Cyanobacteria in High Latitude Lakes, Rivers and Seas

13

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Contents

Summary

Cyanobacteria often account for a large and sometimes dominant fraction of phototrophic biomass and primary production in high latitude lakes, ponds, streams and wetlands. Picocyanobacteria are usually the most abundant photosynthetic cell type in the plankton of Arctic lakes and rivers, and in East Antarctic saline lakes they have been recorded at cell concentrations of up to 1.5×10^7 per mL. In striking contrast to their success in high latitude lakes, picocyanobacteria are generally absent or sparse in polar seas, with the exception of regions that receive advective inputs of picocyanobacteria from more favourable growth environments. Colonial bloom-forming cyanobacteria are conspicuously absent from most polar freshwaters, but future climate change may favour their development in some areas via warmer temperatures for growth, more stable water columns that favour gas-vacuolate species and richer nutrient conditions as a result of more active catchment processes. Mat-forming cyanobacteria are a ubiquitous element of polar aquatic ecosystems including lakes, ponds, streams and seeps. These consortia of diverse microbial taxa often occur as benthic crusts and films, and in some locations form luxuriant communities up to tens of cm in thickness. They have many biological features that make them well suited to life in the extreme polar environment, including tolerance of persistent low temperatures, freeze-thaw-cycles, high and low irradiances, UV-exposure and desiccation.

13.1 Introduction

The first accounts of cyanobacteria in the polar regions came from reports by explorers who noticed unusual biological communities growing on or beneath the ice. In the expedition sent by Robert Falcon Scott to explore the McMurdo Dry Valleys, Antarctica in 1909, Griffith Taylor wrote: "*We came across a lake two miles long. It was of course frozen, but*

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B.A. Whitton (ed.), *Ecology of Cyanobacteria II: Their Diversity in Space and Time*,
DOI 10.1007/978-94-007-3855-3_13, © Springer Science+Business Media B.V. 2012

beneath the ice the water was very deep and we could see extensive water plants" (Taylor 1916). These lakes have no aquatic macrophytes, but they do contain luxuriant, brightly coloured communities of cyanobacterial mats. Several decades earlier on his epic traverse of the Greenland Ice Cap, Nordenskiöld noted that the botanist on his expedition, Dr. Beggren, "*soon discovered, partly on the surface of the ice, partly in the above mentioned powder (cryoconite rock dust), a brown polycellular alga*" (Leslie 1879). This was later identified as the cryoconite community dominated by the nitrogen-fixing cyanobacterium *Calothrix parietina* (Gerdel and Drouet 1960). James Murray, the biologist on Shackleton's 1907–1909 expedition to Ross Island Antarctica, dug through the ice to the bottom of a frozen lake and found a benthic mat "*that on careful thawing released a multitude of living things for study*" (Murray 1910), probably the first evidence that cyanobacterial mats are refugia for diverse communities of organisms in the polar environment.

Over the last few decades there have been many advances in understanding of high latitude lakes, ponds and flowing waters, and of the composition and functioning of their biological communities. It is now well established that cyanobacteria are a major and often dominant component of polar aquatic ecosystems, with strong similarities in community types and ecology between the Arctic and Antarctica. Ecologically, most aquatic cyanobacteria fall into three functional groups (Vincent 2009): picocyanobacteria, bloom-formers, and mat-formers. The first of these groups, picocyanobacteria, are widespread in the oligotrophic freshwaters that characterize high latitude regions, and in some locations these smallest of phototrophs achieve extremely high concentrations. In contrast, there is an intriguing absence or sparse representation of picocyanobacteria in the adjacent polar oceans. Bloom-forming cyanobacteria are currently absent from most polar aquatic environments, but they have been observed in subarctic waters and may be increasingly prevalent with ongoing environmental change in the polar regions. Mat-forming species are the most successful cyanobacteria at high latitudes. These achieve spectacular biomass levels at some sites, although they are more commonly present as mm-thick mats, films and aggregates, and can also be associated with aquatic mosses (Vincent 2000; Singh and Elster 2007; Nakai et al. 2012).

In this review, we examine each of the ecological groups of cyanobacteria in the polar regions, with emphasis on high latitude lake, pond, river and stream communities. In a companion chapter (Chap. 14) we examine cyanobacterial diversity and function in more extreme habitats of the cryosphere: snow, ice, rock and soils. Many of the habitats and communities described below are illustrated in the online article associated with this book chapter (Vincent and Quesada: Cyanobacterial diversity and dominance in polar aquatic ecosystems).

13.2 Picocyanobacteria

Applications of fluorescence microscopy, flow cytometry and molecular methods have resulted in a rapid expansion in knowledge about picocyanobacteria in aquatic ecosystems (see Chaps. 8 and 20). Their high surface-to-volume ratio makes them especially well suited to life in oligotrophic waters. Given the low nutrient status of most high latitude lakes and rivers, picocyanobacteria are widely distributed and abundant in the aquatic ecosystems of both polar regions, as expected. However, they are conspicuously absent or rare in polar seas, yet these may also be nutrient-poor in some locations. *Prochlorococcus marinus*, which is highly successful in the tropical ocean, declines sharply in cell concentration at about latitudes 45°N and 45°S and there have been no confirmed reports of its occurrence in the Arctic Ocean. After extensive surveys of the Arctic picoplankton by flow cytometry, Li (2009) concluded that this taxon "*is known and confirmed to be absent from subpolar and polar waters*". No freshwater representatives of *Prochlorococcus* or the filamentous *Prochlorothrix* are known from the Arctic or Antarctica.

The picocyanobacterial genus *Synechococcus* is well represented in polar freshwaters as well as in Arctic and Antarctic saline lakes (Table 13.1), but in the ocean it steadily declines with increasing latitude south and north (Fig. 13.1), and is typically sparse or undetectable in subpolar and polar marine environments. In a 2,780-km north–south transect during winter into the Southern Ocean (Doolittle et al. 2008), phycoerythrin-rich picocyanobacteria were below the limits of detection once temperatures dropped below 1.3°C, south of the Antarctic Polar Front. *Prochlorococcus* was only detected north of the Subtropical Convergence, in water temperatures above 10°C. In the most extensive survey of picoplankton in the Arctic to date, from the Pacific Ocean through the Canadian Arctic Archipelago to the Atlantic Ocean, there was a striking increase in picocyanobacteria at either end of the transect, and the Arctic Ocean was almost devoid of picocyanobacteria (Fig. 13.2). This dichotomy of abundant *Synechococcus* in lakes yet near absence in the polar oceans has been attributed to the inhibitory effect of extreme low temperatures in the polar marine environment on cyanobacterial growth rates, which prevents them keeping pace with loss processes such as grazing, viral lysis and advection (Vincent 2000). Picoeukaryotes do not exhibit the same latitudinal decline as picocyanobacteria and are sometimes the dominant phytoplankton in the polar oceans. In the Southern Ocean transect, picoeukaryotes represented more than 99% of the picophytoplankton community in waters cooler than 1°C (Doolittle et al. 2008). An especially common picoeukaryote in the Arctic Ocean is a genetically distinct prasinophyte of the genus *Micromonas*. This genotype is psychrophilic and has relatively fast growth rates at low

Table 13.1 Concentrations of picocyanobacteria in high latitude waters.

