Darner dragonfly (Aeshna cyanea) nymph extending its labium.
Photo: Jan Hamrsky
4. Status and Trends in Arctic Freshwater Biodiversity

4.1. Introduction

This chapter provides assessments of spatial and temporal trends in freshwater biodiversity of lakes and rivers for each biological FEC, including algae from benthic samples, phytoplankton, water plants (macrophytes), zooplankton, benthic macroinvertebrates, and fish. Primary producers are represented by both microscopic (algae) and macroscopic (water plants) organisms, while animals include primary (zooplankton, benthic macroinvertebrates) and secondary consumers (invertebrate predators, fish). Aquatic food webs are driven by the photosynthesis of primary producers and by the microbial decomposition of organic matter entering lakes and rivers from their terrestrial environment. The sources represent the autotrophic and heterotrophic pathways, respectively, in aquatic food webs (Figure 4-1). Primary production (photosynthesis) and decomposing leaf litter (detritus) form the base of food webs that supplies food for primary consumers (herbivores and detritivores) and predators at higher trophic levels.

Primary production in lakes and rivers is dependent on access to sunlight and is thus limited to the shallow zones of lakes. Allochthonous inputs (e.g., terrestrial vegetation) contribute food for primary consumers (Figure 4-2), but may be limited at higher latitudes. Benthic algae can grow attached to stones, water plants or sediments in the shallow areas of lakes, while planktonic algae (or phytoplankton) are free-floating in the open water, i.e., the pelagial zone (Figure 4-2). In nutrient-poor, clear-water Arctic lakes, photosynthesis by benthic algae is the main source of food for higher trophic levels and can occur at deeper depths due to increased light penetration. Pelagic phytoplankton production can become relatively more important in more nutrient-rich lakes, where light penetration is decreased. In the deep and dark profundal zone of large lakes, no photosynthesis occurs, and biological production is entirely dependent on organic matter settling to the bottom. In rivers, food webs are more simplified with low biomass of plankton, and benthic algae and allochthonous materials form the base of the food web (Figure 4-3). The illustrations in Figure 4-2, Figure 4-3, and Figure 4-4 highlight reference conditions for ecosystem processes and biodiversity in lakes, rivers and glacial-fed rivers and the potential impact to these freshwater ecosystems as a result of climate change.

This chapter focuses on the dominant FECs within lakes and rivers, assessing status and trends in lake algae from benthic samples, phytoplankton, macrophytes, zooplankton, benthic macroinvertebrates, and fish, as well as river algae from benthic samples, benthic macroinvertebrates, and fish. In line with freshwater monitoring tradition, our assessments primarily focus on changes in the assemblages of these FECs, rather than on single taxa. Key aims for the assessments were to provide an overview of the spatial and temporal trends in current biodiversity of FECs for rivers and lakes in the Arctic and sub-Arctic regions, including assessment of alpha and beta diversity, and evaluation of historical changes that have occurred; to determine any data gaps in spatial coverage across these regions; and to establish a baseline for future monitoring for these geographical regions. Additionally, we provide the steps required to optimize future global bioassessments. By collecting and assessing data from the circumpolar region, we have attempted to establish the state of knowledge for these FEC groups, while allowing for future re-assessments of status and trends as more data become available.

Figure 4-1 A generic food web diagram for a lake or river, indicating the basic trophic levels (boxes) and energy flow (arrows) between those levels. Reproduced from Culp et al. (2012a).
Figure 4-2 (a) Typical Arctic lake food web, including primary and secondary consumers, and indicating vertical placement of food web components in the water column, and (b) Arctic lake food web following climate-change induced inputs of sediments and nutrients, indicating resulting food web shifts with declines in water transparency.

Figure 4-3 (a) Typical Arctic river food web, including primary and secondary consumers, and (b) Arctic river food web impacted by inputs from permafrost thaw slump, with increased suspended solids and increased deposited sediment causing burial of benthic producers and consumers.
4.1.1. Analytical Approach

Our data assessment emphasizes the importance of alpha and beta diversity indicators. The species diversity of a region (gamma diversity) is comprised of both local species diversity (alpha diversity) and the variation in species diversity among sites (beta diversity). These measures of diversity are scale-dependent, and their pattern of change should be considered along multiple spatial and temporal scales. However, the feasibility of such a multi-scale assessment is limited by data availability, and in particular, the spatial and temporal coverage of available data. Although spatial coverage of stations is extensive in some regions with established routine monitoring (e.g., Fennoscandia), sparse coverage in other areas limits the scope of such assessments.

To standardize the spatial scale of the circumpolar analysis of diversity, stations were classified on the basis of the terrestrial ecoregion in which they were found (Terrestrial Ecoregions of the World, TEOW; Olson et al. 2001). These geographic and climatic regions allowed stations to be grouped based on regional conditions, which would be expected to affect habitat conditions within freshwater ecosystems (see Figure 4-5 for a complete map of ecoregions included in the assessment). Although ecoregions based on global freshwater basins have been derived (e.g., Freshwater Ecoregions of the World, FEOW; Abell et al. 2008), this classification groups together several terrestrial ecoregions that would be expected to differ ecologically due to differences in biogeography and climate. For example, Alaska is largely included in one freshwater ecoregion despite the contrast between coastal areas and the mountainous Brooks and British Ranges. Svalbard, which is classified as Arctic Desert in TEOW, is grouped with northern Norway, Finland, the Kola Peninsula, and northwestern Russia as a single freshwater ecoregion in FEOW. Furthermore, Greenland was not assigned freshwater ecoregions, whereas it has been split into northern and southern ecoregions in TEOW. It was determined that the freshwater ecoregions were at too great a spatial scale for assessment, and climate-based terrestrial ecoregions were instead chosen to better allow assessment of the freshwater response to climate change.

Stations were further grouped into hydrobasins within the ecoregions for some analyses (Lehner and Grill 2013). Hydrobasins are standardly-derived basins that reflect natural flow patterns over the landscape, are at a smaller scale than ecoregions, and allow for the grouping of hydrologically-related systems instead of deriving catchment areas for all stations in the database. Because fish stations were more spatially concentrated, analysis of fish data used level 7 hydrobasins, whereas analysis of other FECs used the larger level 5 hydrobasins (to ensure a sufficient number of stations within each hydrobasin).

Because of differences in the number of stations sampled in each ecoregion, rarefaction curves were used to estimate alpha diversity within each ecoregion at a chosen number of stations (see detailed explanation in section 4.1.1.1), thus controlling for variability in sampling effort. This approach allowed for comparison of standardized estimates of alpha diversity across the circumpolar region that were less affected by local sample frequency. Beta diversity was estimated at the hydrobasin level to determine average beta diversity within each ecoregion and assess dominant components of beta diversity (see detailed explanation in section 4.1.1.2).

Figure 4-4 (a) Typical glacier-fed river food web, including primary producers and consumers and low-moderate glacial inputs, (b) glacier-fed river food web in the early stages of climate change, with increased glacial inputs, and (c) glacier-fed river in the late stages of climate change, when glacial inputs have ceased due to glacier retreat.
Figure 4-5 Terrestrial ecoregions that were included in the assessment of the circumpolar region. Only ecoregions with stations in the CBMP database were included in assessment. Source: Terrestrial Ecoregions of the World (TEOW; Olson et al. 2001)
4.1.1.1. Alpha Diversity

It is well established that the number of species encountered at a station correlates proportionally to the sampling effort, i.e., the total area sampled (Rosenberg and Resh 1993, Gotelli and Colwell 2001). Thus, the number of species observed increases as the sampling effort (number of samples) within a water body is increased or as more water bodies are sampled, reaching a plateau above a certain threshold that may depend on the sampling method. Because sampling effort varied among countries and within ecoregions, we applied rarefaction procedures to allow for sound comparisons of alpha diversity (or taxonomic richness) among our data. In this procedure, species accumulation curves were generated for each ecoregion (using the program EstimateS; Colwell 2013, Colwell and Elsensohn 2014), and curves were extrapolated to a higher number of sampled stations when necessary (e.g., see Colwell et al. 2004, Colwell et al. 2012). These curves can be used to estimate the accumulation of new species with added sampling effort, but they can also be used as rarefaction curves, to compare among different regions at a standard number of samples (e.g., if region A included 50 sampled stations and region B included 100 stations, diversity could be rarefied along the curve for region B to 50 stations for a more standardized comparison). Rarefaction curves were randomized 100 times, and the average taxonomic diversity (with upper and lower 95% confidence intervals) was rarefied for every station along the curve (to the maximum number of stations in an ecoregion or to a predetermined extrapolation point). Rarefied alpha diversity was then extracted from the curve at a set number of stations for all ecoregions to allow comparison of taxonomic richness at a standardized sampling level. A sub-analysis was completed for each FEC using ecoregions with high levels of sampling to rarely diversity to a greater number of stations, thus assessing patterns where spatial coverage of monitoring was high. All ecoregions with two or more stations were then rarefied (with extrapolation of the species accumulation curve, as needed) to a standard level of 10 stations for broad-scale assessment. Besides providing better comparisons of alpha diversity among water bodies, rarefaction procedures also alleviate the effects of sampling artifacts related to spatial scale or sampling effort that can vary across localities or regions.

Alpha diversity can be estimated as the number of species encountered, i.e., species richness. However, where identification to species level is not possible, or where taxa have been combined at a higher level to avoid mixed-level taxonomy, alpha diversity can describe family-level richness or simply taxonomic richness, which is the number of taxonomic units at a station. The taxonomic level at which alpha diversity was assessed differed depending on the FEC (see section 4.1.1.3)

4.1.1.2. Beta Diversity and Its Components

Beta diversity describes the level of dissimilarity in assemblage structure among stations within a defined region (Whittaker 1972). If beta diversity is high, stations likely have very large differences in taxonomic composition, whereas low beta diversity indicates that similar taxa are found at all stations. Beta diversity is complementary to alpha diversity, which simply assesses the number of taxa, and is defined as the diversity among ecosystems or the degree of assemblage differentiation in a region. Hence, beta diversity not only accounts for the relationship between local and regional diversity, but also informs about the degree of differentiation among biological assemblages. For example, it is possible for two stations to have a similar number of species (similar levels of alpha diversity), but to have different sets of species found at each station (high beta diversity across these stations).

There are many different ways to estimate beta diversity (Tuomisto 2010a, b), but one that is both simple and effective is to use Sørensen’s dissimilarity coefficient, β_{Sør} (Jost 2007, Baselga 2010). β_{Sør} ranges from 0 to 1, with 0 indicating that the same taxa are found at all stations, and 1 indicating that stations have completely different sets of taxa. This measure of beta diversity has the added benefit that it can be partitioned into the portion of beta diversity that is due to spatial turnover and the portion that is due to nestedness (Baselga 2010, Baselga and Orme 2012, Baselga et al. 2012). These components describe the way in which taxonomic composition differs across stations. For example, spatial turnover refers to replacement of taxa from one station to another, indicating that stations contain unique species (Baselga 2010, Baselga et al. 2012). In contrast, nestedness describes species loss from one station to another, and indicates that taxonomic composition at some stations is a subset of what is found at the richest station (Baselga 2010, Baselga et al. 2012). Figure 4-6 provides visual examples of differences between these components of beta diversity, as presented in Baselga (2010). In Figure 4-6a, there is nestedness across sites, as sites A2 and A3 contain a subset of the species found at A1. Figure 4-6b indicates an example of strong spatial turnover with equal richness across sites, as compositional differences among sites are due to unique species at each site. Figure 4-6c indicates a situation with both turnover and nestedness, as turnover is evident between sites C2 and C3 (unique species at each site, not found at the other site), but the species at both C2 and C3 are nested within the species found at site C1. Northward migration of species into the Arctic might be expected to increase spatial turnover within an area, as more new species begin to contribute to station differences. Estimating the relative contribution of spatial turnover and nestedness to beta diversity can provide important information for monitoring (Socolar et al. 2016). In a region with high spatial turnover, it would be necessary to sample a large number of stations to ensure accurate assessment of species richness (as new species would be introduced at each additional station). However, where nestedness dominates, it may be sufficient to monitor the stations with the highest richness to make accurate regional diversity estimates, though this depends in part on spatial scale of assessment.
4.1.1.3. Data Considerations for FECs

The database compiled by CBMP-Freshwater contains extensive information from over 9000 stations across the circumpolar Arctic (with stations defined as sampling locations with unique geographic coordinates) from which samples have been collected one or more times. For substantially fewer sites, there exists time series data that exceed 10 years. Paleolimnological data were also collected to allow for an assessment of historical trends beyond the contemporary time period. Data were collected and harmonized to standardize units of measurement and nomenclature as outlined in section 2.4.2.

An important consideration in the assessment of data collected by the different Arctic countries is that sampling methods must be comparable. For some biological FECs, the methods used were very similar across the circumpolar Arctic. However, differences were evident with respect to sampled habitats, sampling equipment, mesh size, and sample processing. Due to these differences it was necessary to simplify data (e.g., as presence/absence) or select subsets of data collected with more similar methods to account for these differences. Below, we outline the primary considerations for each of the FECs:

- **Algae from benthic samples:** Data on soft algae (non-diatoms) were only available for Norway, Greenland, and parts of Canada, and therefore the circumpolar analysis focused on diatoms, which were sampled across all regions. Data included lake rocky shoreline scrapes, top sediments of lakes, lake sediment cores (full cores and top/bottom cores), and river scrapes. Analysis generally focused on each group separately, though data from tops of cores were included in the analysis of lake top sediments. Counts or relative abundance data were available for most regions, with the exception of Greenland that only had presence/absence data, and therefore was excluded from some analyses. An adjusted taxonomic nomenclature was used that combined ambiguous or easily misidentified species at the genus level or into species complexes. Where information on sampling dates and depths of sediment core samples was not available or chronology was deemed to be problematic or not reliable, these data were excluded from the paleolimnological analysis.

- **Phytoplankton:** Data included a mix of presence/absence, counts, biovolume, and density,
most stations had biovolume data. Biovolume of phytoplankton taxa can be calculated in multiple ways, and it was necessary to identify the procedure used for each dataset and apply a correction for some data to make them all comparable. There was some mixed-level taxonomy (genus only or genus and species), and corrections were made to avoid taxonomic redundancy.

**Macrophytes:** Sampling methods for macrophytes varied substantially, ranging from simple observational notes to experimental designs with quadrats and measurements of biomass. To allow for broad-scale comparisons, all data were converted to presence/absence. Some regions had less emphasis on identification of mosses, and this was accounted for with subset analyses of moss data. Analysis was at the species level.

**Zooplankton:** Zooplankton data included vertical hauls (composite samples through the water column) and depth-specific samples. The latter were summed across the entire water column to make them comparable with composite samples. Mesh size of sample nets varied across studies, and an effort was made to select samples with comparable mesh sizes. Not all datasets included identification and enumeration of rotifers (i.e., studies were focused only on crustacean taxa), and therefore analysis was completed once with the subset of samples that included data on the full zooplankton assemblage (including rotifers), and once using all samples but selecting only crustacean taxa for analysis. Datasets that included identification only at a coarse level (e.g., order) were generally excluded from analysis and corrections were made to avoid mixed-level taxonomy. Pelagic samples were selected for analysis, and littoral crustacean taxa were removed from the data prior to analysis to ensure a focus on the pelagic habitat and assemblages.

**Benthic macroinvertebrates:** Data for lake benthic macroinvertebrates were obtained from the littoral, sub-littoral, and profundal zones where samples were collected using a variety of samplers (e.g., kick nets, stone scrubs, Surber samplers, dredges, Ekman grab, Ponar, corers). When top sediments were collected using corers, only Chironomidae (midges) were identified and enumerated to support paleolimnological work. Analysis therefore focused on subsets of data based on habitat, sampling method, and whether the full assemblage was assessed. Littoral data collected with kick nets or stone scrubs were combined for analysis, and profundal data collected with dredges or grab samplers were combined for a second analysis. Chironomidae were only identified to family level for many of these samples, so analysis was conducted at the taxonomic level of family or higher. A subset of profundal stations (including the paleo top cores) with Chironomidae to genus level were also analyzed. River samples had greater similarity in sampling methods and habitats than lakes, and analysis focused on samples from rocky substrates collected by kick nets. Mesh size was generally around 400-500 μm, though in some rare cases samples with a mesh size of 200 μm were used if no other samples were available for the region (generally only in Norway). Taxonomic level varied for river samples, and some samples were excluded if taxonomic level was too high (e.g., order level for USA samples) or excluded important groups (e.g., Finland samples that did not identify or enumerate chironomids and/or oligochaete worms). Because samples from Finland, USA, and some areas of Canada only identified chironomids to the family level, analysis was conducted on family-level data for the circumpolar region.

**Fish:** Sampling methods varied widely across the circumpolar region, with many different types of sampling equipment (e.g., gill nets, hoop nets, seine nets, electrofishing, minnow traps, angling) and different mesh sizes. In addition, a large number of datasets (particularly for Canada) targeted individual species or groups of species (e.g., those important for commercial fishing) and thus did not identify or enumerate species in the full fish assemblage. To account for this and improve comparability of data, analysis focused on data from samples that enumerated the full fish assemblage, and data were converted to presence/absence to focus on composition trends rather than patterns in abundance. Analysis was at the species level.

*Photo: Árni Einarsson*
Cyclotella Antiqua, a benthic algae species.
Photo: Kathleen Rühland
4.2. Algae from Benthic Samples

4.2.1. Introduction

Benthic algae are here defined in terms of the habitat in which samples were collected (e.g., lake sediments or streambeds), and thus include taxa collected from benthic habitats, regardless of whether they are otherwise defined as planktonic or benthic species. This definition allows for the comparison of all monitoring data collected by a particular method, without a need to classify species as benthic or planktonic. The Benthic Algae FEC describes primary producers that mainly occur in aquatic habitats, and includes both diatoms (class Bacillariophyceae) and soft algae (non-diatoms such as cyanobacteria, green algae, etc.). Algae from benthic samples are a heterogeneous group, ranging in size from micrometer-long small diatoms, cyanobacteria, or green algae to meter-long filamentous green algae. In benthic habitats, algae generally form a slippery, millimeter thick biofilm or thicker algal mats of around a centimeter. Benthic algae are important in food webs, and are often the main primary producers in open and shallow river stretches or lakes in the Arctic (refer to, e.g., Stevenson and Pan 1999, Wetzel 2001).

Studies of Arctic fresh waters have revealed that lake and stream benthic algae mats are commonly dominated by cyanobacteria, diatoms, and green algae (Conjugatophyceae and Chlorophyceae) (Wrona et al. 2013). Periphytic algal assemblages in Arctic streams are commonly composed of similar classes of algae, though assemblages are dominated by diatoms and cyanobacteria in the Canadian high Arctic (Lento et al. unpublished). In general, these algae provide important nutritional benefits to higher trophic levels, with diatoms in particular having substantial amounts of important fatty acids (Torres-Ruiz et al. 2007). Grazing of algae by herbivores can be affected by algal traits (e.g., morphology), nutritional value that can be modified by algal composition and environmental factors (Müller-Navarra et al. 2000, Ravet et al. 2003), as well as by invertebrate and fish predation on herbivores.

