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Summary

This chapter explores the occurrence and dominance of cyanobacteria in some of the harshest environments on earth, the cryosphere, where extreme cold and the near absence of liquid water provide severe constraints on growth and survival. They are present in ice-based ecosystems including snow, glacier ice, lake ice and ice-shelves, and sometimes achieve remarkably high biomass concentrations. Cold desert ecosystems in the Arctic and Antarctica also contain a variety of habitats colonized by cyanobacteria, although their diversity is low, and similar taxa are present in different geographic locations under similar ecological conditions. The strategy for microbial success in these environments is not adaptation towards optimal growth at low temperatures, but instead rests on tolerance to environmental extremes. An ability to survive prolonged dormancy is also an important feature accounting for the widespread occurrence of cyanobacteria in these environments.

14.1 Introduction

Cyanobacteria are near-ubiquitous organisms that occur in most sun-exposed ecosystems on Earth. In many ecosystems cyanobacteria are seasonally dominant, for example eutrophic lakes in summers in temperate regions. In extreme ecosystems such as high salinity (Chap. 15), thermal (Chap. 3) and oil polluted environments (Chap. 16), cyanobacteria can become exceptionally abundant and dominate through much or all of the year. Among these extreme environments is the cryosphere, which contains some of the harshest conditions for life as a result of extreme cold and the scarcity of liquid water. The cryosphere is defined here as the regions where temperatures remain below 0°C during most of the year, notably alpine regions and both Polar Regions, the Arctic and Antarctica. Most potential habitats in the cryosphere are within or covered by ice. However, some locations are snow and ice-free for much of the year – alpine and polar deserts.

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These latter environments have been considered analogues for the possible development of life on frozen planets or moons (Wynn-Williams 2000), while the ice-bound ecosystems have provided insights into how life may have survived during global freeze-up events on early Earth (Vincent and Howard-Williams 2000). Cyanobacteria are frequently found in the ice as well as cold desert habitats, and use a variety of strategies to mitigate the harshness of their surroundings (Vincent 2007). For example, some communities live inside rocks where the humidity can be higher and the thermal variation is buffered (Nienow and Friedmann 1993), while others form dark-colored mats on or within ice that absorbs sunlight, which increases the temperature enough to melt some ice in summer and provide liquid water conditions (Mueller and Pollard 2004). Cyanobacteria inhabiting the cryosphere do not appear to be very diverse, and are mostly comprised of a few morphospecies (Nienow and Friedmann 1993; Wynn-Williams 2000). Global molecular studies are now well underway, and are providing some evidence of locally restricted (endemic) taxa (Taton et al. 2003), but also the cosmopolitan distribution of closely related genotypes throughout the cryosphere (Jungblut et al. 2010).

Contrary to expectation, cyanobacteria growing in the cryosphere are not cold-adapted psychrophiles (Vincent 2000). Instead, and with very few exceptions (Nadeau and Castenholz 2000), they are psychrotrophic (cold-tolerant) organisms, able to survive and slowly grow at low temperatures, but with temperature optima well above the temperatures found at their habitats (Tang et al. 1997). This lack of adaptative tuning to a low temperature regime may be an optimal strategy in these ecosystems where temperatures can fluctuate widely in few hours (Fig. 14.1), reaching high values at which organisms fully adapted for growth in the cold could suffer severe physiological stress and mortality. Under these suboptimal conditions cyanobacterial growth rate is modest (Vincent 2007), but in spite of this, they can achieve conspicuously large standing crops, and they colonize most habitats (see also Chap. 13).

Apart from extreme cold, cyanobacteria growing in the cryosphere also need to cope with the consequences of freeze-up and ice formation. During the latter, solutes are excluded from the growing ice, resulting in osmotic stress on cells. If the ice crystals are formed inside the cells, they can lead to the physical disruption of the membranes, and destruction of cell integrity (Vincent 2007). Cyanobacteria from the Polar Regions have a variety of strategies to reduce the damage produced by both osmotic shock and physical disruption. Exopolysaccharides are thought to be a primary mechanism of protection by reducing the water loss and by restricting ice crystal formation to sites outside the cells (Wynn-Williams 2000; Vincent 2007). Some cyanobacteria also produce osmoregulatory intracellular proteins, which regulate the osmotic stress imposed by desiccation and antifreeze compounds which are thought to act as cryo-

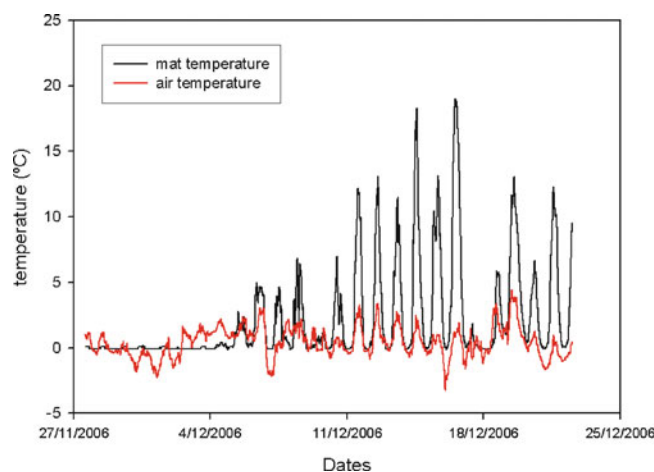


Fig. 14.1 Daily temperature variations in November–December 2006 in a microbial mat in Byers Peninsula (Livingston Island, South Shetland Islands) (Unpublished results, D. Velázquez, personal communication, 2007)

protectants (Raymond and Fritsen 2000). Some of the information in this chapter is based on the extensive review by Wynn-Williams (2000). Some of the habitats and communities described below are illustrated in the online article associated with this book chapter (Quesada and Vincent: Cyanobacterial diversity and dominance in the cryosphere).

14.2 Polar Desert Ecosystems

Cold deserts occur in both the North and South Polar Regions, and contain some of the most inhospitable environments for life. Besides suffering the rigours of extreme cold, the persistent lack of liquid water and repeated freeze-thaw cycles allow only the most resistant organisms to survive. Cyanobacteria often dominate these cryoecosystems, but occupy restricted habitats such as under or within rocks, where they are physically protected to some degree from the harsh ambient conditions.

