



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).

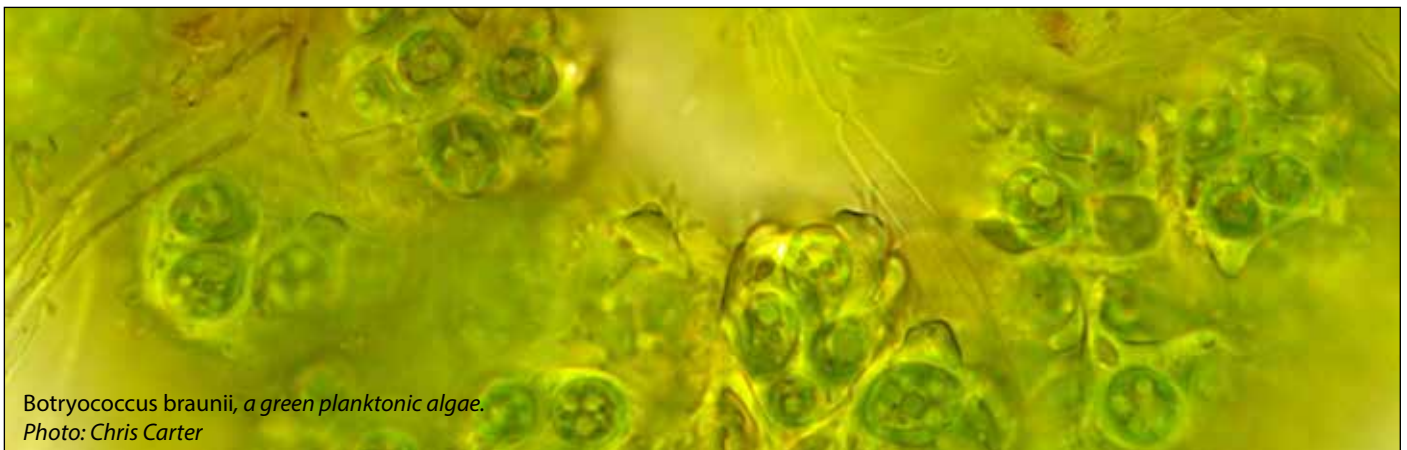
Species richness and biomass can range greatly across Arctic lakes depending on environmental conditions that regulate their need for resources, including factors such as temperature, precipitation, UV radiation levels, spread of viruses and fungi, and predation by zooplankton (Prowse et al. 2006b, Reynolds 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.



