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Preface

This book describes my journey from Csp to CowN. After getting trained in protein structure–function studies, the big challenge in front of me was the selection of the right candidate. While going through a published review article on Antarctic microbiota, Csps attracted me a lot. Luckily, DST financed the first project for the development of a cold-adapted/tolerant mutant of PGPR. Later on in this journey, M. Sc. and Ph.D. students accompanied me to different distances and selected destinations. Surprisingly, the last financial support was again from DST/SERB as a young scientist project to one of our associate editors, wherein CowN was. Moreover, these low-temperature warriors were isolated from high altitude agroecosystems, which gave immense satisfaction to my concept thought.

This book consists of 19 chapters based on four major themes: diversity of cold-adapted microorganisms; their adaptation and survival strategies; use of omics approaches in the respective field; and their application in agriculture and biotechnology. We trust the readers will find the precise and latest update on microbial cold adaptation in this book besides our small contribution in the field.

We gratefully acknowledge the help, support, and suggestions provided by the colleagues and well-wishers. Moreover, the contributing authors are greatly acknowledged for their cooperation and patience. Any suggestion for the improvement of this book will be highly appreciated and these will be incorporated in the subsequent editions.

Mathura, India	Reeta Goel
Raipur, India	Ravindra Soni
Sirmaur, India	Deep Chandra Suyal
Mysore, India	Mahejibin Khan

Contents

About the Editors

Reeta Goel is a Professor and former Head of the Department of Microbiology, G. B. Pant University of Agriculture & Technology, Uttarakhand, India. She has also served as visiting scientist at various institutes in the USA and has more than 35 years of teaching and research experience in the area of plant–microbe interactions, microbial ecology, biodegradation, and metagenomics, especially with reference to higher altitudes. Moreover, she has worked extensively in the field of genomics and proteomics of cold-adapted microorganisms. She has published over 100 research articles, book chapters, and edited books. She has six patents in her credit, including one US Patent, and received numerous awards for her contributions to science and technology. Presently, she is serving as a distinguished Professor at GLA University, Mathura, UP, India after her retirement.

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Cyanobacteria in Cold Ecosystem: Tolerance and Adaptation

1

Khushboo Dasauni, Divya, and Tapan K. Nailwal

Abstract

Cyanobacteria are dominant primary producers and near ubiquitous, inhabiting diverse range of ecosystems. They are found in freshwater, marine system to extreme environment such as the Antarctic, Arctic, and alpine regions. It seems paradoxical that most polar cyanobacteria are psychrotolerant rather than psychrophilic. Fluctuation in temperature, availability of nutrients and liquid water, and irradiance can alter the microbial community dynamics. Cyanobacteria use screening compounds, antifreeze proteins, antioxidants, membrane proteins, ion regulation, etc. to thrive in extremely challenging conditions. This chapter reviews various mechanisms of acclimatization of cyanobacteria at low temperatures of the Arctic and Antarctic.

Keywords

Acclimatization · Cyanobacteria · Psychrotolerant · Antifreeze protein · Arctic region · Antarctic region

1.1 Introduction

Cyanobacteria (blue-green algae) are the only known photosynthetic prokaryotes capable of fixing both carbon dioxide and nitrogen. They are considered as among the first microorganisms to inhabit the earth, therefore playing a key role in nutrient cycling and energy flow on earth. Unicellular, surface-attached, multicellular, filamentous colony and mat-forming are the various morph types of cyanobacteria.

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Polar or low-temperature ecosystems are the largest untouched or unlocked biological resources of our planet. In these regions, temperature remains below 0 °C during most part of the year. Cyanobacteria are frequently found in cryospheric ecosystems such as polar deserts, permafrost, cryoconites, snow lake ice, glacial ice, etc. Swedish-Finnish explorer Adolf Erik and his team are one of the first to discover cyanobacteria thriving in cryoconite of cryosphere during their expedition to green ice cap in 1870. Commonly found polar cyanobacteria belong to the orders *Chroococcales* (*Gloeocapsa* (several species), *Chroococcidiopsis*, *Aphanocapsa*, *Hormathonema*), *Oscillatoriales* (*Lyngbya* and *Leptolyngbya*), and *Nostocales* (*Anabaena* (several species) and *Microchaete*). Some of these assemblages are conspicuously pigmented, such as the red *Gloeocapsa* community. Cryospheric cyanobacteria are required to deal with the challenges of fluctuating low temperature, high irradiance (PAR and UVR), desiccation, availability of nutrient and liquid water, and, now due to global warming, elevated temperature. Though cyanobacteria are dominant organisms in cryo-ecosystems, it seems paradoxical that most polar cyanobacteria are psychrotolerant rather than psychrophilic. It has been reported that cyanobacteria are able to survive in extreme conditions of polar region and are hypothetically also capable of acclimatization under hard environmental conditions and could contribute to the field of astrobiology research. Here we review current literature on ecology and the functional role played by cyanobacteria in various Arctic and Antarctic environments. We will focus on the ecological importance of cyanobacterial communities in polar regions and assess what is known regarding their general mechanism of adaptation (Nienow and Friedmann 1993).

1.2 Significance of Cold Ecosystem

Arctic and Antarctic polar regions together have attention gathering impact on global biogeochemical cycle and share a large proportion of the earth's surface area. Various different habitats in polar ecosystem include soil, permafrost, cryptic niche (biological soil crust, hypoliths and endoliths), ice, snow, and a number of aquatic habitats. Low water temperature in cryo-ecosystems shows increased carbon dioxide solubility accounting for 30% of global uptake that helps sequester a huge amount of carbon from atmosphere enriched with greenhouse gases. Mobilizing frozen methane deposits into ocean water and atmosphere as a result of rising Arctic temperature ultimately exacerbates the global warming. Sulfur particles formed via conversion of polar phytoplankton metabolite dimethylsulfoniopropionate (DMSP) to dimethylsulfide (DMS), a volatile gas, help seed clouds which mitigate climate warming. On the other hand, polar microbial population plays a primarily key role in various biogeochemical cycles, food webs, and re-mineralization processes. These microbial communities are dominated by various orders of cyanobacteria which form the base of food webs and account for large proportion of polar biomass despite extremely low temperature and other stress factors prevailing in polar ecosystems. Poor ideal level of nutrient availability for biological activity restricts the diversity of microbial communities in polar environment. Physiological and phenotypic characteristic of species determines its vulnerability to extreme weather events resulting in some species being more susceptible to challenging stress than others (Nienow and Friedmann 1993).