14.2.1 Lithic Environments

Lithobiontic microorganisms have been described at many sites in the Arctic and Antarctica, and occupy three types of habitat: *epilithic* organisms inhabit rock surfaces; *endolith* organisms inhabit the rock interior (Fig. 14.2); *hypolith* communities inhabiting the soil-rock interface, particularly where pebbles are translucent (Omelson 2008; Nienow and Friedmann 1993; Cockell and Stokes 2004). Within these different habitats the lithobiontic organisms can occupy different micro-regions: *euendolith* micro-organisms can bore actively into the rock, and inhabiting the resultant hole (Cockell and Herrera 2007); *cryptoendolith* micro-organisms inhabit the spaces between the grains of porous rocks (Omelson

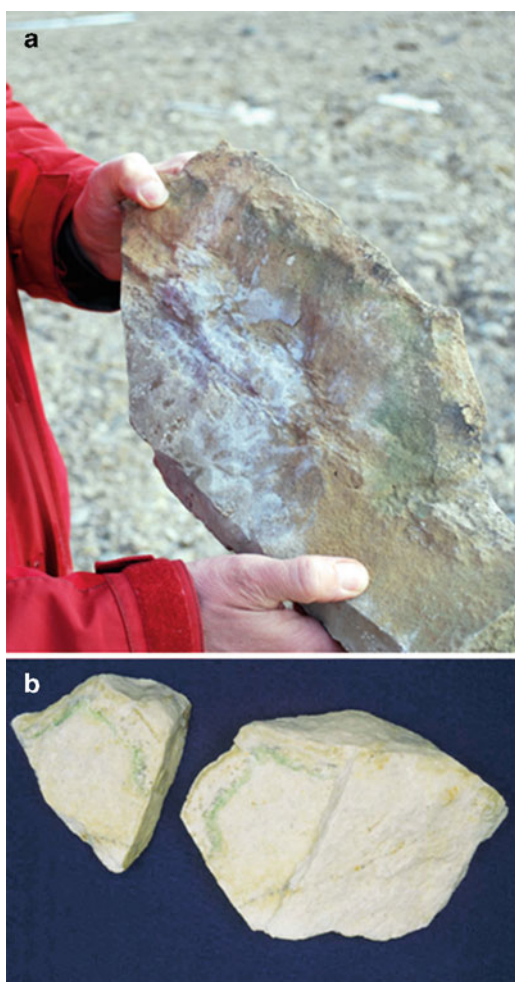


Fig. 14.2 Endolithic cyanobacteria in a sandstone rock from: (a) the High Arctic; and a quartz rock from: (b) the McMurdo Dry Valleys

et al. 2007); *chasmoendolithic* micro-organisms inhabit rock cracks and fissures (Büdel et al. 2008).

In the most severe polar desert environments such as the McMurdo Dry Valleys, few organisms can grow on exposed rock surfaces, but cyanobacteria and associated microbes are frequently found in endolithic or hypolithic environments. In less severe climates such as maritime Antarctica, epilithic communities are more frequent and diverse; conversely, in these habitats endoliths are rare, although also more diverse. Cyanobacteria are present in most polar cryptoendolithic polar habitats (Table 14.1), although they do not always dominate the total community biomass. The most abundant taxa belong to the orders Chroococcales: *Gloeocapsa* (several species), *Chroococcidiopsis*, *Aphanocapsa*, *Hormathonema*; and Oscillatoriales: *Lyngbya* and *Leptolyngbya*; and Nostocales: *Anabaena* (several species) and *Microchaete*. Some of these assemblages are conspicuously pigmented, such as the red *Gloeocapsa* community (Nienow and Friedmann 1993). The same genera are also found in chasmoendolithic communities, which are often dominated by *Chroococcidiopsis*, with associated populations

of *Cyanothece* (Büdel et al. 2008). *Gloeocapsa* and *Chroococcidiopsis* also dominate Arctic hypolithic communities (Cockell and Stokes 2004). In coastal and maritime Antarctica these cyanobacterial taxa are accompanied by other genera such as *Merismopedia*, *Plectonema* and *Nostoc* (Nienow and Friedmann 1993).

Phototrophic lithobionts are limited by the amount of irradiance received within their sequestered habitats, and this restricts the rock type and depth of microbial penetration into the rock (Friedmann and Ocampo 1976). Most lithobiontic cyanobacteria require translucent rocks for colonization and growth. Primarily sandstone rocks (quartz) are colonized, but photolithobiontic communities are also found in evaporites (as gypsum) (Hughes and Lawley 2003), limestone and granite (De los Ríos et al. 2007). The irradiance transmission characteristics of the rock materials as well as those of the organisms growing inside the lithic environment result in a well marked stratification of the communities. Modelling analyses (Nienow et al. 1988) suggested that irradiance was 70–90% absorbed per mm of rock, although some mineral crusts can increase this attenuation very markedly. In polar deserts the availability of liquid water is a critical limiting factor for all organisms. Liquid water becomes available in endolithic ecosystems immediately after snow melt on the rock surface, although snowfall is infrequent. However, dew and rime can form in cold deserts such as the Taylor Valley (Antarctica) in much higher frequency than snowfall (Büdel et al. 2008). Once this liquid water is available for the endolithic community it can be retained there because of the slow evaporation due to reduced gas exchange with the atmosphere (Kappen et al. 1981), and desiccation tolerance is further aided by extracellular polysaccharides produced within the community (Knowles and Castenholz 2008).