Aquatic environment and site	Concentration range (cells mL^{-1})	References
Marine		
AO, east–west transect across Canada	0–10	Li (2009)
Greenland Sea	nd-5×10^3	Gradinger and Lenz (1995)
Coastal AO, eastern Beaufort Sea	$0.2–7 \times 10^4$	Waleron et al. (2007)
Coastal AO, western Beaufort Sea	$10–10^2$	Cottrell and Kirchman (2009)
Saline lakes		
Meromictic lakes, CHA	$10^3–6 \times 10^4$	Van Hove et al. (2008)
Vestfold Hills lakes, Antarctica	$10^4–1.5 \times 10^7$	Powell et al. (2005)
Freshwater lakes		
Freshwater lakes, Vestfold Hills	nd	Powell et al. (2005)
Canadian subarctic lake	$0.2–7 \times 10^4$	Rae and Vincent (1998)
Byers Peninsula, MA	$10^2–10^4$	Toro et al. (2007)
Eutrophic lakes, Signy Island, MA	$10^4–10^8$	Hawes (1990)
Rivers		
Great Whale River, Canadian subarctic	$1.6–4 \times 10^4$	Rae and Vincent (1998)
Mackenzie River, Canadian Arctic	$2–5 \times 10^4$	Vallières et al. (2008)

CHA Canadian High Arctic, *MA* maritime Antarctica, *AO* Arctic Ocean, *nd* not detectable

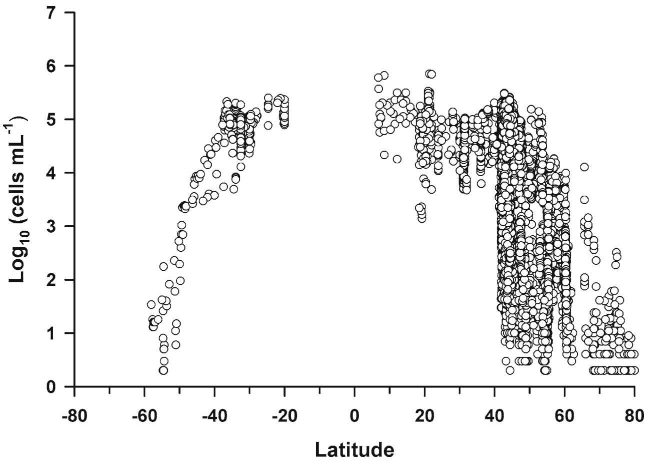

Fig. 13.1 Latitudinal trends in picocyanobacteria (*Synechococcus* plus *Prochlorococcus*), from latitudes 60°S to 80°N. (This figure was prepared by WKW Li based on data published in Li 2009)

temperature (Lovejoy et al. 2007), which may explain its striking success relative to *Synechococcus*. Future changes in the temperature regime of the Arctic Ocean as a result of global warming could ultimately lead to a shift from picoeukaryotes to picocyanobacteria, with implications for food quality and trophic processes (Vincent 2010).

Picocyanobacteria have been recorded at a few sites in the polar oceans, notably in places that have inputs of picocyanobacteria from elsewhere, for example the Beaufort Sea influenced by the Mackenzie River (Waleron et al. 2007) and the Greenland Sea influenced by advection from the North Atlantic (Gradinger and Lenz 1995). The latter study concluded that northward flowing Atlantic water in spring brings high concentrations of picocyanobacteria into the Greenland Sea, which is initially devoid of these cells, and that the presence of picocyanobacteria in this region is the result of advection from the south combined with the high survival potential of these organisms once below the threshold of grazing pressure. *Synechococcus* cells have been recorded in coastal waters of the Arctic Ocean off Barrow, Alaska. Cell concentrations were similar in summer and winter (up to 10^2 cells mL^{-1}), leading Cottrell and Kirchman (2009) to suggest that their growth in the dark may be supported by heterotrophy. These populations might also be the result of advection via coastal currents of Pacific Ocean water, combined with the high survivability of cyanobacterial cells, as in the Greenland Sea.

Studies of lakes in subarctic Québec have shown that picocyanobacteria represent 30–60% of the planktonic biomass, as measured by chlorophyll a (Bergeron and Vincent 1997), and their photosynthetic activity may be more resistant to UV radiation than for larger phytoplankton cells (Laurion and Vincent 1998). Cell concentrations of *Synechococcus* vary greatly in polar lakes, from undetectable in some freshwaters, to 1.5×10^7 cells mL^{-1} in Ace Lake and other saline lakes of the Vestfold Hills in east Antarctica (Table 13.1). In the Vestfold Hills lakes, peak populations were observed deep within the water column where nutrient concentrations are higher (Powell et al. 2005). In an analogous meromictic lake in the High Arctic, deep mixing during an unusual period of ice out was accompanied by a threefold increase in picocyanobacteria, with peak concentrations in the deeper, more phosphorus-rich waters (Veillette et al. 2011). Detectable populations of picoplanktonic cyanobacteria were also observed in the deep chlorophyll maximum of Lake Vanda in the McMurdo Dry Valleys of Antarctica (Vincent and Vincent 1982).

Picocyanobacteria are also a common constituent of high latitude rivers fed by lakes or where the flowing water transit time is long enough to allow the development of a phytoplankton community. In the Great Whale River, subarctic Canada, picocyanobacteria achieved concentrations up to

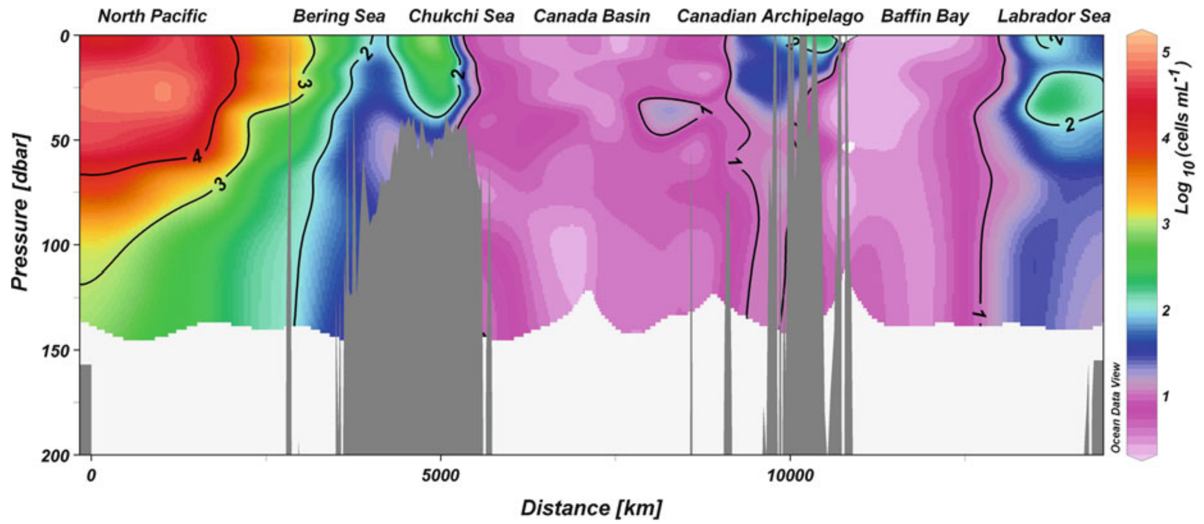

Fig. 13.2 The Arctic as a picocyanobacterial void in the World Ocean. This flow cytometry transect extended eastwards from the Pacific Ocean through the Arctic Ocean to the Labrador Sea at the edge of the Atlantic Ocean. (By permission of WKW Li and C Lovejoy [International Polar Year Symposium, Oslo, Norway, June 2010])

