



Pigment production by cold-adapted bacteria and fungi: colorful tale of cryosphere with wide range applications

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Abstract

Pigments are an essential part of everyday life on Earth with rapidly growing industrial and biomedical applications. Synthetic pigments account for a major portion of these pigments that in turn have deleterious effects on public health and environment. Such drawbacks of synthetic pigments have shifted the trend to use natural pigments that are considered as the best alternative to synthetic pigments due to their significant properties. Natural pigments from microorganisms are of great interest due to their broader applications in the pharmaceutical, food, and textile industry with increasing demand among the consumers opting for natural pigments. To fulfill the market demand of natural pigments new sources should be explored. Cold-adapted bacteria and fungi in the cryosphere produce a variety of pigments as a protective strategy against ecological stresses such as low temperature, oxidative stresses, and ultraviolet radiation making them a potential source for natural pigment production. This review highlights the protective strategies and pigment production by cold-adapted bacteria and fungi, their industrial and biomedical applications, condition optimization for maximum pigment extraction as well as the challenges facing in the exploitation of cryospheric microorganisms for pigment extraction that hopefully will provide valuable information, direction, and progress in forthcoming studies.

Keywords Cryosphere · Microbial pigments · Cold-adapted microbes · Carotenoid · Melanin

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Introduction

Think for a while, without hemoglobin how oxygen molecules can be carried within a living body or without chlorophyll and other necessary pigments; how plants and other primary producers could prepare their food? Surely impossible. It shows life on this planet depends on pigments. Pigments have been used as coloring agents since the prehistoric era. Sir William Henry Perkin prepared the earliest synthetic dye in 1856 named mauvine. The development of mauvine initiated a historical revolution of synthetic dyes (Walford 1980). Initially, the synthetic dyes gained much attraction due to several characteristics such as easy to develop, economical, no undesirable flavors, excellent coloring properties, and needed in a small amount to use. However, most of the synthetic dyes used had never been tested for their toxic nature for health and adverse effects on the environment (Downham and Collins 2000). In general, synthetic dyes are made up of chemical compounds composed of lead, mercury, copper, chromium, sodium chloride, benzene, and toluene that are harmful to human health. Several

synthetic colorants previously permitted by the Food and Drug Administration (FDA) to use in medicines, food, and cosmetics development were later found carcinogenic (Rao et al. 2017). Some of these synthetically-derived colorants banned by the FDA include ethyl acrylate, benzophenone, eugenyl methyl ether (methyl eugenol), pulegone, myrcene, and pyridine. Similarly, several synthetic dyes like cochineal red, tartrazine, and sunset yellow initiate allergies directly or indirectly by combining with other colorants. The Center for Science in the Public Interest in Washington appealed to the FDA in 2008 to disallow synthetic food colorants since of their association with behavioral harms among children (Potera 2010). Most synthetic dyes previously used for various purposes are now quit due to apparent hazards such as carbon black (extensively used as printing ink pigment) a potential carcinogen and benzidine a causative agent of bowel cancer (Rao et al. 2017). Moreover, the unethical release of untreated dye effluents from industries persists for a longer time due to higher stability. Due to the aforementioned drawbacks of synthetic dyes, global demand for natural pigments has been increased (Manikprabhu and Lingappa 2013). Being aware of the adverse effects causing by synthetic dyes, now consumers prefer natural ingredients in their food instead of artificial (Downham and Collins 2000). This has raised the demand for naturally derived pigments.

The use of natural colorants is believed to be relatively safe, since their nature is biodegradable, harmless, and non-carcinogenic (Cristea and Vilarem 2006). Globally, the trend is shifting towards the consumption of biodegradable and environmentally friendly commodities; therefore, the demand for natural colorants is increasing in pharmaceutical, dyestuff, foodstuff, and cosmetics. Waste materials that are environmental pollutants have been used for microbial pigment production, which made this process more sustainable (Joshi et al. 2003; Kamla et al. 2012). Natural biocolorants that are an alternative to synthetic pigments could be obtained from plants and microorganisms. Natural pigments obtained from microbes are more ideal over plants due to the solubility, and stability of pigments and the easy availability of microbes for culturing (Rao et al. 2017). The fast growth of microorganisms in inexpensive medium, easy downstream processing, and their constant cultivation independent of the seasonal variations are advantages of microbes over plants as a source of pigment production (Manikprabhu and Lingappa 2013). Moreover, the use of plants on a large scale can cause damage to the precious species; therefore, the practice is not sustainable (Downham and Collins 2000). Additionally, the yearly growth rate of natural dyes has been projected 5–10% compared to synthetically derived dyes having a lower growth rate of 3–5% (Parmar and Phutela 2015). Pigments produced by microorganisms are not merely colors but consist of diverse chemical components having multidimensional biological activities (Kim

2013). Among microorganisms, bacteria, fungi, and microalgae offer an alternate source for natural pigments (Joshi et al. 2003; Choi et al. 2015; Rao et al. 2017; Pandey et al. 2018; Ramesh et al. 2019).

