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Element cycling and aquatic function in a changing Arctic

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Abstract

Arctic systems are under intense pressure from anthropogenic activities, with climate change in particular inducing rapid change in the interlinked cycling of water and various biogeochemical constituents, and thus also the ecological processes that depend on these cycles. This special issue for *Limnology and Oceanography* explores our changing Arctic, with contributions across the watershed-lake-river-estuary-coastal-open ocean continuum, and foci ranging from physical and chemical processes to food webs. Some specific areas of focus include legacy pollution from mines, greenhouse gas emissions from lakes, riverine fluxes of materials, as well as the balance between primary production and respiration in the water column and benthos in marine systems. While varied in focus, as a collection the papers in this special issue do provide direction into key avenues for future effort. For example, while Arctic systems are historically understudied due to financial and logistical costs, long-term monitoring efforts are clearly critical for documenting change, despite the challenges. In freshwater systems, predicting biogeochemistry, and thus ecology, based on landscape characteristics and lake morphology is an ongoing practice that seems particularly promising for both upscaling and decisions on focusing future research effort. In marine and coastal systems, complementing specific local studies with large-scale cross-disciplinary monitoring programs is clearly required for elucidating long-term trends. While baseline research is critical for documenting the Arctic as it currently stands, and constitutes the majority of current research efforts, ongoing support for long-term observatories and expanding remote sensing capabilities is a fundamental requirement for tracking change.

Water's many remarkable properties (including highest heat capacity, highest heat of vaporization, and second highest heat of fusion of all liquids, universal solvent properties, pH buffering capacity) all contribute to a substance that is inherently resistant to change. This is amply demonstrated in the response of water to anthropogenically derived greenhouse gases, in the manner that bicarbonate-rich oceans absorb and neutralize CO_2 from the atmosphere to partially mitigate warming. The high heat capacity of water also enables oceans to soak up a portion of the heat trapped by greenhouse gases, and then transport that heat around the globe to mitigate local impacts in the tropics. The high heat of vaporization partially minimizes evaporative losses of surface water from soils, lakes, and rivers in a rapidly warming Arctic. The high heat of fusion leads to resistance of phase changes between water, snow, and ice and buffers local atmospheric temperatures. Therefore, when water in its various phases begins to hit thresholds for change, it is an ominous sign for ecological systems and the associated biogeochemical cycles that depend on the constancy of water. The resistance of water to change also enables a corollary effect: once change has occurred, it then reverses slowly. For example, heat once absorbed by surface water is lost slowly, causing effects that last for months to years and fundamentally affect ice cover and stratification regimes in lakes and the open ocean. While ecological systems are typically well adapted to temporary seasonal fluctuations, extended and permanent change adds yet another layer of stress with cascading effects on biogeochemical cycles all throughout the landscape-lake-river-estuary-coast-open ocean continuum.

Although water cycles around the globe have been disrupted by climate change, polar regions and high elevations have been especially vulnerable due to extensive snow and ice, and the positive feedback that occurs with melting, primarily the decrease in albedo. In addition to the general warming climate across the Arctic, there are also numerous localized environmental and ecological changes associated with the phase shifts between snow/ice and liquid water that

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occur with receding glaciers, melting ice sheets, reduced snowpack, changing lake dynamics, thawing permafrost, earlier riverine freshets, and reduced ice cover and thickness in the Arctic Ocean both spatially and temporally. For species that thrive on either side of freezing temperatures, the threshold changes are significant. For example, several marine mammal species rely on multiyear sea ice and are now challenged with significant loss and fragmentation of their habitat (Meier et al. 2014). The loss of ice habitat, also in general, means more pelagic primary production and less ice algal primary production, in addition to greater warming of oceanic surface waters that further propagates this shift in primary production.

However, climate change disrupts many other aspects of the water cycle as well. Altered oceanic currents result in temporal and quantitative shifts in the upwelling of nutrients, and associated changes in advective heat flux further change local climate around those currents. In the Arctic, thawing permafrost changes groundwater flow (Walvoord and Kurylyk 2016), and as woody plants encroach there are shifts in evapotranspiration that impact potential water yields for lakes, streams, and rivers (e.g., Krogh et al. 2017). Changing precipitation patterns also impact areal water yields, and there is evidence that riverine discharge has increased by upward of ~ 10% across the pan-Arctic (Holmes et al. 2018). The coupled increased export of biogeochemically active elements (e.g., Tank et al. 2016; Drake et al. 2018) potentially alters coastal biogeochemistry. Changing temperatures affect stratification patterns and ice coverage in lakes, which in turn impacts lake ecology and elemental cycles. Finally, the phase change of water also impacts its reflective properties. The melting of ice and snow decreases the reflectance resulting in increased heat absorption, which is one of the processes that cause the temperature of the Arctic to increase faster than the global average (Serreze and Barry 2011).

This review takes its cues from the changing water cycle in the Arctic and explores how these fundamental changes affect the ecology and biogeochemistry within the diverse aquatic continuum represented by this special issue: lakes, streams, rivers, coastal zones, through to the open ocean. Some systems have compounded effects between anthropogenically driven climate change and other anthropogenically driven disturbances (e.g., mining, pollution). Effects in some systems represented in this special issue are largely localized, while others have global feedbacks. All Arctic systems are changing in real time and will continue to do so throughout the 21st century.