Nitrogen availability does not seem to be a limiting factor for the phototrophic growth in endolithic habitats. Experiments by Vestal and coworkers (Johnston and Vestal 1986, 1991), adding combined nitrogen compounds (nitrate and ammonium) demonstrated that N probably was not limiting for the phototrophic organisms. On the other hand P can be limiting for this kind of community as shown by Banerjee et al. (2000) for three endolithic communities in sandstones from the Dry Valleys (Antarctica), where both the lithogenic P and the input from precipitation should be minimal. These authors demonstrated that organic P recycling via phosphatase activities plays a key role in the dynamics of the community. The nutrients used by the slow-growing endolithic community can be of the allochthonous origin (dust, nitrate deposition), of lithogenic origin and then recycling should play a crucial role in the nutrient dynamics.

Temperature is another factor that may often limit the activity of phototrophic organisms in polar habitats. Direct solar irradiance is the primary source of heat for the lithic communities. Under some circumstances the rock surface can heat to as much as 20°C above ambient air temperatures

Table 14.1 Dominant cyanobacterial genera described in cryospheric habitats, with examples of locations

Genus	Habitat	Location	References
<i>Anabaena</i>	Permafrost, Soil, Endolithic, Cryoconite	DV, Arctic, MA, AI	Friedmann et al. (1988) and Vishnivetskaya (2009) Mataloni et al. (2000) Brinkmann et al. (2007) Mueller and Pollard (2004) and Thompson (1989)
<i>Aphanocapsa</i>	Soil, Endolithic,	DV, MA	Friedmann et al. (1988) Fermani et al. (2007)
<i>Aphanothece</i>	Hypolithic, Chasmoendolithic Cryoconite	VH, MA, Arctic, DV	Broadly (1981, 1986) Omelson et al. (2007) Mueller and Pollard (2004)
<i>Calothrix</i>	Soil, Hypolithic, Chasmoendolithic, Epilithic	MR, VH, ED, MA, VL	Broadly (1981, 1986, 1989) Cavacini (2001)
<i>Chamaesiphon</i>	Soil, Epilithic, Cryoconite, Snow Lake Ice	MA, AI, DV, HM	Broadly (1979) Priscu et al. (1998) Liu et al. (2006) Christner et al. (2003)
<i>Chroococidiopsis</i>	Soil, Hypolithic Chasmoendolithic, Endolithic, Epilithic	MR, VH, DM, DV, ED, Arctic, MA	Broadly (1981, 1986, 1989) Friedmann et al. (1988) Ryan et al. (1989) Cockell and Stokes (2004) Brinkmann et al. (2007) and Thompson (1989)
<i>Cyanothece</i>	Soil, Chasmoendolithic, Endolithic, Epilithic,	ED, MA, AI, DV	Broadly (1989) Büdel et al. (2008) De los Ríos et al. (2004)
<i>Eucapsis</i>	Cryptoendolithic	DV	Friedmann et al. (1988)
<i>Gloeocapsa</i>	Soil, Hypolithic, Cryptoendolithic, Chasmoendolithic, Cryoconite	VH, DV, ED, Arctic, MA	Broadly (1981, 1986, 1989) Friedmann et al. (1988) Cockell and Stokes (2004) Mueller and Pollard (2004)
<i>Hormathonema</i>	Soil, Cryptoendolithic,	DV	Friedmann et al. (1988)
<i>Homoeothrix</i>	Chasmoendolithic, Epilithic	MR, ED, MA	Broadly (1981, 1989)
<i>Leptolyngbya</i>	Permafrost, Soil, Cryptoendolithic, Cryoconite, Glacial Ice, Lake Ice	Arctic, DV, MA, AI, VL	Vishnivetskaya (2009) and Friedmann et al. (1988) Cavacini (2001) Mataloni et al. (2000) Brinkmann et al. (2007) Priscu et al. (1998) Mueller and Pollard (2004) Stibal et al. (2006)
<i>Lyngbya</i>	Soil, Hypolithic Chasmoendolithic, Endolithic, Cryoconite	MR, DV, MA, VL, Arctic	Broadly (1981) Friedmann et al. (1988) Mueller and Pollard (2004)
<i>Microchaete</i>	Soil, Endolithic	DV	Friedmann et al. (1988)
<i>Microcoleus</i>	Soil, Cryoconite, Glacial Ice	MA, AI, Arctic, DV	Komárek et al. (2008) and Brinkmann et al. (2007) Mueller and Pollard (2004) Stibal et al. (2006)
<i>Myxosarcina</i>	Epilithic	MA	Broadly (1981)
<i>Nodularia</i>	Soil, Hypolithic, Chasmoendolithic,	VH, MA, VL	Broadly (1981, 1986)

(continued)

Table 14.1 (continued)

Genus	Habitat	Location	References
<i>Nostoc</i>	Permafrost, Soil, Hypolithic, Chasmoendolithic, Epilithic, Cryoconite	MR, VH, DM, DV, ED, MA, AI, VL, Arctic	Broady (1981, 1986, 1989) Vishnivetskaya (2009) Büdel et al. (2008) Mueller and Pollard (2004) and Thompson (1989)
<i>Oscillatoria</i>	Soil, Endolithic, Cryoconite	VH, MA, Arctic, DV	Cameron (1972) Mataloni et al. (2000) Mueller and Pollard (2004)
<i>Phormidium</i>	Permafrost, Soil, Hypolithic, Chasmoendolithic, Endolithic, Epilithic, Cryoconite, Glacial Ice, Lake Ice,	DM, DV, ED, Arctic, MA, AI, VL	Ryan et al. (1989) Seaburg et al. (1979) Vishnivetskaya (2009) Priscu et al. (1998) Mueller and Pollard (2004) Stibal et al. (2006) and Thompson (1989)
<i>Plectonema</i>	Hypolithic, Chasmoendolithic	MR, VH, MA	Broady (1981, 1986) Nienow and Friedmann (1993)
<i>Pleurocapsa</i>	Hypolithic, Chasmoendolithic, Epilithic	VH, MA	Broady (1981, 1986)
<i>Pseudanabaena</i>	Soil	MA	Mataloni et al. (2000)
<i>Schizothrix</i>	Soil, Endolithic	DV	Cameron (1972)
<i>Scytonema</i>	Soil, Hypolithic, Epilithic,	DM, MA, VL	Ryan et al. (1989) Broady (1986) Cavacini (2001) and Thompson (1989)
<i>Stigonema</i>	Soil, Epilithic, Chasmoendolithic,	ED, MA	Broady (1989)
<i>Synechococcus</i>	Soil, Hypolithic, Cryptoendolithic, Epilithic, Cryoconite, Snow	DM, MA, AI, HM, Arctic, DV	Ryan et al. (1989) Broady (1979) Brinkmann et al. (2007) Liu et al. (2006) Omelon et al. (2007) Mueller and Pollard (2004) and Thompson (1989)
<i>Tolypothrix</i>	Soil, Hypolithic, Chasmoendolithic	VH, MA, AI	Broady (1979, 1981, 1986) Mataloni et al. (2000)

