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Diversity and ecology of psychrophilic microorganisms

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Abstract

Cold environments represent the majority of the biosphere on Earth and have been successfully colonized by psychrophilic microorganisms that are able to thrive at low temperatures and to survive and even maintain metabolic activity at subzero temperatures. These microorganisms play key ecological roles in their habitats and include a wide diversity of representatives of all three domains (*Bacteria*, *Archaea*, *Eukarya*). In this review, we summarize recent knowledge on the abundance, on the taxonomic and functional biodiversity, on low temperature adaptation and on the biogeography of microbial communities in a range of aquatic and terrestrial cold environments.

Keywords: Psychrophilic microorganisms; Cold ecosystems; Biodiversity; Adaptation; Biogeography

1. Introduction

The Earth is a cold planet. About 85% of the biosphere is permanently exposed to temperatures below 5 °C. Cold habitats span from the Arctic to the Antarctic, from high-mountains to the deep ocean. The major fraction of this low temperature environment is represented by the deep sea (nearly 71% of the Earth is covered by oceans and 90% of the ocean volume is below 5 °C), followed by snow (35% of land surface) permafrost (24% of land surface), sea ice (13% of the Earth's surface) and glaciers (10% of land surface). Other cold environments are cold water lakes, cold soils (especially subsoils), cold deserts, and caves.

Temperature has a strong influence on whether a given kind of organism can survive and/or thrive, which is both indirect, through its influence on water (which has to be liquid), and direct, through its influence on the organic molecules composing the living cells (Poindexter, 2009). Cold environments are colonized by a wide diversity of microorganisms, including bacteria, archaea, yeasts, filamentous fungi and algae. A survey of recently described novel bacterial and fungal species and genera from various cold habitats showed that psychrophiles represent a vast resource of novel microorganisms (Table 1S). Special challenges to microorganisms in cold ecosystems include reduced enzymatic reaction rates, limited bioavailability of nutrients, and often extremes in pH and salinity. Depending on the local conditions, water activity (the amount of water available to microorganisms) may also be limiting. To thrive successfully in low temperature environments, psychrophiles have evolved a complex range of structural and functional adaptations (see Section 5). Consequently, there is evidence of a wide range of metabolic activities, even at subzero temperatures, in cold ecosystems.

In this review, we focus on microbial biodiversity and abundance as well as on the functional activity, adaptation and biogeography of psychrophilic microorganisms in various cold environments, considering the most recent knowledge on selected aquatic and terrestrial cold ecosystems.

2. Aquatic cold environments

2.1. Atmosphere and clouds

Viable bacteria, often dominated by Gram-positives, have been found at altitudes of the atmosphere up to the stratosphere

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and mesosphere (41–77 km) where the temperature may reach −100 °C (Griffin, 2008; Pearce et al., 2009; Wainwright et al., 2004). Microbial survival in this low temperature environment is also impacted by high UV radiation, oxidative stress, low nutrients and desiccation. Cells originating from different terrestrial, aquatic, animal and plant surfaces are transported with aerosol particles vertically and horizontally over short and long distances depending on meteorological and seasonal conditions. A recently created model of the global atmospheric transport of bacteria has estimated the mass of bacteria emitted annually in the atmosphere to be 40–1800 Gg (1 Gg = 10^9 g) (Burrows et al., 2009). Microbial cells reside in the atmosphere for different length of time (days to weeks), and are subsequently transported (or deposited with precipitation) to different ecosystems, which is relevant to the field of microbial biogeography (see Section 4).

The ubiquitous presence of microorganisms in the atmosphere has raised the question of their metabolic activity and possible active role in atmospheric processes and particularly in cloud formation (Morris et al., 2008). Clouds are an important part of the atmosphere formed as water vapors are cooled and condensed into water droplets or ice crystals. Cloud water is considered a more favorable microbial habitat than dry air because cloud droplets stay liquid at temperatures far below 0 °C where cells can metabolize organic compounds (Sattler et al., 2001) and affect atmospheric chemistry (Deguillaume et al., 2008). Diverse bacteria and fungi have been found in tropospheric cloud water, in the range of 10^3-10^5 per ml including novel species (e.g. *Deinococcus aethius, Bacillus stratosphericus* (Table 1S); Ahert et al., 2007; Amato et al., 2005, 2007b). Furthermore, the ability of microbial cells to act as cloud condensation and ice-forming nuclei, thus impacting cloud formation and precipitation development, has drawn significant scientific interest. Bauer et al. (2002) showed that airborne bacteria can be activated as cloud condensation nuclei at suitable supersaturation conditions. Recently, a possible role of microbial glyco- and lipoprotein biosurfactants enhancing cloud condensation efficiency was suggested (Ekstrom et al., 2010).

The phenomenon of ice nucleation (IN), related to a specific protein on the cell surface of plant-associated species *Pseudomonas* and *Xanthomonas* was extensively explored genetically and biotechnologically since the 1970s. However, the ecological role of biological ice nucleators in atmospheric processes is still unclear and has been investigated recently using novel methodological approaches (Mohler et al., 2007). Typically airborne microbial cells with IN activity can catalyze ice crystal formation in clouds at relatively high temperatures (up to −2 °C) and induce rain or snow precipitation. Their ubiquitous distribution and abundance (4–490 ice nuclei per l) in rain and snow over different continents, reported by Christner et al. (2008a, 2008c), has been linked to seasonal and precipitation chemistry variations with suggested impact on meteorological processes. Another comprehensive study of IN activity and community composition using tagged pyrosequencing of atmospheric samples over Colorado showed minimal variability of the bacterial and fungal composition and abundance during different atmospheric conditions, but a significant increase of IN activity in clouds during high humidity periods, indicating a strong capacity of ice nucleators to respond to environmental triggers (Bowers et al., 2009). Interestingly, representatives of the genus *Psychrobacter* with IN activity, common in many permanently frozen environments, were dominant in air samples but not in fresh snow. These differences show that although snow and clouds may be linked as ecosystems, they have distinct microbial communities.

2.2. Snow

Snow is a massive component of the cryosphere, which covers permanently or seasonally up to 35% of the Earth's land surface, predominantly in the Northern Hemisphere. Specific ecologically important characteristics are seasonal temperature fluctuation, aerobic conditions and very high light and UV irradiation (Cockell and Cordoba-Jabonero, 2004; Jones, 1999). As a habitat, snow is related to the atmosphere due to the constant aeolian fluxes of dust, microbial cells and other biological material deposited with precipitation. Snow is also the source for the formation of glaciers and may impact soils temporarily covered with snow (Hodson et al., 2008; Pearce, 2009; Pearce et al., 2010).

