

Review Article

Diversity of Bacteria from Antarctica, Arctic, Himalayan Glaciers and Stratosphere

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This review explores the bacterial diversity of Antarctica, Arctic, Himalayan glaciers and Stratosphere with a view to establish their abundance, their identity and capability to adapt to cold temperatures. It also highlights the unique survival strategies of these psychrophiles at the molecular, cellular, tissue and organism level. It also establishes their utility to mankind in the spheres of health, agriculture and medicine. A major part of the review includes studies carried by scientists in India in the above extreme cold habitats.

Keywords: Diversity; Himalayan; Stratosphere; Antarctica

Bacterial abundance of Antarctica, Arctic, Himalayas and Stratosphere

Antarctica, Arctic and Himalayan regions are considered as highly arid, oligotrophic and extreme cold habitats on the planet Earth and the aforementioned parameters are known to influence microbial diversity. In the Himalayan regions and Arctic, microbial diversity studies were restricted only to soil, ice, water and sediment whereas in Antarctica in addition sea-ice, fast-ice, sediment, cyanobacterial mats, sub-glacial lake water, cryptoendolithic sand stones, air samples, ice cores etc. were also studied. Among all the habitats from the three geographic locations, microbial abundance in soil was found to be highest, followed by sediment, water and ice. The bacterial abundance was lowest in Arctic (5.2×10^4 to 2.5×10^5 cfug⁻¹ soil) and highest in Himalayan regions (4.2×10^7 to 30.7×10^8 cfug⁻¹ soil).

Antarctica

In Antarctica, abundance ranged from 0.2×10^2 to 0.6×10^{12} cells g⁻¹ of ice (Carpenter *et al.*, 2000; Priscu *et al.*, 1999; Delille and Gleizon, 2003; Shivaji *et al.*,

2004; Shivaji *et al.*, 2013c), 0.2×10^2 to 10^7 cells ml⁻¹ of water (Lo Giudice *et al.*, 2012) and 8×10^6 to 2.4×10^7 cells g⁻¹ of sediment (Stibal *et al.*, 2012) and 10^5 to 10^{10} cells g⁻¹ of soil (Shivaji *et al.*, 1988; 1989a, 1989b; Aislabie *et al.*, 2009). The numbers were also abundant in cyanobacterial mats (Reddy *et al.*, 2000, 2002a, 2002b, 2003a, 2003b, 2003c, 2003d, 2004) and have been reviewed by Shivaji and Reddy (2009) and Chattopadhyay *et al.* (2014). In Antarctica, higher bacterial abundance corresponded with high *in situ* sea-salt Na⁺ and dust concentration, suggesting that bacteria might have been transported and deposited into ice along with dust particles and marine aerosols (Antony *et al.*, 2012b).

Arctic

The bacterial abundance in major habitats from Arctic region was comparable to that observed in Antarctica and it ranged from 1.2 to 2.3×10^7 cells g⁻¹ of sediment (Forschner *et al.*, 2009), 5.2×10^4 to 1.7×10^9 cells g⁻¹ of permafrost (Hansen *et al.*, 2007), 0.9×10^3 to 2.4×10^6 cells ml⁻¹ of ice (Møller *et al.*, 2011) and in case of water the abundance was 5×10^5 cells ml⁻¹ (Møller *et al.*, 2011).

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Himalayan Glaciers

In the Himalayan glaciers the total bacterial abundance was low in case of water (1.1 to 25×10^4 cells ml^{-1}) (Liu *et al.*, 2011) and higher in case of sediments wherein it ranged from 0.9×10^7 to 30.7×10^8 cell per gram sediment (Shivaji *et al.*, 2011b; Pradhan *et al.*, 2010; Srinivas *et al.*, 2011).

Bacterial Diversity of Antarctica, Arctic and Himalayas at the Phyla Level

Cultured bacteria constitute only a miniscule fraction (<1%) of the total diversity and thus enumerating their abundance at taxonomic levels would not be correct. Nevertheless one could list their occurrence and diversity at various taxonomic levels without emphasizing on their abundance. The cultivable bacterial diversity was explored extensively from various habitats of Antarctica, Arctic and Himalayan glaciers such as soil, water, algal mats, ice and sediments (reviewed by Shivaji and Reddy, 2009; Chattopadhyay *et al.*, 2014). The most commonly occurring bacteria were affiliated to *Proteobacteria*, *Cytophaga-Flavobacterium-Bacteroidetes*, *Actinobacteria* and *Firmicutes* and the less common were communities belonging to *Deinococcus-thermus* and *Spirochaetes* (Chattopadhyay *et al.*, 2014). Members of *Epsilonproteobacteria* were absent (Reddy *et al.*, 2016). Antony *et al.* (2012a) studied bacterial diversity in an ice core from coastal Dronning Maud Land, East Antarctica and fourteen bacterial isolates belonging to the genera *Methylobacterium*, *Brevundimonas*, *Paenibacillus*, *Bacillus* and *Micrococcus* were retrieved. Among the *Bacillus* species, *Bacillus aryabhatai* which has been reported only from the upper stratosphere, was isolated and is the first record from the Earth's surface. It was also observed that the diversity of retrievable heterotrophic bacteria in Kongsfjorden, an Arctic fjord was represented by *Firmicutes*, *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes* and observed that the composition of heterotrophic bacterial community was linked to the changes in the water masses and/or phytoplankton bloom dynamics occurring in Arctic summer (Sinha *et al.*, 2017).

