

ORIGINAL ARTICLE

Arctic freshwater biodiversity: Establishing baselines, trends, and drivers of ecological change

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Abstract

1. Climate change is predicted to have dramatic effects on Arctic freshwater ecosystems through changes to the abiotic template that are expected to influence biodiversity. Changes are already ongoing in Arctic systems, but there is a lack of coordinated monitoring of Arctic freshwaters that hinders our ability to assess changes in biodiversity.
2. To address the need for coordinated monitoring on a circumpolar scale, the Arctic Council working group, Conservation of Arctic Flora and Fauna, established the Circumpolar Biodiversity Monitoring Program, which is an adaptive monitoring program for the Arctic centred around four ecosystem themes (i.e., Freshwater, Terrestrial, Coastal, Marine). The freshwater theme developed a monitoring plan for Arctic freshwater biodiversity and recently completed the first assessment of status and trends in Arctic freshwater biodiversity.
3. Circumpolar Biodiversity Monitoring Program–Freshwater has compiled and analysed a database of Arctic freshwater monitoring data to form the first report of the state of circumpolar Arctic freshwater biodiversity. This special issue presents the scientific analyses that underlie the Circumpolar Biodiversity Monitoring Program–Freshwater report and provides analyses of spatial and temporal diversity patterns and the multiple-stressor scenarios that act on the biological assemblages and biogeochemistry of Arctic lakes and rivers.
4. This special issue includes regional patterns for selected groups of organisms in Arctic rivers and lakes of northern Europe, Russia, and North America. Circumpolar assessments for benthic diatoms, macrophytes, plankton, benthic macroinvertebrates, and fish demonstrate how climate change and associated environmental drivers affect freshwater biodiversity. Also included are papers on spatial and temporal trends in water chemistry across the circumpolar region, and a systematic review of documented Indigenous Knowledge that demonstrates its potential to support assessment and conservation of Arctic freshwaters.

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5. This special issue includes the first circumpolar assessment of trends in Arctic freshwater biodiversity and provides important baseline information for future assessments and studies. It represents the largest compilation and assessment of Arctic freshwater biodiversity data to date and strives to provide a holistic view of ongoing change in these ecosystems to support future monitoring efforts. By identifying gaps in monitoring data across the circumpolar region, as well as identifying best practices for monitoring and assessment, this special issue presents an important resource for researchers, policy makers, and Indigenous and local communities that can support future assessments of ecosystem change.

KEYWORDS

Arctic, biomonitoring, climate change, freshwater, policy

1 | INTRODUCTION

Arctic lakes and rivers are under increasing pressure as climate change is predicted to cause direct and indirect effects on freshwater ecosystems, their biodiversity (the diversity within species, between species and of ecosystems), and the ecosystem services they support. Observations and projected change to physical and chemical properties of these ecosystems indicate increasingly important impacts on the hydrological and hydrogeomorphic processes that fundamentally shape the abiotic environment of Arctic freshwater systems (Huser et al., 2022; Wrona et al., 2006). Such shifts in ecosystem state include alterations to water temperature (Roberts et al., 2017), ice cover patterns (Prowse et al., 2011), water balance and quantity regimes (Wrona et al., 2005), thawing permafrost (Kokelj et al., 2013), and glacial retreat (Milner et al., 2017). Potential increases in vital chemical constituents, such as dissolved organic carbon and phosphorus, are also critical ecosystem state changes (Wrona et al., 2013). A detailed assessment of the broad-scale effects of climate change on Arctic freshwater systems is provided by Wrona et al. (2005), including how various abiotic processes (e.g., hydrologic regimes) will adjust rapidly (e.g., temperature threshold exceedance) or more gradually (e.g., thawing permafrost and glaciers).

A primary impact of these abiotic changes will be effects on freshwater biodiversity through modification of the distribution and abundance of aquatic plants, invertebrates, and fish (Wrona et al., 2013, 2016). For example, release of sediments from permafrost slumps leads to substantial physical disturbance and a loss of invertebrate and algal biomass in rivers (Chin et al., 2016; Levenstein et al., 2018), while the release of solutes during permafrost thaw can cause shifts in primary producers and system productivity in lakes (Thienpont et al., 2013). Furthermore, incorporation of old carbon from permafrost thaw into freshwater food webs can negatively impact the nutritional status of fish (O'Donnell et al., 2020), which has implications for ecosystem services. While increased nutrient release from permafrost thaw is observed or is predicted for many areas of the Arctic (Frey & McClelland, 2009; Vonk et al., 2015), oligotrophication of already low-nutrient systems has been observed in some areas of the

sub-Arctic (Arvola et al., 2011; Huser et al., 2018). Observed increases in tundra vegetation cover, a.k.a. the *Greening of the Arctic* (Elmendorf et al., 2012; Pouliot et al., 2009), primarily driven by increased nutrient uptake by rooted plants and more efficient trapping of N and P (Aerts et al., 2006), may ultimately contribute to the oligotrophication of many northern lakes and rivers (Huser et al., 2018), and subsequent effects on biodiversity and productivity. Other effects on biodiversity relate to the impact of increased competition from southern species expanding northwards (Reist et al., 2006) and the associated extinction of cold-adapted species that make up a large share of the unique biodiversity of the Arctic (Culp, Lento, et al., 2012; Lento et al., 2019). These stressors are expected to modify distributions of microbiota, aquatic plants, invertebrates, and fish, and produce changes to freshwater food webs and fisheries around the Arctic.