Historically, diversity studies focused on photosynthetic snow algae causing snow coloration with their high activity as primary producers in this intensively illuminated environment (Hoham and Duval, 2001). Recently, dominant *Hymenobacter* bacterial species were also found in red snow (Fujii et al., 2010). During the last 10 years, the bacterial abundance and diversity of different seasonal and permanent snow ecosystems were examined using both molecular and cultivation methods (reviewed in Miteva et al., 2009). In summary, microbial abundance in snow cover varies with altitude and latitude. Different authors found cell numbers ranging from 10^3 to 10^5 per ml in melted snow, which usually positively correlated with Ca^{2+} concentrations, serving as a proxy for dust. Abundance was lower in Antarctic than in mountainous and Arctic snow and increased with altitude (Carpenter et al., 2000; Liu et al., 2006). Significant prokaryotic diversity has been detected, including heterotrophic bacteria, cyanobacteria and eukaryotes, with many related to known psychrophilic and psychrotolerant species (Amato et al., 2007a; Segawa et al., 2005). Interestingly, unlike other cold environments, no novel species have been described from snow. Comparisons of snow cover samples by depth, season or geographic location revealed some patterns. The significant in-depth diversity shifts between surface snow, serac snow and ice were most likely due to post-depositional community changes caused by rapid changes in environmental conditions (Liu et al., 2007; Xiang et al., 2009b). Another important observation was that snow bacterial community structure fluctuated seasonally (Larose et al., 2010; Liu et al., 2006; Segawa et al., 2005). Similar seasonal and diel dynamics was detected in photosynthetic activity of snow algae from Svalbard, Norway (Stibal et al., 2007). However, these variations were specific for different geographic locations (e.g. Mt. Everest and Tateyama mountain, Japan), suggesting that

different atmospheric currents deposited different bacteria to these sites. Finally, snow samples from the surface of four Tibetan plateau glaciers located in different climatic zones showed high diversity and significant differences between glaciers with only 15 out of 82 bacterial genera common for all glaciers (Liu et al., 2009b). In addition to being active photochemical reactors, microorganisms in dry polar snow were shown to be involved in active exchange of reactive nitrogen species with the atmosphere and were thus contributing to biogeochemical cycling at low temperature (Amoroso et al., 2010). The importance of snow to biogeochemical cycling was also supported by the strong correlation between snow cover dynamics and fungal and bacterial diversity in alpine tundra soils (Zinger et al., 2009).

2.3. Cryoconite holes

Cryoconite "ice dust" holes are specific water-filled ice depressions (<1 m wide and <0.5 m deep) with dark material on the bottom that are commonly found on the surface of all snow-free glaciers. They are formed by airborne debris which absorbs more solar radiation and melts down into the ice. Most cryconite holes are open to the atmosphere, while those in Antarctica (Mc Murdo Dry Valley) are covered by an ice lid and in some cases are connected to the subsurface runoff system (reviewed in Hodson et al., 2008; MacDonnell and Fitzsimons, 2008). Diversity studies of polar and alpine cryoconite holes detected abundant microbial communities including photosynthetic cyanobacteria and algae, heterotrophic bacteria, viruses, yeasts, diatoms and metazoa, many of which showed remarkably good cold adaptation and growth characteristics (Anesio et al., 2007; Christner et al., 2003a; Margesin et al., 2002; Vincent, 2007; Zhakia et al., 2008). The description of a number of novel cold-adapted bacterial (*Pedobacter cryoconitis*, *Sphingomonas glacialis*) and yeast taxa (*Rhodotorula glacialis*, *Mrakiella cryoconiti)* (Table 1S) indicates the unique community compositions of these glacial habitats (Margesin et al., 2003; Margesin and Fell, 2008; Zhang et al., 2010), which also vary seasonally, geographically and with changes of the local physico-chemical parameters (Edwards et al., 2010).

These supraglacial mini-ecosystems are considered "hot spots" of microbial metabolic activity, which explains the strong interest in their biogeochemical processes, chemical gradients and nutrient cycling. Numerous studies have shown that microbial photosynthesis and primary production are the major drivers of cryoconite hole processes, providing organic carbon for the heterotrophic bacteria (Bagshaw et al., 2007; Foreman et al., 2007; Stibal et al., 2008). The calculated global net carbon fixation of 64 Gg yearly is comparable to many moderate temperature environments and indicates the need for further studies of the dynamics of the cryoconite hole processes and their ecological role (Anesio et al., 2009).

2.4. Glaciers

Compared to other parts of the cryosphere, glacier ice is considered the most harsh environment for living organisms due to subfreezing temperatures ranging from −56 °C to −10 °C, high hydrostatic pressure, low nutrient and water availability, darkness, etc. However, the vast polar and non-polar glaciers and ice sheets, covering 15,861,766 km^2, contain an enormous reservoir of microbial life (9.61×10^{25} cells) that is uniquely preserved in chronological layers for thousands of years (Priscu and Christner, 2004; Priscu et al., 2007). Glaciers are dynamic ecosystems with different thermal regimes, physical, hydrological and geochemical characteristics in their supraglacial (cryoconite holes), deep ice or subglacial portions (Hodson et al., 2008). This section refers to deep glacial ice. Microbial cells originating from geographically close and distant places are deposited with snow and gradually embedded in the deeper ice layers reaching 3–4 km at the poles. Major sources of microbial cells are terrestrial dust, marine surface aerosols and volcanic ashes. Microbial abundance varies between glaciers and with depth and altitude and ranges from $<10^2$ to 10^6–10^7 cells per ml. The pioneering work of Abyzov (1993) in Antarctica showed that these fluctuations are directly proportional to the dust load in annual snow precipitation with higher cell numbers deposited during colder conditions. Similar correlations were reported for Tibetan and Greenland ice (Miteva et al., 2009; Xiang et al., 2005; Yao et al., 2006; Zhang et al., 2008).

Diversity studies of glaciers are methodologically challenging because they rely on drilling deep ice cores, need rigorous decontamination, use limited sample volumes of low microbial content for DNA isolation and cultivation is possible for a small fraction of the population. Regardless, recent methodological advances intensified microbiological studies of polar and non-polar glaciers and showed widely variable morphological, physiological and phylogenetic microbial diversity (reviewed in Miteva, 2008). Detected glacier microorganisms were dominated by major bacterial phylogenetic groups: *Actinobacteria*, *Firmicutes*, *Proteobacteria*, CFB (*Cytophaga-Flavobacterium-Bacteroides*), and included psychrophilic microbial eukaryotes (fungi, yeasts), some plant and bacterial viruses and a few *Archaea*. Similar taxonomic representation was found in the first recently published glacier ice metagenome analysis (Simon et al., 2009) which revealed the potential for degrading a variety of organic substrates. Despite the few detected photosynthetic genes, the importance of autotrophic lifestyle in this low nutrient environment was indicated by a significant number of genes for carbon fixation. Another prominent gene group was related to aerobic metabolism, which correlated with finding predominantly aerobic and facultative aerobic organisms.

Many bacterial and fungal isolates have been recovered from ancient ice samples in Greenland, Antarctica and Tibet, the oldest reaching 750,000 years (Abyzov, 1993; Christner et al., 2000, 2001, 2003b; Liu et al., 2009a; Miteva and Brenchley, 2005; Miteva et al., 2009; Turchetti et al., 2008; Xiang et al., 2009a; Zhang et al., 2008, 2009b), including about 20 novel species (Table 1S). Common physiological and cellular features of isolated microorganisms are colony pigmentation, ability to grow at low temperatures with low nutrient concentrations, specific membrane structure, synthesis of cryoprotectants,

exopolymers, cold-active enzymes and ice-binding proteins (Margesin et al., 2005, 2007; Bej and Mojib, 2010). In particular, the ice-binding (or antifreeze) proteins of glacier bacteria that inhibit the growth of ice crystals have been studied recently (Christner, 2010; Raymond et al., 2008). Interestingly, metagenome analysis found a large number of genes related to all these functions (Simon et al., 2009).

