Drake, T.W., Guillemette, F., Hemingway, J.D., Chanton, J.P., Podgorski, D.C., Zimov, N.S., and Spencer, R.G.M. 2018a. The ephemeral signature of permafrost carbon in an Arctic fluvial network. J. Geophys. Res. Biogeosci. **123**: 1475–1485. doi:10.1029/2017JG004311.

Drake, T.W., Holmes, R.M., Zhulidov, A.V., Gurtovaya, T., Raymond, P.A., McClelland, J.W., and Spencer, R.G.M. 2018b. Multidecadal climate-induced changes in Arctic tundra lake geochemistry and geomorphology. Limnol. Oceanogr. **64**: S179–S191. doi:10.1002/lno.11015.

Drake, T.W., Tank, S.E., Zhulidov, A.V., Holmes, R.M., Gurtovaya, T., and Spencer, R.G.M. 2018c. Increasing alkalinity export from large russian arctic rivers. Environ. Sci. Technol. **52**(15): 8302–8308. doi:10.1021/acs.est.8b01051.

Drake, T.W., Wickland, K.P., Spencer, R.G.M., McKnight, D.M., and Striegl, R.G. 2015. Ancient low–molecular-weight organic acids in permafrost fuel rapid carbon dioxide production upon thaw. Proc. Natl. Acad. Sci. U. S. A. **112**: 13946–13951. doi:10.1073/pnas.1511705112. PMID: 26504243.

Dranga, S.A., Hayles, S., Gajewski, K., and Henry, G. 2018. Synthesis of limnological data from lakes and ponds across Arctic and boreal Canada. Arct. Sci. **4**(2): 167–185. doi:10.1139/as-2017-0039.

Duan, L., Man, X., Kurylyk, B.L., and Cai, T. 2017. Increasing winter baseflow in response to permafrost thaw and precipitation regime shifts in northeastern China. Water **9**(1): 25. doi:10.3390/w9010025.

Edwards, A., Cameron, K.A., Cook, J.M., Debbonaire, A.R., Furness, E., Hay, M.C., and Rassner, S.M. 2020. Microbial genomics amidst the Arctic crisis. Microb. Genom. 39–47. doi:10.1099/mgen.0.000375.

Egli, M., Mirabella, A., and Sartori, G. 2008. The role of climate and vegetation in weathering and clay mineral formation in late quaternary soils of the swiss and italian alps. Geomorphology **102**(3): 307–324. doi:10.1016/j.geomorph.2008.04.001.

Elder, C.D., Schweiger, M., Lam, B., Crook, E.D., Xu, X. Walker, J., et al. 2019. Seasonal sources of whole-lake $cH_4$ and $CO_2$ emissions from interior Alaskan thermokarst lakes. J. Geophys. Res. Biogeosci. **124**: 1209–1229. doi:10.1029/2018JG004735.

Elder, C.D., Xu, X., Walker, J., Schnell, J.L., Hinkel, K.M. Townsend-Small, A., et al. 2018. Greenhouse gas emissions from diverse Arctic Alaskan lakes are dominated by young carbon. Nat. Clim. Change **8**: 166–171. doi:10.1038/s41558-017-0066-9.

Engram, M., Arp, C.D., Jones, B.M., Ajadi, O.A., and Meyer, F.J. 2018. Analyzing floating and bedfast lake ice regimes across Arctic Alaska using 25 years of space-borne SAR imagery. Rem. Sens. Environ. **209**: 660–676. doi:10.1016/j.rse.2018.02.022.

Estop-Aragonés, C., Olefeldt, D., Abbott, B.W., Chanton, J.P., Czimczik, C.I. Dean, J.F., et al. 2020. Assessing the potential for mobilization of old soil carbon after permafrost thaw: a synthesis of $^{14}C$ measurements from the northern permafrost region. Glob. Biogeochem. Cycles **34**: e2020GB006672. doi:10.1029/2020GB006672.

Evans, S.G., Yokeley, B., Stephens, C., and Brewer, B. 2020. Potential mechanistic causes of increased baseflow across northern eurasia catchments underlain by permafrost. Hydrol. Process. **11**: 2676–2690. doi:10.1002/hyp.13759.

Fang, X., and Stefan, H.G. 2009. Simulations of climate effects on water temperature, dissolved oxygen, and ice and snow covers in lakes of the contiguous united states under past and future climate scenarios. Limnol. Oceanogr. **54**: 2359–2370. doi:10.4319/lo.2009.54.6_part_2.2359.

Farmer, D.M. 1975. Penetrative convection in the absence of mean shear. Quart. J. R. Meteorol. Soc. **101**: 869–891. doi:10.1002/qj.49710143011.

Farquharson, L.M., Romanovsky, V.E., Kholodov, A., and Nicolsky, D. 2022. Sub-aerial talik formation observed across the discontinuous permafrost zone of Alaska. Nat. Geosci. **15**: 475–481. doi:10.1038/s41561-022-00952-z.

Feng, D., Gleason, C.J., Lin, P., Yang, X., Pan, M., and Ishitsuka, Y. 2021. Recent changes to arctic river discharge. Nat. Commun. **12**: 6197. doi:10.1038/s41467-021-27228-1.

Finstad, A.G., Andersen, T., Larsen, S., Tominaga, K., Blumentrath, S.A. de Wit, H., et al. 2016. From greening to browning: catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scales in Nordic lakes. Sci. Rep. **6**: 31944. doi:10.1038/srep31944. PMID: 27554453.

Forel, F.A. 1891. Allgemeine biologie eines suesswassersees. [General biology of freshwater lakes]. In O. Zacharias, O. Die Tier- und Pflanzenwelt des Suesswassers [The flora and fauna of freshwaters]. *Edited by* J.J. Weber. Arno Press, Leipzig, pp. 1–26.

Forsström, L., Sorvari, S., Rautio, M., and Korhola, A. 2005. Seasonality of phytoplankton in subarctic lake saanajärvi in NW finnish lapland. Polar Biol. **28**: 846–861. doi:10.1007/s00300-005-0008-2.

Fouché, J., Christiansen, C.T., Lafrenière, M.J., Grogan, P., and Lamoureux, S.F. 2020. Canadian permafrost stores large pools of ammonium and optically distinct dissolved organic matter. Nat. Commun. **11**(1): 4500. doi:10.1038/s41467-020-18331-w.

Fowler, R.A., Osburn, C.L., and Saros, J.E. 2020. Climate-driven changes in dissolved organic carbon and water clarity in arctic lakes of west greenland. J. Geophys. Res. Biogeosci. **125**: e2019JG005170. doi:10.1029/2019JG005170.

Freeman, E.C., Creed, I.F., Jones, B., and Bergström, A.K. 2020. Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes. Glob. Change Biol. **26**(9): 4966–4987. doi:10.1111/gcb.15189.

Frenken, T., Alacid, A., Berger, S.A., Bourne, E.C., Gerphagnon, M. Grossart, H.P., et al. 2017. Integrating chytrid fungal parasites into plankton ecology: research gaps and needs. Environ. Microbiol. **19**: 3802–3822. doi:10.1111/1462-2920.13827. PMID: 28618196.

Frey, K.E., and McClelland, J.W. 2009. Impacts of permafrost degradation on Arctic river biogeochemistry. Hydrol. Process. **23**: 169–182. doi:10.1002/hyp.7196.

Frey, K.E., and Smith, L.C. 2005. Amplified carbon release from vast west Siberian peatlands by 2100. Geophys. Res. Lett. **32**: L09401. doi:10.1029/2004gl022025.

Frey, K.E., Siegel, D.I., and Smith, L.C. 2007. Geochemistry of west siberian streams and their potential response to permafrost degradation. Water Resour. Res. **43**(3): W03406. doi:10.1029/2006WR004902, 2.

Friberg, N., Milner, A.M., Svendsen, L.M., Lindegaard, C., and Larsen, S.E. 2001. Macroinvertebrate stream communities along regional and physico-chemical gradients in western greenland. Freshw. Biol. **46**: 1753–1764. doi:10.1046/j.1365-2427.2001.00857.x.

Fritz, S.C. 2008. Deciphering climatic history from lake sediments. J. Paleolimnol. **39**: 5–16. doi:10.1007/s10933-007-9134-x.

Gardner, J.R., Yang, X., Topp, S.N., Ross, M.R.V., Altenau, E.H., and Pavelsky, T.M. 2021. The color of rivers. Geophys. Res. Lett. **48**: e2020GL088946. doi:10.1029/2020GL088946.

Gillman, M.A., Lamoureux, S.F., and Lafrenière, M.J. 2017. Calibration of a modified temperature-light intensity logger for quantifying water electrical conductivity. Water Resour. Res. **53**(9): 8120–8126. doi:10.1002/2017WR020634.

Gillooly, J.F., and Dodson, S.I. 2000. Latitudinal patterns in the size distribution and seasonal dynamics of new world, freshwater cladocerans. Limnol. Oceanogr. **45**: 22–30. doi:10.4319/lo.2000.45.1.0022.

Gislason, S.R., Oelkers, E.H., Eiriksdottir, E.S., Kardjilov, M.I., Gisladottir, G. Sigfusson, B., et al. 2009. Direct evidence of the feedback between climate and weathering. Earth Planet. Sci. Lett. **277**(1): 213–222. doi:10.1016/j.epsl.2008.10.018.

Goedkoop, W., Culp, J.M., Christensen, T., Christoffersen, K.S., Fefilova, E. Guðbergsson, G., et al. 2022. Improving the framework for assessment of ecological change in the arctic: a circumpolar synthesis of freshwater biodiversity. Freshw. Biol. **67**: 210–223. doi:10.1111/fwb.13873.

Golosov, S., Maher, O.A., Schipunova, E., Terzhevik, A., Zdorovennova, G., and Kirillin, G. 2007. Physical background of the development of oxygen depletion in ice-covered lakes. Oecologia **151**: 331–340. doi:10.1007/s00442-006-0543-8. PMID: 17115190.

Golosov, S., Terzhevik, A., Zverev, I., Kirillin, G., and Engelhardt, C. 2012. Climate change impact on thermal and oxygen regime of shallow lakes. Tellus Ser. A Dyn. Meteorol. Oceanol. **64**: 17264. doi:10.3402/tellusa.v64i0.17264.

Graly, J.A., Drever, J.I., and Humphrey, N.F. 2017. Calculating the balance between atmospheric CO2 drawdown and organic carbon oxidation in subglacial hydrochemical systems. Glob. Biogeochem. Cycl. **31**(4): 709–727. doi:10.1002/2016GB005425.

Graly, J.A., Humphrey, N.F., and Harper, J.T. 2016. Chemical depletion of sediment under the greenland ice sheet: chemical depletion of sediment under the greenland ice sheet. Earth Surf. Proc. Landf. **41**(13): 1922–1936. doi:10.1002/esp.3960.

Gregory-Eaves, I., Smol, J.P., Finney, B.P., and Edwards, M.E. 1999. Diatom-based transfer functions for inferring past climatic and environmental changes in alaska, U.S.A. Arct. Antarct. Alp. Res. **31**(4): 353–365. doi:10.1080/15230430.1999.12003320.

Grosbois, G., Power, M., Evans, M., Koehler, G., and Rautio, M. 2022. Stocks, production and transfer of polyunsaturated fatty acids in an arctic lake food web. Ecosphere **13**: e03881. doi:10.1002/ecs2.3881.

Grosse, G., Jones, B., and Arp, C. 2013. Thermokarst lakes, drainage, and drained basins. In: *Treatise on Geomorphology*. *Edited by* J.F. Shroder. Academic Press, San Diego, CA. pp. 325–353.

Gudasz, C., Bastviken, D., Steger, K., Premke, K., Sobek, S., and Tranvik, L.J. 2010. Temperature-controlled organic carbon mineralization in lake sediments. Nature **466**: 478–482. doi:10.1038/nature09186. PMID: 20651689.

Guo, L., Ping, C.-L., and Macdonald, R.W. 2007. Mobilization pathways of organic carbon from permafrost to Arctic rivers in a changing climate. Geophys. Res. Lett. **34**: L13603. doi:10.1029/2007GL030689.

Hamilton, P.B., Gajewski, K., Atkinson, D.E., and Lean, D.R.S. 2001. Physical and chemical limnology of 204 lakes from the Canadian Arctic archipelago. Hydrobiologia **457**: 133–148. doi:10.1023/a:1012275316543.

Hampton, S.E., Galloway, A.W., Powers, S.M., Ozersky, T., Woo, K.H. Batt, R.D., et al. 2017. Ecology under lake ice. Ecol. Lett. **20**: 98–111. doi:10.1111/ele.12699. PMID: 27889953.

Harms, T.K., and Jones, J.B. 2012. Thaw depth determines reaction and transport of inorganic nitrogen in valley bottom permafrost soils. Glob. Change Biol. **18**: 2958–2968. doi:10.1111/j.1365-2486.2012.02731.x.

Hauser, D.D.W., Whiting, A.V., Mahoney, A.R., Goodwin, J., Harris, C. Schaeffer, R.J., et al. 2021. Co-production of knowledge reveals loss of indigenous hunting opportunities in the face of accelerating Arctic climate change. Environ. Res. Lett. **16**: 095003. doi:10.1088/1748-9326/ac1a36.