1.3 Ecology and Biogeochemistry of Cyanobacteria

Cryo-ecosystem active cyanobacteria are challenged with extreme environmental parameters of high altitude and latitude. These environmental parameters include high UV radiation, desiccation tolerance, and freeze and thaw damage. Cyanobacteria within microbial communities are the only dominant and most widely distributed photoautotrophs contributing to structural stability, moisture retention, and fertility of surrounding microbes (Belnap and Gardner 1993). They are considered a dominant contributor of essential ecosystem services (carbon and nitrogen cycle). Classical and modern microbiological techniques have revealed the presence of cyanobacteria as primary colonizer in a wide range of polar niche such as permafrost, ice shelves, rocks, ponds, lakes, and glaciers (Vincent 2000). Variability in environmental factors restricts development of other photoautotrophic clades, while domination of cyanobacterial autotrophy supports a diverse number of heterotrophic microorganisms (such as *Actinobacteria*, *Proteobacteria*, *Firmicutes*, and *Bacteroidetes*) as well as a small number of organisms at higher trophic level (De los Rios et al. 2014; Yung et al. 2014). Besides polar cyanobacterial cohorts, polar ecosystems are also inhabited by a number of eukaryotic photoautotrophs which include diatoms, green algae, and mixotrophic organisms. Studying and understanding the mechanism of adaptation of these dominant cyanobacteria helps understand the whole ecosystem dynamics in cryo-ecosystems (Curtis 2006). Cyanobacteria exhibit biogeographical patterns; as such, their diversity is often linked to latitudinal gradients, with highest diversity and density found between 70 and 80 °S (south) (Namsaraev et al. 2010) (Table 1.1).

Table 1.1 Types of lithic environment

Lithic environment	Definition	References
Epilithic	Rock surface-inhabiting organisms	Omelon (2008)
Endolithic	Organisms inhabiting the interior of rock	Nienow and Friedmann (1993)
Hypolithic	Communities inhabiting the soil-rock interface	Cockell and Stokes (2004)
Euendolithic	Microorganisms can bore actively into the rock and inhabit the resultant hole	Cockell and Herrera (2007)
Cryptoendolithic	Microorganisms inhabit the space between grains of porous rocks	Omelon et al. (2007)
Chasmoendolithic	Microorganisms inhabiting rocks cracks and fissures	Budel et al. (2008)

1.3.1 Cryptic Niches

Cryptic niches include biological soil crust (BSC), hypoliths, and endoliths that provide physical stability, allowing slow-growing cyanobacterial and other specialized microbial communities to develop (Agawin and Agusti 1997). Antarctic BSCs are composed of unique filamentous cyanobacteria such as *Nostoc commune* and *Tolypothrix*, *Calothrix*, and *Leptolyngbya* species (Budel and Colesie 2014), while BSC communities in high Arctic favor members of *Nostocales*, *Chroococcales*, and *Oscillatoria*.

1.3.2 Hypoliths

In an extreme cold ecosystem, the underside of rocks acts as a "refuge" for photoautotrophic microorganisms. The community performs photosynthesis with irradiance levels less than 0.1% of incident light. Hypolithons are protected from UV radiation, wind scouring, and trapped water. This provides bioavailable liquid water for hypolithons (Makhalanyane et al. 2014; Ramond et al. 2015). Among hypolithons cyanobacteria forms the base of community structure and functional processes, and a clonal-based analysis of hypolith samples showed close homology to *Nostocales* and *Oscillatoriales* dominance. Arctic hypoliths are also dominated by cyanobacteria, and species found include *Gloeocapsa atrata* Kützing, *Gloeocapsa punctata* Nägeli, *Gloeocapsa kuetzingiana* Nägeli and *Chroococcidiopsis*-like cells; unicellular algal chlorophytes are also present (Cockell and Stokes 2004).

In another study by Pointing et al. (2009), colonized quartz rock examination was done, and observations indicated dominance of oscillatorian cyanobacterial morphotypes, belonging to genus *Leptolyngbya*. De los Rios et al. (2014) demonstrated the unique spatial organization by hypoliths dominated by cyanobacteria and found that most were structured by filamentous cyanobacteria and associated with extracellular polymeric components, largely forming a biofilm. The presence of extracellular polymeric substances has a major impact on survival of these cyanobacteria especially in water-limited environment as EPS plays a key role in water retention. On the other hand, Arctic hypoliths are dominated by a diverse range of cyanobacterial species like *Gloeocapsa*, *Chroococcidiopsis*-like cells, and unicellular algal chlorophytes (Cockell and stokes 2004).

1.3.3 Endoliths

Study on gypsum crusts on Alexander Island, West Antarctic Peninsula, revealed the predominance of *Cyanobacterium chlorogloea* sp. (Makhalanyane et al. 2014). Cyanobacteria are dominant colonists in endolith niches, and their colonization mode depends on micro-morphological and structural properties of the rock (Hughes and Lawley 2003). In a similar study conducted in Canadian High Arctic, analysis of endolthic communities of gypsum crust indicated predominance of phototrophic cyanobacteria which included *Nostoc* species, *Loriellopsis* sp., and *Chroococcidiopsis* sp. (Ziolkowski et al. 2013). In Mcmurdo Dry Valley, Antartica, endolithic communities were dominated by three communities: *Gloeocapsa*, *Hormathonema*, and *Chroococcidiopsis*. Bu del et al. (2008) through their studies of endoliths from Antarctica reported presence of different genera of cyanobacteria such as *Chroococcidiopsis*, *Cyanothece*, and *Nostoc* species.

1.3.4 Cryoconites

Cryoconites play a key role in glacial ecosystems exhibiting different boundaries, nutrient cycling, and energy flow. Cyroconites act as refugia from harsh environment for a diverse range of microbes as well as different species of cyanobacteria. These are cylindrical cavities of thin layer of sediment present in the ice surfaces. These layers of sediments provide a favorable environment for microbial colonization and growth, thereby acting as biomass seeding sources in polar regions (Mueller et al. 2001). Dominating species of cyanobacteria in cryoconites are *Phormidium*, *Nostoc*, and various species of the genus *Leptolyngbya* (Cameron et al. 2012).

1.3.5 Aquatic Habitats

Studies have suggested presence of cyanobacterial species in inland aquatic systems of Antarctica to be low in diversity. However, 20 years later (Taton et al. 2003), in their study using 16S rRNA gene and internal transcribed spaces (ITS), regions came up with 15 phylotypes present on microbial mats of Lake Fryxell in McMurdo Dry Valley, Antartica, and belonged to genera *Geitlerinema*, *Nostoc*, *Hydrocoryne*, *Leptolyngbya*, *Lyngbya*, *Pseudonabaena*, *Phormidium*, *Oscillatoria*, *Schizothrix*, and *Nodularia* (Table 1.2).