The ability of microorganisms to survive trapped in glaciers for long periods has raised the question whether they are metabolically active. Price (2000, 2009) suggested three habitats for live metabolically active microbial cells within the polycrystalline ice: 1) the liquid veins between ice crystals; 2) the thin liquid layer coating the mineral grains; and 3) the interior of individual ice crystals. Because of the extreme in situ conditions, microbial activity may be restricted to basic maintenance needed to repair molecular damage with increased metabolic potential under suitable conditions. This hypothesis has been supported by microscopic observations of cells partitioned in veins (Mader et al., 2006) and numerous demonstrations of microbial activity at subfreezing temperatures down to −39 °C (reviewed in Bakermans, 2008). Because glacial ice preserves ancient DNA (Willerslev and Cooper, 2005), Earth glaciers provide an excellent model to refine strategies for searching for life on icy extraterrestrial bodies.

Several recent studies have explored the relationships between the excellent existing historical records of past climates in glacier ice and the parallel chronological archive of microbial life (Miteva et al., 2009; Yao et al., 2006, 2008). The detected diversity patterns in ice layers deposited under different climate conditions support the idea that local and global climates have influenced the abundance, origin and composition of glacier microbial populations and may lead to microbial markers as new tracers of past climates.

2.5. Polar and alpine lakes

Cold lakes on Earth are represented by polar and high altitude alpine lakes with significant limnological diversity ranging from freshwater to hypersaline, from highly acidic to alkaline, from highly oxygenated to anoxic, permanently ice-covered or ice free (due to different temperature regimes) (Vincent et al., 2008). The number of lakes in the Arctic (1432) is much greater than in Antarctica (174) because of the different geography, environmental conditions and origin (Ryanzhin et al., 2010).

2.5.1. Arctic lakes

The total area of natural lakes in Arctic regions is estimated to be >80,000 km^2 (Ryanzhin et al., 2010). Recent studies suggest that bacterial processes in coastal arctic ecosystems are likely to occur throughout all seasons. Bacterial production varied from 1 mg C m^{-2} day^{-1} in winter to 80 mg C m^{-2} day^{-1} in summer, and mean bacterial abundance in the water column ranged from 1×10^5 cells per ml in winter to 7×10^5 cells per ml in summer (Garneau et al., 2008). However, distinct temperature optima for activity (12 °C and 20 °C), as observed in lakes and streams in northern Alaska, point to the presence of different groups of bacteria (Adams et al., 2010).

Cyanobacteria, especially representatives of *Oscillatoriales*, *Nostocales* and *Chroococcales*, play a dominant role in High Arctic lakes, streams and ice communities (Bonilla et al., 2005; Jungblut et al., 2010; Tang et al., 1997). This is seen as a result of a number of competitive advantages, such as tolerance to desiccation, freeze-thaw cycles and solar radiation, and the ability to grow over a wide temperature range (Tang et al., 1997). Several of the ribotypes detected in the High Arctic were found to be similar to those in Antarctica and in alpine regions (Jungblut et al., 2010).

Euryarchaeota and *Crenarchaeota* colonize different cold habitats. They dominate among archeal communities in High Arctic lakes, which are highly stratified (Galand et al., 2008a; Pouliot et al., 2009). *Euryarchaeota* dominated in the oxic layers, but were also found in the anoxic zone. Nitrification by archaea within the oxycline (a sharp gradient in oxygen concentration) was evidenced by the presence of ammonia monooxygenase A gene variants (Pouliot et al., 2009). In an arctic shelf ecosystem, such as riverine and coastal waters *Euryarchaeota* were mainly associated with particle-rich waters, while *Crenarchaeaota* were almost exclusively found as free-living inhabitants of marine waters, i.e. waters that are less influenced by riverine input (Galand et al., 2008a).

Stamukhi lakes represent frequent ecosystems in the Arctic. These lakes are the result of freshwater retention behind the thick barrier of rubble ice (stamukhi) that forms at the outer limit of land-fast sea ice, and play a key role in processing riverine inputs to the ocean. A recently studied stamukhi lake in the western Canadian High Arctic contained *Betaproteobacteria, Bacteroidetes* and *Euryarchaeota*, whereas ciliates were the dominant fraction among eukaryotes. Bacterial and eukaryotic communities in this lake differed in composition and diversity from the source waters (marine and freshwater) of the lake, while archeal communities were similar in the lake and its freshwater source. Bacterial abundance was not related to heterotrophic production rates (Galand et al., 2008b).

In the Arctic region, the total area of ice shelves is lower than in Antarctica. In addition, global warming has contributed to a massive reduction of the arctic ice shelve (Mueller et al., 2005). Microbial metabolism (respiration) in ice shelves in the Canadian High Arctic was detected at temperatures as low as −10 °C. *Bacteroidetes*, *Proteobacteria* and *Actinobacteria* constituted the major fraction among bacteria; archeal communities were represented by *Euryarchaeota* (Bottos et al., 2008).

2.5.2. Alpine lakes

Alpine mountain lakes are covered with a 1.5–3 m thick ice sheet for a period of 6–9 months per year. The ice cover is characterized by a sandwich-like structure of alternating layers of ice and slush (Psenner et al., 1999), which form a highly productive habitat with even higher carbon turnover rates than in the warmer pelagic zone due to the accumulation of nutrients from the lake catchment area and atmospheric deposition (Waldhuber et al., 2002). UV exposure levels are high in alpine lakes due to a thinner atmosphere, high water transparency and very low contents of dissolved organic carbon (Rose et al.,

2009). Climate-driven changes in dissolved organic matter enrichments also affect the composition and activity of microbial communities (Perez and Sommaruga, 2007).

Pro- and eukaryotic lake ice microbial communities originate from various sources, such as lake water, soil, littoral sediment, or atmosphere (Psenner et al., 1999). The drastic changes in the physical and chemical structure of the ice cover during its formation, growth and ablation determine biomass and composition of microbial assemblages (Felip et al., 2002). Bacterial abundance and community composition vary in the different lake ice layers. Slush layers contained up to 6×10^5 cells per ml (total cell counts); up to 4×10^5 cells per ml were found in lake water and snow. Members of *Betaproteobacteria* dominated in all layers, *Alphaproteobacteria* were found to a lower extent in slush and lake water and low representation of CFB was only found in slush (Alfreider et al., 1996). Microbial production and activity were highest in slush layers, low in lake water and not detectable in snow. The preferred temperature range for production and activity of lake water bacteria was near 15 °C, while both production and activity decreased considerably at temperatures above 5 °C in slush layers of the lake ice (Alfreider et al., 1996). This has been interpreted as a result of low predation pressure and high nutrient contents in lake ice, since high nutrient contents enhance growth rates at low temperatures (Felip et al., 1996).