In this overview article, we introduce this special issue on biodiversity trends and factors leading to ecological change in Arctic lakes and rivers. Culp, Lento, et al. (2012) concluded that the understanding of temporal and spatial biodiversity patterns of Arctic freshwater ecosystems is hindered by the lack of coordinated monitoring and assessment. Therefore, in the first section we introduce the aim of the Freshwater Monitoring Group of the Arctic Council, which was to develop a coordinated biomonitoring plan for Arctic freshwaters and identify major environmental pressures on these ecosystems, with the goal of producing the first circumpolar assessment of status and trends in Arctic freshwater biodiversity (Lento et al., 2019). The ecosystem-based monitoring approach aims to incorporate the interactions of components at multiple scales that are necessary to investigate complex compositional, functional, and structural changes in biodiversity (Meltote, 2013). The next section provides definitions of biodiversity used in the assessments, discusses the use of biomonitoring data for such an assessment, and introduces our focus on assessing α and β diversity of lakes and rivers within the geographical boundaries for the Arctic, as established by CAFF and the Arctic Biodiversity Assessment. This section is followed by a description of the data used for the assessment of Arctic freshwater biodiversity in Canada, Faroe Islands, Finland, Greenland, Iceland, Norway, Russia, Sweden, and the U.S.A. In the final section of the

paper, a summary of each special issue papers is provided. The two categories of studies in the special issue include those that examine regional patterns for one or more groups of organisms (e.g., benthic diatoms, invertebrates, fish), and those that investigate patterns for a specific group of organisms (e.g., benthic invertebrates) on a circumpolar scale. The final paper in the issue compares and contrasts important patterns gained by the circumpolar assessment and provides key questions and next steps for future work.

2 | COORDINATION OF MONITORING AND ASSESSMENT THROUGH ARCTIC COUNCIL INITIATIVES

The growing awareness that Arctic ecosystems are changing rapidly and dramatically prompted the Arctic Council to recommend that adaptive, long-term ecosystem and biodiversity monitoring efforts should be intensified to capture changes and should be focused to address key knowledge gaps and better inform development and implementation of conservation and management strategies for the Arctic (ACIA, 2004; Meltofte, 2013). In response, the Arctic Council working group, Conservation of Arctic Flora and Fauna (CAFF), established the Circumpolar Biodiversity Monitoring Program (CBMP) to address the need for adaptive, coordinated, and standardised monitoring of Arctic environments for the freshwater, terrestrial, coastal, and marine ecosystems (CAFF, 2018; Christensen et al., 2020; Petersen et al., 2004). The mandate of CAFF is to support circumpolar biodiversity monitoring efforts and promote the communication of findings to policymakers and Arctic residents, as well as to encourage sustainable practices in the Arctic countries to assess Arctic freshwater biodiversity and associated ecological change. These initiatives were launched during the International Polar Year of 2007–2008 and aim to describe baselines for change in Arctic biodiversity.

The CBMP is one of CAFF's cornerstone activities (Figure 1) and uses an adaptive monitoring framework (Lindenmayer & Likens, 2009) with iterative steps that link management and scientific questions, conceptual models, experimental monitoring design, data collection, data analysis, data interpretation, and reporting. This initiative involves an international network of scientists, governments, Indigenous Peoples organisations, and conservation groups, working together to develop and improve long-term monitoring of Arctic biodiversity by supporting rapid detection, communication, and response to significant trends in biodiversity, and to identify the factors driving such trends (CAFF, 2018; Christensen et al., 2020; Culp, Lento, et al., 2012). The CBMP aims to harmonise and integrate efforts to monitor the Arctic's living resources and biodiversity and communicate this information to stakeholders, including national and international policymakers, and Indigenous Peoples living in the Arctic (Culp, Goedkoop, et al., 2012). To achieve these goals, each CBMP working group developed circumpolar monitoring plans and assessments.

Effective conservation and management of Arctic ecosystems requires comprehensive long-term information on the status of species, habitats, and ecological processes and functions, as well as

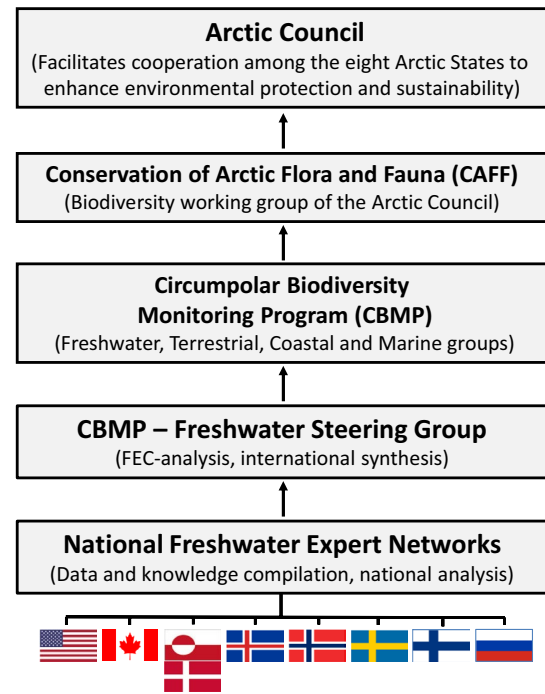


FIGURE 1 Reporting and process structure of the Arctic Council's Conservation of Arctic Flora and Fauna (CAFF) working group and the specific relationship of the Freshwater Circumpolar Biodiversity Monitoring Program (CBMP) to CAFF. The Freshwater CBMP is led by representatives of the eight Arctic Council countries who each gather data and compile information on the focal ecosystem components (FECs) through their national Freshwater Expert Networks for national and international synthesis. Other CBMP steering groups focus on terrestrial, coastal and marine ecosystems