Hawkings, J., Wadham, J., Tranter, M., Telling, J., Bagshaw, E. Beaton, A., et al. 2016. The greenland ice sheet as a hot spot of phosphorus weathering and export in the Arctic. Glob. Biogeochem. Cycl. **30**: 191–210. doi:10.1002/2015GB005237.

Hazuková, V., Burpee, B.T., McFarlane-Wilson, I., and Saros, J.E. 2021. Under ice and early summer phytoplankton dynamics in two arctic lakes with differing DOC. J. Geophys. Res. Biogeosci. **126**: e2020JG005972. doi:10.1029/2020JG005972.

Heino, J., Culp, J.M., Erkinaro, J., Goedkoop, W., Lento, J., Ruhland, K.M., and Smol, J.P. 2020. Abruptly and irreversibly changing arctic freshwaters urgently require standardized monitoring. J. Appl. Ecol. **57**: 1192–1198. doi:10.1111/1365-2664.13645.

Herman-Mercer, N., Schuster, P.F., and Maracle, B.K. 2011. Indigenous observations of climate change in the lower yukon river basin, Alaska. Hum. Organ. **70**: 244–252. doi:10.17730/humo.70.3.v88841235897071m.

Hessen, D.O., Bakkestuen, V., and Walseng, B. 2007. Energy input and zooplankton species richness. Ecography. **30**: 749–758. doi:10.1111/j.2007.0906-7590.05259.x.

Hindshaw, R.S., Aciego, S.M., and Tipper, E.T. 2018. Li and u isotopes as a potential tool for monitoring active layer deepening in permafrost dominated catchments. Front. Earth Sci. **6**: 102. doi:10.3389/feart.2018.00102.

Hines, J.E., Dickson, D.L., Turner, B.C., Wiebe, M.O., Barry, S.J., Barry, T.A., et al. 2000. Population status, distribution and survival of shortgrass prairie Canada geese from the inuvialuit settlement region, western Canada Arctic. Can. Wildl. Serv. Occas. Pap.(103): 27–58.

Hiyama, T., Yang, D., and Kane, D.L. 2021. Permafrost hydrology: linkages and feedbacks. In *Arctic Hydrology, Permafrost and Ecosystems*. *Edited by* D. Yang and D.L. Kane. Springer, Cham. doi:10.1007/978-3-030-50930-9_16.

Hobbie, J.E., Peterson, B.J., Bettez, N., Deegan, L., O'Brien, W.J., Kling, G.W., et al. 1999. Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. Polar Res. **18**(2): 207–214. doi:10.1111/j.1751-8369.1999.tb00295.x.

Holm, H.C., Fredricks, H.F., Bent, S.M., Lowenstein, D.P., Ossolinski, J.E., Becker, K.W., et al. 2022. Global ocean lipidomes show a universal relationship between temperature and lipid unsaturation. Science **376**: 1487–1491. doi:10.1126/science.abn7455. PMID: 35737766.

Holmes, R.M., McClelland, J.W., Peterson, B.J., Tank, S.E., Bulygina, E., Eglinton, T.I., et al. 2012. Seasonal and annual fluxes of nutrients and organic matter from large rivers to the arctic ocean and surrounding seas. Estuar. Coasts **35**: 369–382. doi:10.1007/s12237-011-9386-6.

Houser, J.N. 2006. Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. Can. J. Fish. Aquat. Sci. **63**: 2447–2455. doi:10.1139 /f06-131.

Huey, R.B., and Stevenson, R.D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. **19**: 357–366. doi:10.1093/icb/19.1.357.

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., et al. 2020. Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. Proc. Natl. Acad. Sci. U. S. A. **117**: 20438–20446. doi:10.1073/pnas.1916387117. PMID: 32778585.

Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J.W., Schuur, E.A.G., Ping, C.-L., et al. 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences **11**: 6573–6593. doi:10.5194/bg-11-6573-2014.

Hughes-Allen, L., Bouchard, F., Laurion, I., Séjourné, A., Marlin, C., Hatté, C., et al. 2021. Seasonal patterns in greenhouse gas emissions from thermokarst lakes in central yakutia (Eastern siberia). Limnol. Oceanogr. **66**: S98–S116. doi:10.1002/lno.11665.

Huryn, A.D., Slavik, K.A., Lowe, R.L., Parker, S.M., Anderson, D.S., and Peterson, B.J. 2005. Landscape heterogeneity and the biodiversity of arctic stream communities: a habitat template analysis. Can. J. Fish. Aquat. Sci. **62**: 1905–1919. doi:10.1139/f05-100.

Imbeau, E., Vincent, W.F., Wauthy, M., Cusson, M., and Rautio, M. 2021. Hidden stores of organic matter in northern lake ice: selective retention of terrestrial particles, phytoplankton and labile carbon. J. Geophys. Res. – Biogeosc. **126**: e2020JG006233. doi:10.1029/2020JG006233.

IPCC. 2022. *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. *Edited by* H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría , et al., . Cambridge University Press, UK.

Isidorova, A., Mendonca, R., and Sobek, S. 2019. Reduced mineralization of terrestrial OC in anoxic sediment suggests enhanced burial efficiency in reservoirs compared to other depositional environments. J. Geophys. Res. Biogeosci. **124**: 678–688. doi:10.1029/2018jg004823.

Jane, S.F., Hansen, G.J., Kraemer, B.M., Leavitt, P.R., Mincer, J.L., North, R.L., et al. 2021. Widespread deoxygenation of temperate lakes. Nature **594**: 66–70. doi:10.1038/s41586-021-03550-y. PMID: 34079137.

Jansen, J., MacIntyre, S., Barrett, D.C., Chin, Y.-P., Cortés, A., Forrest, A.L., et al. 2021. Winter limnology: how do hydrodynamics and biogeochemistry shape ecosystems under ice? J. Geophys. Res. Biogeosci. **126**: e2020JG00637. doi:10.1029/2020JG006237.

Jansen, J., Thornton, B.F., Jammet, M.M., Wik, M., Cortés, A., Friborg, T., et al. 2019. Climate-sensitive controls on large spring emissions of cH$_4$ and CO$_2$ from northern lakes. J. Geophys Res. Biogeosci. **124**: 2379–2399. doi:10.1029/2019/JG005094.

Jassby, A.D. 1998. Interannual variability at three inland water sites: implications for sentinel ecosystems. Ecol. Appl. **8**: 277–287. doi:10.1890/1051-0761 (1998) 008[0277:IVATIW]2.0.CO;2.

Jeffries, M., Morris, K., and Liston, G. 1996. A method to determine lake depth and water availability on the north slope of alaska with spaceborne imaging radar and numerical ice growth modelling. Arctic **49**(4): 367–374. doi:10.14430/arctic1212.

Jensen, T.C., Walseng, B., Hessen, D.O., Dimante-Deimantovica, I., Novichkova, A.A., Chertoprud, E.S., et al. 2019. Changes in trophic state and aquatic communities in high arctic ponds in response to increasing goose populations. Freshw. Biol. **64**: 1241–1254. doi:10.1111/fwb.13299.

Jeppesen, E., Christoffersen, K., Rautio, M., and Lauridsen, T.L. 2021. Ecology of Arctic lakes and ponds. In: *Arctic Ecology*. *Edited by* D.N. Thomas. Wiley-Blackwell, Hoboken, NJ. pp. 159–180.

Jeppesen, E., Landkildehus, F., Lauridsen, T.L., and Amsinck, S.L. 2001. Fish and crustaceans in northeast greenland lakes with special emphasis on interactions between arctic charr (*Salvelinus alpinus*), *lepidurus arcticus* and benthic chydorids. Hydrobiologia **442**: 329–337. doi:10.1023/A:1017508211819.

Jeppesen, E., Lauridsen, T.L., Christoffersen, K.S., Landkildehus, F., Geertz-Hansen, P., Amsinck, S.L., et al. 2017. The structuring role of fish in greenland lakes: an overview based on contemporary and paleoecological studies of 87 lakes from the low and the high Arctic. Hydrobiologia **800**: 99–113. doi:10.1007/s10750-017-3279-z.

Jepsen, S.M., Voss, C.I., Walvoord, M.A., Minsley, B.J., and Rover, J. 2013. Linkages between lake shrinkage/expansion and sublacustrine permafrost distribution determined from remote sensing of interior Alaska, USA, Geophys. Res. Lett. **40**: 882–887. doi:10.1002/grl.50187.

Jepsen, S.M., Walvoord, M.A., Voss, C.I., and Rover, J. 2016. Effect of permafrost thaw on the dynamics of lakes recharged by ice-jam floods: case study of yukon flats, Alaska. Hydrol. Process. **30**: 1782–1795. doi:10.1002/hyp.10756.

Johnston, S.E., Striegl, R.G., Bogard, M.J., Dornblaser, M.M., Butman, D.E., Kellerman, A.M., et al. 2020. Hydrologic connectivity determines dissolved organic matter biogeochemistry in northern high-latitude lakes. Limnol. Oceanogr. **65**: 1764–1780. doi:10.1002/lno.11417.

Jones, B.M., Grosse, G., Arp, C.D., Jones, M.C., Anthony, K.M.W., and Romanovsky, V.E. 2011. Modern thermokarst lake dynamics in the continuous permafrost zone, northern seward peninsula, Alaska. J. Geophys. Res. Biogeosci. **116**: 1–13. doi:10.1029/2011jg001666. PMID: 24349901.

Jones, C.E., Kielland, K., and Hinzman, L.D. 2015. Modeling groundwater upwelling as a control on river ice thickness. Hydrol. Res. **46**: 566–577. doi:10.2166/nh.2015.026.

Jones, I.D., Winfield, I.J., and Carse, F. 2008. Assessment of long-term changes in habitat availability for Arctic charr (*Salvelinus alpinus)* in a temperate lake using oxygen profiles and hydroacoustic surveys. Freshw. Biol. **53**: 393–402.

Jones, N.T., and Gilbert, B. 2016. Changing climate cues differentially alter zooplankton dormancy dynamics across latitudes. J. Anim. Ecol. **85**: 559–569. doi:10.1111/1365-2656.12474. PMID: 26590065.

Jorgenson, M.T., and Grosse, G. 2016. Remote sensing of landscape change in permafrost regions. Permafr. Periglac. Process. **27**: 324–338. doi:10.1002/ppp.1914.

Kahlert, M., Rühland, K.M., Lavoie, I., Keck, F., Saulnier-Talbot, E., Bogan, D., et al. 2022. Biodiversity patterns of Arctic diatom assemblages in lakes and streams: current reference conditions and historical context for biomonitoring. Freshw. Biol. **67**: 116–140. doi:10.1111/fwb.13490.

Kalff, J., and Welch, H.E. 1974. Phytoplankton production in char lake, a natural polar lake, and in meretta lake, a polluted polar lake, cornwallis island, northwest territories. J. Fish. Res. Board Can. **31**: 621–636. doi:10.1139/f74-094.

Karlsson, J., and Säwström, C. 2009. Benthic algae support zooplankton growth during winter in a clear-water lake. Oikos **118**: 539–544. doi:10.1111/j.1600-0706.2008.17239.x.

Karlsson, J., Bergström, A.-K., Byström, P., Gudasz, C., Rodríguez, P., and Hein, C. 2015. Terrestrial organic matter input suppresses biomass production in lake ecosystems. Ecology **96**: 2870–2876. doi:10.1890/15-0515.1. PMID: 27070007.

Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., and Jansson, M. 2009. Light limitation of nutrient-poor lake ecosystems. Nature **460**: 506–509. doi:10.1038/nature08179. PMID: 19626113.

Karlsson, J.M., Lyon, S.W., and Destouni, G. 2012. Thermokarst lake, hydrological flow and water balance indicators of permafrost change in western siberia. J. Hydrol. **464–465**: 459–466. doi:10.1016/j.jhydrol.2012.07.037.

Keller, K., Blum, J.D., and Kling, G.W. 2010. Stream geochemistry as an indicator of increasing permafrost thaw depth in an arctic watershed. Chem. Geol. **273**(1–2): 76–81. doi:10.1016/j.chemgeo.2010.02.013.

Kelly, S., Moore, T.N., de Eyto, E., Dillane, M., Goulon, C., Guillard, J., et al. 2020. Warming winters threaten peripheral arctic charr populations of Europe. Clim. Change **163**: 599–618. doi:10.1007/s10584-020-02887-z.

Kenney, M.A., Janetos, A.C., and Lough, G.C. 2016. Building an integrated US national climate indicators system. Clim. Change **135**: 85–96. doi:10.1007/s10584-016-1609-1.

Keva, O., Taipale, S.J., Hayden, B., Thomas, S.M., Vesterinen, J., Kankaala, P., and Kahilainen, K.K. 2021. Increasing temperature and productivity change biomass, trophic pyramids and community-level omega-3 fatty acid content in subarctic lake food webs. Glob. Change Biol. **27**: 282–296. doi:10.1111/gcb.15387.

Kicklighter, D.W., Cai, Y., Zhuang, Q., Parfenova, E.I., Paltsev, S., Sokolov, A.P., et al. 2014. Potential influence of climate-induced vegetation shifts on future land use and associated land carbon fluxes in northern eurasia. Environ. Res. Lett. **9**: 035004. doi:10.1088/1748-9326/9/3/035004.

