Chapter 9
Cyanobacteria in Polar and Alpine Ecosystems

Anne D. Jungblut and Warwick F. Vincent

Abstract Cyanobacteria are commonly found in freshwaters, soils and glacial environments in polar and alpine regions. Studies to date indicate these cold-dwelling phototrophs are psychrotolerant rather than psychrophilic, with temperature optima for growth that lie well above the temperature ranges of their ambient environment. Cyanobacterial mats occur at the bottom of lakes, ponds and streams and within meltwater habitats on glaciers and ice shelves. They can accumulate large biomass stocks and may account for the dominant fraction of total ecosystem productivity in such environments. Certain taxa in these benthic communities are known to produce cyanotoxins, including microcystins. Planktonic cyanobacteria are also found in many high latitude lakes, specifically picocyanobacteria, but they are conspicuously absent or poorly represented in polar seas, probably as a result of their minimal growth rates in extreme cold. Cyanobacteria also occur in a variety of nonaquatic habitats in the cold regions, including on and within rocks, and as a major constituent of soil crusts in polar and alpine deserts. The nitrogen-fixing capabilities of some cyanobacteria make them especially important for the natural enrichment of soils that have been newly exposed after glacial retreat. The evolution and biogeography of cyanobacterial ecotypes in the cold biosphere is a current focus of genomic analysis and pole-to-pole comparisons, and these studies are providing insights into how microbial ecosystems survived prolonged periods of cold and freeze-up on early Earth.

Contents

A.D. Jungblut (✉)
Life Sciences Department, Natural History Museum, London SW7 5BD, UK
e-mail: a.jungblut@nhm.ac.uk

W.F. Vincent
Centre d'Études Nordiques (CEN), Quebec City, QC G1V 0A6, Canada

Department of Biology, Laval University, Quebec City, QC G1V 0A6, Canada

9.1 Introduction

Perennially cold environments in which temperatures remain below 5 °C are common throughout the biosphere (Margesin and Häggblom 2007). In these habitats, cold temperatures are often accompanied by freeze-thaw cycles, extreme fluctuations in irradiance including ultraviolet radiation and large variations in nutrient supply and salinity. As a result of these constraints, polar and alpine environments contain a reduced biodiversity of plants and animals, but they are rich in microscopic life, including cyanobacteria.

Cyanobacteria are phototrophic, oxygenic Gram-negative bacteria. They are of special importance for freshwater and terrestrial ecosystems in polar and alpine regions, where they are major primary producers, key taxa in food webs and drivers of carbon and nitrogen cycling. Their presence in the polar regions was first observed during early expeditions to the Arctic and Antarctica. In 1870, the Swedish-Finnish explorer Adolf Erik Nordenskiöld described the extensive growth of cyanobacteria in the cryosphere (the ensemble of cold environments containing snow and ice) across the Greenland Ice Cap (Leslie 1879). Somewhat later in Antarctica, James Murray, the biologist on the Shackleton's 1907–1909 expedition to Ross Island, also gathered detailed information on cyanobacterial diversity and their importance (Murray 1910). Current research shows a diverse range of cyanobacteria in polar and alpine habitats and that these organisms have broad tolerances to the abiotic stresses that prevail in these environments. This has made them of great interest for the reconstruction of microbial life, diversification and geobiological weathering processes on early Earth, and polar cyanobacterial mats and their ice-based habitats have been identified as potential analogues for biotopes present during the major glaciation events of the Precambrian (Vincent and

Howard-Williams 2000; Vincent et al. 2004a, b; Sumner et al. 2015; Hoffman 2016).

In this chapter, we first introduce the taxonomic status and general characteristics of cyanobacteria. We examine their ecophysiological traits that allow them to survive and often thrive in such cold environments. Cyanobacterial diversity in freshwater, soil and cryosphere ecosystems in the Arctic, Antarctic and alpine regions is presented, and we conclude this review by consideration of the biogeographical distribution and evolution of polar cyanobacteria.

9.2   Taxonomy and Diversity

The classification of Cyanobacteria has been controversial for centuries, and several taxonomic schemes have been proposed. These organisms were initially described as algae in the eighteenth century, and the first classification system was based on the International Code of Botanical Nomenclature as described by Oren (2004). In the botanical taxonomy, two major works are especially noteworthy. Firstly, Geitler (1932) produced a flora that compiled all European taxa, which already encompassed 150 genera and 1500 species based on the morphology. Secondly, the recent revisions by Anagnostidis and Komárek (e.g. Komárek and Anagnostidis 2005) aimed to define more consistent genera, still based on the morphology. After the prokaryotic nature of cyanobacteria became more obvious on the basis of ultrastructural and molecular studies, it was proposed that their nomenclature should be governed by the International Code for Nomenclature of Bacteria (Stanier et al. 1978). Currently, the bacterial phylum Cyanobacteria encompasses five subsections (corresponding to the five orders in the botanical classification) in Bergey's Manual of Systematic Bacteriology (Castenholz 2001): *Chroococcales* (unicellular), *Pleurocapsales* (large cells subdividing into smaller baeocysts), *Oscillatoriales* (simple filamentous), *Nostocales* (filamentous, non-branching heterocyst-forming) and *Stigonematales* (filamentous, branching, heterocyst-forming).

In recent years, several other classifications have been suggested. Hoffmann et al. (2005a, b) recommended the recognition of four subclasses considering both phylogenetic inferences and morphological features: *Nostocophycideae*, *Oscillatoriophycideae*, *Synechococcophycideae* and *Gloeobacteriophycideae* with nine orders *Nostocales*, *Chroococcidiopsidales*, *Spirulinales*, *Pleurocapsales*, *Chroococcales*, *Oscillatoriales*, *Synechococcales* and *Gloeobacteriales* (Hoffman et al. 2005b; Komárek et al. 2014). It is the first system that recognises that coccoid and filamentous morphologies are polyphyletic. This is also the classification that has been adopted by the Greengenes 16S rRNA gene reference database (DeSantis et al. 2006) that is commonly used for high-throughput sequencing community structure analysis.

To date, only a few names of cyanobacterial taxa have been validly published according to bacterial rules, reflecting not only technical difficulties but also the

confusion due to the existence of two nomenclature systems (Oren 2004). Current taxonomic studies on cyanobacteria are now adopting a polyphasic approach, which combines genotypic studies with morphological and phenotypic analyses.

Cyanobacteria often have quite simple morphologies and some of these characters exhibit plasticity with environmental parameters, so that their taxonomic usefulness can be limited. Moreover, a number of botanical taxa have been delimited based on minute morphological differences (e.g. sheath characteristics, slight deviations in cell dimensions or form), and many authors have shown that the genetic diversity does often not coincide with that based on morphology (e.g. Rajaniemi et al. 2005; Taton et al. 2006b). To address these problems, studies on environmental samples (natural mixed assemblages of microorganisms) are typically using molecular taxonomic markers, most often the 16S rRNA gene. The obtained 16S rRNA sequences are compared and often grouped into OTUs (operational taxonomic units) or phylotypes on the basis of their similarity and taxonomic assignment performed based on either phylogenetic interference or percentage similarity match to public databases (Taton et al. 2006a, b; Komárek et al. 2012; Martineau et al. 2013; Jancusova et al. 2016). Another taxonomic marker is the internal transcribed spacer regions (ITS). It is highly variable and therefore not suitable for phylogenetic interference of distinctly related taxa or even between genera. However, within species and 16S rRNA genotypes, ITS-based analyses have shown that the resolution of the 16S rRNA gene is often not sufficient to distinguish between ecotypes as demonstrated for the non-polar marine cyanobacterium *Prochlorococcus* (Rocap et al. 2002).

9.3 General Characteristics and Ecophysiology

Cyanobacteria are oxygenic photosynthetic bacteria and possess photosystems I and II, which are located on thylakoid membranes (except in the genus *Gloeobacter*). The cells usually have a characteristic blue-green coloration due to the proteins phycocyanin (blue) and allophycocyanin (blue). They additionally have chlorophyll *a*, and some species also contain the protein phycoerythrin that colours the cells red. The protein pigments are organised into specialised light-capturing structures called phycobilisomes, which transfer their absorbed energy to the reaction centres of photosystem II. In a few taxa, other chlorophylls have been observed, including chlorophylls *b*, *d*, and *f* (Miyashita et al. 1996; Chen and Scheer 2013). Some cyanobacteria are also able to fix atmospheric nitrogen, and several species produce toxic secondary compounds. Cyanobacteria have various storage bodies for carbon, nitrogen, phosphate and the enzyme ribulose 1,5-biphosphate carboxylase/oxygenase (RubisCO) (Castenholz 2001).

9.3.1 Cold Temperatures

In general, high latitude and high altitude cyanobacteria tend to be cold tolerant (psychrotolerant), with suboptimal growth at low temperatures, rather than psychrophiles that grow optimally at low temperature (Tang et al. 1997; Tang and Vincent 1999; Nadeau et al. 2001). They have a variety of mechanisms that allows them to tolerate and continue to grow, albeit often at slow rates, in the cold and to tolerate freeze-thaw conditions (Vincent 2007). To maintain membrane fluidity at low temperatures, polyunsaturated fatty acids with decreased chain lengths are incorporated into the membrane. In addition, the production of compatible solutes (e.g. trehalose) and update of choline and betaine help to reduce the freezing point of the intracellular fluid. On the cellular level, genomic and metagenomic analysis of the cyanobacterium *Phormidium priestleyi* and cyanobacterial-based microbial mats in the Arctic and Antarctic identified several genes potentially implicated in the adaptation to cold environments linked to DNA replication, a translation initiation factor for protein biosynthesis and chaperones for protein folding (Varin et al. 2012; Chrismas et al. 2016).