Changing hydrology of lakes and impacts on biogeochemistry

As the Arctic system warms and experiences altered precipitation and evapotranspiration regimes (e.g., Bring et al. 2016), changes to northern lakes will span the physical, chemical, and biological (e.g., Vincent et al. 2012). Globally, warming is causing broad-scale changes to thermal stratification regimes (Kraemer et al. 2015; Woolway and Merchant 2019), with decreasing winter ice cover and increasing summertime heating resulting in an increased likelihood and duration of stratification (Cadieux et al. 2017). Where warming additionally leads to increased delivery of chromophoric dissolved organic matter to aquatic systems, stronger near-surface absorption of thermal energy from light may further strengthen stratification and lead to shallower mixed layers (Wauthy and Rautio 2020*b*). Where stratification is already established, however, longer ice-free seasons may also enable mixed layers to deepen (Northington et al. 2019). These changes in stratification, while variable depending on the present stratification status of the lake (as governed by latitude, lake depth, and transparency; Lewis 1983; Woolway and Merchant 2019), can lead to pronounced changes in biogeochemistry and ecology. For example, longer duration of stratification in Greenland has been associated with a longer period of hypolimnetic anoxia and greater water column inventories of CH_4 (Cadieux et al. 2017), while strengthened stratification in northern Canadian thaw ponds has been shown to affect zooplankton distribution (Wauthy and Rautio 2020*a*). In contrast, when longer ice-free seasons cause thermoclines to deepen, reduced water column primary production can result (Northington et al. 2019). Perhaps the most striking example of the effects of changing stratification regimes comes from High Arctic lakes that transition from being perennially ice-covered, to briefly losing ice cover during the summer months (e.g., Veillette et al. 2010). As shown by Bégin et al. (2021) in this issue, this transition can enable the complete mixing of a previously stratified lake, and thus lead to cooler lake temperatures, pronounced swings in dissolved oxygen, and increased chlorophyll *a* concentrations.

Closely coupled with changes in summer stratification is the effect of decreasing duration of ice cover on limnological processes during winter. For example, the increase in summer inventories of water column CH_4 described for Greenland lakes, above, was accompanied by a substantial decline in CH_4 buildup under ice as the duration of winter ice cover declined (Cadieux et al. 2017). Similarly, in subarctic Sweden, spring overturn emissions of CO_2 and CH_4 were strongly regulated by the length of wintertime ice cover (Jansen et al. 2019). The impacts of winter physical characteristics on chemical limnological condition are exemplified by the study of Palmer et al. (2021), who show that the wintertime inflow of oxygenated streamwater to a subarctic lake affected by past mining activities substantially reduces the development of water column anoxia. This, in turn diminishes the reductive dissolution of arsenic-bearing iron (oxy)hydroxides and under-ice arsenic concentrations. Although the effect of changing duration of ice cover on lake ecology is overall sparsely studied in Arctic and subarctic lakes, we do expect substantial ecological and biogeochemical effects to occur (Hampton et al. 2017).

As changing stratification and ice cover regimes are altering within-lake processes, changes in precipitation, evapotranspiration, and the flux of water and associated solutes from land will also fundamentally alter waterbody function. Over broad spatial scales, global climate models indicate that the Arctic freshwater cycle is intensifying via increasing precipitation, evapotranspiration, and riverine discharge (Rawlins et al. 2010). At local scales, decreases in water residence time have been documented as a result of glacial melt in glacier-fed lakes (Lehnherr et al. 2018). However, decreasing lake area has also been documented over several broad regions, and attributed, in part, to warming and increased evapotranspiration (Finger Higgens et al. 2019). Such changes in residence time and associated land-water connectivity can have broad-scale biogeochemical implications: for example, changing the composition of dissolved organic matter (DOM) in lakes (Kellerman et al. 2015) as a result of increases in DOM processing enhanced by increasing residence time. In this issue, Laurion et al. (2021) suggest that even in lakes affected by direct inputs of permafrost thaw substrates, dry (i.e., longer residence time) periods may lead to DOM substrate limitation for both microbial and photochemical mineralization. As Richardson et al. (2021) show, longer water residence times are also associated with lower lake water concentrations of total and methyl mercury, and decreases in the ratio of mercury to dissolved organic carbon (DOC), which is an important predictor of the bioavailability of mercury within food webs. These changes were proposed to occur as a result of processes such as increased photodemethylation and sedimentation in lakes with high residence times.

In addition to the effects of changing amounts of water and solutes flowing to lakes from their catchments, permafrost thaw at the margins of lakes is also likely to alter biogeochemistry and ecology. Lake margin thermokarst (i.e., thaw-induced landscape collapse) decreases DOC concentrations in some lake regions (Kokelj et al. 2005) but increases DOC concentrations in others (Wauthy et al. 2018), as determined by soil composition and the ability of mineral soils to bind DOM in these sedimentation-prone environments (e.g., Vonk et al. 2015). Changes in water color that can accompany thaw may have profound effects on stratification and light penetration (Caplanne and Laurion 2008; Watanabe et al. 2011), and therefore also the balance between benthic and pelagic productivity in often-shallow Arctic lakes (Vonk et al. 2015; Kivilä et al. 2019). Several studies in this issue reinforce the profound effect that this changing balance may have on ecological function. For example, Vesterinen et al. (2021) show that benthic macroinvertebrates can serve as a much poorer quality food source for higher trophic levels than their pelagic (zooplankton) counterparts, while Xing et al. (2021) illustrate that benthic, sediment-associated microbial communities have significantly greater richness and phylogenetic diversity than microbes in the water column, in both Greenland and on the Tibetan Plateau. While increases in nutrient loading with thaw (e.g., Tank et al. 2020) may also critically affect aquatic systems, this aspect of changing lake function is only beginning to be investigated (Wauthy and Rautio 2020*b*).