potential drivers of change. Thus, the freshwater group of the CBMP (CBMP-Freshwater) developed a detailed monitoring plan that identifies major environmental pressures on Arctic freshwater ecosystems (Culp, Goedkoop, et al., 2012). These pressures are summarised as: (1) thermal regime change and associated changes to timing of ice-on and ice break-up due to climate change-driven shifts in air temperature and precipitation (Prowse et al., 2011); (2) permafrost thaw and changes in the hydrological regime resulting in higher loads of nutrients, solids, and organic matter (e.g., Kokelj et al., 2013); (3) long-range transboundary air pollutants (Macdonald, 2007; Veillette et al., 2012), and point source and diffuse pollution originating from anthropogenic development (Heino et al., 2009); (4) fisheries over-harvesting (Christiansen et al., 2013); (5) climate-driven changes to catchment vegetation from grasses to shrub-dominated flora (e.g., Elmendorf et al., 2012); and (6) flow alterations and regulation due to hydropower dams and other forms of development that lead to substantial habitat fragmentation and destruction (Bunn & Arthington, 2002; Dynesius & Nilsson, 1994). Following the structure of previous CBMP working groups (e.g., CAFF, 2017), the response variables for the monitoring framework are categorised by focal ecosystem components (FECs), which are organism groups that are ecologically pivotal, contain charismatic species, such as Arctic charr (*Salvelinus alpinus*), or include sensitive indicators of biodiversity

change. Expert consensus defined six FECs for initial assessment of Arctic freshwater biodiversity based on their central role in ecosystem function and the likelihood that they are extensively represented in existing databases for the Arctic. These FECs are benthic algae (although only diatom data were available for most countries), phytoplankton, macrophytes, zooplankton, benthic macroinvertebrates, and fish. Historically, freshwater biomonitoring has been based on estimating numerical abundance and taxonomic composition, thus our assessment was necessarily restricted to consideration of structural attributes. Future assessments of Arctic freshwater biodiversity should include functional attributes (e.g., decomposition rate) as such information becomes available.

Our list of FECs reflects further limitations in data availability for Arctic freshwaters for such groups as bacteria and fungi. Given the importance of microbiota in overall ecosystem biodiversity, biomass, food web carbon flows, and biogeochemical processes of freshwater ecosystems, this is an important gap in our assessment. Nevertheless, this was an unavoidable restriction because freshwater biomonitoring data sets for microbiota are few across circumpolar Arctic freshwaters, and not great enough to undertake broad spatial analyses. National monitoring programmes in the north do not generally include these organism groups, thus limiting data sources to academic research programmes. The unique freshwater microbial communities and ecosystems in the north are only recently being understood, for example, through the application of molecular techniques (Cavaco et al., 2019; Galand et al., 2008; Vincent et al., 2009). Clearly, this rapidly developing knowledge on Arctic microbial diversity should be an area of consideration for the future.

The goal of the CBMP-Freshwater monitoring group was to plan, initiate, and support long-term monitoring and assessment of status and trends in Arctic freshwater biodiversity (Culp, Goedkoop, et al., 2012). A critical first step towards implementation of this goal was an assessment of the current state of knowledge with respect to Arctic freshwater biodiversity for each of the identified FECs. To achieve this, CBMP-Freshwater coordinated a large international effort to identify and collect contemporary and historical data from the circumpolar region and assess spatial and temporal trends in these data to determine the current state of biodiversity in Arctic freshwaters. This immense endeavour resulted in the first circumpolar assessment of status and trends in Arctic freshwater biodiversity (Lento et al., 2019), which forms the foundation for the papers in this special issue. Here, we describe the process behind this assessment, and outline the papers that follow in this special issue.

3 | DEFINING AND DETECTING FRESHWATER BIODIVERSITY IN THE ARCTIC

The CBMP has adopted the Convention on Biological Diversity's definition of biodiversity, which is, "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes

of which they are a part; this includes diversity within species, among species and of ecosystems" (United Nations, 1992, p. 3). Under this definition, biodiversity includes species richness at local scales (α diversity) and at larger, regional scales (γ diversity), as well as the variation in species composition among regions (β diversity). Changes in the biodiversity of Arctic freshwaters are hypothesised to be strongly associated with increasing temperature, as freshwater communities in the Arctic have generally been limited to those species that have adapted to the cold temperatures and short period of ice-off in this biome (Danks et al., 1994; Gladyshev et al., 2015; Vincent & Laybourn-Parry, 2008; Wrona et al., 2013). The expected northward movement of eurythermic (warm-adapted) species with continued climate warming will affect biodiversity by changing the composition of species within and among regions (β diversity), and by changing the number of species found at local scales (α diversity) and regionally across the Arctic (γ diversity), with the magnitude of change in each type of diversity depending on the relative rates of gain and loss in eurythermic and stenothermic (cold-adapted) species (Culp, Lento, et al., 2012; Lento et al., 2019; Vincent et al., 2011). In isolated ecosystems (e.g., high Arctic or high-altitude), where dispersal is limited, the climate-driven loss of stenotherms may not be compensated by eurythermic species' migration, and an overall decline in local or regional biodiversity is expected. This effect is expected to be strongest for fish whose dispersal patterns rely on habitat connectivity.

Freshwater biomonitoring and assessment have a long (>100 year) tradition in quantifying changes in abundance and diversity of selected FECs (e.g., algae, macrophytes, invertebrates, and fish) caused by specific stressors, such as organic loading, oxygen deficiency, and acidification, or indicating a general deterioration of ecological integrity (see Johnson et al., 1993 and references cited therein). Bioassessment approaches have developed in many countries and often follow standardised procedures with respect to sampling technique (e.g., stratified habitat, mesh sizes) and effort (e.g., time of sample collection), as well as sample treatment (e.g., preservative, subsampling). In some cases, standardised approaches have been inter-calibrated regionally, for example, among European Union countries as part of the Water Framework Directive (Poikane et al., 2016), allowing for large-scale inter-comparability of monitoring data. Freshwater bioassessment focuses on species that have a wide distribution and well-known, specific habitat requirements (Hering et al., 2006; Resh, 2008), which makes them suitable indicator species for the different metrics of pollution or ecological quality/integrity that have been developed. Although monitoring to support bioassessment may not specifically target biodiversity as an endpoint, the data generated from these standardised approaches provide a sound way to systematically assess biodiversity patterns. Rarefaction can be used to further improve comparability of data from different sources, collected with similar methods, by eliminating sample size biases that can occur when comparing data from multiple monitoring programmes (Gotelli & Colwell, 2001).