Earth's cryosphere has been thought too hostile to harbor life for a long time. However, being extreme ecological conditions, diverse microbial communities exist in the glacial ecosystem (Anesio et al. 2017; Hassan et al. 2018; Rafiq et al. 2019) that maintain active biochemical routes (Anesio and Laybourn-Parry 2012). The microbial communities inhabiting the cryosphere are constantly exposed to several stress conditions such as extremely low temperatures, oligotrophic conditions, freeze–thaw cycles, ultraviolet (UV) radiations, and higher salinity. To cope with these hostile conditions, microorganisms adapt several protective strategies including morphological alteration and production of various metabolites. Most of these metabolites have important biotechnological and industrial applications (Cavicchioli et al. 2011). Among these metabolites, pigments are charismatic traits of these cold-adapted microorganisms that are studied to exploit for several industrial applications. Pigments production mostly occurs within cytoplasm as a responsive agent to hostile ecological conditions presenting several ecological functions (Pagano and Dhar 2015). Physiochemically extreme environments such as the cryosphere provide a suitable setup to microorganisms for pigment production with unique qualities and applications. In this review, pigments produced by cold-adapted bacteria and fungi in the cryosphere and their potential applications in various industries are discussed. Moreover, condition optimization for maximum pigment yield as well as the challenges facing in the exploitation of cryospheric microorganisms for pigment extraction are discussed.

Challenges in cryosphere and microbial adaptation mechanisms

Cryosphere has been dominated and colonized by diverse microorganisms collectively termed as psychrophiles or cold-adapted microorganisms. Life span and activity of several microorganisms significantly reduce below 0 °C (Tribelli and López 2018). However, psychrophilic and psychrotrophic microorganisms withstand the hostile environments of cryosphere and adapt to grow below 5 °C (close to zero). Low temperature reduces thermal energy with increased viscosity of solvents and solubility of gases such as oxygen molecules and reactive oxygen species (ROS), reduced solubility of nutrients and solutes, decreased diffusion as well as amplify desiccation, osmotic stress, and ice development. Moreover, life in the cryosphere experience several environmental stresses including high salinity, low availability of nutrients, oxidative stress, low water activity,

and freeze–thaw cycles. High-pressure stress is subjected to microbial population inhabiting in deep-sea and sub-glacial habitats. Additionally, psychrophilic microbes are exposed to extremes of light, exposure to UV radiations, and bright light at high elevation and low light in frosted lakes, permafrost, and deeper ice sheets. To cope with these life-endanger challenges microorganisms adapt and develop certain sophisticated strategies (Margesin and Collins 2019; Collins and Margesin 2019). Previously, several microbiological, physiological, biochemical, biophysical, and molecular-based approaches have been adapted to identify biogeographical distribution, physiological adaptation, diversity, and ecological role of psychrophiles. However, recent advances in ‘omics’ technologies such as genomics, metagenomics, transcriptomics, and proteomics have uncovered novel adaptation mechanisms and environmental functions of microorganisms in the cryosphere (Singh et al. 2014; Barauna et al. 2017; Tribelli and Lopez 2018). Several mechanisms adapted by microorganisms to cope with the hostile environment of cryosphere are shown in Fig. 1.

At low temperatures, psychrophiles alter their cellular envelope and components to provide shape, support, and protection to cells; regulate nutrient uptake and solute transport; and participate in cell division, adhesion, signaling, and sensing. This alteration is against the low temperature that reduces membrane permeability, fluidity, diffusion rates, and cause cell rupturing due to freeze–thaw cycles and ice formation. Psychrophiles modify the composition of fatty acid in lipid bilayer present in the cell membranes and become homeoviscous (D’Amico et al. 2001; Siddiqui