1.4 Ecophysiology of Polar Cyanobacteria and Functional Role of Arctic and Antarctic Cyanobacteria

Current scientific exploration shows that both Arctic and Antarctic cyanobacterial species are essential for ecosystem services (Wagner and Adrian 2009). Fluctuation in temperature and availability of nutrients and liquid water can alter microbial community dynamics (Chan et al. 2013). For example, global warming leading to warmer water in polar lakes and ponds and nutrient accumulation from catchment often results in cyanobacterial blooms (Wagner and Adrian 2009). Application of modern molecular phylogenetic techniques can enhance the understanding of functionality of cryo-microbial communities. Experimental studies by various scientific communities have made it clear that cyanobacteria are central to such ecosystems (Fernandez-Valiente et al. 2001). Recent evidence suggests that even moderate change or reduction in microbial community will affect the whole functional

Table 1.2 Genera of dominant cyanobacteria with their cryospheric habitat

Genus	Habitat	References
Anabaena	Permafrost, soil, endolithic, cryoconite	Friedmann et al. (1987), Vishnivetskaya (2009), Mataloni et al. (2000), Mueller and Pollard (2004)
Aphanocapsa	Soil, endolithic	Friedmann et al. (1987), Fermani et al. (2007)
Calothrix	Soil, hypolithic, chasmoendolithic, epilithic	Broady (1981, 1986, 1989), Cavacini (2001)
Chroococcidiopsis	Soil, hypolithic, chasmoendolithic, endolithic, epilithic	Friedmann et al. (1987), Ryan et al. (1989), Cockell and Stokes (2004)
Eucapsis	Cryptoendolithic	Friedmann et al. (1987)
Gloeocapsa	Soil, hypolithic, cryptoendolithic, chasmoendolithic, cryoconite	Broady (1981, 1986, 1989), Friedmann et al. (1987), Cockell and Stokes (2004)
Leptolyngbya	Permafrost, soil cryptoendolithic, cryoconite, glacial ice, lake ice	Vishnivetskaya (2009), Friedmann et al. (1987), Cavacini (2001), Mataloni et al. (2000)
Lyngbya	Soil, hypolithic, chasmoendolithic, cryoconite	Broady (1981)
Microchaete	Soil, endolithic	Friedmann et al. (1987)
Microcoleus	Soil, cryoconite	Komárek et al. (2008), Mueller and Pollard (2004)
Myxosarcina	Epilithic	Broady (1981)
Nodularia	Soil, hypolithic, chasmoendolithic	Broady (1981)
Nostoc	Permafrost, soil, hypolithic, chasmoendolithic, cryoconite	Budel et al. (2008), Mueller and Pollard (2004)
Oscillatoria	Soil, endolithics, cryoconite	Cameron (1972), Mataloni et al. (2000), Mueller and Pollard (2004)

dynamics of cold ecosystem (Philippot et al. 2013; Singh 2014). Recent metagenomic analysis of genes responsible for stress response to various environmental stress parameters in microbial mat communities which are dominated by cyanobacteria (in Arctic and Antarctic) includes sigma B, EPS, cold shock proteins, and membrane modifications (Varin et al. 2012). Under low temperatures, proteins are more susceptible to tertiary and quaternary structural damage, while nucleic acid content becomes more stable, unable to support basic processes like replication, transcription, and translation (D'Amico et al. 2006). Thus, cyanobacteria for survival produce specialized proteins and other biomolecules such as cold shock proteins, antifreeze protein, and glycine betaine. Cyanobacteria survival is also accompanied by higher production of unsaturated fatty acid to retain membrane fluidity as loss of fluidity highly affects the nutrient transport (Los and Mironov 2013). DEAD-box RNA helicases are also expressed in abundance which help maintain cellular processes even under thermodynamic constraints (Rocak and Linder 2004). To cope up with the challenges of freezing and desiccation, cyanobacteria have adapted the strategy of entering to dormant state followed up by low metabolic activity (Vincent et al. 2004).

Cyanobacteria-driven biofilms provide exopolymer matrix which supports biological as well as biogeochemical interaction. These cyanobacterial biofilms secrete a large number of exopolysaccharides (EPS). EPS matrixes also play a structural role and are responsible for creation and maintenance of microenvironment to support growth and metabolism of cyanobacterial consortia. De los Rios et al. (2014) showed that EPS also provides cryoprotection and desiccation protection for a diverse range of microorganisms.

1.5 Polar Region: Extreme Environmental Parameters and Stress Factors

Generally, cyanobacteria surviving in high latitude and altitude are cold tolerant known as psychrotrophs, and they show suboptimal growth at low temperature as against psychrophiles that show optimal growth at low temperature (Tang and Vincent 1999). Psychrotrophs exhibit a variety of mechanisms to tolerate and grow at extremely low temperatures. They have adapted to freeze-thaw conditions by enhancing the production of polyunsaturated fatty acids accompanied with short chain length to be incorporated in their membrane. Cyanobacteria also produce compatible solutes which reduce freezing point of intracellular solutes such as trehalose, which also reduces cell desiccation. Cyanobacteria also produce and secrete extracellular polymeric substances which help minimize ice nucleation around the cells. Through these ways, cyanobacteria consortiums are able to withstand long-term seasonal dormancy phases in frozen environment. Later, these freeze-dried cyanobacterial mats resume photosynthesis and high metabolics upon rethawing (Vincent 2007). Temperature, liquid water availability, and irradiance are crucial stress factors in cryo-ecosystem. Different adaptation and acclimatization responses are due to various combinations of seasonal and diurnal variation, range of values, and periodicity of these major stress factors. Studies have reported dynamic fluctuation of temperature in polar regions. For example, average temperature during vegetation season ranges from 0 to 5 °C, where temperature can be much higher or lower than air temperature particularly at localized microenvironments. Elster et al. (2012) demonstrated that the temperature of dry hummock top ranges from 2 to 10 °C in the beginning of vegetative season, and with time when hummock bottom is completely submerged in water, the temperature becomes constant around 0 °C. Therefore, decrease in liquid water availability from aquatic to dry habitats is a characteristic of seasonal variation. These seasonal variations are responsible for causing precipitation events. Polar streams, rock surfaces, or wet hummock tundra meadows are exposed to variable wet and dry periods during vegetation season. Another stress encountered by microbial consortia is when temperature for a short period of time rapidly increases to 0 °C and liquid water prevails for 1 or 2 weeks. This event of rain on snow takes place from January to February and results in significant reduction in survival rate of cyanobacteria. Irradiance is yet another key factor and includes PAR (400–700 nm) and UVR (280–400 nm). Polar nights as well as continuous irradiance during polar day cause stress to thriving life. PAR is the main known source of energy for photoautotrophic microorganism. UVR is known to have greater impact on polar aquatic and terrestrial ecosystems. Microclimate can be very different from macroclimate; such dynamic differences can be observed in thermal springs or within cryoendolithic communities (Friedmann et al. 1987).