Novel Bacterial Genera and Species from Antarctica, Arctic, Himalayas and Stratosphere

Several new species of bacteria have been described

from Antarctica, Arctic, Himalayan glaciers and stratosphere (160, 67, 19 and 7 novel species respectively). Most of the new species were identified as belonging to already existing genera except a few which were assigned to new genera. So far, 37 novel genera have been described from Antarctica and 9 novel genera from Arctic (Table 1 and 2). Antony *et al.* (2009) based on phenotypic and molecular markers identified *Cellulosimicrobium cellulans* from Antarctic snow.

Studies on the bacterial diversity of the stratosphere have been very limited. Difficulties in sampling the stratosphere under aseptic conditions have been one of the limiting factors. Recent studies have reported several bacteria from air samples collected at an altitude of 10 to 41 km and seven new species have been reported (Table 3). No new genera have been reported from the Stratosphere (Shivaji *et al.*, 2006; 2009) (Table 3). Several genera from the Arctic (*Arcticibacter*, *Huanghella*, *Dasania* and *Augustibacter*) and Antarctica (*Actimicrobium*, *Antarcticimonas*, *Antarctobacter*, *Constrictibacter*, *Granulosicoccus*, *Marisediminicola*, *Methylosphaera*, *Pricia*, *Psychrosinus*, *Rhodoglobus*, *Rhodoligotrophos*, *Robiginito-maculum*, *Roseibaca*, *Roseicitreum*, *Sejongia*, *Subsaxibacter*, *Subsaximicrobium*, *Zhongshania* and *Oleispira*) (Yakimov *et al.*, 2003; Bowman *et al.*, 1997) were endemic to Antarctica and have not been reported from any other geographic region. Endemism of a particular genus may depend on the physico-chemical nature of the habitat. Further, the observed commonality in diversity between the regions implies that geographic separation may not have a major role in influencing the diversity and supports the hypothesis that everything is everywhere but the environment selects (O' Mastay 2008). The best example is the genus *Cryobacterium* that was originally described from Antarctica but its representatives were later on, identified from several other cold habitats such as Arctic and Himalayas. Further, a novel family, *Granulosicoccaceae*, was reported from Antarctic water (Lee *et al.*, 2007).

Bacterial Diversity of Antarctica, Arctic and Himalayas by Non-culturable Approach

Antarctica

Non-cultivable methods, such as 16S rRNA gene

Table 1: Novel bacterial genera from various habitats of Antarctica and Arctic* assigned by polyphasic taxonomy