Most algae species in Arctic freshwaters are not restricted to polar regions, and their distributions reflect local geology and water chemistry conditions rather than thermal preferences (Wrona et al. 2013). Biomass of algae from benthic samples in lakes and rivers declines with increasing latitude, which may reflect the shorter growing season at high latitudes (Wrona et al. 2013). Arctic diatom diversity in both lakes and rivers is predicted to be affected by pH, nutrients, and metals, as found in temperate regions (Smol and Stoermer 2010). Additionally, lake diatom assemblage composition is expected to be driven by differences in the thickness and seasonal duration of ice cover, as these can affect light levels, length of the stratification period, and change across the 10°C July isotherm (Pienitz et al. 2004). In high Arctic regions, shallow, small water bodies might be most sensitive to the effects of climate change, and might display the most pronounced community shifts (Pienitz et al. 2004). Large-scale assessments of algal distributions from benthic samples in Arctic lakes and streams have not been previously done, and thus the broad-scale effect of climate change and human development on this FEC is unknown. In Arctic regions, diatom sampling is preferred over sampling the full assemblage (diatoms and non-diatoms) because of the greater ease of processing and identification of diatoms. Moreover, research on algae from benthic samples in Arctic lakes and rivers generally considers only diatoms or estimates biomass of the entire biofilm through bulk chlorophyll assessment. Thus, a broad-scale assessment of algal biodiversity from benthic samples using existing data must focus on the diatom component of these samples. Diatoms are advantageous for monitoring because they are sessile and thus cannot escape impacts, they grow quickly, react readily to environmental changes, and integrate impacts over a period of weeks. They are often the dominant algal group in benthic samples, are ubiquitous, and are diverse (> 100 taxa possible per cm2). Sample collection is simple, and the glass diatom frustule is preserved well over time (and in sediments), facilitating species-level identification. Diatom ecology and taxonomy is well-studied, and environmental preferences of species are well known, including the response to stressors such as eutrophication, acidification, pollution, salinisation and toxicants (Pienitz et al. 2004, Smol and Stoermer 2010, Villeneuve et al. 2013). These characteristics make diatoms valuable indicators of environmental change in freshwater ecosystems.
4.2.2. Objectives and Approach

Circumpolar assessment of contemporary diatom assemblages was completed for lake surface-sediment samples (i.e., top sediments or tops of cores) and river benthic scrapes. For this analysis, stations were grouped by ecoregion, which are terrestrial regions with similar geography and climate (Olson et al. 2001). Alpha diversity was assessed for each ecoregion by rarefying to a standard set of stations, while beta diversity was estimated within ecoregions and broken down into its components, i.e., turnover and nestedness. Diatom assemblages in lake surface sediments and shoreline scrapes, as well as in river benthic scrapes were also evaluated spatially to study contemporary biodiversity and compositional patterns. This was done both on a circumpolar scale and across a latitudinal (temperature) gradient, and for comparisons between North America and Europe. In addition, paleolimnological data (full lake sediment cores and tops/bottoms of cores) were used to assess long-term changes in biodiversity of lake diatom assemblages. The top-bottom approach is commonly applied in paleolimnological studies in order to assess change between two periods of time in a study set including a large number of lakes (e.g., Rühland et al. 2003). The results provide a before-and-after snapshot of lake conditions, often between the pre-industrial period and the late 20th century, when most lakes have experienced some form and degree of anthropogenic impact.

Diatom data were collected from both national monitoring programs and academic research studies, as routine monitoring of diatoms is limited to only a few countries (e.g., Sweden, Finland). Samples included those for which diatom assemblage structure was analyzed from prepared slides and where at least 300 diatom valves were enumerated under the microscope. Diatom nomenclature was harmonized at the genus or species level across the circumpolar region, and taxonomic differences due to variability in laboratory analysis methods were minimized by grouping some taxa into species complexes.

4.2.3. Overall Patterns and Trends

4.2.3.1. Circumpolar Diversity

4.2.3.1.1. Lakes

Lake diatom stations were arguably the most evenly distributed across the circumpolar region of all the FECs, although coverage was patchy in Russia and stations were lacking in the High Arctic of Greenland or Svalbard (Figure 4-7a). Ten ecoregions across the Arctic had sufficient numbers of samples to allow for comparison of rarefied richness estimates at 40 stations. Among these ecoregions, the highest alpha diversity was found in the Arctic Coastal Tundra in Alaska, with an average of 239 taxa (harmonized to include species complexes) in 40 stations, which was significantly higher than all other ecoregions (Figure 4-7b). High alpha diversity was also evident in northern Canada (Middle Arctic Tundra and High Arctic Tundra) and Iceland (Iceland Boreal Birch Forests and Alpine Tundra), where on average over 205-215 taxa were found in 40 stations (Figure 4-7b). Russia and Fennoscandia had slightly lower, but not significantly different alpha diversity levels (in the Taimyr-Central Siberian Tundra and Scandinavian Montane Birch Forest and Grasslands). The lowest alpha diversity was found in southern Greenland, in the Kalaallit Nunaat Low Arctic Tundra, which both had only 28 taxa on average in 40 stations (Figure 4-7b), whereas the southern ecoregions in Canada had low to moderate levels of alpha diversity (126 to 178 taxa in 40 stations).

Similar patterns were evident when rarefied taxonomic richness was compared across all 19 ecoregions at a level of 10 stations. The Arctic Coastal Tundra, Middle Arctic Tundra, and Iceland Boreal Birch Forests and Alpine Tundra remained high alpha diversity ecoregions, but the Scandinavian and Russian Montane Birch Forest and Grasslands had similar richness to these ecoregions when only 10 stations were considered (Figure 4-7c). The highest diversity was in the Southern Hudson Bay Taiga in Canada, with an average of 155 taxa in 10 stations; however, this ecoregion did not differ significantly from those in the range of 135-150 taxa. The High Arctic Tundra was in a lower alpha richness class when only 10 stations were considered, and was similar to the Scandinavian and Russian Taiga and the other Russian ecoregions (East Siberian Taiga, Taimyr-Central Siberian Tundra, and Northwest Russian-Novaya Zemlya tundra), where 120-130 taxa were found on average in 10 stations. The Kalaallit Nunaat Low Arctic Tundra continued to have the lowest alpha diversity across all regions, but low richness was also found in a mountainous Alaskan ecoregion (Brooks-British Range Tundra) and in eastern and southeastern Canadian ecoregions (Baffin Coastal Tundra, Eastern Canadian Forests, and Eastern Canadian Shield Taiga), where average alpha diversity ranged from 65 to 98 taxa in 10 stations (Figure 4-7c).

Beta diversity \( \beta_{SOR} \) ranged from 0.50 to 0.88 when averaged across hydrobasins in an ecoregion, which indicated that there was generally moderate to high dissimilarity in community structure among stations within hydrobasins. The highest dissimilarity among stations (\( \beta_{SOR} = 0.88 \)) was found in the Kalaallit Nunaat Low Arctic Tundra, which had the lowest alpha diversity. Thus, despite the low number of taxa, stations in the ecoregion were highly dissimilar. Furthermore, lake beta diversity was dominated by the turnover component in all ecoregions, which indicated that there was a high degree of species replacement across stations (Figure 4-7d), and a low contribution of nestedness to beta diversity (ranging from 3% to 23%, but at 15% or lower for 16 ecoregions). This suggests that spatially-extensive sampling is necessary to capture the majority of species across these ecoregions.
Figure 4-7 Circumpolar assessment of lake diatoms, indicating (a) the location of lake diatom stations, underlain by circumpolar ecoregions; 
(b) ecoregions with many lake diatom stations, colored on the basis of alpha diversity rarefied to 40 stations; (c) all ecoregions with lake diatom 
stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis 
of the dominant component of beta diversity (i.e. species turnover, nestedness, approximately equal contribution, or no diversity) when averaged 
across hydrobasins in each ecoregio.
4.2.3.1.2 Rivers
River diatom data included large gaps in Russia, Iceland, and in the western Canadian low Arctic and sub-Arctic regions (Figure 4-8a). Eight ecoregions had a sufficient number of stations to allow for comparison of richness rarefied at the level of 40 stations. Among these, there were distinct and significantly different groupings of ecoregions with similar alpha diversity. The highest alpha diversity was in the Arctic Coastal Tundra in Alaska, which on average had 252 taxa in 40 stations (Figure 4-8b). The Fennoscandian ecoregions (Scandinavian and Russian Taiga, and Scandinavian Montane Birch Forest and Grasslands) were similar in alpha diversity, which ranged from 180 to 197 taxa. The northern Canadian ecoregions of the Middle Arctic Tundra and High Arctic Tundra had similar alpha diversity at 115-116 taxa on average in 40 stations (Figure 4-8b). Finally, the lowest richness was found in the eastern and southern Canadian ecoregions (Torngat Mountain Tundra, Eastern Canadian Shield Taiga, and Low Arctic Tundra), which ranged from 91 to 95 taxa on average in 40 stations.

Figure 4-8 Results of circumpolar assessment of river diatoms, indicating (a) the location of river diatom stations, underlain by circumpolar ecoregions; (b) ecoregions with many river diatom stations, colored on the basis of alpha diversity rarefied to 40 stations; (c) all ecoregions with river diatom stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.
Comparison of richness values rarefied to 10 stations allowed the inclusion of two additional ecoregions in Greenland and one in Fennoscandia. Both of the Greenland ecoregions had the lowest alpha diversity estimates across the study area (Figure 4-8c). The Kalaallit Nunaat Low Arctic Tundra had an average of 3 taxa in 10 stations, whereas that for the Kalaallit Nunaat High Arctic Tundra averaged 28 taxa in 10 stations, with both values being significantly lower than those for the remaining ecoregions (Figure 4-8c). The Scandinavian Coastal Conifer Forests had low alpha diversity, similar to the Torngat Mountain Tundra, which is also a coastal ecoregion. Comparing the remaining ecoregions at only 10 stations (rather than at 40) resulted in less clear groupings of ecoregions in the low to moderate classes of alpha diversity (e.g., those ranging 52–72 taxa in 10 stations), with some shifts in the similarity of ecoregions. For example, High Arctic Tundra became more similar to the Low Arctic Tundra than to the Middle Arctic Tundra (Figure 4-8c). The observation that groupings of ecoregions were less evident when only 10 stations were sampled emphasizes the importance of sampling a sufficient number of stations in order to capture the range of species present and, consequently, accurately characterize alpha diversity within ecoregions.

Beta diversity within an ecoregion was highly variable for river diatoms, as $\beta_{\text{SCR}}$ ranged from 0.2 (indicating strong similarity among stations in an ecoregion) to 0.81 (indicating strong dissimilarity among stations). Seven of the ecoregions had moderate dissimilarity among stations, with $\beta_{\text{SCR}}$ between 0.5 and 0.65. The lowest beta diversity was in the Kalaallit Nunaat Low Arctic Tundra ($\beta_{\text{SCR}} = 0.2$) and the Scandinavian Coastal Conifer Forests ($\beta_{\text{SCR}} = 0.37$). In contrast, the highest beta diversity was in the Torngat Mountain Tundra ($\beta_{\text{SCR}} = 0.81$) and the Scandinavian Montane Birch Forest and Grassland ($\beta_{\text{SCR}} = 0.75$). Interestingly, one of the lowest beta (Scandinavian Coastal Conifer Forest) and the highest beta (Torngat Mountain Tundra) ecoregions had similar alpha diversity estimates at 10 stations (56 and 52 taxa, respectively). These ecoregions also differed with respect to the dominant component of beta diversity, as the Torngat Mountain Tundra was dominated by taxonomic turnover (90% of beta), whereas the Scandinavian Coastal Conifer Forests had more similar contributions of turnover and nestedness (64% and 36% of beta, respectively; Figure 4-8d). Across all ecoregions, turnover generally remained the dominant component of beta diversity. However, in the Kalaallit Nunaat Low Arctic Tundra, beta diversity was completely due to nestedness (Figure 4-8d), which reflected the low richness and low number of stations in this ecoregion.

4.2.3.2. Regional Diversity

Circumpolar analysis of ecoregions showed high biodiversity in both lakes and rivers along the northern Alaskan coast, in the Canadian Arctic Archipelago, and in Fennoscandia. At the site scale, lake stations with high alpha diversity were found throughout the circumpolar region (Figure 4-9), whereas clusters of high diversity river stations were somewhat more evident in Alaska and Fennoscandia (Figure 4-10). However, data were more spatially limited for rivers, which may have affected the distribution of taxonomic hotspots. Differences in diversity across the circumpolar regions may be related to a number of factors, including time since glaciation, underlying geology type, and site-specific substrate and nutrient conditions. For example, a number of samples from Alaska were collected in marshy habitats with sandy substrates and high levels of organic material, which may have led to different taxonomic composition than would be expected in rocky habitats. Furthermore, northern Alaska and the Arctic Archipelago are primarily underlain by sedimentary and sedimentary/volcanic bedrock, in contrast to the non-sedimentary bedrock underlying the southern Canadian Arctic regions. These geological differences may have contributed to contrasting diversity across these regions, as diatom species composition is strongly affected by underlying geology through its effect on water chemistry (Grenier et al. 2006).

Figure 4-9 (left) Global species richness of diatom communities in Arctic lakes, with stations over the global mean taxonomic richness in red, and (right) local species richness of diatom communities in Arctic lakes across a latitudinal gradient.
Samples with the highest diatom richness, for both lakes and rivers, were generally in the latitude range of 60-75°N (Figure 4-10). However, the decline in richness outside this latitudinal range was small, and partly due to the fact that fewer samples were collected at the highest latitudes (above 75°N), particularly in rivers. Taxa accumulation curves indicated that an asymptote was not reached for either lake or river samples in any Arctic zone (sub-, low, or high Arctic; Figure 4-11), which suggests that raw richness estimates were affected by sampling effort. Taxa accumulation curves for lakes were similar until approximately 100 samples, above which high Arctic lakes had significantly lower taxonomic richness than sub- or low Arctic samples (Figure 4-11). Similar results were observed for lakes, though the species accumulation curve for the low Arctic appeared to reach a richness value that was significantly higher than the estimate for the sub-Arctic (with no overlap of 95% confidence intervals for the two regions) at around 225 samples. Differences among Arctic zones were more evident for river data. The high Arctic had significantly lower taxonomic richness than the other two zones at 50 samples, whereas the low Arctic reached significantly higher richness than the sub-Arctic at approximately 75 samples. Patterns in lakes and rivers across Arctic zones were thus similar, but differences were stronger and more evident for river samples.

Figure 4-10 (left) Global species richness of diatom communities in Arctic streams, with stations over the global mean taxonomic richness in red, and (right) local species richness of diatom communities in Arctic streams across a latitudinal gradient.

Figure 4-11 Taxa accumulation curves for (left) lakes and (right) rivers in the high Arctic (red), low Arctic (green), and sub-Arctic (blue) zones.
4.2.3.3. Compositional Patterns

Diatom taxa that were found to dominate the samples from across the circumpolar region are generally also common in other regions of the world, consistent with the suggestion that most algal species are not limited to the polar regions (Wrona et al. 2013). Within the studied regions, among-site differences in diatom assemblages were small, resulting in gradual shifts in composition across regions rather than clear thresholds of change. Many of the taxa that were present across the Arctic have an ecological preference for low nutrient levels and neutral pH, though a number of the identified taxa display a wide range of tolerances to environmental conditions and can be found in nutrient-rich conditions.

Diatom samples were grouped into biotypes with self-organizing maps (SOMs) to determine natural groupings of sites based on assemblage structure similarity and to evaluate spatial distributions of taxa. There were gradual changes between groups of sites rather than sharp differences, which indicated that there were no profound shifts in species taxa composition among regions. Clusters of samples did not differ significantly between North America and Europe/Russia, which indicated that taxa composition was not linked to longitudinal position (Figure 4-12). Instead, some of the similarity among sites was related to latitude, with apparent clusters of taxa associated with high latitude and low temperatures, particularly for the most spatially extensive dataset of lake top sediments (Figure 4-12).

Lake top sediment samples were characterized by six SOM clusters (biotypes), one of which represented a diatom assemblage that only occurred at very high latitudes (>70°N) and cold temperatures (< -15°C degrees annual average). This cluster was also characterized by a high number of unique species, contributing to the distinction of these northern samples. There were four SOM biotypes found for rivers, two of which were associated with high latitudes (>70°N). Of the high latitude biotype in rivers, only one was associated with cold temperatures (< -7°C annual average degrees). Lake shoreline samples were collected only at lower latitudes and thus did not allow for assessment of compositional differences between Arctic zones. Shoreline samples were characterized by three SOM biotypes, one of which was associated with higher latitudes than the others (>60°N) and colder temperatures (approximately < -7°C annual average degrees).

Figure 4-12 Diatom groups from Self Organizing Maps (SOMs) in lake top sediments, showing the geographical distribution of each group (with colors representing different SOM groups).
4.2.3.4. Temporal Trends

4.2.3.4.1. Lake sediment core top-bottom analysis

Analysis of differences between the tops and bottoms of lake cores was completed for 116 lakes, only 5 of which were located outside of North America. We divided the lakes into four categories based on geographical location, climate and vegetation (Boreal forest = BF, transition zone = T, Low Arctic = LA, High Arctic = HA). For certain analyses, sites were also categorized into 3 depth categories: ponds (< 2m), shallow lakes (2.1–6 m) and deep lakes (> 6.1 m). Figure 4-13 illustrates the number of lakes per geographic zone for each of the depth categories.

The dataset for the top-bottom analysis included 452 diatom taxa, many of which were rare (e.g., found in low numbers at a single station). To eliminate rare taxa and reduce noise, only taxa that represented at least 2% in at least one sample were retained for the analysis, which reduced the number of species in the data set from 452 to 174. We then used the Bray-Curtis (B-C) dissimilarity coefficient to evaluate the difference in assemblage composition between ~1800 CE and contemporary sediments within each study lake. High values of this coefficient (which ranges from 0 to 100%) indicate strong dissimilarity between samples, whereas low values indicate that samples are similar. Mean values of the B-C dissimilarity coefficient were compared to assess if depth (pond, shallow, deep) and geographical zone (BF, T, LA, HA) influenced similarity between the bottoms and tops of cores.

B-C dissimilarity coefficient analysis showed a very wide range of similarity between tops and bottoms of cores among the stations (Bray-Curtis ranging between 14% and 91%; geographical distribution presented in Figure 4-14). Although the number of lakes outside North America was limited, the results suggested that systems in northern Siberia have changed more over time than those in northern Finland. In North America, western and high Arctic clusters (Tuktuuyuktuk, Alaska, Ellesmere Island and other high Arctic Islands) displayed the largest change between now and c. 200 years ago. These were followed by the central Canadian sites (NWT and Hudson Bay lowlands). Finally, lakes in the central and eastern Canadian Arctic (lower islands of the Arctic Archipelago, Baffin Island and Northernmost Ungava) showed the least change in diatom assemblages in the past c. 200 years.

