Psychrophiles: Ecological significance and potential industrial application

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DATES:
Received: 31 July 2017
Revised: 15 Dec. 2017
Accepted: 17 Jan. 2018
Published: 30 May 2018

KEYWORDS:
frozen ecosystem; biodiversity; cold-active proteins; carotenoid pigments; food industry; pharmaceutical industry

HOW TO CITE:
Hamdan A. Psychrophiles: Ecological significance and potential industrial application. S Afr J Sci. 2018;114(5/6), Art. #2017-0254, 6 pages. http://dx.doi.org/10.17159/sajs.2018/20170254

ARTICLE INCLUDES:
× Supplementary material
× Data set

FUNDING:
None

The bulk of earth's biosphere is cold (<5 °C) that sustains a broad diversity of microbial life by triggering physiological response(s) to ensure survival in cold and frozen ecosystems. The strategy of adaptation to cold environments includes changes in membrane composition and induction of a set of specific cold-active proteins, polyunsaturated lipids and exopolysaccharides. These adaptive features provide an enormous natural reservoir of enzymes that function effectively in cold environments, and these cold-active enzymes have been targeted for innovative applications useful to humankind. This review provides an overview of the existence, distribution and adaptation strategies of psychrophilic microorganisms worldwide with great emphasis on their recently emerged industrial applications in the textile industry, food and dairy industry, brewing and wine industry, laundry detergent industry, and others.

Significance:

- The outcome of these studies may also help in the exploration of the possibility of life in distant frozen planets.

Introduction

A great proportion of the earth's biosphere (>85%) permanently experiences temperatures below 5 °C.[1] The largest coverage of these cold environments is successfully colonised by a wide diversity of extremophilic microorganisms, including bacteria, archaea, yeasts, filamentous fungi and algae.[2,3] In 1887, Forster first reported the existence of bacteria capable of growth at 0 °C, especially in sea water and ocean fish.[4] Cold-adapted or cold-loving microbes are termed 'psychrophiles', and have cardinal growth temperatures (minimum, optimum and maximum) at or below 0 °C, 15 °C and 20 °C, respectively, while microorganisms that withstand cold temperatures with a higher growth optimum and maximum (above 25 °C) are called 'psychrotolerant'.[5] The ability to thrive at such low temperatures requires a vast array of adaptations to maintain the metabolic rates and sustain growth compatible with life in these severe environmental conditions.[6] Because of their attractive properties, extensive research on psychrophilic microorganisms has been conducted to understand their survival strategies that include genetic and acclimation processes and adaptation mechanisms.[7]

The purpose of this review is to summarise the tremendous significance of this group of microorganisms in fundamental research, pharmaceuticals, medicine and recent biotechnological applications.

Psychrophiles: Historical background

In 1887, Forster early investigated the isolation of microorganisms from fish preserved by cold temperatures that were bioluminescent.[8] Later in 1892, Forster reported other bacterial isolates from various environments (natural water, food, surface and intestines of freshwater and seawater fish) that were able to grow at 0 °C.[4] Schmidt-Nielsen (1902) first mentioned the term 'psychrophile' to describe bacteria capable of growing at 0 °C.[9] However, Müller (1903) criticised this term and demonstrated that while these organisms were able to grow at low temperature they actually grew more rapidly at elevated temperatures.[10] Thus, Kruse (1910) suggested that these bacteria might be better called 'psychrotolerant', but this suggestion or others of similar nature did not gain acceptance and the term 'psychrophile' has retained.[11] This confusion was ended in 1975, when Morita proposed a definition to the term 'psychrophile' for cold-adapted or cold-loving microbes, having minimum, optimum and maximum growth temperatures at or below 0 °C, 15 °C and 20 °C, respectively.[12]

Habitats and biodiversity

Cold habitats dominate the vast majority of our planet, covering three-quarters of the earth's surface, and span from the Arctic to the Antarctic and from high-mountain regions to the deep ocean.[13,14] The major fraction of this low temperature environment is represented by the deep sea (90% of the ocean volume), followed by snow (35% of land surface), permafrost (24% of land surface), sea ice (13% of the earth's surface) and finally glaciers (10% of land surface). Other cold environments are cold-water lakes, cold soils, cold deserts and caves.[15] These earth dominant environments are successfully colonised by enormously diverse communities of psychrophilic bacteria, archaea, algae, yeast[16-20], insects[21] and fish[22], that are able to thrive and even maintain metabolic activity at subzero temperatures.

Bacteria represent very important members of the sea ice habitat, including many unique taxa.[23] Heterotrophic gas-vacuolate bacteria, not reported in other marine habitats, have been discovered in and near sea ice.[24] Among those cold-adapted bacteria, the genus *Colwellia* provides an unusual case. Members of this genus produce extracellular enzymes capable of degrading high-molecular-weight organic compounds. These traits make *Colwellia* species important to carbon and nutrient cycling wherever they occur in the cold marine environment, from contaminated sediments to ice formations as analogs for possible habitats on other planets and moons (e.g. Mars and Europa).[13]

Representatives of the family Vibrionaceae are among the most commonly reported bacteria to populate almost all extreme environments.[25] Nevertheless, a wide range of phylogenetic diversity within the genera