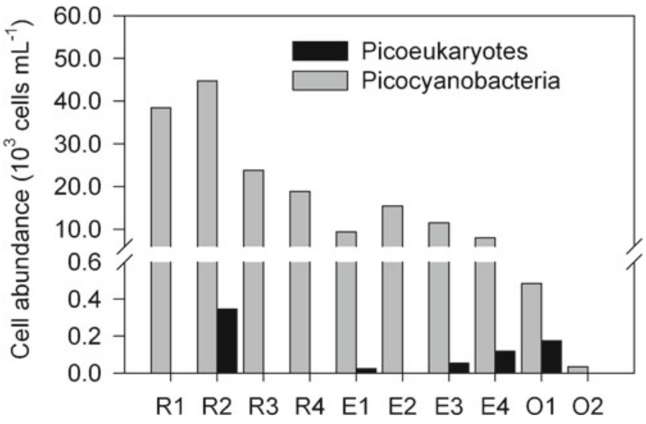

Fig. 13.3 Abundance of picocyanobacteria along a transect in the Mackenzie River, Canadian Arctic. *R1–R4* were freshwater stations in the river, *R5* and *R7* were located across the estuarine transition from freshwater to saltwater, and *R8* and *R9* in the coastal ocean. (Redrawn from the data in Vallières et al. 2008)

10^4 mL^{-1} and the picoplankton fraction (<2 µm) contributed about half of the chlorophyll *a* biomass (Rae and Vincent 1998). A 300-km transect down the Mackenzie River, in Canada's Northwest Territories, showed that picocyanobacterial concentrations ranged up to 5×10^4 cells mL^{-1}, but dropped precipitously across the estuary to around 30 cells mL^{-1} in the offshore ocean (Fig. 13.3). In the freshwater river sites, many of the picocyanobacteria occurred in cell aggregates (Vallières et al. 2008).

Initial analyses of the pigment characteristics of *Synechococcus* isolates from High Arctic lakes implied a high level of genetic diversity (Vézina and Vincent 1997). Molecular characterization of assemblages from northern Ellesmere Island similarly indicates considerable diversity among northern strains (Van Hove et al. 2008). The 16S rRNA gene clone library analysis of picocyanobacteria in the Beaufort Sea off the mouth of the Mackenzie River showed that most were closely related to freshwater and brackish *Synechococcus*. No typically marine *Synechococcus* sequences nor any *Prochlorococcus* sequences were recovered, consistent with the hypothesis that most of the picocyanobacteria in this coastal region of the Arctic Ocean come from the river (Waleron et al. 2007).

Thin trichome oscillatorians are often reported in Antarctic lakes plankton; for example, oscillatorian cyanobacteria in the bacterioplankton were found in five out of six lakes in maritime Antarctica (Schiaffino et al. 2009). These organisms also contribute to the deep chlorophyll maxima in McMurdo Dry Valley lakes (e.g. Vincent and Vincent 1982; Spaulding et al. 1994). Studies on the light-capturing abilities of thin oscillatorians have shown that these approach the efficiencies of picocyanobacteria (S. Vézina and Vincent, unpublished data). Some of these populations may be the result of resuspension from benthic mats that often grow over polar stream beds and the lake littoral zone (see below).

13.3 Bloom-Forming Cyanobacteria

Bloom-forming cyanobacterial taxa such as *Anabaena*, *Microcystis* and *Aphanizomenon* are largely absent from the polar regions. A detailed phytoplankton analysis of two lakes in the Canadian High Arctic, ultraoligotrophic Char Lake and sewage polluted Meretta Lake, showed that cyanobacteria made only a small contribution to total nano- and micro- phytoplankton biomass (<10%) in both lakes and that, unlike temperate lakes, there was no increase in the proportional representation of this group in the enriched system (Kalff et al. 1975). Similarly, in a mesocosm experiment conducted in Char Lake, nutrient enrichment (+ P and to a greater extent, +NP) caused an increase in algal biomass, but there was no shift towards cyanobacteria, unlike the usual phytoplankton community response to nutrients in warmer lakes (Schindler 1974). These results imply that bloom-formers are absent not only as a result of the low nutrient status of most waters, but probably also because of other factors, such as low temperatures. Some bloom-formers are known to grow at cool temperatures, at least in culture (e.g. *Aphanizomenon flos-aquae*; Mehnert et al. 2010). However, in temperate latitudes blooms become more likely as the water column warms above 15°C, in part because bloom-forming cyanobacteria tend to have high temperature optima for maximum growth. This temperature-correlated effect may also be the result of an increased frequency and strength of diurnal thermoclines (near-surface temperature and density gradients), which accompany warming and potentially favour gas vacuolate species that can adjust their position in a stable water column (Vincent 2009).

The Arctic, and also maritime Antarctica, are heating rapidly as a result of global climate change, and polar microbial ecosystems are beginning to show the effects of this warming in Antarctica (Quayle et al. 2002) and the Arctic (Vincent 2010). In the longer term, high latitude lakes may become more conducive to bloom-forming cyanobacteria as a result of warmer waters, and increased nutrient input from catchments. Limnological observations at Saqvaqjuac (lat. 63°N), on the western side of Hudson Bay, Canada, are informative in this regard (Welch et al. 1989). Whole lake fertilization experiments in three of the lakes of this coastal region resulted in a strong increase in the concentration of chrysophytes, cryptophytes, dinoflagellates and green algae. As in Char Lake, colonial cyanobacteria (including *Gomphosphaeria*, *Aphanothece*, *Aphanocapsa* and *Anabaena*) were only minor constituents of the phytoplankton and did not respond to the fertilization, even under low N:P ratios. However, naturally enriched lakes close to the sea had blooms of cyanobacteria (*Anabaena* and *Oscillatoria*). This indicates the potential for such communities to develop in the North, although the controlling mechanisms are still unclear.

13.4 Mat-Forming Species

The most conspicuous cyanobacterial communities in the polar regions are mats, films and crusts over the bottom substrata of lakes, ponds, streams and other water-containing ecosystems. These are often highly pigmented, and can form mucilaginous layers, typically 0.5–5 mm thick, but sometimes much thicker (see below). In many aquatic ecosystems of the Arctic and Antarctic, these benthic communities dominate total biomass as well as total primary productivity.

The cyanobacterial-based mat communities are consortia of diverse taxa that are interdependent via their trophic and biogeochemical relationships. The assemblage is often based on a well-developed matrix of thin, filamentous cyanobacteria and a cohort of other autotrophic organisms, which collectively support short trophic chains to bacteria, protists and simple metazoans such as rotifers, nematodes and tardigrades. The chemical and physical micro-environments within the mats differ greatly from bulk properties of their surroundings, and are influenced by the local climate, water, ice and sediment characteristics as well as by the physical and biological organization of the community. Microbial mats can be considered self-organized ecosystems in which biological processes take place under much more benign conditions than in the surrounding polar environment.