Locations: DV Dry Valleys, VH Vestfold Hills, MR Mawson Rocks, ED Edward VII Peninsula, DM Dronning Maud Land, MA Maritime Antarctica, AI Alexander Island, VL Victoria Land

(Omelon et al. 2006), thereby directly speeding up all biological activities but also thawing ice and thus increasing the liquid water availability. A factor distinguishing aquatic versus terrestrial ecosystems in the Polar Regions is the stability of the temperature regime. While in polar aquatic ecosystems temperature is usually low and relatively stable, in terrestrial habitats temperature fluctuates rapidly depending upon exposure to the sun; when these temperatures are close to freezing point, freezing and thawing processes can take place several times within few hours. For example, McKay and Friedmann (1985) measured in the McMurdo Dry Valleys a temperature fluctuation at the rock surface of 8°C over 42 min, crossing the freezing

point 14 times. However, these rapid fluctuations are not expected or observed in the endolithic habitat due to the poor heat transmission of the rocks. Moreover, the abundant exopolysaccharides present in some of the cryptoendolithic communities increase the extent freezing tolerance (Knowles and Castenholz 2008).

The endolithic microbial communities show very low diversity but at least three trophic levels are typically included: primary producers (cyanobacteria, algae and lichens), consumers (fungi) and decomposers (heterotrophic bacteria). Walker and Pace (2007) have demonstrated, comparing the genetic identification of four endolithic communities from different parts of the world, that the communities

are quite similar, and present extremely low diversity, indicating also a high degree of microbial cosmopolitanism. However, Horath and Bachofen (2009) suggest that there is insufficient data to support the attributed simplicity and ubiquity of cyanobacteria in this kind of habitat. Some of the cyanobacteria found in endolithic habitat seem to be also present in other habitats as soils or semi-aerophytic environments (De los Ríos et al. 2007).

Endolithic communities represent the largest biomass (in organic C) compartment of Antarctic polar desert ecosystems, with organic carbon stocks of the order 10^2 g m^{-2} (Büdel et al. 2008; Nienow and Friedmann 1993), and with chlorophyll *a* contents in the range of tens of mg m^{-2} , which is only one order of magnitude lower than the values typically found in dense cyanobacterial mats in polar ponds (Chap. 13). It has been suggested that extremely low turnover rates take place within these microecosystems with an estimated age for lipids around 17,000 years (Vestal 1988; Johnston and Vestal 1991). Radiocarbon analyses in some endolithic communities indicate ages of the order of magnitude of 10^3 years (Bonani et al. 1988). However, the results presented by Büdel et al. (2008) indicate that these values depend very much on the water availability; the presence of the appropriate conditions for the dew formation may help to speed up all biological processes, reducing turnover rates to the order of hundreds of years. The cryptoendolithic community described by Büdel et al. in the granites of the Taylor Valley consisted of *Chroococcidiopsis*, *Cyanothece* and *Nostoc* and had a mean chlorophyll *a* content of 24 mg m^{-2} and an estimated mean biomass of 168 mg m^{-2} .

Endolithic environments may provide the most favourable terrestrial habitats for some cyanobacteria in extreme polar deserts, as indicated by the high cyanobacterial pigmentation and biomass sometimes observed below rock surfaces. Inside the rock, cyanobacteria may avoid many of the problems associated with the surface environment, with greatly improved liquid water availability, access to higher and more constant temperatures, protection against harmful UV radiation (Wynn-Williams 2000), and reduced habitat loss rates caused by wind erosion and rock surface detachment (Cockell and Herrera 2007).

14.2.2 Striped Ground and Polygonal Patterns

Hypolithic organisms are widely distributed in the Polar Regions, including areas of periglacial rock sorting (Thomas 2005). Hypolithic cyanobacteria are present under translucent rocks such as quartz (Cowan and Tow 2004), but also occur under opaque rocks such as dolomites (Cockell and Stokes 2006). They may represent an important source of biological activity and organic carbon for depauperate polar desert ecosystems. Cockell and Stokes (2004) have estimated the primary production of hypolithic cyanobacteria from

High Arctic locations to be close to $1 \text{ g C m}^{-2} \text{ year}^{-1}$, which is similar to the values for other phototrophs in these ecosystems. In hypolithic habitats, the sheltered environment beneath the rock provides a refugium, with much better microclimatic conditions than the upper rock surface. Liquid water availability seems to be one of the factors enhanced in the under-rock environment and one of the factors explaining the distribution of cyanobacteria in this habitat (Pointing et al. 2007). Rocks also protect organisms living underneath from high UVR (Cockell and Stokes 2006). Temperature changes are also very much attenuated, as in the endolithic habitat, providing a kind of greenhouse condition that is favourable for shade-adapted cyanobacteria (Wynn-Williams 2000). Intriguingly, hypolithic communities are especially common in patterned ground, where rock movements caused by the freeze-thaw cycles and the presence of ice in the soil provide a favourable combination of environmental conditions for cyanobacterial colonisation and growth (Cockell and Stokes 2004). On Devon and Cornwallis Islands (High Canadian Arctic) and on Alexander Island (Antarctica), 100% of the stones placed at the edges of the polygons in patterned grounds showed an evident hypolithic cyanobacterial community. However, the rocks inside the polygons showed much a lower colonization percentage (68% and 5% colonization in the Arctic and in the Antarctic, respectively). Conspicuous cyanobacterial biomass has been also described at the edge of large rocks at the periphery of frost sorted polygons (Hodgson et al. 2010).