Botryococcus braunii, a green planktonic algae.
Photo: Chris Carter

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

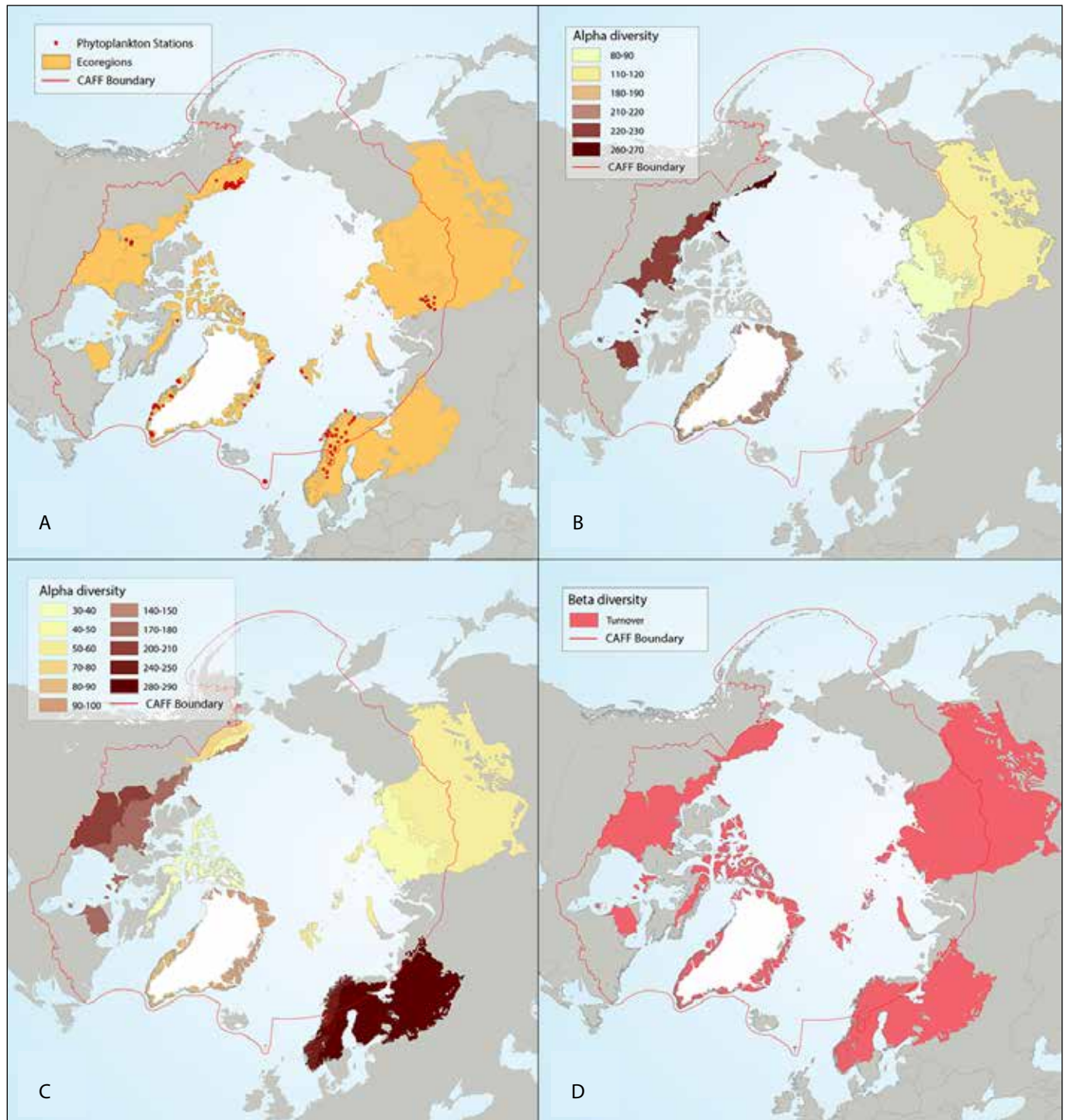


Figure 4-17 Results of circumpolar assessment of lake phytoplankton, indicating (a) the location of phytoplankton stations, overlain by circumpolar ecoregions; (b) ecoregions with many phytoplankton stations, colored on the basis of alpha diversity rarefied to 35 stations; (c) all ecoregions with phytoplankton 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.

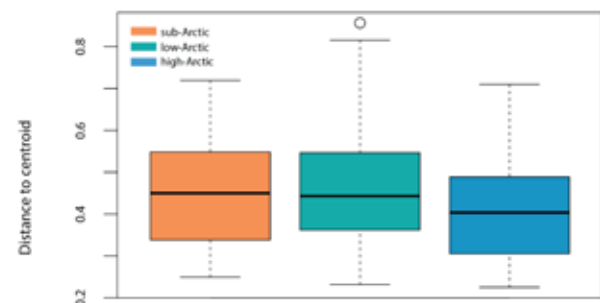


Figure 4-18 Box plot represents the homogeneity of assemblages in high Arctic ($n=190$), low Arctic ($n=370$) and sub-Arctic lakes ($n=1151$), i.e., the distance of individual lake phytoplankton assemblages to the group centroid in multivariate space. The mean distance to the centroid for each of the regions can be seen as an estimated of beta diversity, with increasing distance equating to greater differences among assemblages.



Macrophytes in lake, Rybachy peninsula near Murmansk, Russia
Photo: svic/Shutterstock.com

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.

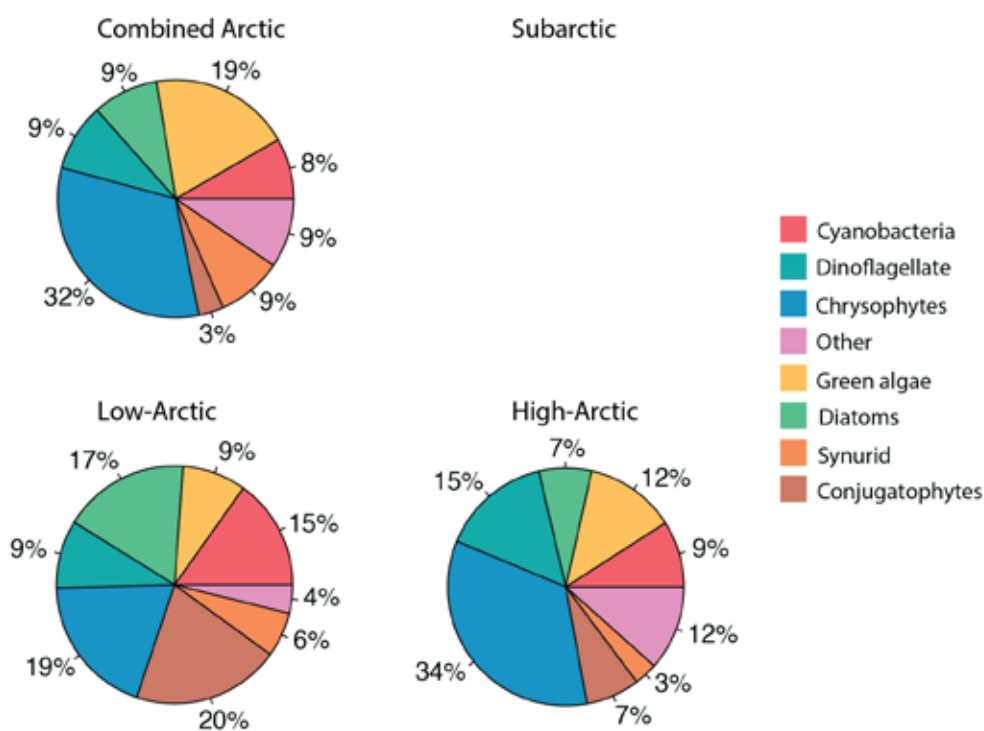


Figure 4-19 Phytoplankton percent composition by dominant classes across the three Arctic regions, using relative presence across stations calculated from from presence-absence data.