1.6 Polar Cyanobacteria: Response to Various Stress Factors

1.6.1 General Mechanism of Adaptation

Duration of stress and stress intensity determines the stress effect and course of stress reaction (Schulze 2005). Stress response also depends on adaptation capabilities of microbial communities. These cryo-microbial communities in nature are exposed to combinations of different types of stresses at the same time. For example, high PAR is followed by UVR. As a result of multiple stresses, stress responses in turn are highly complex involving various protection mechanisms. Basic stress response is categorized as active (stress tolerance) and passive (stress avoidance) according to Schulze (2005). For algae and cyanobacteria, the following terms are defined: adaptation, genetically fixed responses to outer environmental conditions (Elster 1999), and acclimation, response to sporadic extremes of environment that is not genetically fixed, but biochemical (e.g., synthesis of screening pigments), morphological (e.g., cell wall modification), or physiological (e.g., state transitions) changes occur. Elster (1999) defined this type of response as “acclimatization.” Stress reaction usually triggers specific processes, for example, state transitions (Allen 2003), metabolic changes like increased synthesis of polyunsaturated fatty acids (Shivaji et al. 2007), or modification of cell ultrastructure, viz., increased number of photosystem units in membranes.

1.6.2 Stress Avoidance

Stress avoidance is done by microbial communities using escape strategies to avoid harsh conditions or insulate cells from the surroundings. Escape mechanisms involve migration to acceptable (favorable) conditions or suitable habitats. For migration, unicellular and filamentous forms use gliding movement (Hoiczyk 2000; McBride 2001), and planktonic species use buoyancy mechanisms involving gas vacuoles to control and monitor their position in the water column (Oliver 1994). Habitat

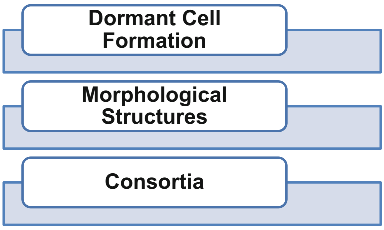

Fig. 1.1 Strategies of polar cyanobacteria use for stress avoidance

selection is a favorable option for non-motile living forms. Habitat selection is advantageous as it provides favorable conditions than outside such as rock interior is warmer and wetter, protecting against PAR and UVR) (Friedmann et al. 1987). Gilichinsky et al. (2008) observed that permafrost samples were dominated by viable non-heterocystous filamentous cyanobacteria of the family *Oscillatoriales* (Fig. 1.1).

1.6.3 Stress Tolerance

When stress factors damage the cell, stress tolerance mechanism comes into play. Stress response events that help restore the cell's function are known as stress reactions. The point when cell structure as well as function is disturbed, signaling molecules trigger appropriate receptor to carry a cascade of reactions, resistance of organism increases up to a maximal level, and resistance need not to last constantly as it can decrease again during long-term and intensive stress (Schulze 2005).

1.6.4 Dormant Cell Formation

One of the mechanisms of protection from harsh environment is to produce akinetes whose formation has not been observed in polar cyanobacteria (Lubzens et al. 2010), and it can rarely be seen in genera *Anabaena* or *Hydrocoryne*. Nonpolar cyanobacteria do exhibit the ability to form akinetes, which is defined as a resting stage where the cell wall is thick and large amounts of intracellular storage compounds are present. This allows survival under extremely harsh conditions. Trigger mechanisms for akinete formation from vegetative cells are probably species specific (Van den Hoek et al. 1995). It is reported that hormogonia and hormocyst are polar akinete in polar regions. Hormogonia and hormocyst are formed via fragmentation of vegetative or mother filaments and possess ability to migrate to favorable conditions.

Tashyreva and Elster (2016) in their study on polar *Microcoleus* (a filamentous species of cyanobacteria) observed that at the end of vegetative season, a dense sheet starts to develop, and later in spring, a large number of hormogonia is released. They also stated that at the end of vegetative season, freezing, desiccation, and nitrogen starvation trigger the acclimatization process. This promotes development of resistance to winter (Tashyreva and Elster 2016). Under stress conditions of vegetative season, hormogonia and hormocysts may still form in large number and spread actively or passively via gliding or by water, respectively, to a suitable habitat. Despite very low survival rate, few hormogonia manage to outlast severe conditions and later act as inoculums for colonization of habitat. Since filaments are more delicate to desiccation, freezing, and biochemical modifications, therefore, production of osmotically active compounds, or formation of other types of dormant cells, like cyst-like cells in chroococcidiopsis (Caiola et al. 1996), could facilitate continued cell existence (Tashyreva and Elster 2012, 2016).

1.6.5 Morphological Structures

To cope with hostile external conditions, cyanobacteria promote differential development of morphological structure. These morphological structures can help survive in times when migration toward suitable environment is restricted. Against desiccation and freezing, polar cyanobacteria develop various types of extracellular mucilaginous envelopes and sheaths (De los Ríos et al. 2004; Makhalanyane et al. 2014; Tashyreva and Elster 2016; Deming and Young 2017). The surrounding envelops protect via different compounds that screen the cell against PAR and UVR. Colonial forms are more resistant to stress (Xiong et al. 1996), probably because surface cells protect those inside the colony. Formation of a colony of cells or filaments was indeed observed after exposure to high irradiance and nutrient depletion (Callieri et al. 2012).

1.6.6 Consortia

In polar environments, the consortium of different species develops into several structures like firm layered structures, microbial mats, and biofilms. These colonial patterns are often characterized by an outer or upper layer of cell containing screening pigments. A sheath pigment, scytonemin, protects subsurface layers. This shows that the condition is more favorable in the interior of the mat than outside (Vincent et al. 1993). Such microbial mats are found at aerial-liquid-solid interfaces as periphyton in seepages or at the aerial-solid interface on the soil surface as a soil crust. These microbial mats and biofilms show more resistance response to a number of stress factors (Elster and Benson 2004). Tashyreva and Elster et al. (2012) demonstrated an extreme case of avoidance strategy by lichen formation where fungal filaments play a role in structural and chemical protection and provide water to phycobiont, and in return cyanobactreium offers organic nutrients to the mycobiont. Here lichen system provides an advantage of good water management in polar regions, which are often exposed to water stress.

1.6.7 Low Temperature

In a study, oscillatorian cyanobacteria isolated from melt water ponds which are psychrophilic (temperature range from 0 to 8 °C). Polar cyanobacteria also exhibit longer doubling time than psychrophilic eukaryotic algae and heterotrophic bacteria (Vincent 2007) (Fig. 1.2).

1.6.8 Temperature Perception

Cold adapted microbial plus cyanobacterial consortia possess temperature sensors which trigger signal transduction in cells. The scheme of acclimatization reaction in synechocystis PCC6803 was studied by Murata and Wada (1995) and Nishida and Murata (1996), and they reported that the fall in external temperature decreases fluidity of cellular membrane which is sensed by membrane-bound sensors. Receptors of cold shocks could possibly be membrane proteins. Temperature sensors trigger a cascade of reaction that ultimately leads to expression of desaturase genes leading to restoration of membrane fluidity with accumulation of desaturated fatty acids.