Circumpolar Biodiversity Monitoring Program–Freshwater's assessment of Arctic freshwater biodiversity (Lento et al., 2019) focused on analysing diversity patterns in biomonitoring data from lakes and rivers. For each FEC, spatial and (where possible) temporal patterns in taxonomic richness were assessed at local or regional scales (α and γ diversity) and regional differences in taxonomic composition (β diversity) detected. This effort required international collaboration to identify, obtain, and harmonise data from across the circumpolar region. Specific details with respect to harmonisation are presented in several of the papers in this issue, but an overview of data collection and harmonisation is provided below.

4 | DATA COLLECTION AND HARMONISATION

Data that underlie the different studies of this special issue were collected from Canada, Faroe Islands, Finland, Greenland, Iceland, Norway, Russia, Sweden, and the U.S.A. The southern geographic boundaries of this assessment followed the Arctic boundary as defined by CAFF (political boundary) or the lower limit of the sub-Arctic as defined by the Arctic Biodiversity Assessment (Meltøfte, 2013), whichever was more inclusive (Figure 2). The Arctic was sub-divided into sub-Arctic, low, and high Arctic following the boundaries

determined by the Arctic Biodiversity Assessment using climate and vegetation patterns (Meltøfte, 2013).

The biodiversity data used in the various papers of this special issue originated from a combination of national monitoring databases, government- and industry-funded monitoring programmes, academic research, peer-reviewed published literature, and the grey literature. Data were primarily from the contemporary period (collected from 1950 to present), although efforts were made to obtain historical data (collected from 1800 to 1950). However, time series were rare, except for some long-term monitoring data, and most sample locations only had single sampling events. Paleolimnological data (specifically, diatom data from lake sediment cores) were obtained to allow for an assessment of historical trends beyond the contemporary period. In total, data from more than 9000 stations were compiled in the CBMP–Freshwater database (Figure 3), with stations defined as sampling locations with unique geographic coordinates from which samples have been collected one or more times. The spatial distribution of stations was patchy across much of the Arctic, particularly in remote Arctic regions, due in part to the difficulty and cost associated with accessing those regions (Mallory et al., 2018). Metadata and (where allowed) data from the database have been made available on CAFF's Arctic Biodiversity Data Service (ABDS; found at abds.is).

Several harmonisation steps were required to guarantee the comparability of data from such a wide geographic area and large



FIGURE 2 Arctic freshwater boundaries from the Arctic Council's Arctic Biodiversity Assessment developed by Conservation of Arctic Flora and Fauna (CAFF) (Meltøfte, 2013), showing the three sub-regions of the Arctic, namely the high (dark purple), low (purple), and sub-Arctic (light purple), and the CAFF boundary (black line)

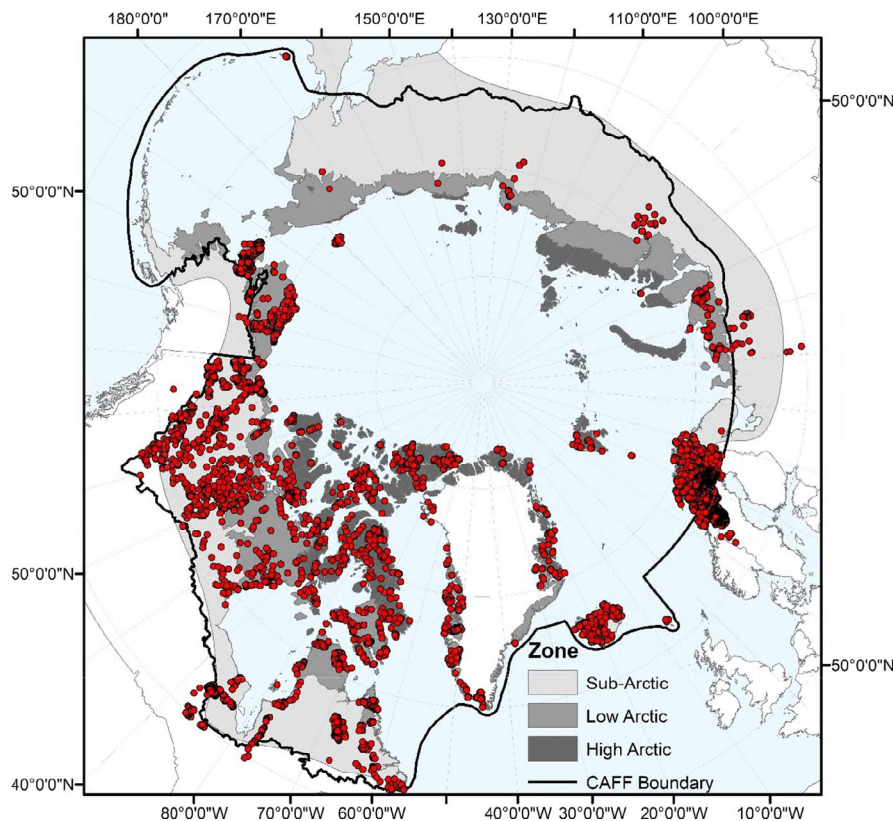


FIGURE 3 Circumpolar map of all stations in the Circumpolar Biodiversity Monitoring Program–Freshwater database, including stations with biotic and/or abiotic data for lakes or rivers. Conservation of Arctic Flora and Fauna Boundary and Arctic Biodiversity Assessment Arctic zone boundary layers from caffi.is

number of sources. Data and metadata were compiled by each country using a standardised format, then reviewed and revised as needed to ensure compliance with the data schema for a single circumpolar database on freshwater biodiversity and supporting variables. Although quality assurance and quality control procedures were generally completed by data providers, we also examined the data to ensure that there were no obvious outliers or indications of errors in measurement units. In addition, a standardised nomenclature table was created for each FEC (fish, benthic invertebrates, zooplankton, macrophytes, benthic diatoms, and phytoplankton) to harmonise and align taxonomic identifications from the raw data. Sampling method protocols were recorded with the metadata.