Kirchman, D.L. 2018. *Processes in Microbial Ecology*. Oxford University Press, Oxford, UK.

Kirf, M., Roy, H., Holtappels, M., Fischer, J.P., Schubert, C.J., and Wehrli, B. 2015. Redox gradients at the low oxygen boundary of lakes. Aquat. Sci. **77**: 81–93. doi:10.1007/s00027-014-0365-4.

Kivilä, E.H., Luoto, T.P., Rantala, M.V., Kiljunen, M., Rautio, M., and Nevalainen, L. 2019. Environmental controls on benthic food web functions and carbon resource use in subarctic lakes. Freshw. Biol. **64**(4): 643–658. doi:10.1111/fwb.13250.

Kivilä, H., Rantala, M.V., Antoniades, D., Luoto, T.P., Nevalainen, L., and Rautio, M. 2022. Sea level rise may contribute to the arctic greening of coastal water bodies, implications from ontogeny of greiner lake. Nunavut. CATENA **211**: 105969. doi:10.1016/j.catena.2021.105969.

Kling, G.W., Kipphut, G.W., and Miller, M.C. 1991. Arctic lakes and rivers as gas conduits to the atmosphere: implications for tundra carbon budgets. Science, **251**: 298–301.

Kling, G.W. 1995. Land-water interactions: the influence of terrestrial diversity on aquatic ecosystems. In *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. 320pp.

Klobucar, S.L., Gaeta, J.W., and Budy, P. 2018. A changing menu in a changing climate: using experimental and long-term data to predict invertebrate prey biomass and availability in lakes of Arctic Alaska. Freshw. Biol. **63**: 1352–1364. doi:10.1111/fwb.13162.

Knight, R., Vrbanac, A., Taylor, B.C., Aksenov, A., Callewaert, C., Debelius, J., et al. 2018. Best practices for analysing microbiomes. Nat. Rev. Microbiol. **16**: 410–422. doi:10.1038/s41579-018-0029-9. PMID: 29795328.

Knoll, L.B., Sharma, S., Denfeld, B.A., Flaim, G., Hori, Y., Magnuson, J.J., et al. 2019. Consequences of lake and river ice loss on cultural ecosystem services. Limnol. Oceanogr. Lett. **4**: 119–131. doi:10.1002/lol2.10116.

Knoll, L.B., Williamson, C.E., Pilla, R.M., Leach, T.H., Brentrup, J.A., and Fisher, T.J. 2018. Browning-related oxygen depletion in an oligotrophic lake. Inland Wat. **8**: 255–263. doi:10.1080/20442041.2018.1452355.

Knopp, J.A., Levenstein, B., Watson, A., Ivanova, I., and Lento, J. 2020. Systematic review of documented indigenous knowledge of freshwater biodiversity in the circumpolar arctic. Freshw. Biol. **67**: 194–209. doi:10.1111/fwb.13570.

Kokelj, S.V., and Burn, C.R. 2005. Geochemistry of the active layer and near-surface permafrost, mackenzie delta region, northwest territories, Canada. Can. J. Earth Sci. **42**(1): 37–48. doi:10.1139/e04-089.

Kokelj, S.V., and Jorgenson, M.T. 2013. Advances in thermokarst research. Permafr. Periglac. Process. **24**(2): 108–119. doi:10.1002/ppp.1779.

Kokelj, S.V., Jenkins, R.E., Milburn, D., Burn, C.R., and Snow, N. 2005. The influence of thermokarst disturbance on the water quality of small upland lakes, mackenzie delta region, northwest territories, Canada. Permafr. Periglac. Process. **16**(4): 343–353. doi:10.1002/ppp.536.

Kokelj, S.V., Lacelle, D., Lantz, T.C., Tunnicliffe, J., Malone, L., Clark, I.D., and Chin, K.S. 2013. Thawing of massive ground ice in mega slumps drives increases in stream sediment and solute flux across a range of watershed scales. J. Geophys. Res. Earth Surf. **118**(2): 681–692. doi:10.1002/jgrf.20063.

Kokelj, S.V., Lantz, T.C., Tunnicliffe, J., Segal, R., and Lacelle, D. 2017. Climate-driven thaw of permafrost preserved glacial landscapes, northwestern Canada. Geology **45**(4): 371–374. doi:10.1130/G38626.1.

Korhola, A., Sorvari, S., Rautio, M., Appleby, P.G., Dearing, J.A., Hu, Y., et al. 2002. A multi-proxy analysis of climate impacts on the recent development of subarctic lake saanajärvi in finnish lapland. J. Paleolimnol. **28**(1): 59–77. doi:10.1023/a:1020371902214.

Korosi, J.B., McDonald, J., Coleman, K.A., Palmer, M.J., Smol, J.P., Simpson, M.J., and Blais, J.M. 2015. Long-term changes in organic matter and mercury transport to lakes in the sporadic discontinuous permafrost zone related to peat subsidence. Limnol. Oceanogr. **60**: 1550–1561. doi:10.1002/lno.10116.

Koue, J., Shimadera, H., Matsuo, T., and Kondo, A. 2020. Numerical simulation for seasonal and inter-annual change of dissolved oxygen in lake biwa, Japan. Int. J. Geomat. **18**: 56–61. doi:10.21660/2020.66.9366.

Kuhn, C., and Butman, D. 2021. Declining greenness in Arctic-boreal lakes. Proc. Nat. Acad. Sci. U. S. A. **118**: E2021219118. doi:10.1073/pnas.2021219118.

Kuhn, C.D., Bogard, M., Johnston, S.E., John, A., Vermote, E.F., Spencer, R., et al. 2020. Satellite and airborne remote sensing of gross primary productivity in boreal alaskan lakes. Environ. Res. Lett. **15**: 105001. doi:10.1088/1748-9326/aba46f.

Labrecque, S., Lacelle, D., Duguay, C.R., Lauriol, B., and Hawkings, J. 2009. Contemporary (1951–2001) evolution of lakes in the old crow basin, northern yukon, Canada: remote sensing, numerical modeling, and stable isotope analysis. Arctic **62**: 225–238. doi:10.14430/arctic134.

Lacelle, D., Fontaine, M., Pellerin, A., Kokelj, S.V., and Clark, I.D. 2019. Legacy of holocene landscape changes on soil biogeochemistry: a perspective from paleo-active layers in northwestern Canada. J. Geophys. Res. Biogeosc. **124**(9): 2662–2679. doi:10.1029/2018JG004916.

Lafrenière, M.J., and Lamoureux, S.F. 2013. Thermal perturbation and rainfall runoff have greater impact on seasonal solute loads than physical disturbance of the active layer. Permafr. Periglac. Process. **24**: 241–251. doi:10.1002/ppp.1784.

Lamhonwah, D. 2020. *Hydrological and Hydrochemical Responses From Thawing Permafrost in the Canadian Arctic*. PhD thesis. Queen's University, Kingston. p. 197.

Lamhonwah, D., Lafrenière, M., Lamoureux, S., and Wolfe, B. 2017. Evaluating the hydrological and hydrochemical responses of a high Arctic catchment during an exceptionally warm summer. Hydrol. Process. **31**: 2296–2313. doi:10.1002/hyp.11191.

Lantz, T.C., and Kokelj, S.V. 2008. Increasing rates of retrogressive thaw slump activity in the mackenzie delta region, N.W.T., Canada. Geophys. Res. Lett. **35**: L06502. doi:10.1029/2007GL032433.

Lantz, T.C., and Turner, K.W. 2015. Changes in lake area in response to thermokarst processes and climate in old crow flats, yukon. J. Geophys. Res. Biogeosci. **120**: 513 524. doi:10.1002/2014JG002744.

Larocque, I., Hall, R.I., and Grahn, E. 2001. Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). J. Paleolimnol. **26**(3): 307–322. doi:10.1023/a:1017524101783.

Larouche, J.R., Abbott, B.W., Bowden, W.B., and Jones, J.B. 2015. The role of watershed characteristics, permafrost thaw, and wildfire on dissolved organic carbon biodegradability and water chemistry in Arctic headwater streams. Biogeosciences **12**: 4221–4233. doi:10.5194/bg-12-4221-2015.

Larsen, A., Schwoerer, T.T., Simmons, T., and Fulkerson, J. 2020. *Elodea*: Alaska's first invasive aquatic plant continues to march across the state. Alaska Park Sci. **19**: 92–99.

Laske, S.M., Amundsen, P.A., Christoffersen, K.S., Erkinaro, J., Guðbergsson, G., Hayden, B., et al. 2022. Circumpolar patterns of arctic freshwater fish biodiversity: a baseline for monitoring. Freshw. Biol. **67**: 176–193. doi:10.1111/fwb.13405.

Lau, M.P., and del Giorgio, P. 2020. Reactivity, fate and functional roles of dissolved organic matter in anoxic inland waters. Biol. Lett. **16**: 20190694. doi:10.1098/rsbl.2019.0694. PMID: 32097596.

Lauridsen, T.L., Mønster, T., Raundrup, K., Nymand, J., and Olesen, B. 2020. Macrophyte performance in a low arctic lake: effects of temperature, light and nutrients on growth and depth distribution. Aquat. Sci **82**: 18. doi:10.1007/s00027-019-0692-6.

Laurion, I., Vincent, W.F., MacIntyre, S., Retamal, L., Dupont, C., Francus, P., et al. 2010. Variability in greenhouse gas emissions from permafrost thaw ponds. Limnol. Oceanogr. **55**: 115–133. doi:10.4319/lo.2010.55.1.0115.

Law, A.C., Anderson, N.J., and McGowan, S. 2015. Spatial and temporal variability of lake ontogeny in south-western greenland. Quat. Sci. Rev. **126**: 1–16. doi:10.1016/j.quascirev.2015.08.005.

Laybourn-Parry, J., and Marshall, W.A. 2003. Photosynthesis, mixotrophy and microbial plankton dynamics in two high arctic lakes during summer. Polar Biol. **26**(8): 517–524. doi:10.1007/s00300-003-0514-z.

Leavitt, P.R., Fritz, S.C., Anderson, N.J., Baker, P.A., Blenckner, T., Bunting, L., et al. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnol. Oceanogr. **54**: 2330–2348. doi:10.4319/lo.2009.54.6_part_2.2330.

Lehnherr, I., St Louis, V.L., Sharp, M., Gardner, A.S., Smol, J.P., and Schiff, S.L. 2018. The world's largest high arctic lake responds rapidly to climate warming. Nat. Commun. **9**: 1290. doi:10.1038/s41467-018-03685-z.

Lento, J., Culp, J.M., Levenstein, B., Aroviita, J., Baturina, M.A., Bogan, D., et al. 2022a. Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. Freshw. Biol. **67**: 159–175. doi:10.1111/fwb.13805.

Lento, J., Goedkoop, W., Culp, J., Christoffersen, K.S., Fannar Lárusson, K., Fefilova, E., et al. 2019. *State of the Arctic Freshwater Biodiversity*. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland. ISBN 978-9935-431-77-6.

Lento, J., Laske, S.M., Lavoie, I., Bogan, D., Brua, R.B., Campeau, S., et al. 2022b. Diversity of diatoms, benthic macroinvertebrates, and fish varies in response to different environmental correlates in arctic rivers across North America. Freshw. Biol. **67**: 95–115. doi:10.1111/fwb.13600.

Leppi, J.C., Arp, C.D., and Whitman, M.S. 2016. Predicting late winter dissolved oxygen levels in arctic lakes using morphology and landscape metrics. Environ. Manag. **57**: 463–473. doi:10.1007/s00267-015-0622-x.

Levenstein, B., Lento, J., and Culp, J. 2021. Effects of prolonged sedimentation from permafrost degradation on macroinvertebrate drift in Arctic streams. Limnol. Oceanogr. **66**: S157–S168. doi:10.1002/lno.11657.

Lewis, T., Lafrenière, M.J., and Lamoureux, S.F. 2012. Hydrochemical and sedimentary responses of paired high arctic watersheds to unusual climate and permafrost disturbance, cape bounty, melville island, Canada. Hydrol. Process. **26**(13): 2003–2018. doi:10.1002/hyp.8335.

Lewis, T.L., Heglund, P.J., Lindberg, M.S., Schmutz, J.A., Schmidt, J.H., Dubour, A.J., et al. 2016. Trophic dynamics of shrinking subarctic lakes: naturally eutrophic waters impart resilience to rising nutrient and major ion concentrations. Oecologia **181**(2): 583–596. doi:10.1007/s00442-016-3572-y. PMID: 26857253.

Liljedahl, A.K., Gädeke, A., O'Neel, S., Gatesman, T.A., and Douglas, T.A. 2017. Glacierized headwater streams as aquifer recharge corridors, subarctic Alaska. Geophys. Res. Lett. **44**: 6876–6885. doi:10.1002/2017GL073834.

Lindstrøm, E.A., and Skulberg, O. 2008. *Did y mosphenia geminata*—a native diatom species of norwegian rivers coexisting with the atlantic salmon. In Proceedings of the 2007 international workshop on Didymosphenia geminata. Can. Tech. Rep. Fisher. Aquat. Sci., Nanaimo - British Columbia, Fisheries and Oceans Canada, vol. **2795**: pp. 35–40.