Cyanobacteria must withstand prolonged seasonal desiccation and freezing. *Phormidium*-dominated microbial mats in the Arctic have been shown to be perennial and appear to survive the winter in the vegetative state as they were metabolically active shortly before and after freezing (Tashyreva and Elster 2016). Similarly, Antarctica microbial mats have been shown to resume photosynthesis within minutes to hours after re-thawing (Vincent 2007). However, the tolerance to desiccation varies between genera. While taxa belonging to *Nostoc* are anhydrobiotic, *Microcoleus* was found not to be truly anhydrobiotic as it survived extensive dehydration (to 0.23 g water g^{-1} dry mass) but not complete desiccation (to 0.03 g water g^{-1} dry mass). Laboratory experiments also suggested that nitrogen starvation prior to desiccation increased the tolerance to reduced water availability in Arctic *Microcoleus* stains (Tashyreva and Elster 2016).

9.3.2 Salt Stress

Typical hypersaline environments are saline ponds and lakes in terrestrial polar ecosystems (Vincent 1988) in permanently cold environments, and salinity can be an important driver of community assemblages (Sabbe et al. 2004; Jungblut et al. 2006). Sudden increases in salt concentration are counterbalanced by a rapid accumulation of salts to maintain the osmotic equilibrium. Long-term survival strategies involve uptake of inorganic ions to balance the extracellular ion concentrations, as well as the production of organic osmolytes (Oren 2000) and similar mechanisms as to protect from desiccation. Studies on microbial mats in Ward Hunt Lake, Canadian High Arctic, have shown that the photosynthetic communities are

highly resistant to the major increases in salinity that may be associated with solute concentration during freeze-up (Lionard et al. 2012).

9.3.3   High and Low Irradiance

UV radiation and high-energy photosynthetically active radiation (PAR) can induce photoinhibition, phycobiliprotein degradation, chlorophyll bleaching and DNA damage or the production of reactive oxygen species, and the net damage may be exacerbated at low temperatures (Vincent 2007). Cyanobacteria have evolved a variety of DNA repair mechanisms, such as excision repair and photoreactivation, to cope with UV-induced DNA damage (Castenholz and Garcia-Pichel 2000). However, these processes are reduced at lower temperatures. Furthermore, the cyanobacteria produce photoprotective screening (gloeocapsin, scytonemin, mycosporine) and quenching pigments (carotenoids), and many Antarctic cyanobacteria are able to avoid UV radiation exposure by migrating to deeper layers within the microbial mats (Castenholz and Garcia-Pichel 2000). High concentrations of scytonemin can lead to a black coloration in many cyanobacterial mats and soil crusts (Vincent 2007). Conversely, phototrophs in polar and alpine regions must also contend with low irradiances caused by prolonged snow and ice cover. The cyanobacteria utilise highly efficient light-capturing complexes, with photosynthetic quantum yields close to the theoretical maximum (Hawes and Schwarz 2001; Vincent 2007).

9.3.4   Cyanobacterial Toxin Production

Many cyanobacteria can produce toxic substances, known collectively as cyanotoxins. The mechanisms of toxicity include hepatotoxicity, neurotoxicity, dermatotoxicity, tumour promotion and genotoxicity and are therefore of great importance for public health and freshwater ecology. Several studies have also found cyanotoxins in cyanobacteria-based microbial mats from freshwater ecosystems in polar regions. Microcystins are hepatotoxins and inhibit protein phosphatases, and acute exposure can lead to liver failure and death (Chorus and Bartram 1999). Microcystins have been detected in meltwater ponds on the McMurdo Ice Shelf, Miers Valley (McMurdo Dry Valleys), and Adelaide Island, Antarctica, as well as in thermokarst ponds on Bylot Island, Canadian High Arctic. Concentrations ranged from 1 ng g^{-1} to 16 µg g^{-1} dry mass (Hitzfield et al. 2000; Jungblut et al. 2006; Wood et al. 2008; Kleinteich et al. 2012, 2013). Culture studies with Arctic mats showed that warming caused changes in species composition and an increase in toxins that could have been the result of increased cellular toxin production or a shift in community structure towards more toxic species (Kleinteich et al. 2012).

Common planktonic microcystin producers, such as *Microcystis*, are absent from polar freshwater ecosystems, and benthic *Nostoc* populations have been proposed as the most likely potential microcystin producers based on morphological and DNA analysis (Jungblut et al. 2006; Wood et al. 2008). In addition, Kleinteich et al. (2013) also detected cylindrospermopsin in freshwater ponds on Adelaide Island, Antarctica, but the genus *Cylindrospermosis*, the main producer of this toxin in temperate and tropical environments, was not found. The ecological or physiological functions of toxins in polar ecosystems are not fully understood at present. For microcystins, potential roles include protection against grazers, quorum sensing, gene regulation or iron scavenging, or they may be ancestral relics of past pathways and functions (Kaebernick and Neilan 2001; Moffitt and Neilan 2004; Rantala et al. 2004).

9.4 Polar Inland Waters

Cyanobacteria often form cohesive, highly pigmented biofilms and mats, from mm- to dm-scale thicknesses that coat the benthic environments in ponds and streams in the Arctic and Antarctic (e.g. Tanabe et al. 2010; Andersen et al. 2011; Lionard et al. 2012; de los Ríos et al. 2015). Due to the high biomass accumulations of cyanobacteria-based microbial mats with rich heterotrophic and microbial eukaryote communities in terrestrial aquatic ecosystems, they are therefore seen as hotspots of biodiversity in comparison to soil environments in the cold, arid polar desert in permanently ice-free regions.

9.4.1 Benthic Communities in Shallow Ponds

In Antarctica, a great variety of shallow meltwater ponds are present that span a wide range of environmental conditions. During the austral summer they are ice-free and brightly lit habitats, whereas they can fully freeze during winter but can also experience high variability in irradiance and temperatures including daily freeze-thaw cycling, depending on weather conditions. These aquatic ecosystems are characterised by high benthic biomass accumulations of cyanobacteria-based microbial mats. Some of these microbial mats can have vertical zonation of organisms and functions in response to light gradients. Many of these cyanobacteria-based microbial mats have an orange, carotenoid-rich upper layer that likely reduces UV and oxidative stress, underlain by green deep chlorophyll maximum layer, which in turn may be further underlain by an anoxic bottom layer that contains anoxygenic phototrophs such as purple bacteria. At the molecular level, these ponds can show a large cyanobacterial diversity (Taton et al. 2003; Kleinteich et al. 2014; Archer et al. 2015); for example, Kleinteich et al. (2014)

identified 274 cyanobacterial OTUs from 30 meltwater ponds from Adelaide Island, Antarctic Peninsula, using 16S rRNA gene high-throughput sequencing.

9.4.2 Benthic Communities in Lakes

Lakes similarly span a wide range of environmental conditions in the Arctic and Antarctic. Many of them are covered with ice for most of the year or even have a perennial ice cover. Studies on perennially ice-covered Lake Hoare in the McMurdo Dry Valleys have shown that PAR irradiance exerts an overall control on microbial photosynthetic production, composition and mat structure (Vopel and Hawes 2006). Other characteristics such as nutrients and salinity also influence the cyanobacterial richness and community structure (Sabbe et al. 2004; Jungblut et al. 2012; Zhang et al. 2015). The most spectacular cyanobacteria-based mats have been described to date from the McMurdo Dry Valley lakes, such as Lakes Vanda, Hoare, Fryxell and Joyce, and Lake Untersee in Dronning Maud Land, East Antarctica, with striking differences in shape and form. Microbial mats can range from prostrate (flat) to decimetre thick, three-dimensional branched pinnacle and cone-shaped growth morphologies that form through accumulation of annual layers during the summer months (Anderson et al. 2011; Jungblut et al. 2016; Sumner et al. 2016).

It is still not well understood what triggers the three-dimensional growth, but Sumner et al. (2016) proposed for Lake Vanda that first small tufts initiate from random irregularities in prostrate mat and that these then grow into pinnacles over the course of several years. As pinnacles increase in size and age, their interiors become colonised by a more diverse community of cyanobacteria with high photosynthetic potential. Biomass accumulation within this subsurface community causes pinnacles to swell, expanding laminae thickness and creating distinctive cylindrical bases and cuspate tops. This change in shape suggests that pinnacle morphology emerges from a specific distribution of biomass accumulation that depends on multiple microbial communities fixing carbon in different parts of pinnacles. However, local habitat conditions such as physical and chemical variables must also play some role as microbial mat structures can vary greatly among lakes.

Differences along vertical lake profiles can also be observed. In Lake Fryxell (Taylor Valley), cyanobacterial mat morphologies and cyanobacterial assemblages and microbial mat communities appear to be a result of local habitat conditions likely defined by irradiance and oxygen and sulphide concentrations. Dissolved oxygen falls from 20 mg L^{-1} to undetectable over one vertical metre from 8.9 to 9.9 m depth, and three macroscopic mat morphologies were associated with different parts of the oxygen gradient. Cuspate pinnacles occurred in the upper hyperoxic zone, which displayed complex topography, and were dominated by phycoerythrin-rich cyanobacteria attributable to the genus *Leptolyngbya* and a diverse but sparse assemblage of pennate diatoms. A less topographically complex

"ridge-pit" mat was located immediately above the oxygen limit and contained *Leptolyngbya* and an increasing abundance of diatoms. Finally, flat prostrate mats occurred in the upper anoxic zone, dominated by a green cyanobacterium phylogenetically identified as *Phormidium pseudopriestleyi* and a single diatom, *Diadesmis contenta* (Jungblut et al. 2016).