Achromobacteria, Alcaligenes, Altermonas, Aquaspirillum, Arthrobacter, Bacillus, Bacteroides, Brevibacterium, Clostridium, Colwellia, Cytophaga, Flavobacterium, Gelidibacter, Methanococcoides, Methanogenium, Methanosarcina, Microbacterium, Micrococcus, Moritella, Octadecabacter, Phormidium, Photobacterium, Polaribacter, Polaromonas, Pseudomonas, Psychroserpens, Shewanella, *Psychrobacter* and *Vibrio* have been found to be psychrophilic across the domain Bacteria.[26-29]

In general, fungi are relatively rare in deep sea habitats compared to bacteria.[30] Fungal isolates reported in frozen environments belong mainly to the genera *Rhodotorula, Penicillium, Ustilago*, *Alternaria, Aureobasidium, Cladosporium, Geomyces, Ulocladium, Valsa* and *Verticillium*.[31-33]

Existence and metabolic adaptation

Survival of psychrophiles in harsh and extremely cold environments is interesting and requires a vast array of unique adaptive features from all their cellular components.[34,35] Chintalapati et al.[36] categorised three phases of cold-shock response. Phase I, Acclimation Phase, immediately follows cold exposure, leading to reduced growth rate as a result of reduced membrane fluidity, and several cold-shock proteins are produced. During Phase II, Recovery Phase, cells are considered 'cold-adapted' and resume growth and bulk protein synthesis restarts. During Phase III, Stationary Phase, non-cold-shock proteins are synthesised, allowing cells to proceed to slow-rate growth at low temperature.[37]

In general, bacteria owe the ability to cope with such challenges to complex strategies. One important strategy is directed towards their extremely efficient DNA repair mechanism sustained under frozen conditions.[38] This evidence for active DNA repair mechanism in icy environments is a true reflection of their physiological potential and survival in frozen substrates for extended time frames of up to 600 000 years.[39]

Regulation of membrane fluidity

Another important and the most frequent adaptive strategy relates to the ability of the cell to regulate or modulate the fluidity of the membrane in freezing environments. The membrane is the first barrier that can sense environmental changes and it acts as an interface between external and internal environments, so as to overcome the deleterious effects of harsh conditions.[36] Shivaji and Prakash[35] reported that membranes become more rigid at cold temperatures, which activates a membrane-associated sensor resulting in upregulation of genes involved in membrane fluidity modulation for exchange of metabolites from and to the cell.

Consequently, changes in the membrane lipid composition facilitate this process. This is achieved by modifications in the lipids' fatty acyl chains that serve to maintain optimum membrane fluidity.[40] In general, lower growth temperatures govern the activation of a group of cold-shock-activated enzymes called 'desaturases' which convert saturated acyl fatty acids to unsaturated ones and aid the increase in the proportion of unsaturated acyl chains, reduction in the acyl chain length and increased methyl-branched fatty acids.[36] Fungal cell membranes show evidence of similar changes at cold ecosystems to maintain their fluid state. The degree of unsaturated fatty acids increases at low temperatures in *Candida, Leucosporidium* and *Torulopsis* as reported by Kerekes and Nagy[41].

Carotenoid pigments

Predominance of carotenoid pigments, in several bacteria isolated from Antarctic sea ice, has been reported to play an important role in the maintenance of membrane structure, fluidity and protection from UV radiation.[42] Accumulation of C-50 carotenoid, Bacterioruberin, observed in the psychrotrophic strain, *Arthrobacter agilis*, was postulated to play a crucial role in the regulation of membrane fluidity at low temperatures.[43] Furthermore, several polar and non-polar carotenoid pigments, synthesised by *Micrococcus roseus* and *Sphingobacterium antarcticus* Antarctic strains, were found to bind vesicles, made of both synthetic and natural lipids, and to rigidify them.[44]

Anti-freeze proteins

Anti-freeze proteins (AFPs) are ice-binding proteins that have the ability to decrease the freezing point of water and show extracellular ice re-crystallisation inhibition activity during latter stages of the warming cycle.[45,46] Furthermore, AFPs have been well known in promoting super cooling of the body fluids at subzero temperatures to prevent freezing of blood in polar fish.[47] In addition, those proteins have been reported in insects and plants.[48,49] Duman and Olsen[50] first demonstrated the presence of AFPs in cold-adapted bacteria and the bacterium *Moraxella* sp. was the first reported Antarctic strain to produce an AFP.[51] Some psychrophilic AFPs have been purified from cell extracts of *Micrococcus cryophilus, Pseudomonas putida* and *Rhodococcus erythropolis*.[52]

Cryoprotectants

Cryoprotectants are exopolymeric substances (e.g. sugars, alcohols and amino acids), produced in high amounts and believed to prevent cold-induced aggregation of proteins and maintain optimum membrane fluidity under unfavorable low temperature.[53,54] In 1994, Ko et al.[55] demonstrated the growth-enhancing effect of glycine betaine on *Listeria monocytogenes* at low temperature. Furthermore, trehalose showed evidence in preventing protein denaturation and aggregation in psychrophilic bacteria.[56] In fungi, trehalose is an important stress protectant and stabiliser of membranes, accumulated in fungal hyphae in large quantities at low temperatures.[57]

Cold-shock proteins

Cold-shock proteins have been extensively characterised and are considered the most prominent response of cells to cold shock in order to counteract the detrimental effect of temperature downshift; they play a critical role in cold adaptation.[58] Cold-shock proteins have been functionally linked to the regulation of cellular protein synthesis, particularly at the level of transcription and initiation of translation. They also act as chaperones by preventing the formation of mRNA secondary structures (mRNA 'folding') and maintenance of chromosome structure.[59,60] These stress proteins, together with cold-acclimation proteins, have been detected and exclusively overexpressed during the entire growth of several Antarctic bacteria.[56] Furthermore, Kawahara et al.[61] believed that the cold acclimation protein (Hsc 25) produced in an ice-nucleating bacterium *Pantoea ananas* KUIN-3, was capable of refolding cold-denatured enzymes that sustain biological activities following an abrupt temperature downshift.