Closely associated with these direct thermokarst-associated effects is our growing realization of the importance of the tied factors of lake origin, evolution, and morphometry for controlling and constraining the chemical and biological response to change in northern lakes. While this principle is well understood generally in temperate lakes and a predominant focus in the limnological sciences (e.g., Kalff 2002), it has been less specifically considered in studies of northern lakes. In this special issue, several authors reinforce this importance of landscape, lake origin, and lake evolution for lake function. For example, Zabelina et al. (2021) show that CO_2 emissions from Bolshezemelskaya (northeastern European) tundra lakes are more strongly determined by lake area than any other parameter, with emissions increasing by over an order of magnitude from large to small lakes. Hughes-Allen et al. (2021) show that greenhouse gas emissions from thermokarst-origin lakes in Central Yakutia (Russia) are inextricably linked to lake age, with recent thermokarst lakes acting as strong CO_2 sources throughout all seasons, whereas hydrologically closed alas lakes (formed via thermokarst processes during the early Holocene warm interval) act as CO_2 sinks during spring and fall, and much more modest CO_2 sources in winter. This finding is similar to earlier work by Anthony et al. (2014), who report that Yedoma thermokarst lakes shift from being CO_2 sources, to CO_2 sinks, as they age over millennia. Finally, Préskienis et al. (2021) further illustrate the importance of lake origin and morphometry for controlling greenhouse gas dynamics, by examining deep kettle lakes, relatively shallow thermokarst lakes, ponds formed over ice-wedge troughs, and ponds formed in the depressions of coalescent polygons in a polygonal tundra landscape of the Canadian High Arctic. These four lake origin types showed consistency in greenhouse gas dynamics within classes, but wide divergence between classes. For example, while coalescent polygon ponds were summer CO_2 sinks, nearby trough ponds were strong summer CO_2 sources. Similarly, CO_2 ages ranged from modern (ice wedge trough ponds) to millennial-aged (thermokarst lakes). As described in Préskienis et al. (2021), a better understanding of functional differences among discernable lake types is clearly required for accurate upscaling across Arctic landscapes.

Changing riverine delivery of materials to the coastal ocean

Warming climate will change multiple drivers of riverine fluxes to the Arctic coastal zone. Thawing permafrost and subsequent leaching and erosion releases both organic and inorganic materials into waterways and alters stream ecology. In this special issue, it is shown that increased sediment loads from thaw slumps resulted in lower macroinvertebrate abundance but higher proportional drift (i.e., higher proportions of macroinvertebrates in drift as compared to the benthos) relative to undisturbed sites (Levenstein et al. 2021). Succession from tundra to more woody plants will change the nature of organic matter released into waterways (e.g., McGowan et al. 2018), will alter evapotranspiration (Raz-Yaseef et al. 2017) thereby impacting runoff yields (Krogh et al. 2017), and will likely alter nutrient retention efficiency by the landscape, thus changing nutrient release to waterways (e.g., McGowan et al. 2018). Changing precipitation patterns will also lead to alterations in both the timing and amount of riverine discharge. Earlier spring thaw and later fall freeze-up will increase the growing season, creating a domino effect related to riverine constituents. The fate of newly released organic matter and nutrients depends in part on in situ processing within the rivers (Rocher-Ros et al. 2021). However, the timing and magnitude of at least one of those in situ processes, gross primary production, depends on the interplay between early and late season release of nutrients from the landscape when there is adequate light availability (Myrstener et al. 2021). Nevertheless, the fundamental driver of varying fluxes of riverine constituents is variation in river discharge.

A number of studies have characterized changing discharge in various Arctic rivers. McClelland et al. (2006) estimated 11–14% increases in Eurasian river discharge to the Arctic Ocean from 1964 to 2000, but a decrease from North American rivers both to the Arctic Ocean (~ 4%) and to the Hudson, James, and Ungava Bays (~ 12%). A more recent analysis of 72 Arctic rivers from 1975 to 2015 confirms the increasing discharge from Eurasian rivers but also found that North American rivers now have a net increase as well (Durocher et al. 2019). One prominent message is that regional differences are significant and will need to be carefully analyzed when estimating current and future fluxes of riverine constituents. For example, in this issue, high-resolution headwater stream measurements demonstrate that in some catchments, DOC correlates to discharge while nitrate does not, but that the reverse is observed in other catchments (Shogren et al. 2021). Additional concerns include variations in the length of time analyzed as well as the influence of regular climate cycles (e.g., Pacific Decadal Oscillation) that may obscure trends that are due to anthropogenic forcing. For example, expanding the analyzed record for the Mackenzie River to 1939–2013 provides an estimation of increasing discharge of about 1.5% per decade, but the Pacific Decadal Oscillation can be responsible for changes in discharge of 25–30% across a 10-yr period from major tributaries to the Mackenzie River (Rood et al. 2017).

Primary drivers for increased discharge have focused on increasing precipitation, thawing permafrost, and mass loss of glacial ice. Across the time period 1971–2017, precipitation in the Arctic appears to be increasing at a rate of 1.5–2% per decade, with greater increases during the cold months compared with warm months (Box et al. 2019). In contrast, glacial ice mass loss from 2003 to 2015 in the Arctic has been estimated at 421 $\mathrm{km}^3\ \mathrm{yr}^{-1}$ (Box et al. 2018), which represents approximately 10% of total riverine discharge to the Arctic. However, > 60% of the ice mass loss is from Greenland (Cazenave et al. 2018), so a more realistic average increased contribution of glacial ice to Arctic rivers if excluding Greenland is approximately 4%, with the obvious caveat that the contribution to any individual river will depend on the relative amount of glacial ice mass within the watershed. There has been less research on the contributions of thawing permafrost to increased runoff, at least from a mass balance perspective. The impacts of thawing permafrost on changing flowpaths from surface runoff to groundwater runoff undoubtedly changes water residence times and yields from the landscape, but quantifying the release of water from permafrost as ice melts has been poorly addressed. The National Snow and Ice Data Center indicates that if all the permafrost in the world is thawed, it would release enough water to raise global sea levels by 3–10 cm (https://nsidc.org/cryosphere/frozenground/climate.html, 24 January 2021), which corresponds to approximately 11,000–36,000 Gt of water. If 40% of this stored water is released by the end of the century, as projected in some models (e.g., Chadburn et al. 2017), this amount would correspond to approximately 55–180 $\mathrm{km}^3\ \mathrm{yr}^{-1}$ contributions to the hydrologic cycle, or 1–4% of average Arctic riverine discharge.