In contrast, in Lake Joyce, Taylor Valley (McMurdo Dry Valleys), the water is supersaturated with calcium carbonate (Green et al. 1988), and this leads to the formation of three-dimensional microbial mats with well-developed calcite skeletons associated with the active microbial mats (Mackey et al. 2015). Interestingly, in Lake Joyce, depth-specific distributions of these calcitic microbialites, their organic carbon, photosynthetic pigments and photosynthetic potential cannot be explained by current growth conditions; it was therefore proposed that they are a legacy of past lake conditions before a 7-m lake level rise between 1973 and 2009, thus representing sentinels of environmental change (Hawes et al. 2011).

At the other pole, cyanobacteria play an important role in Arctic lakes, ponds and streams and have been well studied in the Canadian High Arctic (Bonilla et al. 2005). The benthic microbial mats in lakes often have a cohesive layering, which is established through an extra polysaccharide matrix and often have a characteristic pigment stratification (Bonilla et al. 2005; Jungblut et al. 2010; Lionard et al. 2012). The most common groups are *Oscillatoriales* and *Nostocales*, with some *Chroococcales*; however, elaborate microbialite structures have not yet been found in Arctic lake ecosystems.

9.4.3 Benthic Communities in Flowing Water Ecosystems

Streams, runnels and seepages are other aquatic features in permanently cold ecosystems in the Arctic and Antarctic. They are more ephemeral than lakes and meltwater ponds and only have liquid water during the warmer summer months from glacial and snow meltwater. Benthic microbial mats grow in these environments (Vincent 1988; Elster et al. 1997). These communities remain dormant during the winter, then rapidly resume biological activity when water wets the dry channels (Vincent et al. 1993; Tashyreva and Elster 2016). Filamentous cyanobacteria, such as *Phormidium*, *Leptolyngbya* and *Pseudanabaena*, are important for formation of the microbial mat matrix structure as found in ponds and lakes in the McMurdo Dry Valleys. Stream mats are usually less well developed and can be made of two macroscopically different layers with a more pigmented upper layer and more photosynthetically active lower layers. Other components of the communities are heterotrophic bacteria and diatoms and significant co-occurrence patterns have been identified between the different taxonomic groups, which suggests ecological interaction between these groups in stream mat communities in the McMurdo Dry Valleys (Stanish et al. 2013). The stream water also contains cyanobacteria in the plankton, which are similar taxa in the benthic stream mats,

and they likely originate from dispersed benthic mat material rather than represent a distinct planktonic community (Jungblut unpublished).

Microbial mats also grow in water-filled depressions in the soil, such as the ice-free central plateau of Byers Peninsula, Livingston Island (South Shetland Islands), which form meltwater catchment areas for lakes and can cover extensive surface areas of up to several hundred square metres. These microbial mats are typically bi-layered, with an upper layer of non-active biomass and the sheath pigment scytonemin and a basal layer that contains most of the active photosynthetic microbiota. Cyanobacteria in these mats were *Leptolyngbya*, *Phormidium*, *Anabaena*, *Tychonema*, *Synechococcus*, *Oscillatoria*, *Gloeobacter*, *Calothrix*, *Microcoleus*, *Pseudanabaena and Tolypothrix*, and a comparison of samples from spring, summer and autumn found differences suggesting microbial succession within these communities (Velázques et al. 2017).

Interestingly, when looking at the trophic interactions of these mats, a Bayesian mixing model suggested that carbon flow from cyanobacteria to upper trophic levels was limited to tardigrades and rotifers, whereas fungal and bacterial activity were likely the main connectors between consumers and producers via a heterotrophic loop. This suggests that a homeostatic state displayed in freshwater microbial mats from maritime Antarctica provides stability to the microbial mats under the fluctuating environmental conditions commonly found in permanently cold shallow terrestrial aquatic ecosystems in Antarctica (Velázques et al. 2017).

Cyanobacterial mat communities are less well described from the Arctic. High biomass accumulations of *Nostoc* can be found in runnels, but further work is required to better understand the trophic interactions and relationship with the environmental conditions of these microbial mats. A detailed analysis by a range of microscopy techniques of a black pigmented stream mat on Ellesmere Island in High Arctic Canada showed that it contained *Gloeocapsa*, *Nostoc*, cf. *Tolypothrix*, *Calothrix* and cf. *Tychonema*, with the filaments binding together aggregates of calcium carbonate and other mineral particles; a pink coloured mat in the same stream also contained abundant populations of *Phormidium*, *Pseudanabaena* and *Leptolyngbya* (de los Ríos et al. 2015). A study on shallow seeps on Svalbard found extensive mats dominated by *Phormidium* that maintained large, viable overwintering populations (Tashyreva and Elster 2016).

9.4.4 Planktonic Communities in Lakes

Bloom-forming cyanobacteria are mostly absent from polar and alpine waters, reflecting the typically oligotrophic (low nutrient) status of these aquatic environments as well as their low temperatures and the lack of water column stability in summer that would favour gas-vacuolate taxa (Vincent and Quesada 2012). However, picoplanktonic forms of cyanobacteria can be present in high abundance in lakes. These usually have a lower contribution to total biomass and primary production than phototrophic microbial eukaryotes such as chrysophytes,

dinoflagellates and green algal flagellates and may be a food supply for mixotrophic algae. Picocyanobacteria can also be grazed by crustacean zooplankton in high latitude waters, although they are a relatively poor quality food source for growth (Przytulska et al. 2015).

The abundance of planktonic picocyanobacteria is dependent on nutrient availability and light (Vincent 2000a) and more often nutrient limited than benthic cyanobacterial mat communities, based on in situ growth experiments in the High Arctic (Bonilla et al. 2005). In a High Arctic lake, improved irradiance conditions combined with entrainment of nutrient-rich deeper waters into the surface by mixing after loss of its ice cover resulted in a threefold increase in concentrations of picocyanobacteria (Veillette et al. 2011).

In relation to the composition, a study on lakes in the Vestfold Hills (Ace Lake, Pendant Lake and Clear Lake) found 16S rRNA sequences of *Synechococcus*-like picocyanobacteria but distinct from other *Synechococcus* genotypes, such as *Synechococcus* PS840 from the Russian marine coast (Waleron et al. 2007). In Lakes Vanda and Hoare, cyanobacteria-specific 16S rRNA gene clone analysis revealed sequences with highest BLAST similarity up to 99% to *Limnothrix redekei* and *Chamaesiphon subglobosus*, which are also genotypes found in the microbial mats (Jungblut unpublished). Interestingly, although picocyanobacteria are often the most common photosynthetic cell type in many lakes in the polar regions, they are absent or only poorly represented in polar seas (Vincent 2000a; Vincent and Quesada 2012).

9.5 Ice-Based Habitats in the Polar Regions

Similar to lakes, ponds and streams, cyanobacteria can also form large biomass accumulations in Arctic and Antarctic ice-based ecosystems (Vincent 1988; Quesada and Vincent 2012) and dominate many microbial consortia formed in ice-based habitats, such as cryoconite holes on glaciers and meltwater ponds on ice shelves both in the Arctic and Antarctic.

9.5.1 Glacial Ecosystems

Cryoconite (literally "cold rock dust") gives rise to vertical, cylindrically formed holes in the ice surface that contain a thin layer of sediment overlain by water. The formation of these habitats is initiated through the absorption of solar radiation by the sediment and the subsequent ablation of the surrounding ice (Wharton et al. 1985). Two different types of cryoconite holes can be found depending on summer conditions, such as those that are open to the air annually and those that remain closed by a perennial ice lid. Typically cryoconite holes on glaciers in the Arctic

and Greenland Ice Sheet open up every summer, whereas in the Antarctic, there are also closed cryoconite holes (Webster-Brown et al. 2015).

Studies of cryoconite have described diverse microbial communities of cyanobacteria, heterotrophic bacteria and microbial eukaryotes (Cameron et al. 2012; Mueller et al. 2003; Edwards et al. 2014; Stibal et al. 2015; Webster-Brown et al. 2015) from regions such as Svalbard, Greenland Ice Shelf, Canadian Arctic, southern Victoria Land and the McMurdo Dry Valleys in Antarctica. In closed cryoconite hole communities on the Koettlitz, Diamond and Wright glaciers in southern Victoria Land, Webster-Brown et al. (2015) found 73 cyanobacterial OTUs belonging to the genera *Chamaeosiphon*, *Leptolyngbya*, *Pseudanabaena*, *Phormidesmis*, *Phormidium*, *Hormoscilla*, *Nostoc* and *Oscillatoria* using a combination of high-throughput sequencing and 16S rRNA gene clone library-based survey. Some of these cyanobacterial taxa were also identified by Christner et al. (2003) in a 16S rRNA clone library survey of open cryoconite holes from Canada Glacier, Taylor Valley in the McMurdo Dry Valleys, Antarctica, and by Edwards et al. (2011) in Svalbard. Environmental samples and isolates from four glaciers in Svalbard included the morphotypes *Chlorogloea*, *Microcoleus* and *Pseudophormidium* (Stibal et al. 2006). Many cyanobacterial genera appear to be present in supraglacial ecosystems in the Arctic and Antarctic but with large differences among sites. Variations in community structure among several glaciers in southern Victoria Land, Antarctica, were attributed to both initial wind-borne inocula from local and regional sources as well as to differences in habitat properties, such as pH of the meltwaters in the cryoconite holes (Webster-Brown et al. 2015).

Food webs in these glacial systems tend to be simple, with algae and cyanobacteria as the primary producers and heterotrophic bacteria and fungi as microbial recycling agents in cryoconite holes (Porazinska et al. 2004; Foreman et al. 2007). Cyanobacteria are not only key taxa for photosynthesis in these environments but also aggregate and bind together wind-blown debris leading to the formation of granular cryoconites. Filamentous, non-heterocystous genera, such as *Phormidium, Phormidesmis* and *Leptolyngbya,* appear to be especially important in this process. It has therefore been suggested that cyanobacteria are habitat engineers of granular microbial-mineral cryoconite aggregates in glacial ecosystems (Hodsion et al. 2010; Langford et al. 2010; Cook et al. 2015; Gokul et al. 2016).