13.4.1 Community Structure

Four types of benthic communities commonly occur in polar freshwaters. Firstly, the rocky substrata of shallow streambeds and ponds may be coated by black or brown coloured crusts. These are typically dominated by *Gloeocapsa*, *Schizothrix* or *Calothrix*, and are often rich in UV-screening pigments such as scytonemin (Proteau et al. 1993) or the related compound gloeocapsin. Secondly, tundra ponds often contain extensive black, dark yellow or olive-green sheets of *Nostoc commune*, which sometimes detach and float to the surface (Vincent 2000). This nitrogen-fixing species also occurs over the bottom or edge of some Antarctic stream beds. A third type of community is formed by loose spherical colonies of *Nostoc*; e.g. in meltwater pools on the McMurdo Ice Shelf, Antarctica, and in Two Basin Lake, Canadian High Arctic (Quesada et al. 1999). The fourth community, and by far the most common, is composed of benthic films and mats dominated by filamentous, mucilage-producing Oscillatoriales (Fig. 13.4). These organisms are responsible for the three-dimensional structure of the communities, and the most common genera are *Leptolyngbya*, *Phormidium*, *Microcoleus* and *Oscillatoria*.

Even within a single localized area of the polar regions there can be a large biodiversity of cyanobacteria. For example, on James Ross Island, Antarctica, 75 cyanobacterial morphotypes were observed in various habitats of the area (Komárek and Elster 2008; Komárek et al. 2008), including several types of monospecific communities. Almost all the coccoid morphotypes (in particular a large *Chroococcus*) were restricted to seepages, and were never the taxonomic dominants in the communities. The most commonly represented genus was *Leptolyngbya,* with different species in different habitats *(e.g. L. fritschiana, L. vincentii and L. borchgrevinkii). Phormidium* was also widely distributed; *Phormidium priestleyi* was found in downstream flowing waters, while *P. autumnale* was common in streams and

Fig. 13.4 A carotenoid-rich microbial mat in Discovery Pond at latitude 83°N, on the northern coast of Ellesmere Island in the Canadian High Arctic. The mat community is dominated by oscillatorian cyanobacteria embedded within a mucilaginous matrix of exopolymeric substances. (Photo WF Vincent)

seepages (Komárek et al. 2008). This latter taxon is important throughout Antarctica, and appears to be an isolated clade within the traditional genus *Phormidium*. On the basis of its distinctive morphological and molecular characteristics, it shows a greater affinity to the genus *Microcoleus* (Strunecký et al. 2010).

The application of molecular methods is showing that the cyanobacterial diversity of the polar regions is very much greater than previously thought. Even within the same apparent morphospecies there may be considerable genetic variation. For example, amplified fragment length polymorphism (AFLP) analysis of variation within *Nostoc commune* from collections in Victoria Land, Antarctica, showed that samples could be split according to habitat (irrigated soil communities versus ponds), rather than latitude (Novis and Smissen 2006).

Studies of Antarctic oscillatorians based on morphological and molecular methods have reported endemic as well as cosmopolitan taxa (Taton et al. 2003, 2006a, b; Jungblut et al. 2005; Comte et al. 2007; Komárek et al. 2008). In the most comprehensive analyses to date on microbial mat diversity in the Antarctic, Taton et al. (2003, 2006a, b) analyzed mats from Lake Fryxell (Dry Valleys), four coastal lakes in the Prydz Bay area (East Antarctica) and two meltwater samples from Livingston Island (Antarctic Peninsula). Using clone libraries based on 16S rRNA gene sequences, a total of 63 operational taxonomic units (OTUs) were defined, of which 44 were unique to Antarctica (70%) at the time of publication. In ponds at the far southern Dufek Massif (82ºS), cyanobacterial diversity was impoverished, but the sequenced clones seemed to be more closely related to clones from other Antarctic regions than to sequences from non-Antarctic regions (Fernández-Carazo et al. 2011). Conversely, a clone library analysis of oscillatorian mats at the northern limit of the High Arctic found several High Arctic ribotypes that were >99% similar to Antarctic and alpine sequences. These results included close matches to taxa that had been previously considered endemic to Antarctica, for example one sequence that was 99.8% similar to *Leptolyngbya antarctica* sequenced from the Larsemann Hills, Antarctica. More than 68% of all identified ribotypes at each High Arctic site matched only cyanobacterial sequences from perennially cold ecosystems, and these were <97.5% similar to sequences from warmer environments. These results imply the global distribution of low-temperature cyanobacterial ecotypes throughout the cold terrestrial biosphere (Jungblut et al. 2010). Similar results were obtained by Comte et al. (2007) and Michaud et al. (2012), with some genotypes showing a bipolar distribution. The restriction of endemic cyanobacteria to within one or both polar regions is becoming progressively less apparent. For example, the taxon *Phormidium murrayi,* previously considered to be endemic to Antarctica, has been found in New Zealand streams (Heath et al. 2010), and *Phormidium* sp. from Lake Fryxell has been found to be genetically highly similar (96–99%) to a strain present in saline lakes on the Chilean Altiplano (Dorador et al. 2008). However, most of these studies are based on a limited number of genes, and more detailed genomic analysis is required to fully assess the important question of endemicity versus cosmopolitanism.

Like microbial mats elsewhere, polar cyanobacterial mat and film communities are complex consortia containing viruses, heterotrophic bacteria, archaea and microbial eukaryotes. For example, analysis of 16S rRNA genes from mats collected from the moat of Lake Fryxell in the McMurdo Dry Valleys showed a high bacterial diversity, including the gliding bacteria *Stigmatella, Myxococcus, Cytophaga, Flavobacterium, Marinilabilia* and *Flexibacter*, and anaerobic saccharolytic taxa such as *Clostridium* and *Eubacterium*. Only two distinct archaeal clone sequences were recovered (Brambilla et al. 2001). Similarly, in high arctic microbial

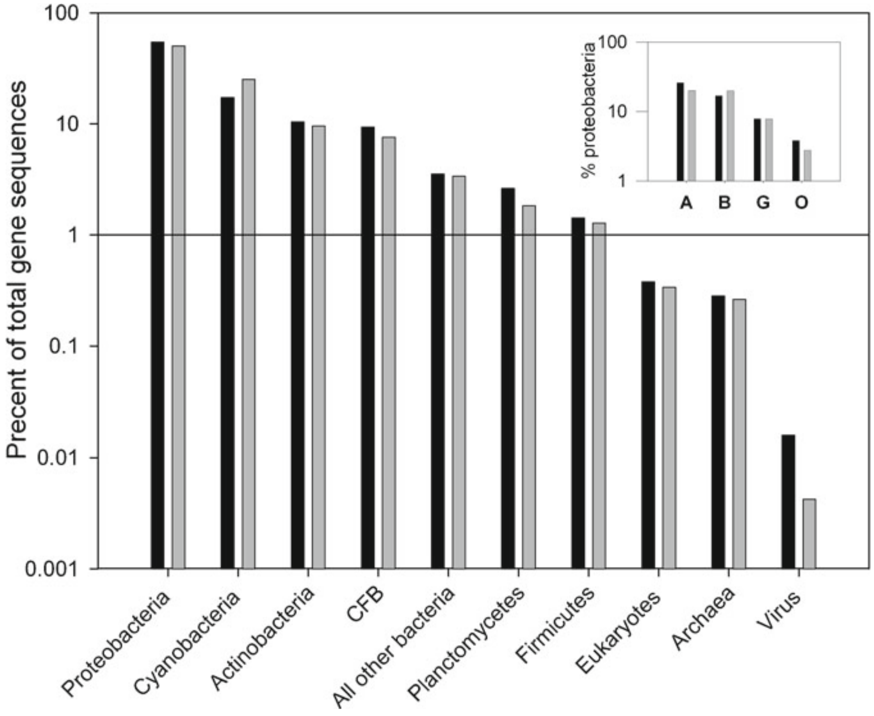

Fig. 13.5 Microbial biodiversity in polar cyanobacterial mats. This shows the distribution of protein-coding gene sequences according to major taxonomic groups, based on metagenomic analysis of mat communities from the Ward Hunt Ice Shelf (*black bars*) and Markham Ice Shelf (*grey bars*) in the High Arctic. Insert: contribution of the major classes of Proteobacteria (*A* Alphaproteobacteria, *B* Betaproteobacteria, *G* Gammaproteobacteria, *O* other Proteobacteria). Note the log scale of the *y-axis* in both graphs. (Modified from Varin et al. 2010)