1.6.9 Lipids

Based on fatty acid composition, cyanobacteria belong to four different groups. Alteration in fatty acid composition during exposure to low polar temperature in cyanobacterial membranes depends on the group to which cyanobacterium belongs. When temperature shifts to extreme low, fatty acid composition of membrane changes and results in an increased ratio of unsaturated fatty acids, increase in cis-double bonds, methyl branching, and shortening of fatty acid chain (Gounot and Russell 1999). It involves changes in level of desaturation together with acyl chain length (Shivaji et al. 2007). In a study conducted on polar *Calothrix* sp. Samples, it was shown that membrane phospholipid containing branched long chain fatty acids improves cold tolerance (Řezanka et al. 2009). In another study, it was shown that in *Synechocystis* sp., level of unsaturated fatty acid changes due to unsaturation of existing fatty acid and not because of de novo synthesis.

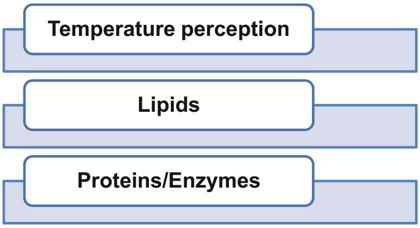

Fig. 1.2 Survival strategies of cyanobacteria at low temperature

1.6.10 Proteins/Enzymes

Conservation of structural and functional integrity of cellular proteins at extreme low temperature is challenging for polar cyanobacteria and other microbial communities. At low temperature, decaying of compact protein structure can be observed, further resulting in individual subunit dissociation (Primalov 1979). Catalytic activity of enzymes too gets affected at low temperature. Protein folding must take play in such a way as to maintain structural and functional integrity (Walles et al. 1999). Sensitivity to low temperature could be different for various enzymes even when isolated from the same species, and different enzymes have developed different responses to low temperature (Loppes et al. 1996). When compared to mesophilic enzymes, enzymes from cold adapted organisms are more active at lower temperature, and their catalytic activity is more temperature independent, though their active site is less stable (Feller and Gerday 2003).

Still, few enzymes follow opposite scenario, for example, the highly conserved enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) catalytic activity was observed to be low in psychrophilic algae in comparison with mesophiles. Lower enzymatic activity in RuBisCO is compensated with synthesis of greater amount of enzyme subunits in psychrophilic alga (Devos et al. 1998). Many microbial species together with diverse cyanobacterial communities undergo dormancy or hibernation to survive in polar environment. Cold shock proteins are synthesized as they are essential for restoration of growth under lower temperature, and they function at transcriptional and translational levels (Raymond-Bouchard and Whyte 2017). Cold shock proteins act differently in psychrophiles and mesophiles. The number of cold shock protein is higher and is directly proportional to the intensity of stress, i.e., the higher the cold stress, the greater the production of cold shock proteins. Another group of proteins called cold acclimation proteins (CAPs) are also considered to play a role in promoting growth in polar environments along with cold shock proteins (Berger et al. 1997).

1.6.11 Freeze/Melting Cycles

In polar regions especially polar hydroterrestrial and terrestrial ecosystems, cyanobacteria are more frequently subjected to freeze-thaw cycle. There are many factors on which sensitivity of cell to freezing and melting depends (Elster et al. 2012), like the physiological state of cell, rate of cooling, freezing and melting, and also the chemical composition of freezing medium. It was observed that polar cyanobacteria are more resistant to freezing than polar algae and could possibly survive freezing up to −100 °C (Šabacká and Elster 2006). Polar freezing and melting in turn are responsible for inducing many stresses like temperature change, change in water content and phase, and change in concentration of many compounds that often leads to alteration in pH, salt precipitation, and intracellular ice crystal. The rate of freezing and melting is very slow (Elster et al. 2012). Ice crystals penetrate the intracellular structure which could damage cells (Tanghe et al. 2003). ROS

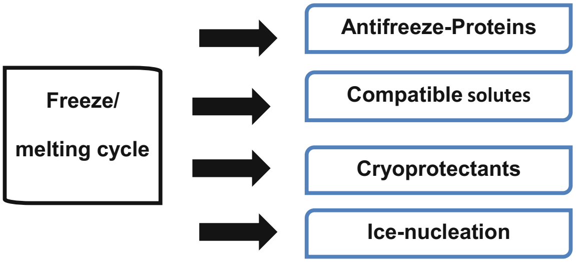

Fig. 1.3 Survival strategies against freeze/melting cycle

production together with in−/outflow of water with osmotic gradient also damages the cell. Synthesis of AFPs and dimethylsulfoxide (DMSO) prevents ice crystal formation and could account for freeze avoidance strategy, while freeze tolerance mechanism involves phenomenon of ice nucleation (Cockell et al. 2000) (Fig. 1.3).

1.6.12 Antifreeze Proteins

AFPs function by depressing the freezing point and avoiding recrystallization of ice (Chao et al. 1996). In a study on Antarctic cyanobacterial mats (dominated by *Nostoc* sp. and *Phormidium*), presence of AFPs was observed (Raymond and Fritsen 2000). These AFPs include a diverse range of proteins and are present at low concentration in cells.

1.6.13 Compatible Solutes and Cryoprotectants

Psychrophilic and psychrotolerant cyanobacteria are expected to synthesize and accumulate compatible solutes, though their accumulation in them is not well studied (Klähn and Hagemann 2011). However, marine algae have been known to produce cryoprotectant or compatible solutes, for example, DMSO which provides protection against freezing injury (Day et al. 2005; Day and Brand 2005). In halotolerant cyanobacteria, a similar compound was found, namely, dimethylsulfoniopropionate (DMSP) which can also serve as a cryoprotectant like DMSO (Kirst et al. 1991; Karsten et al. 1992). EPS (extracellular polysaccharides) present in thick mucilaginous envelopes and sheaths are also observed to slow down water movement during freeze and thaw (to prevent sudden alteration in cell volume) and, therefore, can also be considered as a sort of cryoprotectant (Deming and Young 2017). EPS are known to consist of glucose, xylose, galactose, and uronic acid (Helm et al. 2000). Chain-forming carbohydrates contain hydrophilic solutes. So, the extracellular matrix provides cryoprotection to cells during encapsulation. This effectively protective encapsulation has been demonstrated in coccal algae and yet not sufficiently studied in polar cyanobacteria (Elster et al. 2008; Lukešová et al. 2008).