The dominance of *Betaproteobacteria* and *Actinobacteria* in high mountain lakes has been demonstrated in a number of studies on microbial community composition (Hörtnagl et al., 2010; Pernthaler et al., 1998; Sommaruga and Casamayor, 2009). In six alpine lakes located across an altitude gradient, both the surface microlayer and its underlying water were predominantly inhabited by *Betaproteobacteria*, which also contributed to most of the microbial activity in both layers in all lakes, followed by *Actinobacteria* (Hörtnagl et al., 2010). *Bacteroidetes* dominated in plankton samples from two remote high altitude lakes in the Mount Everest region (Sommaruga and Casamayor, 2009). Interestingly, up to 81% of the phylotypes detected in six lakes in that region had high 16S rRNA gene sequence similarity to those reported from other alpine lakes and glaciers worldwide. Nonetheless, local environmental conditions influenced taxon sorting (Sommaruga and Casamayor, 2009).

Pelagic microbial communities in high mountain lakes are seasonally variable, annually recurrent and vertically stratified (Pernthaler et al., 1998). *Betaproteobacteria* were dominant throughout the year and represented 24% of total bacterial counts, while *Alphaproteobacteria* (11% of total counts) were dominant in spring. Bacteria of the CFB cluster were less abundant but significantly contributed most of the year to the total microbial biomass. Rod-shaped archaea, not further classified, were observed in the autumn during the period of ice cover formation (Pernthaler et al., 1998).

2.5.3. Antarctic lakes

The majority of ice-covered lakes on Earth are located in Antarctica. The continent contains more than 150 subglacial lakes most of which are interconnected by subglacial rivers, a large number of inland perennially ice-covered lakes in the ice free Mc Murdo Region and many coastal lakes with seasonally variable ice cover (see reviews by Hodson et al., 2008; Green and Lyons, 2009; Laybourn-Parry and Pearce, 2007; Priscu and Foreman, 2009; Sattler and Storrie-Lombardi, 2010).

Certainly, the largest, subglacial Lake Vostok, has been and still is the focal point of interest, although the lake itself has not yet been penetrated. The 200 m of accretion ice has been formed by refreezing on the bottom of the 4 km deep ice sheet. A large number of microbiological and biogeochemical studies of this basal ice have provided valuable information about the lake environment, which is extremely oligotrophic and highly oxygenated. Despite the extremely low number (400 cells per ml), diverse prokaryotic organisms including a thermophilic proteobacterium *Hydrogenophilus thermoluteolus* have been detected and isolates were related to all major phylogenetic groups (Bulat et al., 2004; Christner et al., 2001, 2008b; D'Elia et al., 2008, 2009; Priscu et al., 2008).

The Antarctic perennially ice-covered lakes include both freshwater and highly saline environments (seven times sea water salinity). The ice cover may reach 3–6 m and the water columns of these lakes are highly stable and exclusively microbial ecosystems. These lakes are considered "oases" of life in a polar desert and microbiological studies have revealed diverse and abundant (10^5–10^6 cells per ml) populations of bacteria, archaea, eukaryota and viruses within the ice cover and in the lake water, sediment and mats including over 30 novel psychrophilic species and genera (Table 1S) (Mosier et al., 2007; Laybourn-Parry and Pearce, 2007; Sawstrom et al., 2008; Stingl et al., 2008). The stable stratification of some lakes has enabled the development of high-density populations of low complexity (e.g. the dominant green sulfur bacterium from Ace Lake (Ng et al., 2010). Interestingly, the first psychrophilic methanogen *Methanogenium frigidum* and the psychrotolerant *Methanococcoides burtonii* were isolated from this lake (Franzmann et al., 1992, 1997). Hence, because of the geographic isolation and extreme environmental conditions in Antarctica, these microbially dominated pristine lake ecosystems provide models for studying microbial biogeography and evolution.

2.6. Deep sea and sea ice

Approximately 71% of the Earth's surface is covered by ocean and more than half of this area is over 3000 m deep. The deep sea is defined as the lowest layer in the ocean, below the thermocline, at a depth of 1000 fathoms (1 fathom = 1.8288 m) or more. This extreme environment is characterized by low temperature (2–4 °C); hydrothermal vents with temperatures up to 370 °C occur occasionally. The abyssal zone (3000–6000 m) and the hadal zone (>6000 m; the deepest part of the marine environment) are additionally characterized by high hydrostatic pressure (up to 110 MPa) and the absence of solar radiation. Nutrient availability is low; however, there is a high content of dissolved oxygen (for

example, about 4 ml dissolved oxygen per liter at 6000 m depth (Lauro and Bartlett, 2008; Nogi, 2008).

Microorganisms living in the deep sea have evolved several unusual features that allow them to thrive in their environment (Abe, 2004; Deming, 2009b). Most isolated strains are psychropiezophilic, i.e. psychrophilic and piezophilic (optimal growth at pressures >0.1 MPa), and cannot be cultured at temperatures higher than 20 °C (Nogi, 2008). Inhabitants from the deep sea form distinct clades with phyla from polar regions, which suggests that adaptation to low temperature might have evolved prior to acclimation to the deep sea (Lauro et al., 2007).

Communities of bacteria, archaea, protists and yeasts account for most of the biomass in the ocean and are responsible for 98% of primary production (Whitman et al., 1998). Microbial abundance in the deep sea is low; however, there is enormous phylogenetic diversity, which may be clearly underestimated by culture-based surveys. The composition of microbial communities should be much higher than estimates of a few thousand distinct kinds of microorganisms per ml of sea water (Sogin et al., 2006).

Among psychrophilic and piezophilic bacteria in the deep sea, members belonging to the class *Gammaproteobacteria* predominate. Most of these culturable bacteria were affiliated to novel genera *Colwellia*, *Moritella*, *Photobacterium*, *Psychromonas, Marinomonas* and *Shewanella* represented by many novel species (Dang et al., 2009; Lauro et al., 2007; Nogi, 2008) (Table 1S). They are characterized by a high amount of unsaturated fatty acids in their cell membranes. The widespread production of extracellular hydrolytic enzymes, such as amylases, proteases, lipases and DNAses, points to the ecological role of these bacteria in the biocycling of elements in the deep sea (Dang et al., 2009). Sulfate reduction in deep sea sediments can be attributed to *Deltaproteobacteria*, mostly members of the genus *Desulfovibrio* (Kaneko et al., 2007). Few Gram-positive bacteria were found; they belonged to the genus *Carnobacterium* and are closely related to *C. pleistocenicum* from permafrost (division *Firmicutes*) (Lauro et al., 2007). *Clostridium* strains appear only to survive in the form of spores in deep sea sediments; the spores were resistant to pressure and low temperature, while their vegetative cells appeared not to be adapted for growth in this environment (Lauro et al., 2004).

The dominant group of archaea in the deep sea might be chemoautotrophic. Ammonia-oxidizing archaea (*Crenarchaeota*) have been detected in water samples at 2000–3000 m depth columns and in sediments of the ocean (Francis et al., 2005; Nakagawa et al., 2007). They are assumed to play a significant, but previously unrecognized role in the global nitrogen cycle (Francis et al., 2005). Their abundance and ability to function at 4–10 °C indicates that psychrophilic ammonia-oxidizing archaea may be responsible for nitrification in the deep ocean (Nakagawa et al., 2007; Kalanetra et al., 2009).