et al. 2013). Contents of unsaturated fatty acids, short-chain, methyl branched, and/or cis-isomeric can manage the low temperature stress (Hassan et al. 2020) by lowering the liquid phase phospholipid bilayer to gel phase and sustain their function. For this adaptation, upregulation and overrepresentation of genes occur that encode proteins involved in membrane biogenesis and biosynthesis and desaturation of fatty acids (desaturases that also guard against ROS), biosynthesis of branched-chain fatty acids (KAS-II, KAS-III) and cis-isomerization (fatty acid cis/trans isomerases) (Medigue et al. 2005; De Maayer et al. 2014; He et al. 2015; Goordial et al. 2016). Furthermore, psychrophiles upregulate the membrane transport proteins that could counter the reduced diffusion rates at lower temperatures (Bakermans et al. 2007; De Maayer et al. 2014). Long-chain polyunsaturated fatty acids (LC-PUFAs) (Yoshida et al. 2016) also shield the membrane by generating hydrophobic edges between the lipid bilayers, which prevents the entrance of ROS augmented at low temperatures. Polyunsaturated fatty acids (PUFAs) can act as chaperons for proteins in the membrane, which could be functional in cell division and the efflux process (Okuyama et al. 2008; Yoshida et al. 2016). Turk et al. (2011) reported higher membrane fluidity in psychrotolerant yeast *Rhodospiridium diobovatum* suggesting that LC-PUFAs maintain the integrity and functionality of the plasma membrane. Similarly, psychrophiles upregulate certain genes encoding peptidoglycan biosynthesis and thicken their peptidoglycan (Mykytczuk et al. 2013), which can protect psychrophiles against freeze–thaw cycle, ice formation, and osmotic pressure. The lipopolysaccharides

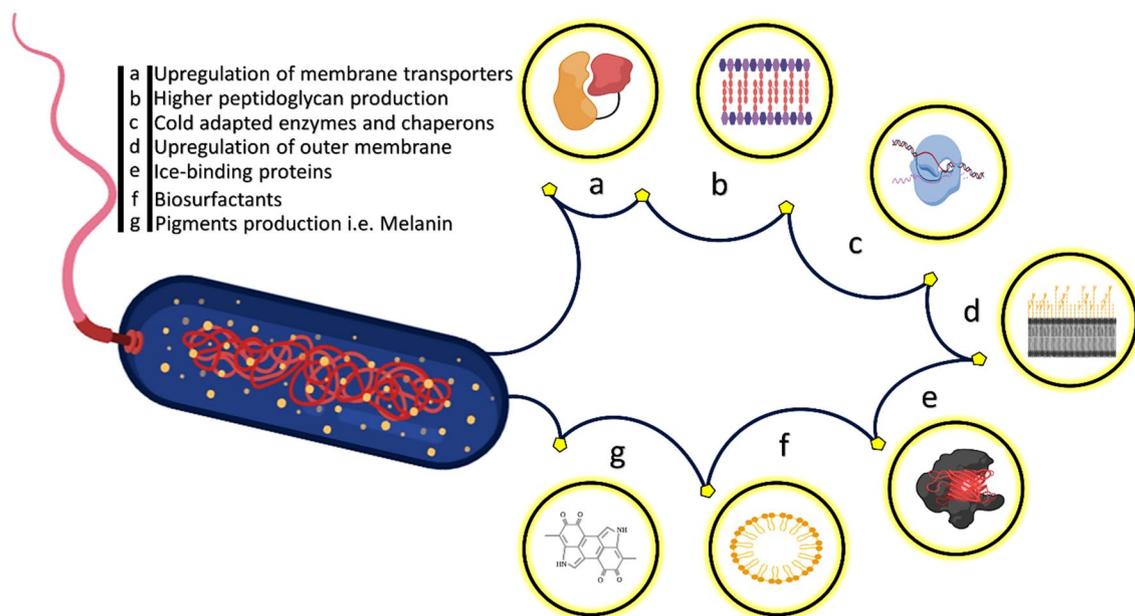


Fig. 1 Common strategies adapted by psychrophiles to cope with low temperatures and other stresses in the cryosphere