mats bacterial diversity was high, but only one clade of Archaea was recovered (Bottos et al. 2008). Analyses of cryoconite hole mats on McMurdo Dry Valley glaciers that lie upstream from the Dry Valley lakes had representatives from eight bacterial lineages (*Acidobacterium, Actinobacteria,* Cyanobacteria, Cytophagales, *Gemmimonas, Planctomycetes, Proteobacteria,* and Verrucomicrobia), metazoa (nematode, tardigrade, and rotifer), *Choiromyces*, a ciliate (*Spathidium*) and green algae (Christner et al. 2003), and had similarities with lake ice consortia (Priscu et al. 1998) and microbial mats from Lake Fryxell. More recent studies have shown a high percentage of *Cytophaga*-flavobacteria cells in cryoconite sediments (Foreman et al. 2007). Microbial eukaryotes are often conspicuous elements of polar microbial mats (e.g., on the Markham Ice Shelf; Vincent et al. 2004a, b), and constituted ca. 20% of the protein-coding genes in a metagenomic study of Arctic cyanobacterial mats (Varin et al. 2010). This latter study also showed that the ribosomal and protein-coding genes from these mats were dominated by Proteobacteria, not Cyanobacteria, with a small contribution by Archaea and viruses (Fig. 13.5). Fungi are also present in Antarctic microbial mats (Verleyen et al. 2010) and may play an important functional role in mat decomposition processes.

The rich microbial biodiversity of polar cyanobacterial mats has generated interest for bioprospection, with the possibility that these consortia may contain microbes that produce molecules of biomedical or biotechnological potential. Some of the isolates and communities produce unusual lipids (e.g. Rezanka et al. 2009) and toxins (e.g. Hitzfeld et al. 2000; Wood et al. 2008), and a variety of antimicrobials have been identified from cyanobacterial isolates (e.g. Taton et al. 2006a; Asthana et al. 2009). The potential of Antarctica cyanobacteria for commercial production of carotenoids (Shukla and Kashyap 2003), phycocyanin (Shukla et al. 2008) and UV-screening scytonemin (Singh et al. 2010) has also been explored.

13.4.2 Mat Structure and Pigments

Microbial mats consist of diverse microbiota embedded within a polymeric gel matrix. In the polar regions, the main structural elements of the mats are usually filamentous cyanobacteria, which excrete exopolymeric substances (EPS) that bind together the assemblage. The application of novel methods in electron and confocal microscopy has produced many insights into the architecture of these assemblages, and has shown that these biofilms have an anastomosing network of holes and channels (de los Ríos et al. 2004; Fig. 13.6), which may provide conduits for nutrient transfer as well as microhabitats for smaller cells such as bacteria and even channels for the movement of gliding, filamentous cyanobacteria (Vincent and Quesada 1994).

One of the most striking features of polar cyanobacterial mats is their colouration and pigment content, to the extent that the biopotential of some high latitude isolates has been considered for commercial pigment production (Shukla and Kashyap 2003; Shukla et al. 2008). The cyanobacterial pigments include both light-harvesting and photoprotective

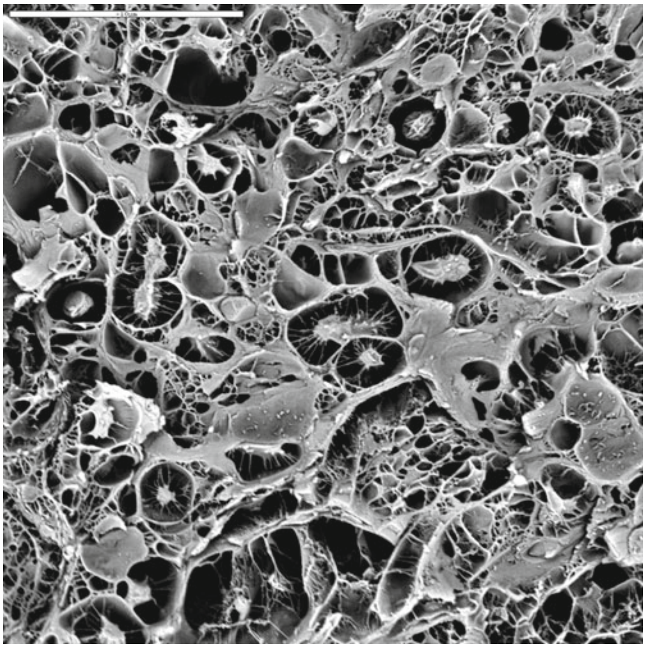

Fig. 13.6 Freeze-fracture electron micrograph of a microbial mat from the High Arctic showing its open, pore-containing structure. The scale bar is 10 μm. The scale bar is 10 μm. (A. de los Rios, with permission)

molecules, and typically dominate the total ecosystem pigment stocks. For example, in shallow ponds and lakes from Alaska, High Arctic Canada and Low Arctic (SubArctic) Canada, the chlorophyll *a* and carotenoid content of the mats (mg m^{-2}) was more than 100 times that of the phytoplankton in the overlying water column (Bonilla et al. 2009). The mats vary greatly in colour depending on species composition and light regime. Some are dull green or blue-green in colour, for example some *Nostoc* colonies and communities of oscillatorians that have migrated to the surface of mats under dim light conditions (e.g. Salt Pond on the McMurdo Ice Shelf). This coloration is dictated by the high concentrations of light-capturing phycobiliproteins in the cells, particularly phycocyanin, sometimes combined with phycoerythrin giving the communities a darker appearance. *Nostoc commune* mats that are exposed to bright light, for example in shallow Arctic tundra ponds (Vincent 2000) or in Antarctic stream beds, are often golden-brown, olive-green or black in appearance as a result of high concentrations of the UV-screening pigment scytonemin (Proteau et al. 1993). Mats and crusts of *Calothrix* (e.g., Antarctic stream bed communities and the Greenland ice cap cryoconite assemblages) are also black pigmented with scytonemin (e.g., Gerdel and Drouet 1960; Vincent 1988).

The luxuriant oscillatorian mat communities and living stromatolites at the bottom of Antarctic ice-capped lakes (e.g. McMurdo Dry Valleys lakes; Lake Untersee, Andersen et al. 2011) are often pink in colour as a result of high concentrations of the light-capturing pigment phycoerythrin and the absence of UV blocking pigments. Five types of microbial mats were initially identified in Antarctic ice-capped lakes (Wharton et al. 1983; Parker and Wharton 1985): (i) Moat mats that occur around the edge of the lake where the ice melts each summer; (ii) Lift-off mats that trap bubbles of nitrogen and oxygen in upright columnar structures up to 1 cm in diameter and that may eventually detach from the sediments; (iii) Pinnacle mats that form small cone–shaped structures; (iv) aerobic prostrate mats; (v) anaerobic prostrate mats. Larger mat structures have been subsequently discovered in some Antarctic lakes (illustrated in the online article associated with this book), including microbialites (macroscopic sedimentary structures derived from microbial growth) in Lake Joyce (Wharton et al. 1983), dome-shaped structures in Untersee (Andersen et al. 2011) and cyanobacteria-coated moss pillars in freshwater lakes near Syowa Station (Imura et al. 1999; Nakai et al. 2012).