Only a few reports are available on the occurrence of yeasts and filamentous fungi in the deep sea. Fungi in general are relatively rare in deep sea habitats, as demonstrated by a study on the fungal diversity in 11 deep sea samples collected at depths from 15,000 to 4000 m around the world. Only 32 fungal 18S-types have been recovered, with a predominance of distantly related yeasts and only 4 putative filamentous fungal types (Bass et al., 2007). The isolation frequency of yeasts decreases as the depth of the sampling site is increased (Kutty and Philip, 2008). Deep sea regions contain ca. 10 or fewer yeast cells per liter, although favorable local nutrient conditions may result in 3000–4000 cells per liter. Yeasts isolated down to a depth of 4000 m include basidiomycetous and ascomycetous representatives and belong mainly to the genera *Rhodotorula*, *Cryptococcus*, *Debaryomyces*, *Torulopsis* and *Candida* (for references, see the review by Kutty and Philip, 2008).

Sea ice is one of the most extreme and extensive cold habitats, covering an area of over 30 millions km^2 in the polar oceans (Collins et al., 2010). Its seasonally variable semi-solid ice matrix with a net of brine channels provides a microbial habitat of low temperature (0 to −35 °C), high salinity (35-200 psu), high pH and low solar irradiation. The abundant microbial communities found in sea ice of northern and southern polar oceans have shown dynamic spatial and temporal heterogeneity with greater abundance in the upper and the lowest layers (Bowman and Deming, 2010; Collins et al., 2008; Gosink et al., 1993; Junge and Swanson, 2008; Sullivan and Palmisano, 1984). These remarkably diverse communities, dominated by diatoms, have been found to persist in sea ice and contribute to the primary production in the polar oceans (Collins et al., 2010). Important findings based on studies of model organisms such as *Colwellia psychrerythrea* and *Psychromonas ingrahamii* and their habitats showed unusually high culturability compared to sea water, significant physiological plasticity for acclimation at constantly changing conditions, evidence for endemic species. For comprehensive reviews on sea ice microbial adaptation, diversity and biogeography see Staley and Gosink (1999), Mock and Thomas (2005) and Deming (2009a).

3. Terrestrial cold environments

3.1. Cold soils

3.1.1. Arctic soils

Limiting factors for microbial activity in arctic soils are extreme temperatures, freeze-thaw cycles, low annual precipitation, low soil moisture and low contents of available nutrients.

Microbial communities in Finnish Lapland (Männistö and Häggblom, 2006; Männistö et al., 2007) are dominated by Gram-negative bacteria consisting mainly of members of the *Alpha-*, *Beta-* and *Gammaproteobacteria* and the CFB phylum; abundance of Gram-positives seems to be low. Pseudomonads represented 60% of all isolates in Arctic tundra soils. A high abundance of members of the phylum *Acidobacteria* was found in low pH soils. Nonetheless, almost 30% of clones from Arctic tundra soils belonged to unclassified bacteria, which may play a significant yet unknown ecological role (Gilichinsky et al.,

2008). Differences in microbial community composition could be attributed to variations in bedrock materials rather than to altitude or vegetation (Männistö et al., 2007). In contrast, Wallenstein et al. (2007) reported a significant influence of vegetation on bacterial and fungal community structure in Alaskan soils. Tussock soils contained high amounts of recalcitrant compounds and were dominated by *Acidobacteria* and *Ascomycota*, while *Proteobacteria* and *Zygomycota* were more abundant in shrub soils with higher amounts of bioavailable carbon sources. The production of a wide range of extracellular enzymes, such as proteases, lipases, cellulases and amylases, with high activities at low temperatures, points to the ecological role of Arctic bacteria in their cold environment (Männistö and Häggblom, 2006).

Psychrophilic active methanotrophs (*Methylobacter*, *Methylosinus*) in Arctic soils, especially in peat wetlands, are of importance for the regulation of increased methane emission due to climatic warming (Trotsenko and Khmelenina, 2005; Wartiainen et al., 2003). Methanogenic archaea that catalyze methane production via hydrogenotrophic or acetoclastic methanogenesis at low temperatures were affiliated with *Euryarchaeota* (Hoj et al., 2005). They may compete (for hydrogen) with psychrophilic homoacetogenic bacteria (*Acetobacterium*), which are important hydrogen consumers in cold anoxic sediments (Kotsyurbenko et al., 2001).

3.1.2. Alpine soils

The term "alpine" implies a high altitude belt above continuous forests on mountains. Alpine soils are subjected to large temperature fluctuations, a high number of frost and ice days, regular freeze-thaw-events and high precipitation. Microbial communities may vary seasonally (Lipson, 2007).

An increase in altitude and thus in environmental harshness generally results in a decrease in microbial abundance and activity, as well as in shifts in microbial community composition. With increasing altitude, a significant increase in the relative amounts of culturable psychrophilic heterotrophic bacteria, fungi and FISH-detected (thus active) Gram-negative bacteria was found in the Austrian Central Alps. *Proteobacteria* dominated at high altitudes, while the number of members of the CFB group decreased. Microbial (dehydrogenase) activity decreased with altitude; however, activity at higher altitudes was characterized by a lower apparent optimum temperature and a significantly higher relative activity in the low temperature range compared to soils from lower altitudes (Margesin et al., 2009).

Diversity of the psychrophilic bacterial community in high altitude cold soils of the Himalayan mountains decreased with increasing altitude. The culture-independent approach revealed a dominance (73%) of *Preoteobacteria,* with *Betaproteobacteria* as the most abundant class (31%). However, viable cultured bacteria consisted of almost equal amounts of Gram-negative bacteria (51%, with a dominance of *Gammaproteobacteria* (39%) and low amounts of *Bacteroidetes* (6%)) and Gram-positive bacteria (48%, with a dominance of *Firmicutes* (32%). Isolates produced a number of hydrolytic enzymes; the most frequently observed enzyme was lipase (Gangwar et al., 2009). The ability to solubilize phosphate at low temperatures has been observed with pseudomonads (Selvakumar et al., 2009). Soils at high altitudes (3000–5400 m) in the Anapurna Mountains, Nepal, are characterized by low water activity due to dry climate, and consequently these soils contained psychrophilic fungi with xerophilic characteristics; the most extreme xerophiles belonged to the ascomycetous genera *Eurotium* and *Aspergillus* (Petrovic et al., 2000). Another example of alpine soil bacterial xerophiles are novel species from the genus *Deinococcus,* which are also radiation-resistant (Table 1S). *Chytridiomycota* dominated fungal diversity in periglacial soils at high altitudes in the Himalayas and Rockies (Freeman et al., 2009).

Ammonia-oxidizing bacteria and archaea were found in high altitude soils (4000–6500 m) of Mount Everest. Their abundance was influenced by altitude. Archeal ammonia oxidizers were more abundant than bacterial ones at altitudes below 5400 m, while the situation was reversed at higher altitudes (Zhang et al., 2009a).

3.1.3. Antarctic soils

Antarctic terrestrial ecosystems differ from those in the Arctic as they are colder (subzero temperatures down to −60 °C), drier (moisture content of 1–10%), lower in available nutrients and often alkaline, since soils accumulate salts from precipitation and weathering due to the extreme aridity.