(LPS) layer in psychrophiles are shortened in length lacking the O-chain component (Corsaro et al. 2017) that may enhance the flexibility and stability of the outer membrane. Genes encoding for the synthesis of outer membrane components, proteins, and LPS (largely glycosyl transferases) was reported upregulated at lower temperatures (Frank et al. 2011; De Maayer et al. 2014). Benforte et al. (2018) reported that how a mutation in the glycosyl transferase gene (*wapH*) reduced the growth pattern of the Antarctic bacterium at lower temperatures. Several psychrophiles have higher genome contents encoding for compatible solute biosynthesis and uptake genes that could accumulate compatible solutes in molar concentrations, with glycine betaine, glycerol, mannitol, trehalose, sarcosine, sucrose, and sorbitol (Mykytczuk et al. 2013; Ghobakhlou et al. 2015; Goordial et al. 2016) that could restore osmotic balance and cell shrinkage. Fungi synthesize certain compatible solutes to cope with osmotic pressure and dehydration in the cryosphere such as mannitol that acts as a cryoprotective (Feofilova et al. 1994). Psychrophiles produce antifreeze proteins (AFPs) that bind to ice and inhibit ice development and recrystallization. AFPs preserve the liquid present in the close vicinity of cells (Raymond et al. 2008). These AFPs also stabilize cell membranes, structural integrity, and position the cell for increase contact towards nutrients and oxygen in the phototrophic region (Lorv et al. 2014; Bar Dolev et al. 2016; Voets 2017). Another protein called ice-nucleating proteins (INPs) reported in psychrophiles prevent cryoinjury of the cell by inhibiting intracellular ice formation (Lorv et al. 2014). Cold-adapted bacteria produce a high concentration of extracellular polymeric substances (EPS) at low temperatures (Mykytczuk et al. 2013; Caruso et al. 2018) which could form a protective shell around the cells. EPS produced by psychrophilic microorganisms could act as osmoprotective, ROS scavenging, and cryoprotective (Ewert and Deming 2013; Deming and Young 2017). Along with low temperature adaptation, biosurfactant (glycolipid) reported from Antarctic yeast showed ice recrystallization inhibition activity (Kitamoto et al. 2001), also such biosurfactants act as osmolytes (Perfumo et al. 2018). The main adverse effect of low temperature is on the cellular reaction rate of mesophilic microorganisms that either halts their cellular growth or cause death due to cellular lysis. However, psychrophiles produce enzymes that perform high catalytic activities in cold environments, therefore, optimally grow at low temperatures (Santiago et al. 2016; Collins and Gerday 2017). Psychrophiles overcome the obstacle of reduced enzyme activity by developing a changed system for the transportation of nutrients and waste products; altered cellular processes of transcription and translation, and cell division cycle, and decrease the fluidity of membrane to grow in low temperature (D'Amico et al. 2006). Cold-adapted organisms produce chaperones that efficiently fold proteins and

DNA/RNA and stabilize the secondary structures of these molecules at low temperatures. Psychrophiles upregulate the production of protein and DNA/RNA chaperones as cold acclimation proteins (Lim et al. 2000). Recently by adapting omics approaches have discovered various traits that are common to psychrophiles (Tribelli and Lopez 2018). One such trait is the metabolic adjustment at sub-zero temperature that takes place in psychrophiles such as the down-regulation of primary metabolic pathways and replacement with alternate secondary pathways and accumulations and digestion of spare compounds. Cellular metabolic routes like glycolysis, tricarboxylic acid cycle, electron transport chain, and pentose phosphate pathway get downregulated in cold-adapted microorganisms (Medigue et al. 2005; Piette et al. 2011; Tribelli et al. 2015). Such metabolic reprogramming could protect oxidative stress and conserve energy for long-term survival. Another important protective mechanism adapted by psychrophilic microorganisms is the production of pigments. Psychrophiles reported from ice-cores and glaciers were capable to produce pigments (Shen et al. 2018). Melanin pigment reported in fungi protects stresses such as ionizing radiation, desiccation, oxidizing agents, and UV radiations (Butler and Day 1998; Gorbushina 2003). Antarctic fungal species having melanin were reported, which were resistant to UV radiation (Hughes et al. 2003). Several fungal strains produce mycosporines that absorb UV radiations (Sommaruga et al. 2004). Similarly, psychrophilic bacteria produce carotenoid as a protection mechanism in cryospheric environments (Vila et al. 2019). Moreover, these pigments also play role in photoprotection (in combination with other molecules like mycosporine and scytonemin like amino acids, and act as a protector against intense light range and UV irradiation), act as cryoprotectants, antioxidants, and antimicrobials (Dieser et al. 2010; Pandey et al. 2018).

Role of pigments in cold-adapted microbes

In general, pigments are secondary metabolites produced by microbes and are not necessarily produced by all kinds of microorganisms. Cold-adapted bacteria and fungi inhabiting cryospheric environments produce a diverse range of pigments (Table 1). The pigment production by microbes in extremely low temperature environments is a mechanism to survive ecological stresses. They consume pigment molecules as an energy source (Madigan et al. 2012), for the process of photosynthesis (Siefirrmann-Harms 1987), as a confrontation tool against stress (Martin-Cerezo et al. 2015), oxidants, extreme temperature and desiccation (Wada et al. 2013), and for safety against UV irradiation (Becker-Hapak et al. 1997). Moreover, pigments also act as an antimicrobial agent against other bacteria (Suresh et al. 2015) and sometimes act as a shield to protect the cell against natural

Table 1 Pigments produced by cold-adapted bacteria and fungi, characterization, and biological activities