1.6.14 Ice Nucleation Proteins

In bacteria, proteins present in the outer cell membrane act as template for ice nucleation which helps prevent desiccation. Ice nucleation separates water source present near the cell surface, and ice particles spreading outward from the cell can be observed. In this way, damage to the cell via ice formation reduces to minimum (Lee et al. 1995). Freezing temperatures required for ice nucleation activity are −13 °C, −15 °C, and −18 °C for Antarctic soil *Phormidium scotii*, *Pseudophormidium* sp., and *Phormidium attenuatum*, respectively, indicating that the cyanobacteria do not use ice nucleation mechanism for freezing protection (Worland and Lukešová 2000).

1.6.15 Dessication

Poikilohydric organisms such as microalgae, lichens, and mosses are defined as organisms that can tolerate desiccation (Alpert 2000, 2005). Cyanobacteria are also poikilohydric. Desiccation causes failure of various physiological processes, therefore impairing essential cellular process. In a study, long-term survival of desiccation in cyanobacterial *Nostoc* sp. was observed where *Nostoc* sp. was successfully revived after 55 (Shirkey et al. 2003), 87 (Lipman 1941), and more than 100 years (Cameron 1962). Cyanobacteria follow diverse strategies to minimize osmotic and mechanical stresses which are also common in poikilohydric organisms, indicating early evolutionary relatedness of these photosynthetic organisms (Fig. 1.4).

These strategies include complex interaction networks and processes at several cellular levels. In cyanobacterial consortia, desiccation leads to inhibition of nitrogen fixation and decline in photosynthesis and also affects respiration (Potts 2000; Qiu and Gao 2001). Even upon rehydration, it takes hours to recover photosynthetic function and days for nitrogenase activity recovery. Cyanobacterial tolerance to extreme desiccation is mainly due to its ability to tolerate extreme low water potentials. In a study by Potts and Friedmann (1981), it was shown that cryptoendolithic *Chroococcus* and *Chroococcidiopsis* were able to fix carbon dioxide at unusually low potential (Potts and Friedmann 1981; Palmer and Friedmann 1990). In another study, it was observed that *Nostoc* sp. carry out usual photochemical and nitrogen fixation activity even after losing 50% of its original weight when present at fully hydrated state. Stress response during desiccation is reported in *Calothrix* sp. and *Nostoc* sp., respectively. These responses include enhanced rate of lipid production and accumulation of polyunsaturated membrane lipids. Superoxide

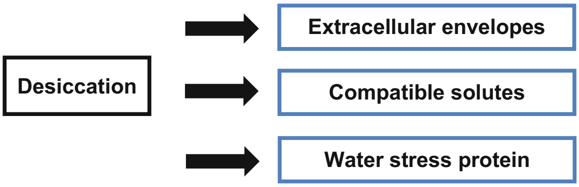

Fig. 1.4 Survival strategies in response to desiccation

dismutase and catalase are the oxygen scavenging enzymes produced to reduce or prevent membrane damage due to ROS generation. As a desiccation tolerance strategy, cyanobacteria modify protein structure by acetylation, phosphorylation, and glycosylation. Photoreactivation, excision repair, and post-replication repair are the DNA protection mechanisms adapted by polar cyanobacteria.

1.6.16 Extracellular Envelopes

In polar regions, microbial species are usually desiccation resistant as they develop thick mucilage envelopes and sheaths (Tamaru et al. 2005). The major component of this envelop is a mucopolysaccharide that helps delay desiccation and retains water (Caiola et al. 1996; Pereira 2009). In *Nostoc commune* colonies, it has been demonstrated that EPS are responsible for possible water storage function and, therefore, keep cells in hydrated state (Kvíderová et al. 2011). Prolonged desiccation does affect the size and biochemical composition, resulting in larger cellular envelops in *Chrococcidiopsis* sp. (Caiola et al. 1996).

1.6.17 Water Stress Proteins

Another challenging parameter in the polar region is availability of water. Many microbial species including cyanobacterial species have water stress proteins (WSPs), late embryogenesis abundant (LEA) proteins, and dehydrin among them. LEA proteins have mechanism to stabilize other proteins and cellular membrane during drying (in presence of trehalose) (Close 1997). Dehydrins exhibit a functional role of inhibition of coagulation of macromolecules. Both proteins are found to be present in cyanobacteria (Close and Lammers 1993). Disaccharides such as trehalose, sucrose, and glucosylglycerol are considered compatible solutes especially in water-stressed mesophilic cyanobacteria (Reed et al. 1984; Klähn and Hagemann 2011). Some WSPs have been detected in *Nostoc commune* colonies that perform modification in extracellular envelop (or extracellular glycan) (Potts 1999).

1.6.18 Salinity

Osmotic and ionic components are required to combat with salinity stress through their specific response (Epstein 1985; Läuchli and Epstein 1990). Osmotic component is linked to water efflux, and response mechanism helps minimize or reduce water loss. Ionic component acts against toxic effects caused by higher concentration of ions and nutritional misbalance by performing selective or specific ion transport (Elster 1999). Cyanobacterial response to increase tolerance to salinity includes reduction in total lipid content and undergoes desaturation of membrane lipids. Salt tolerance mechanism also involves regulation of ion and water membrane channels (Singh et al. 2002). Salt stress often generates ROS, and cyanobacteria

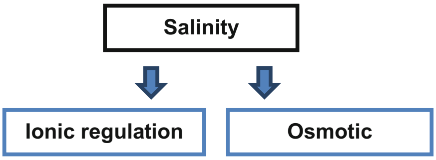

Fig. 1.5 Survival strategies against salinity in cold ecosystems

deals with it by activating quenching mechanisms (Latifi et al. 2009). Response involves several steps: (1) active Na^+ extrusion (ionic regulation), (2) uptake/synthesis of compatible solutes (osmotic regulations), (3) modification of membrane lipid composition, and (4) increased energetic capacity due to increased photosynthesis and respiration (Joset et al. 1996) (Fig. 1.5).

1.6.19 Ionic Regulation

Ion regulation is a crucial process that takes place in every microbial as well as eukaryotic cell. It can be achieved by active and passive ion transport. Active ion transport provides rapid response to changes in intracellular Na^+ concentration. When extracellular concentration of Na^+ increases, to maintain osmotic balance as a result, intracellular Na^+ concentration increases steeply and later declines slowly to attain physiological value (Packer et al. 1987; Blumwald et al. 1983). Active ion transport eliminates excess Na^+ to maintain an intracellular range of 10–30 mM. K^+ uptake too helps in adjustment of turgor (Apte 2001). These active ion transport systems such as antiport Na^+/H^+ are powered by P-ATPase (Joset et al. 1996).