Litchman, E., and Klausmeier, C.A. 2008. Trait-based community ecology of phytoplankton. Annu. Rev. Ecol. Evol. Syst. **39**: 615–639. doi:10.1146/annurev.ecolsys.39.110707.173549.

Littlefair, C.A., Tank, S.E., and Kokelj, S.V. 2017. Retrogressive thaw slumps temper dissolved organic carbon delivery to streams of the peel plateau, NWT, Canada. Biogeosciences **14**: 5487–5505. doi:10.5194/bg-14-5487-2017.L.

Lougheed, V.L., Tweedie, C.E., Andresen, C.G., Armendariz, A.M., Escarzaga, S.M., and Tarin, G. 2020. Patterns and drivers of carbon dioxide concentrations in aquatic ecosystems of the arctic coastal tundra. Glob. Biogeochem. Cycles **34**: e2020GB006552. doi:10.1029/2020GB006552.

Louiseize, N.L., Lafrenière, M.J., and Hastings, M.G. 2014. Stable isotopic evidence of enhanced export of microbially derived NO_3- following active layer slope disturbance in the Canadian high arctic. Biogeochemistry **121**(3): 565–580. doi:10.1007/s10533-014-0023-x.

Luo, D., Wu, Q., Jin, H., Marchenko, S.S., Lü, L., and Gao, S. 2016. Recent changes in the active layer thickness across the northern hemisphere. Environ. Earth Sci. **75**(7): 555. doi:10.1007/s12665-015-5229-2.

Luoto, T.P., Brooks, S.J., and Salonen, V.-P. 2014. Ecological responses to climate change in a bird-impacted high Arctic pond (Nordaustlandet, svalbard). J. Paleolimnol. **51**(1): 87–97. doi:10.1007/s10933-013-9757-z.

Maasri, A., Jähnig, S.C., Adamescu, M.C., Adrian, R., Baigun, C., Baird, D.J., et al. 2022. A global agenda for advancing freshwater biodiversity research. Ecol. Lett. **25**: 255–263. doi:10.1111/ele.13931. PMID: 34854211.

MacDonald, E.N., Tank, S.E., Kokelj, S.V., Froese, D.G., and Hutchins, R.H.S. 2021. Permafrost-derived dissolved organic matter composition varies across permafrost end-members in the western Canadian arctic. Environ. Res. Lett. **16**: 024036. doi:10.1088/1748-9326/abd971.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C., and Velichko, A.A. 2006. Rapid early development of circumarctic peatlands and atmospheric $cH_4$ and $CO_2$ variations. Science **314**: 285–288. doi:10.1126/science.1131722. PMID: 17038618.

MacDonald, L.A., Farquharson, N., Merritt, G., Fooks, S., Medeiros, A.S., Hall, R.I., et al. 2015. Limnological regime shifts caused by climate warming and lesser snow goose population expansion in the western hudson bay lowlands (Manitoba, Canada). Ecol. Evol. **5**: 921–939. doi:10.1002/ece3.1354.

MacDonald, L.A., Turner, K.W., Balasubramaniam, A.M., Wolfe, B.B., Hall, R.I., and Sweetman, J.N. 2012. Tracking hydrological responses of a thermokarst lake in the old crow flats (Yukon territory, Canada) to recent climate variability using aerial photographs and paleolimnological methods. Hydrol. Process. **26**: 117–129. doi:10.1002/hyp.8116.

MacIntyre, S, Bastviken, D., Arneborg, L., Crowe, A.T., Karlsson, J., Andersson, A., et al. 2021b. Turbulence in a small boreal lake: consequences for air-water gas exchange. Limnol. Oceanogr. **66**: 827–854. doi:10.1002/lno.11645.

MacIntyre, S., Amaral, J.H., and Melack, J.M. 2021a. Turbulence in the upper mixed layer under light winds and heating: implications for gas fluxes. J. Geophys. Res. Oceans **126**: e2020JC017026. doi:10.1029/2020JC017026.

MacIntyre, S., Cortés, A., and Sadro, S. 2018a. Sediment respiration drives circulation and production of $cO_2$ in ice-covered Alaskan Arctic lakes. Limnol. Oceanogr. Lett. **3**: 302–310. doi:10.1002/lol2.10083.

MacIntyre, S., Crowe, A.T., Cortes, A., and Arneborg, L. 2018b. Turbulence in a small Arctic pond. Limnol. Oceanogr. **63**: 2337–2358. doi:10.1002/lno.10941.

MacIntyre, S., Fram, J.P., Kushner, P.J., Bettez, N.D., O'Brien, W.J., Hobbie, J.E., and Kling, G.W. 2009. Climate-related variations in mixing dynamics in an Alaskan Arctic lake. Limnol. Oceanogr. **54**: 2401–2417. doi:10.4319/lo.2009.54.6_part_2.2401.

Malik, H.I., and Saros, J.E. 2016. Effects of temperature, light, and nutrients on five *cyclotella* sensu lato taxa assessed with in-situ experiments in arctic lakes. J. Plankton Res. **38**: 431–442. doi:10.1093/plankt/fbw002.

Malik, H.I., Northington, R.M., and Saros, J.E. 2017. Nutrient limitation status of Arctic lakes affects the responses of *cyclotella* sensu lato taxa to light: implications for distribution patterns. Polar Biol. **40**: 2445–2456. doi:10.1007/s00300-017-2156-6.

Malone, L., Lacelle, D., Kokelj, S., and Clark, I.D. 2013. Impacts of hillslope thaw slumps on the geochemistry of permafrost catchments (Stony creek watershed, NWT, Canada). Chem. Geol. **356**: 38–49. doi:10.1016/j.chemgeo.2013.07.010.

Mann, P.J., Eglinton, T.I., McIntyre, C.P., Zimov, N., Davydova, A., Vonk, J.E., et al. 2015. Utilization of ancient permafrost carbon in headwaters of Arctic fluvial networks. Nat. Commun. **6**: 7856. doi:10.1038/ncomms8856. PMID: 26206473.

Mariash, H.L., Devlin, S.P., Forsström, L., Jones, R.I., and Rautio, M. 2014. Benthic mats offer a potential subsidy to pelagic consumers in tundra pond food webs. Limnol. Oceanogr. **59**: 733–744. doi:10.4319/lo.2014.59.3.0733.

Mariash, H.L., Rautio, M., Mallory, M.L., and Smith, P.A. 2019. Experimental tests of water chemistry response to ornithological eutrophication: biological implications in Arctic freshwaters. Biogeosciences **16**(23): 4719–4730. doi:10.5194/bg-16-4719-2019.

Mariash, H.L., Smith, P.A., and Mallory, M. 2018. Decadal response of arctic freshwaters to burgeoning goose populations. Ecosystems **21**: 1230–1243. doi:10.1007/s10021-017-0215-z.

Matheus Carnevali, P.B., Herbold, C.W., Hand, K.P., Priscu, J.C., and Murray, A.E. 2018. Distinct microbial assemblage structure and archaeal diversity in sediments of arctic thermokarst lakes differing in methane sources. Front. Microbiol. **7**: 1192. doi:10.3389/fmicb.2018.01192.

Mathias, J.A., and Barica, J. 1980. Factors controlling oxygen depletion in ice-covered lakes. Can. J. Fish. Aquat. Sci. **37**: 185–194. doi:10.1139/f80-024.

Matveev, A., Laurion, I., and Vincent, W.F. 2019. Winter accumulation of methane and its variable timing of release from thermokarst lakes on subarctic peatlands. J. Geophys. Res. Biogeosci. **124**: 3521–3535. doi:10.1029/2019JG005078.

McCallister, S.L., Ishikawa, N.F., and Kothawala, D.N. 2018. Biogeochemical tools for characterizing organic carbon in inland aquatic ecosystems. Limnol. Oceanogr. Lett. **3**: 444–457. doi:10.1002/lol2.10097.

McClelland, J.W., Déry, S.J., Peterson, B.J., Holmes, R.M., and Wood, E.F. 2006. A pan-arctic evaluation of changes in river discharge during the latter half of the 20th century. Geophys. Res. Lett. **33**: L06715. doi:10.1029/2006GL025753.

McClelland, J.W., Holmes, R.M., Peterson, B.J., Raymond, P.A., Striegl, R.G., Zhulidov, A.V., et al. 2016. Particulate organic carbon and nitrogen export from major Arctic rivers. Glob. Biogeochem. Cycles **30**: 629–643. doi:10.1002/2015GB005351.

McCrystall, M.R., Stroeve, J., Serreze, M., Forbes, B.C., and Screen, J.A. 2021. New climate models reveal faster and larger increases in Arctic precipitation than previously projected. Nat. Commun. **12**: 6765. doi:10.1038/s41467-021-27031-y.

McGowan, S., Anderson, N.J., Edwards, M.E., Hopla, E., Jones, V. Langdon, P.G., et al. 2018a. Vegetation transitions drive the autotrophy–heterotrophy balance in Arctic lakes. Limnol. Oceanogr. Lett. **3**(3): 246–255. doi:10.1002/lol2.10086.

McGowan, S., Anderson, N.J., Edwards, M.E., Langdon, P.G., Jones, V.J., et al. 2016. Long-term perspectives on terrestrial and aquatic carbon cycling from palaeolimnology. WIREs Water **3**: 211–234. doi:10.1002/wat2.1130.

McGowan, S., Gunn, H.V., Whiteford, E.J., Anderson, N.J., Jones, V.J., and Law, A.C. 2018b. Functional attributes of epilithic diatoms for palaeoenvironmental interpretations in south-west greenland lakes. J. Paleolimnol. **60**: 273–298. doi:10.1007/s10933-017-9968-9.

McIntosh Marcek, H.A., Lesack, L.F.W., Orcutt, B.N., Wheat, C.G., Dallimore, S.R., Geeves, K., and Lapham, L.L. 2021. Continuous dynamics of dissolved methane over 2 years and its carbon isotopes ($\delta^{13}$c, $\delta^{14}$C) in a small arctic lake in the mackenzie delta. J. Geophys. Res. Biogeosci. **126**: e2020JG006038. doi:10.1029/2020JG006038.

Medeiros, A.S., Taylor, D.J., Couse, M., Hall, R.I., Quinlan, R., and Wolfe, B.B. 2014. Biological and nutrient responses to catchment disturbance and warming in small lakes near the alaskan tundra–taiga boundary. Holocene **24**: 1308–1319. doi:10.1177/0959683614540955.

Mesquita, P.S., Wrona, F.J., and Prowse, T.D. 2008. Effects of retrogressive thaw slumps on sediment chemistry, submerged macrophyte biomass, and invertebrate abundance of upland tundra lakes. Hydrol. Process. **22**: 145–158.

Metcalfe, D.B., Hermans, T.D.G., Ahlstrand, J., Becker, M., Berggren, M., Björk, R.G., et al. 2018. Patchy field sampling biases understanding of climate change impacts across the Arctic. Nat. Ecol. Evol. **2**: 1443–1448. doi:10.1038/s41559-018-0612-5. PMID: 30013133.

Michelutti, N., Douglas, M., Lean, D., and Smol, J.P. 2002. Physical and chemical limnology of 34 ultra-oligotrophic lakes and ponds near wynniatt bay, victoria island, arctic Canada. Hydrobiologia **482**: 1–13. doi:10.1023/A:1021201704844.

Michelutti, N., Douglas, M.S.V., Antoniades, D., Lehnherr, I., St. Louis, V.L., St.Pierre, K., et al. 2020. Contrasting the ecological effects of decreasing ice cover versus accelerated glacial melt on the high Arctic's largest lake. Proc. R. Soc. B **287**(1929): 20201185. doi:10.1098/rspb.2020.1185.

Michelutti, N., Wolfe, A.P., Vinebrooke, R.D., Rivard, B., and Briner, J.P. 2005. Recent primary production increases in arctic lakes. Geophys. Res. Lett. **32**: L19715. doi:10.1029/2005gl023693.

Mohit, V., Culley, A., Lovejoy, C., Bouchard, F., and Vincent, W.F. 2017. Hidden biofilms in a far northern lake and implications for the changing Arctic. npj Biofilms Microbiomes **3**: 17. doi:10.1038/s41522-017-0024-3. PMID: 28702216.

Monteith, D.T., Stoddard, J.L., Evans, C.D., De Wit, H.A., Forsius, M., Høgåsen, T., et al. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature **450**: 537–540. doi:10.1038/nature06316. PMID: 18033294.

Mueller, D.R., Van Hove, P., Antoniades, D., Jeffries, M.O., and Vincent, W.F. 2009. High arctic lakes as sentinel ecosystems: cascading regime shifts in climate, ice cover, and mixing. Limnol. Oceanogr. **54**: 2371–2385. doi:10.4319/lo.2009.54.6_part_2.2371.

Natali, S.M., Watts, J.D., Rogers, B.M., Potter, S., Ludwig, S.M., Selbmann, A.-K., et al. 2019. Large loss of CO2 in winter observed across the northern permafrost region. Nat. Clim. Change **9**: 852–857. doi:10.1038/s41558-019-0592-8.