Cold-active enzymes

Cold-active or 'cold-adapted' enzymes are those enzymes that display high catalytic efficiency at low temperature compared to their mesophilic counterparts.[62] Furthermore, Struvay and Feller[63] reported multiple adaptive features developed by constrained psychrophiles to design enzymes perfectly compatible to the given environment. In the first attempt, psychrophiles produce enzymes that are highly flexible in structure, having an up to 10-fold higher specific activity (k_{cat}) than their mesophilic homologues, thus providing better access to the active site of substrates at lower temperatures.[64] These cold-active enzymes offset the inhibitory effect of low temperatures on reaction rates and maintain adequate metabolic fluxes to the growing organism. Secondly, the apparent maximal activity of cold-active enzymes is shifted towards low temperatures to cope with the increased viscosity of the aqueous environment induced under cold conditions. In this context, these enzymes are heat labile and frequently inactivated at temperatures that are not detrimental for their mesophilic counterparts.[65] Finally, apart from their high catalytic efficiency, the adaptation to cold is not usually perfect, as the specific activity exhibited by most psychrophilic enzymes around 0 °C remains generally lower than that of their mesophilic counterparts at 37 °C.

Pioneering studies compared cold-active enzymes to their conventional mesophilic forms and observed significant differences in amino acid composition, mostly in the active site domain, responsible for their activity under cold conditions.[66] The criteria for structural alterations include increased clusters of glycine residues (providing local mobility) and reduction in proline and arginine residues in loops, which provides enhanced chain flexibility between secondary structures and the capability of forming multiple salt bridges and hydrogen bonds, respectively.[6] However, surprisingly, Aghajari et al.[67] reported great similarity in the three-dimensional structure of a cold-adapted α-amylase enzyme of a psychrophilic bacterium, *Alteromonas hulopfuncris*, to those of mammalian α-amylases.

A variety of cold-active enzymes – xylanases and laminarases[68], chitinases[69], α-amylase and β-galactosidase[70,71], lipases and proteases[20,72], aminopeptidase[73] and protein-tyrosine phosphatase[74] – have been reported in cold-adapted bacteria to aid in their survival under cold conditions.

Biotechnological applications

Over recent years, considerable attention has been focused on psychrophilic microorganisms that proliferate in extremely cold niches and the fascinating biotechnological potential of their cold adaptation. Although Witter[11] reported the significant opportunity of psychrophilic bacteria in the dairy industry and in keeping milk fresh under refrigeration facilities for longer holding times as far back as 1961, studies on psychrophiles have been accentuated by the advancements and applications in avoiding potentially disastrous situations in various industries, including those concerned with food production, waste processing, mining, environmental bioremediations, agriculture, and medicine and molecular diagnostics.[75,76]

Bioremediation

Because of increasing human activities and demand for fossil fuel energy, spillage of petroleum products is a growing menace to the environment. Psychrophiles hold tremendous potential as 'environmental cleaners' to successfully degrade pollutants of petroleum hydrocarbons in extreme cold conditions.[77,78] Whyte et al.[79] reported that the microbial catabolic pathways responsible for the degradation of petroleum hydrocarbons, including *n*-alkanes and polycyclic aromatic hydrocarbons, are widespread in cold regions. Furthermore, several indigenous, cold-adapted microbial populations that use petroleum hydrocarbons have been detected, including *Rhodococcus*[80], *Pseudomonas*[81] and *Pseudoalteromomas*[82].

Food industry

It has indeed emerged that cold-active enzymes represent an extremely powerful tool in the food industry. There is an increasing industrial trend to treat foodstuffs under low temperature conditions in order to avoid detrimental effects on taste, texture and nutritional value, and also to save energy. Cold-active β-galactosidase, which hydrolyses lactose to glucose and galactose at refrigerating temperature, is a potentially important enzyme in the dairy industry. It can be used to produce lactose-free milk-derived foods for lactose-intolerant people, who represent approximately 30% of the world population.[83] Furthermore, it can be used to convert lactose in whey to D-tagatose – a natural high-added-value sweetener with low caloric and glycemic index.[63] Hoyoux et al.[84] patented a cold-active β-galactosidase from an Antarctic psychrophile, *Pseudoalteromonas haloplanktis*, for its capacity to hydrolyse lactose during milk storage at low temperatures.