S. No.	Novel genera	Habitat	16S rRNA gene accession number
Antarctica			
<i>Alphaproteobacteria</i>			
1	<i>Antarctobacter heliothermus*</i>	Lake water	Y11552
2	<i>Constrictibacter antarcticus*</i>	Rock	AB510913
3	<i>Loktanella salsilacus</i>	Mats	AJ440997
4	<i>Rhodoligotrophos appendicifer*</i>	Water	AB617575
5	<i>Robiginitomaculum antarcticum*</i>	Sea water	EF495229
6	<i>Roseibaca ekhonensis*</i>	Saline Water	AJ605746
7	<i>Roseicitreum antarcticum*</i>	Sediment	FJ196006
8	<i>Roseisalinus antarcticus</i>	Lake water	AJ605747
9	<i>Roseovarius tolerans</i>	Lake water	Y11551
10	<i>Staleyagutti formis</i>	Lake water	Y16427
<i>Betaproteobacteria</i>			
11	<i>Actimicrobium antarcticum*</i>	Sea water	HQ699437
12	<i>Polaromonas vacuolata</i>	Sea ice	U14585
<i>Gamaproteobacteria</i>			
13	<i>Granulosicoccus antarcticus#</i>	Sea water	EF495228
14	<i>Methylosphaera hansonii*</i>	Lake water	U67929
15	<i>Oleispira antarctica</i>	Sea water	AJ426420
16	<i>Psychromonas antarcticus</i>	Sediment	Y14697
17	<i>Saccharospirillum impatiens</i>	Lake water	AJ315983
18	<i>Zhongshania antarctica*</i>	Sea water	FJ889619
CFB group bacteria			
19	<i>Aequorivita antarctica</i>	Sea water	AY027802
20	<i>Antarcticimonas flava*</i>	Sea water	EF554365
21	<i>Gelidibacter algens</i>	Sea ice	U62914
22	<i>Gillisia limnaea</i>	Mats	AJ440991
23	<i>Hymenobacter roseosalivarius</i>		
Soil	Y18833		
24	<i>Lacinutrix copepodicola</i>	Sea ice	AY694001
25	<i>Polaribacter filamentus</i>	Sea ice	U73726
26	<i>Psychroflexus torquis</i>	Sea ice	U85881
27	<i>Psychroserpens burtonensis</i>	Sea ice	U62913
28	<i>Sejorgia antarctica*</i>	Soil	AY553293
29	<i>Subsaxibacter broadyi*</i>	Sea ice	AY693999
30	<i>Subsaximicrobium wynnwilliamsii*</i>	Sea ice	AY693997
<i>Firmicutes</i>			
31	<i>Psychrosinus fermentans*</i>	Water	DQ767881
High G+C Gram-positives			
32	<i>Cryobacterium psychrophilum</i>	Soil	AJ544063
33	<i>Friedmanniella antarctica</i>	Soil	Z78206

34	<i>Marisediminicola antarctica</i> *	Sediment	GQ496083
35	<i>Modestobacter multiseptatus</i>	Soil	Y18646
36	<i>Rhodoglobus vestalii</i> *	Water	AJ459101
	Arctic		
	<i>Gamaproteobacteria</i>		
37	<i>Dasania marina</i> *	Sediment	AY771747
	<i>Deltaproteobacteria</i>		
38	<i>Desulfofaba gelida</i>	Sediment	AF099063
39	<i>Desulfofrigus oceanense</i> *	Sediment	AF099064
40	<i>Desulfotalea psychrophila</i> *	Sediment	AF099062
	CFB group bacteria		
41	<i>Arcticibacter svalbardensis</i> *	Soil	JQ396621
42	<i>Huanghella arctica</i> *	Soil	JQ303016
43	<i>Polaribacter filamentus</i>	Sea ice	U73726
	Firmicutes		
44	<i>Tumebacillus permanentifrigoris</i>	Permafrost	DQ444975
	High G+C Gram-positives		
45	<i>Angustibacter luteus</i>	Soil	AB512285

*Represent genera that are endemic to Antarctica or Arctic. From Chattopadhyay et al., 2014

metagenomics, indicated the occurrence of *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, *Deltaproteobacteria*, *Epsilonproteobacteria*, *Cytophaga-Flavobacterium-Bacteroidetes* (CFB) group of bacteria, *Actinobacteria*, *Firmicutes*, *Acidobacteria* and *Verrucomicrobia* in Antarctica, Arctic and Himalayas albeit with different relative percentages. For instance, *Firmicutes* and *Acidobacterium* were clearly an abundant community in the Himalayan soils compared to Antarctica and Arctic and *Alphaproteobacteria* and *Deltaproteobacteria* were dominant in Antarctica and Arctic. In the Himalayan glaciers the bacterial diversity exhibited an altitude gradient with a gradual decline in the number of genera with increase in altitude.

In the Antarctic soils bacterial diversity varied with respect to soil type (Bottos et al., 2014; Shivaji et al., 2004) with *Proteobacteria* (47.0%) dominating in Antarctic Peninsula soils and *Actinobacteria* and *Bacteroidetes* (42.0% and 31% respectively) in West Antarctic soils and transantarctic Mountain soils (Bottos et al., 2014) respectively. Shivaji et al. (2011a) observed stratification of bacteria with respect to oxygen requirement in Antarctic soils and also

identified quite a few clones belonging to *Caldiserica* group, a thermophilic candidate phylum (Shivaji et al., 2004; Aislabie et al., 2006; 2013). Bowman et al. (2000) detected more than 200 distinct phylotypes in anoxic marine sediment with close to 31.0% belonging to a novel deep branch within the low GC Gram-positives. While Antony et al. (2016) identified a diverse assemblage of prokaryotic (*Proteobacteria*, *Actinobacteria*, *Firmicutes*, *Bacteroidetes*, *Deinococcus-Thermus*, *Planctomycetes*, *Verrucomicrobia* and *Euryarchaeota*) communities capable of producing the enzymes lipase, protease, amylase, β -galactosidase, cellulase, and/or lignin modifying enzyme in regions of East Antarctica, with respect to compounds present in snow and tested whether their functional signature reflected the snow environment.