Efforts were made to obtain data on supporting variables (e.g., water chemistry and habitat data), although these variables were not always available for each biodiversity station and were not always recorded consistently across all countries. To obtain comparable supporting variables for all circumpolar stations, a geographic information system (ArcMap Version 10.3; ESRI, St. Paul, Minnesota) was used to extract geospatial data from circumpolar data layers. Available circumpolar remote sensing and geospatial data were summarised for standardly-derived global catchments (hydrobasins; Lehner & Grill, 2013) and for ecoregions (using Terrestrial Ecoregions of the World; Olson et al., 2001) for use in analyses in the papers in this special issue's papers, and more details about the chosen variables can be found in each paper.

By using the available data collected through various biomonitoring and research programmes, we were able to undertake unique investigations of FEC biodiversity patterns at regional, continental,

and circumpolar scales. Through enormous collaborative effort by scientists of the eight Arctic Council States, this approach allowed production of the first circumpolar-scale database for the six FECs. An implicit characteristic of large-scale analysis of observational-based data is an inherent variability in the data that is due to the large number of data sources. Differences in sample collection method, timing of sampling, and sample processing and reporting can introduce error into diversity estimates and must be controlled for or corrected if assessments are to be scientifically sound. As described in greater detail in each paper of the special issue, we undertook extensive quality assurance and quality control measures to ensure that the data for FECs were comparable among sources. For example, we considered and evaluated the collection method and level of taxonomic resolution, in some cases removing data when they were not deemed comparable, and we undertook corrective procedures, such as rarefaction, prior to metric calculation and statistical analyses. Presence/absence data provided an alternative option for analysis of taxonomic richness and composition when data sets could not be combined quantitatively, and specific details on the use of qualitative or quantitative data are provided in each paper. Following selection based on sample comparability, a final set of approximately 8300 stations was chosen for inclusion in biotic and abiotic assessments, including a broad spatial distribution of lake stations (Figure 4a,b) and more restricted distribution of river stations (Figure 4c,d). Spatial distributions of stations for each individual assessment are indicated in special issue papers.

Our database and associated analytic approaches do have potential limitations, such as the paucity of available long-term datasets

and unavoidable gaps in spatial coverage. Our estimates of biodiversity, particularly at smaller scales, are likely underestimates in some regions because of these gaps; however, we were most interested in investigating freshwater biological pattern at the hydrobasin and ecoregion scales, as opposed to more detailed evaluations of within site variation. Furthermore, these limitations are balanced by the important outcomes stemming from the massive accumulation of circumpolar freshwater data, and associated analytical effort, that allowed us to produce a new and unique understanding of circumpolar biodiversity in Arctic lakes and rivers.

5 | ASSESSING FRESHWATER BIODIVERSITY ACROSS THE CIRCUMPOLAR REGION

Papers in this special issue address different aspects of the ongoing ecological change in Arctic ponds, lakes, streams, and rivers by analysing spatial patterns and temporal trends for key freshwater organism groups. The special issue includes regional studies, which examine biodiversity of multiple organism groups within specific geographical regions (e.g., northern Europe, Russia, North America),