In this context, application of cold-active pectinases in the fruit juice industry is highly demanding to retain the quality and nutritional properties of the fruit juice and facilitate different processing steps – liquefaction, clarification and juice extraction – at low temperatures. Furthermore, residual enzyme activity could be easily eliminated by enzyme inactivation by moderate heat input after treatment.[85] In wine industries, cold-active pectinases, isolated from yeasts and fungi, are believed to increase the production and retention of volatile compounds, thereby improving the aromatic profile of wines.[86]

Also, it is worth mentioning that cold-active xylanases, hydrolysing β-1,4-xylan present in all flours, are one of the key ingredients of industrial dough conditioners used at cool temperatures required for dough resting to improve bread quality. Following careful baking trials, xylanase from the Antarctic bacterium *Pseudoalteromonas haloplanktis*, effectively improved the mechanical dough properties and final bread quality with a positive effect on loaf volume.[63]

Medical and pharmaceutical applications

There is a growing interest in studying psychrophilic bacteria as new tools in pharmaceutical and cosmetic applications. Consequently, several promising psychrophilic strains were detected as a valuable source of new active antimicrobial compounds at low temperatures, as reported by Tomova et al.[87] Recently, compounds produced by the halophilic Antarctic actinomycete *Nocardioides* sp. strain A-1, with antimicrobial activity against *Xanthomonas oryzae* which causes bacterial blight disease in rice-producing countries, exhibited promising application in agriculture for plant protection.[88] In addition, it was found that Antarticine-NF3, an antifreeze glycoprotein produced by the Antarctic bacterium *Pseudoalteromonas*, is effective for scar treatment and has been included in cosmetic regeneration creams.[89]

Furthermore, polyunsaturated fatty acids, produced to improve membrane permeability and nutrient transport in psychrophilic bacteria, may constitute an economic alimentary source for aquaculture industries with favorable activities on cholesterol and triglyceride transport for optimal nervous system and cardiovascular health.[90]

At the industrial level, the polar yeast *Candida antarctica* is used to produce two cold-active lipases, A and B, sold as Novozym 435 by Novozymes (Bagsvaerd, Denmark) involved in a very large number of applications related to pharmaceuticals and cosmetics.[91]

Detergent and fabric industry

Considering the versatile properties of cold-active enzymes – such as high catalytic efficiencies at low temperature, lower thermal stability and novel substrate specificities – they offer a large reservoir of potentially novel biotechnological exploitation.[75] Nowadays, the detergent field, which represents 30–40% of all enzymes produced worldwide, requires more enzymes that are capable of working at low temperatures in the context of energy saving. Cold-adapted enzymes actively used in detergent formulations – lipases, proteases and α-amylases – are systematically introduced to improve the efficiency of detergents and reduce the amount of chemicals used in order to protect the texture and colours of fabrics and reduce wear and tear during washing.[6,64,92] Currently, cold-active subtilisins, isolated from Antarctic *Bacillus* species, are incorporated in cold-active detergents that combine storage alkaline stability and cold activity required for optimal washing results.[63]

Furthermore, the application of cold-adapted cellulases in fabric production and denim finishing could increase the smoothness and softness of tissues, decolourisation of textile effluents and textile bleaching and allows the development of environmentally friendly technologies in fibre processing.[93]

Conclusion

Over recent years, a wealth of knowledge has been accumulated on psychrophilic microorganisms and their cold-shock response catalysts. Because of their unique biological features, psychrophiles can be significantly exploited in biotechnological industries such as the pharmaceutical, enzyme production, bioremediation, biosensor, cosmetic, agriculture, domestic purposes and textile industries. The outcome of these studies may also help to explore the possibility of life in distant frozen planets and their satellites.

References

1. Gounot AM. Microbial life in permanently cold soils. In: Margesin R, Schinner F, editors. Cold-adapted organisms, ecology, physiology, enzymology and molecular biology. New York: Springer; 1999. p. 4–15. https://doi.org/10.1007/978-3-662-06285-2_1

2. Kirchman DL, Moran XA, Ducklow H. Microbial growth in the polar oceans – role of temperature and potential impact of climate change. Nat Rev Microbiol. 2009;7:451–459. https://doi.org/10.1038/nrmicro2115

3. Laybourn-Parry J, Pearce D. Heterotrophic bacteria in Antarctic lacustrine and glacial environments. Polar Biol. 2016;39:2207–2225. https://doi.org/10.1007/s00300-016-2011-1

4. Morita R. Psychrophilic bacteria. Bacteriol Rev. 1975;39:144–167.

5. Helmke E, Weyland H. Psychrophilic *versus* psychrotolerant bacteria. Occurrence and significance in polar and temperate marine habitats. Cell Mol Biol. 2004;50:553–561.