Microbial diversity and abundance in terrestrial Antarctic have been recently reviewed (Bej et al., 2010). Culture-dependent and culture-independent methods often revealed different pictures (Aislabie et al., 2006; Babalola et al., 2009; Smith et al., 2006). For example, Antarctic Dry Valley soils (cold deserts) harbored *Actinobacteria* as one of the major phylogenetic groups, while the majority of the cultured isolates (>80%) were *Streptomycetes*, which were only detected at a low frequency by metagenomics (Babalola et al., 2009). A high number of phylotypes have not yet been cultured. In general, diversity of viable bacteria and fungi is low (although influenced by local environmental conditions), which supports the hypothesis that extreme environments harbor relatively low species diversity (Gilichinsky et al., 2007; Negoita et al., 2001; Smith et al., 2006). Nonetheless, several novel bacterial and fungal representatives could be isolated (Table 1S). Indicators of vital and enzymatic activities showed the existence of potentials for mineralization and biosynthesis (Negoita et al., 2001). The occurrence and biodiversity of microorganisms is higher in the C-horizon than in the top layer, which is typical of cryptoendolithic communities (Gilichinsky et al., 2007).

Archaea are not abundant in Antarctic soils (Aislabie and Bowman, 2010); the majority belong to *Crenarchaeota* and one of their putative functions in soil is nitrification. Ammonia oxidizers have also been found among bacteria (Shravage et al., 2007). Similarly, yeasts and filamentous fungi are present in low numbers (Vishniac, 1996). Among yeasts, capsular *Cryptococcus* species and the related genus *Mrakia* dominate in Antarctic desert soils and are well adapted to local conditions by growth at low temperatures and minimal nutritional requirements.

3.2. Permafrost

Permafrost is one of the most extreme environments on Earth and covers more than 20% of the Earth's land surface. Permafrost has been defined as lithosphere material (soil, sediment or rock) that is permanently exposed to temperatures ≤0 °C, remains frozen for at least 2 consecutive years (Pewe, 1995) and can extend down to more than 1000 m into the subsurface. Permafrost regions occur at high latitudes, but also at high elevations; a significant part of the global permafrost is represented by mountains.

Detailed characteristics of Arctic, Antarctic and mountain permafrost have been recently reviewed (Margesin, 2009). The Arctic permafrost is characterized by a mean annual temperature of −10 °C, low nitrogen content and an organic carbon content of 0.05–7%. The Antarctic permafrost is generally ice-cemented, but may be loose in drier soils; further characteristics are alkaline pH conditions, low contents of clay and organic matter; temperatures range from −18.5 °C to −27 °C. Mountain permafrost can be found at low and high latitudes. It is invisible, extremely variable and heterogeneous, and due to topography and variable surface conditions, temperature does not simply increase with depth.

Permafrost soils contain ca. 20–70% of ice and 1–7% of unfrozen water in the form of salt solutions with low water activity (a_w = 0.8–0.85) (Gilichinsky, 2002). In addition, microorganisms in this environment have to thrive at constant subzero temperatures, oligotrophic conditions, complete darkness and constant gamma radiation. They are resistant to freeze-thaw stress, to radiation, and also, surprisingly, to a wide range of antibiotics combined with the presence of mobile genetic elements (Petrova et al., 2009), which might be part of a generalized bacterial response to stress conditions.

Considerable abundance and diversity of microorganisms, including bacteria, archaea, phototrophic cyanobacteria and green algae, fungi and protozoa, are present in permafrost. The characteristics of these microorganisms reflect the unique and extreme conditions of the permafrost environment. Substantial growth and metabolic activity (respiration and biosynthesis) of permafrost bacteria and fungi at temperatures down to −20 °C and even −39 °C have been demonstrated (Bakermans, 2008; Panikov et al., 2006; Panikov and Sizova, 2007).

Microorganisms in permafrost have been studied by culture-dependent and culture-independent methods (for reviews, see Gilichinsky et al., 2008; Steven et al., 2006, 2009). The microbial long-term survival in permafrost has been questioned; however, there is evidence that bacteria are able to survive in 500,000-year-old permafrost (Johnson et al., 2007). Despite the fact that only a small fraction of the microbial community is culturable, the low recovery of viable cells from permafrost can be explained by a large amount of dwarfed, very small (≤1 μm) cells, which are typical of the viable but non-culturable state (Oliver, 2005). Other factors that hamper the isolation of viable cells are old age of permafrost and a large amount of ice in permafrost samples. On the other hand, care has to be taken when interpreting the presence of DNA sequences, since it is not proof of viability or even activity (Willerslev et al., 2004).

Bacterial communities in permafrost include aerobes and anaerobes. The reducing conditions in permafrost favor the preservation of anaerobes such as acetoclastic and hydrogenotrophic methanogens, sulfate reducers, Fe(III)reducers and denitrifiers (Gilichinsky et al., 2008). Denitrifiers and acetoclastic methanogens were found in high numbers in old permafrost layers (Rivkina et al., 1998). Ancient permafrost sediments also contain a wide diversity of methanotrophic bacteria (e.g., *Methylomicrobium*, *Methylobacter*) able to oxidize and assimilate methane at subzero temperatures (for a review, see Trotsenko and Khmelenina, 2005). The genera *Exiguobacterium* (Gram-positive and facultatively anaerobic) and *Psychrobacter* (Gram-negative) have been repeatedly isolated from ancient Siberian permafrost (Rodrigues et al., 2009; Vishnivetskaya et al., 2009) (Table 1S). Members of both genera are adapted to long-term freezing (at temperatures as low as −12 °C where intracellular water is not frozen), they grow at subzero temperatures and display several features of psychrophiles, such as membrane composition and IN activity (Ponder et al., 2005; Rodrigues et al., 2009).

Bacterial abundance in permafrost varies depending on the environment. According to direct microscopic counts, Siberian and Antarctic permafrost yield 10^7–10^8 and 10^5–10^6 cells per *g* dry mass, respectively (Gilichinsky et al., 2008). The viable fraction (<0.1–1%) in various permafrost regions could be assigned to at least 70 genera, with a predominance of Gram-positive representatives of the phyla *Actinobacteria* and *Firmicutes*. Very old permafrost contains an increased amount of *Actinobacteria* (Willerslev et al., 2004). *Gammaproteobacteria* (esp. *Xanthomonadaceae*) dominate among *Proteobacteria*, while members of the CFB phylum have been found at a low extent (Gilichinsky et al., 2008; Steven et al., 2006, 2009; Vishnivetskaya et al., 2006). Culture-independent methods revealed the dominance of Gram-positive bacteria (up to 45 and 57% in Siberian and Antarctic permafrost, respectively) and *Gammaproteobacteria* (Gilichinsky et al., 2008; Vishnivetskaya et al., 2006).