In North America, continent-wide long-term climatic changes, such as deglaciation, are known to follow a west-east spatio-temporal gradient (Dyke 2004). This is also true of recent climatic warming, evidenced by the degree of change observed in biotic assemblages over the past c. 200 years (Smol et al. 2005). The low degree of change in many eastern Canadian lakes may reflect the temperature stability that has been noted in this area, as the easternmost regions of the Canadian Arctic have not warmed as much as the west and the far north (Prowse et al. 2006a). At sites on central high Arctic islands including Victoria, Prince of Wales and Devon, in eastern and southern Baffin Island, as well as in northernmost Ungava, across the Hudson Strait, changes in diatom assemblages over the past 200 years have remained minor. This is likely to change in the near future, as climate warming and long-distance atmospheric deposition of pollutants increasingly encroach into the region (e.g., Saulnier-Talbot et al. 2015).

The highest latitudes in the Canadian Arctic region have some of the largest temporal variability among stations. This region includes some of the lakes with the largest change over the last c. 200 years, but also includes stations that have recorded very low levels of change. The duration of ice cover is the main environmental variable that has been driving the changes in diatom assemblage composition in this region (Griffiths et al. 2017), with the ice-free season changing from almost none to several weeks per summer. However, not all lakes in the Canadian Arctic region are subject to homogeneous decreases in ice-cover (Keatley et al. 2008), which can explain the large variation in temporal patterns among lakes at high latitudes. Temporal shifts in diatom communities may be less evident where there has not be a change to ice cover duration due to lake morphometry (e.g., deeper lakes, such as Elison Lake; Smol and Douglas 2007, Keatley et al. 2008), localized conditions (e.g., Skeleton Lake, where shading and shelter from wind have sustained ice

Figure 4-13 Number of deep lakes (light speckled grey), shallow lakes (solid dark grey) and ponds (dark speckled grey) in each geographical zone (BF, T, LA, HA). BF = Boreal Forest, T = Transition Zone, LA = Low Arctic, HA = High Arctic.
Figure 4-14 Map showing the magnitude of change in diatom assemblages between bottom (pre-industrial) and top (modern) section of the cores, estimated by Bray-Curtis (B-C) dissimilarity. Boundaries for the B-C dissimilarity categories are based on distribution quartiles (0-30%, 30-40%, 40-50% and >50%), where the lowest values (blue dots) represent the lowest degree of change in diatom assemblage composition between top and bottom sediment core samples in each lake.

cover; Keatley et al. 2008) (e.g., Skeleton Lake, where shading and shelter from wind have sustained ice cover; Keatley et al. 2008), or where the climate signal is dampened by other impacts (e.g., Eider Pond, which is dominated by the effects of bird colonies; Michelutti et al. 2010).

In some areas of the Arctic, there were clear shifts in taxa that contributed strongly to dissimilarity between bottom and top core samples. The large change recorded in the Russian sites reflected a transition in the assemblages from small *Fragilarias sensu lato* to epiphytic taxa (especially *Achnanthidium minutissimum*) in one lake, and from a strong dominance of *Aulacoseira humilis* (over 50% of the assemblage) to a more diverse assemblage dominated by small *Fragilarias sensu lato* in the other lake. Changes in the diatom assemblages of lakes located in the Central Canadian Arctic (continental NWT and Hudson Bay Lowlands) were characterised by a switch from a predominance of small, benthic *Fragilarias sensu lato* species to planktonic taxa such as *Discostella stelligera* (Rühland et al. 2003), reflecting changes in the length of the ice-free season and in stratification of the water column (Saros et al. 2016). Temporal change within lakes showed a high degree of similarity across this region. In contrast, in the subarctic Hudson Bay lowlands, temporal change was highly variable between lakes. In this region, diatom assemblages also responded to climatic warming and decreased ice-cover with an increase in planktonic species, relative to the pre-1850 period (Rühland et al. 2014).

Geographic zone and depth did not have a significant effect on B-C dissimilarity (two-way ANOVA; p > 0.05). However, mean within-zone and -lake type B-C dissimilarities suggested that ponds have changed more than shallow and deep lakes and that changes in boreal forest and transition zones are more pronounced than in the low Arctic and high Arctic. Ponds in the boreal forest and in the high Arctic changed more than those in the transition and low Arctic zones; shallow lakes in the transition and low Arctic zones changed more than in the boreal forest and high Arctic; and deep lakes in the boreal forest and transition zones changed more than those in the low Arctic and high Arctic zones (Table 4-1). This strong spatial heterogeneity suggests that different lake types respond differently to change in different biomes.

**Table 4-1** Lake depth categories that have changed the most in each geographic zone.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Ponds</th>
<th>Shallow lakes</th>
<th>Deep lakes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal Forest</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Transition Zone</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Low Arctic</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>High Arctic</td>
<td></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>
4.2.3.4.2. Identification of Sentinel Species

A SIMPER analysis (similarity percentage) was conducted using the Top-Bottom data to identify individual taxonomic groups that contributed most to the observed differences between pre-industrial and present-day assemblages. This multivariate analysis quantifies the contribution of each variable in a group and can help to identify the variables responsible for the differences between groups (here, fossil versus modern samples). For selected indicator taxa, we plotted the bottom vs. top relative abundances to evaluate the concordance between past and modern data (1:1 plot). The distribution of relative abundances along the 1:1 line indicates the shifts in abundance of these taxa between past and present (below the 1:1 line indicates higher abundances in fossil samples while above the 1:1 line indicates higher abundances in modern samples).

A number of diatom taxa showed large changes in relative abundances between bottom and top samples of the cores. In the boreal forest, the most striking assemblage change was from a predominance of small *Fragilaria* sensu-lato to the planktonic species *Discostella stelligera* in all the deep lakes and in most shallow lakes. This was also the case in many low Arctic lakes, and to a lesser degree was also visible in the transition lakes. In the high Arctic, there was a change from small *Fragilaria* sensu lato to a more diverse assemblage dominated by other small benthic taxa such as *Achnanthes minutissima*, which were found at higher relative abundances in modern samples than in fossil samples for ponds. Ponds in the boreal forest showed a shift to lower relative abundances of *Nitzschia fonticola* in modern compared with fossil sediments. *Pseudostaurosira brevistriata* similarly declined in modern samples relative to fossil samples in lakes of all sizes in the transition zone.

When samples were pooled across all Arctic zones and lake sizes, there was evidence that the Discostella complex showed a higher relative abundances in modern sediments than in fossil sediments (Figure 4-15), indicating a major temporal shift in the prevalence of this group. Increased relative abundance in modern sediments was also evident for *Psammothidium marginulatum/scoticum/levenderi* (Figure 4-15). Whereas both of these groups increased in dominance in modern sediments, there were other taxonomic groups that became less prevalent in modern samples, including *Aulacoseira perglabra* complex and *Staurosirella pinnata* complex (Figure 4-15). Such a shift in taxa could indicate changes in lake stratification over time in response to climatic changes.

4.2.3.4.3. Downcore Analysis

Diatom composition was analyzed along the length of the core (downcore) to evaluate gradual temporal changes in assemblage structure and biodiversity since the early 19th century. This analysis provided a representation of ecological reorganization that was similar, albeit more in-depth, to the analysis of top and bottom core samples. Only cores that had robust chronologies were retained for this analysis (a total of 52). Samples along the length of the core were compared in multivariate analysis (Detrended Correspondence Analysis) to obtain a measure of beta diversity, which indicated the degree of dissimilarity across the c. 200 years of sediments analyzed from the core. The years in which the sediments were sampled varied considerably. As such, some cores may have been retrieved before the beginning of significant warming in certain areas of the study region, affecting the degree of change between recent and past.

Sediment core analysis results showed high variability in beta diversity across downcore samples, which indicated
that rates of change in diatom assemblage composition were not the same across the sampled lakes. Nevertheless, some regional trends were observed. The areas that showed the least change since c. 1800 (lowest beta diversity) included northernmost Québec and eastern Baffin Island in Canada, the Central Canadian Archipelago and northern Finland (Figure 4-16). Sites in the Canadian high Arctic and northeastern Northwest Territories, Canada showed moderate overall change, whereas the largest changes were observed in the westernmost cluster of sites, near the Beaufort Sea in Canada, and southernmost sites (southern Hudson Bay; Figure 4-16). Variability in relative change among lakes was high at these sites. However, these results are similar to those obtained by Smol et al. (2005).

4.2.4. Gaps in Knowledge and Monitoring

Lake top sediment samples covered a large extent of the circumpolar region, but this coverage was primarily due to academic research, and thus does not represent repeated monitoring. Additional data from academia do exist (for example, additional samples are available from paleolimnological training datasets for Europe, including samples on Svalbard and on the Kola Peninsula in Russia), and these could be integrated into the CBMP database for future assessments. Any further assessment of diatoms from lake sediments must rely primarily on academic data, as these samples are not generally part of monitoring programs, with the exception of monitoring by industry and local- or regional-scale government monitoring (e.g., the province of Québec in Canada). However, the advantage of diatom samples in lakes is that long-term changes can be inferred from collecting sediment cores, thus compensating for the lack of routine monitoring activities.

River samples were more sparse, and were lacking from Russia, Iceland, Greenland, Svalbard, and central and western Canada. Although river algae monitoring takes place in some Arctic countries (e.g., Norway, Sweden, Finland), it is limited elsewhere in the circumpolar region (though some local- or regional-scale government monitoring occurs, e.g., the province of Québec in Canada). Furthermore, even in countries where monitoring occurs, the samples may not always be comparable if they focus on non-diatoms (e.g., in Norway) or do not follow comparable procedures (e.g., if they do not digest samples, thus potentially obscuring diatom taxa and making species-level identification impossible). Obviously, there is a clear need to increase the spatial scope of river diatom monitoring in order to capture the full variability in biodiversity across the circumpolar region.

Paleolimnological data for lakes similarly had gaps, in particular across most countries outside North America, resulting from the need to acquire downcore and top-bottom core data from academic sources, as this work is not conducted as part of routine monitoring. In some cases, core data were obtained from published research, but critical information on dates and/or depths may have been missing, or data were obtainable as presence/absence only, when analysis focused on relative abundances. Additional paleolimnological data repositories exist and could be accessed to improve data coverage, particularly for Europe where there was little collection of data of this type. Furthermore, it would be beneficial to make a targeted effort to approach paleolimnological researchers who have not been involved in the CBMP process, to request access to full core data that could fill the gaps in spatial coverage and allow for a broader assessment of long-term trends.

Figure 4-16 Map showing the magnitude of change in diatom assemblages for downcore samples, with beta diversity used as a measure of the compositional differences between samples at different depths along the core. Boundaries for the beta diversity categories are based on distribution quartiles (0-0.1, 0.1-1.24, 1.24-1.5, >1.5), where the lowest values (blue dots) represent the lowest degree of change in diatom assemblage composition along the length of the core in each lake.
Achnanthes minutissima.
Photo: Chris Carter
4.3. Phytoplankton

4.3.1. Introduction

Primary producers living in the water column (pelagic zone) of lakes are microscopic phytoplankton that include single cells and small-cell colonies that rely on dissolved nutrients and light for growth. Although phytoplankton cells account for < 1% of photosynthetic biomass on earth, they are responsible for about 50% of global net primary production and are the primary source of energy in lake ecosystems (Field et al. 1998). Phytoplankton communities of Arctic lakes typically include diatoms, dinoflagellates, chrysophytes, and benthic cyanobacteria, while chlorophytes and pelagic cyanobacteria are less common (Sheath 1986, Forsström et al. 2005). Few, if any, species of phytoplankton are exclusively found in the Arctic; diatoms species are numerous but chrysophytes (e.g., Dinobryon) and dinoflagellates (e.g., Gymnodinium) are represented by fewer species. Species such as Dinobryon are adapted to utilise bacteria as an energy source, thus they can grow during winter with little or no light and then switch to photosynthesis as light becomes available. In addition, the dynamics of phytoplankton community composition have important implications for biogeochemical cycling processes (Winder and Sommer 2012).

Species richness and biomass can range greatly across Arctic lakes depending on environmental conditions that regulate their need for resources, including factors such as temperature, precipitation, UV radiation levels, spread of viruses and fungi, and predation by zooplankton (Prowse et al. 2006b, Reynolds 2006). Species numbers can total up to several hundred per lake and be correlated negatively with latitude and negatively with altitude (and thus water temperature; Stomp et al. 2011). Phytoplankton biomass and community composition is commonly regulated by the availability of light and the key nutrients, nitrogen (N) and phosphorus (P) (Sterner and Elser 2002, Mette et al. 2011). Under N-deficient conditions, Cyanobacteria can become dominant because this group is capable of converting atmospheric N2 (i.e., nitrogen fixation) to biologically-available N forms (Pick and Lean 1987). In clear, nutrient-poor Arctic lakes, phytoplankton production is low and dominated by small species. Phytoplankton species are often the preferred food source for filter feeders; however, in nutrient-poor lakes some pelagic feeders can obtain a higher proportion of their diet from benthic primary production (Vadeboncoeur et al. 2003, Mariash et al. 2014). Small-bodied taxa like the Chrysophyte, Cryptomonas, are often the most dominant pelagic algal groups; however, diatoms and dinoflagellates can also be numerically dominant (Christoffersen et al. 2008).

Phytoplankton species distribution and composition has been well studied in some regions of the Arctic but is not standardly included in monitoring programs. There has been no large-scale description of the biogeographical distribution of phytoplankton species in the Arctic regions (Wrona et al. 2013); however, studies from lower latitudinal gradients (e.g., Stomp et al. 2011) point to a decrease in diversity towards the North that may reflect responses of environmental drivers to geographical gradients (latitude, longitude and altitude). Since important abiotic factors driving phytoplankton growth, such as nutrients and temperature, decrease towards higher latitudes, species richness is expected to be lower in the Arctic compared to temperate regions. Nevertheless, phytoplankton richness can be relatively high in oligotrophic boreal lakes (Forsström et al. 2005), and this is especially the case for shallow lakes with many semi-planktonic species of desmids and diatoms. Mass blooms of harmful, toxin-producing cyanobacteria or other nuisance species are rarely reported in the water column, although they often dominate the microbial mat communities in Arctic lakes (Bonilla et al. 2005).

4.3.2. Objectives and Approach

The aim of this assessment is to provide a summary of phytoplankton biodiversity in lakes from the high Arctic to the sub-Arctic regions to provide a baseline for future monitoring programs, detect any changes that have occurred over time and identify gaps in spatial coverage across the Arctic. The assessment also includes summaries of spatial and temporal patterns of biodiversity and biomass in Arctic lakes. Sample locations were grouped into ecoregions of similar geography and climate (Olson et al. 2001) at a circumpolar scale, and alpha diversity, beta diversity, and its component parts (turnover and nestedness) were evaluated within ecoregions. Spatial and temporal patterns in phytoplankton diversity and species composition were also assessed at a regional scale (by country and by Arctic region) for the circumpolar Arctic. This assessment of phytoplankton diversity, which is based on contemporary data, provides a baseline with which future monitoring results can be compared and identifies gaps in the current distribution of phytoplankton monitoring.
4.3.3. Overall Patterns and Trends

4.3.3.1. Circumpolar Diversity

For the among-ecoregion comparisons, alpha diversity (taxon richness) was assessed for 6 ecoregions that had 30–69 lakes/stations (Figure 4-17a). When data were rarefied to assess taxonomic richness at 35 stations for each ecoregion, the highest alpha diversity was found for the Arctic Coastal Tundra in Alaska (268 taxa), followed by the Low Arctic Tundra in Canada and the Kalaallit Nunaat High Arctic Tundra in Greenland (with 225 and 219 taxa, respectively; Figure 4-17b). Alpha diversity was lower in southern Greenland, where lakes on the Kalaallit Nunaat Low Arctic Tundra had 186 taxa, and in the ecoregions sampled in Russia (lakes on the East Siberian Taiga had 112 taxa and those on the Taimyr-Central Siberian Tundra had 81 taxa; Figure 4-17b). Differences between ecoregions were significant for all but the Low Arctic Tundra and the Kalaallit Nunaat High Arctic Tundra.

Another eight ecoregions had data for 19 or fewer stations and were not included in among-ecoregion comparisons above, as extrapolation to 35 stations was far outside the range of stations per ecoregion. To include ecoregions with

![Figure 4-17](image-url) Results of circumpolar assessment of lake phytoplankton, indicating (a) the location of phytoplankton stations, underlain by circumpolar ecoregions; (b) ecoregions with many phytoplankton stations, colored on the basis of alpha diversity rarefied to 35 stations; (c) all ecoregions with phytoplankton stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.
fewer sampled stations, the analysis was conducted on all ecoregions with rarefaction and extrapolation used to assess taxonomic richness at a sampling effort of 10 stations in a region. The Scandinavian and Russian Taiga, the Scandinavian Montane Birch Forest and Grasslands, and the Northern Canadian Shield Taiga had the highest alpha diversity at 280, 247, and 201 taxa, respectively (Figure 4-17c). These estimates of taxonomic richness were all significantly different (no overlap among 95% confidence intervals). In this assessment at 10 stations, there was significantly lower taxonomic richness in the Arctic Coastal Tundra (144 taxa), the Low Arctic Tundra (170 taxa) and the Kalaallit Nunaat High Arctic Tundra (100 taxa), which were the ecoregions with the highest alpha diversity when more stations were considered in the analysis (Figure 4-17c). Alpha diversity estimates for these three ecoregions were also significantly different from one another. The other eight regions had 40–87 taxa, but for some of these only between 2 and 6 stations were included, suggesting a potential for large error in the estimate of alpha diversity at 10 stations. This assessment highlighted the importance of increasing sampling effort within ecoregions to include more stations, as patterns of diversity may differ greatly depending on how many stations are sampled and how much variability exists among those stations.

Without extrapolation to a larger number of stations, there remained evidence that the Scandinavian ecoregions, in particular, had higher alpha diversity than other regions. For example, the Scandinavian and Russian Taiga had a total of 351 taxa found across the full 19 stations that were sampled in this ecoregion, and the Scandinavian Montane Birch Forest and Grasslands had 333 taxa across its 19 stations. In contrast, the Arctic Coastal Tundra (in Alaska) had an estimate of 202 taxa at 19 stations and only reached a total of 343 taxa across the 64 stations that were sampled in that ecoregion, whereas the Kalaallit Nunaat Low Arctic Tundra (in Greenland) had an estimate of 132 taxa at 19 stations and only reached a total of 256 taxa across its 69 stations. Presumably, differences in alpha diversity between the Scandinavian ecoregions and the ecoregions in Greenland and in North America would have been even greater had a comparable number of stations been sampled.