Counterbalancing increased inputs of water to the landscape are potential increases in evapotranspiration, due to increasing temperature, residence times, changing winds (e.g., La Sorte and Fink 2017), and changes in vegetation. The role of vegetation was captured by a study on the north slope of Alaska, in which average evapotranspiration varied in 2013 from 0.008 $\mathrm{mm\ h}^{-1}$ for shrubs up to 0.027 $\mathrm{mm\ h}^{-1}$ for moss, a threefold variation across a single season (Raz-Yaseef et al. 2017). Evapotranspiration values for 2014 were higher, with moss and open water evapotranspiration at 0.040 $\mathrm{mm\ h}^{-1}$ and 0.039 $\mathrm{mm\ h}^{-1}$, respectively, while bare soil and lichens were both measured at 0.021 $\mathrm{mm\ h}^{-1}$, with intermediate rates for sedges (0.027 $\mathrm{mm\ h}^{-1}$) and grasses (0.030 $\mathrm{mm\ h}^{-1}$) (Raz-Yaseef et al. 2017). The well-documented concept of a "greening Arctic" (e.g., Myers-Smith et al. 2020) in combination with these data shows the large potential for changing evapotranspiration associated with climate change to affect the amount of precipitation that flows into streams and rivers (Krogh et al. 2017). Additionally, a greening Arctic will fundamentally change the composition of organic matter discharged to streams as well as nutrient cycling (e.g., McGowan et al. 2018).

Elucidating the cascading effects of a single phenomenon such as the greening Arctic highlights the intertwined and complex interactions between hydrological, ecological, and biogeochemical systems as it relates to changing riverine fluxes. Cross-site and cross-constituent variation in concentration-discharge relationships, coupled with changing flow paths and uptake due to warming means that discharge that increases 10% may cause either synergistic or antagonistic changes in constituent flux. This disconnect is shown nicely in this issue by contrasting changes in concentrations with seasonal discharge between three headwater systems (Shogren et al. 2021). More broadly, a frequently stated hypothesis has suggested that climate-change-induced increases in fluxes of Arctic riverine DOC would likely derive a significant proportion from thawing permafrost and the concomitant release of frozen organic matter. Thus, even for watersheds with similar discharge, those with higher relative amounts of thawing permafrost might yield larger DOC increases. However, research specifically aimed at quantifying permafrost carbon at the mouths of rivers has largely failed to identify DOC with a permafrost signature (e.g., Raymond et al. 2008; Spencer et al. 2015), and bio- and photolability experiments suggest that released permafrost carbon can often be highly labile (e.g., Mann et al. 2015). Complex interactions between DOC and sediments (Groeneveld et al. 2020), and flow paths (Walvoord and Striegl 2007), and the superimposed effects of temperature and changing vegetation on the flux of carbon from land to water (Laudon et al. 2012) also come into play. Conversely, larger sediment loadings from permafrost thaw are likely to be more persistent (Kokelj et al. 2020), especially in areas of thermokarst, and nutrients and dissolved ions may be increasing more universally (Tank et al. 2020). Characterizations of discontinuous vs. continuous permafrost, the formation of taliks, and regional differences in landscape characteristics all indicate that there has not been and will not be a single universal response to changes in groundwater flow, groundwater discharge, or the relative timing and efficiencies of land–water transfer of biogeochemical constituents related to permafrost thaw (Vonk et al. 2019).

Characterizing the pan-Arctic riverine response to climate change is hampered by differences in scale between the most and least studied systems. The six largest rivers have been comparatively well studied, and generate about half the total discharge, depending on how the pan-Arctic region is defined, but these rivers include large proportions of taiga (boreal forests) and nonpermafrost landscape. The remaining river discharge comes from much smaller rivers that largely drain tundra, with at least one study estimating areal yields of DOC that are a third less in these smaller tundra rivers compared to the six largest rivers (Lobbes et al. 2000), while another study demonstrates the potential for significantly higher DOC yields from a mid-sized high latitude river (Johnston et al. 2018). Contrasting findings such as these once again emphasize the heterogeneous changes in delivery of river-borne constituents to the coastal ocean. There are also two modes of permafrost thaw that are likely to have differing effects on riverine loads. While thermal changes are more likely to release dissolved constituents, including DOC, physical disturbances that accompany thawing can result in proportionally greater loading of particulate organic carbon (POC) and sediments (Beel et al. 2020). Similarly, identifying changes in fluxes of Arctic riverine material and attributing them specifically to climate change is challenging, due to interannual variability and the lack of long-term chemical measurements with consistent methodology. Several studies have utilized a space-for-time approach to predict what will happen in the future by spanning their research across north–south transects that include both permafrost-affected and permafrost-free zones. A study in western Siberia compared stream water chemistry in permafrost-influenced catchments to permafrost-free catchments and found statistically higher concentrations of dissolved organic nitrogen, total dissolved nitrogen, and total dissolved phosphate in the permafrost-free catchments, thus indicating that a warming climate was likely to increase riverine discharges of all three constituents (Frey et al. 2007). However, subsequent studies of small- to medium-sized rivers (10–100,000 km^2) in this same general region a decade later reached the opposite conclusion, that N, P, Si, K, Ca, dissolved inorganic carbon (DIC), and DOC are all higher in permafrost-affected rivers than permafrost-free rivers and that therefore a warming climate will lead to decreases (Vorobyev et al. 2017). A more recent study, also in the Western Siberian Lowland, further suggests that all of these constituents except DIC and Ca will decrease by factors of two to five (Pokrovsky et al. 2020), and that DIC, Ca, SO_4, Sr, Ba, Mo, and U will increase by factors of two to three. A general consensus of space-for-time analyses is that there will be regional variability in whether warming leads to increases or decreases in dissolved constituents, as exemplified by Si for which riverine concentrations are predicted to decrease in western Siberia, while increasing in Alaska (Carey et al. 2020).