As compared to soil and sediments bacterial diversity in the water is generally reduced (Laybourn-Parry, 1997) and a shift in diversity is observed with depth wherein the dominant *Bacteroidetes*, *Betaproteobacteria* and *Actinobacteria* in the surface layers are replaced by *Gammaproteobacteria* and unclassified bacteria in deeper zones as in McMurdo ice shelf, Victoria land and in the

Table 2: Novel bacterial species from various habitats of Himalayas* assigned by polyphasic taxonomy

S. No.	Novel species	Habitat	16S rRNA gene accession number
	Alphaproteobacteria		
1	<i>Rhodobacter changlensis</i>	Soil	AM399030
2	<i>Rhodobacter megalophilus</i>	Soil	AM421024
	Deltaproteobacteria		
3	<i>Desulfovibrio psychrotolerans</i>	Soil	AM418397
	CFB group bacteria		
4	<i>Dyadobacter hamtensis</i>	Soil	AJ619978
	Firmicutes		
5	<i>Bacillus cecembensis</i>	Soil	AM773821
6	<i>Exiguobacterium himgiriensis</i>	Soil	JX999056
7	<i>Exiguobacterium indicum</i>	Soil	AJ846291
8	<i>Paenibacillus glacialis</i>	Soil	EU815294
9	<i>Paenisporosarcina indica</i>	Soil	FN646595
10	<i>Planococcus stackebrandtii</i>	Soil	AY437845
	High G+C Gram-positives		
11	<i>Actinoalloteichus spitiensis</i>	Soil	AY426714
12	<i>Dietzia kunjamensis</i>	Soil	DQ156908
13	<i>Agrococcus lahaulensis</i>	Soil	AY972480
14	<i>Kocuria himachalensis</i>	Soil	AY987383
15	<i>Leifsonia pindariensis</i>	Soil	AM900767
16	<i>Leifsonia kafniensis</i>		AM889135
17	<i>Ornithinimicrobium kibberense</i>	Soil	AY636111
18	<i>Rhodococcus kroppenstedtii</i>	Soil	AY726605
19	<i>Cryobacterium roopkundensis</i>	Soil	EF467640

*From Chattopadhyay *et al.* (2014)

Amundsen sea polyna (Archer *et al.*, 2014; Kim *et al.*, 2014). Prabakaran *et al.* (2007) demonstrated dynamic change in bacterial community following hydrocarbon contamination of sea water which revealed that genera *Psychrobacter*, *Arcobacter*, *Formosa*, *Polaribacter*, *Ulvibacter* and *Tenacibaculum* are present in hydrocarbon contaminated water and the abundance of *Sulfitobacter* group was high in sea water and decreased in contaminated seawater.

In a recent study, Singh *et al.* (2015a) studied the response of bacterio plankton to iron fertilization of the Southern Ocean, Antarctica based on metagenome approach. More than 97.35% of the sequences represented four bacterial lineages *i.e.* *Alphaproteobacteria*, *Gammaproteobacteria*,

Bacteroidetes and *Firmicutes* and confirmed their role in scavenging of phytoplankton blooms induced following iron fertilization. In addition, this study identified three unique phylogenetic clusters LOHAFEX Cluster 1 (affiliated to *Bacteroidetes*), 2 and 3 (affiliated to *Firmicutes*) which were not detected in any of the earlier studies on iron fertilization (Fig. 1). Further these clusters varied in their response to iron fertilization. For instance LOHAFEX Cluster 2 increased in abundance following iron fertilization which corresponded with phytoplankton bloom whereas LOHAFEX Cluster 3 disappeared after iron fertilization implying that high iron concentration may not be conducive for their survival (Singh *et al.*, 2015a).

In sea ice *Gammaproteobacteria*,

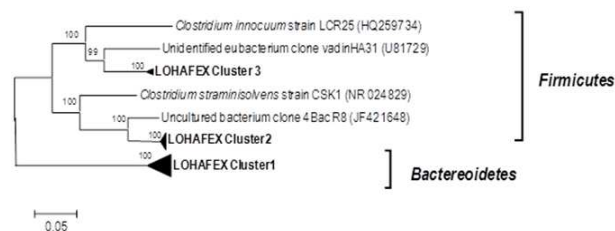


Fig. 1: Phylogenetic affiliation of Lohafex cluster1, Lohafex cluster 2 and Lohafex cluster 3 with Firmicutes and Bacteroidetes. Cluster 1 had 12 OTUs represented by 547 clones, Cluster 2 had 9 OTUs with 741 clones and Cluster 3 had 3 OTUs with 407 clones respectively

Alphaproteobacteria and *Bacteroidetes* are the predominant groups (Bowman *et al.*, 1997; Kuhn *et al.*, 2014). Temporal community analyses over a period of two years indicated a shift in community wherein *Acinetobacter* and *Cohnella* (*Firmicutes*) replaced *Paenibacillus* and *Jeotgalibacillus* in a span of two years (Doyle *et al.*, 2013).