Beta diversity among ecoregions ranged between 0.31 and 0.90. Beta diversity exceeded 0.80 for the Arctic Coastal Tundra, the Arctic Foothill Tundra, the East Siberian Taiga, the Low Arctic Tundra, the North Canadian Shield Taiga, Scandinavian Montane Birch Forest and Grasslands, and the Taimyr-Central Siberian Tundra. This means that the lakes in these regions showed the highest among-station diversity, i.e., showed a high differentiation in phytoplankton assemblages. Beta diversity was low in the Brooks-British Range Tundra, the High Arctic Tundra, the Kalaallit Nunaat High Arctic Tundra, and the Scandinavian and Russian Taiga. Homogeneous conditions in the catchment, resulting in rather similar water body types and water quality can contribute to this. Turnover was the dominant component of beta diversity in all ecoregions (Figure 4-17d), accounting for at least 70% of the total beta diversity. This reflected the important contribution of the introduction of new species across stations, and indicates the importance of spatially extensive monitoring of phytoplankton in lakes, to ensure the full variability due to species turnover is captured.

4.3.3.2. Regional Diversity

Beta diversity was assessed for each Arctic region (sub-Arctic, low Arctic, and high Arctic) by comparing the mean statistical distance of lakes to the centroid for each Arctic region in multivariate space, where larger distances are indicative of greater differences among assemblages. The low and high Arctic lakes on average had higher beta diversity than the sub-Arctic lakes when the distance to the centroid was used as an estimate of beta diversity (Figure 4-18). However, the average distance to the centroid was not significantly different among the three regions, mainly due to the large variability among sub-Arctic lakes. Sub-Arctic lakes are more heterogeneous due to a higher variability in catchment characteristics (e.g., vegetation cover, permafrost, nutrient concentrations) than lakes at higher latitudes. The fact that there were more samples from the sub-Arctic region (and more samples per lake) as well as wider geographic sample coverage likely also contributed to this pattern.
4.3.3.3. Compositional Patterns

There were 8-10 phytoplankton classes present within each Arctic region. Chrysophytes and Chlorophyceae (green algae) were the most dominant phytoplankton groups across all geographical regions (Figure 4-19), with the exception of Russia where cyanobacteria was most abundant across lake sites. The most common phytoplankton classes in the sub-Arctic regions were Chrysophyceae and Chlorophyceae. The next most common were Cyanophyceae, Bacillariophyceae (diatoms), Synurophyceae, and Dinophyceae with more than 1000 occurrences in the sub-Arctic (Figure 4-19). In the low Arctic, the assemblage composition was more balanced, with nearly 71% of the community equally represented by conjugatophytes, chrysophytes, diatoms, and cyanobacteria (Figure 4-19). In the high Arctic, chrysophytes clearly dominated, making up 34% of the community, whereas Dinoflagellates and green algae together contributed to 27% of the community on average (Figure 4-19).

4.3.3.4. Temporal Trends

Phytoplankton alpha diversity was compared based on the time period of collection to evaluate whether general patterns in species richness among Arctic regions has varied over time. The oldest records, from 1940-1980, showed high taxa richness, but these data covered very few years and sites (n< 34), making it difficult for direct comparison with the later contemporary years (n> 100) (1980-2000 and 2000-2015; Figure 4-20). Across both of the later time periods, there were significant differences in taxa numbers between Arctic regions (p = 0.03), with lakes in the high Arctic and low Arctic generally both having < 20 taxa, compared to the sub-Arctic sites that had approximately 30 taxa per site. Average richness was slightly higher from 2000-2015 than it was from 1980-2000 in the high Arctic and sub-Arctic, whereas the low Arctic showed a larger increase in richness in the later time period, but neither trend was significant. However, these patterns may have been affected by increased frequency and geographic coverage of sampling stations in later years.

Figure 4-19 Phytoplankton percent composition by dominant classes across the three Arctic regions, using relative presence across stations calculated from presence–absence data.
Figure 4.20 Phytoplankton species richness averaged by time periods ±SE in each Arctic region.

4.3.3.4.1. Temporal Trends in Total Biovolume and Composition

Temporal trends in community composition were more closely evaluated for lakes with greater than 10 years of phytoplankton biovolume data. Lakes with long time series were identified in Finland, Greenland, and Sweden. Whereas Finland and Greenland each had two lakes with greater than 10 years of data, Sweden had 12 lakes with more than 10 years of phytoplankton monitoring data. Productivity differed among lakes, with generally high productivity (>250 mm³ L⁻¹) for the two Greenland lakes and for Pallasjärvi in Finland. The Swedish lakes and Inarijärvi in Finland had a lower productivity of on average less than 100 mm³L⁻¹. Shifts in biovolume were compared among lakes to identify monotonic (i.e., single-directional) temporal trends.

From the late 1980s to present, total biovolume of phytoplankton increased in Inarijärvi in Finland and in several Swedish lakes, while biovolume decreased in Langemandsso in Greenland. Temporal trends in Greenland and Finland were variable in general, with some apparent outliers often masking trends. For example, when an extremely high value in 2014 (biovolume = 854 mm³ L⁻¹) was excluded, there was a significant decrease in total biovolume in Greenland lake Langemandsso (Mann-Kendall trend test (M-K) p = 0.024; Sen’s slope of trend = -11.59). Finland’s Inarijärvi had extremely variable total biovolume of phytoplankton prior to 1995, but from 1995 to 2014 there was evidence of a significant increasing trend (MK p = 0.001; slope = 1.19) despite an extremely high value in 2001. For Sweden, the trends were more clear across lakes, which were either sampled from circa 1988 to present (e.g., Abiskojaure, Jutsajaure, Stor-Tjulträsket), or sampled from circa 2000 to present. Clear significant increasing trends (all with p < 0.05) in total biovolume were evident in the Swedish lakes Abiskojaure (slope = 0.64), Båtkjäure (slope = 1.63), Övre Fjätjsjön (slope = 2.41), Jutsajaure (slope = 3.92), and Stor-Tjulträsket (slope = 2.30). Remaining Swedish lakes either displayed no trend over time, or had trends driven by a single outlier year. Overall, these trends indicate that total biovolume is decreasing in some of the highest productivity lakes and increasing in many low productivity lakes, leading to a more similar level of phytoplankton biovolume across these systems.

Though there was evidence of significant temporal trends in overall biovolume, it was often less clear which groups of phytoplankton contributed to those trends. In Greenland and Finland, trends in Chrysophyceae appeared to most closely reflect overall biovolume trends, with increasing biovolume of chrysophytes in Finland lakes and decreasing chrysophyte biovolume in Greenland lakes (though this decrease was only significant for Sommerfuglesø, which did not display a significant trend in overall biovolume). However, Chrysophyceae only showed a clear trend in one Swedish lake (Abiskojaure), and there was little evidence of broad trends in other phytoplankton classes in Swedish lakes, which indicated that shifts in biovolume over time could not be attributed to a single group.

4.3.3.4.2. Cyanobacteria response to a Changing Climate

Four main climate drivers of phytoplankton can be summarized as i) water temperature, ii) water column irradiance and clarity, iii) stratification regime and residence time, which are also influenced by local precipitation patterns, and iv) availability of nutrients (Paerl and Huisman 2008). More specifically in the Arctic, the seasonality of phytoplankton communities is directly affected by changes in ice coverage (Vincent 2007, Prowse et al. 2011c). Not only will earlier ice-off dates and later ice-on dates increase the length of the growing season, but they will shift the peak spring phytoplankton bloom earlier (Prowse et al. 2011c). Furthermore, a decrease in the period of ice cover and increased nutrient inputs could contribute to increased prevalence of cyanobacteria blooms (Prowse et al. 2011c). Current climate trends are showing rising temperatures in the Arctic, lengthening of the ice-off period, and changes in precipitation patterns (IPCC 2007).
Cyanobacteria are often considered to be a nuisance or even toxic phytoplankton group, as they are capable of creating thick surface blooms and outcompeting other phytoplankton. Although mostly thought to inhabit warm-temperate climates, they are commonly found in Polar regions (Vincent 2007). The circumpolar database confirmed these patterns, as cyanobacteria were found in low Arctic and sub-Arctic lakes, including about half the Russian lakes, some northern Fennoscandian lakes, as well as a few lakes in western Greenland and Canada (Figure 4-21). Blooms of toxic algae do not generally occur in Arctic lakes (Wrona et al. 2013), and toxin presence has only been confirmed in one case (Trout-Haney et al. 2016), though such occurrences might become more prevalent if climate change leads to warmer temperatures and higher nutrient inputs to lake and river systems. Cyanobacteria often dominate the benthic mats and algae in the littoral areas in cold habitats (Vincent 2007), but there was evidence of pelagic cyanobacteria in some of the high Arctic lakes in our dataset.

Temporal patterns in cyanobacteria biovolume were used as an indicator of how climate change has affected lake phytoplankton assemblages in the Arctic. With Cyanobacteria favouring warmer waters and abundant nutrients, we predicted an expanded geographical range and increased dominance of cyanobacteria since 1990, concordant with a period of increased warming. However, our results showed no overall increase in the regional distribution of cyanobacteria from 1980-2000 compared with 2001-2015. There was limited evidence of unidirectional trends in cyanobacteria biovolume across long-term data records from Greenland, Finland, or Sweden.

Despite the lack of long-term trends, cyanobacteria biovolume showed similar peaks across a number of lakes that may have corresponded with shifts in temperature. Long-term records were examined for Finland and Sweden (which had lakes with more consistent time series, with fewer gaps in recent years) to identify the years in which
cyanobacteria biovolume appeared to peak (that is, was notably increased relative to other years on record), and 66% of these peaks (37 of 56 high values of cyanobacteria biovolume) occurred during one of the hottest years on record (Table 4-2). High biovolume of cyanobacteria was most prominent in 2014, the hottest year on record since 1880, when 64% of lakes had a peak value (and in some cases these values were the highest recorded for cyanobacteria across the lake's time series; e.g., Pahajärvi had a peak of 2944 mm³/L in 2014, compared with the next highest value of 192 mm³/L in 2006). More than 20% of the lakes showed peak cyanobacteria biovolume in 2013 and 2003 (ranked the 5th hottest years), 2006, 2007, and 2010 (ranked the second hottest year; Table 4-2). An additional 32% of the peaks in cyanobacteria biovolume across lake times series (19 of 56 high values) were found to follow a hot year (e.g., a peak was noted in 2004, 2008, or 2011), and there were also five lakes sampled in Greenland that had cyanobacteria blooms of > 2000 mm³/L in 2004. These peaks in years following record hot years could reflect a delayed reaction to temperature increases, particularly as there appeared to be certain lakes that regularly showed these off-pattern peaks. Peaks in these years may also have occurred as a delayed response to consecutive warm years (e.g., 2004 followed record hot years in 2003 and 2004; 2008 followed hot years in 2005 through 2007; and 2011 followed record hot years in 2009 and 2010). Notably, these off-pattern peaks in cyanobacteria were generally not followed by another high biovolume value in the next year when temperatures were once again elevated. Since rising temperature and decreased ice potentially enhance cyanobacterial dominance (Paerl and Huisman 2008), continued monitoring of cyanobacteria in all Arctic regions may be useful in tracking associated climate and nutrient changes in Arctic water bodies.

4.3.4. Gaps in Knowledge and Monitoring

Monitoring of phytoplankton is not completed regularly in all Arctic countries, and data are therefore patchy both in spatial coverage and temporal coverage. The best coverage of phytoplankton data exists in Fennoscandia and Greenland, though most data are located in low Arctic or sub-Arctic regions, and high Arctic coverage is sparse (particularly in Svalbard). Monitoring designs vary among these countries, with a different focus on maximizing spatial or temporal data coverage in different regions. For example, monitoring in Finland, Sweden, and Greenland takes place at a small number of sites, but focuses on preserving long time series. In contrast, phytoplankton monitoring in Norway includes repeated sampling within a year in many stations (in some cases including monthly sampling), but the suite of sites differs from year to year. Thus stations may have only 6 years of biovolume data over a 15-year period, with many gaps in the time series.

There is virtually no consistent phytoplankton monitoring in North America. Data for Canada, Russia, and USA were largely sourced from academic research or from monitoring data collected by industry, which tends to include a large number of stations from a small number of lakes, though sampling is repeated annually and often monthly for those stations. Academic data can provide spatial coverage for limited areas, but rarely includes repeated sampling over a long time period, thus limiting the number of time series that can be examined. The result is that there is insufficient data, particularly for Canada, to accurately describe biodiversity across this region.

The need for more monitoring sites across North America, Russia, and other northern areas of the Arctic is clear. Norway began monitoring approximately 15 lakes in northern regions in 2017, which will begin to fill some gaps. But to allow for comparison and assessment across phytoplankton monitoring data, future monitoring efforts must endeavor to improve consistency in sample processing methods (particularly with respect to the estimation of biovolume) and taxonomic resolution. Data collected for this assessment included a mixture of biovolume (estimated by multiple methods), biomass, density, abundance, and presence/absence. Such a range of measurements are difficult to combine in a way that retains maximum information (i.e., retaining more information than presence/absence).

Furthermore, phytoplankton data included a mix of species-level and genus-level data, which can complicate assessment of taxonomic structure. Where possible, potential taxonomic redundancy from multi-level nomenclature was removed from the data, but future efforts should focus on obtaining species-level data where possible.

<table>
<thead>
<tr>
<th>Rank (1 = Warmest)</th>
<th>Year</th>
<th>Percent of lakes with cyanobacteria peak</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2014</td>
<td>64%</td>
</tr>
<tr>
<td>2 (tie)</td>
<td>2010</td>
<td>21%</td>
</tr>
<tr>
<td>2 (tie)</td>
<td>2005</td>
<td>15%</td>
</tr>
<tr>
<td>4</td>
<td>1998</td>
<td>18%</td>
</tr>
<tr>
<td>5 (tie)</td>
<td>2013</td>
<td>36%</td>
</tr>
<tr>
<td>5 (tie)</td>
<td>2003</td>
<td>36%</td>
</tr>
<tr>
<td>7</td>
<td>2002</td>
<td>18%</td>
</tr>
<tr>
<td>8</td>
<td>2006</td>
<td>29%</td>
</tr>
<tr>
<td>9 (tie)</td>
<td>2009</td>
<td>14%</td>
</tr>
<tr>
<td>9 (tie)</td>
<td>2007</td>
<td>29%</td>
</tr>
</tbody>
</table>
Watermilfoil (Myriophyllum alterniflorum).
Photo: Mps197/Shutterstock.com
4.4.1. Introduction

Macrophytes are a diverse group of aquatic plants large enough to see with the naked eye. There are 644 described species of vascular macrophytes in the Nearctic region and 497 species in the Palearctic region (Chambers et al. 2008), though Arctic zones of these biogeographical regions are expected to be less diverse. Macrophytes are taxonomically and phenologically wide ranging, from macroalgae (such as macroscopic species of green algae or Chlorophyta), to mosses and liverworts (Bryophyta), ferns (Pteridophyta) and seed-bearing plants (Spermatophyta) (Chambers et al. 2008). Macroscopic forms of Cyanobacteria, Xanthophyta (yellow-green algae) and Rhodophyta (red algae) can also be classified as aquatic macrophytes. Morphological forms of aquatic macrophytes include emergent (rooted plants with foliage extending into the air), floating-leaved (plants rooted to the lake or stream bottom with leaves that float on the water surface), submersed (plants growing completely submerged under the water and attached to, or closely associated with the substrate), and free-floating macrophytes (plants that typically float on or under the water surface) (Chambers et al. 2008). In addition, the depth distribution of macrophytes in lakes and rivers is often determined by the light penetration through water.

Macrophytes are an important functional component of lake ecosystems. They remove nutrients (e.g., nitrogen and phosphorus) from the water column (e.g., Gumbricht 1993, Jeppesen et al. 1998) and decrease wave energy and water currents, which leads to increased sedimentation and stabilization of sediment within macrophyte beds (e.g., Carpenter and Lodge 1986, Sand-Jensen 1997). Moreover, these beds provide habitat for fish, invertebrates, and epiphytes, and are an important food source for some invertebrates (e.g., insects) and vertebrates (e.g., fish, birds, moose) (Lodge 1991, Newman 1991). Wrona et al. (2013) indicate there are several major environmental factors that affect macrophyte distribution including nutrient levels, water clarity and water temperature (including ice regimes). Because macrophyte presence and abundance is closely associated with these environmental factors as well as substrate type, the composition of macrophyte communities can provide diagnostic information on water quality and is part of many countries’ assessment criteria (Jeppesen et al. 1998, Søndergaard et al. 2010).

4.4.2. Objectives and Approach

This circumpolar assessment provides a summary of broad spatial patterns of aquatic macrophyte biodiversity in the Arctic. To accomplish this we examined presence/absence data for macrophyte species-level data compiled for 440 lakes in all Arctic countries except Russia (Figure 4-22a). We examined spatial distribution patterns of macrophyte species composition, alpha diversity (i.e., species richness), and beta diversity and its component parts (i.e., turnover and nestedness) for regions with numerous data records. Using this approach, we produced a baseline for current macrophyte species distribution and composition to which future monitoring results can be compared. Knowledge gaps related to macrophyte monitoring in lakes and rivers were also identified.

4.4.3. Overall Patterns and Trends

4.4.3.1. Circumpolar Diversity

Among the three ecoregions with the largest number of sampling stations, there was significantly lower alpha diversity in the Iceland Boreal Birch Forests and Alpine Tundra (estimate of 35 species at 70 stations) than in either the Scandinavian and Russian Taiga or the Scandinavian Montane Birch Forest and Grasslands (estimate of 111 and 112 species at 70 stations, respectively; Figure 4-22b). Macrophyte distribution ranges are thought to be largely determined by seed dispersal via migratory birds and human activity, though continental drift and geographic proximity may have influenced dispersal patterns (Les et al. 2003, Chambers et al. 2008). These processes may have contributed to lower observed alpha diversity in Iceland compared to the continental Scandinavian ecoregions. When compared to one another using 100 stations, alpha diversity estimates were similar for the two Scandinavian ecoregions (120 species in the Scandinavian and Russian Taiga and 130 species in the Scandinavian Montane Birch Forest and Grasslands), indicating generally high diversity within these two ecoregions.

Rarefaction of species across all ecoregions, using 10 stations as the assessment threshold, showed alpha diversity estimates were lowest (< 15 species) for the tundra ecoregions of the Brooks-British Range, Kalaallit Nunaat High Arctic, Kola Peninsula and High Arctic (Figure 4-22c). Three of the ecoregions with the lowest species richness were located at the highest latitudes (average latitude > 70°N for the stations in the ecoregion), suggesting that alpha diversity of macrophytes declines in high-latitude Arctic regions. This is consistent with past research, which has suggested that there are latitudinal and altitudinal gradients in alpha diversity (Chambers et al. 2008), with aquatic vascular macrophytes showing a decline in species richness with latitude (Wrona et al. 2013). The highest alpha diversity (> 45 species) was in lakes of the Arctic Coastal Tundra, Northwest Territories Taiga, Scandinavian and Russian Taiga and Scandinavian Montane Birch Forest and Grasslands (Figure 4-22c). Interestingly, the Scandinavian and Russian taiga ecoregion had the highest estimated alpha diversity when only 10 samples were used (60 species), whereas it generally had lower alpha diversity than the Scandinavian Montane Birch Forest and Grasslands when a more representative sample size (e.g., over 70 stations) was considered. This result highlights the importance of sampling a sufficient number of stations across these regions.