Cyanobacteria growing in the hypolithic habitat apparently rest between lithic environments and edaphic (soil) habitats, however the genetic diversity of these organisms in the Dry Valleys indicated that they were more similar to aquatic and semi-aquatic cyanobacterial mats than to the soil microbiota (Wood et al. 2008). Morphologically the diversity of cyanobacteria in this habitat is quite poor, with *Chroococcidiopsis* the dominant genus, and *Gloeocapsa*-like cyanobacteria also frequent. However this morphological simplicity could be misleading. Pointing et al. (2007) working on non-polar hypoliths and comparing morphological observations and genetic tools suggested that some non-Chroococcales could adopt Chroococcales shapes in hypolithic ecosystems.

14.2.3 Soils

Soils may be the least hospitable habitat for cyanobacteria in the Polar Regions (Vincent 1988). Organisms inhabiting soil surfaces are exposed to bright solar radiation (including UV-A and UV-B), low humidity due to the wind effect, high amplitude fluctuations in temperature even within the same day, high salinity and osmotic stress, variable snow cover, and physical erosion and scouring associated with the intense winds that are frequent at high latitudes. In spite of all these limitations, phototrophic communities are often found in polar

soils, and cyanobacteria are usually the dominants (Vincent 1988; Fernández-Carazo et al. 2011; Michaud et al. 2012). Edaphic cyanobacteria have been found at several sites around Antarctica and the Arctic (Vincent 1988), including polar deserts and more humid environments. However, it has been suggested that the presence of cyanobacteria in the most arid soils, such as those from the McMurdo Dry Valleys, is due to wind dispersion (Michaud et al. 2012) and that the soil populations are not actively growing (Aislabie et al. 2006). Consistent with this hypothesis, Wood et al. (2008) and Michaud et al. (2012) found that the cyanobacterial diversity in Dry Valley soils was very similar to that found in nearby microbial mats. Cyanobacteria from the three main orders (Chroococcales, Oscillatoriales and Nostocales) are frequently reported in Antarctic soils (Cavacini 2001; Wood et al. 2008). Humidity has been postulated as the main factor limiting the development of these edaphic cyanobacteria, but the chemical composition of soils may also play an important role, controlling the rate of supply of limiting elements and of toxic elements (Wood et al. 2008). Proximity to the inoculum source seems to be also a factor affecting the development of edaphic communities (Wood et al. 2008). Floristically, in most of the investigated soils the Oscillatoriales *Leptolyngbya* and *Phormidium* are the most common genera (Cavacini 2001; Mataloni et al. 2000). The occurrence of different cyanobacterial taxa seems to be related with the extent and duration of liquid water conditions (Vincent 1988). In mineral soils periodically flushed with water, Nostocales tend to dominate, but in moist to wet soils Oscillatoriales are the most frequent. Chroococcales are associated with other taxa in moist but unflushed sites. This distribution is related to the desiccation tolerance of each taxon, which is related to EPS concentration and characteristics (Wynn-Williams 2000). Yergeau et al. (2007) demonstrated in an Antarctic latitudinal gradient, extending from the subantarctic Falkland Islands (51°S) to the Ellsworth Mountain Range (79°S), that both diversity and species richness in fell-field microbial communities decreased as a function of increasing latitude. However, the proportion of cyanobacterial operational taxonomic units (OTU) was higher at higher latitudes (Yergeau et al. 2007). In the High Arctic (Svalbard, 78°N), 18 different cyanobacterial species were enumerated from barren soils, belonging to seven genera including *Leptolyngbya* and *Phormidium* (Kastovska et al. 2005).

Cyanobacteria are also abundant in high mountain environments. They become the dominant group in periglacial soils at 5,400 m altitude in Peru (Schmidt et al. 2009). The authors demonstrated that environmental conditions are even harsher than those in Polar Regions, with the temperature amplitude within 1 day reaching 36°C and with the fastest instantaneous cooling rate ever recorded of 1.83°C h⁻¹. Schmidt et al. (2009) identified a large number of cyanobacterial clones and a high diversity of genotypes that were only related to taxa from other high mountain sites and not to the Polar Regions.

Ancient communities of edaphic cyanobacteria have been preserved in permafrost. These cyanobacteria are not only fossil remnants from past ages, but in some cases they have been shown to be viable despite apparently being trapped and frozen in the permafrost for millions of years (Erokhina et al. 2000; Vishnivetskaya et al. 2002, 2003; Vishnivetskaya 2009). Several cyanobacterial strains belonging to the Oscillatoriales and Nostocales have been isolated from Arctic permafrost (Vishnivetskaya et al. 2003; Vishnivetskaya 2009) and show a close phylogenetic similarity to cyanobacteria found nowadays in microbial mats or endolithic environments, notably the genera *Leptolyngbya*, *Microcoleus*, *Phormidium*, *Nostoc* and *Anabaena*.

14.3 Ice-Based Ecosystems

Ice-based ecosystems have a number of characteristics that distinguish them from polar terrestrial ecosystems. One of the main differences is liquid water availability, which may be much greater in ice-based habitats as a result of radiative heating and local melting. Additionally, the environment is thermally more stable than in highly variable soil and rock regimes; temperatures are persistently cold, and changes are buffered by the isolating and high albedo characteristics of the ice and snow. Cyanobacteria occur in many types of ice-bound habitat, ranging from those that are annual or instable such as lake-ice (in lakes that melt out completely in summer) or snow, to those that are more stable in time, such as ice-shelves, glacier ice and cryoconites. The environmental conditions and the ecology of ice based ecosystems are described in detail in Laybourn-Parry et al. (2012).