9.5.2   Ice Shelf Ecosystems

Another important class of ice-based habitats is represented by meltwater ponds that form on ice shelves in the Arctic and Antarctic. These contain liquid water during the summer months but completely freeze over the winter. The biota of these habitats must therefore contend with extreme temperature changes, freezing and desiccation stress and high salinities. In Antarctica, the ponds on the McMurdo Ice

Shelf have low nutrient concentrations, especially nitrogen, due to the marine origin of the sediments (Hawes et al. 1993); their characteristics are described by Wait et al. (2006).

Thick benthic cyanobacterial mats coat the base of ice shelf melt ponds and are diverse communities of *Chroococcales*, *Nostocales* and *Oscillatoriales* as well as other bacterial phyla and microeukaryotes, as revealed by microscopy, culture isolation, environmental sequencing and lipid biomarker analysis (Howard-Williams et al. 1989; Nadeau et al. 2001; Jungblut et al. 2005, 2010). Salt content, measured as conductivity, can vary greatly from 100 to 70,000 μS cm^{-1}, from freshwater to brines that are more saline than sea water, and salt concentrations appear to be a key driver of cyanobacterial community assemblages in these benthic ecosystems (Jungblut et al. 2005). These meltwater ponds are also usually limited in nitrogen and cyanobacteria, especially heterocyst-forming genera such as *Nostoc*, are thought to play a more important role in the nitrogen budget than heterotrophic bacteria. Filamentous, oscillatorian cyanobacteria dominate the microbial mats in these ice shelf meltwater ponds (Fernandez-Valiente et al. 2007; Jungblut and Neilan 2010), but nitrogen-fixing *Nostoc* colonies are also present.

Similar to the south polar region, ice shelves as well as glaciers provide a variety of habitats for cyanobacteria in addition to other biota in the Arctic (Säwström et al. 2002; Varin et al. 2010; Jungblut et al. 2017). However, the total area of ice shelves is lower than that of Antarctica, where 40% of coastline is fringed by ice shelves. Furthermore, the recent breakup of the Ward Hunt Ice Shelf (Mueller et al. 2003) and the loss of the Markham Ice Shelf (Mueller et al. 2008) signal the massive reduction of these habitats through global warming.

Microbial mats in the Arctic can be prolific at some locations (Vincent et al. 2004a, b) but are generally less developed than in Antarctica; this may be due to the increased grazing pressure and also a lesser habitat stability as meltwater ponds are more ephemeral on Arctic ice shelves (Vincent 2000a). As in Antarctica, the north polar cyanobacteria communities are also dominated by oscillatorian morphotypes and genotypes such as *Leptolyngbya*, *Phormidesmis*, *Phormidium* and *Oscillatoria*. Jungblut et al. (2010) found overlaps in the abundance of genera in Arctic and Antarctic ice shelf mats and also identified Arctic sequences that had similarities up to 99% to *Leptolyngbya antarctica* that was thought to be endemic to Antarctica.

More unicellular genera were found on Arctic ice shelves than in Antarctica, including *Chamaesiphon*, *Gloeocapsa*, *Merismopedia*, cf. *Chlorogloea* sp., cf. *Aphanocapsa* sp., *Chroococcus* sp. and *Synechococcus*. This may be due to the wind-blown material from the nearby terrestrial lakes and streams (Harding et al. 2011). *Nostoc* and *Tolypothrix* can also be found; however, the genus *Nodularia* was not detected using 16S rRNA gen clone library sequencing. In total, 10 ribotypes and 19 morphotypes were identified, but this is still an underestimation, and high-throughput analyses are required for the more complete understanding of the cyanobacterial richness in ice shelf ecosystems.

9.6 Polar Soil and Rock Habitats

Cyanobacteria are often the primary colonisers of permafrost soils in areas where meltwater flushes occur through snowmelt or glacial meltwater (Pointing et al. 2015). Colonisation by cyanobacteria can increase soil stability and contribute to nutrient concentrations. Niederberger et al. (2015) showed that cyanobacteria and diverse groups of heterotrophic bacteria contributed to nitrogen fixation in wetted soils in the McMurdo Dry Valleys by comparing DNA, transcript *nifH* genes and acetylene reduction assays. However, in the Dry Valleys of Antarctica, the soils are old and weathered and have low carbon and nutrient concentrations (Vincent 1988; Cary et al. 2010), and cyanobacteria do not seem to be ubiquitously present in soil samples in the McMurdo Dry Valleys as cyanobacteria were only detected in some of the studied soil samples using 16S rRNA gene high-throughput sequencing (Van Horn et al. 2013) and ARISA (Magalhaes et al. 2012). Wood et al. (2008) also concluded that moisture content of Antarctic Dry Valley soils was a poor indicator of cyanobacteria distribution and that other variables such as soil elemental composition may play a role in influencing edaphic cyanobacterial habitat suitability.

Terrestrial dark crusts are found throughout the Arctic and Antarctica and are commonly dominated by cyanobacteria. A study performing 16S rRNA gene high-throughput sequencing on dark soil crusts growing in water tracks in the Ward Hunt Lake catchment, Canadian high Arctic (Stevens et al. 2013), found communities dominated by *Oscillatoriales* and OTUs grouping within *Nostocales*, *Chroococcales* and *Acaryochloris*, as well as a diverse heterotrophic community that included *Acidobacteria*, *Proteobacteria*, *Bacteroides* and *Verrucumicrobia*. Although there was no clear relationship between overall community structure and water availability, cyanobacteria were present in higher abundance in the water tracks with more regular water.

Cyanobacteria are also often identified in biofilms below and within the rocks where the microclimate gives protection against environmental stresses, such as high UV radiation, temperature extremes, desiccation and physical removal by wind in hyperarid polar deserts. They can be found in depth below the rock surface, depending on the optical characteristics of the rocks and the level of available PAR. Depending on the spatial location of the communities, they are hypolithic (beneath rocks), endolithic (in pore spaces of rocks), chasmoendolithic (in cracks and fissures of rocks) or cryptoendolithic (in the pore space between mineral grains forming sedimentary rocks) (Pointing et al. 2009; Makhalanyane et al. 2013; Stomeo et al. 2013).

Hypolithic communities under translucent rocks can be found in Antarctica, for example, in the Miers Valley of the McMurdo Dry Valleys. These microbial assemblages differ from soil communities, and cyanobacteria appear particularly during the first stage of developmental succession. The increased nutrient enrichment of the hypolithic microenvironment resulting from cyanobacterial colonisation could set the stage for subsequent heterotrophic fungal colonisation and the eventual development of bryophyte-based communities (Cowan et al. 2010). A

phylogenetic inference analysis found that hypolithic 16S rRNA cyanobacterial sequences formed clades with Oscillatoriales, such as *Phormidium priestleyi* and *Leptolyngbya frigida*, and Nostocales such as *Nostoc* (Pointing et al. 2009; Khan et al. 2011) in hypoliths in the McKelvey and Miers valleys. In the Arctic, hypolithic cyanobacteria are also commonly observed under opaque rocks subjected to periglacial movements (Cockell and Stokes 2004); however there is still a lack of 16S rRNA gene community structure analysis and phylogenetic analysis for a biogeographic and ecological comparison.

Chasmoliths and endoliths have also been studied in the McKelvey Valley in Antarctica and appear to have bacterial, eukaryotic and functional gene communities that are distinct from hypolithic and soil bacterial communities (Pointing et al. 2009; Chan et al. 2013). 16S rRNA gene cyanobacterial communities were dominated by *Chroococcidiopsis*, which had already been identified by morphology in sandstones of the Dry Valleys by Friedmann and Ocampo (1976). This genus is remarkably resistant to desiccation and has close relatives in hot deserts (Fewer et al. 2002). Other 16S rRNA sequences identified in this habitat have included *Acaryochloris* and *Tolypothrix* (Miyashita et al. 1996; de los Ríos et al. 2007; Pointing et al. 2009), and microscopic analysis has identified *Gloeocapsa*-like cyanobacteria in other types of continental Antarctic rocks such as sandstones. In the Arctic, cryptoendolithic communities are also common in sandstone outcrops of Eureka, Ellesmere Island, and consist of similar cyanobacterial morphotypes as in Antarctic rocks (Omelon et al. 2006); however, there is still a lack of molecular analysis.

9.7 Marine Ecosystems

The abundance of picocyanobacteria decreases markedly from temperate latitudes to polar regions (Marchant et al. 1987; Fouilland et al. 1999; Vincent and Quesada 2012). This decrease is likely due to temperature-limited growth rates (Vincent 2000a; Marchant 2005) in combination with continuous losses due to grazing, advection and mixing (Vincent 2000a; Vincent and Quesada 2012). In a 16S rRNA gene study of bacterial communities in the Beaufort Sea and Amundson Gulf, cyanobacteria were not part of the top 50 most abundant bacterial taxa (Comeau et al. 2011) and represented only 0.5% of the relative abundance in the epishelf lake in Milne Fjord, Canadian High Arctic, whereas phototrophic microbial eukaryotes were more abundant (Thaler et al. 2017). Interestingly a study of their molecular diversity in the Beaufort Sea identified picocyanobacteria using a cyanobacteria-specific amplification protocol, but they were affiliated with freshwater and brackish *Synechococcus* lineages and not with oceanic ones (Waleron et al. 2007). This was further confirmed by Blais et al. (2012), who also identified cyanobacterial nitrogenase reductase genes (*nifH*) from the Beaufort Sea, but again had highest match to cyanobacteria in freshwater or terrestrial habitats, such as the heterocyst-forming and nitrogen-fixing genus *Nostoc*. Their origin, therefore,

seemed allochthonous for the Arctic Ocean as it is much influenced by large riverine inputs. Similar findings have also resulted from Antarctic marine studies (e.g. Koh et al. 2012) where cyanobacteria were rare in the Antarctic ice communities and most closely related to freshwater *Cyanobacteria* from neighbouring terrestrial sources. Interestingly, Wilmotte et al. (2002) detected 16S rRNA sequences of picocyanobacteria that were closely related to temperate oceanic *Synechococcus*, such as WH8103 and WH7803 (Wilmotte et al. 2002) from the Subantarctic Front (51°S), suggesting that some marine genotypes may occur in polar waters.