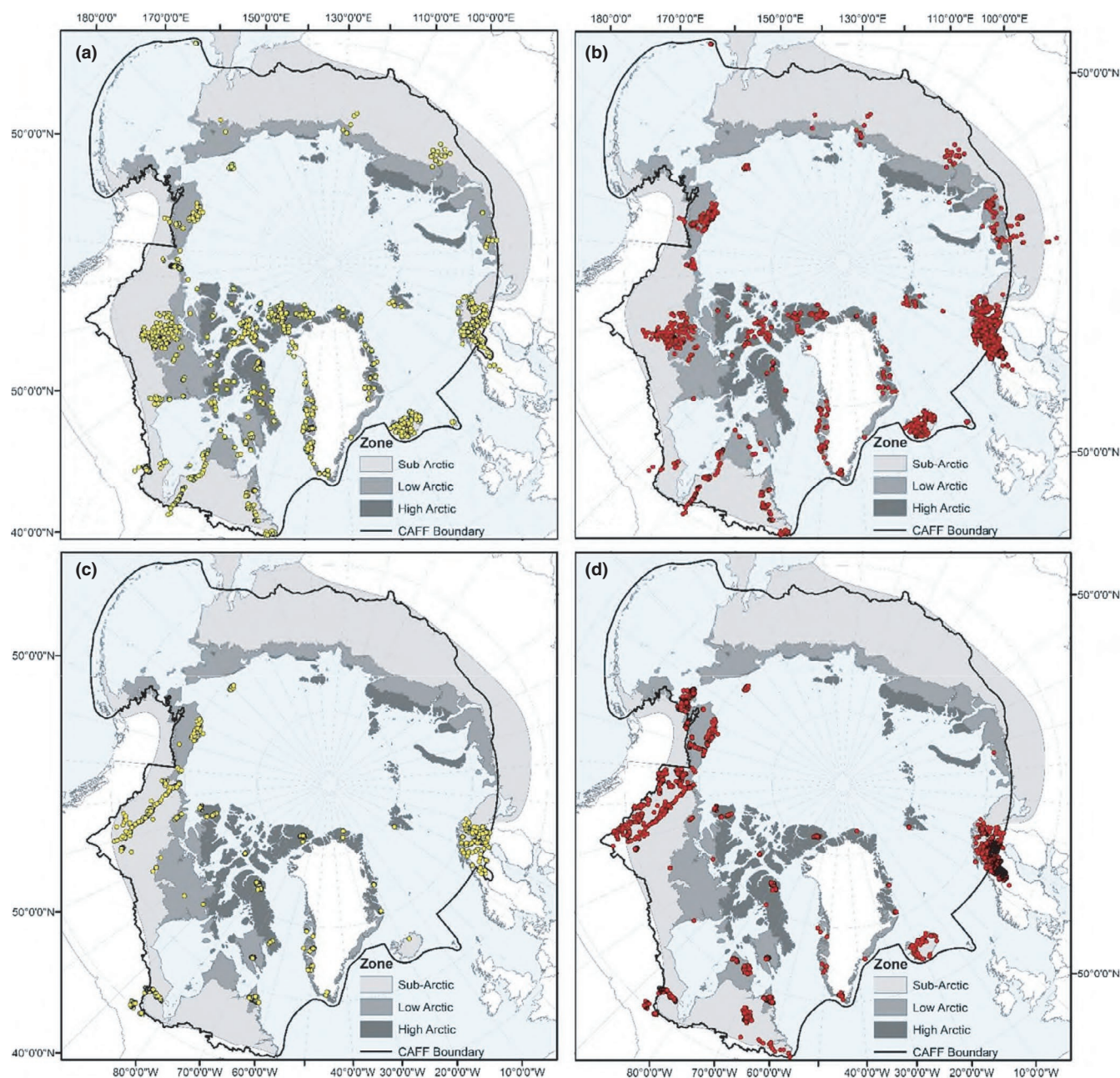


FIGURE 4 Circumpolar map of stations used in assessments in this special issue, including (a) lake stations with water chemistry data, (b) lake stations with biotic data, (c) river stations with water chemistry data, and (d) river stations with biotic data. Conservation of Arctic Flora and Fauna Boundary and Arctic Biodiversity Assessment Arctic zone boundary layers from caff.is

as well as circumpolar studies that examine patterns on a pan-Arctic scale for individual organism groups. In addition, a paper on circumpolar water chemistry trends provides context for recorded and anticipated changes to the chemical habitat template for aquatic organisms. Finally, a systematic review of documented Indigenous Knowledge (IK) indicates the potential to support circumpolar assessments of ecosystem change and biodiversity through consideration of IK. The key findings for each paper are summarised below while Goedkoop et al. (2022) integrate all the work and emphasises future needs for monitoring and research.

The special issue begins with an assessment of water chemistry in 2,032 lake and 482 river sites across the Arctic (Huser et al., 2022) that provides an overview of ongoing and historical change in the abiotic template of these ecosystems for 1970–2015. Recent water chemistry data indicate that spatial variation in pH, alkalinity, and ions reflects natural geologic gradients across the Arctic, whereas spatial patterns in nutrients are indicative of lower nutrient levels at higher latitudes and systems affected by permafrost thaw slumps. Most notably, results of temporal analysis indicate decreasing trends in total phosphorus at lower latitudes and increasing trends at higher latitudes. This difference is hypothesised to result from different drivers at low and high latitudes, with deposition, climate, and vegetation changes in the south leading to oligotrophication, and deepening of the active layer in the north leading to increased nutrient availability. Freshwater organisms respond to these changes in their chemical and physical habitat, and such shifts in nutrient availability may have large implications for Arctic freshwater biodiversity and food web structure.

The five regional assessments of Arctic freshwater biodiversity include three papers examining diversity of lakes and rivers in northern Europe. In the first assessment, Lau et al. (2022) use a novel whole ecosystem biodiversity approach that integrates multiple organism groups and trophic levels (i.e., FECs) to analyse patterns and environmental descriptors in an extensive data set of 74 sub-Arctic lakes in Finland, Sweden, Norway, and the Faroe Islands. They show that the richness_{relative} of phytoplankton, macrophytes, and fish decreased, but those of the intermediate trophic levels (i.e., macroinvertebrates and zooplankton) increased, with decreasing latitude and/or elevation. Fish richness_{relative} and diversity correlate positively with temporal variation in climate (temperature and/or precipitation), with lake nutrient concentrations (e.g., TN), and with hydrobasin vegetation cover (e.g., taiga forest). Conversely, taxon richness of macroinvertebrates and zooplankton decreases with increasing temporal variation in climate. The authors interpret the observed similarity in patterns for richness_{relative} of fish, macrophytes, and phytoplankton as a similar response by each organism group to environmental correlates, or a response to habitat creation by macrophytes. They suggest that fish could be an overall indicator of lake biodiversity, as average richness_{relative} for FECs is highest where fish richness_{relative} is high. The observed trophic-level-specific biodiversity patterns along the environmental gradients indicate the need for whole-ecosystem monitoring and management of biodiversity in high-latitude lakes that is focused on the entire food web.

Brittain et al. (2022) address the broad-scale patterns of riverine α and β diversity for an extensive data set of benthic diatom and macroinvertebrate communities across northern Norway, Sweden, and Finland (Fennoscandia), and correlate these to geographic location, climate, and environmental variables. They focus on partitioning β diversity into component parts of replacement and richness difference. For macroinvertebrate assemblages, richness difference is the most important component of β diversity, whereas the replacement component is most important for diatom assemblages. Significant differences in α diversity are evident among three drainage basins (Baltic Sea, Barents Sea, Norwegian Sea) for both macroinvertebrates and diatoms, and several taxa are identified as basin-unique indicators. Alpha diversity is higher where the climate is continental than oceanic areas in the west that had greatly reduced flora and fauna. Climate variables, particularly temperature, are the strongest correlates of biodiversity in Fennoscandian Arctic rivers for both macroinvertebrates and diatoms, although sedimentary geology, which relates to water chemistry, is also important. The authors conclude that climate variables are the overall most important correlates of biodiversity patterns and stress the need for conservation of catchments in each region to protect riverine biodiversity.