1.6.20 Osmotic Regulation

In *Synechocystis* sp., the processes of uptake/synthesis of compatible compounds takes place simultaneously along with ion transport to maintain positive turgor (Reed et al. 1984; Joset et al. 1996). However, very less has been explored about the osmotic regulation in polar cyanobacteria. Cyanobacteria surviving under combined stress of desiccation and salinity in hypersaline deserts do synthesize necessary compatible solutes, for example, glycinebetaine, the most commonly synthesized compatible solute (Klähn and Hagemann 2011; Oren 2007).

1.6.21 Irradiance (PAR) and Ultraviolet Radiation (UVR)

Orthodoxically, cyanobacteria in polar regions have the ability to tolerate high doses of UVR and are less sensitive to it (Seckbach and Oren 2007). They exhibit different morphological and community organization patterns such as bigger cells or grow in large colonies, coenobia, or mats which provides protection to internal cells or filaments (Pattanaik et al. 2007). Screening strategies are species specific. For

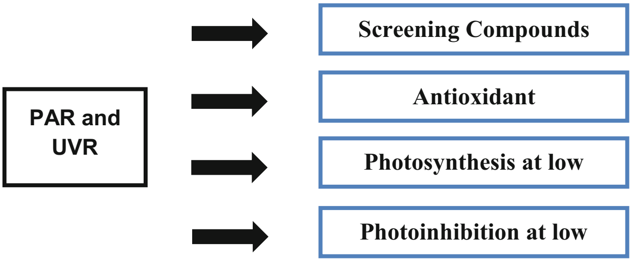

Fig. 1.6 Survival strategies of polar cyanobacteria against PAR and UVR

example, outer layers of *Scytonema* mats are characterized by actively moving filaments, whereas the upper layer cells in oscillatoracean mats contain low pigment concentration thereby protecting internal cells (Quesada et al. 1999) (Fig. 1.6).

High level of UVR exposure to cyanobacteria may cause photo-inhibition, photochemical damage, and cellular component degradation; as a consequence of which, generation of ROS takes place. Primary target of ROS is DNA leading to harmful mutations (Quesada and Vincent 1997; Xue et al. 2005). Consequences of high-dose exposure of UVR include slow growth rate and damage to photosynthetic apparatus, nitrogenase complex, and cellular membranes. As an adaptive mechanism, cyanobacteria possess four lines of defense which also favor cyanobacteria acclimatization under high light (Vincent 2000).

- Selection of habitat
- Production of screening compounds
- Production of antioxidants
- Repair mechanisms

Sunlight is the main source of energy for phototrophic clades including cyanobacteria. Variations in the availability of PAR together with its spectral composition and intensity impose challenges to cyanobacterial communities (Falkowski and Raven 2007; Markager and Vincent 2000). In water, blue and blue-green light prevails more, while red light diminishes in very short time. Its intensity can vary from minute intensities in cryptoendolithic communities of 0.1 μmol m^{-2} s^{-1} up to full sunlight of 1500 μmol m^{-2} s^{-1} (Nienow et al. 1988). To survive in cold habitats, cyanobacteria are required to acclimatize to a broad range of PAR values (Vincent 2000).

1.6.22 Photosynthesis and Photoinhibition at Low Temperature

Rate of photosynthetic reaction depends mainly on factors like temperature, sunlight, water, and CO_2. Photosynthesis occurs at temperature ranges of −7 to +75 °C (Castenholz 1969). It is observed that rate of photosynthesis first increases to an optimum temperature and then declines (Davison 1991). Generally, at cold temperature, rate of individual steps of electron transport, carbon dioxide diffusion, enzymatic activity, and turnover of membrane protein is slow. This limits photosynthesis in phototrophic clades when exposed to higher irradiance resulting in photoinhibition (called as photo-inhibition of low temperature) (Powels and Berry 1983; Smillie and Hetherington 1988). In a study, it was shown that *Synechocystis* sp. are resistant to photoinhibition due to lipid desaturation, through light regulation of desaturase genes expression, resulting in higher photosynthetic productivity (Sakurai 2003). Therefore, cryo-cyanobacteria attain higher photosynthetic rates even at low temperatures considering their upper temperature limits of photosynthesis are still lower than algae of warmer region (Kuebler et al. 1991).

1.6.23 Screening Compounds

Cyanobacterial consortia often exhibit colored colonies. Cyanobacteria produce pigments that absorb in UV and blue regions of electromagnetic spectrum (Quesada and Vincent 1997). The major screening compound mycosporine-like amino acid (MAA) accumulates in cytoplasm of cyanobacteria and shows absorbance maxima at 310–360 nm (Oren and Seckbach 2001; Pattanaik et al. 2007). Another screening pigment scytonemin (yellowish-brown) shows maximal absorbance at 370–390 nm (Oren and Seckbach 2001; Pattanaik et al. 2007). Scytonemin is a stable pigment and provides prolonged protection. Cyanobacterial mats exhibit black and dark coloration due to the presence of scytonemin in extracellular sheath. *Gloeocapsa* species of cyanobacteria lacks scytonemin and exhibits brown coloration due to the presence of a different screening pigment in the envelope, the gloeocapsin. Colored *Gloeocapsa* sp. were reported by Nováček (1930, 1934), and the observation of Jaag (1945) may imply possible effects of environmental conditions, namely, pH, on sheath pigment color in *Gloeocapsa*. Presence of gloeocapsin is usually connected with absence of scytonemin in some cyanobacterial species, thus suggesting independent development of scytonemin and gloeocapsin-based protective strategies (Storme 2015). It has been reported that even common cellular compounds have screening property against excess UVR. There is an observation by Araoz and Häder (1999) that synthesis of phycoerytherin increases with increased exposure to UVR due to faster rate of repair of photosynthetic apparatus, whereas phycobiliprotein (PBP) do show absorbance in UVR region but still can be easily damaged by it (Häder 2001). In cyanobacterial mats, mucilaginous sheath performs a dual function to provide resistance against UVR, firstly by providing matrix for extracellular screening compound and secondly EPS showing UVR absorption (Ehling-Schulz et al. 1997). Dark red gloeocapsin in the envelopes of *Gloeocapsa* sp. is responsible for the brown coloration of crusts on rocks (Sheath et al. 1996); however, further data on its properties are lacking.

1.6.24 Antioxidants

Cryo-cyanobacteria have adapted a system of enzymatic and non-enzymatic antioxidant to scavenge ROS. These ROS are formed in cyanobacteria when exposed to high PAR and UVR (Pattanaik et al. 2007). In cryo-cyanobacteria, non-enzymatic oxidants include carotinoids, tocopherol, ascorbic acid (act rapidly to URV induced damage (Ehling-Schulz et al. 1997), and reduced glutathione though not considered as very effective ROS quenchers (Wolfe-Simon et al. 2005). SOD, catalase, and glutathione reductase as well as enzymes of ascorbate-glutathione cycle however account for enzymatic antioxidant systems of cyanobacteria growing in the polar regions (Pattanaik et al. 2007).