Type of microorganism	Name of organism	Habitat	Pigment	Color	Biological function	References
Bacteria	<i>Micrococcus roseus</i>	Antarctic soil	Carotenoid	Yellow	Regulation of membrane fluidity	Chattopadhyay et al. (1997)
	<i>Arthrobacter agilis</i>	Sea ice, Antarctica	Carotenoid	Yellow	Membrane stabilization at low temperature	Fong et al. (2001)
	Microbial mat; multiple bacteria isolated	Ward Hunt Ice Shelf, Nunavut, Canada	Carotenoid, Scytonemins	Yellow	Protection against reactive oxygen species, coping radiations, and other stresses	Mueller et al. (2005)
	Multiple bacteria isolated	Antarctic sites: Pony Lake and Cotton Glacier	Carotenoid	Yellow, orange, and dark rose red	Prevent against freeze–thaw cycles. Protection against UV radiation	Dieser et al. 2010
	<i>Sanguibacter suarezii</i> KK6, <i>Kocuria turfanensis</i> KK7, <i>Kocuria rosea</i> KK12, and <i>Planococcus maritimus</i> KK21	Leh and Ladakh soil, Himalayas	Carotenoid (Lycopene)	Yellow and orange	Survival strategy in a cold environment	Kushwaha et al. (2014)
	<i>Arthrobacter</i> isolates	Scott Base, Granite Harbour, Mirna Bluff and Marble Point (Antarctic)	Carotenoid	Genes reported	Cold adaptation by stabilizing cell membrane, resistance to oxidative stress	Dsouza et al. (2015)
	30 different heterotrophic pigmented bacteria were isolates	Fildes Peninsula, King George Island, Antarctica	Carotenoid	Yellow and orange	Survival strategy in a cold environment	Vila et al. (2019)
	Novel species very close to <i>Janthinobacterium lividum</i>	Organic residue of a water tank keeping rainbow trout	Mixture of violacein and deoxyviolacein	Violet	Antibacterial activity and enhance competitive ability	Nakamura et al. (2002)
	<i>Corynebacterium glutamicum</i> ATCC	ATCC	Decaprenoxanthin (Carotenoid); Lycopene (Carotenoid)	Yellow and red	Photoprotection and light-harvesting	Heider et al. (2012)
	<i>Sphingomonas faeni</i> and other	Anthropogenic cold environments	Astaxanthin (Carotenoid)	Yellow	Antagonistic effect against competitors	Mageswari et al. (2015)
	<i>Janthinobacterium</i> sp. HHS7	Xinjiang glacier, China	Violacein	Violet	Adaptation to extremely low temperature	Lu et al. (2009)
	11 psychrophilic <i>Flavobacterium</i> strains	Laigu, Zepu, Renlongba, and Gawalong glaciers in Bome County, Tibetan Autonomous Region, P.R. China	Flexirubin-type pigment	Yellow	Adaptation to extremely low temperature	Liu et al. (2019)

Table 1 (continued)

Type of microorganism	Name of organism	Habitat	Pigment	Color	Biological function	References
	<i>Pseudomonas Cryobacterium</i> , <i>Psychrobacter</i> , <i>Flavobacterium</i> , and many others	Yuzhufeng Glacier, Tibetan Plateau, China	carotenoids such as α - and β -carotene, 19'-butanoyloxy-fucoaxanthin, fucoxanthin, diatoxanthin, peridinin and zeaxanthin, with α -carotene as the dominant carotenoid	(orange, reddish-orange, yellow, pink, brown, and white)	Survival strategy in a cold environment	Shen et al. (2018)
	Genus <i>Arthrobacter</i> ; <i>Arthrobacter psychrophilicus</i> sp. nov	Alpine ice cave, Austria	Unidentified	Yellow	Survival strategy in a cold environment	Margesin et al. (2004)
	Thirty-seven heterotrophic bacterial isolates	Franz Josef and Fox Glaciers, New Zealand	Unidentified	Yellow and orange	Survival strategy in a cold environment	Foght et al. (2004)
	Multiple bacteria isolated	Prydz Bay, Eastern, Antarctica	Unidentified	Yellow, red, orange, pink	Survival strategy in a cold environment	Bowman et al. (1997)
	Multiple bacterial isolates are reported	Gulkana Glacier, Alaska	Unidentified	Pink, orange, white, cream, and yellow	Resistance and adaptation to cold temperatures	Segawa et al. (2011)
	Multiple bacterial isolates are reported	Siachen Glacier, Pakistan	Unidentified	Several colors pigments	Adaptation against cold temperature	Rafiq et al. (2017)
	<i>Proteobacteria</i> , <i>Firmicutes</i> , <i>Actinobacteria</i> , <i>Bacteroidetes</i>	Himalayan Glaciers in Uttarakhand, India	Unidentified	Lemon yellow, orange, brown, violet, pinkish-red and pale yellow	Adaptation against cold temperature	Panwar et al. (2019)
	<i>Janthinobacterium</i> sp. strain Ant5-2	Lake Podprudnoye, Schirmacher Oasis, East Antarctica	Violacein	Purple violet	photoprotective role. UV and cold tolerance	Mojib et al. (2013)
	total of 31 g-positive bacteria was reported	King George Island, Antarctica Peninsula)	Unidentified	Yellow, red, orange, and amber	inhibit potential surface competitors	Leiva et al. (2015)
	<i>Lysobacter oligotrophicus</i>	Antarctica	(Lo-melanin) melanin	Dark-brown	Protection against UV-B irradiation. Scavenge ROS	Kimura et al. (2015)
	<i>Hymenobacter actinoscleris</i> and <i>Chryseobacterium chaponense</i>	King George Island, Antarctica	Carotenoids	Yellow and red	tolerate excessive UV irradiation	Órdenes-Aenishanslins et al. (2016)
	<i>Pedobacter terrae</i>	Doumer Island, Antarctica	Different pigments belong to carotenoids group	Red	Antioxidant activity, protection against UV radiation	Correa-Llantén et al. (2012)