6. Feller G, Gerday C. Psychrophilic enzymes: Hot topics in cold adaptation. Nat Rev Microbiol. 2003;1:200–208. https://doi.org/10.1038/nrmicro773

7. Zakhia F, Jungblut A-D, Taton A, Vincent W, Wilmotte A. Cyanobacteria in cold ecosystems. In: Margesin R, Schinner F, Marx J-C, Gerday C, editors. Psychrophiles: From biodiversity to biotechnology. Berlin: Springer; 2008. p. 121–135. https://doi.org/10.1007/978-3-540-74335-4_8

8. Georlette D, Blaise V, Collins T, D'Amico S, Gratia E, Hoyoux A, et al. Some like it cold: Biocatalysis at low temperatures. FEMS Microbiol Rev. 2004;28:25–42. https://doi.org/10.1016/j.femsre.2003.07.003

9. Feller G, Gerday C. Psychrophilic enzymes: Molecular basis of cold adaptation. Cell Mol Life Sci. 1997;53:830–841. https://doi.org/10.1007/s000180050103

10. Morita R, Moyer C. Psychrophiles, origin of. Encyclopedia of biodiversity. 2001;4:917–924. https://doi.org/10.1016/B0-12-226865-2/00362-X

11. Witter LD. Psychrophilic bacteria – A review. J Dairy Science. 1961;44:983–1015. https://doi.org/10.3168/jds.S0022-0302(61)89851-2

12. Junge K, Christner B, Staley J. Diversity of psychrophilic bacteria from sea ice – and glacial ice communities. In: Horikoshi K, editor. Extremophiles handbook. Tokyo: Springer; 2011. p. 793–815.

13. Deming JW, Eicken H. Life in ice. In: Sullivan WT, Baross JA, editors. Planets and life: The emerging science of astrobiology. Cambridge: Cambridge University Press; 2007. p. 292–312.

14. Rodrigues DF, Tiedje JM. Coping with our cold planet. Appl Environ Microbiol. 2008;74:1677–1686. https://doi.org/10.1128/AEM.02000-07

15. Lauro FM, Bartlett DH. Prokaryotic lifestyles in deep sea habitats. Extremophiles. 2008;12:15–25. https://doi.org/10.1007/s00792-006-0059-5

16. Cavicchioli R. Cold-adapted Archaea. Nat Rev Microbiol. 2006;4:331–343. https://doi.org/10.1038/nrmicro1390

17. Kalanetra KM, Bano N, Hollibaugh T. Ammonia-oxidizing Archaea in the Arctic ocean and Antarctic coastal waters. Environ Microbiol. 2009;11:2434–2445. https://doi.org/10.1111/j.1462-2920.2009.01974.x

18. Margesin R, Miteva V. Diversity and ecology of psychrophilic microorganisms. Res Microbiol. 2011;162:346–361. https://doi.org/10.1016/j.resmic.2010.12.004

19. Buzzini P, Branda E, Goretti M, Turchetti B. Psychrophilic yeasts from worldwide glacial habitats: Diversity, adaptation strategies and biotechnological potential. FEMS Microbiol Ecol. 2012;82:217–241. https://doi.org/10.1111/j.1574-6941.2012.01348.x

20. Lamilla C, Pavez M, Santos A, Hermosilla A, Llanquinao V, Barrientos L. Bioprospecting for extracellular enzymes from culturable Actinobacteria from the South Shetland Islands, Antarctica. Polar Biol. 2017;40:719–726. https://doi.org/10.1007/s00300-016-1977-z

21. Doucet D, Walker VK, Qin W. The bugs that came in from the cold: Molecular adaptations to low temperatures in insects. Cell Mol Life Sci. 2009;66:1404–1418. https://doi.org/10.1007/s00018-009-8320-6

22. Giordano D, Russo R, Di Prisco G, Verde C. Molecular adaptations in Antarctic fish and marine microorganisms. Mar Genomics. 2012;6:1–6. https://doi.org/10.1016/j.margen.2011.09.003

23. Helmke E, Weyland H. Bacteria in sea ice and underlying water of the eastern Weddell Sea in midwinter. Mar Ecol Prog Ser. 1995;117:269–287. https://doi.org/10.3354/meps117269

24. Staley JT, Irgens RL, Herwig RP. Gas vacuolated bacteria found in Antarctic sea with ice algae. Appl Environ Microbiol. 1989;55:1033–1036.

25. D'Amico S, Collins T, Marx JC, Feller G, Gerday C. Psychrophilic microorganisms: Challenges for life. EMBO Rep. 2006;7:385–389. https://doi.org/10.1038/sj.embor.7400662

26. Staley JT, Gosink JJ. Poles apart: Biodiversity and biogeography of sea ice bacteria. Annu Rev Microbiol. 1999;53:189–215. https://doi.org/10.1146/annurev.micro.53.1.189

27. Deming JW. Psychrophiles and polar regions. Curr Opin Microbiol. 2002;5:301–309. https://doi.org/10.1016/S1369-5274(02)00329-6

28. Miteva V. Bacteria in snow and glacier ice. In: Margesin R, Schinner F, Marx J-C, Gerday C, editors. Psychrophiles: From biodiversity to biotechnology. Berlin: Springer; 2008. p. 31–50. https://doi.org/10.1007/978-3-540-74335-4_3

29. Zhang X, Ma X, Wang N, Yao T. New subgroup of *Bacteroidetes* and diverse microorganisms in Tibetan plateau glacial ice provide a biological record of environmental conditions. FEMS Microbiol Ecol. 2008;67:21–29. https://doi.org/10.1111/j.1574-6941.2008.00604.x

30. Bass D, Howe A, Brown N, Barton H, Demidova M, Michelle H, et al. Yeast forms dominate fungal diversity in the deep oceans. Proc Roy Soc B Biol Sci. 2007;274:3069–3077. https://doi.org/10.1098/rspb.2007.1067

31. Robinson CH. Cold adaptation in Arctic and Antarctic fungi. New Phytologist. 2001;151:341–353. https://doi.org/10.1046/j.1469-8137.2001.00177.x

32. Ozerskaya SM, Ivanushkina NE, Kochkina GA, Fattakhova RN, Gilichinsky DA. Mycelial fungi in cryopegs. Int J Astrobiol. 2004;4:327–331. https://doi.org/10.1017/S1473550405002260

33. D'Elia T, Veerapaneni R, Theraisnathan V, Rogers SO. Isolation of fungi from Lake Vostok accretion ice. Mycologia. 2009;101:751–763. https://doi.org/10.3852/08-184

34. Bej AK, Aislabie J, Atlas RM. Polar microbiology: The ecology, biodiversity and bioremediation potential of microorganisms in extremely cold environments. Boca Raton, FL: CRC Press; 2010.