14.3.1 Snow and Lake Ice

Cyanobacteria appear to be relatively rare in melting snow banks (Vincent 2000) or other non-stable cryoecosystems, probably because their slow growth is unable to keep pace with continuous losses by the percolating meltwater. However, they have been described in snow from glaciers in several areas of the world including Alaska, where two Oscillatoriales morphospecies were the only representatives (Takeuchi 2001), a Chilean Patagonia glacier, and in the Altai Mountains in Russia, where another Oscillatoriales morphospecies was found (Takeuchi and Koshima 2004; Takeuchi et al. 2006). On the Rombuk Glacier on Mount Everest, two groups of cyanobacteria were found in the snow at 6,500 m altitude, with genetic similarities to the Chroococcales genera *Synechococcus* and *Chamaesiphon* (Liu et al. 2006). In the Polar Regions, records for snow cyanobacteria are scarce and some authors such as Marshall and Chalmers (1997) suggest that are not actively growing in such environments, but merely transported and deposited on

snowpacks by the wind. The only report about Antarctic active cyanobacteria in snow is from an extensive snow cover on the Byers Peninsula (Livingston Island, maritime Antarctica) that was colonized by green algae, but also with *Leptolyngbya* as a substantial fraction of the biomass and several morphospecies of *Phormidium* (Velázquez et al. 2011). In the High Arctic, several cyanobacterial genotypes were found in the snow, and these were very similar to those found in the surrounding microbial mats (Harding et al. 2011).

Other transient cryo-ecosystems such as lake ice have not been investigated in detail, although in Antarctic lakes fragments of cyanobacterial mats wind blown are trapped during the ice formation and may remain active when they warm up due to solar radiation, even within the ice. In the perennial ice of the McMurdo Dry Valley lakes, cyanobacteria can remain for longer periods and be physiologically active (Prisco et al. 1998, 2005). Michaud et al (2012) identified a high cyanobacterial diversity from aeolian deposits in the McMurdo Dry Valleys as well as in the lake ice and suggested that these cyanobacteria can establish in the lake community when the liquid water is reached in summer partial melting.

Another example of unstable cryo-ecosystems is the annual sea-ice. In polar marine ecosystems cyanobacteria are not particularly abundant (Chap. 13), and there is little information regarding the occurrence of cyanobacteria in annual sea-ice. However, cyanobacteria have been recorded in multi-year Arctic sea-ice (Bowman et al. 2012).

14.3.2 Glacial Ice and Cryoconite Ecosystems

A cryoecosystem that is attracting increasing attention by microbial ecologists is the ice surface of glaciers where rock dust ('cryoconite') accumulates and initiates local melting. This material can build up to substantial levels, reaching values over 300 g m⁻² for example on the Urumqi Glacier in the Tien Shan Mountains, China (Takeuchi and Li 2008). Many authors have found living cyanobacteria within these deposits (e.g. Takeuchi and Li 2008). This habitat provides favourable conditions for phototrophs, since the radiation absorption by the dust particles increases the surface temperature, causing the ice underneath to melt and release liquid water, which additionally may leach nutrients from the particles. The phototrophs are more abundant in the surface layers than in deeper layers indicating that their presence is not only a result of the dust deposition but also because of the active growth of these organisms (Xiang et al. 2009). This phototrophic growth and autochthonous carbon production also contributes towards the development of heterotrophic communities within the ice. Cyanobacteria have been described from polar glaciers (e.g. Mueller et al. 2001; Stibal et al. 2006) as well as from mountain glaciers around the world

(Xiang et al. 2009). In an Arctic glacier the cyanobacterial communities found in supraglacial sediments (glacial kame) were dominated by *Leptolyngbya*, *Nostoc* and *Phormidium* (Stibal et al. 2006), while in high mountain glaciers the cyanobacterial communities were exclusively dominated by Oscillatoriales (Xiang et al. 2009).

More substantial melting of the glacier ice can give rise to cryoconite melt-holes consisting of cylindrical cavities, up to 50 cm deep, which retain dark sediment at the bottom and are filled with meltwater (Mueller et al. 2001). Cryoconite holes are abundant in the lower part of polar glaciers as well as on alpine glaciers of the temperate zone. In the cryoconite holes explored to date in Antarctica, cyanobacteria are the dominant biota, and their photosynthesis provides the basis for associated heterotrophic organisms, including a variety of micro-invertebrates as nematodes, rotifers and tardigrades (Mueller et al. 2001). Nutrient concentrations in the meltwater of the cryoconites are consistently low and phosphorus may be the limiting element (Mueller et al. 2001). The cyanobacterial community inhabiting cryoconites is quite similar all around the world, it is dominated by Oscillatoriales, notably *Leptolyngbya* spp. *Crinalium* spp., and *Phormidium* spp. Chroococcales are also abundant and typically represented by *Aphanothece*, *Aphanocapsa*, *Gloeocapsa* and *Synechococcus*. However, in most cryoconite holes in the White Glacier in the Canadian High Arctic, desmids rather than cyanobacteria dominated the community, possibly as a result of the lower pH of the meltwaters here (Mueller et al. 2001; Mueller and Pollard 2004). The cyanobacterial species distribution on cryoconites has been found to be quite similar to the species distribution in soils, ponds and mats in the proximities of the glaciers, indicating the wind distribution of these cryo-colonizers (Christner et al. 2003). The biological activity of primary producers in cryoconites has been described as a potentially significant important source of organic carbon to the polar environment (Säwström et al. 2002). However, in more dynamic glaciers, with shorter persistence of the cryoconites, autochthonous carbon input has been considered to be minor compared with the organic matter transported and accumulated in the cryoconite sediments (Stibal et al. 2008).