Table 1 (continued)

Type of microorganism	Name of organism	Habitat	Pigment	Color	Biological function	References
	Multiple isolates were reported	coastal Antarctic Station Dumont d'Urville, European alpine snow pits, Nevado Illimani, Bolivia, and Antarctic Station Artigas, King George Island	Unidentified	Multiple colors	UV radiation protection	González-Toril et al. (2008)
	<i>Leeuwenhoekiella aequorea</i> , <i>Pseudomonas pelagia</i> , <i>Halomonas boliviensis</i> , <i>Rhodococcus yunnanensis</i> , <i>Algoriphagus ratkowskyi</i>	Kongsfjorden, a glacial fjord on the west coast of Svalbard,	(Zeaxanthin) carotenoid	Yellow and red	cryptoprotective agent in regulating membrane fluidity	Singh et al. (2017)
	<i>Kocuria polaris</i> sp. nov	McMurdo Dry Valley, Antarctica	Carotenoid	Orange		Reddy et al. (2003)
	<i>Arthrobaacter</i> sp. G20	Caspian Sea	Carotenoid	Red		Afra et al. (2017)
	Cyanobacterial mats	Antarctic stromatolitic and endolithic cyanobacterial communities	Scytonemin		Photoprotection	Wynn-Williams et al. (1999)
	Lichen and cyanobacterial samples	Antarctic desert habitats,	β -carotene, Scytonemin, phycocyanin, etc		UV protection	Wynn-Williams and Edwards (2002)
	Cyanobacteria-dominated microbial mats (several isolates)	McMurdo Sound region, Antarctica	Scytonemin, carotenoids,	Multiple colors		Vincent et al. (1993)
Fungi	Several yeasts were isolated	Antarctica (Admiralty Bay, King George Island, and Port Foster Bay and Deception Island)	Carotenoids and Other pigments	Several colors	Protection against UV radiation	Vaz et al. (2011)
	<i>Dioszegia</i> sp., <i>Rhodotorula mucilaginosa</i> , <i>Rhodotorula laryngis</i>	Italian alpine glacier (Tonale Pass, TN, Italy)	Carotenoids	Orange to salmon-colored	Protection against UV radiation	Amaretti et al. (2014)
	<i>Thelebotus microsporius</i>	McLeod Island, Larsemann Hills, in the Prydz Bay area of East Antarctica	β -carotene (Carotenoid)	Bright orange to yellow-orange	Stress tolerance of UV radiation and extreme cold	Singh et al. (2014)
	<i>Xanthophylomyces dendrorhous</i>	King George Island, Antarctic Peninsula	Astaxanthin, phoenicoxanthin, β -carotene, (Carotenoid)	red, pale-yellow and yellow	photoprotective role	Contreras et al. (2015)
	<i>Penicillium</i> sp. (GBPL_P155)	Himalayan region of India	Carotenoid (Derivatives)	Dark orange pigment	Survival of the cold temperature	Pandey et al. (2018)

Table 1 (continued)