35. Shivaji S, Prakash J. How do bacteria sense and respond to low temperature? Arch Microbiol. 2010;192:85–95. https://doi.org/10.1007/s00203-009-0539-y

36. Chintalapati S, Kiran MD, Shivaji S. Role of membrane lipid fatty acids in cold adaptation. Cell Mol Biol. 2004;50:631–642.

37. Weber MH, Marahiel MA. Bacterial cold shock responses. Sci Progr. 2003;86:9–75. https://doi.org/10.3184/003685003783238707

38. Christner BC. Incorporation of DNA and protein precursors into macromolecules by bacteria at -15°C. Appl Environ Microbiol. 2002;68:6435–6438. https://doi.org/10.1128/AEM.68.12.6435-6438.2002

39. Johnson SS, Hebsgaard MB, Christensen TR, Mastepanov M, Nielsen R, Munch K, et al. Ancient bacteria show evidence of DNA repair. Proc Natl Acad Sci USA. 2007;36:14401–14405. https://doi.org/10.1073/pnas.0706787104

40. Russell NJ. Membrane components and cold sensing. In: Margesin R, Schinner F, Marx J-C, Gerday C, editors. Psychrophiles: From biodiversity to biotechnology. Berlin: Springer; 2008. p. 177–190. https://doi.org/10.1007/978-3-540-74335-4_11

41. Kerekes R, Nagy G. Membrane lipid composition of a mesophilic and psychrophilic yeast. Acta Alimentaria. 1980;9:93–98.

42. Armstrong GA. Genetics of eubacterial carotenoid biosynthesis: A colourful tale. Annu Rev Microbiol. 1997;51:629–659. https://doi.org/10.1146/annurev.micro.51.1.629

43. Fong NJC, Burgess ML, Barrow KD, Glenn DR. Carotenoid accumulation in the psychrotrophic bacterium *Arthrobacter agilis* in response to thermal and salt stress. Appl Microbiol Biotechnol. 2001;56:750–756. https://doi.org/10.1007/s002530100739

44. Chattopadhyay MK, Jagannadham MV. Maintenance of membrane fluidity in Antarctic bacteria. Polar Biol. 2001;24:386–388. https://doi.org/10.1007/s003000100232

45. Gilbert JA, Hill PJ, Dodd CE, Laybourn-Parry J. Demonstration of antifreeze protein activity in Antarctic lake bacteria. Microbiology. 2004;150:171–180. https://doi.org/10.1099/mic.0.26610-0

46. Christner BC. Bioprospecting for microbial products that affect ice crystal formation and growth. Appl Microbiol Biotechnol. 2010;85:481–489. https://doi.org/10.1007/s00253-009-2291-2

47. Jia Z, DeLuca CI, Chao H, Davies PL. Structural basis for the binding of a globular antifreeze protein to ice. Nature. 1996;384:285–288. https://doi.org/10.1038/384285a0

48. Duman JG, Wu DW, Xu L, Tursman D, Olsen TM. Adaptations of insects to subzero temperatures. Q Rev Biol. 1991;66:387–410. https://doi.org/10.1086/417337

49. Sun X, Griffith M, Pasternak JJ, Glick B. Low temperature growth, freezing survival and production of antifreeze protein by the plant growth promoting rhizobacterium *Pseudomonas putida* GR12–2. Can J Microbiol. 1995;41:776–784. https://doi.org/10.1139/m95-107

50. Duman JG, Olsen TM. Thermal hysteresis protein activity in bacteria, fungi and phylogenetically diverse plants. Cryobiology. 1993;30:322–328. https://doi.org/10.1006/cryo.1993.1031

51. Yamashita Y, Nakamura N, Omiya K, Nishikawa J, Kawahara H, Obata H. Identification of an antifreeze lipoprotein from *Moraxella* sp. of Antarctic origin. Biosci Biotechnol Biochem. 2002;66:239–247. https://doi.org/10.1271/bbb.66.239

52. Muryoi N, Sato M, Kaneko S, Kawahara H, Obata H, Yaish MW, et al. Cloning and expression of *afpA*, a gene encoding an antifreeze protein from the arctic plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2. J Bacteriol. 2004;186:5661–5671. https://doi.org/10.1128/JB.186.17.5661-5671.2004

53. Krembs C, Eicken H, Junge K, Deming JW. High concentrations of exopolymeric substances in Arctic winter sea ice: Implications for the polar ocean carbon cycle and cryoprotection of diatoms. Deep Sea Res. 2002;49:2163–2181. https://doi.org/10.1016/S0967-0637(02)00122-X