Negandhi, K., Laurion, I., and Lovejoy, C. 2016. Temperature effects on net greenhouse gas production and bacterial communities in Arctic thaw ponds. FEMS Microbiol. Ecol. **92**: 1–12. doi:10.1093/femsec/fiw117.

Negandhi, K., Laurion, I., Whiticar, M.J., Galand, P.E., Xu, X.M., and Lovejoy, C. 2013. Small thaw ponds: an unaccounted source of methane in the Canadian high arctic. PLoS ONE **8**: e78204. doi:10.1371/journal.pone.0078204. PMID: 24236014.

Nelligan, C., Jeziorski, A., Ruhland, K.M., Paterson, A.M., and Smol, J.P. 2019. Long-term trends in hypolimnetic volumes and dissolved oxygen concentrations in boreal shield lakes of south-central Ontario, Canada. Can. J. Fish. Aquat. Sci. **76**: 2315–2325. doi:10.1139/cjfas-2018-0278.

Nitze, I., Cooley, S.W., Duguay, C.R., Jones, B.M., and Grosse, G. 2020. The catastrophic thermokarst lake drainage events of 2018 in northwestern alaska: fast forward into the future. Cryosphere **14**: 4279–4297. doi:10.5194/tc-14-4279-2020.

Nitze, I., Grosse, G., Jones, B.M., Romanovsky, V.E., and Boike, J. 2018. Remote sensing quantifies widespread abundance of permafrost region disturbances across the arctic and subarctic. Nat. Commun. **9**: 5423. doi:10.1038/s41467-018-07663-3. PMID: 30575717.

Novichkova, A.A., and Azovsky, A.I. 2017. Factors affecting regional diversity and distribution of freshwater microcrustaceans (Cladocera, copepoda) at high latitudes. Polar Biol. **40**: 185–198. doi:10.1007/s00300-016-1943-9.

O'Brien, W.J., Barfield, M., Bettez, N.D., Gettel, G.M., Hershey, A.E., McDonald, M.E., et al. 2004. Physical, chemical, and biotic effects on arctic zooplankton communities and diversity. Limnol. Oceanogr. **49**: 1250–1261. doi:10.2307/3597951.

O'Brien, W.J., Hershey, A.E., Hobbie, J.E., Hullar, M.A., Kipphut, G.W., Miller, M.C., et al. 1992. Control mechanisms of arctic lake ecosystems: a limnocorral experiment. Hydrobiologia **240**: 143–188. doi:10.1007/BF00013459.

O'Donnell, J.A., Aiken, G.R., Walvoord, M.A., and Butler, K.D. 2012. Dissolved organic matter composition of winter flow in the yukon river basin: implications of permafrost thaw and increased groundwater discharge. Glob. Biogeochem. Cycles **26**: GB0E06. doi:10.1029/2012GB004341.

O'Gorman, E.J., Pichler, D.E., Adams, G., Benstead, J.P., Cohen, H. Craig, N., et al. 2012. Impacts of warming on the structure and functioning of aquatic communities: individual-to ecosystem-level responses. Adv. Ecol. Res. **47**: 81–176. doi:10.1016/B978-0-12-398315-2.00002-8.

O'Neill, H.B., Roy-Leveillee, P., Lebedeva, L., and Ling, F. 2020. Recent advances (2010–2019) in the study of taliks. Permafr. Periglac. Process. **31**: 346–357. doi:10.1002/ppp.2050.

Opfergelt, S. 2020. The next generation of climate model should account for the evolution of mineral-organic interactions with permafrost thaw. Environ. Res. Lett. **15**: 091003. doi:10.1088/1748-9326/ab9a6d.

Orihel, D.M., Baulch, H.M., Casson, N.J., North, R.L., Parsons, C.T., Seckar, D.C., and Venkiteswaran, J.J. 2017. Internal phosphorus loading in Canadian fresh waters: a critical review and data analysis. Can. J. Fish. Aquat. Sci. **74**: 2005–2029. doi:10.1139/cjfas-2016-0500.

Palmer, M.E., Yan, N.D., and Somers, K.M. 2014. Climate change drives coherent trends in physics and oxygen content in North American lakes. Clim. Change **124**: 285–299. doi:10.1007/s10584-014-1085-4.

Paltan, H., Dash, J., and Edwards, M. 2015. A refined mapping of arctic lakes using landsat imagery. Int. J. Rem. Sens. **36**: 5970–5982. doi:10.1080/01431161.2015.1110263.

Paquette-Struger, B., Wrona, F.J., Atkinson, D., and Di Cenzo, P. 2018. Seasonal variations in the limnology of noell lake in the western canadian arctic tracked by in situ observation systems. Arctic **71**: 149–166. doi:10.14430/arctic4716.

Paquette, M., Fortier, D., and Lamoureux, S.F. 2020b. Cryostratigraphical studies of ground ice formation and distribution in a high arctic polar desert landscape, resolute bay, nunavut. Can. J. Earth Sci. 759–771. doi:10.1139/cjes-2020-0134.

Paquette, M., Fortier, D., Lafrenière, M., and Vincent, W.F. 2020a. Periglacial slopewash dominated by solute transfers and subsurface erosion on a high arctic slope. Permafr. Periglac. Process. **31**: 472–486. doi:10.1002/ppp.2066.

Paquette, M., Fortier, D., Mueller, D.R., Sarrazin, D., and Vincent, W.F. 2015. Rapid disappearance of perennial ice on Canada's most northern lake. Geophys. Res. Lett. **42**: 1433–1440. doi:10.1002/2014GL062960.

Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., et al. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. **21**(8): 3049–3082. doi:10.1890/10-2341.1.

Pastick, N.J., Jorgenson, M.T., Goetz, S.J., Jones, B.M., Wylie, B.K., Minsley, B.J., and Jorgenson, J.C. 2019. Spatiotemporal remote sensing of ecosystem change and causation across Alaska. Glob. Change Biol. **25**: 1171–1189. doi:10.1111/gcb.14279.

Payette, S., Delwaide, A., Caccianiga, M., and Beauchemin, M. 2004. Accelerated thawing of subarctic peatland permafrost over the last 50 years. Geophys. Res. Lett. **31**: L18208. doi:10.1029/2004GL020358.

Paytan, A., Lecher, A.L., Dimova, N., Sparrow, K.J., Garci-Tigreros Kodovska, F., Murray, J., et al. 2015. Methane transport from the active layer to lakes in the arctic using toolik lake, alaska, as a case study. Proc. Nat. Acad. Sci. U. S. A. **112**(12): 3636–3640. doi:10.1073/pnas.1417392112.

Perren, B.B., Axford, Y., and Kaufman, D.S. 2017. Alder, nitrogen, and lake ecology: terrestrial-aquatic linkages in the postglacial history of lone spruce pond, southwestern alaska. PloS ONE **12**: e0169106. doi:10.1371/journal.pone.0169106. PMID: 28076393.

Peterson, B.J., Holmes, R.M., McClelland, J.W., Vörösmarty, C.J., Lammers, R.B., Shiklomanov, A.I., et al. 2017. Overview of sea ice growth and properties. In *Sea Ice*. Edited by D.N. Thomas. John Wiley, Chichester, UK. p. 652.

Petrone, K.C., Hinzman, L.D., Shibata, H., Jones, J.B., and Boone, R.D. 2007. The influence of fire and permafrost on sub-arctic stream chemistry during storms. Hydrol. Process. **21**(4): 423–434. doi:10.1002/hyp.6247.

Pick, F.R. 2016. Blooming algae: a canadian perspective on the rise of toxic cyanobacteria. Can. J. Fish. Aquat. Sci. **73**: 1149–1158. doi:10.1139 /cjfas-2015-0470.

Pienitz, R., and Vincent, W.F. 2000. Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. Nature **304**: 484–487. doi:10.1038/35006616.

Pilla, R.M., Williamson, C.E., Adamovich, B.V., Adrian, R., Anneville, O., Chandra, S., et al. 2020. Global trends in lake thermal structure: deep waters are warming less consistently than surface waters and thermal stability. Sci. Rep. **10**: 20514. doi:10.1038/s41598-020-76873-x. PMID: 33239702.

Pilla, R.M., Williamson, C.E., Zhang, J., Smyth, R.L., Lenters, J.D., Brentrup, J.A., et al. 2018. Browning-related decreases in water transparency lead to long-term increases in surface water temperature and thermal stratification in two small lakes. J. Geophys. Res. Biogeosci. **123**: 1651–1665. doi:10.1029/2017JG004321.

Pinel-Alloul, B., André, A., Legendre, P., Cardille, J.A., Patalas, K., and Salki, A. 2013. Large-scale geographic patterns of diversity and community structure of pelagic crustacean zooplankton in canadian lakes. Glob. Ecol. Biogeogr. **22**: 784–795. doi:10.1111/geb.12041.

Power, M., Power, G., Grosbois, G., and Rautio, M. 2022. Occurrence of slimy sculpin, *cottus cognatus* (Richardson) on southern victoria island, nunavut. Polar Biol. **45**: 507–512. doi:10.1007/s00300-021-02979-1.

Prėskienis, V., Laurion, I., Bouchard, F., Douglas, P.M.J., Billett, M.F., Fortier, D., and Xu, X. 2021. Seasonal patterns in greenhouse gas emissions from lakes and ponds in a high arctic polygonal landscape. Limnol. Oceanogr. **66**: S117–S141. doi:10.1002/lno.11660.

Prowse, T.D., Alfredsen, K., Beltaos, S., Bonsal, B., Duguay, C., Korhola, A., et al. 2011. Changing lake and river ice regimes: trends, effects, and implications. In Arctic Monitoring and Assessment Program (AMAP), Oslo, Norway. pp. 63–74

Przytulska, A., Bartiowicz, M., and Vincent, W.F. 2017. Increased risk of harmful cyanobacterial blooms in northern high-latitude lakes through climate warming and phosphorus enrichment. Freshw. Biol. **62**: 1986–1996. doi:10.1111/fwb.13043.

Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.E., et al. 2020. Scientists' warning on invasive alien species. Biol. Rev. **95**: 1511–1534. doi:10.1111/brv.12627.

Rasilo, T., Hutchins, R.S., Ruiz-Gonzalez, C., and del Giorgio, P.A. 2017. Transport and transformation of soil-derived CO$_{2,}$ CH$_{4,}$ and DOC sustain CO$_2$ supersaturation in small boreal streams. Sci. Total Environ. **579**: 902–912. doi:10.1-16/j.scitotenv.2016.10.187.

Rautio, M., and Vincent, W.F. 2006. Benthic and pelagic food resources for zooplankton in shallow high-latitude lakes and ponds. Freshw. Biol. **51**: 1038–1052. doi:10.1111/j.1365-2427.2006.01550.x.

Rawlins, M., Yang, D., and Ge, S. 2021. Regional and basin streamflow regimes and changes: climate impact and human effect. In *Arctic Hydrology, Permafrost and Ecosystems. Edited by* D. Yang and D.L. Kane. Springer , Cham, Germany. pp. 159–186. doi:10.1007/978-3-030-50930-9_16.

Rawlins, M.A., Steele, M., Holland, M.M., Adam, J.C., Cherry, J.E., Francis, J.A., et al. 2010. Analysis of the arctic system for freshwater cycle intensification: observations and expectations. J. Clim. **23**(21): 5715–5737. doi:10.1175/2010JCLI3421.1.

Raymond, P.A., McClelland, J.W., Holmes, R.M., Zhulidov, A.V., Mull, K., Peterson, B.J., et al. 2007. Flux and age of dissolved organic carbon exported to the Arctic ocean: a carbon isotopic study of the five largest Arctic rivers. Glob. Biogeochem. Cycles **21**: GB4011. doi:10.1029/2007GB002934.

Read, J.S., and Rose, K.C. 2013. Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. Limnol. Oceanogr. **58**: 921–931. doi:10.4319/lo.2013.58.3.0921.

Redfield, G.W., and Vincent, W.F. 1979. Stages of infection and ecological effects of a fungal epidemic on the eggs of a limnetic copepod. Freshw. Biol. **9**: 503–510. doi:10.1111/j.1365-2427.1979.tb01534.x.

Rehder, Z., Zaplavnova, A., and Kutzbach, L. 2021. Identifying drivers behind spatial variability of methane concentrations in east Siberian ponds. Front. Earth Sci. **9**: 617662. doi:10.3389/feart.2021.617662.

Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., et al. 2021. General effects of climate change on arctic fishes and fish populations. Ambio **35**(7): 370–380. doi:10.1579/0044-7447 (2006) 35[370:GEOCCO]2.0.CO;2.

Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., King, J.R., and Beamish, R.J. 2006. An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. Ambio **35**: 381–387. doi:10.1579/0044-7447(2006)35%5b381:AOOEOC%5d2.0.CO;2. PMID: 17256642.

Remmer, C.R., Neary, L.K., Kay, M.L., Wolfe, B.B., and Hall, R.I. 2020. Multi-year isoscapes of lake water balances across a dynamic northern freshwater delta. Environ. Res. Lett. **15**: 104066. doi:10.1088/1748-9326/abb267.

Rey, D., Walvoord, M., Minsley, B., Rover, J., and Singha, K. 2019. Investigating lake-area dynamics across a permafrost-thaw spectrum using airborne electromagnetic surveys and remote sensing time-series data in yukon flats, alaska. Environ. Res. Lett. **14**: 02001. doi:10.1088/1748-9326/aaf06f.