Beta diversity of macrophyte assemblages ranged between 0 (no inter-station differences in species composition) and 1 (no inter-station overlap in species) within the ecoregions. Ecoregions with the highest inter-station differences (β_{inter} > 0.80) included the Arctic Coastal Tundra, Brooks-British Range Tundra, Kalaallit Nunaat High Arctic Tundra, Kalaallit Nunaat Low Arctic Tundra, Northwest Territories Taiga, Scandinavian Coastal Conifer Forests, and Scandinavian Montane Birch Forest and Grasslands. Beta diversity was lowest (high inter-station composition overlap) in the remote ecoregions with low connectivity, such as the Faroe Islands Boreal Grasslands, High Arctic Tundra, and Kola Peninsula Tundra. For most ecoregions, turnover was the dominant component of beta diversity.
diversity as it accounted for more than 70% of the total beta diversity (Figure 4-22d). This indicates that variation in diversity within an ecoregion is due species replacement across stations, rather than finding a subset of the species found at the richest station. The High Arctic Tundra ecoregion had no beta diversity as species composition was the same among stations, and beta diversity of the Kola Peninsula Tundra was a result of both turnover and nestedness.

4.4.3.2. Regional Diversity

Species richness of circumpolar macrophytes varied widely among lakes in the sub-Arctic region, ranging from 0 to a maximum of 29 species when mosses and algae were excluded (Figure 4-23). The highest alpha diversity was observed in Fennoscandia and the Faroe Islands, and alpha diversity was significantly lower in Greenland (Figure 4-23). Species richness was highly variable in Fennoscandia, owing in part to the wide variety of stations and ecoregions sampled in that area (Figure 4-23). Beta diversity in these regions was primarily driven by species turnover, indicating that differences among stations were due to the replacement of species.

4.4.3.3. Compositional Patterns

All major taxonomic groups were included in the circumpolar dataset, although there were several lakes without macrophytes or with only aquatic mosses. The most common taxa were *Myriophyllum alterniflorum*, *Potamogeton gramineus*, and *Ranunculus reptans*. Aquatic moss species comprised a higher percentage of total species richness with increasing latitude. Bryophytes (or charophytes) commonly dominate the macrophyte assemblages in high latitude lakes (e.g., Welch and Kalff 1974, Vincent and Hobbie 2000) where macrophyte growth rate is extremely low (e.g., Sand-Jensen et al. 1999). Multivariate analysis of macrophyte assemblages for highly-sampled regions indicated some separation among countries based on species composition (Figure 4-24). In particular, macrophyte species composition in Greenland and Norway differed from stations in Sweden and Finland.
which were highly similar (Figure 4-24). Species composition in a number of Greenland stations was distinct from all other countries included in the analysis.

In Arctic lakes, aquatic macrophyte abundance and composition is largely driven by physicochemical conditions including climate, which imposes latitudinal and altitude zonation patterns; local weather that modifies the regional patterns; water clarity, which is largely determined by natural or anthropogenic erosional activities; and nutrients, which are inherently in low supply and increase with human activity (Chambers et al. 2008). Harsh climate and ice conditions restrict the distribution of helophytes (i.e., perennial marsh plants with overwintering buds underwater) in the littoral zone, and the number of submerged vascular plants decreases as they are successively replaced by mosses at northern latitudes. This compositional change is likely due to the superior competitive ability of mosses under low light and temperature conditions (Sand-Jensen et al. 1999). Most of the lakes included in the analysis were in pristine condition, but there was some evidence of nutrient enrichment as indicated by the presence of freely-floating lemnids (*Lemna trisulca*) and ceratophyllids (*Ceratophyllum demersum*).

### 4.4.3.4. Temporal Trends

Paleoecological analysis has identified shifts in macrophyte taxonomic composition in response to changing environmental conditions. For example, pollen records from a number of lakes in Greenland show a loss of aquatic angiosperms and their replacement by aquatic mosses (8000 - 1000 BP), associated with lake oligotrophication (i.e., the reduction in salt concentrations, ions and nutrients) (Fredskild 1983, 1992). Similarly, analysis of the depth distribution and abundance of aquatic pollen taxa from six Alaskan lakes indicated increases in macrophyte abundance 14,000-12,000 and 8000 BP, likely due to temperate-linked changes in productivity and/or changes in water depth (Edwards et al. 2000).

### 4.4.4. Gaps in Knowledge and Monitoring

Extensive data were available for some areas of the Arctic (e.g., Fennoscandia), but data were sparse elsewhere, particularly for Canada, Alaska, and Russia. No data were obtained from Russian lakes, and data for Canada and Alaska were extracted from a small number of published papers. In the case of Canada, this resulted in a moderate number of samples covering a small geographic area. Data from Alaska included a single species list that summarized observations from over 100 lakes that covered a wide geographic area, with no details about the lakes in which macrophyte species were found. Macrophyte monitoring is not part of regular assessments in these countries, thus limiting the spatial scope of available data.

Across the entire circumpolar region, there are very few lakes that are monitored regularly. As a result, time series data are generally not available, and many lake observations are outdated (e.g., 1970s or earlier) with no repeated visits to the same lakes. Such data do not allow for the detection of shifts in macrophyte distribution and may not provide an accurate view of contemporary patterns in diversity.

There may also be inconsistencies in sampling methods and taxonomic identification; this can introduce variability that constrains data comparisons. For example, identification of aquatic mosses and Charophytes is sometimes difficult and may result in errors. Moreover, monitoring may not include the identification or enumeration of aquatic mosses, helophytes, or bryophytes, which may be of particular concern if these groups are dominant in a region. Improvements to the monitoring of macrophytes are necessary across the circumpolar region, and should focus on regular and repeated monitoring of representative lakes with standardized monitoring protocols.
Daphnia longispina.
Photo: Deiter Ebert / Flickr/CC 2.0
4.5. Zooplankton

4.5.1. Introduction

Zooplankton are small, heterotrophic invertebrates that live in the water column (pelagic zone) of standing water bodies (i.e., lakes, ponds, pools), although some species have juvenile and resting stages that may occur in benthic habitats. The zooplankton of freshwaters (including the Arctic) are represented by three major groups: rotifers (Rotifera), cladocerans (Cladocera) and copepods (Copepoda). Arctic lakes are dominated by rotifers of the Monogononta class, cladocerans of all families including many genera of Ctenopoda, Anomopoda, Haplopora and Onychopoda, and copepods of the orders Calanoida and Cyclopoida. In Arctic ponds and small water bodies, cladocerans of the families Chydoridae and Macrothricidae, and copepods from the order Harpacticoida come into account. Zooplankton assemblages are composed of true pelagic taxa, but can also contain benthic species, particularly in small water bodies. In order to obtain a complete picture of biodiversity in these ecosystems and compare them with biodiversity in shallow water bodies, it is necessary to analyze the composition of both aquatic assemblages. However, data for littoral or benthic taxa and stages of zooplankton are generally less available than pelagic data, which may preclude assessment of this component of the zooplankton assemblage.

The distribution of zooplankton species in Arctic lakes differs along a longitudinal gradient, with the greatest species richness corresponding with proximity to areas without recent glaciation (e.g., Alaska, northern Greenland; Wrona et al. 2013). Recolonization of lake zooplankton following the Pleistocene period was from these areas, and thus species richness declines with distance from locations such as Alaska and northern Greenland (Samchyshyna et al. 2008, Rautio et al. 2011). Zooplankton diversity is also increased by proximity to coastal regions, where species richness is increased by freshwater species that originate from marine ecosystems (Rautio et al. 2008).

Zooplankton density, biomass, and community composition are regulated by the abundance of food resources (i.e., planktonic and/or benthic algae and bacteria), predation, and indirectly by the nutrient status of lakes. Despite the low nutrient conditions that are typical of the Arctic, zooplankton density and biomass can be relatively high in shallow Arctic lakes because of the presence of benthic algal mats that are important feeding habitats (e.g., Rautio and Vincent 2006, Mariash et al. 2014). Eutrophication primarily has an indirect effect on zooplankton through increased primary production and changes in food quantity/quality. In low-productivity waters, even small inputs of nutrients may lead to increased production and biomass of zooplankton as well as richness. In contrast, in lakes with higher natural nutrient levels and in lakes with heavy nutrient loads, the main response may be a shift in zooplankton composition. Many zooplankton species are sensitive to predation from macroinvertebrates and fish. In fish-free lakes, zooplankton assemblages include large-bodied species, but the presence of fish will drive the size distribution of zooplankton towards smaller species (O’Brien et al. 2004). Increased fish predation, as a consequence of invasive species or changes in lake trophy, often have strong effects on zooplankton composition, with a shift from larger to smaller cladocerans and copepods and changes in the size distribution of individual species.

Industrial pollution and climate change both have the potential to affect the biodiversity of zooplankton in Arctic lakes. For example, metal and acid contamination in the areas along the boundary between Russia (Kola Peninsula) and Norway (South-Varanger) affects the zooplankton community composition in lakes, leading to reduced species richness, changes in species composition, and reduced complexity of the zooplankton assemblage (Vandish 2002, Shustova et al. 2009). Lakes on the Kola Peninsula have very simple zooplankton communities with low species numbers (Vandish 2002), similar to patterns that have been observed in temperate regions of Canada (Yan and Strus 1980). Changes in water temperature influence zooplankton through shifts in the composition of dominant species, changes to phenology of certain species, and introduction of alien species to northern regions (Rautio et al. 2011). Increased water temperature may also affect stratification of deep lakes and cause shifts in the vertical distribution of species in the water column. Other drivers related to climate change, including increased UV, shifts in precipitation, and increased turbidity, have the potential to impact the diversity, biomass, and feeding efficiency of zooplankton.
4.5.2. Objectives and Approach

This assessment provides an evaluation of zooplankton biodiversity and composition across the entire Arctic, which allows for analyses of latitudinal differences and trends across all Arctic regions. At a circumpolar scale, stations were grouped into ecoregions of similar geography and climate (Olson et al. 2001) and alpha diversity, beta diversity, and its component parts (turnover and nestedness) were evaluated within ecoregions. Zooplankton data from 3082 samples representing 482 stations and 421 lakes were used in this report. Of these, 416 lakes included data on crustaceans (Figure 4-25a), and 172 lakes included data on both crustacean zooplankton and rotifers (Figure 4-26a). Thus, diversity was assessed separately for the whole zooplankton assemblage (using stations in which Crustacea and Rotifera were sampled and enumerated) and also for just crustacean zooplankton. Spatial patterns in zooplankton diversity were also assessed at a regional scale (by country and by Arctic region) for the circumpolar Arctic. In the regional assessment, beta diversity was assessed in terms of the dispersion of stations around a group centroid in multivariate space (based on assemblage composition). Using contemporary zooplankton data, we produce a baseline to which future monitoring results can be compared and identify gaps in the current distribution of monitoring.

4.5.3. Overall Patterns and Trends

4.5.3.1. Circumpolar Diversity

For a subset of ecoregions with moderate sample frequency (range 25-72 stations; Figure 4-25a), alpha diversity estimates of crustacean zooplankton were rarefied to 25 stations for comparison. Among these ecoregions, alpha diversity of crustacean zooplankton was highest for lakes in the Northwest Russian-Novaya Zemlya Tundra ecoregion, where on average 29 taxa were found, and the Scandinavian and Russian Taiga ecoregion, where 23 taxa were found (Figure 4-25b). Alpha diversity of crustacean zooplankton was lowest in the Brooks-British Range Tundra in Alaska, where seven taxa were found. For the other four ecoregions, alpha diversity ranged from nine to 16 crustacean taxa, with higher diversity found in coastal Alaska and in Canada than was found in Iceland or Greenland. When all ecoregions were compared at a rarefied alpha diversity level of 10 stations, ecoregions in Russia and Fennoscandia remained the most diverse, with 22 crustacean taxa in the Northwest Russian-Novaya Tundra ecoregion, 19 taxa in the Scandinavian

![Figure 4-25 Results of circumpolar assessment of lake zooplankton, focused just on crustaceans, and indicating (a) the location of crustacean zooplankton stations, underlain by circumpolar ecoregions; (b) ecoregions with many crustacean zooplankton stations, colored on the basis of alpha diversity rarefied to 25 stations; (c) all ecoregions with crustacean zooplankton stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.](image)
Montane Birch Forest and Grasslands, and 17 taxa in the Scandinavian and Russian Taiga (Figure 4-25c). The majority of ecoregions (18 ecoregions from across the circumpolar region) had similar alpha diversity estimates, ranging from six to 13 taxa (Figure 4-25c). The lowest diversity was found in the Canadian high Arctic (High Arctic Tundra), Svalbard (Arctic Desert) and mountainous regions of Alaska (Brooks-British Range Tundra), where fewer than seven crustacean taxa were estimated to be found at 10 stations.

A limited set of stations also had data for rotifers (Figure 4-26a), allowing for a more inclusive assessment of alpha diversity patterns. Four ecoregions had moderate levels of sampling of both Crustacea and rotifers, and alpha diversity estimates were rarefied to 25 stations for comparison. Similar to the crustacean analysis, the Northwest Russian-Novaya Zemlya Tundra ecoregion was found to be most diverse, having an average 102 taxa (95% confidence interval 92-111; Figure 4-26b). The Arctic Coastal Tundra was also significantly more diverse than the other ecoregions, and had an average of 62 taxa (95% confidence interval 55-70). The remaining two ecoregions had similar alpha diversity estimates (23-26 taxa). All ecoregions with data for both crustaceans and rotifers were compared at a rarefied alpha diversity level of 10 stations. Ecoregions covered a wider range of alpha diversity (which spanned four to 86 taxa on average per ecoregion) than when only Crustacea were considered. Russian and Fennoscandian ecoregions remained the most diverse ecoregions, though the Scandinavian Montane Birch Forest and Grasslands had the highest richness, with an estimated 86 crustacean and rotifer taxa at 10 stations (though this was not significantly different from the Northwest Russian-Novaya Zemlya Tundra, which had an estimated 67 taxa; Figure 4-26c). In this analysis, the Arctic Desert had the lowest diversity with an estimated four taxa (Figure 4-26c).

Assessment of the full zooplankton assemblage and of crustacean zooplankton provided some evidence of high alpha diversity in coastal regions, particularly in coastal ecoregions of Fennoscandia and Russia. This pattern is consistent with predictions that high richness would be found in coastal areas where there would be more influence from the marine habitat (Rautio et al. 2008). Richness was also high in Alaska (Arctic Coastal Tundra), which supports the prediction of high diversity in areas that were unaffected by recent glaciation (Samchyshyna et al. 2008). The high alpha diversity of rotifers observed for some Russian ecoregions (particularly the Northwest Russian-Novaya Zemlya Tundra)

Figure 4-26 Results of circumpolar assessment of lake zooplankton, including crustaceans and rotifers, and indicating (a) the location of zooplankton stations, underlain by circumpolar ecoregions; (b) ecoregions with many zooplankton stations, colored on the basis of alpha diversity rarefied to 25 stations; (c) all ecoregions with zooplankton stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.
may partly reflect differences in the taxonomic identification approaches used by researchers in different regions (e.g., where taxa may be split into multiple species in some regions but grouped in other regions). Further consultation with taxonomic experts from different regions may be required to confirm taxonomic groupings and further develop nomenclature harmonization.

Beta diversity for crustacean zooplankton, calculated for 21 ecoregions, exceeded 0.80 in three of the ecoregions: the Arctic Coastal Tundra, Arctic Desert, and Kamchatka-Kurile Meadows and Sparse Forests. The high beta diversity values indicated that these ecoregions had the highest differences in crustacean zooplankton assemblage composition among lakes. Eight of the 21 ecoregions had low beta diversity ($\beta_{\text{SOR}} \leq 0.50$), suggesting that the lakes in these regions were more similar in their crustacean zooplankton assemblages. The lowest beta diversity was in the High Arctic Tundra ($\beta_{\text{SOR}} = 0.20$), whereas seven other ecoregions had beta diversity ranging from 0.43 to 0.5; however, these ecoregions all had data from between four and seven lakes, and low beta diversity values may have reflected the fact that assemblage composition was compared among few lakes. Beta diversity for the remaining ecoregions ranged from 0.51 to 0.77, indicating intermediate similarities among assemblages. Species turnover was the most important component of beta diversity in 13 of the 21 ecoregions analyzed, accounting for 70–100% of beta diversity in these ecoregions (Figure 425d). Of the remaining ecoregions, one was dominated by nestedness (Low Arctic Tundra in Canada; 80% of beta diversity) whereas all other ecoregions had approximately equal contribution of turnover and nestedness, with the turnover component accounting for 38-62% of beta diversity. Where nestedness played a larger role, there were generally fewer lakes sampled in an ecoregion, and differences among lakes may not have been captured. These results highlight the importance of monitoring zooplankton in a wide variety of lakes within an ecoregion, as widespread sampling may be necessary to accurately summarize the full diversity of species in an area.

Beta diversity for samples with both crustacean and rotifer data ranged from 0.28 to 0.87 across 12 ecoregions. For some ecoregions, the addition of rotifers resulted in only minor deviations from the results of the crustacean beta diversity analysis. However, there was a strong increase in beta diversity in the Arctic Foothills Tundra (0.5 to 0.8) and the Northern Canadian Shield Taiga (0.51 to 0.73), which indicated that the inclusion of rotifers led to stronger dissimilarity among stations. In contrast, there was a sharp decline in beta diversity estimates for the Arctic Desert (0.81 to 0.29) and Kalaallit Nunaat High Arctic Tundra (0.71 to 0.43), which indicated that consideration of rotifer taxa led to stronger similarity among stations in these high Arctic ecoregions. Nestedness became more important in some ecoregions and contributed approximately equally to beta diversity (e.g., Kalaallit Nunaat High Arctic Tundra and Scandinavian Montane Birch Forest and Grasslands), or even became the dominant component of beta diversity (e.g., Arctic Desert; Figure 426d). Species turnover remained an important component of beta diversity in ecoregions in Alaska, Russia, and southern Greenland.

4.5.3.2. Regional Diversity

Average taxon richness per site decreased with increasing latitude for crustaceans and rotifers. For rotifers, taxa richness was significantly lower in the high Arctic than in the low Arctic ($p < 0.005$), but there was substantial overlap in richness between the high Arctic and the sub-Arctic/alpine zone. When crustacean richness was assessed, there was evidence of significantly lower alpha diversity in the high Arctic than in either low-Arctic or sub-Arctic/alpine lakes ($p < 0.001$; Figure 4-27). Though these patterns in diversity may have been driven in part by lower sample size in the high Arctic, they are also indicative of lower diversity of both crustaceans and rotifers at higher latitudes.
4.5.3.3. Compositional Patterns

The zooplankton dataset included 357 taxa, of which 282 were at the species level. The main groups of zooplankton were calanoid copepods (30 spp.), cyclopoid copepods (37 spp.), cladocerans (66 spp.) and rotifers (121 spp.). Other groups like Harpacticoida, Ostracoda and others were represented with <20 species each. Approximately 40% of all taxa were found in only one or two samples, whereas the most common species groups (Daphnia longispina gr., which likely included several species), and Cyclops scutifer were found in 44% and 37% of the samples, respectively. Among the rotifers, Kellicottia longispina was most widespread, found in 69% of the samples with rotifer data.