Svenning et al. (2022) examine 26 years (1993–2018) of unique catch statistic data from more than 200 rivers in northern Norway and Iceland to assess shifts in the relative abundance of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*) in relation to temperature change. Long-term trends in catch statistics indicate little change in total fish catch, a decreased proportion of the cold stenothermic Arctic charr, and an increase in the proportion of brown trout, and no change for Atlantic salmon. The shift in catch statistics is associated with an increase in air temperatures of approximately 1–2°C during the study period. Continued warming is expected to bring further shifts in the relative abundance of these fish species, with warm-adapted species favored. Beside the economic importance of these species, the shifts in species composition will also affect the lives of Indigenous Peoples of the Arctic for whom Arctic char is an important food source.

Fefilova et al. (2022) investigate planktonic and meiobenthic biodiversity from 1960 to 2017 across seven regions of the continental Russian Arctic (Kola Peninsula in the west to the Indigirka River Basin in eastern Siberia). They examine composition of planktonic and meiobenthic rotifers, cladocerans, and copepods, as well as sub-fossil remains in bottom sediments. Across these regions, total richness of lakes is greater than ponds, and copepod and rotifer species richness increase with latitude (c. 67–73°N). They indicate that many species are unique to a region, while the Bolshezemelskaya tundra and Putorana Plateau have the highest number of rare species. Copepod species richness is positively associated with waterbody area, elevation, and precipitation, while cladoceran richness is positively related to temperature. This finding is consistent with known temperature preferences and tolerances copepods that are dominant in large, cold lakes and ponds in the east. Rotifers are negatively associated with these factors. Finally, northward range expansion of several thermophilic species appears related to climate warming, but

the presence of new microfauna between 1990 to 2010 in the Lena River Delta appears related to ballast water release.

In the fifth regional paper, Lento et al. (2022) evaluate drivers of diversity of diatoms, benthic macroinvertebrates, and fish in North American Arctic rivers. This paper shows that α diversity of benthic macroinvertebrates at the basin scale declines more strongly with increasing latitude than does diversity of diatoms or fish. Alpha diversity of benthic macroinvertebrates is strongly related to long-term average maximum summer air temperature, used as a proxy for maximum water temperature. In contrast, diatom diversity relates to geology and temperature, and fish diversity more strongly relates to glaciation history. Site-scale assemblage composition of benthic macroinvertebrates is most strongly associated with temperature and precipitation, whereas diatom assemblage composition is associated with water chemistry. The authors suggest that of the three FECs, benthic macroinvertebrates might be expected to respond most strongly to temperature changes resulting from ongoing climate change in the Arctic. In contrast, diversity of diatoms and fish may reflect changes to, respectively, nutrient levels and hydraulic connectivity that result from climate change. However, large spatial gaps in monitoring coverage across the North American Arctic limits the acquisition of time series information and impedes our ability to detect ongoing biodiversity change in this region.

In the first of the circumpolar papers, Kahlert et al. (2022) provide a spatial assessment of contemporary diatom species distributions across the circumpolar Arctic and evaluate historical trends using paleolimnological data. The authors identify distinct diatom assemblages, or biotypes, distributed across the circumpolar region for both lakes and streams, including a biotype that is only found in the High Arctic. However, diatom taxa that dominate in remote high-latitude regions were also found elsewhere in the Arctic. Richness of diatoms does not show a clear decline with increasing latitude and is highest between 60°N and 75°N. Results also show that differences in diatom assemblages across the Arctic are gradual in nature rather than showing abrupt species turnover. Analysis of paleolimnological sediment core data indicates substantial change in diatom composition in the high Arctic and areas of western North America in the last 200 years where the effects of climate warming have been greatest. The authors stress the need for routine monitoring of diatoms in Arctic lakes and rivers and harmonisation of sampling and identification of these organisms, including increased use of metabarcoding methods, to support ongoing trend detection.

Schartau et al. (2022) assess spatial trends in phytoplankton and zooplankton data from more than 300 lakes across the Arctic. Taxonomic richness of zooplankton is lower in the high Arctic than at lower latitudes, but this pattern was less clear for phytoplankton. Fennoscandia and inland regions of Russia represented hotspots for, respectively, phytoplankton and zooplankton diversity, whereas isolated regions had lower taxonomic richness. Ecoregions with high α diversity generally also had high β diversity, and turnover was the most important component of β diversity in all ecoregions. Variation in taxonomic diversity of both phytoplankton and zooplankton appears most strongly related to latitudinal differences in

air temperatures, but barriers to dispersal may also be an important factor limiting diversity on islands. They conclude that plankton is a key group for the monitoring of ecological change in Arctic lakes due to their fast response to environmental change and their key role in aquatic food webs. However, the importance of turnover in regional diversity patterns indicates that more extensive sampling is required to fully characterise the species pool of Arctic lakes.