The most commonly observed oscillatorian mat communities throughout both polar regions are in shallow waters, and are often orange, pink or purple as a result of carotenoids (Fernández-Valiente et al. 2007) that protect against the damaging effects of bright PAR and UV radiation (see below). Many of these have similar morphologies and detachment characteristics to the moat and lift-off mat categories as described in the McMurdo Dry Valley lakes; e.g., the microbial mat communities of freshwater lakes in the Hope Bay region of the Antarctic Peninsula, which vary greatly in texture, colour and thickness depending on community structure, substrate and sediment content (Bonaventura et al. 2006). The mats usually have a layered structure, with the surface enriched in photoprotective pigments and the basal layer enriched in light capturing pigments, including phycocyanin and chlorophyll a (Vincent et al. 1993; Quesada and Vincent 1997; Mueller et al. 2005). Most of the active cyanobacterial biomass resides in this ‘deep chlorophyll maximum’, where the cells grow under a shade regime of dim orange light that is devoid of blue and UV wavebands (Vincent et al. 1993). There are now many published reports of these brightly coloured, layered communities from both polar regions, and here we provide two such examples.

The shallow waters of Ward Hunt Lake at the northern limit of High Arctic Canada contain extensive mats that average about 4 mm in thickness. Vertical sectioning of these mats shows that they are composed of a black layer irregularly distributed over the surface of a pink layer, which in turn is underlain by a blue-green coloured basal layer (Bonilla et al. 2005). Microscopic observations show that the black layer is composed of large colonies with radially oriented filaments of *Tolypothrix* sp.; the pink layer is dominated by thin filamentous species (including *Leptolyngbya* and *Pseudanabaena)* and colonies of *Nostoc* spp., and the blue-green layer is composed of diverse filaments of both narrow and wide taxa from the order Oscillatoriales (*Lyngbya* spp.,

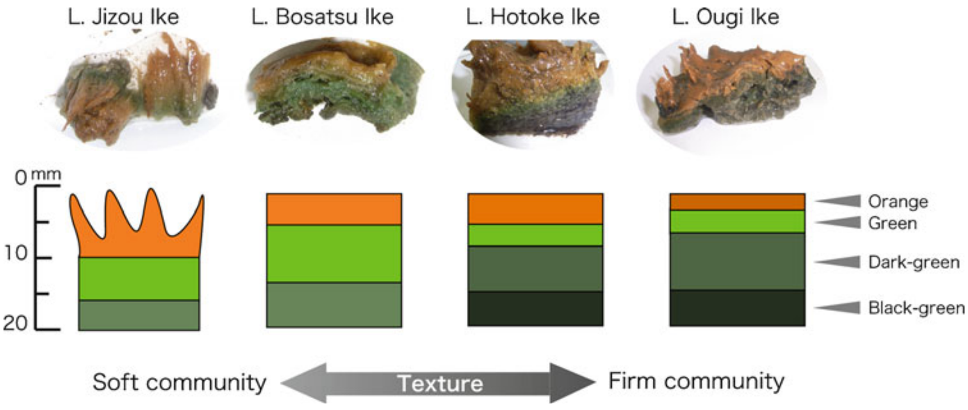

Fig. 13.7 Vertical sections through cyanobacterial mats from four lakes of the Skarvsnes area, East Antarctica. (From Tanabe et al. 2010; with permission)

Oscillatoria spp., *Leptolyngbya* sp.). Small diatoms such as *Achnanthes* and *Cymbella*, and the chlorophytes *Mougeotia* and *Closterium* are found in both the pink and blue-green layer. The absolute concentrations of scytonemin and its ratio to chl *a* are maximal at the top of the mat, and also the ratio of total carotenoid to chl a is maximal in the upper mat surface. The mats contain high concentrations of the cyanobacterial carotenoids canthaxanthin, echinenone, myxoxanthophyll, and a related glycoside closely resembling 4-keto-myxoxanthophyll, the most abundant carotenoid in the mats. The highest concentrations of violaxanthin and chl b have been found in the basal blue-green layer, indicating the increased importance of Chlorophyta in the lower community. Phycocyanin and allophycocyanin absorbance ratios to 750 nm are also highest in the basal stratum, indicative of the acclimation towards light-harvesting under dim light in this lower stratum (Bonilla et al. 2005).

The Skarvsnes area, east Antarctica, provides a compelling set of examples of pigmented microbial mats in the South Polar Region. This ice-free area contains about 50 shallow lakes and the pigment characteristics of mats in four of these lakes have been analysed in detail (Tanabe et al. 2010). As in the Arctic, the dominant pigments in the mats are from cyanobacteria (scytonemin, aphanizophyll, myxoxanthophyll, echinenone, canthaxanthin, zeaxanthin), followed by green algae (Chl b, violaxanthin, antheraxanthin, and lutein) and diatoms (Chl c, fucoxanthin and diadinoxanthin). There were large differences in colour zonation down the mat profile (Fig. 13.7). Scytonemin was found only in the top to middle sections, while Chl *a* concentrations were always highest in the deep, green layers. The total carotenoid, total xanthophyll (violaxanthin, diadinoxanthin, zeaxanthin, antheraxanthin, lutein) and scytonemin ratios to Chl *a* were highest in the uppermost, orange layer. In Larsemann Hills region (East Antarctica), 62 microbial mats were investigated regarding their pigment compositions. The variables affecting pigmentary composition. The authors identified lake depth, as a result of its influence on the light climate, as the most relevant variable defining the carotenoid and UV-protecting pigments composition in microbial mats (Hodgson et al. 2004).

13.4.3 PAR and UVR Responses

Polar cyanobacterial mats live under the two extremes of high and low irradiance conditions, and are capable of acclimating to both extremes. Under dim light, for example in the deep shade communities of McMurdo Dry Valley lakes, the high cellular concentrations of phycobiliproteins confer an ability to grow under extreme shade. Laboratory gas-exchange measurements by Hawes and Schwarz (1999, 2001) showed that the communities have an unusually efficient light-capturing capacity, with photosynthetic quantum yields close to the theoretical maximum. These results were subsequently confirmed by in situ oxygen micro-electrode measurements of photosynthesis in the mats under the perennial ice (Vopel and Hawes 2006).