Arctic

The soil microbial communities are very similar to that observed in Antarctica. In soil, sediment, permafrost and ice genera belonging to the class *Proteobacteria* are most dominating and members of the class *Actinobacteria*, *Firmicutes* and *Bacteroidetes* contribute 3 to 25% (Collins *et al.*, 2010; Wilhelm *et al.*, 2011). In addition,

Gammaproteobacteria, *Verrucomicrobia*, *Gemmatimonadetes* and *Deltaproteobacteria* were also reported. The bacterial communities did not show any response to intermittent flow in water tracks over high Arctic permafrost (Steven *et al.*, 2013). It was also observed that low pH supported the *Proteobacteria* at the expense of *Acidobacteria* and high pH supported *Bacteroidetes* (Ganzert *et al.*, 2014). Sea-ice contained bacterial lineages that belonged to *Proteobacteria*, *Bacteroidetes*, *Planctomycetes* and *Chloroflexi* (Junge *et al.*, 2002; Brinkmeyer *et al.*, 2003; Bottos *et al.*, 2008) and sea water harboured significant proportions of *Proteobacteria* (>50%) and *Bacteroidetes* (25%) and *Actinobacteria* and *Verrucomicrobia* were present below 25% (Kirchman *et al.*, 2010). Interestingly, a seasonal variation in bacterial abundance and change in phylotypes (belonging to the phyla *Firmicutes*, *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes*) was observed in Kongsfjorden, an Arctic fjord (Sinha *et al.*, 2017).

Himalayan Glaciers

The three habitats, soil, water and sediments from the Pindari, Kafni and Roopkund glaciers shared common taxa affiliated to *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, *Chlamydiae*, *Firmicutes*, *Nitrospirae*, *Proteobacteria* and *Verrucomicrobia*. However,

Table 3: Novel bacterial species from Stratospheric air samples assigned by polyphasic taxonomy

Height (Kms)	Strain	Identity based on 16S rRNA gene similarity (%)	Year
24.10-38.87	(24 K and 28K)	<i>Bacillus aerius</i> *	2001
28.0	(28 K)	<i>Bacillus aerophilus</i> *	2001
39.65-41.06	(41KF2a)	<i>Bacillus stratosphericus</i> *	2001
39.65-41.06	(41KF2b)	<i>Bacillus altitudinus</i> *	2001
27-30	(B3W22)	<i>Bacillus isronensis</i> *	2005
40-41.4	(B8W22)	<i>Bacillus aryabhatai</i> *	2005
40-41	(pVAS-1)	<i>Janibacter hoylei</i> *	2005
35-40	(B5W22-1)	<i>Micrococcus flavus</i> (99)	2005
35-40	(B5W22-2)	<i>Streptomyces maritimus</i> (99)	2005
20-24	(PVAS-8 and 5)	<i>Stenotrophomonas rhizophila</i> (99)	2005
30-35	(PVAS-4)	<i>Acinetobacter radoresistense</i> (100)	2005
35-40	(PVAS-6)	<i>Acinetobacter calcooaceticus</i> (99)	2005
35-40	(PVAS-10)	<i>Bacillus pumilus</i> (99)	2005
40-41	(PVAS-2 and 3)	<i>Methylobacterium chloromathanicum</i> (99)	2005

sediments from the glaciers differed in their diversity in that sediments from Kafni glacier contained clones affiliated to *Spirochaetae* and *Tenericutes* (Srinivas *et al.*, 2011; Shivaji *et al.*, 2011b) whereas samples from Pindari and Roopkund had sequences affiliated to *Gemmatimonadetes* and *Planctomycetes*. Gangwar *et al.*, (2009) observed that *Proteobacteria* was the highest in soil (45 to 70%) followed by *Actinobacteria* (10 to 86%) and *Bacteroidetes* (6.4 to 28%) (Gangwar *et al.*, 2009; Srinivas *et al.*, 2011). The difference in community composition in the three habitats studied so far can be attributed to the nature of the soil. So far 135 diverse genera were identified from various environments of Himalayas and the number of genera followed the trend *Actinobacteria* (28.0%), *Betaproteobacteria* (21.5%), *Alphaproteobacteria* (9.6%), *Gamaproteobacteria* (8.9%), *Deltaproteobacteria* (11.1%), *Bacteroidetes* (11.1%), *Firmicutes* (3.7%), *Acidobacteria* (1.4%), *Verrucomicrobia* (3.0%) and *Epsilonproteobacteria* (1.5%). Further, Gupta *et al.*, (2015) identified the rare taxa (*Firmicutes*, *Nitrospirae*, *Armatimonadetes* (former candidate division OP10), *Planctomycetes*, *TM7*, *Chloroflexi* and *Deinococcus-Thermus*) in Drass sector of Himalayan region and uniquely *Acidobacteria* (32.1%) was the most dominant community.