Lento et al. (2022) evaluate α and β diversity of benthic macroinvertebrates in >1,500 lakes and rivers across the circumpolar region. Rarefied α diversity of benthic macroinvertebrates declines with increasing latitude in both lakes and rivers, although more strongly across mainland regions than islands. Furthermore, this paper finds a strong relationship between diversity and temperature, with the lowest diversity found at the coldest maximum summer air temperatures (used as a proxy for water temperature). Taxonomic composition of lake and river assemblages reflects physiological limitations of cold temperatures at the highest latitudes, where only a few taxa predominate that are adapted to survive the extreme cold. However, their analyses also show that the degree of spatial connectivity appears to be limiting diversity on islands. Connectivity also plays a role in regional taxonomic differences, as β diversity among regions is greatest when mainland regions and island regions are compared. The strong association with temperature supports the prediction that warming will increase Arctic macroinvertebrate diversity, although low diversity on islands suggests that this increase will be limited by biogeographical constraints. Furthermore, they stress that long-term harmonised monitoring across the circumpolar region is necessary to detect future changes to diversity and inform science-based management, that an expansion of the number of lake and river sites is needed to improve detection of temporal trends, and that taxonomic resolution of these groups can be increased by using barcoding techniques.

Fish play an important role in Arctic freshwater ecosystems, both in terms of ecosystem function and as a resource to humans, and thus it is vital to understand Arctic fish species distribution, richness, and biodiversity. Laske et al. (2022) address this problem by examining patterns of γ , α , and β diversity of freshwater fish across the Arctic. Their results show that both γ and β diversity are reduced in the high Arctic compared to other zones. Although little variation in the composition and richness of species occurs in the High Arctic, diversity in the sub-Arctic and boreal zones varies across large spatial extents. The authors find that geographic isolation, area, and topography are strong drivers of γ , α , and β diversity. Physical isolation reduces the total number of species and average richness of hydrobasins and change in species composition is due mainly to loss of species, rather than the replacement of species. Relative to adjacent low elevation ecoregions, those with mountain ranges have reduced γ and α diversity. Beta diversity of fish probably also reflected geographic distance, heterogeneity of habitats, and environmental gradients among ecoregions. Improvement in future assessments requires reduction of existing spatial and temporal data gaps, for example, by accessing data archives in addition to conducting more sampling. Clearly, the implementation of more robust monitoring

framework is needed to improve tracking of temporal and spatial changes in among- and within-species fish biodiversity across the Arctic.

The last topical paper in the special issue by Knopp et al. (2022) provides a systematic review of documented IK from the circumpolar region. Arctic freshwaters and the biodiversity they contain provide vital ecosystem services to Arctic Indigenous communities. Due to their close connection to the land, Arctic Indigenous Peoples have a vast and unique knowledge of freshwater organisms and their habitats, as well as the changes that have taken place in freshwater ecosystems, yet few attempts have been made to summarise existing records of this knowledge. Knopp et al. (2022) complete the first circumpolar systematic review of documented IK to support our understanding of the scope of this knowledge and its potential to support monitoring and conservation efforts in Arctic freshwaters. Faunal observations in documented IK are most commonly about fish, and 59 species have been recorded, including several that are not part of the CBMP monitoring database. Furthermore, documented IK fish observations expand the spatial and temporal coverage of fish data from the CBMP monitoring database, particularly in Russia. Documented IK includes several observations of habitat change, many of which are consistent with climate warming. These observations include permafrost thaw, and changes to ice cover and thickness. The emergent themes identified in this study highlight the important contributions that IK can make to understanding biodiversity and ecosystem change in Arctic freshwaters. The authors provide numerous suggestions for further work in this area, including targeted searches for documented IK and increased effort to understand the context of the knowledge. The latter is vital to ensuring that IK is incorporated into biodiversity assessment in a way that is respectful to IK holders.

The special issue concludes with a paper by Goedkoop et al. (2022) that provides an overview and summary of biodiversity trends from a whole-ecosystem perspective and outlines the initiatives necessary to ensure adequate monitoring of Arctic freshwater biodiversity in the future. This paper synthesises the findings of the special issue papers by highlighting key patterns in diversity across Arctic regions and organism groups and identifying the key environmental correlates of change for each FEC. The authors further relate these patterns to projected changes in Arctic freshwater ecosystems to predict the anticipated effects of continued climate change on biodiversity in these ecosystems. The paper includes an assessment of the current state of biodiversity monitoring in Arctic countries and a summary of the major gaps that jeopardise future assessments of biodiversity status and trends, highlighting the lack of routine monitoring of many FECs in several countries, the limited spatial coverage for some FECs that are routinely monitored, and the need for more harmonisation of sample methods and processing to ensure data comparability. Using the findings of the special issue papers and this overview of the state of monitoring, the authors provide key recommendations for monitoring of Arctic freshwater biodiversity, relevant to policymakers, researchers, and Indigenous and

local communities. These recommendations include the establishment of monitoring networks following a hub-and-spoke sampling model to facilitate improvements to spatial coverage of data, use of ecoregions to identify areas requiring additional sampling, increased effort to develop community-based monitoring programmes and to engage with Indigenous communities, increased use of emergent technologies such as metabarcoding, eDNA, and remote sensing, and maintenance of time series through routine monitoring at priority locations.

This special issue and the associated *State of the Arctic Freshwater Biodiversity Report* (Lento et al., 2019) represent milestones in providing key scientific input to a comprehensive assessment of status and trends for Arctic freshwater biodiversity and existing monitoring efforts. The wide range of topics addressed in this special issue provides important findings and advice useful to both scientists and policy makers (CAFF, 2019). The rapid change of Arctic ecosystems highlights the need for the CBMP-Freshwater initiative to establish baselines against which future biodiversity change can be assessed and through which future Arctic freshwater monitoring efforts can be coordinated among Arctic countries. Furthermore, Arctic countries need to initiate long-term biological monitoring at selected locations. This is a necessity if we are to make evidence-based assessments in the future of the ecological effects of climate change in Arctic freshwaters.

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DATA AVAILABILITY STATEMENT

There are no data in this paper. The CBMP-Freshwater database described in this paper can be found on the Arctic Biodiversity Data Service (ABDS; abds.is).

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