Distributional patterns differed among species groups. Many of the common and highly abundant species, i.e., crustaceans (Bosmina longirostris, Bosmina longispina/coregoni gr., Daphnia longispina gr.) and rotifers (Asplanchna priodonta, Conochilus unicorns, Kellicottia longispina) are common throughout the Holarctic area. Some species were common, but were not found in all regions. For example, the cladoceran Daphnia pulex gr., commonly associated with fishless lakes, was observed in 31% of the stations, but was lacking in Scandinavia. The reason for this may be that Scandinavian lakes are relatively large and deep and contain fish. Additionally, Holopedium gibberum was observed in 26% of the circumpolar lakes, but was absent in the eastern part of Russia. Other common species with a more restricted spatial distribution were Bythotrophes longimanus, Limnosida frontosa, and Heterocope appendiculata, which were found in Scandinavia and Eastern and Western Siberia, but not in Canada or parts of Beringia (Alaska), in agreement with the described Eurasian distribution of these species. Leptodora kindtii and Cyclops abyssorum had a similar distribution in the data, but have been found in North America in the past.

Comparison of the relative abundance of each of the main crustacean groups (Calanoida, Cyclopoida and Cladocera) across Arctic zones indicated that the dominance of cladocerans in sub-Arctic lakes (approximately 50% of all specimens) was diminished by an increased presence of cyclopoid copepods in the low Arctic and high Arctic (Figure 4-28). Conversely, the relative abundance of calanoid copepods was similar between the sub-Arctic and low Arctic, and declined in the high Arctic zone (Figure 4-28). It is known that copepods are more cold-adapted than cladocerans, and are thus potentially able to tolerate high Arctic conditions. Cladocerans have advantages in colonization of arctic areas thanks to a cyclic parthenogenesis that includes lentic stages (ephiphia), but they are more sensitive to the ratio of P:N in waterbodies (Novichkova and Azovsky 2017), and may be limited in the nutrient-poor systems of the high Arctic.

4.5.3.4. Gaps in Knowledge and Monitoring

Data for this assessment were lacking particularly from Canada and Russia, but there were several regions of the Arctic where spatial coverage was less extensive than for other FECs. Zooplankton are not generally included in routine monitoring in North America, with the exception of monitoring by industry. The lack of data in some European countries may be due to the fact that zooplankton is not a so-called “ecological quality element” according to the European Water Framework Directive. Greenland and Norway are the primary regions with routine monitoring at established stations, whereas monitoring data from other regions are often from impact studies rather than long-term programs intended to evaluate natural variation or monitor for effects of climate change. Throughout the circumpolar region, therefore, there is a need to rely in part or in whole on data from academia, industry, or other non-government research. As a result, there is limited availability of time series, and in some areas, limited assessment of the full zooplankton assemblage (e.g., areas with research focused on crustaceans or just on cladocerans or copepods).

There were some historical data from Greenland (records from the early 1900s from published papers), but data were generally from within the last 30 years for most countries. Time series were rare, and only nine stations in the database (from Greenland, Norway, and USA) had ≥ 10 years of sampling data. Some paleolimnological cladoceran data were obtained for the database, but these data covered a small spatial scale and additional data would be required to improve assessment of long-term historical changes.

Current assessments are limited by a lack of routine monitoring, which would be necessary to detect changes in response to climate change and anthropogenic stressors. To facilitate the future status assessment for freshwater zooplankton across the circumpolar region, there is need to standardize sampling methods and habitats. For example, data included a variety of samplers (with different mesh sizes) and sampling approaches (depth-specific or depth-integrated sampling), and the depth/region of the lake where samples were collected was not always available. For many of the samples, >50% of the taxa are generally associated with littoral habitats (very few truly pelagic species). We assume that the vast majority of these sites are very shallow, and therefore that most samples represent a mixed habitat (littoral + pelagic). However, future monitoring would preferably include the collection of quantitative samples with vertical net-hauls from open waters and horizontal net-hauls from the littoral zone. Furthermore, identification of the complete sample (crustaceans and rotifers) should be completed using the most recent nomenclature.

Figure 4-28 Average relative abundance of the main zooplankton groups (calanoid copepods, cyclopoid copepods, cladocerans) for the sub-Arctic (n=150), low-Arctic (n=154), and high-Arctic (n=55) regions. Samples with a single taxon have been excluded.
The larval stage of non-biting midges (Chironomidae) occurs in aquatic environments. Chironomidae are cold-tolerant and are therefore the dominant benthic macroinvertebrate group in many Arctic freshwater systems. Because they are so abundant, they are an important component of aquatic and terrestrial food webs, and provide food sources for fish and other organisms. Photo: Jan Hamrsky
4.6. Benthic Macroinvertebrates

4.6.1. Introduction

Benthic macroinvertebrates are a diverse group of animals including insect larvae, crustaceans, worms, molluscs, and mites that are generally visible to the naked eye, and that are typically collected using nets with a mesh size of 0.25–0.5 mm. They live on or close to the bottom substrates of rivers and lakes, i.e., in sediments, on stony substrates and/or rocky shores. Benthic macroinvertebrate monitoring in lakes is generally either of the littoral species that inhabit the shallow waters along the shoreline or the profundal species that live in the soft sediments of the deep, dark parts of lakes. Macroinvertebrates in rivers are commonly collected in stony riffle habitats or in the sandy/clay sediments of pool habitats as well as in association with water plants. Benthic macroinvertebrates feed on water plants, algae, detritus, and other macroinvertebrates, and form the trophic link between the base of the food web (i.e., the primary producers) and predators higher up in the food chain such as invertebrate predators, fish and waterfowl. Many benthic macroinvertebrate taxa have a wide distribution and well-defined ecological niches, which make them good indicators of ecological condition.

The diversity of benthic macroinvertebrate assemblages in the Arctic has not been studied on a circumpolar scale, but regional assessments have suggested that species-specific physiological tolerance to cold temperatures may play a role in determining assemblage structure (Milner et al. 2001, Wrona et al. 2013, Culp et al. In Press). Riverine studies from higher northern latitudes (> 40° N) indicate that alpha diversity of benthic macroinvertebrate decreases with increasing latitude, shifting from high abundances of mayflies (Ephemeroptera), caddisflies (Trichoptera) and stoneflies (Plecoptera) to communities dominated by true flies (Diptera) (e.g., Oswood 1997, Castella et al. 2001, Scott et al. 2011). At lower latitudes, the benthic macroinvertebrate community in rivers typically includes the mayfly families Baetidae and Heptageniidae, stoneflies belonging to the Nemouridae and Chloroperlidae, oligochaete worms, and the water mites or Hydracarina. Further North, cold water temperatures and scarce food resources limit benthic macroinvertebrate survival and growth (Wrona et al. 2013), and adaptations such as freeze-avoidance or freeze-tolerance (Irons III et al. 1993) are necessary for survival (Danks 1992, Danks et al. 1994). The predominant taxa at the highest latitudes are the non-biting midge (family Chironomidae) subfamily Diamesinae, which dominates in glacial streams where maximum temperatures are 0–2°C, while worms (Oligochaeta), crane flies (Tipulidae), and the midge subfamily Orthocladiinae are found in streams with maximum temperatures between 2°C and 4°C (Milner et al. 2001).

Important environmental drivers of benthic macroinvertebrate assemblages in northern rivers include substrate composition, water velocity, nutrients, temperature, catchment geology and catchment vegetation (Lento et al. 2013). Arctic streams and rivers are also highly dynamic systems, with long periods of ice cover followed by peaks in flow during the spring freshet, when melt-water from snow and ice enters the system, leading to high water levels, fast-flowing water, and the potential for flooding (Prowse and Culp 2003, Prowse et al. 2006b, Prowse et al. 2011a). These ecosystems have recurrent high turbidity due to unstable streambeds and high sediment loads. Such physical disturbances are important drivers of macroinvertebrate biodiversity and are especially pronounced during periods of high discharge, such as during ice break-up or in glacial-fed systems, or during periods of anchor ice formation (Milner and Petts 1994, Power and Power 1995). The dynamics of Arctic streams and rivers impose constraints on macroinvertebrate biodiversity and population size, as invertebrates need specific traits to grow and reproduce in these environments (e.g., life history strategies relating to the length of the life cycle and number of generations and life stages, cold tolerance, and feeding habits; Brown et al. 2018).

Arctic lakes have lower invertebrate taxon richness than temperate lakes, but still maintain functionally and taxonomically diverse benthic macroinvertebrate communities (Johnson and Goedkoop 2002, Wrona et al. 2013). Primary production in Arctic lakes is to a large extent from benthic algae, mainly diatoms and cyanobacteria. Due to the high water clarity of Arctic lakes (except glacier-fed lakes), light penetrates and supports benthic primary production even at large depths, thus supplying food for benthic invertebrates. Common taxa in the shallow, highly-productive littoral zone of Arctic lakes are midges (Chironomidae), crane flies (Tipulidae), case-building caddisflies in the family Limnephilidae, mayflies, especially in the family Ameletidae, and stoneflies belonging to the genus Capnia in the family Capniidae. In contrast, the profundal zone of lakes largely consists of homogeneous sediments and is characterized by relatively low diversity. Chironomids, amphipod crustaceans, and oligochaete worms are common taxa in the profundal zone. Fishless lakes frequently contain predation-sensitive macroinvertebrate fauna, such as the crustacean Lepidurus arcticus (Branchiopoda, Notostraca) and the beetle Colymenthes. These organisms may be highly abundant in fishless lakes, but are very rare on larger spatial scales.
Freshwater biomonitoring of benthic invertebrates in lakes and rivers has a long tradition (Rosenberg and Resh 1993), starting with the early work by Kolkwitz and Marsson (1909) and progressively developing into multiple, pollution-specific indicator taxa that are used to construct biological metrics. These metrics quantify effects on ecosystems by both point-source pollution and large-scale diffusive pollution on macroinvertebrate communities (e.g., Wiederholm 1980, Armitage et al. 1983, Raddum and Fjellheim 1984) by summarizing knowledge of the tolerance range of multiple macroinvertebrate species along environmental stress gradients into a single value. Such metrics (e.g., EPT and tolerance metrics) have been developed for ecological integrity, acidification, and eutrophication and form the core of assessment tools in many countries, but are not adapted to Arctic water bodies. Similarly, as lakes and rivers are closely linked to landscape modifications, macroinvertebrate communities will react to climate-induced changes in landscape-level processes such as changes in temperature, ice-regimes, and vegetation. As biomonitoring using benthic macroinvertebrates is a well-established approach, standard methods exist for the sampling, processing, and analysis of samples that can facilitate large-scale assessments of their diversity.

4.6.2. Objectives and Approach

Benthic macroinvertebrate assemblages were assessed for rivers and for lake littoral and profundal zones. Analysis focused on samples collected using similar approaches (e.g., kick net in lake littorals and rivers, grab samples in profundal zone of lakes). Analysis was conducted at the lowest taxonomic level that allowed maximum inclusion of stations, which was generally at family level or higher as a large number of stations did not identify chironomids to lower taxonomic units (though limited analysis was done at the genus level for chironomids in lake profundal zones). The circumpolar assessment of benthic macroinvertebrates provided a summary of broad spatial patterns of biodiversity in Arctic streams and lakes. Stations were grouped into ecoregions with similar geography and climate (Olson et al. 2001) and rarefaction curves were used to compare alpha diversity across ecoregions at a standardized number of stations (to control for differences in sampling effort). We assessed beta diversity within ecoregions (averaging beta diversity across hydrobasins in each ecoregion), as well as the proportion of beta diversity that was due to turnover or nestedness.

4.6.3 Overall Patterns and Trends

4.6.3.1 Circumpolar Diversity

4.6.3.1.1. Lake Littoral Zones

Lake littoral invertebrate samples were not collected across the entire circumpolar region, but primarily came from Fennoscandia, Iceland, and USA, with a small number of stations in southern Greenland, Faroe Islands, and northern Russia (Kola Peninsula and Wrangel Island; Figure 4-29a). There were four ecoregions in the highly sampled regions with sufficient sampling to allow the assessment of littoral zone alpha diversity rarefied to 80 stations. Among these ecoregions, the lowest alpha diversity was found in the Iceland Boreal Birch Forests and Alpine Tundra, which had an average of 16 taxa in 80 stations (Figure 4-29b). This may have been due in part to the sampling method used in this country, as invertebrate samples were collected using rock scrapes rather than kick nets. Although these methods are broadly comparable, rock scrapes have been shown to collect fewer taxa than kick nets (Lento and Morin 2014). The Arctic Coastal Tundra in Alaska had significantly higher alpha diversity, with an average of 37 taxa in 80 stations (Figure 4-29b). The Fennoscandian ecoregions had the highest taxonomic richness, with an average of 56 taxa in the mountainous Scandinavian Montane Forests and Grasslands and an average of 70 taxa in the circumpolar Arctic. Using this approach and contemporary data, we produce a baseline to which future monitoring results can be compared and identify gaps in the current distribution of benthic macroinvertebrate monitoring.
of 24 taxa), the Kola Peninsula Tundra (average of 24 taxa), the Scandinavian Montane Forests and Grasslands (average of 34 taxa) and the Scandinavian and Russian Taiga (average of 42 taxa), with the latter two ecoregions having significantly higher alpha diversity than the low diversity ecoregions (Figure 4-29c). The similarity in diversity estimates for the most taxonomically-poor ecoregions suggests that barriers to dispersal, such as proximity to mainland and presence of mountains, limits biodiversity in these northern lakes. Even in areas of high biodiversity, such as Fennoscandia and northern Alaska, there was evidence of lower diversity where the presence of mountainous ecoregions likely limited dispersal. Beta diversity within ecoregions ranged from 0.19 to 0.77, indicating a relatively large range in the level of similarity between lakes. The lowest beta diversity ($\beta_{SOR} = 0.19$) was in the Faroe Islands Boreal Grasslands, where only four lakes were sampled over a relatively small area, alpha diversity was low, and composition among lakes was extremely similar. Other ecoregions with low to moderate beta diversity included the Kola Peninsula Tundra ($\beta_{SOR} = 0.43$) and the Iceland Boreal Birch Forests and Alpine Tundra ($\beta_{SOR} = 0.56$). In all three of these ecoregions, nestedness contributed to beta diversity, either as the predominant component (in the case of the Kola Peninsula) or approximately equally to taxonomic turnover (Figure 4-29d). Thus, among-lake differences in composition in these ecoregions were due primarily or in part to a loss of species. In the remaining ecoregions, within which $\beta_{SOR}$ ranged from 0.65 to 0.78, turnover was generally the dominant component of beta diversity (with the exception of the Kalaallit Nunaat Low Arctic Tundra, where there were equal contributions of turnover and nestedness), indicating that the replacement of taxa across lakes drove differences in composition.

Figure 4-29 Results of circumpolar assessment of lake littoral benthic macroinvertebrates, indicating (a) the location of littoral benthic macroinvertebrate stations, underlain by circumpolar ecoregions; (b) ecoregions with many littoral benthic macroinvertebrate stations, colored on the basis of alpha diversity rarefied to 80 stations; (c) all ecoregions with littoral benthic macroinvertebrate stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.
4.6.3.1.2. Lake Profundal Zones

Lake profundal zone samples were obtained for sub-Arctic and low Arctic regions of Canada and Fennoscandia. Profundal samples had predictably lower taxonomic richness for benthic invertebrates than littoral zone samples. Sample richness was also less variable than was found in the littoral zone samples, resulting in smaller confidence intervals around richness estimates. Alpha diversity was rarefied to 20 stations for comparison among ecoregions. The lowest diversity was found in the Low Arctic Tundra (average of 8 taxa in 20 stations) and the Northern Canadian Shield Taiga (average of 9 taxa, significantly higher than the Low Arctic Tundra estimate), both in central Canada. The remaining ecoregions had similar alpha diversity, ranging from 17 to 26 taxa on average in 20 stations. These included the Central Canadian Shield Forests and Southern Hudson Bay Taiga in Central and southern Canada, and the Scandinavian and Russian Taiga and Scandinavian Montane Birch Forest and Grasslands in Fennoscandia.

A total of 24 ecoregions had river benthic macroinvertebrate stations, and were comparable at a rarefied alpha diversity level of 10 stations. The lowest diversity was in the Arctic Desert ecoregion on Svalbard, with an average of 2 taxa in 10 stations (Figure 4-30c). Low diversity (ranging from 6 to 11 taxa in 10 stations) was also evident in other high Arctic and low Arctic island ecoregions, including the Kalaallit Nunaat High Arctic Tundra and Kalaallit Nunaat Low Arctic Tundra in Greenland, Iceland Boreal Birch Forests and Alpine Tundra, Wrangel Island Arctic Desert in Russia, and High Arctic Tundra in Canada (Figure 4-30c). The highest alpha diversity was evident in sub-Arctic mainland ecoregions, including the Scandinavian and Russian Taiga (average of 47 taxa in 10 stations), and the Muskwa-Slake Lake Forests (44 taxa), Southern Hudson Bay (53 taxa), and Central Canadian Shield Forests (56 taxa) ecoregions in Canada. Across the sampled region, alpha diversity generally was lower at the highest latitudes, on remote islands, and in mountainous ecoregions. In contrast, the highest alpha diversity was evident at the lowest latitudes on the mainland where connectivity allows for greater dispersal of taxa from southern regions. Thus, alpha diversity may reflect a combination of dispersal constraints and thermal tolerances.

Beta diversity for rivers was variable across ecoregions, with average $\beta_{SOR}$ ranging from 0.21, implying strong similarity among stations, to 0.95, which indicated a large among-site variability in assemblage structure. Beta diversity was highest in the Southern Hudson Bay Taiga ecoregion, which indicated that the largest differences among stations were evident within one of the most diverse ecoregions. Turnover was the predominant component of beta diversity (>70%) in most ecoregions (Figure 4-30d), but there was an increased contribution of nestedness in colder ecoregions and ecoregions potentially affected by dispersal limitations. In particular, both turnover and nestedness contributed approximately equally to beta diversity in Brooks-British Range Tundra and Arctic Foothills Tundra in Alaska, the High Arctic Tundra in Canada, the Kalaallit Nunaat High Arctic Tundra and Low Arctic Tundra in Greenland, and the Wrangel Island Arctic Desert in Russia (Figure 4-30d). Furthermore, beta diversity was completely attributed to nestedness in the Arctic Desert in Svalbard, which was not surprising, as only two taxa were found in this ecoregion. For the remaining ecoregions, the dominance of the turnover component of beta shows that taxon replacement was the main driver of among-river compositional differences.