14.3.3 Ice Shelves

Ice shelves are sheets of ice from 10 to more than 100 m thick that are connected to land, but floating on the sea. They are found in coastal areas of both Polar Regions, but are vastly more extensive in Antarctica. The McMurdo Ice Shelf is the best known in Antarctica. It covers 1,500 km² and is one of the most spectacular ice-based ecosystems on Earth (Hawes et al. 2008). Sediment accumulates on the surface of this ice shelf by coming up from the sea bottom through the

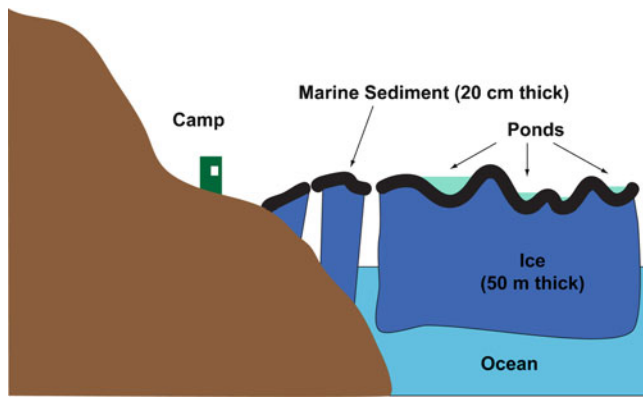


Fig. 14.3 Scheme of the McMurdo Ice-Shelf by Bratina Island. For clarity, drawings not to scale. Based on a field sketch by C. Howard-Williams

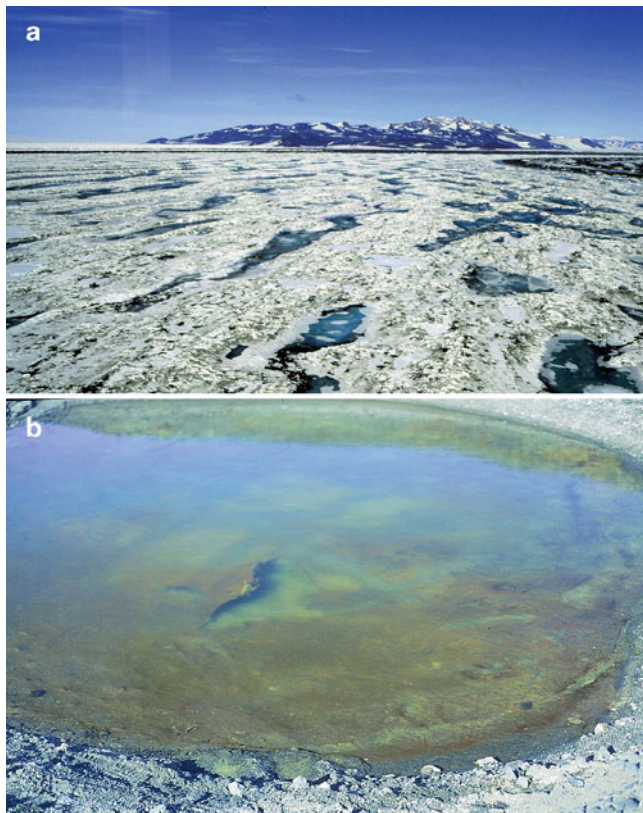


Fig. 14.4 McMurdo ice-shelf. (a) aerial photo showing the ‘dirty ice’, where numerous ice-based aquatic ecosystems are found; (b) detail of one of the ponds, showing cyanobacterial mats covering the bottom

basal accretion of ice, and the surface melting and ablation. This sediment forms a 10–20 cm thick layer (Fig. 14.3) that absorbs radiation and increases the temperature enough to melt the ice, producing ponds and wind-oriented lakes that can persist for decades or longer. In summer, when these lakes are ice-free in the surface, they function as traps for wind dispersed particles, including both sediments and

inocula of new colonizers (Michaud et al. 2012). In the most stable ponds, cyanobacteria dominate the ecosystems forming extensive microbial mats, from mm to cm in thickness (Fig. 14.4). The microbial mats are formed by a matrix of *Leptolyngbya* (De los Ríos et al. 2004) accompanied by *Phormidium* and *Oscillatoria*, *Nostoc* and *Nodularia*, and several Chroococcales such as *Gloeocapsa*, *Synechococcus* and *Chroococcus*. Some green algae can also be found in the mats, as well as an associated diatom flora, the latter dominated by the genera *Navicula*, *Nitzschia*, *Pinnularia* and *Achnanthes* (Howard-Williams et al. 1990).

The microbial mats found in ice-shelf ponds and lakes are functionally similar to those found in other polar aquatic ecosystems (see Vincent and Quesada, this volume). Cyanobacterial N_2 -fixation has been found responsible for an important proportion of the N input in the McMurdo Ice Shelf cryo-ecosystems, which seem to be N-limited (Fernández-Valiente et al. 2001).

Environmental conditions in the ice shelf ponds and lakes vary according to the type of sediment accumulated at a particular location. Thus, chemical diversity is as high as or even higher than in terrestrial based ponds and lakes. On the McMurdo Ice shelf, for instance, very low salinity ponds are found in very short proximity (hundreds of meters) to sulphate rich brines several times the salinity of sea water, and support cyanobacterial communities of different taxa (Vincent 2000; Vincent et al. 2004; Hawes et al. 2008).

In the High Arctic, ice shelves are restricted to the remnants of a continuous glacial fringe that at the beginning of the twentieth century occurred along 500 km of the northern coastline of Ellesmere Island, Canada. These remaining ice shelves are extremely vulnerable to climate change (Mueller et al. 2003). Over the period 2000–2008, they experienced considerable fracturing and attrition, including complete break-out and loss of the Ayles Ice Shelf and the Markham Ice Shelf (Vincent et al. 2009).

The High Arctic ice shelves have an undulating surface topography with localized deposits of sediments derived from three sources: wind-blown material; glacial moraine pushed onto the ice shelves by glaciers and other dynamic ice processes; and marine sediments that freeze into the bottom of the ice sheet and move to the surface by basal accretion of ice and surface ablation, as described above for the McMurdo Ice Shelf. Cyanobacterial mat consortia are found in association with the sediments, at the bottom of meltwater ponds or sometimes exposed to the air. Three types of mats can be distinguished in terms of visual appearance and community structure, and may represent a successional sequence (Mueller et al. 2006): sediments with little or no visible accumulation of microbial biomass, ‘matlet’ communities composed of loose flocs of olive-brown aggregates, and communities of accumulated matlets up to 10 mm thick, overlain by a thin (100 μ m), more cohesive orange layer at the surface.