54. Mancuso Nichols CA, Guezennec J, Bowman JP. Bacterial exopolysaccharides from extreme marine environments with special consideration of the southern ocean, sea ice, and deep-sea hydrothermal vents: A review. Mar Biotechnol. 2005;7:253–271. https://doi.org/10.1007/s10126-004-5118-2

55. Ko R, Smith LT, Smith GM. Glycine betaine confers enhanced osmotolerance and cryotolerance on *Listeria monocytogenes.* J Bacteriol. 1994;176:426–431. https://doi.org/10.1128/jb.176.2.426-431.1994

56. Phadtare S. Recent developments in bacterial cold-shock response. Curr Issues Mol Biol. 2004;6:125–136.

57. Tibbett M, Sanders FE, Cairney JWG. The effect of temperature and inorganic phosphorus supply on growth and acid phosphatase production in arctic and temperate strains of ectomycorrhizal *Hebeloma* spp. in axenic culture. Mycol Res. 1998;102:129–135. https://doi.org/10.1017/S0953756297004681

58. Hebraud M, Potier P. Cold shock response and low temperature adaptation in psychrotrophic bacteria. J Mol Microbiol Biotechnol. 1999;1:211–219.

59. Chaikam V, Karlson DT. Comparison of structure, function and regulation of plant cold shock domain proteins to bacterial and animal cold shock domain proteins. BMB Rep. 2010;43:1–8. https://doi.org/10.5483/BMBRep.2010.43.1.001

60. Phadtare S. Unwinding activity of cold shock proteins and RNA metabolism. RNA Biol. 2011;8:394–397. https://doi.org/10.4161/rna.8.3.14823

61. Kawahara H, Koda N, Oshio M, Obata H. A cold acclimation protein with refolding activity on frozen denatured enzymes. Biosci Biotechnol Biochem. 2000;64:2668–2674. https://doi.org/10.1271/bbb.64.2668

62. Samie N, Noghabi K, Gharegozloo Z, Zahiri H, Ahmadian G, Sharafi H, et al. Psychrophilic α-amylase from *Aeromonas veronii* NS07 isolated from farm soils. Process Biochem. 2012;47:1381–1387. https://doi.org/10.1016/j.procbio.2012.05.007

63. Struvay C, Feller G. Optimization to low temperature activity in psychrophilic enzymes. Int J Mol Sci. 2012;13:11643–11665. https://doi.org/10.3390/ijms130911643

64. Gerday C, Aittaleb M, Bentahier M, Chessa JP, Claverie P, Collins T, et al. Cold-adapted enzymes: From fundamentals to biotechnology. Trends Biotechnol. 2000;18:103–107. https://doi.org/10.1016/S0167-7799(99)01413-4

65. Miyazaki K, Wintrode PL, Grayling RA, Rubingh DN, Arnold FH. Directed evolution study of temperature adaptation in a psychrophilic enzyme. J Mol Biol. 2000;297:1015–1026. https://doi.org/10.1006/jmbi.2000.3612

66. Siddiqui KS, Cavicchioli R. Cold-adapted enzymes. Annu Rev Biochem. 2006;75:403–433. https://doi.org/10.1146/annurev.biochem.75.103004.142723

67. Aghajari N, Feller G, Gerday C, Haser R. Structures of the psychrophilic *Alteromonas haloplanctis* alpha-amylase give insights into cold adaptation at a molecular level. Structure. 1998;6:1503–1516. https://doi.org/10.1016/S0969-2126(98)00149-X

68. Humphrey DR, George A, Black GW, Cummings SP. *Flavobacterium frigidarium* sp. nov., an aerobic, psychrophilic, xylanolytic and laminarolytic bacterium from Antarctica. Int J Syst Evol Microbiol. 2001;51:1235–1243. https://doi.org/10.1099/00207713-51-4-1235

69. Bendt A, Huller H, Kammel U, Helmke E, Schweder T. Cloning, expression and characterization of a chitinase gene from the Antarctic psychrotolerant bacterium *Vibrio* sp. strain Fi:7. Extremophiles. 2001;5:119–126. https://doi.org/10.1007/s007920100179

70. Lu M, Fang Y, Li H, Liu H, Wang S. Isolation of a novel cold-adapted amylase-producing bacterium and study of its enzyme production conditions. Ann Microbiol. 2010;60:557–563. https://doi.org/10.1007/s13213-010-0090-8

71. Krishnan A, Convey P, Gonzalez-Rocha G, Alias S. Production of extracellular hydrolase enzymes by fungi from King George Island. Polar Biol. 2016;39:65–76. https://doi.org/10.1007/s00300-014-1606-7

72. Arora P. *Staphylococcus lipolyticus* sp. nov., a new cold-adapted lipase producing marine species. Ann Microbiol. 2013;63:913–922. https://doi.org/10.1007/s13213-012-0544-2

73. Huston AL, Methe B, Deming JW. Purification, characterization, and sequencing of an extracellular cold active aminopeptidase produced by marine psychrophile *Colwellia psychrerythraea* strain 34H. Appl Environ Microbiol. 2004;70:3321–3328. https://doi.org/10.1128/AEM.70.6.3321-3328.2004

74. Tsuruta H, Tamura J, Yamagata H, Aizono Y. Specification of amino acid residues essential for the catalytic reaction of cold-active protein-tyrosine phosphatase of a psychrophile, *Shewanella* sp. Biosci Biotechnol Biochem. 2004;68:440–443. https://doi.org/10.1271/bbb.68.440

75. Cavicchioli R, Charlton T, Ertan H, Mohd Omar S, Siddiqui K, Williams T. Biotechnological uses of enzymes from psychrophiles. Microbial Biotechnol. 2011;4:449–460. https://doi.org/10.1111/j.1751-7915.2011.00258.x

76. Banerjee R, Halder A, Natta A. Psychrophilic microorganisms: Habitats and exploitation potentials. Eur J Biotechnol Biosci. 2016;4:16–24.