4.6.3.1.3. Rivers

River benthic macroinvertebrate stations had better spatial coverage across the circumpolar region than lake regions, and were particularly prevalent in Canada (Figure 4-30a). There were six ecoregions in Canada and Fennoscandia with a sufficient number of stations to allow for comparison of family richness rarefied to 100 stations. The lowest alpha diversity was in two mountainous ecoregions: the Ogilvie-
Figure 4-30 Results of circumpolar assessment of river benthic macroinvertebrates, indicating (a) the location of river benthic macroinvertebrate stations, underlain by circumpolar ecoregions; (b) ecoregions with many river benthic macroinvertebrate stations, colored on the basis of alpha diversity rarefied to 100 stations; (c) all ecoregions with river benthic macroinvertebrate stations, colored on the basis of alpha diversity rarefied to 10 stations; (d) ecoregions with at least two stations in a hydrobasin, colored on the basis of the dominant component of beta diversity (species turnover, nestedness, approximately equal contribution, or no diversity) when averaged across hydrobasins in each ecoregion.
4.6.3.2. Regional Diversity

The relationship between alpha diversity and latitude was explored to evaluate whether there was evidence of a decline in richness with increasing latitude, as suggested in previous studies (e.g., Scott and Crossman 1973, Castella et al. 2001). Because many ecoregions covered a wide range of latitudes, stations were grouped at a smaller spatial scale into level 5 hydrobasins, and analysis focused only on hydrobasins with at least 4 stations. To ensure comparability of richness estimates across hydrobasins with different levels of sampling, rarefied alpha diversity was compared at the level of 10 stations.

Rarefied taxonomic richness for lake littoral macroinvertebrates showed evidence of a declining trend in alpha diversity above 68°N for samples in Fennoscandia and Alaska (Figure 4-31). Other hydrobasins were located on remote islands (e.g., Iceland, Wrangel Island, Greenland, Faroe Islands) and rarefied alpha diversity in these hydrobasins was lower than those in Fennoscandia and Alaska by approximately 10 or more taxa, regardless of latitude. The low diversity of island ecoregions across all latitudes provided strong evidence for an island biogeography effect on BMI diversity in lakes. For example, Iceland has limited EPT taxa due to dispersal constraints for these taxa. In island hydrobasins, the effect of dispersal constraints on BMI diversity appeared to be stronger than latitudinal constraints, as diversity was similar across all latitudes for these hydrobasins. In contrast, in mainland (e.g., higher connectivity) hydrobasins where dispersal was less limited, a decline in diversity with increasing latitude was the predominant trend, likely related to thermal tolerances.

The river data assessment showed stronger evidence of a latitudinal decline in alpha diversity of benthic invertebrates (Figure 4-32). River data covered a wider range of latitudes (from 49°N to 83°N) and revealed clear evidence of higher taxonomic richness at the lowest latitudes and a strong decline in taxonomic richness above 68°N (Figure 4-32). However, these data also covered a wider range of longitudes, and there was evidence that the strength of the latitudinal decline in diversity differed by longitude/region, related in part to longitudinal temperature gradients across the Arctic. For example, a west-east temperature gradient exists in North America, with more historical warming in the west than along the eastern Canadian Arctic coast, and colder temperatures in the east at similar latitudes. Eastern Canadian hydrobasins clearly showed a stronger decline in diversity that began at lower latitudes than in other regions of the Arctic, and generally had lower diversity than western Canada or USA/ western Canada hydrobasins at similar latitudes (Figure 4-32). Furthermore, the eastern Canadian Arctic is colder than Fennoscandia at similar latitudes. Within the mid-latitudes, western North American stations and Fennoscandia stations had higher average alpha diversity than eastern Canadian stations, consistent with patterns expected to occur with warmer temperatures. The lowest alpha diversity values in the mid-latitudes were attributed to the Kalaallit Nunaat Low Arctic Tundra in Greenland (average richness of 12 taxa at 10 stations and average latitude 61°N) and a hydrobasin in the Middle Arctic ecoregion on southern Baffin Island in eastern Canada (average richness of 16 taxa at 10 stations and average latitude of 63.8°N). Both areas (southern Greenland and southern Baffin Island) have experienced less warming since 1990 than other areas of the Arctic (NASA GISS).
4.6.3.3. Compositional Patterns

The most abundant taxa were compared spatially across highly-sampled areas of the Arctic to identify similarities and differences in composition. Geographic areas for comparison were selected by broadly grouping stations in highly-sampled areas by locale (see Figure 4-33 and Figure 4-34 for locations chosen for lake and river BMI, respectively). Data were summarized by selecting the most abundant taxonomic families in each area, comprising a total of 85% of the organisms found in the area. To account for regional differences at the family level, data were summarized by order level or higher, providing a broad picture of composition across geographic areas. Lake littoral samples were generally numerically dominated by Dipteran taxa (true flies, primarily chironomids) and oligochaete worms in all Arctic areas (Figure 4-33). The numerical abundance of Diptera and Oligochaeta was strong enough in Greenland that these were the only two groups that contributed to the dominant portion of the assemblage. Ephemeroptera (mayflies) were not generally abundant in littoral samples, but Trichoptera (caddisflies) were among the important taxa in Alaska and Plecoptera (stoneflies) were abundant in Fennoscandia. Alaska and Fennoscandia also differed with respect to non-insects, as nematode worms were important in Alaska whereas isopods were among the abundant taxa in Fennoscandia. However, differences with respect to

Figure 4-33 Summary of the taxa accounting for 85% of the lake littoral benthic macroinvertebrates collected in each of several highly-sampled geographic areas, with taxa grouped by order level or higher in pie charts placed spatially to indicate sampling area. Pie charts correspond to (1) Alaska, (2) Greenland low Arctic, (3) Iceland, and (4) Fennoscandia.
nematode abundance may have reflected differences in sample sorting, as nematodes are often not counted in lake littoral samples of Fennoscandia.

River benthic invertebrate assemblages were compared across more areas of the Arctic, and showed large differences in composition and dominance, both latitudinally and longitudinally. Diptera alone made up 85% of the assemblage in the high Arctic islands (Ellesmere Island in Canada, and Svalbard), as well as in Iceland (Figure 4-34). The high Arctic in Greenland was dominated by Diptera, but oligochaetes were also abundant in these systems, and composition of the most abundant groups was extremely similar between the low and high Arctic regions of Greenland. At lower latitudes, other groups contributed more to assemblage composition. Alaska and northern Baffin Island in eastern Canada had similar composition of oligochaetes and nematode worms, but Alaska also had high abundance of mollusks whereas Ephemeroptera were more common on Baffin Island. Ephemeroptera were highly abundant in several areas of eastern and southern Canada (Baffin Island, northern Labrador, and south of Hudson Bay), but were not abundant in other areas of the Arctic. In contrast, Plecoptera and Trichoptera were far more abundant in Fennoscandia, western Canada, and south of Hudson Bay than they were in eastern Canada. Overall, Fennoscandia had the largest contribution from non-Dipteran organisms.

Figure 4-34 Summary of the taxa accounting for 85% of the river benthic macroinvertebrates collected in each of several highly-sampled geographic areas, with taxa grouped by order level or higher in pie charts placed spatially to indicate sampling area. Pie charts correspond to (1) Alaska, (2) western Canada, (3) southern Canada, south of Hudson Bay, (4) northern Labrador, (5) Baffin Island, (6) Ellesmere Island, (7) Greenland high Arctic, (8) Greenland low Arctic, (9) Iceland, (10) Svalbard, and (11) Fennoscandia.
4.6.3.4. Temporal Trends in Lakes

Few long-term records of benthic macroinvertebrates exist from biological monitoring in Arctic lakes. In Lake Abiskojaure (68°N) and Lake Stor-Tjulträsk (66°N) in Sweden, the stony littoral zones (1 m depth) have been monitored annually since 1988 (Figure 4-35). Taxonomic richness (alpha diversity) of littoral macroinvertebrates shows a high inter-annual variability for both lakes. This is mainly due to the low densities of many taxa, i.e., many taxa occur only with a single or few individuals in a sample. While there is no obvious trend in Lake Abiskojaure, richness in the more southern Lake Stor-Tjulträsk has been increasing significantly (Mann-Kendall trend test, p <0.001) since the 1990s. Taxonomic richness has been calculated using a standardized list of taxa. Note, however, that two major groups of benthic macroinvertebrates, the Chironomidae (midges) and Oligochaeta (worms) have not been identified to species. The plots in Figure 4-35 therefore show underestimates of true alpha diversity.

4.6.4. Gaps in Knowledge and Monitoring

There were large gaps in the spatial coverage of lake benthic invertebrate data, due in part to a lack of routine monitoring in many areas. However, a larger issue with regards to lake monitoring is that different countries and researchers focus on a different lake habitats, leading to a heterogeneous dataset that does not allow for broad comparisons. For example, Fennoscandia, Iceland, Alaska, and a few stations in Greenland have data from the littoral zone of lakes, with data collected using kick nets or rock scrapes (broadly comparable with respect to taxonomic composition, though rock scrapes have been shown to collect fewer taxa; Lento and Morin 2014). In contrast, Canada, Russia, and most of Greenland have data from the profundal zone, with grab samplers or dredges used to collect benthic macroinvertebrates. Data from the two quite different habitats and sampler types are not comparable, as profundal samples collected by grabs or dredges are dominated by organisms that prefer to burrow in soft sediments, such as midges and worms. Lake littoral samples, collected using a kick net (i.e., D-net) or rock and sediment scrapes, include more taxa that live on rocky substrates, such as mayflies, stoneflies, and caddisflies. Profundal samples are naturally less diverse than littoral samples, precluding broad comparisons across the circumpolar region. Moreover, in many areas (such as the Canadian high Arctic), only top sediment samples or sediment cores are collected for paleolimnological samples (or training datasets) using chironomids. These samples, although spatially extensive, offer a further limitation on circumpolar assessments, particularly when lake littoral and profundal samples do not identify past the family level for Chironomidae. In order to support future assessment efforts, there should be a standard sampling approach for lake benthic macroinvertebrate assemblages, ideally focused on the more taxonomically-rich littoral zone.

Spatial coverage of river benthic macroinvertebrate data was strong across the circumpolar region, though data were generally lacking for Russia. Despite this gap, river benthic macroinvertebrates had one of the best spatial extents of all the FECs, due in large part to the prevalence of this group in monitoring programs, the relatively standardized sampling approaches used across the circumpolar region (generally kick nets or similar, with comparable mesh size in most regions), and the fact that it is the only FEC to have a national database in Canada, with data contributed to the database from academia and government. As a result, most ecoregions in Canada were represented by river benthic macroinvertebrate samples, allowing for strong spatial assessments. However, despite the strong spatial coverage, much of the sampling that has occurred (particularly in Canada) has been single-event sampling, and thus time series are scarce. An additional limitation to the strength and scope of diversity assessment is inconsistency in the taxonomic level of identification across the Arctic. In Alaska, Finland, and some stations in Canada, Chironomidae were not identified past family level (or were not counted at all for some samples in Finland). Chironomidae are ubiquitous in the Arctic and make up a large proportion of the benthic macroinvertebrate assemblage, and identification at even the subfamily level can help identify more subtle shifts in composition across broad regions (e.g., Culp et al. In Press). Future assessments can continue to make use of the strong spatial coverage of data and accessibility of data from national databases, but monitoring activities should endeavour to include a focus on Chironomidae and include re-sampling of stations to establish time series if possible.

Figure 4-35 30-year trends in alpha diversity of benthic macroinvertebrates in the stony littoral zones (1 m depth) of two Scandinavian Arctic/alpine lakes: Lake Abiskojaure (upper panel) and Lake Stor-Tjulträsk (lower panel).
4.7. Fish

4.7.1. Introduction

Fish are often the top consumer in freshwater habitats, feeding on an array of prey including zooplankton, macroinvertebrates, and other fish. Over 100 species of fish, from 18 families, are reported from freshwaters throughout the circum-Arctic region (Wrona et al. 2013). Five families account for most of the freshwater taxonomic diversity and include Salmonidae (salmon, trout, and whitefish), Cottidae (sculpins), Cyprinidae (carps and minnows), Percidae (perch), and Petromyzontidae (lamprey) (Wrona et al. 2013). Much of the diversity in Arctic fish species occurs within one family, the Salmonidae. Within the Salmonidae family, there is a high degree of phenotypic and ecological diversity throughout the circumpolar Arctic (Klemetsen 2010), and those species that are closely related are often considered as a species complex that includes phenotypic, systematic, and taxonomic variation. Furthermore, fish of the same species may occur sympatrially (e.g., in the same lake), but occupy different niches -- and the use of different resources is often accompanied by differentiation of physical or morphometric characteristics (Knudsen et al. 2007, Siwertsson et al. 2010). For example, the Arctic char (Salvelinus alpinus) species complex, including the North American Dolly Varden (S. malma) and at least 10 other Siberian chars (Wrona et al. 2013), is widely spread across the Arctic and exhibits a broad range of behavioral and morphological variation (Reist et al. 2013). Within a species, char exhibit a range of biodiversity characteristics including variation in life history (see Box 4-1), trophic status, and size structure, resulting in a highly adaptable taxonomic group (Snorras et al. 1994, Wrona et al. 2013). In fact, diadromous Arctic char is the only fish species present through much of the extreme high Arctic (~75° N latitude; Wrona et al. 2013).

At large spatial scales (e.g., continents or regions), historical and modern features of climate, geology, and hydrology influence species distributions. Dispersal barriers, landscape differences, and climate events such as glaciations, sea level rise and fall, and flooding regimes have influenced present day patterns of species richness and distribution (Tonn 1990, Matthews 1998, Hugueny et al. 2010). For example, the North Atlantic region is species-poor as it was colonized only by anadromous species, whereas Beringia and northwest Canada are relatively speciesic because of high variation in space and time of glaciation events that allowed for multiple refugia from glaciation and recolonization pathways (Mims et al. 2010, Wrona et al. 2013). Within northern regions, high variability in environmental conditions across the landscape can support equally high variation in the richness of species at smaller spatial scales (Tonn 1990). Climate change will likely alter the geographic range of species – affecting both local and regional biodiversity – through the northward expansion of southern “non-native” species and the contraction or loss of “native” Arctic species (Wrona et al. 2006b, Culp et al. 2012b, Hayden et al. 2017).

At local scales, a number of environmental drivers affect fish diversity through direct impacts on distribution, growth, and phenology (Culp et al. 2012a, Culp et al. 2012b). Water temperature can have significant impacts on the timing of ontogeny and incubation, on growth and energy requirements of all life stages, and may affect the timing of migrations in diadromous fishes. Connectivity is a strong driver of fish distributions and community composition and is affected by water availability and human development (Schindler and Smol 2006, Dias et al. 2014, Laske et al. 2016). Nutrient concentrations can also affect body size and production of fish (Hayden et al. 2017). While these examples illustrate local-scale influences of environmental shifts on fish diversity, interacting effects across local and regional spatial scales complicate the prediction of species shifts with changing environmental drivers (Box 4-2).

Box 4-1. Fish Life History

At high latitudes, fish life history strategies predominantly promote survival and reproduction in environments that are suboptimal or resource-limited (North America, Mims et al. 2010). Many Arctic fish species are large-bodied, long-lived, late-maturing, highly fecund, and often migratory (e.g., Atlantic salmon; Niemelä et al. 2006, Erkinaro et al. 2018). Migration is common among many species of Arctic fishes. Migrations can either be fully within freshwater habitats (e.g., Arctic Grayling; West et al. 1992, Heim et al. 2016), or between fresh- and saltwater habitats (i.e., diadromy; Gross et al. 1988). Strictly, anadromous fish migrate from sea to freshwater to reproduce, while catadromous fish migrate from freshwater to reproduce in the sea (Mecklenburg et al. 2002). Among the Arctic fishes that migrate between fresh- and saltwater, 39 species (families: Acipenseridae [sturgeons], Gasterosteidae [sticklebacks], Osmeridae [smelts], Petromyzontidae [lampreys], and Salmonidae [salmon, trout, and whitefish]) are anadromous, and two are catadromous (family Anguillidae [eels]; Wrona et al. 2013).

In northern climates, anadromy is the dominant migratory strategy because it allows fishes to exploit the highly productive marine environment, thereby increasing growth rates and reproductive advantages (Gross et al. 1988, Wrona et al. 2013). Anadromous migratory behavior may be reduced at the lower latitudes where feeding and rearing resources are more available to fish in freshwater (Reist et al. 2006). At higher latitudes, anadromy and its benefits to Arctic char (the only fish species in the extreme high Arctic) decrease because of limited access to marine habitats (Svenning and Gullestad 2002).
4.7.2. Objectives and Approach

The circumpolar fish assessment provides a summary of broad spatial patterns of species diversity in Arctic rivers/streams and lakes, including those in sub, low, and high Arctic regions. Fish diversity was evaluated across continental (104 – 107 km2) and regional scales (103 - 105 km2). Specifically, we assessed fish diversity by examining spatial distribution patterns of species composition, alpha diversity, and beta diversity and its component parts (turnover and nestedness). Data were assessed for the circumpolar region by evaluating alpha diversity (species richness) at the ecoregion scale. Beta diversity and its components were calculated within ecoregions for this circumpolar assessment. Regional-scale assessments were completed for highly-sampled ecoregions in Alaska, Iceland, and Fennoscandia, where data were aggregated at the hydrobasin scale to compare diversity patterns at more standardized spatial scales. Diversity measures for this regional assessment included ecoregion-scale gamma diversity (species richness), basin-scale alpha diversity (species richness), and basin-scale beta diversity (species compositional differences). At the regional scale, hydrobasins were divided across ecoregions of similar geography and climate (Olson et al. 2001). Only stations with data for the entire fish assemblage were included in analyses of biodiversity (Figure 4-36a). We identified gaps in the current distribution of fish monitoring, providing a baseline of information for comparison with future monitoring.

4.7.3. Overall Patterns and Trends

Freshwater fish biodiversity was assessed using fish presence data from 3148 stations spanning c. 240° longitude and 23° latitude and 25 ecoregions (Figure 4-36a). Two-thirds (n = 2116) of the stations occurred in lotic systems, with the remainder in lentic systems (n = 1058). In several ecoregions and countries the provided data were robust - having high numbers of both lotic and lentic sample stations. For example, in Fennoscandia (Norway, Sweden, and Finland) 1807 stations were available for analysis, including 1585 lotic stations and 237 lentic stations. Overall, only six ecoregions (24 %) were represented by more than 100 stations, and 12 ecoregions (48 %) were represented by more than 10 stations. The remaining 13 ecoregions were represented by fewer than 10 stations, and often stations of only one type - lentic or lotic. Poor data coverage among the circumpolar ecoregions results from lack of sampling, sampling focused only on particular species, or lack of data contribution to the CBMP freshwater database. Within the 25 ecoregions included in this assessment, 100 fish species of 52 genera and 15 families are known to occur (Figure 4-36b). Sixty-five of the species are in the two most specious families: the Salmonidae, with 34 species from 8 genera, and the Cyprinidae, with 31 species from 21 different genera (Appendix A). The remaining 35 species are from 13 families of 23 genera.