Unique Features of Bacteria from Antarctica, Arctic, Himalayas and Stratosphere

A vast majority of the species isolated from Antarctica, Arctic and Stratosphere are psychrophilic. However, a few species like *Alicyclobacillus pohliae* (42-60°C) (Imperio *et al.*, 2008), *Aneurinibacillus terranovensensis* (20-55°C), (Allan *et al.*, 2005), *Anoxybacillus amylolyticus* (45-65°C) (Poliet *et al.*, 2006), *Bacillus fumrioli* (25-55°C) (Logan *et al.*, 2000), *Brevibacillus levickii* (15-55°C) (Allan *et al.*, 2005), *Paenibacillus cineris* (8-50°C) and *Paenibacillus cookie* (15-50°C) (Logan *et al.*, 2004) are moderately thermophilic and interestingly all these species were isolated from soil. Further, 68% of novel species described so far are pigmented, indicating that pigmentation is a common phenomenon in Antarctic bacteria. Pigment is known to be involved in stress adaptation to low temperatures (Jaganadham *et al.*, 1996; Jaganadham *et al.*, 2000; Chattopadyay *et al.*, 1997).

At the DNA level it was observed that the 16S rDNA operons possessed specific psychrotolerant signatures such as the transitions from C and G to T and A, higher uracil content and G:U mismatches compared to mesophilic strains of *Bacillus* (Prüss *et al.*, 1999; Lauro *et al.*, 2007). Further swollen sporangia were observed in psychrophilic strains of the genus *Bacillus* compared to their nearest mesophilic counterparts (Abd El-Rahman *et al.*, 2002; Larkin and Stokes, 1967; Priest *et al.*, 1988). *Bacillus cecembensis*, a psychrophilic species from Himalayas contained C_{16:1}ω7c alcohol in its membrane while it is absent in its nearest mesophilic neighbour (Reddy *et al.*, 2008). In fact all the psychrophiles have a preponderance of unsaturated fatty acids compared to mesophilic counterparts. These bacteria also have cold active and heat labile enzymes (Ray *et al.*, 1992; Reddy *et al.*, 1994; Chattopadhyay *et al.*, 1995) and have genes that are essential for their survival at low temperature (Singh *et al.*, 2009; Singh and Shivaji, 2010; Sundareswaran *et al.*, 2010). Some other aspects of adaptation to low temperature are highlighted in the following section of this article.

Strategies Involved in Cold Adaptation

Studies have indicated that psychrophilic bacteria adapt to low temperatures by adopting multiple strategies such as their ability to miniaturize and undergo fragmentation as in an Arctic strain of *Psychrobacter* (Ewert and Deming, 2014), ability to produce cold-tolerant and/or thermolabile enzymes (Feller and Gardaí, 2003; Singh *et al.*, 2014a) and ability to sense changes in temperature by modulating membrane fluidity (Ray *et al.*, 1994). Studies have demonstrated that preferential synthesis of membrane-fluidizing fatty acids (unsaturated, short-chain and anteiso-fatty acids) coupled with involvement of some carotenoid pigments appear to help them in the homeoviscous adaptation of membrane fluidity (Chintalapati *et al.*, 2004, Chattopadhyay and Jagannadham, 2001). Temperature-dependent changes in the DNA topology is also postulated to play an important role in sensing ambient temperature (Shivaji and Prakash, 2010). The ability of some bacteria, isolated from the extreme cold habitats, to continue both catabolism and anabolism at sub-zero temperatures has been demonstrated (Sengupta and Chattopadhyay, 2013). It has also been demonstrated that bacteria preferentially transcribe cold-inducible