Type of microorganism	Name of organism	Habitat	Pigment	Color	Biological function	References
Multiple fungal isolates were reported	Batura Glacier, Karakoram, Pakistan	Unidentified	Multiple colors		Adaptation against cold temperature	Hassan et al. (2018)
Multiple endophytic fungal isolates were reported	Admiralty Bay, King George Island, South Shetland Islands, Antarctica	Melanin	Dark blackish		Protection against environmental stresses in cold habitats	Rosa et al. (2009)
<i>Antarctomyces pellizariae</i> sp. nov.,	Coppermine Peninsula, Robert Island, in the South Shetland Islands, Antarctica	Unidentified	Blue		Cryo-protection of fungus	de Menezes et al. (2017)
<i>Cystofilobasidium capitatum</i> and <i>Sporobolomyces ruberrimus</i>	Zooplankton (Antarctica)	β -Carotenoid			Resistance to ultraviolet B (UVB)	Moliné et al. (2009)
<i>Sporobolomyces salmonicolor</i> , <i>Cryptococcus albidus</i> , and <i>Cryptococcus laurentii</i>	Livingston Island, Antarctica	β -carotene			Resistance to ultraviolet A (UVA)	Dimitrova et al. (2010)
<i>Sporobolomyces salmonicolor</i>	Livingston Island, Antarctica	β -Carotene, torularhodin, and torulene			Antioxidant activity	Dimitrova et al. (2013)
<i>Rhodotorula mucilaginosa</i> , <i>Rhodotorula larynges</i> , <i>Dioszegia</i> sp.	(King George Island, Antarctica)	2- γ -Carotene, Torulene, γ -carotene, and lycopene, Torulene, and lycopene, OHK torulene	Pink, pale red, red, orange		UV-C radiation tolerance	Villarreal et al. 2016
<i>Nadsoniella nigra</i>	Antarctica	Melanin	Black		Increase resistance in piglets and reduction of morbidity and mortality	Chyzyhanska and Beręgova (2009)
Several yeasts strains	Antarctic biotopes	Melanin	Coal-black		Protection against UV radiations	Tashirev et al. (2010)
<i>Cryptococcus</i> sp. and <i>Torrubitella</i> sp	Sedimentary rocks (Union Glacier) Antarctic	Mycosporine	Pink and cream			Barahona et al. (2016)
<i>Dioszegia patagonica</i>	(King George Island)	Carotenoid	Orange			Trochine et al. (2017)
<i>Arthrobotrys ferrox</i>	Moss samples (Wood Bay, Victoria Land Antarctica)	Carotenoid and mycosporines			Resistance to ultraviolet-B (UVB)	Arcangeli et al. (1997, 2000); Arcangeli and Cannistraro (2000)
6 yeast strains and 11 bacterial strains	Galindez Island in the Argentine Islands in the north-western Antarctic Peninsula	Carotenoids and other pigments	Multiple colors		UV resistance	Vasiljeva-Tonkova et al. (2014)

antimicrobial compounds secreted by other bacteria (van Duin et al. 2002). High diversity of pigment molecules are reported from microorganisms inhabiting in glaciers (Foght et al. 2004), ice cores (Zhang et al. 2008), and marine surface waters (Agogu  et al. 2005) which shows that this pigment production is essential to cope with the environmental stresses in the cryosphere. Such as carotenoid modulate the cellular membrane fluidity of bacteria as an adaptive strategy in the cryosphere. Polar microbial communities are concurrently exposed to UV radiations, highly active photosynthetic radiations, and extremely low temperatures which make them more prone to photo-damage (Roos and Vincent 1998). Therefore, the adaptation of protective strategies by microorganisms is crucial in these habitats. In such harsh environmental conditions, pigment production efficiently decreases photo-damage and could provide resources for osmoregulation, thus provide tolerance against salinity, desiccation, and freeze–thaw cycles and prevent serious damages such as inhibition of metabolic processes and cellular repair mechanisms (Mueller et al. 2005). Depend upon the composition and concentration of pigments, the production could visibly provide coloration to snow such as green due to chlorophylls, various yellow shades due to xanthophylls, and orange to red due to carotenoids (Anesio et al. 2017).

Pigments produced by cold-adapted bacteria and fungi

Carotenoid

Carotenoids are the main natural pigments widely produced by plants and microorganisms and initially were reported by H.W.F Wackenroder (Wackenroder 1831). Currently, carotenoids signify the largest and highly diverse known group of natural pigments, and 1183 carotenoid structures are compiled from 702 source organisms by Carotenoid Database Japan (<https://carotenoiddb.jp>). Carotenoid is the family of tetraterpenoids consists of an extensively conjugated polyene, which absorbs blue light and appears from yellow to red in shade (Fraser and Bramley 2004). The structure of carotenoids acquires the form of a polyene hydrocarbon chain that is occasionally terminated by rings with or without extra oxygen atoms. Carotenoids are classified into carotenes, which are hydrocarbons (torulene, lycopene, and α - to ϵ -carotenes) or xanthophylls that possess keto, hydroxyl, and/or carboxyl groups (lutein, zeaxanthin, torularhodin, and astaxanthin,) (Table 2). Naturally, carotenoids are extensively produced by plants and microorganisms as a photo-protectants. The color of carotenoids ranging from yellow to deep red depending on the structure (Alija et al. 2005; Rao and Rao 2007). The maximum absorption capacity of carotenoids is ranged from 440 to 520 nm, having a