Very few data are available on alpine permafrost. The most abundant and diverse viable isolates in alpine permafrost in China were members of Gram-positive bacteria, with a dominance of the genus *Arthrobacter* (Bai et al., 2006). Molecular analyses, however, showed the dominance of various classes of *Proteobacteria* (Yang et al., 2008). The Tibet Plateau permafrost region contained 10^2–10^5 viable bacteria per *g* dry sample; notably, almost 90% of these isolates were Gram-positive (with a high dominance of *Actinobacteria*), and only 10% were Gram-negative and members of *Alphaproteobacteria*. The isolates were adapted to growth at low temperatures and alkaline conditions and produced a wide range of extracellular enzymes such as proteases, amylases and cellulases (Zhang et al., 2007).

Among archaea, *Euryarchaeota* (*Methanomicrobiaceae*, *Methanosarcinaceae*, *Methanosaetaceae*) and – to a lesser extent – *Crenarchaeota,* have been detected in Siberian and alpine permafrost. Some of the methanogens are halophiles (Ganzert et al., 2007; Rivkina et al., 2007; Yang et al., 2008). Methanogenic activity at low temperatures increased with

increasing depth, but a relation between activity and diversity of methanogens in permafrost soils could not be shown (Ganzert et al., 2007).

There are only very few reports on yeasts in permafrost. Viable basidiomycetous yeasts were found in significant amounts (up to 9000 cfu g^{-1} dry mass) in Siberian permafrost soil with an estimated age of 3 million years (Dmitriev et al., 1997) and could be affiliated with the genera *Cryptococcus*, *Rhodotorula* and *Sporobolomyces* (Dmitriev et al., 1997; Golubev, 1998). Abundance of mycelial (filamentous) fungi in permafrost varies from below 10 to 10^5 fungal colonies per *g* sample. No relation between fungal abundance and depth or age of permafrost could be detected (Kochkina et al., 2001; Ozerskaya et al., 2009). The index of abundance (ratio of the number of species to the total abundance) often tends to zero. Arctic permafrost is inhabited by considerable taxonomic diversity of Asco- and Basidiomycetes. The most common genera are *Geomyces*, *Cladosporium* and *Aspergillus*, while the highest number of species was found among the genus *Penicillium* (for a complete list of fungal biodiversity in arctic permafrost, see Ozerskaya et al., 2009).

The presence of photoautotrophic microorganisms in permafrost is surprising. Despite complete darkness, viable cyanobacteria (and green algae) have been found in Siberian permafrost samples (Vishnivetskaya, 2009). It is hypothesized that these photoautotrophs survive in permafrost for up to millions of years in a dormant or resting state, but they are readily reversible to proliferation without losing their photosynthetic capacity (Vishnivetskaya et al., 2003).

4. Microbial biogeography: an ecological perspective on cold biosphere diversity

Modern technologies and interdisciplinary approaches allow assessing spatial and temporal microbial diversity patterns relative to measurable environmental parameters that refer to the emerging field of microbial biogeography (Fierer, 2008; Green et al., 2008). Microbial biogeography is defined as the science that documents the spatial distribution of prokaryotic taxa in the environment on a local, regional and continental scale (Ramette and Tiedje, 2007). Several processes shape these patterns, such as dispersal, speciation and extinction, which were first introduced in eukaryotic ecology and recently applied to prokaryotes. Particularly relevant to biogeographical studies of the cold biosphere is dispersal, which is defined as the transport of free-living cells over large geographic distances made possible through a combination of favorable climatic factors (winds, storms), disseminating vectors (oceanic currents, dust, plant seeds, birds, insects) and the existence of mechanisms that enhance survival during atmospheric transport and lead to colonization of new habitats under favorable environmental settings. Thus, the different dispersal and colonization rates and survival abilities of microbial cells, as influenced by the intensity and length of varying environmental factors, likely shape the diversity patterns (Fierer, 2008).

How environmental heterogeneity and spatial limitations contribute to the formation of microbial biogeographic patterns is still disputable between opposing viewpoints, endemism versus cosmopolitan distribution. The traditional perception of cosmopolitan microbial distribution, "everything is everywhere but the environment selects" introduced at the beginning of the 20th century (Baas-Becking, 1934; Beijerinck, 1913), has been supported by studies showing the occurrence of similar phylotypes in similar habitats in geographically different regions (Finlay and Clarke, 1999). However, recent studies have provided evidence for local endemism of microbial populations in specific geographically isolated locations and of spatial patterns of microbial diversity (Papke et al., 2003; Souza et al., 2008; Whitaker et al., 2003). Different authors have pointed out that endemicity of free-living microorganisms can occur and known cosmopolitan taxa may display non-random patterns of abundance and co-occurrence depending on the analytical method's resolution (Green et al., 2008; Martiny et al., 2006; Pearce and Galand, 2008; Ramette and Tiedje, 2007). For example, Cho and Tiedje (2000) isolated fluorescent *Pseudomonas* strains from four continents showing cosmopolitan distribution based on 16S rRNA gene sequences, but geographically unique genotypes were revealed with rep-PCR fingerprinting which detects microdiversity.

Questions about endemism and cosmopolitan distribution have been raised for microorganisms inhabiting low temperature ecosystems, but they remain unanswered. Cold environments on Earth, and the poles in particular, provide ideal model systems of similar ecological characteristics, separated geographically by climatic barriers (Staley and Gosinks, 1999). It is also known that the fluxes of dust carrying microbial cells to both poles have different origins, e.g. eastern Asian deserts are the main source of dust deposited over Greenland, while dust in Antarctic ice originates mostly from Patagonia. However, most diversity studies of worldwide polar and non-polar glaciers at 16S rRNA gene resolution have consistently detected representatives of similar genera of *Actinobacteria, Proteobacteria* and *Cytophaga-Flavobacteria,* suggesting that members of these genera likely possess similar survival mechanisms (Christner et al., 2008b). Recently, Rodrigues et al. (2009) detected a higher abundance and diversity of two psychrophilic genera, *Psychrobacter* and *Exiguobacterium,* in Antarctica and in Siberian permafrost than in other climatic zones, and Vishnivetskaya et al. (2009) showed that psychrophilic and thermophilic *Exiguobacterium* strains from different environments formed two distinct divisions. Another study showed the importance of local environmental factors for community composition of remote high altitude lakes in the Mt. Everest region (Sommaruga and Casamayor, 2009). Endemicity was suggested for some eukaryotic and bacterial species in sea ice (Gast et al., 2004) and for cyanobacteria in Antarctic lakes (Laybourn-Parry and Pearce, 2007), while Jungblut et al. (2010) found global distribution of cold-adapted cyanobacteria throughout the cold terrestrial biosphere. Clearly, despite the growing recognition that microbes exhibit biogeographic patterns, further studies are needed for better understanding global microbial diversity and the environmental and evolutionary forces shaping it.

5. Cold adaptation: The basis of successful colonization and survival

Current knowledge on the microbial ecology and diversity of the Earth's cryosphere has shown that even the most extreme cold and frozen environments harbor enormously diverse, viable and metabolically active microbial populations representing major phylogenetic groups. Despite the variable metabolic capabilities and other differences in environmental conditions, the key feature of all cold-adapted microorganisms is the successful surmounting of the negative effects of low temperatures by evolving a range of structural and functional adaptations (for recent reviews, see Bej et al., 2010; Deming, 2009b; Feller, 2007; Gostincar et al., 2010; Margesin et al., 2008; Shivaji and Prakash, 2010; Siddiqui and Cavicchioli, 2006).