genes at low temperature as a survival strategy and cold-inducible promoters regulate the expression of such genes at low temperature. In a review, Singh *et al.* (2014b) have compiled all the advances on cold inducible promoters and regulation of gene expression at low temperature. Ability to transcribe and translate (Ray *et al.*, 1998) and re-initiation of replication (Sinha *et al.*, 2013) at cold temperatures is a characteristic feature of cold adaptation. Degradation of RNA is a crucial step in the regulation of gene expression and the RNA-degradosome, a protein complex involved in RNA degradation, was found to be substantially different in an Antarctic bacterium compared to those in *E. coli* (Purusharth *et al.*, 2007). In *Methanobrevibacterium smithii* R15, exosome-mediated RNA degradation at low temperature was accelerated (Chen *et al.*, 2012). In natural environments bacteria are most often challenged with more than one stress factor. Consequently, they have to adapt to more than one stressor for survival (Rothschild and Mancinelli, 2001). Association between tolerance of bacteria to low temperature and some other stress factors was highlighted earlier (Chattopadhyay, 2008). Adaptation of some Antarctic isolates to high osmotic stress, high pH and high oxidative stress besides freezing, was also demonstrated and the prospective role of an enzyme in tolerance of one isolate to multiple stress factors was also evidenced (Sengupta *et al.*, 2015).

Specific Genes Involved in Cold Adaptation

Attempts have been made to ascertain whether a single gene or multiple genes are required for growth at low temperature. *Pseudomonas syringae* Lz4W, a psychrophilic bacterium capable of growing at temperatures between 2 and 30°C, yielded 30 cold-sensitive mutants following transposon mutagenesis. Two of these mutants CSM1 and CSM2 were characterized and the results indicated that both had a single transposon insertion. In CSM1 the gene *trmE* coding for tRNA modification GTPase was disrupted whereas in CSM2 the gene *AAT* coding for aspartate aminotransferase was disrupted. In both the mutants growth was retarded when cultured at 4°C but not when it was cultured at 22°C and 28°C compared to the growth of wild-type cells. Both these genes were cold-inducible and plasmid-mediated complementation of the genes to the mutants alleviated the cold-sensitive phenotype of the mutants (Singh and Shivaji, 2010; Singh *et al.*, 2010; Sundareswaran *et al.*, 2010).

Earlier studies have also indicated that *pnp* (encoding polynucleotide phosphorylase), *oppA* (involved in the transport of oligo-nucleotides) and *recD* have been identified as genes required for low-temperature growth. Presence of antifreeze proteins could also be a strategy to overcome freezing as demonstrated in Arctic cryoconite bacteria (Singh *et al.*, 2014c).

Lessons from Genome Sequencing of Psychrophiles

Next-generation sequencing (NGS) has facilitated whole-genome sequencing of multiple organisms from different and distinct habitats and has helped to generate specific genomic information so as to understand and appreciate unique features of organisms such as their adaptation to extreme environments. For instance the presence of cold-resistant proteins, cold-shock protein, soluble acyl-ACP desaturase, ATP-dependent RNA helicase, DEAD/DEAH box family proteins, putative ribonuclease H1 are examples of proteins involved in cold resistance in polar microbial genomes. Based on the genome sequence of psychrophilic *Pseudomonas extremaustralis* (Raiger *et al.*, 2015) genes required for osmoregulation, cold adaptation, exopolysaccharide production and degradation of complex compounds were detected. In addition genes coding for cold-shock proteins (Csps) and cold acclimation proteins (Caps) were present only in *Pseudomonas extremaustralis* which is a psychrophile and not in *P. syringae* pv. *syringae* B278a and *P. aeruginosa* PAO1, which are mesophiles. Thus, it was suggested that these proteins contribute to cold adaptation of *P. extremaustralis*. We and others have recently reported the genome sequence of a number of psychrophiles from different cold habitats like Antarctica (Sreenivas *et al.*, 2014; Reddy *et al.*, 2013, 2014; Kumar *et al.*, 2013a,b), Arctic (Shivaji *et al.*, 2013a; 2013b; Kumar *et al.*, 2013a; Kapseet *et al.*, 2017; Singh *et al.*, 2016), Himalayan glaciers (Reddy *et al.*, 2014) and Stratosphere (Shivaji *et al.*, 2012). A comparative genome analysis of Csps in the psychrophilic *Sphingobacterium antarcticum*, *Oceanisphaera arctica* and *Exiguobacterium indicum* indicated that CspA was present in all of them, Csp C, D, E and G were present in at least one of the 3 isolates whereas Csp B and I were absent (unpublished). The implications of this observation with respect to cold adaptation warrant further studies.

Draft genome sequence of a lake-isolate of *Hymenobacter*, tolerant to ultraviolet radiation and oxidative stress besides low temperature, was published some time back (Koo *et al.*, 2014). Comparative genomics also suggested a decrease in charged amino acids in psychrophiles when compared with mesophiles and thermophiles. In a recent study when the genomes of Arctic and Antarctic *Octadecabacter arcticus* and *O. antarcticus* were compared high genome plasticity was observed and they possessed genes representing a new type of xanthorhodopsins as an adaptation to icy environments.