While fluxes of riverine materials to the coastal ocean will undoubtedly change, the ultimate impact will depend not just on amounts but on the timing of delivery. Earlier warming and later freezing will increase the timeframe over which surficial soils can release materials to rivers, and hence the coastal zone. A shift in precipitation patterns away from snow and toward rain will dampen the impact of spring freshets (e.g., Ahmed et al. 2020) that can represent up to two thirds of the annual discharge of certain constituents, like DOC (Holmes et al. 2012). Given potential light limitations in how riverine materials are processed and utilized in the coastal ocean, earlier delivery could potentially bypass primary productivity and photooxidation processes in the coastal zone and either move those processes to further out in the ocean or reduce them altogether.

Changing ecology and biogeochemistry in the coastal zone out to the open ocean

The Arctic coastline extends for more than 100,000 km and constitutes at least 35% of the global coastline (Lantuit et al. 2012). The coastline spans 30° of latitude and includes a multitude of coastscapes ranging from deep narrow fjords impacted by glaciers to open sedimentary coasts with lagoons and estuaries. Extending beyond the coast are broad, shallow shelves that encircle the deep central basins and comprise 50% of the area of the Arctic Ocean (Jakobsson et al. 2003). The three domains—coast, shelf, and deep sea—are all forced and connected by lateral transports; with the coastal zone influenced by river outflow while the shelves and deep sea are mainly impacted by currents from the subarctic Pacific and Atlantic oceans (Wassmann et al. 2020). However, the extensive coastal ecosystems surrounding the Arctic Ocean means that no other ocean is as influenced by freshwater and terrestrial processes. For example, the Arctic Ocean holds 1% of global seawater but receives about 11% of terrestrial runoff (McClelland et al. 2012), with its constituents of organic matter, nutrients, contaminants, and particles. Thus, changes in timing and increasing amounts of water flow in the terrestrial and limnic spheres due to climate change intensify and modify the hydrological connectivity between land and sea. In the coastal ocean, the impact of changes on land combines with marine drivers to produce complex dynamics that are highly variable in space and time. The spring freshet may last just a few weeks (McClelland et al. 2016; Citterio et al. 2017) and together with concurrent melting of sea ice this induces steep physical and biogeochemical gradients within the coastal zone (Mortensen et al. 2011; Carmack et al. 2015; Dezutter et al. 2021). The timing and the extent of this annual event has important implications for the overall structure and function of both the benthic and pelagic ecosystem (Sejr et al. 2010; Middelboe et al. 2018; Matsuno et al. 2020).

Productivity serves as a key ecosystem function that is affected by light and nutrient availability for primary producers and the availability of allochthonous and autochthonous organic matter for secondary producers. The decrease in duration and extent of sea ice cover can improve light availability for marine primary producers, and increase productivity in the open ocean (Lewis et al. 2020). However, decreased sea ice cover also increases fetch, coastal erosion, and sediment resuspension in shallow areas, which together with turbid riverine runoff and wind-driven mixing, counteract the otherwise enhanced light availability following reduced time of ice coverage (Murray et al. 2015; Bonsell and Dunton 2018). To further complicate projections of climate change effects, succession and photoadaptive response of pelagic primary producers might induce nonlinear responses in pelagic productivity (Croteau et al. 2021). The impact of meltwater on nutrient availability in Arctic marine systems is also complex. In general, meltwater increases stratification that limits vertical mixing and thus nutrient replenishment to the photic zone (Tremblay and Gagnon 2009; Randelhoff et al. 2020). However, meltwater released from the base of tidewater glaciers results in buoyancy-driven upwelling that increases nitrate input to the photic zone (Cape et al. 2019), which in turn can increase primary and secondary production (Meire et al. 2017). Thus, the accelerated melting of ice sheets and glaciers is likely an important local driver for change in coastal ecosystems.

Large areas of the seabed along the Arctic coastline receive sufficient light to sustain benthic primary production (Gattuso et al. 2020) and an increasing number of reports document significant contributions of benthic primary production to system production in Arctic settings (Glud et al. 2002, 2009; Attard et al. 2016). Benthic primary production is generally less constrained by nutrient limitation due to greater supply of nutrients at depth and from the sediment. Depending on the substratum and water depth, the seabed might be covered by microalgae, macroalgae, seagrasses, or crustose corallines all contributing to the sustenance of local and deeper benthic food webs via lateral transport (Wiedmann et al. 2020). Clearly, the biological and biogeochemical function of shallow water settings in the future will depend on the extent to which environmental changes favor pelagic or benthic primary production. Ongoing hydrological, physical, and biogeochemical changes appear to stimulate the northward migration and areal expansion of seagrass and macroalgae (Kortsch et al. 2012; Krause-Jensen et al. 2020) and the growth of resilient crustose corallines (fundamental ecosystem engineers in deeper waters) (Williams et al. 2021). Thus, predictions for the future Arctic need to better address the importance of benthic primary producers and the energy they provide for coastal food webs and constrain the regional variability in their response to ongoing environmental changes.