At the other extreme, cyanobacterial mats exposed to full light in shallow or semi-aquatic ecosystems experience a range of light climate conditions. At the mat surface, cells are exposed to the full solar spectrum at high irradiance, but in the subsurface layers certain wavelengths are absorbed and irradiance is attenuated (Fig. 13.8). At only 2 mm from the mat surface the maximum irradiance reaching the cells may be only 5% of that at surface. This profile is caused by the high surface concentrations of photoprotective pigments which allow the cells deeper in the mat community to grow under milder conditions, free of UV radiation (e.g. Quesada et al. 1999; Tanabe et al. 2010). Experiments under controlled laboratory conditions showed that protective carotenoid pigmentation in an Antarctic mat-forming oscillatorian increased as a function of increasing UVR and PAR, and also with decreasing temperature (Roos and Vincent 1998). Similarly, a comparison of mat communities across northern

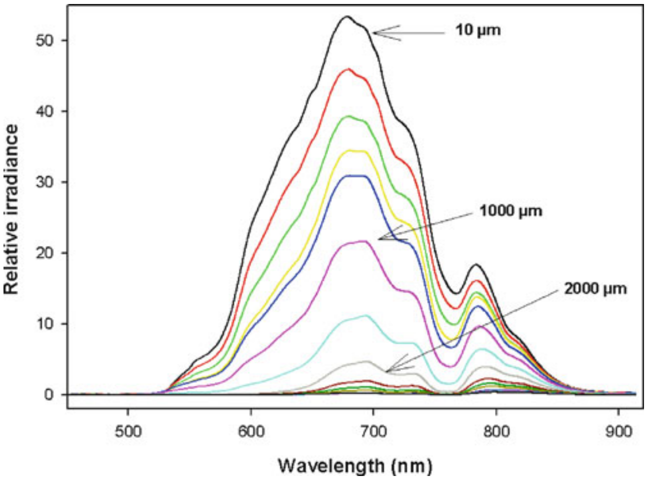

Fig. 13.8 Spectral irradiance in a depth profile within a cyanobacterial mat from Byers Peninsula (Livingston Island, Antarctica). Each line is an irradiance spectrum, at 200-µm depth intervals, relative to the surface irradiance. (A. Quesada, unpublished data)

Canada and Alaska showed that photoprotective pigments increased with increasing latitude, decreasing water temperature and increased UVR transparency of the overlying water (Bonilla et al. 2009). These cyanobacterial photoprotectants are ingested and bio-accumulated by some crustacean grazers on the mat communities, and may thereby provide some UV protection to higher trophic levels (Rautio et al. 2009).

As in microbial mats at lower latitudes, many oscillatorians in high latitude mats are capable of adjusting their position in the mats by their gliding motility (Vincent and Quesada 1994; Nadeau et al. 1999). Mat samples brought indoors sometimes visibly darken as the trichomes rich in light-capturing pigments, but deficient in light-protecting carotenoids and UV screening pigments, migrate to the surface. This migration behaviour allows the cells to avoid damaging exposure to UVR and bright PAR, while allowing them to rise to the surface and continue photosynthesis during periods of low incident irradiance, such as during freeze-up of the lake or pond habitat.

13.4.4 Nutrient Supply

Dissolved inorganic nutrients such as soluble reactive phosphorus and ammonium tend to be one or more orders of magnitude higher in the interstitial waters of polar mat communities than in the overlying water column (Vincent et al. 1993; Villeneuve et al. 2001), and there is also molecular evidence of that these mats are active sites of nutrient regeneration and scavenging (Varin et al. 2010). Metagenomic DNA analysis of 11.5 million base pairs showed that the ribosomal and protein-coding genes of two high Arctic ice shelf mat communities were dominated by Proteobacteria, not Cyanobacteria, implying a broad range of bacterial decomposition and nutrient recycling processes in addition to phototrophy. Viruses were also present (*Alpha*-, *Beta*-, *Gamma-proteobacteria* phages and cyanophages), and these also likely contribute to cellular lysis and recycling. The nitrogen-related genes were dominated by ammonium-assimilation systems, implying that the microbial mats are sites of intense mineralization. Nutrient scavenging systems including genes for transport proteins and enzymes converting larger molecules into more readily assimilated inorganic forms (allantoin degradation, cyanate hydrolysis, exophosphatases, phosphonatases). This analysis underscored the capability of polar microbial mat consortia to retain and recycle nutrients in an otherwise oligotrophic environment (Varin et al. 2010).

In some polar mat communities, nitrogen supply is supplemented by nitrogen fixation. For example, in a mat community for the McMurdo Ice Shelf, N_2-fixation was estimated to contribute about 30% of the total N budget (Fernández-Valiente et al. 2001). Molecular analysis of these communities has shown that although N_2-fixing bacteria other than cyanobacteria were represented in the DNA clone libraries for the nitrogenase gene nifH, gene expression was exclusively by the cyanobacterium *Nostoc* (Jungblut and Neilan 2010), in agreement to the physiological results by Fernández-Valiente et al. (2001) which indicated that N_2-fixation was light-dependent and most probably by heterocystous cyanobacteria. In other cyanobacterial mats from the same region, microscopic observations indicated that *Anabaena* sp. and *Nodularia* sp. were present and also likely contributed to N_2-fixation. Nitrogen-fixation by cyanobacterial communities is also well known from Arctic lakes and ponds (e.g. Bergmann and Welch 1990).

13.4.5 Salinity

Cyanobacteria mats in shallow waters are subject to pronounced variations in solute concentration throughout their growing season. During ice-formation, ions are excluded and a brine is formed in the water overlying the cyanobacterial mats, which are therefore exposed to major shifts in salinity (Schmidt et al. 1991; Hawes et al. 1999; Mueller and Vincent 2006). Many mat forming cyanobacteria appear to have a strong tolerance to these salinity variations (e.g. Lionard et al. 2012), however to an extent that varies among species, and conductivity is a variable that separates the distribution of taxa. For example, two morphotypes of *Oscillatoria priestleyi* appeared to be halophilic and restricted to high conductivity waters (4.2–55 mS cm^{-1}), while four *P. autumnale* morphotypes occurred over a wide range of conductivities (75–7,000 µS cm^{-1}) and one narrow-trichome oscillatorian morphotype was found only at the lowest conductivity, leading Broady and Kibblewhite (1991) to suggest that different genotypes may have different salinity preferences.

Sabbe et al. (2004) conducted a similar analysis at Larsemann Hills and Bølingen Islands (East Antarctica) and found a relationship between diatom composition but not cyanobacterial morphospecies and salinity. However, in a subsequent more detailed study based on molecular methods (DGGE analysis) at five ice-free oases, salinity emerged as a key variable in the ordination analyses for separating different cyanobacterial genotypes (Verleyen et al. 2010). Similarly, in a clone library analysis of cyanobacterial distribution on the McMurdo Ice Shelf, salinity was an important discriminating variable (Jungblut et al. 2005). When a large pond drained on this ice shelf leaving 13 residual ponds, there was little difference in biomass among the ponds two seasons later; however there were differences in community structure that appeared to be related to differences in salinity (Sutherland 2009).

13.4.6 Freeze-Up and Desiccation Tolerance

Cyanobacterial mats in the polar regions may experience complete freeze-up of their aquatic environment, or evaporation to dryness given the low precipitation-evaporation balance at many sites. Both of these conditions imply an increase in osmolarity, through freeze- or evaporative- concentration. For example, in a study on Ross Island ponds, the benthic communities experienced relatively freshwater conditions in late summer but salinities up to five times that of seawater, and liquid water temperatures down to −12°C, during the final stages of freeze-up in winter (Schmidt et al. 1991). Ice crystal formation that accompanies freeze-up can also mechanically damage cell membranes, particularly if the crystals are formed within the cells (Vincent 1988). Mat-forming cyanobacteria in the polar regions have a variety of strategies to minimize these osmotic and mechanical stresses including production of mucopolysaccharides (exopolymeric substances) and compatible solutes (Vincent 2007, and refs therein). Experiments on Antarctic microbial mats have shown a high level of tolerance to desiccation, but to an extent that differs among different mat types (Hawes et al. 1992). The extreme tolerance of cyanobacteria as a group to osmotic stress and desiccation is also suggested by their ability to tolerate very low water potentials (Wynn-Williams 2000). Recovery from desiccation conditions appears to vary among species and polar communities. In Antarctica, some *Nostoc* mats were began respiration and photosynthesis only 10 min after rewetting, while *Phormidium* based microbial mats did not achieve complete recovery even after 10 days of rewetting (Hawes et al. 1992). Metagenomic studies have revealed a broad spectrum of stress genes in both Arctic and Antarctic cyanobacterial mats, including sigma B genes that may be involved in acclimating to freeze-up and osmotic stresses (Varin et al. 2012).