Rey, D.M., Walvoord, M.A., Minsley, B.J., Ebel, B.A., Voss, C.I., and Singha, K. 2020. Wildfire-initiated talik development exceeds current thaw projections: observations and models from alaska's continuous permafrost zone. Geophys. Res. Lett. **47**: e2020GL087565. doi:10.1029/2020GL087565.

Reyes-González, D., De Luna-Valenciano, H., Utrilla, J., Sieber, M., Peña-Miller, R., and Fuentes-Hernández, A. 2022. Dynamic proteome allocation regulates the profile of interaction of auxotrophic bacterial consortia. Roy. Soc. Open Sci. **9**: 212008. doi:10.1098/rsos.212008.

Riordan, B., Verbyla, D., and McGuire, A.D. 2006. Shrinking ponds in subarctic alaska based on 1950–2002 remotely sensed images. J. Geophys. Res. Biogeosci. **111**: G04002. doi:10.1029/2005jg000150.

Roach, J., Griffith, B., Verbyla, D., and Jones, J. 2011. Mechanisms influencing changes in lake area in alaskan boreal forest. Glob. Change Biol. **17**: 2567–2583. doi:10.1111/j.1365-2486.2011.02446.x.

Roberts, K.E., Lamoureux, S.F., Kyser, T.K., Muir, D.C.G., Lafrenière, M.J., Iqaluk, D., et al. 2017. Climate and permafrost effects on the chemistry and ecosystems of high arctic lakes. Sci. Rep. **7**(1): 13292. doi:10.1038/s41598-017-13658-9. PMID: 29038475.

Rogers, S. 2018. Nunavut community still relies on reverse osmosis for drinking water. Nunatsiaq News. Iqaluit, Canada. Available from https://nunatsiaq.com/stories/article/65674nunavut_community_still_relies_on_reverse_osmosis_for_drinking_wa/ [accessed 6 October 2022].

Rolls, R.J., Hayden, B, and Kahilainen, K.K. 2017. Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. Ecol. Evol. **7**: 4109–4128. doi:10.1002/ece3.2982. PMID: 28649324.

Romero-Mujalli, G., Hartmann, J., and Börker, J. 2019. Temperature and $cO_2$ dependency of global carbonate weathering fluxes – implications for future carbonate weathering research. Chem. Geol. **527**: 118874. doi:10.1016/j.chemgeo.2018.08.010.

Rose, A.L. 2016. The influence of reactive oxygen species on local redox conditions in oxygenated natural waters. Front. Earth Sci. **4**: 96. doi:10.3389/feart.2016.00096.

Rosén, P., Cunningham, L., Vonk, J., and Karlsson, J. 2009. Effects of climate on organic carbon and the ratio of planktonic to benthic primary producers in a subarctic lake during the past 45 years. Limnol. Oceanogr. **54**(5): 1723–1732. doi:10.4319/lo.2009.54.5.1723.

Rueda, F.J., and MacIntyre, S. 2009. Flow paths and spatial heterogeneity of stream inflows in a small multibasin lake. Limnol. Oceanogr. **54**: 2041–2057. doi:10.4319/lo.2009.54.6.2041.

Sardain, A., Sardain, E., and Leung, B. 2019. Global forecasts of shipping traffic and biological invasions to 2050. Nature Sustain. **2**: 274–282. doi:10.1038/s41893-019-0245-y.

Saros, J.E., and Anderson, N.J. 2015. The ecology of the planktonic diatom *cyclotella* and its implications for global environmental change studies. Biol. Rev. **90**(2): 522–541. doi:10.1111/brv.12120.

Saros, J.E., Anderson, N.J., Juggins, S., McGowan, S., Yde, J.C., Telling, J., et al. 2019. Arctic climate shifts drive rapid ecosystem responses across the west greenland landscape. Environ. Res. Lett. **14**(7): 074027. doi:10.1088/1748-9326/ab2928.

Saros, J.E., Northington, R.M., Anderson, D.S., and Anderson, N.J. 2016. A whole-lake experiment confirms a small centric diatom species as an indicator of changing lake thermal structure. Limnol. Oceanogr. Lett. **1**(1): 27–35. doi:10.1002/lol2.10024.

Saros, J.E., Stone, J.R., Pederson, G.T., Slemmons, K.E.H., Spanbauer, T., Schliep, A., et al. 2012. Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleo-ecological approaches. Ecology **93**: 2155–2164. doi:10.1890/11-2218.1. PMID: 23185877.

Saros, J.E., Strock, K.E., McCue, J., Hogan, E., and Anderson, N.J. 2014. Response of *cyclotella* species to nutrients and incubation depth in arctic lakes. J. Plankton Res. **36**: 450–460. doi:10.1093/plankt/fbt126.

Schaeffer, S.M., Sharp, E., Schimel, J.P., and Welker, J.M. 2013. Soil-plant n processes in a high arctic ecosystem, NW greenland, are altered by long-term experimental warming and higher rainfall. Glob. Change Biol. **19**(11): 3529–3539. doi:10.1111/gcb.12318.

Schartau, A.K., Mariash, H.L., Christoffersen, K.S., Bogan, D., Dubovskaya, O.P., Fefilova, E.B., et al. 2022. First circumpolar assessment of arctic freshwater phytoplankton and zooplankton diversity: spatial patterns and environmental factors. Freshw. Biol. **67**: 141–158. doi:10.1111/fwb.13783.

Schindler, D.W., Welch, H.E., Kalff, J., Brunskill, G.J., and Kritsch, N. 1974. Physical and chemical limnology of char lake, cornwallis island (75 N lat.). J. Fish. Res. Board Canada **31**: 585–607. doi:10.1139/f74-092.

Schuur, E.A.G., McGuire, A.D., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., et al. 2015. Climate change and the permafrost carbon feedback. Nature **520**: 171–179. doi:10.1038/nature14338. PMID: 25855454.

Schwab, M.S., Hilton, R.G., Raymond, P.A., Haghipour, N., Amos, E., Tank, S.E., et al. 2020. An abrupt aging of dissolved organic carbon in large arctic rivers. Geophys. Res. Lett. **47**: 1–11. doi:10.1029/2020GL088823. PMID: 33380763.

Schwefel, R., Gaudard, A., Wüest, A., and Bouffard, D. 2016. Effects of climate change on deepwater oxygen and winter mixing in a deep lake (Lake geneva): comparing observational findings and modeling. Water Resour. Res. **52**: 8811–8826. doi:10.1002/2016WR019194.

Schwoerer, T., Little, J.M., Schmidt, J.I., and Borash, K.W. 2019. Hitchhikers on floats to arctic freshwater: private aviation and recreation loss from aquatic invasion. Ambio **49**: 1364–1376. doi:10.1007/s13280-019-01295-7. PMID: 31802430.

Segal, R.A., Lantz, T.C., and Kokelj, S.V. 2016. Acceleration of thaw slump activity in glaciated landscapes of the western canadian arctic. Environ. Res. Lett. **11**: 034025. doi:10.1088/1748-9326/11/3/034025.

Sepulveda-Jauregui, A., Anthony, K.M.W., Martinez-Cruz, K., Greene, S., and Thalasso, F. 2015. Methane and carbon dioxide emissions from 40 lakes along a north-south latitudinal transect in alaska. Biogeosciences **12**: 3197–3223. doi:10.5194/bg-12-3197-2015.

Serikova, S., Pokrovsky, O.S., Ala-Aho, P., Kazantsev, V., Kirpotin, S.N., Kopysov, S.G., et al. 2018. High riverine $CO_2$ emissions at the permafrost boundary of Western Siberia. Nat. Geosci. **11**: 825–829. doi:10.1038/s41561-018-0218-1.

Serreze, M.C., and Barry, R.G. 2011. Processes and impacts of arctic amplification: a research synthesis. Glob. Planet. Change **77**(1–2): 85–96. doi:10.1016/j.gloplacha.2011.03.004.

Shakil, S., Tank, S.E., Kokelj, S.V, Vonk, J.E., and Zolkos, S. 2020. Particulate dominance of organic carbon mobilization from thaw slumps on the peel plateau, NT: quantification and implications for stream systems and permafrost carbon release. Environ. Res. Lett. **15**: 114019. doi:10.1088/1748-9326/abac36.

Sharma, S., Blagrave, K., Magnuson, J.J., O'Reilly, C.M., Oliver, S., Batt, R.D., et al. 2019. Widespread loss of lake ice around the northern hemisphere in a warming world. Nat. Clim. Change **9**: 227–231. doi:10.1038/s41558-018-0393-5.

Sharma, S., Jackson, D.A., Minns, C.K., and Shuter, B.J. 2007. Will northern fish populations be in hot water because of climate change? Glob. Change Biol. **13**: 2052–2064. doi:10.1111/j.1365-2486.2007.01426.x.

Sivarajah, B., Simmatis, B., Favot, E.J., Palmer, M.J., and Smol, J.P. 2021. Eutrophication and climatic changes lead to unprecedented cyanobacterial blooms in a canadian sub-Arctic landscape. Harmful Algae **105**: 102036. doi:10.1016/j.hal.2021.102036. PMID: 34303513.

Slavik, K., Peterson, B.J., Deegan, L.A., Bowden, W.B., Hershey, A.E., and Hobbie, J.E. 2004. Long-term responses of the kuparuk river ecosystem to phosphorus fertilization. Ecology **85**: 939–954. doi:10.1890/02-4039.

Smejkalova, T., Edwards, M.E., and Dash, J. 2017. Arctic lakes show strong decadal trend in earlier spring ice-out. Sci. Rep. **6**: 38449. doi:10.1038/srep38449.

Smith, L.C., Pavelsky, T.M., MacDonald, G.M., Shiklomanov, A.I., and Lammers, R.B. 2007. Rising minimum daily flows in northern eurasian rivers: a growing influence of groundwater in the high-latitude hydrologic cycle. J. Geophys. Res. **112**: G04S47. doi:10.1029/2006JG000327.

Smith, L.C., Sheng, Y., MacDonald, G.M., and Hinzman, L.D. 2005. Disappearing arctic lakes. Science **308**: 1429. doi:10.1126/science.1108142. PMID: 15933192.

Smol, J.P., and Douglas, M.S.V. 2007. Crossing the final ecological threshold in high arctic ponds. Proc. Natl. Acad. Sci. U. S. A. **104**: 12, 395–12, 397. doi:10.1073/pnas.0702777104.

Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S., Jones, V.J., Korhola, A., et al. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. Proc. Nat. Acad. Sci. U. S. A. **102**(12): 4397–4402. doi:10.1073/pnas.0500245102.

Song, C., Dodds, W.K., Rüegg, J., Argerich, A., Baker, C.L., Bowden, W.B., et al. 2018. Continental-scale decrease in net primary productivity in streams due to climate warming. Nat. Geosci. **11**: 415–420. doi:10.1038/s41561-018-0125-5.

Song, C., Wang, G., Mao, T., Huang, K., Sun, X., Hu, Z., et al. 2020. Spatiotemporal variability and sources of DIC in permafrost catchments of the yangtze river source region: insights from stable carbon isotope and water chemistry. Water Resour. Res. **56**: e2019WR02534. doi:10.1029/2019WR025343.

Sorvari, S., Korhola, A., and Thompson, R. 2002. Lake diatom response to recent arctic warming in finnish lapland. Glob. Change Biol. **8**(2): 171–181. doi:10.1046/j.1365-2486.2002.00463.x.

Spawn, S.A., Dunn, S.T., Fiske, G.J., Natali, S.M., Schade, J.D., and Zimov, N.S. 2015. Summer methane ebullition from a headwater catchment in northeastern siberia. Inland Waters **5**: 224–230. doi:10.5268/IW-5.3.845.

Spencer, R.G., Mann, P.J., Dittmar, T., Eglinton, T.I., McIntyre, C., et al. 2015. Detecting the signature of permafrost thaw in arctic rivers. Geophys. Res. Lett. **42**: 2830–2835. doi:10.1002/2015GL063498.

St. Jacques, J.M. S., and Sauchyn, D.J. 2009. Increasing winter baseflow and mean annual streamflow from possible permafrost thawing in the northwest territories, Canada. Geophys. Res. Lett. **36**: L01401. doi:10.1029/2008GL035822.

St. Pierre, K.S., Louis, V.S., Lehnherr, I., Schiff, S.L., Muir, D.C.G., Poulain, A.J., et al. 2019. Contemporary limnology of the rapidly changing glacierized watershed of the world's largest high arctic lake. Sci. Rep. **9**(1): 4447. doi:10.1038/s41598-019-39918-4. PMID: 30872603.

Stackpoole, S.M., Butman, D.E., Clow, D.W., Verdin, K.L., Gaglioti, B.V., Genet, H., and Striegl, R.G. 2017. Inland waters and their role in the carbon cycle of alaska. Ecol. Appl. **27**: 1403–1420. doi:10.1002/eap.1552. PMID: 28376236.

Stalder, L.C., and Marcus, N.H. 1997. Zooplankton responses to hypoxia: behavioral patterns and survival of three species of calanoid copepods. Mar. Biol. **127**: 599–607. doi:10.1007/s002270050050.