9.8 Alpine Habitats

9.8.1 Ice-Based Supraglacial Ecosystems

Glaciers are a key feature of alpine landscapes, and supraglacial ecosystems, such as cryoconite hole communities, can be found from European and New Zealand Alps to the Himalayas. Therefore, it is not surprising that similarities have been found across supraglacial microbial diversity and communities and *Cyanobacteria* and *Proteobacteria* are important taxa in cryoconite assemblages. Although there are similarities in the cryosphere ecosystems across Svalbard, Greenland and Austria, a comparative study also found distinct geographic signals in the communities suggesting that local conditions play a role in shaping the assemblages (Edwards et al. 2014).

9.8.2 Streams and Lakes

In alpine streams, water chemistry, geochemical conditions, hydraulic conditions and permanence of flow are the key factors defining taxonomic diversity. Cyanobacteria have been found as part of microbial mats, epiphytic on mosses and endosymbiotic in lichens in stream habitats of many alpine regions, but there are no specific studies on their molecular diversity or adaptations (McClintic et al. 2003; Rott et al. 2006). Nutrient concentrations show large variations during the year with peaks in late winter and autumn. PAR and UV radiation also range from low levels in the presence of ice and snow cover to high levels during summer months, creating a need for protective mechanisms to survive. Rott et al. (2006) have described different colonisation patterns for several cyanobacterial morphotypes in alpine streams.

Cyanobacteria in alpine freshwater lakes can be found as benthic and planktonic communities. Plankton communities are mostly comprised of *Synechococcus* morphotypes, and their abundance is correlated to nutrient availability, particularly

nitrogen and phosphorus. Benthic communities were studied by Mez et al. (1998) and Sommaruga and Garcia-Pichel (1999).

9.8.3 Rocks and Soils

Cyanobacteria are also a component of alpine soil crusts and of soils from recently deglaciated areas and rock-associated communities, as described for endolithic communities of dolomite rocks in the Swiss Alps (Sigler et al. 2003). Diverse cyanobacteria, such as *Microcoleus*, *Nodosilinea*, *Nostoc* and Chroococcales, were found, based on morphological and 16S rRNA gene phylogenetic analysis in soil crust altitudinal gradients (4600–5900 m) in the Himalayas (Janatková et al. 2013). The presence and role of cyanobacteria in microbial and plant succession in the Andes has also been examined (Schmidt et al. 2008). Cyanobacterial sequences in Andean soils (Nemergut et al. 2007) included those related to the *Chamaesiphon* PCC7430 (96% sequence similarity), diverse *Nostoc* strains (up to 98.5% sequence similarity with the Antarctic ANT.L52B.1), the Antarctic *Leptolyngbya frigida* ANT.LH52.2 (98.5%) and ANT.LH52B.3 (99.6%), or differed from database sequences and thus represented a novel diversity.

Cyanobacteria have also been described from rock habitats ranging from European alpine dolomite layers to rocks in cold desert environment, such as stony desert pavements in the Qaidam Basin in China where communities contained in particular *Chroococcidiopsis*, based on 16S rRNA gene phylogenies, and cyanobacterial communities in comparison to hot desert environments were spatially aggregated at multiple scales in patterns distinct from the underlying rock pattern. Site-level differences in cyanobacterial spatial pattern (e.g. mean inter-patch distance) were linked with rainfall, whereas patchiness within sites was correlated with local geology (greater colonisation frequency of large rocks) and biology (dispersal during rainfall) (Warren-Rhodes et al. 2007).

9.9 Evolution and Biogeography

The origin and biogeography of cyanobacteria found in permanently cold environments, especially in the Arctic and Antarctic, remain topics of much debate. Physiological studies of polar cyanobacterial strains found that they were mostly psychrotolerant and had temperature optima for growth rates in the range 15–20 °C, well above their habitat temperatures, and it was therefore suggested that they likely had their evolutionary origins within temperate latitudes (Tang et al. 1997; Nadeau et al. 2001) and subsequently colonised perennial cold habitats. Phylogenetic interference based on a limited number of 16S rRNA genes of these first polar cyanobacteria isolates showed that they grouped with clades across the cyanobacterial Tree of Life, implying that psychrotolerant phenotypes evolved

several times (Nadeau et al. 2001). A far more comprehensive study based on a 16S rRNA gene tree with a large-scale multi gene analysis (135 proteins and 2 ribosomal RNAs) also identified clades that are common to Arctic, Antarctic and alpine sites in all major lineages (Chrismas et al. 2015). Bayesian ancestral state reconstruction was also performed with 16S rRNA gene sequences from these three cold region environments. This analysis of 270 sequences of cyanobacteria identified 20 clades with each having common ancestors that were likely capable of surviving in the cold (Chrismas et al. 2015).

Linked to the question of where and what evolutionary mechanisms led to the radiation of cyanobacteria with an ability to dealing with extreme cold is the ongoing discussion about cyanobacterial biogeography. A long-standing theory of microbial distribution is that "everything is everywhere, but the environment selects" and that local habitats select for specific microbiota that are globally distributed (Baas-Becking 1934). Castenholz (1992) noted the slow rates of speciation in the cyanobacteria together with their large dispersal abilities, and this in combination with the relatively young age of most polar ice-free environments suggests that endemism is likely to be rare among polar cyanobacteria. On the other hand, several features of Antarctica suggest that microbial endemism may be possible there (Vincent 2000b): (1) Antarctica has been more isolated than other parts of the world for several million years; (2) dispersal processes which favour local species are more efficient than long-range dispersal processes; and (3) there has probably been strong environmental selection for adaptive strategies. Morphological identifications seemed to support this hypothesis, but such characterisation is limited due to morphological plasticity. There are also several phylogenetic studies based on 16S rRNA gene sequences from isolated cyanobacteria and from environmental samples that have identified taxa which appeared to be restricted to specific geographic sites and which may suggest the presence of endemicity (Taton et al. 2006a, b; Strunecky et al. 2011; Komárek et al. 2012). However, comparisons with other geographic locations are still unsatisfactory due to the limited number of reference strains in culture and the limited sampling over the vast polar and alpine regions.

The first comprehensive 16S rRNA gene surveys of cyanobacterial mat assemblages from the High Arctic indicated the presence of cyanobacterial ecotypes that were 99% similar, based on 16S rRNA gene analyses, to taxa previously thought to be endemic to Antarctica. More than 68% of all identified ribotypes at each site matched only cyanobacterial sequences from perennially cold terrestrial ecosystems and were less than 97.5% similar to sequences from warmer environments. This implied the global distribution of low-temperature cyanobacterial ecotypes throughout the cold terrestrial biosphere (Jungblut et al. 2010).

Although several studies have shown the potentially cosmopolitan distribution of cold ecotypes, other work has indicated that there are dispersal barriers on local to global scales leading to distinct populations within 16S rRNA gene genotypes and ecotypes. At the local scale, Novis and Smissen (2006) showed with amplified fragment length polymorphism (AFLP) analysis that *Nostoc commune* formed distinct genetic groups according to the habitat in the McMurdo Dry Valleys,

Antarctica. At the global scale, barriers of dispersal have also been identified between 16S rRNA gene ribotypes of desert-dwelling *Chroococcidiopsis*, as molecular clock analysis of 16S RRNA genotypes from cold arid and hot deserts suggested no evidence of recent interregional gene flow. The temporal phylogeny suggests that the time of most recent common ancestry to all contemporary variants was 2.5 Ga (range: 3.1–1.9 Ga), indicating populations have not shared common ancestry since before the formation of modern continents (Bahl et al. 2011). This suggests that the biogeography of polar cyanobacteria is complex and may vary across taxonomic species and ecotypes. Therefore, further studies are needed with better species sampling and using multilocus gene and genomic analysis for adequate resolution.

9.10 Conclusions

Cyanobacteria evolved under the harsh, highly variable temperature regimes of the Precambrian and their modern representatives retain a remarkable ability to adapt to and survive within extreme conditions. They are among the microbial dominants in soil ecosystems, the hydrosphere and the cryosphere of Arctic, Antarctic and alpine regions. They are keystone taxa as they play a major ecological role in primary colonisation of substrates, primary production, nitrogen input and even as habitat engineers in these permanently cold ecosystems. The application of molecular tools, in particular high-throughput sequencing and metagenomics, in combination with laboratory experimentation has begun to provide new insights into the full diversity of cyanobacteria, their community dynamics and their biogeographical distribution in cold environments on a global scale. However, more studies and especially comparative genomic evaluations are needed to unravel the enigmatic origins and evolution of cyanobacteria in the cold biosphere. This is an urgent task in view of the climatic changes that have already begun to alter the structure and functioning of polar and alpine microbial ecosystems.