77. Margesin R, Schinner F. Biodegradation and bioremediation of hydrocarbons in extreme environments. Appl Microbiol Biotechnol. 2001;56:650–663. https://doi.org/10.1007/s002530100701

78. Zhou Z, Qing J, Jinlai M, Fangming L. Antarctic psychrophile bacteria screening for oil degradation and their degrading characteristics. Mar Sci Bull. 2008;10:50–57.

79. Whyte LG, Bourbonnière L, Bellerose C, Greer CW. Bioremediation assessment of hydrocarbon-contaminated soils from the high Arctic. Bioremediation J. 1999;3:69–79. https://doi.org/10.1080/10889869991219217

80. Ruberto L, Vazquez S, Lobalbo A, Mac Cormack W. Psychrotolerant hydrocarbon-degrading *Rhodococcus* strains isolated from polluted Antarctic soils. Antarct Sci. 2005;17:47–56. https://doi.org/10.1017/S0954102005002415

81. Aislabie J, Saul DJ, Foght JM. Bioremediation of hydrocarbon-contaminated polar soils. Extremophiles. 2006;10:171–179. https://doi.org/10.1007/s00792-005-0498-4

82. Lin X, Yang B, Shen J, Du N. Biodegradation of crude oil by an Arctic psychrotrophic bacterium *Pseudoalteromomas* sp. P29. Curr Microbiol. 2009;59:341–345. https://doi.org/10.1007/s00284-009-9440-9

83. Nam E, Ahn J. Antarctic marine bacterium *Pseudomonas* sp. KNOUC808 as a source of cold-adapted hydrolyzing enzyme. Braz J Microbiol. 2011;42:927–936. https://doi.org/10.1590/S1517-83822011000300011

84. Hoyoux A, Jennes I, Dubois P, Genicot S, Dubail F, Francois JM, et al. Cold-adapted β-galactosidase from the Antarctic psychrophile *Pseudoalteromonas haloplanktis*. Appl Environ Microbiol. 2001;67:1529–1535. https://doi.org/10.1128/AEM.67.4.1529-1535.2001

85. Adapa V, Ramya L, Pulicherla K, Rao K. Cold active pectinases: Advancing the food industry to the next generation. Appl Biochem Biotechnol. 2014;172:2324–2337. https://doi.org/10.1007/s12010-013-0685-1

86. Singh P, Hamid B, Ahmad Lone M, Ranjan K, Khan A, Chaurse V, et al. Evaluation of pectinase activity from the psychrophilic fungal strain *Truncatella angustata*-BPF5 for use in wine industry. Endocytobiosis Cell Res. 2012;22:57–61.

87. Tomova I, Stoilova-Disheva M, Lazarkevich I, Vasileva-Tonkova E. Antimicrobial activity and resistance to heavy metals and antibiotics of heterotrophic bacteria isolated from sediment and soil samples collected from two Antarctic islands. Front Life Sci. 2015;8:348–357. https://doi.org/10.1080/21553769.2015.1044130

88. Gesheva V, Vasileva-Tonkova E. Production of enzymes and antimicrobial compounds by halophilic Antarctic *Nocardioides* sp. grown on different carbon sources. World J Microbiol Biotechnol. 2012;28:2069–2076. https://doi.org/10.1007/s11274-012-1009-2

89. Bisht S. Cold active proteins in food and pharmaceutical industry [article on the Internet]. Biotech Articles. c2011 [cited 2017 Dec. 15]. Available from: http://www.biotecharticles.com/Biotechnology-products-Article/Cold-Active-Proteins-in-Food-and-Pharmaceutical-Industry-719.html

90. Jadhav V, Jamle M, Pawar P, Devare M, Bhadekar R. Fatty acid profiles of PUFA producing Antarctic bacteria: Correlation with RAPD analysis. Ann Microbiol. 2010;60:693-699. https://doi.org/10.1007/s13213-010-0114-4

91. Babu J, Ramteke PW, Thomas G. Cold active microbial lipases: Some hot issues and recent developments. Biotechnol Adv. 2008;26:457–470. https://doi.org/10.1016/j.biotechadv.2008.05.003

92. Maiangwa J, Ali M, Salleh A, Abd Rahman R, Shariff F, Leow T. Adaptational properties and applications of cold-active lipases from psychrophilic bacteria. Extremophiles. 2015;19:235-247. https://doi.org/10.1007/s00792-014-0710-5

93. Araujo R, Casal M, Cavaco-Paulo A. Application of enzymes for textile fibres processing. Biocatal. Biotransform. 2008;26:332–349. https://doi.org/10.1080/10242420802390457