Stone, J.R., and Fritz, S.C. 2004. Three-dimensional modeling of lacustrine diatom habitat areas: improving paleolimnological interpretation of planktic:benthic ratios. Limnol. Oceanogr. **49**: 1540–1548. doi:10.4319/lo.2004.49.5.1540.

Stone, J.R., Saros, J.E., and Spanbauer, T. 2019. The influence of fetch on the holocene thermal structure of hidden lake, glacier national park. Front. Earth Sci. **7**: 28. doi:10.3389/feart.2019.00028.

Strauss, J., Schirrmeister, L., Grosse, G., Fortier, D., Hugelius, G., Knoblauch, C., et al. 2017. Deep yedoma permafrost: a synthesis of depositional characteristics and carbon vulnerability. Earth-Sci. Rev. **172**: 75–86. doi:10.1016/j.earscirev.2017.07.007.

Street, L.E., Dean, JF., Billett, M.F., Baxter, R., Dinsmore, K.J., Lessels, J.S., et al. 2016. Redox dynamics in the active layer of an arctic headwater catchment; examining the potential for transfer of dissolved methane from soils to stream water. J. Geophys. Res. Biogeosci. **121**: 2776–2792. doi:10.1002/2016JG003387.

Streletskiy, D.A., Sherstiukov, A.B., Frauenfeld, O.W., and Nelson, F.E. 2015. Changes in the 1963–2013 shallow ground thermal regime in russian permafrost regions. Environ. Res. Lett. **10**(12): 125005. doi:10.1088/1748-9326/10/12/125005.

Striegl, R.G., Aiken, G.R., Dornblaser, M.M., Raymond, P.A., and Wickland, K.P. 2005. A decrease in discharge-normalized DOC export by the yukon river during summer through autumn. Geophys. Res. Lett. **32**: L21413. doi:10.1029/2005GL024413.

Striegl, R.G., Dornblaser, M.M., Aiken, G.R., Wickland, K.P., and Raymond, P.A. 2007. Carbon export and cycling by the yukon, tanana, and porcupine rivers, alaska, 2001-2005. Water Resour. Res. **43**(2): 1–9. doi:10.1029/2006WR005201. PMID: 20300476.

Striegl, R.G., Dornblaser, M.M., McDonald, C.P., Rover, J.A., and Stets, E.G. 2012. Carbon dioxide and methane emissions from the yukon river system. Glob. Biogeochem. Cycles **26**: GB0E05. doi:10.1029/2012GB004306.

Stroeve, J.C., and Notz, D. 2018. Changing state of arctic sea ice across all seasons. Environ. Res. Lett. **13**: e2019JC016039. doi:10.1088/1748-9326/aade56.

Stroeve, J.C., Serreze, M.C., Holland, M.M., Kay, J.E., Malanik, J., and Barrett, A.P. 2012. The arctic's rapidly shrinking sea ice cover: a research synthesis. Clim. Change **110**: 1005–1027. doi:10.1007/s10584-011-0101-1.

Stuefer, S.L., Arp, C.D., Kane, D.L., and Liljedahl, A.K. 2017. Recent extreme runoff observations from coastal arctic watersheds in alaska. Water Resour. Res. **53**: 9145–9163. doi:10.1002/2017WR020567.

Surdu, C.M., Duguay, C.R., Brown, L.C., and Fernández Prieto, D. 2014. Response of ice cover on shallow lakes of the north slope of alaska to contemporary climate conditions (1950–2011): radar remote-sensing and numerical modeling data analysis. Cryosphere **8**(1): 167–180. doi:10.5194/tc-8-167-2014.

Tank, S.E., Lesack, L.F.W., and Hesslein, R.H. 2009. Northern delta lakes as summertime cO$_2$ absorbers within the Arctic landscape. Ecosystems **12**: 144–157. doi:10.1007/s10021-008-9213-5.

Tank, S.E., Lesack, L.F.W., Gareis, J.A.L., Osburn, C.L., and Hesslein, R.H. 2011. Multiple tracers demonstrate distinct sources of dissolved organic matter to lakes of the mackenzie delta, western canadian arctic. Limnol. Oceanogr. **56**: 1297–1309. doi:10.4319/lo.2011.56.4.1297.

Tank, S.E., Raymond, P.A., Striegl, R.G., McClelland, J.W., Holmes, R.M., Fiske, G.J., and Peterson, B.J. 2012. A land-to-ocean perspective on the magnitude, source and implication of DIC flux from major arctic rivers to the arctic ocean. Glob. Biogeochem. Cycles **26**(4): 1–15. doi:10.1029/2011GB004192.

Tank, S.E., Striegl, R.G., McClelland, J.W., and Kokelj, S.V. 2016. Multidecadal increases in dissolved organic carbon and alkalinity flux from the mackenzie drainage basin to the arctic ocean. Environ. Res. Lett. **11**(5): 054015. doi:10.1088/1748-9326/11/5/054015.

Tank, S.E., Vonk, J.E., Walvoord, M.A., McClelland, J.W., Laurion, I., and Abbott, B.W. 2020. Landscape matters: predicting the biogeochemical effects of permafrost thaw on aquatic networks with a state factor approach. Permafr. Periglac. Process. **31**: 358–370. doi:10.1002/ppp.2057.

Taranu, Z.E., Gregory-Eaves, I., Leavitt, P.R., Bunting, L., Buchaca, T., Catalan, J., et al. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the anthropocene. Ecol. Lett. **18**(4): 375–384. doi:10.1111/ele.12420. PMID: 25728551.

Terhaar, J., Kwiatkowski, L., and Bopp, L. 2020. Emergent constraint on arctic ocean acidification in the twenty-first century. Nature **582**(7812): 379–383. doi:10.1038/s41586-020-2360-3. PMID: 32555488.

Terzhevik, A., Golosov, S., Palshin, N., Mitrokhov, A., Zdorovennov, R., Zdorovennova, G., et al. 2009. Some features of the thermal and dissolved oxygen structure in boreal, shallow ice-covered lake vendyurskoe, Russia. Aquat. Ecol. **43**: 617–627. doi:10.1007/s10452-009-9288-x.

Thienpont, J.R., Ruhland, K.M., Pisaric, M.F.J., Kokelj, S.V., Kimpe, L.E., Blais, J.M., and Smol, J.P. 2013. Biological responses to permafrost thaw slumping in canadian arctic lakes. Freshw. Biol. **58**: 337–353. doi:10.1111/fwb.12061.

Thottathil, S.D., Reis, P.C.J., and Prairie, Y.T. 2019. Methane oxidation kinetics in northern freshwater lakes. Biogeochemistry **143**: 105–116. doi:10.1007/s10533-019-00552-x.

Tipper, E.T., Stevenson, E.I., Alcock, V., Knight, A.C.G., Baronas, J.J. Hilton, R.G., et al. 2021. Global silicate weathering flux overestimated because of sediment–water cation exchange. Proc. Nat. Acad. Sci. U. S. A. **118**(1): 1–6. doi:10.1073/pnas.2016430118.

Tondu, J.M.E., Turner, K.W., Wiklund, J.A., Wolfe, B.B., Hall, R.I., and McDonald, I. 2017. Limnological evolution of zelma lake, a recently drained thermokarst lake in old crow flats (Yukon, Canada). Arct. Sci. **3**: 220–236. doi:10.1139/AS-2016-0012.

Toohey, R.C., Herman-Mercer, N.M., Schuster, P.F., Mutter, E.A., and Koch, J.C. 2016. Multidecadal increases in the yukon river basin of chemical fluxes as indicators of changing flowpaths, groundwater, and permafrost. Geophys. Res. Lett. **43**(23): 120–130. doi:10.1002/2016GL070817.

Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., Striegl, R.G., Ballatore, T.J., et al. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnol. Oceanogr. **54**: 2298–2314. doi:10.4319/lo.2009.54.6_part_2.2298.

Turetsky, M.R., Abbott, B.W., Jones, M.C., Anthony, K.W., Olefeldt, D., Schuur, E.A.G., et al. 2020. Carbon release through abrupt permafrost thaw. Nat. Geosci. **13**: 138–143. doi:10.1038/s41561-019-0526-0.

Turner, K.W., Wolfe, B.B., and Edwards, T.W.D. 2010. Characterizing the role of hydrological processes on lake water balances in the old crow flats, yukon territory, Canada, using water isotope tracers. J. Hydrol. **386**: 103–117. doi:10.1016/j.jhydrol.2010.03.012.

Turner, K.W., Wolfe, B.B., Edwards, T.W.D., Lantz, T.C., Hall, R.I., and Larocque, G. 2014. Controls on water balance of shallow thermokarst lakes and their relations with catchment characteristics: a multi-year, landscape-scale assessment based on water isotope tracers and remote sensing in old crow flats, yukon (Canada). Glob. Change Biol. **20**: 1585–1603. doi:10.1111/Gcb.12465.

Ulseth, A.J., Hall, R.O., Boix Canadell, M., Madinger, H.L., Niayifar, A., and Battin, T.J. 2019. Distinct air–water gas exchange regimes in low- and high-energy streams. Nat. Geosci. **12**: 259–263. doi:10.1038/s41561-019-0324-8.

Vadeboncoeur, Y., Devlin, S.P., McIntyre, P.B., and Vander Zanden, M.J. 2014. Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshw. Sci. **33**(2): 524–536. doi:10.1086/676315.

Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.H., Christoffersen, K., and Lodge, D.M. 2003. From greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. **48**(4): 1408–1418. doi:10.4319/lo.2003.48.4.1408.

Van Geest, G.J., Hessen, D.O., Spierenburg, P., Dahl-Hansen, G.A.P., Christensen, G., Faerovig, P.J., et al. 2007. Goose-mediated nutrient enrichment and planktonic grazer control in arctic freshwater ponds. Oecologia **153**: 653–662. doi:10.1007/s00442-007-0770-7. PMID: 17609984.

Van Zuiden, T.M., Chen, M.M., Stefanoff, S., Lopez, L., and Sharma, S. 2016. Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. Divers. Distrib. **22**: 603–614. doi:10.1111/ddi.12422.

Vander Zanden, M.J., and Vadeboncoeur, Y. 2020. Putting the lake back together 20 years later: what in the benthos have we learned about habitat linkages in lakes? Inland Waters **10**(3): 305–321. doi:10.1080/20442041.2020.1712953.

Vanderploeg, H.A., Ludsin, S.A., Cavaletto, J.F., Höök, T.O., Pothoven, S.A., Brandt, S.B., et al. 2009a. Hypoxic zones as habitat for zooplankton in lake erie: refuges from predation or exclusion zones? J. Exp. Mar. Biol. Ecol. **381**: S108–S120. doi:10.1016/j.jembe.2009.07.015.

Vanderploeg, H.A., Ludsin, S.A., Ruberg, S.A., Höök, T.O., Pothoven, S.A., Brandt, S.B., et al. 2009b. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in lake erie. J. Exp. Mar. Biol. Ecol. **381**: S92–S107. doi:10.1016/j.jembe.2009.07.027.

Vasconcelos, F.R., Diehl, S., Rodríguez, P., Karlsson, J., and Byström, P. 2018. Effects of terrestrial organic matter on aquatic primary production as mediated by pelagic–benthic resource fluxes. Ecosystems **21**(6): 1255–1268. doi:10.1007/s10021-017-0217-x.

Vigneron, A., Cruaud, P., Langlois, V., Lovejoy, C., Culley, A.I., and Vincent, W.F. 2020. Ultra-small and abundant: candidate phyla radiation bacteria are potential catalysts of carbon transformation in a thermokarst lake ecosystem. Limnol. Oceanogr. Lett. **5**: 212–220. doi:10.1002/lol2.10132.

Vigneron, A., Cruaud, P., Lovejoy, C., and Vincent, W.F. 2022. Genomic evidence for functional diversity in DPANN archaea, from oxic species to anoxic vampiristic consortia. ISME Commun. **2**: 4. doi:10.1038/s43705-022-00088-6.

Vigneron, A., Lovejoy, C., Cruaud, P., Kalenitchenko, D., Culley, A., and Vincent, W.F. 2019. Contrasting winter versus summer microbial communities and metabolic functions in a permafrost thaw lake. Front. Microbiol. **10**: 1656. doi:10.3389/fmicb.2019.01656. PMID: 31379798.

Vincent, W.F. 2018. *Lakes: A Very Short Introduction*. Oxford University Press, Oxford, UK.

Vincent, W.F. 2020. Arctic climate change: local impacts, global consequences, and policy implications. In *Palgrave Handbook of Arctic Policy and Politics*. *Edited by* K. Coates and C. Holroyd. Palgrave Macmillan, London, UK. pp. 507–526. doi:10.1007/978-3-030-20557-7_31.

Vincent, W.F., and Hobbie, J.A. 2000. Ecology of arctic lakes and rivers. In: The Arctic: Environment, People, Policies. *Edited by* M. Nuttall and T.V. Callaghan, Harwood Academic Publishers, UK. pp. 197–231.

Vincent, W.F., and Smol, J.P.(eds). 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnol. Oceanogr. **54**(6): 2273–2564.

Vincent, W.F., Canário, J., and Boike, J. 2019. Understanding the terrestrial effects of arctic sea ice decline. Eos, **100**. doi:10.1029/2019EO128471.