References

Andersen DT, Sumner DY, Hawes I, Webster-Brown J, Mackay CP (2011) Discovery of large conical stromatolites in Lake Untersee, Antarctica. Geobiology 9:280–293

Archer SDJ, McDonald IR, Herbold CW, Lee CK, Cary CS (2015) Benthic microbial communities of coastal terrestrial and ice shelf Antarctic meltwater ponds. Front Microbiol 6:485

Baas-Becking LGM (1934) Geobiologie of inleiding tot de milieukunde. van Stockum WP, Zoon NV, The Hague

Bahl J, Lau MCY, Smith GJD, Vijaykrishna D, Cary C, Lacap DC, Lee CK, Papke RT, Warren-Rhodes KA, Wong FKY, McKay CP, Pointing SB (2011) Ancient origins determine global biogeography of hot and cold desert cyanobacteria. Nat Commun 2:163

Blais M, Tremblay J-É, Jungblut AD, Gagnon J, Martin J, Thaler M, Lovejoy C (2012) Nitrogen fixation and identification of potential diazotrophs in the Canadian Arctic. Glob Biogeochem Cycles 26:GB3022. doi:10.1029/2011GB004096

Bonilla S, Villeneuve V, Vincent WF (2005) Benthic and planktonic algal communities in a high arctic lake: pigment structure and contrasting responses to nutrient enrichment. J Phycol 41:1120–1130

Cameron KA, Hodson AJ, Osborn AM (2012) Structure and diversity of bacteria, eukaryotic and archaeal communities in glacial cryoconite holes from the Arctic and the Antarctic. FEMS Microbiol Ecol 91:254–267

Cary SC, McDonald IR, Barrett JE, Coawn DA (2010) On the rocks: the microbiology of Antarctic Dry Valley soils. Nat Rev Microbiol 8:129–138

Castenholz RW (1992) Species usage, concept, and evolution in the Cyanobacteria (blue-green algae). J Phycol 28:737–745

Castenholz RW (2001) Phylum BX. Cyanobacteria. Oxygenic photosynthetic bacteria. In: Boone DR, Castenholz RW, Garrity GM (eds) Bergey's manual of systematic bacteriology (the archaea and the deeply branching and phototrophic bacteria), vol 1. Springer, New York, NY, pp 473–599

Castenholz RW, Garcia-Pichel F (2000) Cyanobacterial responses to UV-radiation. In: Whitton BA, Potts M (eds) The ecology of cyanobacteria. Kluwer, Dordrecht, pp 591–611

Chen M, Scheer H (2013) Extending the limits of natural photosynthesis and implications for technical light harvesting. J Porphyrins Phthalocyanines 17:1–15

Chan Y, Van Nostrand JD, Zhou J, Pointing SB, Farrell RL (2013) Proc Natl Acad Sci USA 110:8990–8995

Chorus I, Bartram J (1999) Toxic cyanobacteria in water. A guide to their public health consequences, monitoring and management. World Health Organization, London

Chrismas N, Anesio AM, Sanches-Baracaldo P (2015) Multiple adaptations to polar and alpine environments within cyanobacteria: a phylogenomic and Bayesian approach. Front Microbiol 6:1070

Chrismas N, Barker G, Anesio AM, Sanches-Baracaldo P (2016) Genomic mechanisms for cold tolerance and production of exopolysaccharides in the Arctic cyanobacterium *Phormidesmis priestleyi* BC1401. BMC Genom 17:533

Christner BC, Kvitoko BH, Reeve JN (2003) Molecular identification of Bacteria and Eukarya inhabiting an Antarctic cryoconite hole. Extremophiles 7:177–183

Cockell CS, Stokes MD (2004) Widespread colonization by polar hypoliths. Nature 431:414

Comeau AM, Li WKW, Tremblay J-E, Carmack EC, Lovejoy C (2011) Changes in Arctic Ocean microbial community structure following the 2007 record sea ice minimum. PLoS ONE 6: e27492

Cook JM, Edwards A, Takeuchi N, Irvine-Fynn TDL (2015) Cryoconite: the dirty biological secret of the cryosphere. Prog Phys Geogr 40:66–111

Cowan DA, Khan N, Pointin SB, Cary SG (2010) Diversity of hypolithic refuge communities in the McMurdo Dry Valleys. Antarct Sci 22:714–720

de los Ríos A, Grube M, Sancho LG, Ascaso C (2007) Ultrastructural and genetic characteristics of endolithic cyanobacterial biofilms colonizing Antarctic granite rocks. FEMS Microbiol Ecol 59:386–395

de los Ríos A, Ascaso C, Wierzchos J, Vincent WF, Quesada A (2015) Microstructure and cyanobacterial composition of microbial mats from the High Arctic. Biodivers Conserv 24:841–886

DeSantis TZ, Hugenholtz P, Larsen N et al (2006) Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. Appl Environ Microbiol 72:5069–5072

Edwards A, Anesio AM, Rassner SM et al (2011) Possible interactions between bacterial diversity, microbial activity and supraglacial hydrology of cryoconite holes in Svalbard. ISME J 5:150–160

Edwards A, Mur LAJ, Girdwood SE et al (2014) Coupled cryoconite ecosystem structure-function relationships are revealed by comparing bacterial communities in alpine and Arctic glaciers. FEMS Microbiol Ecol 89:222–237

Elster J, Syobody J, Komárek J, Marvan P (1997) Algal and cyanoprocaryote communities in a glacial stream, Sverdrup Pass, 79N, Central Ellesmere Island, Canada. Arch Hydrobiol Suppl 119:57–93

Fernandez-Valiente E, Camacho A, Rochera C, Rico E, Vincent WF, Quesada A (2007) Community structure and physiological characterization of microbial mats in Byers Peninsula, Livingston Island (South Shetland Islands, Antarctica). FEMS Microbiol Ecol 59:377–385

Fewer D, Friedl T, Büdel B (2002) *Chroococcidiopsis* and heterocyst-differentiating cyanobacteria are each other's closest living relatives. Mol Phylogenet Evol 23:82–90

Foreman CM, Sattler B, Mikucki J et al (2007) Metabolic activity and diversity of cryoconites in the Taylor Valley, Antarctica. J Geophys Res 112:1–11

Fouilland E, Descolas-Gros C, Courties C, Pons V (1999) Autotrophic carbon assimilation and biomass from size-fractionated phytoplankton in the surface waters across the subtropical frontal zone (Indian Ocean). Polar Biol 21:90–96

Friedmann EI, Ocampo R (1976) Endolithic blue-green algae in the Dry Valleys: primary producers in the Antarctic ecosystem. Science 193:1247–1249

Geitler L (1932) Cyanophyceae. In: Kolkwitz R (ed) Rabenhorst's Kryptogamenflora von Deutschland, Osterreich und der Schweiz. Akademische Verlagsgesellschaft, Leibzig

Gokul JK, Hodson AJ, Saetnan ER, Irvine-Fynn TDL, Westall PJ, Detheride AP, Takeychi N, Bussell J, Mur LAJ, Edwards E (2016) Taxon interactions control the distributions of cryoconite bacteria colonizing a High Arctic ice cap. Mol Ecol 25:3752–3767

Green WJ, Angle MP, Chave KE (1988) The geochemistry of Antarctic streams and their role in the evolution of four lakes of the McMurdo Dry Valleys. Geochim Cosmochim Acta 52:1265–1274

Harding T, Jungblut AD, Lovejoy C, Vincent WF (2011) Microbes in High Arctic snow and implications for the cold biosphere. Appl Environ Microbiol 77:3234–3243

Hawes I, Schwarz AM (2001) Absorption and utilization of irradiance by cyanobacterial mats in two ice-covered Antarctic lakes with contrasting light climates. J Phycol 37:5–15

Hawes I, Howard-Williams C, Pridmore RD (1993) Environmental control of microbial biomass in the ponds of the McMurdo Ice Shelf, Antarctica. Arch Hydrobiol 127:271–287

Hawes I, Sumner DY, Andersen DT, Mackey TJ (2011) Legacies of recent environmental change in the benthic communities of Lake Joyce, a perennially ice-covered Antarctic lake. Geobiology 9:394–410

Hitzfeld B, Lampert CS, Spaeth N, Mountfort D, Kaspar H, Dietrich DR (2000) Toxin production in cyanobacterial mats from ponds on the McMurdo Ice Shelf, Antarctica. Toxicon 38:1731–1748

Hodson A, Cameron K, Bøggild C et al (2010) The structure, biogeochemistry and formation of cryoconite aggregates upon an Arctic valley glacier; Longyearbreen, Svalbard. J Glaciol 56:349–362

Hoffman PF (2016) Cryoconite pans on Snowball Earth: supraglacial oases for Cryogenian eukaryotes? Geobiology 14:531–542

Hoffmann L, Komárek J, Kaštovský J (2005a) System of cyanoprokaryotes (cyanobacteria) – state in 2004. Algol Stud 117:95–115

Hoffmann L, Komárek J, Kaštovský J (2005b) Proposal of cyanobacterial system – 2004. In: Büdel B, Krienitz L, Gärtner G, Schagerl M (eds) Süsswasserflora von Mitteleuropa 19/2. Elsevier/Spektrum, Heidelberg, pp 657–660

Howard-Williams C, Pridmore RD, Downes MT, Vincent WF (1989) Microbial biomass, photosynthesis and chlorophyll a related pigments in the ponds of the McMurdo Ice Shelf, Antarctica. Antarct Sci 1:125–131

Janatková K, Řeháková K, Doležal J, Šimek M, Chlumská Z, Dvorský M, Kopecký M (2013) Community structure of soil phototrophs along environmental gradients in arid Himalaya. Environ Microbiol 15:2505–2516

Jancusova M, Kovacik L, Batista Periera A, Dusinsky R, Wilmotte A (2016) Polyphasic characterization of 10 selected ecologically relevant filamentous cyanobacterial strains from the South Shetland Islands, Maritime Antarctica. FEMS Microbiol Ecol 92:fiw100

Jungblut AD, Neilan BA (2010) NifH-gene diversity and expression in a microbial mat community on the McMurdo Ice Shelf, Antarctica. Antarct Sci 22:177–122