In addition to influencing light and nutrient availability for autochthonous primary production, freshwater runoff from land also contributes allochthonous organic matter to the coastal zone, where it can be an important food source for marine organisms (Paulsen et al. 2017; Harris et al. 2018; Bridier et al. 2021). The mobilization and transport of organic matter stored in melting glaciers and permafrost is expected to affect carbon cycling in the coastal zone, but effects are generally poorly constrained. However, in the East Siberian Shelf, the input of bioavailable organic matter from land results in coastal waters that are oversaturated with CO_2 (Anderson et al. 2009) and consequently low in pH (Semiletov et al. 2016). The amount of organic matter stored in ice sheets and glaciers is orders of magnitude lower than in permafrost (Wadham et al. 2019) but may still be important for local systems due to the high bioavailability (Hood et al. 2009; Hopwood et al. 2020).

Benthic fauna play a crucial role for coastal carbon cycling (Blicher et al. 2009; Renaud et al. 2015) and can be responsible for more than 50% of the benthic O_2 uptake (Glud et al. 1998, 2000; Grebmeier et al. 2006). This uptake partly reflects faunal respiration and partly an enhanced O_2 supply due to bioturbation that allows for microbially driven aerobic mineralization. Bioturbation markedly stimulates the reoxidation of reduced constituents from anaerobic microbial carbon mineralization and irrigation creates a complex three-dimensional mosaic of redox zones in the upper sediment (Berg et al. 2001; Jørgensen et al. 2005). The net effect is an overall enhancement of organic carbon mineralization, microbially driven removal of bioavailable nitrogen, entrapment of phosphorous, and an increased sulfide buffer capacity in the sediment (Aller and Cochran 2019). These are all biogeochemical functions that are essential for sustaining diverse and healthy coastal ecosystems. However, enhanced surface production and terrigenous runoff due to climate-driven changes in ice and terrestrial hydrology are expected to increase sedimentation rates, which could potentially lead to benthic O_2 depletion (Berg et al. 2003). Such a scenario would have profound impacts on the benthos and induce dramatic step-changes in the biogeochemical function of coastal Arctic sediments. For instance, enhanced levels of free sulfide following increased anaerobic mineralization would be detrimental for benthic communities and stimulate internal N and P loading. The efficiency of benthic mineralization regulates the long-term carbon sequestration in marine systems (Canfield 1994). However, despite relatively high productivity and permanently low temperatures, microbial communities of Arctic sediments appear highly efficient in remineralizing deposited organic material. The involved pathways for organic carbon mineralization and carbon sequestration rates in the Arctic appear similar to those at warmer latitudes (Glud et al. 1998; Jørgensen et al. 2021). This partly reflects the activity of well-adapted microbial communities that maintain high metabolic rates and growth yields at low ambient temperature (Sagemann et al. 1998; Robador et al. 2015; Scholze et al. 2021).

As noted, glacier dynamics and the position of the glacial terminus is fundamental to the biological and biogeochemical function of many Arctic fjords. Detailed long-term investigations in Svalbard have clearly documented how spatiotemporal dynamics in glacial-induced upwelling, surface production and deposition shape the benthic communities and the relative importance of the respective diagenetic pathways for carbon mineralization (Jørgensen et al. 2021). Reduced benthic supply of metal oxides and enhanced marine influence following glacial retreat is expected to transform benthic redox conditions from well-oxidized iron-rich environments to sulfidic sediments (Jørgensen et al. 2021), which will have detrimental environmental consequences for benthic and coastal food webs.

Beyond the coast, the shelves are experiencing loss of sea ice cover, and in some regions there is also increased inflow of water from the Atlantic and the Pacific (Polyakov et al. 2020). The implications of these factors include changing nutrient dynamics, altered productivity, and shifts in the pelagic food web structure including species composition and relative abundance (Fossheim et al. 2015; Møller and Nielsen 2020). Calanoid copepods are a key node in Arctic marine food webs and it is therefore essential to parameterize their role in pelagic energy flow (Thingstad et al. 2021). Ongoing environmental change is shifting calanoid communities from lipid-rich high Arctic species to smaller and less nutritious lower latitude species (Carstensen et al. 2012; Henriksen et al. 2012)—a shift that is likely to have important negative implications for top predators such as fish, mammals, and birds in the region (Laidre et al. 2008). The succession of calanoid species due to ongoing climate change is complex and recent work has suggested that cross-species hybridization might occur (Parent et al. 2012). However, this hypothesis has since been challenged and the debate is ongoing (Choquet et al. 2021). Nevertheless, understanding the responses of zooplankton communities toward increasing temperature, changes in stratification, changes in sea-ice coverage, and changes in productivity is essential for projecting ecosystem responses at higher trophic levels and the effects of pelagic-benthic coupling.

The Arctic Ocean holds extensive areas of deep sea that are currently undergoing transformation from permanently ice-covered to seasonally ice-free (Laxon et al. 2013; Overland and Wang 2013). Reduced sea ice cover and freshening of the open ocean will fundamentally change the oceanographic conditions, light availability, and nutrient balance of the surface ocean (Polyakov et al. 2020; Downes et al. 2021). These changes will have substantial implications for pelagic productivity, food web structure (Brown et al. 2020; Piontek et al. 2021; Schanke et al. 2021), and ultimately for the supply of organic material to deep sea benthos (Nöthig et al. 2020; Wiedmann et al. 2020). Generally, the changes are expected to enhance production, turnover, and deposition of organic matter—in particular during the summer months, but responses will vary extensively among regions (Brown et al. 2020; Wassmann et al. 2020). For example, enhanced freshening of the Pacific sector presumably will lead to intensified stratification within the Amerasian Basin, while the Eurasian basin will mainly be affected by enhanced inflow of warmer Atlantic water (Brown et al. 2020). Complex shifts in surface ocean dynamics may regionally affect the atmospheric exchange of greenhouse gasses such as N_2O and CO_2 with potential implications for climate feedbacks and ocean acidification (Torstensson et al. 2021; Zhan et al. 2021). The transformation from a multiyear-ice dominated region to first-year ice environments will presumably induce seasonal biological hot spots along dynamic marginal ice zones with increased importance of ice algae production and deposition, potentially stimulating the nutritional supply to deep-sea communities (Boetius et al. 2013). However, current assessments of carbon deposition in the deep Arctic Ocean do not match the apparent carbon demand, demonstrating how little is known about the present status of nutritional supplies to deep sea communities, let alone projecting their responses to the ongoing transformation of the Arctic Ocean (Wiedmann et al. 2020).