Biotechnological Implications

Microbes are crucial in the cycling of C and other elements such as N, S, and P and play an important role in transformation of dissolved organic matter in Antarctica and other regions (Antony *et al.*, 2017). In an earlier study (Anthony *et al.*, 2012b) demonstrated that carbon utilization by bacterial communities in three surface snow samples from Antarctica collected along a coastal to inland transect utilized diverse substrates like carbohydrates, amino acids, amines, amides, complex polymers, etc. (Antony *et al.*, 2012b). This activity is dependent on the enzymes associated with these organisms which are cold-active and/or thermolabile and such novel enzymes find widespread application in biotechnology industry. In the Arctic also similar organisms with lipase, protease, cellulase, amylase, and urease activities with potential industrial applications have been reported (Singh *et al.*, 2016).

These novel enzymes have been exploited for food processing, for reducing viscosity of fruit juices at low temperature and in leather industries. A thermolabile phosphatase, obtained from an Antarctic bacterium and patented (HKTM) is active in neutral and alkaline pH and is useful in performing sequential steps in a single tube *viz.*, restriction enzyme digestion, dephosphorylation, enzyme inactivation, and ligation or end-labelling. A cold-active lipase, obtained by cloning a lipolytic gene from an Arctic bacterium (*Rhodococcus* ssp. AW25M09) in *E. coli*, has been found to retain activity at high pH, organic solvents (acetonitrile, diethyl ether) and salt (1M NaCl). Thus it appears to be an interesting candidate for industrial applications (De Santi *et al.*, 2014). Such strains could

also be useful in lipase-mediated biodiesel production (Moreno and Rojo, 2014). Bacteria occurring in Polar Regions could also serve as potential candidates for production of unique antimicrobial compounds (Liu *et al.*, 2013; Fondi *et al.*, 2014). Cold-adapted bacteria capable of degrading hydrocarbons are useful in waste water treatment (Margesin and Schinner, 2001) and they are found not only in oil contaminated soil but also in soil that has no history of oil contamination (Shukor *et al.*, 2009). A number of genes responsible for hydrocarbon biodegradation (*e.g.* monooxygenases, dioxygenases) in different oil-contaminated sites (Powell *et al.*, 2006) were also identified. Besides petroleum products, heavy metals are also degraded. A bacterial isolate from the South Shetlands Islands, Antarctica, tentatively identified as a *Pseudomonas* sp. was found to convert sodium molybdate or Mo^{6+} to molybdenum blue (Ahmad *et al.*, 2013). Microorganisms having the capacity to degrade Polychlorinated biphenyls (PCBs) have also been isolated from both the Arctic and Antarctic regions (Master and Mohn, 1998; De Domenico *et al.*, 2004). It has been possible to improve the cold-tolerance of the mesophilic *E. coli* by cloning the genes encoding two chaperonin proteins obtained from an Antarctic organism (Ferrer *et al.*, 2003) and also by cloning a gene encoding an antifreeze protein occurring in a cold-tolerant plant (Deng *et al.*, 2014). The use of such genetically engineered microorganisms with high capacity to degrade pollutants appears to be an attractive option. The potential role of some molecules, which confer tolerance to more than one stressor, was discussed elsewhere (Chattopadhyay, 2013). The multistress-protective potential of these molecules could find application in construction of genetically engineered sturdy bacterial strains, suitable for bioremediation in harsh environments. Some food-borne bacteria evolved with tolerance to various stress conditions (low temperature, low pH, high salt) used for the preservation of food and thus pose serious threat to the health of the consumers. It might also be possible to design inhibitors of these molecules and use them for the safe preservation of food materials (Chattopadhyay, 2013).

Conclusions

Psychrophiles are a predominant community on the planet Earth and define the lower limits of temperature

at which life forms survive and replicate. They need to be studied more intensively to understand their contribution to the ecosystem. Psychrophiles are a bioresource and could serve as workhorses for the biotech industry and improve the quality of life of human beings by contributing to agriculture, medicine and industry. Bioprospecting for biomolecules using cultivable bacteria and the metagenome approach need to be pursued with greater focus. Understanding the survival strategies of psychrophiles would help to

unravel cellular and molecular mechanisms that are obligatory for the survival of life forms at freezing temperatures. Such a knowledge base would strengthen human efforts in agriculture in cold regions and may also address issues related to bioremediation in cold regions of the Earth. There is a need to carry out more comparative genome analysis of psychrophiles from different cold habitats so as to unravel the molecular basis of cold adaptation.

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