Jungblut AD, Hawes I, Mountfort D, Hitzfeld B, Dietrich DR, Burns BP, Neilan BA (2005) Diversity within cyanobacterial mat communities in variable salinity meltwater ponds of McMurdo Ice Shelf, Antarctica. Environ Microbiol 7:519–529

Jungblut AD, Hoeger SJ, Mountford D, Hitzfeld BC, Dietrich DR, Neilan BA (2006) Characterization of microcystin production in an Antarctic cyanobacterial mat community. Toxicon 47:271–278

Jungblut AD, Lovejoy C, Vincent WF (2010) Global distribution of cyanobacterial ecotypes in the cold biosphere. ISME J 4:191–202

Jungblut AD, Wood SA, Hawes I, Webster-Brown J, Harris C (2012) The Pyramid Trough Wetland: environmental and biological diversity in a newly created Antarctic protected area. FEMS Microbiol Ecol 82:356–366

Jungblut AD, Hawes I, Mackey TJ, Krusor M, Doran PT, Sumner DY, Eisen JA, Hillman C, Goroncy AK (2016) Microbial mat communities along an oxygen gradient in a perennially ice-covered Antarctic lake. Appl Environ Microbiol 82:620–630

Jungblut AD, Mueller D, Vincent WF (2017) Arctic ice shelf ecosystems. In: Copland L, Mueller DR (eds) Arctic Ice Shelves and Ice Islands. Springer SBM, Dordrecht

Kaebernick M, Neilan BA (2001) Ecological and molecular investigations of cyanotoxin production. FEMS Microbiol Ecol 35:1–9

Khan N, Tuffin M, Stafford W, Cary C, Lacap DC, Pointing SB et al (2011) Hypolithic microbial communities of quartz rocks from Miers Valley, McMurdo Dry Valleys, Antarctica. Polar Biol 34:1657–1668

Kleinteich J, Wood SA, Kupper FC, Camacho A, Quesada A, Frickey T, Dietrich DR (2012) Temperature-related changes in polar cyanobacterial mat diversity and toxin production. Nat Clim Chang 2:356–360

Kleinteich J, Wood SA, Puddick J, Schleheck D, Kupper FC, Dietrich D (2013) Potent toxins in Arctic environments: presence of saxitoxins and an unusual microcystin variant in Arctic freshwater ecosystems. Chem Biol Interact 206:423–431

Kleinteich J, Hildebrand F, Wood SA, Cirs S, Agha R, Quesada A, Pearce D, Convey P, Küpper F, Dietrich DR (2014) Diversity of toxin and non-toxin containing cyanobacterial mats of meltwater ponds on the Antarctic Peninsula: a pyrosequencing approach. Antarct Sci 26:521–532

Koh EY, Cowie ROM, Simpson AM, O'Toole R, Ryan KG (2012) The origin of cyanobacteria in Antarctic sea ice: marine or freshwater? Environ Microbiol Rep 4:479–483

Komárek J, Anagnostidis K (2005) Cyanoprokaryota 2. Teil Oscillatoriales. Spektrum Akademischer Verlag, Heidelberg

Komárek J, Nedbalová L, Hauer T (2012) Phylogenetic position and taxonomy of three heterocytous cyanobacteria dominating the littoral of deglaciated lakes, James Ross Island, Antarctica. Polar Biol 35:759–774

Komárek J, Kaštovský J, Mareš J, Johansen JR (2014) Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach. Preslia 86:295–335

Langford H, Hodson A, Banwart S, Bøggild C (2010) The microstructure and biogeochemistry of Arctic cryoconite granules. Ann Glaciol 51:87–94

Leslie A (1879) The Arctic voyages of Adolf Erik Nordenskiöld. MacMillan, London

Lionard M, Péquin B, Lovejoy C, Vincent WF (2012) Benthic cyanobacterial mats in the High Arctic: multi-layer structure and fluorescence responses to osmotic stress. Front Aquat Microbiol 3:140

Mackey TJ, Sumner DY, Hawes I, Jungblut A-D, Andersen DT (2015) Branched stromatolites in Lake Joyce, Antarctica. Geobiology 13:373–390

Magalhaes C, Stevens MI, Cary SC, Ball BA, Storey BC, Wall DH, Tuerk R, Ruprecht U (2012) At limits of life: multidisciplinary insights reveal environmental constraints on biotic diversity in continental Antarctica. PLoS ONE 7:e44578

Makhalanyane TP, Valverde A, Lacap DC, Pointing SB, Tuffin M, Cowan DA (2013) Evidence of species recruitment and development of hot desert hypolithic communities. Environ Microbiol Rep 5:219–224

Marchant HJ (2005) Cyanophytes. In: Scott FJ, Marchant HJ (eds) Antarctic marine protists. Australian Biological Resources Study, Canberra, pp 324–325

Marchant HJ, Davidson AT, Wright SW (1987) The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. Proc NIPR Symp Polar Biol 1:1–9

Margesin R, Häggblom M (2007) Thematic issue: microorganisms in cold environments. FEMS Microbiol Ecol 59:215–216

Martineau E, Wood SA, Miller MR, Jungblut AD, Hawes I, Webster-Brown J, Packer MA (2013) Characterisation of Antarctic cyanobacteria and comparison with New Zealand strains. Hydrobiology 711:139–154

McClintic AS, Casamatta DA, Vis ML (2003) A survey of algae from montane cloud forest and alpine streams in Bolivia: macroalgae and associated microalgae. Nova Hedwigia 76:363–379

Mez K, Hanselmann K, Preisig HR (1998) Environmental conditions in high mountain lakes containing toxic benthic cyanobacteria. Hydrobiologia 368:1–15

Miyashita H, Ikemoto H, Kurano N, Adachi K, Chihara M, Miyashi S (1996) Chlorophyll d as a major pigment. Nature 383:402

Moffitt CM, Neilan AB (2004) Characterization of the nodularin synthetase gene cluster and proposed evolution of cyanobacterial hepatotoxins. Appl Environ Microbiol 70:6353–6362

Mueller DR, Vincent WF, Jeffries MO (2003) Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake. Geophys Res Lett 30:2031

Mueller DR, Copland L, Hamilton A, Stern DR (2008) Examining Arctic ice shelves prior to 2008 breakup. EOS Trans Am Geophys Union 89:502–503

Murray J (1910) British Antarctic expedition 1907–1909. Reports on the scientific investigations. Biology 1(Part V):83–187

Nadeau TL, Milbrandt EC, Castenholz RW (2001) Evolutionary relationships of cultivated Antarctic Oscillatoriaceans (cyanobacteria). J Phycol 37:650–654

Nemergut DR, Anderson SP, Cleveland CC, Martin AP, Miller AE, Seimon A, Schmidt SK (2007) Microbial community succession in an unvegetated, recently deglaciated soil. Microb Ecol 53:110–122

Niederberger TD, Sohm JA, Gunderson TE, Parker AE, Tirindelli J, Capone DG, Carpenter EK, Cary SC (2015) Microbial community composition of transiently wetted Antarctic Dry Valley soils. Front Microbiol 6:9

Novis PM, Smissen RD (2006) Two genetic and ecological groups of Nostoc commune in Victoria Land, Antarctia, revealed by AFLP analysis. Antarct Sci 18:573–581

Omelon CR, Pollard WH, Ferris FG (2006) Environmental controls on microbial colonization of high Arctic cryptoendolithic habitats. Polar Biol 30:19–29

Oren A (2000) Salt and brines. In: Whitton BA, Potts M (eds) The ecology of cyanobacteria. Kluwer Academic Press, Dordrecht, pp 281–306

Oren A (2004) A proposal for further integration of the cyanobacteria under the Bacteriological Code. Int J Syst Evol Microbiol 54:1895–1902

Pointing SB, Chan Y, Lacap DC, Lau MC, Jurgens JA, Farrell RL (2009) Highly specialized microbial diversity in hyper-arid polar desert. Proc Natl Acad Sci U S A 106:19964–19969

Pointing SB, Büdel B, Convey P, Gillman L, Körner C, Leuzinger S, Vincent WF (2015) Biogeography of photoautotrophs in the high polar biome. Front Plant Sci 6:692

Porazinska DL, Fountain AG, Nylen TH et al (2004) The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley Glaciers, Antarctica. Arct Antarct Alp Res 36:84–91

Przytulska A, Bartosiewicz M, Rautio M, Dufresne F, Vincent WF (2015) Climate effects on Arctic *Daphnia* via food quality and thresholds. PLoS ONE 10:e0126231

Quesada A, Vincent WF (2012) Cyanobacteria in the cryosphere: snow, ice and extreme cold. In: Whitton BA (ed) Ecology of cyanobacteria II: their diversity in space and time. Springer, New York, NY, pp 387–399

Rajaniemi P, Hrouzek P, Kastovska K, Willame R, Rantala A, Hoffmann L, Komarek J, Sivonen K (2005) Phylogenetic and morphological evaluation of the genera *Anabaena, Aphanizomenon, Trichormus* and *Nostoc* (Nostocales, Cyanobacteria). Int J Syst Evol Microbiol 55:11–26

Rantala A, Fewer D, Hisburges M, Rouhiainen L, Vaitomaa J, Börner T (2004) Phylogenetic evidence for the early evolution of the microcystin synthesis. Proc Natl Acad Sci U S A 101:568–573

Rocap G, Distel DL, Waterbury JB, Chisholm SW (2002) Resolution of *Prochlorococcus* and *Synechococcus* ecotypes by using 16S-23S ribosomal DNA internal transcribed spacer sequences. Appl Environ Microbiol 68(3):1180–1191

Rott E, Cantonati M, Füreder L, Pfister P (2006) Benthic algae in high altitude streams of the Alps-a neglected component of the aquatic biota. Hydrobiology 562:195–216