Feedbacks and scaling

Two challenges in Arctic research have been and continue to be (1) determining the extent to which localized research environments represent the greater Arctic, and (2) overcoming the short funding timescales that make it challenging to distinguish between interannual variability and climate change impacts. These limitations on scaling to the entire system also affect our collective ability to evaluate both the magnitude and direction of feedbacks.

Several studies cited in this review have highlighted the heterogeneity of the pan-Arctic and caution against upscaling regional studies to the entire Arctic (e.g., Shogren et al. 2021; Préskienis et al. 2021; Xing et al. 2021). Nevertheless, the time series measurements on major Arctic rivers initiated through the PARTNERS (Pan Arctic River Transport of Nutrients, Organic Matter, and Suspended Sediments) project and continued through Arctic-GRO (Arctic Great Rivers Observatory) (McClelland et al. 2008) have revealed several measurements and trends that do seem to hold across diverse environments, at least at the watershed outlet scale. Among dissolved constituents and properties, these include similar correlation slopes between the absorption coefficient at 350 nm and both DOC and dissolved lignin concentration, similar relationships between lignin compositions and multiple linear regression of several optical parameters, and similar seasonal trends across systems in composition (Mann et al. 2016). These results allow for higher resolution sampling on a single river like the Yukon to be scaled to Arctic Ocean turnover times for terrestrial DOM inputs (Spencer et al. 2009). Among particulate constituents, broad similarities between the major rivers include the seasonality of C : N, radiocarbon, and C and N stable isotope ratios, although significant geological differences are captured by POC concentrations that are 4–5 times higher in the Yukon River compared to the Yenisey River (McClelland et al. 2016).

Despite these similarities in seasonal patterns and compositional relationships, differences in yields of DOC (Holmes et al. 2012), POC (McClelland et al. 2016), and ions (Tank et al. 2012) point to the importance of understanding landscape variation even when these constituents are integrated over broad spatial scales. Similarly, smaller rivers draining to the Arctic Ocean are dominated by tundra and permafrost, with areal yields of DOM about 50% greater in the largest six rivers compared to smaller rivers in one study (Lobbes et al. 2000), but the opposite in yet another northern high latitude mid-sized river (Johnston et al. 2018), highlighting the need to measure across all significant landscapes in order to characterize current baseline conditions. Under a warming climate, changes and feedbacks between permafrost and tundra compared to boreal forests (taiga) will likely look quite different. It will be critical to characterize the relative impacts of changing groundwater flow, released frozen soil organic matter, and increased (woody) vegetation as part of an overall greening trend in the tundra, compared to increased biomass potential countered by more rapid cycling in boreal forests.

While ongoing studies in large rivers have generated important biogeochemical datasets that are not included in long-term gauging measurements, the basic hydrological data provided by long-term gauging stations allow for the calculation of changing material fluxes that accompany climate change. The fate of biogeochemical constituents is inextricably tied to the amounts and flow of water, with general increasing discharge leading to a freshening of the Arctic Ocean and potentially decreasing the residence time of terrestrial materials before they are exported to lower latitudes either at the surface or in deep-water formations. Similarly, while changes in concentration-discharge relationships certainly are possible with changing climate, they are less likely to have the same magnitude of effect as the broad changes in discharge that will almost certainly change the amount, and seasonality, of land-to-ocean constituent flux, given the strong relationship between discharge and many biogeochemical parameters.

Long-term ecological research (LTER) sites are another means of capturing climate change effects vs. interannual variability, with multiple land-based LTERs above the Arctic Circle located in Alaska (Arctic LTER and Beaufort Lagoon Ecosystem), Sweden (Abisko), and Greenland (Greenland Ecosystem Monitoring Program [GEM]). Research at Abisko spans back over 100 yr, the Arctic LTER (i.e., Toolik Lake) and GEM span more than three decades, while the Beaufort Lagoon Ecosystem was only awarded in 2017. The extended history at these sites have led to several findings related to climate change, including the advancement of spring (Høye et al. 2007), freshening of coastal waters (Sejr et al. 2017), complex dynamics between sea ice and underwater light climate (Bonsell and Dunton 2018), increasing nitrate concentrations in the Kuparuk River (McClelland et al. 2007), changes in the competitive balance of soil nutrient assimilation by microbes and plants (Schmidt et al. 2002; McClelland et al. 2007), decrease in vegetation species richness (Chapin et al. 1995), and differences in aboveground biomass, with some sites and vegetation types more responsive (generally increasing) than others (Kennendy 1984; Van Wijk et al. 2004). However, the particular biomes at each of the three stations are not necessarily expandable to the vast majority of the Arctic, and one recent study highlighted the patchiness of climate change research in the Arctic, noting that nearly a third of all studies comes from either the Toolik or Abisko sites (Metcalfe et al. 2018).