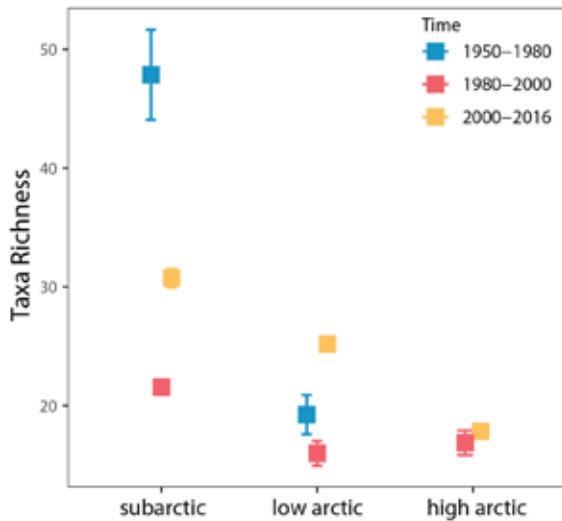


Figure 4-20 Phytoplankton species richness averaged by time periods \pm SE in each Arctic region.

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 ($>250 \text{ mm}^3 \text{ L}^{-1}$) 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 $100 \text{ mm}^3 \text{ L}^{-1}$. 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 Langemandssø 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 = $854 \text{ mm}^3 \text{ L}^{-1}$) was excluded, there was a significant decrease in total biovolume in Greenland lake Langemandssø (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), Båtkåjaure (slope = 1.63), Övre Fjätsjön (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).

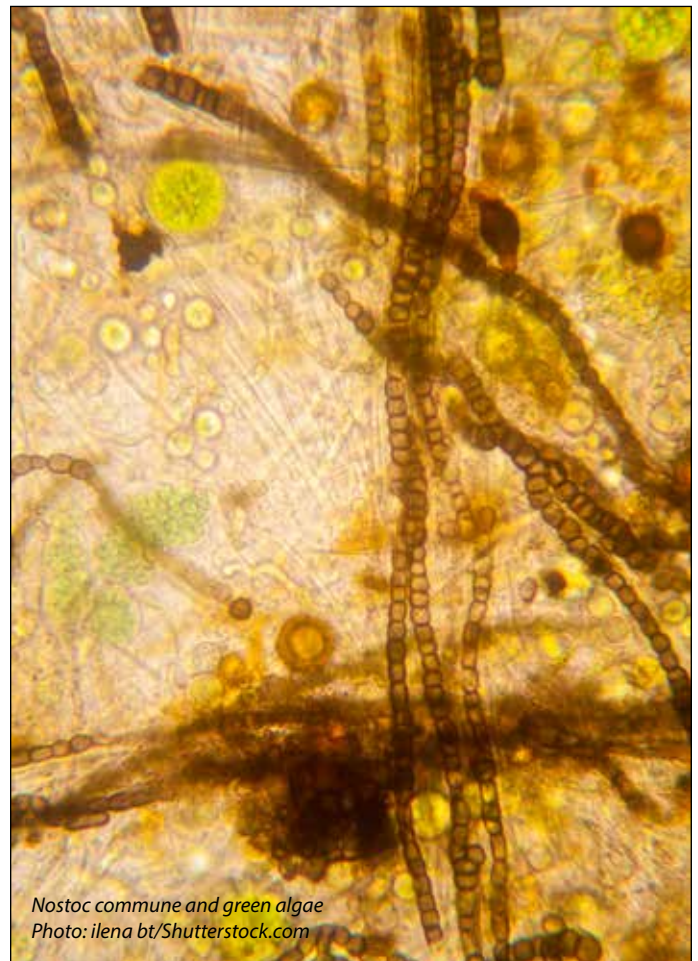




Figure 4-21 Circumpolar Arctic distribution of Cyanophyceae using presence-absence data from all sites sampled between 1980-2015.

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 monitoring 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 4-2 The percent of lakes with a peak in cyanobacteria biovolume in each of the 10 hottest years on record from 1880 to 2014 (temperature rankings from NOAA National Centers for Environmental Information 2015). Percents were calculated using only lakes sampled in a particular year, and a peak was defined as a notable increase in biovolume relative to other years on record, with magnitude of peaks varying by lake and by year.

| Rank (1 = Warmest) | Year | Percent of lakes with cyanobacteria peak |
|--------------------|------|--|
| 1 | 2014 | 64% |
| 2 (tie) | 2010 | 21% |
| 2 (tie) | 2005 | 15% |
| 4 | 1998 | 18% |
| 5 (tie) | 2013 | 36% |
| 5 (tie) | 2003 | 36% |
| 7 | 2002 | 18% |
| 8 | 2006 | 29% |
| 9 (tie) | 2009 | 14% |
| 9 (tie) | 2007 | 29% |