4.7.3.1. Circumpolar Diversity

Large-scale alpha diversity (i.e., species richness within ecoregions) varied among 25 ecoregions, ranging from a single fish species in the Arctic Desert (Arctic charr) to as many as 47 species in the Scandinavian and Russian taiga (Figure 4-36b). Fish alpha diversity varied across continents; northern ecoregions or mountainous ecoregions had lower numbers of fish species. As expected, Islands (e.g., Iceland - 9 species, Greenland - 5 species) also had fewer fish species (Figure 4-36b), representing only one-fourth of all freshwater families when compared to continental ecoregions. Based on a standard sample size (n = 10 stations), alpha diversity of fish varied across ecoregions, ranging from a single species...
in the high Arctic zones (e.g., Arctic Desert and High Arctic Tundra) to between 2 and 13 species in the low Arctic zones (e.g., Interior Yukon-Alaska Alpine Tundra) and subarctic (e.g., Northwest Territories Taiga) ecoregions of North America. In the high Arctic (above 75°N) ecoregions with low richness are both isolated from continents by salt water (e.g., islands such as Svalbard and Ellesmere) and are extremely cold, making it difficult for freshwater species to access and persist in these areas. The relatively high alpha diversity, at 7 to 15 species, in Fennoscandia and western Russia (e.g., Scandinavian and Russian Taiga, Figure 4-36c) is likely due to the combination of history (e.g., glaciations), fish access via streams that run north, and large spatial extent (Reist et al. 2006, Wrona et al. 2013, Stein et al. 2014). Estimates of richness in all ecoregions were generally reduced from those known from academic and government researchers, Traditional Knowledge, and literature (Figure 4-36b, Figure 4-37). For example, alpha diversity at latitudes above 72°N declined to a single species, Arctic charr, based on observations at 36 stations in 17 hydrobasins across four ecoregions. However, eight additional species are known to occur in the Middle Arctic Tundra and one additional species in the High Arctic Tundra of the Archipelago (Figure 4-36b; Scott and Crossman 1973). In addition, TK records can provide additional information about observations of fish species diversity outside of the ecoregions for which monitoring and research data were obtained, such as northern Quebec (Nunavik) and Labrador in Canada, as well as Russia (Figure 4-37).

**Figure 4-37** Fish species observations from Traditional Knowledge (TK) literature, plotted in the approximate geographic location of observed record, with symbol colour indicating the number of fish species recorded and shape indicating the approximate time period of observation. Results are from a systematic literature search of TK sources from Alaska, Canada, Greenland, Fennoscandia, and Russia.
Beta diversity assessment across 25 ecoregions was focused on determining the dominant component of beta diversity (i.e., nestedness or turnover) within an ecoregion. Three ecoregions had insufficient data for calculating beta diversity: Kalaailit Nunaat High Arctic Tundra, Middle Arctic Tundra, and Yamal Gydan Tundra. In the Arctic Foothills Tundra, Brooks-British Range Tundra (North America) and in the Scandinavian and Russian Taiga, the turnover component of beta diversity was greater than the nestedness component (confidence intervals did not overlap; Figure 4-36c). This indicates that the replacement of species across spatial or environmental gradients appeared to drive diversity patterns across a range of ecoregion types in North America and Fennoscandia, including alpine and taiga habitats (See Box 4-2). Generally, a heterogeneous mix of habitats or a broad range of locations (including both lakes and streams) would capture higher biodiversity in these ecoregions, because species and communities are more dissimilar over greater distances (Socolar et al. 2016). The nestedness component of beta diversity was greater only in the Iceland Boreal Birch Forests and Alpine Tundra where only three species were represented in the data, and changes in species composition across the region would result from subsampling the richest fish community. In this instance, monitoring or conserving biodiversity in high richness locations (e.g., sites, lakes, river reaches) may provide the best option of maintaining current biodiversity (Socolar et al. 2016). Beta diversity in all other ecoregions showed no significant differences in turnover and nestedness components, indicating that compositional differences within these ecoregions are due to a combination of stations containing subsets of the species found in richer communities and stations containing additional species not found elsewhere.

Beta diversity in two of the most northern ecoregions (Arctic Desert and High Arctic Tundra) equaled zero, as only a single species (Arctic charr) was captured and there was no change in freshwater fish composition among stations. These locations are species-poor and less accessible to freshwater species, presently and in the past. Reduced colonization potential in these regions prevents the addition of more species, while a hierarchy of species-specific traits may dictate distribution within those regions (Henriques-Silva et al. 2013). In these low richness regions, within-species biodiversity (e.g., polymorphisms) may be of most interest or importance for future monitoring of species.

### 4.7.3.2. Regional Diversity

Regional analysis was completed for five highly-sampled ecoregions, which included the Arctic Coastal Tundra and Brooks-British Range Tundra in Alaska, the Iceland Boreal Birch Forests and Alpine Tundra in Iceland, and the Scandinavian Montane Birch Forest and Grasslands and the Scandinavian and Russian Taiga in Fennoscandia. The regional species pool (based on literature and expert knowledge) in the Iceland Boreal Birch Forests and Alpine Tundra was 8 species, the lowest number among the five ecoregions. In the mountainous ecoregions, the Brooks-British Range Tundra and the Scandinavian Montane Birch Forest and Grasslands, there were 19 and 25 species, respectively. The Arctic Coastal Tundra had a species richness estimate of 26 species, and in the largest ecoregion, Scandinavian and Russian Taiga, 47 species occurred (Figure 4-36b).

When compared across a standard sample size (n = 200 stations), the lowest species richness was found in the Iceland Boreal Birch Forests and Alpine Tundra (3 species, significantly lower than all other ecoregions), which is isolated from other ecoregions by the North Atlantic Ocean. Rarefied alpha diversity was highest in the Scandinavian and Russian Taiga (average of 20 species; Fennoscandian stations only) and the Arctic Coastal Tundra (average of 19 species; Figure 4-38). Species richness estimates were similar for these two ecoregions and did not differ significantly even when rarefaction curves were compared at a sampling frequency of 1500 stations. Rarefied alpha diversity (at 200 stations) in the two mountainous ecoregions was reduced compared to lower elevation Taiga and Coastal Tundra, though only the Brooks-British Range Tundra (average of 9 species) had a significantly lower species richness estimate, whereas confidence intervals for the Scandinavian Montane Birch Forest and Grasslands (average of 15 species) overlapped with those of the lower-elevation ecoregions.

In a subset of 7th level hydrobasins that contained at least 10 sampling stations, the pool of available species ranged from 3 species in Iceland Birch Forest and Alpine Tundra to 21 species in Arctic Coastal Tundra (Figure 4-39a). The average species richness of hydrobasins was typically reduced from the available species pool. Mean basin richness was 9 ± 2.5 species in the Arctic Coastal Tundra, 4.5 ± 1 species in the Brooks-British Range Tundra, 9.5 ± 1.2 species in the Scandinavian and Russian Taiga, and 5.9 ± 1.2 species in the Scandinavian Montane Birch Forest and Grassland (Figure 4-39b). Only in Iceland did the basin richness of 3 ± 0 species mirror the available species pool (Figure 4-39a-b). In Alaska and Fennoscandia, the richness of mountain region basins was consistently lower than the richness of adjacent lowland (tundra or taiga) basins. Mountain regions often have fewer species due to the challenges of accessing habitats (e.g., steep stream gradients) or because of harsher climate conditions (e.g., earlier freeze-up dates).

Beta diversity differed across ecoregions, with higher values ($\beta_{SOR} > 0.70$) in the Arctic Coastal Tundra, Brooks-British Range Tundra, and Scandinavian and Russian Taiga. The Scandinavian Montane Birch Forest and Grasslands and the Iceland Boreal Birch Forests and Alpine Tundra showed moderate beta diversity ($\beta_{SOR}$ values between 0.56 and 0.66). The value of $\beta_{SOR}$ in Iceland Boreal Birch Forests and Alpine Tundra was likely reduced due to its low species richness and isolation. Spatial isolation may have also contributed to differences in the importance of nestedness relative to species replacement. Among the five ecoregions, only the Iceland Boreal Birch Forests and Alpine Tundra showed greater nestedness-resultant similarity compared to turnover (Figure 4-39c). Turnover, the replacement of species in space, was more important relative to nestedness in the remaining four ecoregions (Figure 4-39c), indicating that assemblages would vary across landscapes with either distance between sites or along another environmental gradient (e.g., elevation or temperature).
Figure 4-38 Rarefaction curves of fish species richness in the five ecoregions with robust sampling data. Dashed lines are the 95% confidence intervals. Curves for the Brooks-British Range Tundra and Iceland Boreal Birch Forests and Alpine Tundra were extrapolated to 200 stations (from 63 and 73 stations, respectively), Scandinavian Montane Birch Forest and Grasslands, Scandinavian and Russian Taiga, and Arctic Coastal Tundra were truncated at 400 stations.

Figure 4-39 Fish diversity characteristics in three geographical regions: Alaska, Iceland, and Fennoscandia. Gamma diversity is based the total number of species sampled in hydrobasins of each ecoregion. Alpha diversity shows the mean basin species richness (95% confidence interval) and beta diversity shows the component of beta diversity, nestedness or turnover, that dominated within each of the ecoregions; gamma, alpha, and beta diversity estimates were based on a subset of basins where a minimum of 10 stations were sampled. All maps are drawn to the same scale.
4.7.3.3. Compositional Patterns

Across the total area with available fish presence data, there were discernible differences in the distribution of species (Figure 4-40), including the presence of certain families (e.g., Catostomidae in North America) or exchange in genera (e.g., *Salmo* in Fennoscandia and *Oncorhynchus* in Alaska). Fourteen species of fish had a distributional range across continents - including salmonids (7 spp.), smelts (2 spp.), sticklebacks (2 spp.), burbot (1 spp), pike (1 spp), and lamprey (1 spp.). Three additional species (all salmonids) have been introduced to Fennoscandia and Russia from North America. Generally, ecoregions that spanned greater spatial extents (e.g., Scandinavian and Russian Taiga) had higher numbers of species, and ecoregions that reached lower latitudes often contained minnows (Cyprinidae) and perch (Percidae). The most northern ecoregions contained few fish, sometimes only Arctic char. Latitude limited the species richness, and therefore, the beta diversity (change in species composition) across space. Furthermore, in isolated locations like Iceland, the depauperate fish fauna and their distributional patterns - as subsets of the richest community - resulted in lower overall beta diversity, and a higher index of nestedness compared to turnover. Mountain regions may be similarly isolated, with fish species access reduced due to stream gradients or climate. In the regional analysis, species richness was reduced in the Brooks-British Range Tundra and in the Scandinavian Montane Birch Forest and Grasslands when compared to adjacent, low-elevation ecoregions (e.g., Brooks-British Range Tundra elevation range 800-2400 m, Arctic Coastal Tundra elevation range 0-150 m; [https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions](https://www.worldwildlife.org/biome-categories/terrestrial-ecoregions)). Interestingly, the within-ecoregion beta diversity was comparable, and mountain and low elevation ecoregion beta diversity was primarily supported through species turnover.

Biodiversity analyses were influenced by the availability of data across and within ecoregions. For some areas, limitations based on sample size (the number of stations) hindered our ability to fully examine species richness from the data gathered for the CBMP database. For example, in our regional subset, which contained the most robust data, we could not discern differences in species richness between the Scandinavian Montane Birch Forest and Grasslands and the adjacent Scandinavian and Russian Taiga until nearly 300 stations were sampled. In all other ecoregions but one, we had far fewer than 300 sample stations, and therefore, an inability to compare richness at the hydrobasin level based on collected data. Fortunately, fish distributions are well known, especially compared to other aquatic organisms, and species richness of ecoregions could be determined based on literature, expert knowledge, and indigenous knowledge. While we were able to determine whether beta diversity within ecoregions was due to either replacement or loss of species, this often relied on small sample sizes, with one or two hydrobasins representing large spatial extents. Increasing spatial and temporal coverage, through additional monitoring or improved access to existing data, would improve our ability to determine the status of freshwater fishes.

Figure 4-40 Longitudinal distribution pattern of fish species from Alaska to western Russia. Each number (y-axis) represents a single species, colored by taxonomic family. Species numbers are referenced in Appendix A. Introduced species are represented by circles. See Figure 4-36 for ecoregion abbreviations.
Both climate and land-use affect Arctic freshwaters and their fish communities. For example, Hayden et al. (2017) examined fish communities along a gradient of altitude, human population density, and land-use intensification in the subarctic, Tornio-Muoniojoki catchment (Figure 4-43) over the period of 2009 to 2013. Levels of nutrients (phosphorus, nitrogen, carbon) in lakes increased along the gradient leading to higher ecosystem productivity. This productivity gradient was associated with a change in fish community composition with salmonids (European whitefish, Coregonus lavaretus) dominant in headwater lakes. Fish composition then progressively shifted downstream towards percid (perch, Perca fluviatilis, and ruffe (Gymnocephalus cernua)) and finally cyprinid (roach, Rutilus rutilus) dominance (Figure 4-43). This progressive change was accompanied by a near 50-fold increase in relative biomass of fish, and a 50% decrease in mean body size. This massive increase in fish abundance was correlated with a reduction in the size of invertebrate prey, a shift towards smaller invertebrate species, and decreased invertebrate diversity, particularly in the most productive lakes. They also observed distribution limits and continuous range expansions over the period of record for cool and warm water species such as percids (ruffe, perch), and cyprinids (ide [Leuciscus idus], roach, bleak [Alburnus alburnus]). In contrast, range retractions were evident for the cold water species Arctic charr (Salvelinus alpinus), grayling (Thymallus thymallus), brown trout (Salmo trutta), and burbot (Lota lota). The study concludes that effects of range expansion cannot be predicted by bioclimatic envelope models alone, but that lake-specific abiotic and biotic data must be integrated to realistically assess future fish community diversity. Hence, long-term data from Arctic systems are required to optimally assess the relative roles of different abiotic and biotic factors in determining fish diversity and ecosystem functioning. However, if such long-term data are not available, space-for-time substitution studies have the potential to provide an alternative approach to predict future change in fish diversity.

Changes to thermal and hydrological regimes of freshwaters due to climate change are predicted to affect the distributions and prevalence of salmonids including Atlantic salmon (Salmo salar), brown trout (Salmo trutta), and Arctic charr (Salvelinus alpinus) (Elliott and Elliott 2010, Finstad and Hein 2012). Northern Norway (65–71°N) and Iceland (64–66°N) are among the only regions in the world where distributions of these species overlap. Long-term catch records for these areas provide an opportunity to assess recent changes in the abundance of these fish species and evaluate whether similar trends are evident in both countries.

A 24-year record of fish relative abundance (percent of total abundance) from Iceland shows that Atlantic salmon were most abundant in the west by a margin of about 50-70% (Figure 4-41a), while trout were most abundant in the south by about 10-30% (Figure 4-41b). Communities in the north and east exhibited the strongest changes in relative abundance over time (Figure 4-41c,d). In these regions, previously similar abundances of Atlantic salmon and Arctic charr have diverged as temperatures have increased (Elliott and Elliott 2010, Finstad and Hein 2012).
anadromous Arctic charr (~45% each) have been diverging since 2005 due to declines in the relative proportion of Arctic charr, resulting in a dominance of Atlantic salmon in these systems. At the same time, in the north and east, brown trout have steadily increased (10-15%) since 1992 (at the start of record). Potential temporal shifts in the relative abundance of fish species in Iceland’s river communities will change current patterns of species diversity - lessening the evenness among species in some regions (e.g., diverging percent abundance of Arctic salmon and anadromous Arctic charr in northern rivers) while increasing the evenness of species in others (e.g., brown trout and anadromous Arctic charr in western rivers).

Long-term records from northern Norway indicate that Atlantic salmon has dominated in river-based systems for the entire period of record (1993-2016), and has been increasing in relative abundance over the last several years (Figure 4-42a). The amount of brown trout in the catches has been relatively stable throughout the period, while Arctic charr have shown a decline in relative abundance over the last 10-15 years. In lake-based systems, however, brown trout seems to be the dominant species and has shown a steady increase from 1995 until approximately 2011, while relative abundances of both Atlantic salmon and anadromous Arctic charr declined over the same period (Figure 4-42b). Thus, the relative abundance of anadromous Arctic charr has generally declined in rivers of northern Norway, both in river-based and lake-based systems (Figure 4-42a,b). However, whereas there was an early period of relative stability followed by a decline after 2002 in Norwegian river-dominated systems, similar to the patterns seen in Iceland, there was a more steady decline in anadromous Arctic charr abundance in lake-based systems in northern Norway from 1995 to 2009 (Figure 4-42b).

Coherent changes in two countries that are located on each side of the Norwegian Sea indicate that a common factor such as climate change may be causing these declines in Arctic charr. However, the mechanisms for the changes are not fully understood. In Iceland, water temperature has shown an increase in spring and autumn while the average temperature for the summer months (June – August) has not shown an increase. The effects of increased water temperatures in spring and autumn might affect and possibly cause mismatch in spawning and hatching time of Arctic charr while salmon and trout remain unaffected. The strong contrast in the dominance of brown trout and Atlantic salmon in northern Norway between lake- and river-based systems speaks to the important influence of lakes on fish assemblage composition.

4.7.4 Gaps in Knowledge and Monitoring

While fish are key species in aquatic ecosystems and are important to communities of the North, it is evident that there are significant gaps in monitoring effort and data coverage across the circumpolar region. Although in some cases the spatial extent is limited because existing datasets were not accessible (e.g., some academic sources that were not open access or government-funded programs that are no longer in operation), there remain significant gaps in monitoring effort and coordination of routine monitoring in some areas. Across Canada, for example, a large number of historical studies focused on monitoring commercial or subsistence fisheries, and thus quantified a selection of fish species rather than assessing the diversity of the full assemblage. Furthermore, many sites across North America have only been sampled once, thus precluding temporal analyses of trends. Similarly, there are large areas that have not been sampled sufficiently to allow for analyses of spatial patterns or temporal trends.

Sparse long-term data on fish assemblages exist for the Arctic. Long-term commercial fishing data are common in North America and Europe (e.g., see section 4.7.3.4), but these records generally focus on targeted fish species rather than assessing the full assemblage. There were large spatial gaps in the distribution data that could be obtained on fish assemblages that hinder assessments of fish distribution or biodiversity patterns across large spatial or circumpolar scales. Furthermore, the number of fish species included in the database represents only 42% of all Arctic species (Wrona et al. 2013). In northeastern North America, only four of 38 species (or 10.5%) were included, and only two species (Arctic charr and threespine stickleback) that were surveyed outside of commercial fishing data were used in our analyses. In two regions, which were considered relatively data rich, Beringia (i.e., Alaska) & northwestern Canada and Russia & Scandinavia, only 50% and 57% of the species, respectively, were found in the dataset. (See Appendix A for species lists). Until broader spatial and temporal data coverage is available, the ability to assess changes in biodiversity, especially at large spatial scales, will be limited.
Figure 4-41 Temporal patterns in % abundance of Atlantic salmon, brown trout, and anadromous Arctic charr from catch statistics in Iceland rivers monitored from 1992 to 2016, showing results from (a) west, (b) south, (c) north, and (d) east Iceland.

Figure 4-42 Temporal patterns in % abundance of Atlantic salmon, brown trout, and anadromous Arctic charr from catch statistics in northern Norway rivers monitored from 1993 to 2016, including basins dominated by (a) rivers and (b) lakes.