The dominant phototrophs in all three High Arctic communities are Oscillatoriales, particularly thin trichome representatives of *Leptolyngbya*, *Phormidium* and *Oscillatoria* (Mueller et al. 2006), as in Antarctica. However, nitrogen-fixing cyanobacteria are sparse relative to the McMurdo Ice Shelf communities, probably reflecting the low phosphorus concentrations and high N:P ratios in the High Arctic waters. The mats contain many chlorophytes, in particular *Palmellopsis*, *Chlorosarcinopsis*, *Pleurastrum*, *Chlamydomonas*, *Chlamydocapsa*, *Chlorella*, *Bracteacoccus*, *Chlorococcum*, and *Klebsormidium*. Like the McMurdo mats, these communities also contain abundant small benthic and aerophilic diatoms. The most common diatom species is *Chamaepinnularia* (*Navicula*) *begeri*, with subdominance by species of *Nitzschia*, *Navicula*, *Luticola*, *Achnanthes* and *Pinnularia* (Mueller et al. 2006).

Prior to its break-out in 2008, the Markham Ice Shelf contained the richest microbial mats, with extensive orange communities within and adjacent to meltwater ponds (Vincent et al. 2004). For this ice shelf alone, Mueller et al. (2006) estimated there to be 16,500 t microbial biomass in summer, with an additional 16,000 t on the much larger (and still extant in 2010) Ward Hunt Ice Shelf, and only sparse communities on the other four ice shelves. Analyses of these mats by high performance liquid chromatography (HPLC) showed that they are rich in UV photoprotecting pigments including scytonemin and many carotenoids (Chap. 13). Metagenomic analysis of these mats revealed that they contain a rich microbial flora in addition to cyanobacteria, with their ribosomal and protein-coding gene sequences dominated by Proteobacteria (Varin et al. 2010).

14.4 Cyanobacterial Diversity in the Cryosphere

Cyanobacterial diversity in the Polar Regions is a subject of ongoing debate. Some authors support the idea that several strains are endemic to Antarctica (Taton et al. 2006; Komárek et al. 2008). However, recently Jungblut et al. (2010) and Kleinteich et al. (2012) found that in cyanobacterial mats at least part of the genetic diversity was very similar to the genetic diversity found in Arctic and high mountain cyanobacterial mats, showing high 16S rRNA gene similarity (>99%) with some strains previously considered endemic to Antarctica. Morphological identification of polar cyanobacteria is complicated even at the genus level, and some genera have probably been misidentified. Strunecký et al. (2010) found that the very conspicuous genus *Phormidium* in polar regions can be misidentified and belong to several genera. They also found that strains isolated from both polar regions overlap geographically with ones isolated from temperate regions. This makes it almost impossible to

compare the lists from different authors. Moreover, the genetic tools, although powerful in identifying genetic variation, are based on databases that are still very limited. Jungblut et al. (2010) concluded that, at least at the 16S rRNA gene level, cyanobacteria from polar and alpine regions are more related to each other than to temperate groups. However, they also noted the need for additional analyses using the ITS region (Comte et al. 2007), multilocus sequence analyses (Whitaker et al. 2003) and broader genomic and metagenomic analyses to define the ecotypic diversity of high latitude genotypes.

In Table 14.1 we present a non-exhaustive list of genera described in the cryosphere and the different habitats that they have been described from. It is especially remarkable that *Phormidium* has been found in the full range of habitats considered in this study, although it is also genus that can be easily misidentified. *Leptolyngbya* and *Nostoc* have been described from six different habitats, and as their morphological characteristics are easily distinguishable from other genera, most probably they have not been misidentified. These three genera can be considered cosmopolitan, at least within the cryosphere, since they appear in quite different habitats in terms of liquid water availability. At the other end of the range, *Chroococciopsis* seems to be especially well adapted to the habitats in which liquid water availability is limited, probably due to its extreme ability for desiccation resistance. It has even been suggested that it would be an ideal pioneer microorganism for terra-forming Mars (Friedmann and Ocampo-Friedmann 1995). On the other hand, *Microcoleus* seems to require the more frequent presence of liquid water (Table 14.1). Regarding the latitude at which they have been described, most genera have been found at maritime Antarctic sites, but also at coastal continental sites of Antarctica, with the associated contrasts in environmental conditions. The most common cyanobacterial genera appear to be present at all latitudes in the cryosphere where liquid water is available for some period each year.

14.5 Conclusions

Cyanobacteria are often the dominant organisms in cryoecosystems. This observation might seem paradoxical considering that most Arctic and Antarctic cyanobacteria studied to date are psychrotolerant rather than psychrophilic. Cryoecosystems are among the most extreme ecosystems on Earth, with liquid water limiting for most of the year, thermal conditions that can be highly unstable, and with rapid freeze-thaw cycles and associated fluctuations in water and salt stress. It is likely that these extremes preclude most other phototrophs, and allow cyanobacteria to achieve pre-eminence in these habitats. Cyanobacteria do not show high rates of metabolism and growth under these polar conditions, but

because of their broad tolerances rather than fine adaptation to cold, an ability to survive prolonged dormancy, and their resistance to natural loss processes, they are well suited to the cryosphere. Cyanobacteria in cryoecosystems appear to follow the 'lichen strategy' of remaining dormant and withstanding even the worst of environmental conditions, resuming primary production once conditions become suitable, and storing the new carbon, energy and perhaps even water for ongoing cell division. Psychrophilic adaptation would not be a suitable strategy in non-aquatic cryoecosystems, since high temperatures (>15°C) may be reached even in the coldest ice-free deserts, and the resultant thermal stress could be fatal to cold-adapted species. Furthermore, under these high temperatures, psychrotolerance rather than psychrotrophy would allow high biological activities to be achieved, and even a short period of enhanced performance each season may be enough to achieve a net positive energy and carbon balance. Cryptoendolithic cyanobacteria provide an extreme example of this strategy. These organisms cannot be considered ecologically successful using the traditional criteria of growth rates or metabolic performance, with impressively slow doubling times for the community biomass of hundreds or even thousands of years. Yet cyanobacteria are the most important primary producers in these habitats, until quite recently were considered to be devoid of life, and they have thereby achieved compelling success.

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