1.6.25 Survival Strategies: Insight from Metagenomics

A study tested whether increasing age and associated stress challenges drive adaptive changes in diversity of microbial community and their function. Pleistocene permafrost chronosequence from 19,000 to 33,000 (kyr) was performed with deep metagenomics and 16S rRNA gene sequencing. It was concluded that age affected microbial community composition and also reduced its diversity. Consistent shifts were observed with long-term strategies in cryo-ecosystem; this includes increased reliance of community on scavenging detritus biomass, horizontal gene transfer, chemotaxis, dormancy, environmental sensing, and stress response.

1.6.26 Subzero Temperature Effect

Under subzero temperature, nucleic acid and its secondary structure as well as structural flexibility of proteins are stabilized that inhibits replication, transcription, and translation. At extremely low temperature, concentration of ROS increases and damages DNA, RNA, proteins, and lipids. Stressors on the microbial community accumulate over time, demanding a counteractive adaptation for long-term survival in extremely harsh polar conditions. However, we know little about the ecological strategies utilized by microbial communities in response to the challenges presented by spending millennia in permafrost. The study showed older permafrost samples were enriched with pathways involved in synthesis of cell envelope component, amino acid, peptide, carbohydrate metabolism, environmental sensing, membrane transport, and degradation of recalcitrant biomass as compared to younger permafrost samples.

Along the permafrost chronosequence, the ability to respond to harsh environmental conditions increased, for example, ancient cryo-environment includes nutrients and other resource limitation, low temperature, and high osmolarity (Raivio 2014). Older permafrost samples are also enriched with diverse sensor system genes involved in temperature sensing, protein misfolding, H^+ regulation, salt stress, osmolarity, oxygen limitation, and cell membrane stress. Expression of genes responsible for nutrient and resource sensing ion, trace metal, nitrogen, acetoacetate, malate, and glucose amplified in chronosequence. Chemotaxis pathway also showed significant increase in ancient permafrost.

ATP-binding cassette transporter pathway genes, importer genes responsible for transfer of amino acid, peptides, osmoprotectant, and stress compounds together with exporter genes involved in transfer of LPS layer and cell wall component, increased in abundance along with chronosequence. The study mapped high expression of genes accounting from four of the six classes of secretion machinery and two membrane-spanning systems in older permafrost. These abundantly expressed secretion systems include type IV secretion system which encodes conjugation machinery, type I secretion system that secretes product in extracellular milieu, and type III secretion system involved in interaction with eukaryotic domain of life. Abundance of pathways involving biosynthesis of three cell envelope components—fatty acids, lipopolysaccharides (LPS), and peptidoglycan—increased with age. Fatty acid chains in phospho- and glycolipids form the membrane and are altered to increase membrane fluidity in response to cold (Phadtare 2004).

1.7 Impact of Rise in Global Temperature on Polar Cyanobacteria

Ancient literature and ongoing scientific studies suggest how important Arctic and Antarctic cyanobacterial communities are, for a number of ecosystem processes. The rise in global temperature has resulted in global climate change, which is accompanied with melting of polar glaciers. This causes harmful alteration in community dynamics in polar habitats (Wynn-Williams 1996; Strauss et al. 2012; Chan et al. 2013). One can observe the rise in cyanobacterial blooms in lakes and ponds having warmer water and enriched with nurients due to discharge of untreated industrial and community waste. It is crucial to understand cyanobacterial functionality along with its interaction networks with other microbial species under changing global climate. This can reveal the acclimatization strategies and also tell us in what way global changes are affecting the biogeochemical processes derived by microbes. Studies on soil systems suggest that moderate losses in microbial diversity definitely affect the functionality of the whole ecosystem (Philippot et al. 2013; Singh 2014).

1.7.1 Nitrogen Cycling

Climate change does have impact on microbial communities, for example, it affects nitrogen-fixing microorganisms. Yergeau (2008) did an environmental microarray analysis of Antarctic soil communities, where they observed a rise in cyanobacterial population with increasing latitude. This study revealed a strong connection between community structure and functional gene distribution in Antarctic soils. Results of Principal Coordinate Analysis (PCA) exhibited a relationship between cyanobacteria and genes for nitric oxide reductase (*nor*B). Surprisingly, the study showed a strong relationship between cyanobacteria and genes implicated in nitrogen fixation (*nif*H), ammonium oxidizing bacteria (*amo*A), and other genes associated with nitrogen cycling (nar, nos, nas). However, in a similar study undertaken on Arctic permafrost, cyanobacteria-mediated nitrogen fixation was suggested through the identification of a single type of nitrogenase (*nif*H) (Yergeau et al. 2010). Cyanobacteria also appear to drive nitrogen fixation in moist soil communities (Niederberger et al. 2012). For instance, it has been shown that N_2-fixing activity of cyanobacteria in Arctic regions is primarily governed by moisture gradients associated with topography that determines nutrient availability. The energy demand leads to high photosynthetic and respiration rates (Joset et al. 1996). Since respiration rates are low, photosynthesis seems to be the primary energy source (Apte 2001). Due to the allocation of energy to ion regulation and inhibition of nitrogenase activity, nitrogen fixation may be depressed in N_2-fixing species at high salt concentrations (Apte 2001) as observed in nonpolar *Anabaena* sp. (Apte et al. 1987). On the contrary, optimum nitrogen fixation in marine tropic and subtropic *Trichodesmium* sp. occurs in a salinity range from 3.3% to 3.7%, indicating adaptation of this cyanobacterium to the marine environment.

1.7.2 Carbon Cycling

Cyanobacteria, the globally dominant photoautotrophic lineage, are considered to be particularly important in Antarctic carbon cycling. In a study, using metagenomics, Pearce et al. (2012) reported cyanobacteria being underrepresented in southern maritime Antarctic soil, with only 3.4% of total sequences belonging to this phylum, although 1% of the genes identified were involved in CO_2 fixation. This result is surprising and may be a localized phenomenon, rather than representative of all southern maritime Antarctic soils. In any event, cyanobacteria have been shown to use a number of methods in order to increase photosynthesis (Rae et al. 2013). For example, they are able to produce carboxysomes, which together with CO_2-concentrating mechanisms (CCM) augment chemical conditions in the locality of the primary CO_2-fixing enzyme (RuBisCO), resulting in increased photosynthesis (Rae et al. 2013). In Antarctic habitats, such mechanisms are essential for nutrient input. Interestingly, Functional Forms II and III of RubisCO were assigned to other groups including *Archaea*, *Actinobacteria*, and *Proteobacteria*, the known chemolithotrophs. Cyanobacterium *Nostoc commune* is a prominent primary producer in continental Antarctica and has been used as a model for elucidating the ecological constraints on total carbon fixation particularly for ice-free areas (Novis 2007).