Adaptation to low temperatures depends on the ability to sense changes in temperature. One of the primary cold sensors is the cell membrane that acts as an interface between external and internal environments. At cold temperatures, the membrane becomes more rigid, which activates a membrane-associated sensor. The sensor transduces the signal to a response regulator, which induces upregulation of genes involved in membrane fluidity modulation, and ultimately results in upregulation of a number of genes involved in cold adaptation of bacteria (Shivaji and Prakash, 2010). A survey of genome sequences and proteomic studies of a number of psychrophilic bacteria and archaea shows that the main upregulated functions for growth at low temperatures are protein synthesis (transcription, translation), RNA and protein folding (adaptation of the molecular structure of proteins to ensure increased flexibility at low temperatures), maintenance of membrane fluidity, production and uptake of compounds for cryoprotection (extracellular polysaccharides, compatible solutes), antioxidant activities and regulation of specific metabolic pathways (Bowman, 2008; Medigue et al., 2005; Methé et al., 2005; Kurihara and Esaki, 2008; Ng et al., 2010; Riley et al., 2008; Saunders et al., 2003). Currently the functional low temperature limits of psychrophiles are −12 °C for reproduction and −20 °C for metabolism (reviewed in Bakermans, 2008). Although activity has been recently described at significantly lower subfreezing temperatures, these reports await replication and verification by other researches.

To increase membrane fluidity, microorganisms apply various strategies. When growth temperature is lowered, the most frequently noted change in fatty acid composition is in the extent of unsaturation, as observed with bacteria, archaea, fungi, and algae. Further modes of modulation of membrane fluidity include changes in fatty acid isomerization, an increase in methyl-branched fatty acids, in polar carotenoids and in the ratio of anteiso/iso-branched fatty acids, as well as a decrease in the average chain length of fatty acids and in the ratio of sterol/phospholipids (Deming, 2009b; Russell, 2008; Shivaji and Prakash, 2010).

Psychrophiles produce cold-active enzymes. These enzymes can be up to ten times more active at low and moderate temperatures as compared with their mesophilic homologues. Furthermore, these enzymes are heat-labile and are frequently inactivated at temperatures that are not detrimental for their mesophilic counterparts. The conformation and 3D structures of psychrophilic proteins are not markedly different from their mesophilic homologues. However, cold-active enzymes maintain the appropriate flexibility and dynamics of the active site at temperatures at which their mesophilic and thermophilic counterparts have severely restricted molecular motions (D'Amico et al., 2006; Feller, 2007).

Representatives of all thermal classes of bacteria (psychro-, meso- and thermophilic) display cold-shock response to sudden temperature changes. The cold-shock response in psychrophiles differs from that in mesophiles or thermophiles in two major aspects: cold-shock does not repress the synthesis of housekeeping proteins, and the number of cold-shock proteins is higher and increases with the severity of the cold-shock. In addition, psychrophiles permanently produce one set of proteins (cold-acclimation proteins) during growth at low temperature and increase the steady-state level of these proteins when the temperature is lowered (Phadtare, 2004).

Psychrophilic microorganisms produce various compounds to protect themselves or the extracellular environment against intracellular freezing or to minimize the deleterious effects of ice crystal formation (Christner, 2010; Deming, 2009a, 2009b; Margesin et al., 2008; Shivaji and Prakash, 2010). Osmoprotection of bacterial and fungal cells (Robinson, 2001) is achieved by the accumulation of compatible solutes (polyamines, sugars, polyols, amino acids). Antifreeze proteins (AFPs) are ice-binding proteins that have the ability to modify the ice crystal structure and inhibit the growth of ice in two ways. (i) Prior to freezing, they lower the freezing point of water without altering the melting point (thermal hysteresis activity). (ii) In the frozen state, AFPs show ice re-crystallization inhibition activity, whereby the proteins inhibit the growth of large crystals at the expense of small crystals at subzero temperatures (Gilbert et al., 2004). Bacteria may apply different strategies. Freeze tolerance can be obtained with low levels of thermal hysteresis activity but high re-crystallization inhibition activity. On the other hand, freeze avoidance by high thermal hysteresis activity can inhibit the growth of ice crystals before they propagate into the bacterium (Gilbert et al., 2005).

Bacteria living in cold aquatic environments (e.g. Antarctic and Arctic sea ice) produce high amounts of exopolymeric substances (Krembs et al., 2002; Mancuso Nichols et al., 2005). Key functions of exopolymeric substances include the mediation of adhesion to wet surfaces and the formation of the biofilm matrix, which traps nutrients, protects the cell against unfavorable environmental conditions and mediates biochemical interaction (Mancuso Nichols et al., 2005).

Protection against reactive oxygen species (ROS) is important for survival at low temperatures where the solubility of gases is increased. ROS can result in significant damage to cell structures. Bacterial strategies for the detoxification of ROS include the production of high amounts of antioxidant enzymes (catalase, superoxide dismutases, dioxygen-consuming lipid

desaturases) or the absence of ROS-producing pathways (Medigue et al., 2005; Methé et al., 2005).

Modern genomic studies are needed for better understanding the molecular basis of cold adaptation. As of August 2010, the number of completely sequenced genomes of psychrophiles is only 17 out of 1213 other prokaryotes, and 15 more psychrophilic genome projects are in progress out of 3625 other prokaryotes (see list in Table 1S) (http://www.ncbi.nlm.nih.gov/genomes/lproks.cgi). Further increasing the number of sequenced genomes of psychrophilic microorganisms and wider application of novel metagenomic and metaproteomic technologies will provide valuable information on the mechanisms of cold adaptation and the ecological roles of psychrophiles.

6. Conclusion

Psychrophilic microorganisms are subjected in their natural environments to low temperatures and often experience temperature fluctuations and frequent freeze-thaw events. The evolution of a number of adaptation mechanisms with regard to reproduction, metabolic activities, survival and protection strategies enables these microorganisms to be active at low temperatures and even at subzero temperatures.

There is great interest in, and rapid development of studies on, the microbial ecology of cold ecosystems. Culture-dependent and culture-independent molecular methods have been applied to gain an understanding of the diversity and ecological function of microbial populations in cold ecosystems. The emerging fields of genome and proteome analyses will provide further new insights into psychrophilic lifestyle. Studies on community structures revealed a wide range of diversity (including representatives of Gram-positive and Gram-negative bacteria, archaea, yeasts, filamentous fungi, and cyanobacteria) and indicate that psychrophiles are a large pool of novel and not yet cultured taxa. The development of improved methods to collect samples and isolate and culture psychrophiles may lead to an increase in the recovery of viable cells and novel taxa.

Due to the increasing interest in astrobiology, research in the microbial ecology and diversity of permanently frozen environments, such as ancient permafrost and ice, has increased considerably over the past years. Psychrophiles inhabiting frozen areas provide a prototype for possible life on cryogenic planets of the Solar System.

The emerging field of biogeography has demonstrated that the distribution and abundance of psychrophiles may exhibit geographic patterns, while some dominant species appear endemic to their environments. Polar cold environments provide ideal model systems of similar ecological characteristics separated geographically by climatic barriers.

Appendix. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.resmic.2010.12.004.

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