To understand ongoing climatic responses in open-ocean regions and the Arctic deep sea, ocean-based LTERs such as the HAUSGARTEN observatory in the Fram Strait are essential (Soltwedel et al. 2016). Here chemical, biological, and physical parameters are measured at 21 permanent sampling sites at a depth range of 250–5500 m to monitor changing conditions. Maintaining this LTER is resource demanding, but is a visionary endeavor that is being expanded by the FRAM (FRontiers in Arctic Marine Monitoring) project that will establish an integrated underwater infrastructure to enable synchronous year-round observations from surface to depth in the remote Arctic (Soltwedel et al. 2013).

More recently, remote sensing has become a critical tool in upscaling studies both temporally and spatially. For example, Fichot et al. (2013) developed an algorithm to determine a pan-Arctic distribution of terrestrial DOM in the Arctic Ocean and used a retrospective analysis to determine changing flow patterns in riverine plume waters with potential implications for incorporation of riverine DOM in North Atlantic Deep Water. Matsuoka et al. (2017) modeled pan-Arctic DOC concentrations (± 28%) by ground-truthing remote sensing data with field samples from multiple cruises. They highlight the potential for coupling remotely sensed DOC estimates across space and time with riverine discharge data to evaluate changing trends in DOC fluxes in the Arctic Ocean. Remote sensing has also been critical for determining chlorophyll and primary production in the Arctic Ocean; however, there still remain several challenges for resolving remote sensing estimates with that of three dimensional coupled physical–biological ocean numerical models (Babin et al. 2015). In the terrestrial environment, remote sensing has been instrumental in scaling process studies on the greening of the tundra to pan-Arctic estimates of whether or not the tundra will be a net sink for carbon (increased sequestration in biomass) or whether that will be partially or totally offset by increases in CH_4 emissions (Sitch et al. 2007).

NASA has increasingly supported remote sensing efforts in the Arctic, with field campaigns to the Chukchi and Beaufort Seas (Impacts of Climate change on the Eco-Systems and Chemistry of the Arctic Pacific Environment, i.e., ICESCAPE; https://espo.nasa.gov/icescape/content/ICESCAPE_0, 24 January 2021), a terrestrial field campaign to Alaska (Arctic Boreal Vulnerability Experiment, i.e., ABoVE; https://above.nasa.gov, 24 January 2021) that incorporated significant airborne sensors, and a proposed field campaign centered at the land–ocean interface (Arctic-COastal Land Ocean InteRactionS, i.e., Arctic-COLORS). Arctic-COLORS would invest heavily in ground-truthing remote sensing data with biogeochemical data collected from rivers and the near-coastal region spanning from the Yukon River to the Mackenzie River, with the potential for international partnerships to extend the regions into other areas of the Arctic (https://arctic-colors.gsfc.nasa.gov, 24 January 2021).

An overall goal of scaling is to accurately model and predict the direction and magnitude of climate change feedbacks. The Sitch et al. (2007) review, for example, highlights the necessity of getting the correct balance between carbon sequestration and CH_4 production in a greening tundra. However, the overall heterogeneity of the terrestrial environment and associated issues with scaling make it very challenging to determine feedback responses related to shifting aquatic ecology and biogeochemistry. Within this special issue, most studies focus on current or potential climate change effects, but the uncertainty in scaling precludes an accurate determination as to how those effects would translate quantitatively into a feedback. The best example of a feedback prediction might be the study of Zabelina et al. (2021), which concludes that small ponds emit smaller areal fluxes of greenhouse gasses than large thermokarst lakes, and that if large lakes become less dominant with permafrost thaw (Smith et al. 2005), the overall effect will be a net negative feedback.

Another challenge in determining feedbacks within Arctic systems is simply the dearth of data across a sufficient length of time to determine statistically meaningful climate change trends. Therefore, the stated objective of multiple studies within this special issue was simply to establish baselines (e.g., Dezutter et al. 2021; Downes et al. 2021). This work underscores the importance of tying into long-term datasets or constructing and improving remote sensing products to enable hindcasting for the measurements where this is possible, and investing in long-term monitoring of the ecological and biogeochemical parameters that are not well suited for measurement by proxy, such as microbial community structure or molecular biomarkers.

As described at the outset, our review takes its cues from the changing water cycle in the Arctic, and explores the effect of coupled climate-hydrologic changes on the ecology and biogeochemistry of diverse freshwater to marine environments across the aquatic continuum. While one clear conclusion from the myriad papers in this special issue is the need to continue—and even redouble—our efforts to understand the ecological and biogeochemical functioning of this rapidly changing region, broad patterns across the diverse special issue contributions highlight a number of avenues for future focus. In freshwater systems, for example, multiple studies indicated the possibility for predicting biogeochemical and ecological responses based on landscape (rivers and lakes) and morphological (lakes) characteristics (e.g., Hughes-Allen et al. 2021; Richardson et al. 2021; Shogren et al. 2021; Préskienis et al. 2021). Although these drivers may vary across ecoregions, they are critical to consider for upscaling efforts, and should be further investigated—in particular the potential for integrating two or more fundamental variables into remote sensing products. In marine environments, we still only have rudimentary insight of spatiotemporal dynamics that compromise our ability to project system scale or pan-Arctic response toward ongoing climate change. There is a clear need to complement specific local studies with large-scale cross-disciplinary monitoring programs to fully resolve long-term trends. Work in this special issue comes from both long-term observatories (Shogren et al. 2021), and regions that are much more sparsely investigated (Zabelina et al. 2021). Continued effort on increased and more representative coverage across the Arctic region is critical for understanding the diversity of biogeochemical and ecological response to change, and could be directed by the relative importance of drivers highlighted in this special issue. An additional challenge to consider is the need for cross-disciplinary studies that fully integrate components of the Earth System. Finally, while baseline research is an absolute necessity for documenting the Arctic as it currently stands and constitutes the bulk of the papers in this special issue, ongoing support for long-term observatories is critical for tracking change. Our work is clearly still underway.

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Conflict of Interest

None declared.

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