Vincent, W.F., MacIntyre, S., Spigel, R.H., and Laurion, I. 2008. The physical limnology of high latitude lakes. In: Polar Lakes and Rivers – Limnology of Arctic and Antarctic Aquatic Ecosystems. *Edited by* W.F. Vincent and J. Laybourn-Parry. Oxford University Press, Oxford, UK.

Vincent, W.F., Whyte, L.G., Lovejoy, C., Greer, C.W., Laurion, I., Suttle, C.A., et al. 2009. Arctic microbial ecosystems and impacts of extreme warming during the international polar year. Polar Sci. **3**: 171–180. doi:10.1016/j.polar.2009.05.004.

Voigt, C., Marushchak, M.E., Abbott, B.W., Biasi, C., Elberling, B., Siciliano, S.D., et al. 2020. Nitrous oxide emissions from permafrost-affected soils. Nat. Rev. Earth Environ. **1**: 420–434. doi:10.1038/s43017-020-0063-9.

Vonk, J.E., Mann, P.J., Davydov, S., Davydova, A., Spencer, R.G.M., Schade, J., et al. 2013. High biolability of ancient permafrost carbon upon thaw. Geophys. Res. Lett. **40**: 2689–2693. doi:10.1002/grl.50348.

Vonk, J.E., Tank, S.E., and Walvoord, M.A. 2019. Integrating hydrology and biogeochemistry across frozen landscapes. Nat. Commun. **10**: 5377. doi:10.1038/s41467-019-13361-5.

Vonk, J.E., Tank, S.E., Bowden, W.B., Laurion, I., Vincent, W.F., Alekseychik, P., et al. 2015. Reviews and syntheses: effects of permafrost thaw on arctic aquatic ecosystems. Biogeosciences **12**: 7129–7167. doi:10.5194/bg-12-7129-2015.

Walter Anthony, K., Daanen, R., Anthony, P., Schneidervon Deimling, T., Ping, C.-L., Chanton, J.P., and Grosse, G. 2016. Methane emissions proportional to permafrost carbon thawed in arctic lakes since the 1950 s. Nat. Geosci. **9**: 679–682. doi:10.1038/ngeo2795.

Walvoord, M.A., and Kurylyk, B.L. 2016. Hydrologic impacts of thawing permafrost—A review. Vadose Zone J. **15**(6): 1–20. doi:10.2136/vzj2016.01.001.0.

Walvoord, M.A., and Striegl, R.G. 2007. Increased groundwater to stream discharge from permafrost thawing in the yukon river basin: potential impacts on lateral export of carbon and nitrogen. Geophys. Res. Lett. **34**: L12402. doi:10.1029/2007GL030216.

Walvoord, M.A., Voss, C., Ebel, B., and Minsley, B. 2019. Development of perennial thaw zones in boreal hillslopes enhances potential mobilization of permafrost carbon. Environ. Res. Lett. **14**: 015003. doi:10.1088/1748-9326/aaf0cc.

Walvoord, M.A., Voss, C.I., and Wellman, T.P. 2012. Influence of permafrost distribution on groundwater flow in the context of climate-driven permafrost thaw: example from yukon flats basin, alaska, united states. Water Resour. Res. **48**(7): 1–17. doi:10.1029/2011WR011595.

Wang, J.-J., Lafrenière, M.J., Lamoureux, S.F., Simpson, A.J., Gélinas, Y., and Simpson, M.J. 2018. Differences in riverine and pond water dissolved organic matter composition and sources in canadian high arctic watersheds affected by active layer detachments. Environ. Sci. Technol. **52**: 1062–1071. doi:10.1021/acs.est.7b05506. PMID: 29301070.

Wanninkhof, R. 2014. Relationship between wind speed and gas exchange over the ocean revisited. Limnol. Oceanogr. Methods **12**: 351–362. doi:10.4319/lom.2014.12.351.

Ward, N.D., Bianchi, T.S., Medeiros, P.M., Seidel, M., Richey, J.E., Keil, R.G., and Sawakuchi, H.O. 2017. Where carbon goes when water flows: carbon cycling across the aquatic continuum. Front. Mar. Sci. **4**: 7. doi:10.3389/fmars.2017.0000.

Warner, K.A., and Saros, J.E. 2019. Variable responses of dissolved organic carbon to precipitation events in boreal drinking water lakes. Water Res. **156**: 1–20. doi:10.1016/j.watres.2019.03.036. PMID: 30927627.

Wauthy, M., and Rautio, M. 2020. Permafrost thaw stimulates primary producers but has a moderate effect on primary consumers in subarctic ponds. Ecosphere **11**(6): e03099. doi:10.1002/ecs2.3099.

Wauthy, M., Rautio, M., Christoffersen, K.S., Forsström, L., Laurion, I., Mariash, H.L., et al. 2018. Increasing dominance of terrigenous organic matter in circumpolar freshwaters due to permafrost thaw. Limnol. Oceanogr. Lett. **3**: 186–198. doi:10.1002/lol2.10063.

Wellman, T.P., Voss, C.I., and Walvoord, M.A. 2013. Impacts of climate, lake size, and supra- and sub-permafrost groundwater flow on lake-talik evolution, yukon flats, alaska (USA). Hydrogeol. J. **21**: 281–298. doi:10.1007/s10040-012-0941-4.

Whiteford, E.J., McGowan, S., Barry, C.D., and Anderson, N.J. 2016. Seasonal and regional controls of phytoplankton production along a climate gradient in south-west greenland during ice-cover and ice-free conditions. Arct. Antarct. Alp. Res. **48**(1): 139–159. doi:10.1657/AAAR0015-003.

Wickland, K.P., Aiken, G.R., Butler, K., Dornblaser, M.M., Spencer, R.G.M., and Striegl, R.G. 2012. Biodegradability of dissolved organic carbon in the yukon river and its tributaries: seasonality and importance of inorganic nitrogen. Glob. Biogeochem. Cycles **26**: GB0E03. doi:10.1029/2012GB004342.

Wickland, K.P., Jorgenson, M.T., Koch, J.C., Kanevskiy, M., and Striegl, R.G. 2020. Carbon dioxide and methane flux in a dynamic arctic tundra landscape: Decadal-scale impacts of ice wedge degradation and stabilization. Geophys. Res. Lett. **47**: e2020GL089894. doi:10.1029/2020GL089894.

Wickland, K.P., Waldrop, M.P., Aiken, G.R., Koch, J.C., Jorgenson, M.T., and Striegl, R.G. 2018. Dissolved organic carbon and nitrogen release from boreal holocene permafrost and seasonally frozen soils of alaska. Environ. Res. Lett. **13**(6): 065011. doi:10.1088/1748-9326/aac4ad.

Wik, M., Varner, R.K., Anthony, K.W., MacIntyre, S., and Bastviken, D. 2016. Climate-sensitive northern lakes and ponds are critical components of methane release. Nat. Geosci. **9**: 99–105. doi:10.1038/ngeo2578.

Wild, B., Andersson, A., Bröder, L., Vonk, J., Hugelius, G., McClelland, J.W., et al. 2019. Rivers across the siberian arctic unearth the patterns of carbon release from thawing permafrost. Proc. Natl. Acad. Sci. U.S.A. **116**: 10280–10285. doi:10.1073/pnas.1811797116. PMID: 31061130.

Williamson, C.E., Overholt, E.P., Pilla, R.M., Leach, T.H., Brentrup, J.A., Knoll, L.B., et al. 2015. Ecological consequences of long-term browning in lakes. Sci. Rep. **5**: 18666. doi:10.1038/srep18666. PMID: 26690504.

Williamson, C.E., Saros, J.E., and Schindler, D.W. 2009. Sentinels of change. Science **323**: 887–888. doi:10.1126/science.1169443. PMID: 19213905.

Winfree, M.M., Hood, E., Stuefer, S.L., Schindler, D.E., Cline, T.J., Arp, C.D., and Pyare, S. 2018. Landcover and geomorphology influence streamwater temperature sensitivity in salmon bearing watersheds in southeast alaska. Environ. Res. Lett. **13**(6): 064034. doi:10.1088/1748-9326/aac4c0.

Wolfe, A.P., Baron, J.S., and Cornett, R.J. 2001. Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the colorado front range (USA). J. Paleolimnol. **25**: 1–7. doi:10.1023/A:1008129509322.

Wolfe, B.B., Light, E.M., Macrae, M.L., Hall, R.I., Eichel, K., Jasechko, S., et al. 2011. Divergent hydrological responses to 20th century climate change in shallow tundra ponds, western hudson bay lowlands. Geophys. Res. Lett. **38**: L23402. doi:10.1029/2011gl049766.

Woodward, G., Dybkjær, J.B., Ólafsson, J.S., Gíslason, G.M., Hannesdóttir, E.R., and Friberg, N. 2010. Sentinel systems on the razor's edge: effects of warming on arctic geothermal stream ecosystems. Glob. Change Biol. **16**: 1979–1991. doi:10.1111/j.1365-2486.2009.02052.x.

Wright, D., and Shapiro, J. 1990. Refuge availability: a key to understanding the summer disappearance of daphnia. Freshwat. Biol. **24**: 43–62. doi:10.1111/j.1365-2427.1990.tb00306.x.

Wrona, F.J., Feist, J.D., Lehtonen, D., Kahilainen, K., Forsstrom, L., Amundsen, P.-A., et al. 2013. Freshwater ecosystems. Chapter 13. In *Arctic Biodiversity Assessment*. Arctic Council, Conservation of Arctic Flora and Fauna Working Group, Akureyri, Iceland. pp. 390–433.

Wrona, F.J., Johansson, M., Culp, J.M., Jenkins, A., Mård, J., Myers-Smith, I.H., et al. 2016. Transitions in arctic ecosystems: ecological implications of a changing freshwater system. J. Geophys. Res. Biogeosci. **121**: 650–674. doi:10.1002/2015JG003133.

Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M.J., and Vincent, W.F. 2006. Climate change effects on aquatic biota, ecosystem structure and function. Ambio **35**: 359–369. doi:10.1579/0044-7447 (2006) 35[359:CCEOAB]2.0.CO;2. PMID: 17256640.

Yang, B., Wells, M.G., McMeans, B.C., Dugan, H.A., Rusak, J.A, Weyhenmeyer, G.A., et al. 2020. A new thermal categorization of ice-covered lakes. Geophys. Res. Lett. **48**: e2020GL091374. doi:10.1029/2020GL091374.

Yang, D., Kane, D.L., Hinzman, L.D., Zhang, X., Zhang, T., and Ye, H. 2002. Siberian lena river hydrologic regime and recent change. J. Geophys. Res. Atmos. **107**: 4694. doi:10.1029/2002jd002542.

Yoshikawa, K., and Hinzman, L.D. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near council, Alaska. Permafr. Periglac. **14**: 151–160. doi:10.1002/ppp.451.

Yvon-Durocher, G., Montoya, J.M., Woodward, G., Jones, J.I., and Trimmer, M. 2011. Warming increases the proportion of primary production emitted as methane from freshwater mesocosms. Glob. Change Biol. **17**: 1225–1234. doi:10.1111/j.1365-2486.2010.02289.x.

Zhang, G., and Duan, S. 2021. Lakes as sentinels of climate change on the tibetan plateau. All Earth **33**: 161–165. doi:10.1080/27669645.2021.2015870.

Zhang, X., Bianchi, T.S., Cui, X., Rosenheim, B.E., Ping, C.-L., Hanna, A.J.M., et al. 2017. Permafrost organic carbon mobilization from the watershed to the colville river delta: evidence from $^{14}$C ramped pyrolysis and lignin biomarkers. Geophys. Res. Lett. **44**: 11, 491-11, 500. doi:10.1002/2017GL075543.

Zhang, X., He, J., Zhang, J., Polyakov, I., Gerdes, R., Inoue, J., and Wu, P. 2013. Enhanced poleward moisture transport and amplified northern high-latitude wetting trend. Nat. Clim. Change **3**: 47–51. doi:10.1038/nclimate1631.

Zolkos, S., and Tank, S.E. 2020. Experimental evidence that permafrost thaw history and mineral composition shape abiotic carbon cycling in thermokarst-affected stream networks. Front. Earth Sci. **8**(152): 152. doi:10.3389/feart.2020.00152.

Zolkos, S., Tank, S.E, Striegl, R.G., Kokejl, S.V., Kokoszka, J., Estop-Aragones, C., and Olefeldt, D. 2020. Thermokarst amplifies fluvial inorganic carbon cycling and export across watershed scales on the peel plateau, Canada. Biogeosciences **17**(20): 5163–5182. doi:10.5194/bg-2020-111.

Zolkos, S., Tank, S.E., and Kokelj, S.V. 2018. Mineral weathering and the permafrost carbon-climate feedback. Geophys. Res. Lett. **45**(18): 9623–9632. doi:10.1029.2018GL078748.

Zolkos, S., Tank, S.E., Striegl, R.G., and Kokelj, S.V. 2019. Thermokarst effects on carbon dioxide and methane fluxes in streams on the peel plateau (NWT, Canada). J. Geophys. Res. Biogeosci. **124**: 1781–1798. doi:10.1029/2019JG005038.