Sabbe K, Hodgson DA, Verlyen E, Taton A, Wilmotte A, Vanhoutte KD, Vyverman W (2004) Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes. Freshw Biol 49:296–319

Säwström C, Mumford P, Marshall W, Hodson A, Laybourn-Parry J (2002) The microbial communities and primary productivity of crycoconite holes in an Arctic glacier (Svalbard 79°N). Polar Biol 25:591–596

Schmidt SK, Reed SC, Nemergut DR, Grandy AS, Cleveland CC, Weintraub MN, Hill AW, Costello EK, Meyer AF, Neff JC, Martin AM (2008) The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils. Proc R Soc Lond B Biol Sci 275:2793–2802

Sigler WV, Bachofen R, Zeier J (2003) Molecular characterization of endolithic cyanobacteria inhabiting exposed dolomite in central Switzerland. Environ Microbiol 5:618–627

Sommaruga R, Garcia-Pichel F (1999) UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. Arch Hydrobiol 144:255–269

Stanier RY, Sistrom WR, Hansen TA, Whitton BA, Castenholz RW, Pfennig N, Gorlenko VN, Kondratieva EN, Eimhjellen KE, Whittenbury R, Gherma RL, Trüper HG (1978) Proposal to place nomenclature of cyanobacteria (blue-green-algae) under rules of International Code of Nomenclature of Bacteria. Int J Syst Bacteriol 28:335–336

Stanish LF, O'Neil SP, Gonzales A, Legg TM, Knelman J, McKnight DM, Spaulding S, Nemergut DR (2013) Bacteria and diatom co-occurrence patterns in microbial mats from polar desert streams. Environ Microbiol 15:1115–1131

Stevens B, Lionard M, Kuske CR, Vincent WF (2013) High bacterial diversity of biological soil crusts in water tracks over permafrost in the High Arctic polar desert. PLoS ONE 8:e71489

Stibal M, Sabacká M, Kastovská K (2006) Microbial communities on glacier surfaces in Svalbard: impact of physical and chemical properties on abundance and structure of cyanobacteria and algae. Microb Ecol 52:644–654

Stibal M, Schostag M, Cameron KA et al (2015) Different bulk and active bacterial communities in cryoconite from the margin and interior of the Greenland ice sheet. Environ Microbiol Rep 7:293–300

Stomeo F, Valverde A, Pointing SB, McKay CP, Warren-Rhodes KA, Tuffin MI et al (2013) Hypolithic and soil microbial community assembly along an aridity gradient in the Namib Desert. Extremophiles 17:329–337

Strunecky O, Elster J, Komarek J (2011) Taxonomic revision of the freshwater cyanobacterium *Phormidium murrayi = Wilmottia murrayi*. Fottea 11:57–71

Sumner DY, Hawes I, Mackey TJ, Jungblut AD, Doran PT (2015) Antarctic microbial mats: a modern analogue for Archean lacustrine oxygen oases. Geology 43:887–890

Sumner D, Jungblut AD, Hawes I, Andersen DT, Mackey TJ, Wall K (2016) Growth of elaborate microbial pinnacles in Lake Vanda, Antarctica. Geobiology 14:556–574

Tanabe Y, Ohtan S, Kasamatsu N, Fukuchi M, Kudoh S (2010) Photophysiological responses of phytobenthic communities to the strong light and UV in Antarctic shallow lakes. Polar Biol 33:85–100

Tang EPY, Vincent WF (1999) Strategies of thermal adaptation by high latitude cyanobacteria. New Phytol 142:315–323

Tang EPY, Tremblay R, Vincent WF (1997) Cyanobacterial dominance of polar freshwater ecosystems: are high latitude mat-formers adapted to the low temperature environment? J Phycol 33:171–181

Tashyreva D, Elster J (2016) Annual cycles of two cyanobacterial mat communities in hydro-terrestrial habitats of the High Arctic. Microb Ecol 71:887–900

Taton A, Grubisic S, Brambilla E, De Wit R, Wilmotte A (2003) Cyanobacterial diversity in natural and artificial microbial mats of Lake Fryxell (McMurdo Dry Valleys, Antarctica): a morphological and molecular approach. Appl Environ Microbiol 69:5157–5169

Taton A, Grubisic S, Balhasart P, Hodgson DA, Laybourn-Parry J, Wilmotte A (2006a) Biogeographical distribution and ecological ranges of benthic cyanobacteria in East Antarctic lakes. FEMS Microbiol Ecol 57:272–289

Taton A, Grubisic S, Ertz D, Hodgson DA, Piccardi R, Biondi N, Tredici MR, Mainini M, Losi D, Marinelli F, Wilmotte A (2006b) Polyphasic study of Antarctic cyanobacterial strains. J Phycol 42:1257–1270

Thaler M, Vincent WF, Lionard M, Hamilton AK, Lovejoy C (2017) Microbial community structure and interannual change in the last epishelf lake ecosystem in the North Polar Region. Front Mar Sci 3:275

Van Horn DJ, Van Horn ML, Barret JE, Gooseff MN, Altrichter E, Geyer KM, Zeglin LH, Takacs-Vesbach CD (2013) Factors controlling soil microbial biomass and bacterial diversity and community composition in a cold desert ecosystem: Role of geographic scale. PLoS ONE 8: e66103

Varin T, Lovejoy C, Jungblut AD, Vincent WF, Corbeil J (2010) Metagenomic profiling of Arctic microbial mat communities as nutrient scavenging and recycling systems. Limnol Oceanogr 55:1901–1911

Varin T, Lovejoy C, Jungblut AD, Vincent WF, Corbeil J (2012) Metagenomic analysis of stress genes in microbial mat communities from Antarctica and the High Arctic. Appl Environ Microbiol 78:549–559

Veillette J, Martineau M-J, Antoniades D, Sarrazin D, Vincent WF (2011) Effects of loss of perennial lake ice on mixing and phytoplankton dynamics: Insights from High Arctic Canada. Ann Glaciol 51:56–70

Velázques D, Jungblut AD, Rochera C, Camacho A, Quesada A, Rico E (2017) Seasonal dynamics and trophic interactions of a microbial mat in maritime Antarctic. Polar Biol. doi:10.1007/s00300-016-2039-2

Vincent WF (1988) Microbial ecosystems of Antarctica. Cambridge University Press, Cambridge, 304 pp

Vincent WF (2000a) Cyanobacterial dominance in the polar regions. In: Whitton BA, Potts M (eds) The ecology of Cyanobacteria. Kluwers Academic Press, Dordrecht, pp 321–340

Vincent WF (2000b) Evolutionary origins of Antarctic microbiota: invasion, selection and endemism. Antarct Sci 12:374–385

Vincent WF (2007) Cold tolerance in cyanobacteria and life in the cryosphere. In: Seckbach J (ed) Algae and cyanobacteria in extreme environments. Springer, Heidelberg, pp 287–301

Vincent WF, Howard-Williams C (2000) Life on snowball Earth. Science 287:2421v

Vincent WF, Quesada A (2012) Cyanobacteria in high latitude lakes, rivers and seas. In: Whitton BA (ed) Ecology of cyanobacteria II: their diversity in space and time. Springer, New York, NY, pp 371–385

Vincent WF, Castenholz RW, Downes MT, Howard-Williams C (1993) Antarctic cyanobacteria: light, nutrients, and photosynthesis on the microbial mat environments. J Phycol 29:745–755

Vincent WF, Mueller D, Van Hove P, Howard-Williams C (2004a) Glacial periods on early Earth and implications for the evolution of life. In: Seckbach J (ed) Origins: genesis, evolution and diversity of life. Kluwer Academic Publishers, Dordrecht, pp 481–501

Vincent WF, Mueller DR, Bonilla S (2004b) Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the High Arctic. Cryobiology 48:103–112

Vopel K, Hawes I (2006) Photosynthetic performance of benthic microbial mats in Lake Hoare, Antarctica. Limnol Oceanogr 51:1801–1812

Wait BR, Webster-Brown JG, Brown KR, Healy M, Hawes I (2006) Chemistry and stratification of Antarctic meltwater ponds I: coastal ponds near Bratina Island, McMurdo Ice Shelf. Antarct Sci 18:515–524

Waleron M, Waleron K, Vincent WF, Wilmotte A (2007) Allochthonous inputs of riverine picocyanobacteria to coastal waters in the Arctic Ocean. FEMS Microbiol Ecol 59:356–365

Warren-Rhodes KA, Rhodes KL, Boyle LN, Pointing SB, Chen Y et al (2007) Cyanobacterial ecology across environmental gradients and spatial scales in China's hot and cold deserts. FEMS Microbiol Ecol 61:470–482

Webster-Brown JG, Hawes I, Jungblut AD, Wood SA, Christenson HK (2015) The effects of entombment on water chemistry and bacterial assemblages in closed cryoconite holes on Antarctic glaciers. FEMS Microbiol Ecol 91:fiv144

Wharton RA, McKay CP, Simmons GM, Parker BC (1985) Cryoconite holes on glaciers. Bioscience 35:499–503

Wilmotte A, Demonceau C, Goffart A, Hecq J-H, Demoulin V, Crossley AC (2002) Molecular and pigment studies of the picophytoplankton in a region of Southern Ocean (42-54°S, 141-144°E) in March 1998. Deep-Sea Res II 49:3351–3363

Wood SA, Mountfort D, Selwood AI, Holland PT, Puddick J, Cary SC (2008) Widespread distribution and identification of eight novel microcystins in Antarctic cyanobacterial mats. Appl Environ Microbiol 74:7243–7251

Zhang L, Jungblut AD, Hawes I, Andersen DT, Sumner DY, Mackey TJ (2015) Cyanobacterial diversity in benthic mats of the McMurdo Dry Valley lakes, Antarctica. Polar Biol 38:1097–1110