13.4.7 Controlling Factors

Cyanobacteria isolated from mats in the polar regions have been shown to tolerate a wide range of conditions, and to maintain slow net growth despite the frigid ambient temperatures (Tang and Vincent 1999, 2000). The large standing stocks of benthic cyanobacteria in many polar freshwater environments imply that conditions are highly favourable for their net accumulation, in marked contrast to the typically low biomass of planktonic phototrophs in the overlying water column. However, there are large variations between sites, with the benthic communities ranging from thin sub-millimetre biofilms that require a microscope to detect, to microbial mats that are several cm in thickness. What factors contribute to such a contrast between the plankton and the benthos, and to the pronounced site-to-site variability?

Standing stocks of biomass at any point in time are the result of the integrated balance of production and loss (P/L) processes at timescales ranging from days to decades. Primary production rates in cyanobacterial mats from both polar regions mostly fall within a narrow range ($1–10\ \mu g\ C\,cm^{-2}\ h^{-1}$; Quesada et al. 2008 and references therein). Therefore, the markedly different extents of mat accumulation at different locations within the polar regions may be explained by differences in the P/L balance at each site, including the growing period that is determined by seasonal irradiance and the duration of liquid water supply. The latter is somewhat longer than expected based on freshwater, since ice formation results in increased salinities (see above) that extend the liquid conditions to subzero temperatures. In McMurdo Ice Shelf ponds at latitude 78°S, liquid water was detected at the bottom of <1 m deep ponds as late in the season as April (Hawes et al. 1999; Hawes et al. 2011). However, at that time of year and latitude, irradiance is extremely low and the physiological maintenance costs for phototrophs may be larger than their cellular gains by photosynthesis. Differences in the extent of overwintering biomass may also contribute the variability in standing stocks of microbial mats.

The availability of liquid water is the first prerequisite for microbial activity, and in many polar aquatic environments this resource is highly seasonal; for example, in stream beds that dry up and lakes that freeze to the bottom. Mat-forming cyanobacteria in these habitats seem highly tolerant of these conditions of freeze-up and desiccation (see above), and are able to maintain large overwintering biomass stocks that provide them with a competitive advantage after melt-out the next season. Light availability for photosynthesis is highly seasonal throughout the polar regions, and the underwater solar radiation regime during the growing season varies from prolonged dim light conditions under snow and ice to 24 h of sunshine, including high UV exposure. As noted above, cyanobacteria have a variety of pigment strategies that allows them to minimize photodamage (even when desiccated) and maximize photon capture. Low temperature is another Blackman-type limitation on production rates, given that most polar cyanobacteria have high temperature optima and show extremely slow growth at ambient temperatures (Tang et al. 1997; Velázquez et al. 2011).

In the benthic environment of polar lakes and rivers, several features result in reduced loss rates and thereby push these communities towards slow net accumulation. Grazing losses to benthic herbivores are minimal in many of these waters as a result of the short growing season for invertebrates to complete their life cycles, and other inhospitable features of the polar environment that prevent colonisation by most animal species. Some crustacean species do occur in Antarctic and High Arctic ponds, including fairy shrimps such as *Branchinecta* and *Artemiopsis* that feed at least partially on cyanobacterial mats (Rautio and Vincent 2006). In many lakes and ponds in the Arctic, including the northernmost lake in Canada (Bonilla et al. 2005), chironomid larvae also feed on the mats, and within the mats several species of microinvertebrates are typically found including rotifers, nematodes, tardigrades and flatworms. Some cyanobacteriovorous ciliates are also frequent within cyanobacterial mats (Petz et al. 2007), mostly feeding on thin oscillatorians such as *Leptolyngbya*. These protozoa and invertebrate communities, however, are limited in biomass and duration of feeding activity, with presumed little impact on the standing crop of microbial biomass, although this has yet to be fully tested. The cold temperatures also inhibit bacterial degradation processes, and analyses of bacterial growth rates and respiration generally indicate slow rates of mineralisation of the organic biomass to CO_2. This in combination with adequate nutrient supply may be the reason for the development of the thickest mats in extreme cold environments, for example in ice shelf meltponds and in the phytobenthos of frigid Antarctic lakes. Viruses are known to occur within the mats (Vincent et al. 2000) and include cyanophage (Varin et al. 2010), however loss rates by viral lysis of cyanobacterial cells have not been quantified to date.

Limited nutrient supply can result in both Liebig (yield) and Blackman (growth rates) limitation effects, and in this regard there is a striking contrast between the plankton and phytobenthos of polar lakes. High latitude lake phytoplankton are typically subject to severe nutrient limitation, and respond strongly to nitrogen and or phosphorus addition. In contrast, microbial mats are zones of nutrient scavenging and regeneration, with microenvironmental nutrient concentrations that are much higher than the bulk concentrations in their overlying environments (see above). A series of bioassays at Ward Hunt Lake in the Canadian High Arctic provided evidence of these contrasting nutrient regimes: benthic cyanobacterial mats showed no significant photosynthetic or biomass response to nutrient enrichment over 4–8 days, while the phytoplankton increased several fold after nutrient addition (Bonilla et al. 2005). It is possible that nutrient enrichment at longer timescales (months to years) may favour the gradual accretion of biomass in perennial microbial mats.

Field observations suggest that physical attrition processes may be more effective in controlling cyanobacterial mat biomass than biological loss factors. For example, the incorporation of gas bubbles within the mat structure increases the buoyancy of large portions of mats (Wharton et al. 1983). These lift-off mats float up from the sediments and are then pushed to the lake-edge by the wind, and large accumulations of dead microbial mats are sometimes seen washed up on the shore. Another physical effect is scouring by the lake ice during melt-out, which might be responsible of the absence of microbial mats from the inshore waters of many polar lakes. Fast flowing or sediment laden streams will also lose their microbial mats by scouring, while ponds and streams that dry up in late summer, or ablate to dryness over winter, may lose microbial mat biomass by wind erosion.

13.5 Conclusions

Cyanobacteria are poorly represented in polar marine environments, but they are enormously successful in high latitude lakes, ponds, wetlands and rivers where they may be the biomass and production dominants. These organisms tolerate the broad range of extreme conditions experienced in the Arctic and Antarctica, including freeze-thaw cycles, variable osmolarity, persistent low temperatures and extremes of irradiance including UV radiation. They are especially successful in the benthic environment where they produce nutrient-rich mat communities that contain taxonomically and functionally diverse populations of micro-organisms. Each of the three ecological groups is highly responsive to temperature, and cyanobacteria are likely to prosper from ongoing climate change in the polar regions.

Acknowledgements This work has been partially funded by the Ministry of Science and Innovation (Spain) by grant POL2006-06,635, the Natural Sciences and Engineering Research Council of Canada, and the Network of Centres of Excellence program ArcticNet. We thank David Velázquez and Anne Jungblut for comments on the manuscript, and are especially grateful to Bill Li for providing Figs. 13.1 and 13.2, and to Dale T. Andersen for underwater photographic and video contributions to the online article associated with this chapter.

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