stronger molar absorption coefficient (ca. $10^5 \text{ L mol}^{-1} \text{ cm}^{-1}$) (Marizcurrena et al. 2019). Cryospheric habitats especially glacial environment provide suitable conditions for pigment production by microorganisms. These pigments also protect the bacterial cells either screening or absorbing UV radiation (Dieser et al. 2010). Carotenoids safeguard microbial cells from photo-oxidative injury and other environmental stresses at low temperatures either by inhibiting the ROS generation through thermal degeneracy of the extra energy or satisfying the excited states of singlet oxygen and chlorophyll (Tian and Hua 2010). Moreover, these pigments play a crucial role in the physiological plasticity of Antarctic microorganisms, efficiently respond to a lower temperature and freeze–thaw cycles (Singh et al. 2017). Additionally, carotenoids play a role in cell differentiation and regulation during cell cycles.

Several studies reported carotenoid producing bacteria and fungi from low temperature environments (Table 1). Vila et al. (2019) reported 30 bacterial strains capable of carotenoids production from Fildes Peninsula, King George Island, Antarctica. Kim et al. (2015) isolated carotenoid producing *Planococcus faecalis* from stools of Antarctic penguins. Carotenoid production was reported in heterotrophic bacteria from Antarctica as a strategic tool against ecological stresses (Dieser et al. 2010). The accumulation of C-50 carotenoid (Bacterioruberin and its glycosylated derivatives) observed in psychrotrophic *Arthrobacter agilis* from an Antarctic sea ice sample. This accumulation of pigments might be responsible for the regulation of cellular membrane fluidity at low temperatures (Fong et al. 2001). Moreover, several polar and non-polar carotenoid pigments produced by Antarctic strains of *Sphingobacterium antarcticus* and *Micrococcus roseus* (Chattopadhyay and Jagannadham 2001). Silva et al. (2019) reported carotenoid producing bacterial strains isolated from the Antarctic continent. Three different carotenoids such as zeaxanthin, β -cryptoxanthin, and β -carotene were reported from Antarctic bacterium *Sphingobacterium antarcticus*. Similarly, carotenoid producing cold-adapted *Penicillium* sp was reported in the Himalaya region of India (Pandey et al. 2018). Several carotenoid-producing yeasts were reported in Italian alpine glaciers (Amaretti et al. 2014). Vaz et al. (2011) reported multiple yeasts isolates from Antarctica capable of carotenoid production.

Prodigiosin

Prodigiosin is a red linear tripyrrole pigment primarily reported from *Serratia marcescens* (Boger and Patel 1987). Prodigiosin was named after its extraction from *Bacillus prodigiosus* later given the name of *S. marcescens* (Gerber 1975). Prodigiosin produces only in later growth stages of bacteria (Harris et al. 2004). Biosynthesis of prodigiosin is controlled by quorum sensing (Thomson et al. 2000).

Certain proposed eco-physiological roles of prodigiosin are; air diaspora of bacteria (Burger and Bennett 1985), metabolic precursor for NAD(P)H or proline (Hood et al. 1992), light energy storage (Ryazantseva et al. 1995), ion exchange (Seganish and Davis 2005), energy spilling function in *S. marcescens* (Haddix et al. 2008) and acts as an antimicrobial agent to provide a competitive advantage within communities (Starič et al. 2010). Borić et al. (2011) studied that prodigiosin is protective against UV radiation in *Vibrio* sp. DSM 14379. Prodigiosin was extracted from psychrotrophic bacterial strain *Janthinobacterium lividum* isolated from Alaskan soil (Schloss et al. 2010). Shen et al. (2018) reported several red pigment-producing bacterial strains inside deep ice core collected from the Yuzhufeng Glacier, Tibetan Plateau. Centurion et al. (2019) reported genes in Antarctic volcanic island sediments responsible for the biosynthesis of 3-oxoacyl-[acyl-carrying protein] reductase (K00059) enzyme that belongs to the fatty acid synthesis pathway type II associated to the production of prodigiosin.

Melanin

Melanin is dark in color (brown to dark green, or fully black) and higher molecular weight biological pigment found in hair, feather, skin, eyes, scales, and some interior membranes. Melanin is chemically a polymerized product of phenolic and/or indolic compounds (Tarangini and Mishra 2014). Melanin is further classified into three groups based on structure and color (i) pheomelanins (red or yellow), (ii) eumelanins (black-brown), and (iii) allomelanins (black to dark brown) (Table 2). Due to variations in the occurrence and structure of melanin, its biosynthesis is not from a single route (Solano 2014). Melanin synthesis has been associated in providing resistance against UV- and visible light-irradiations, confrontation the attack of cell wall enzymes, fortification against oxidizing and reducing agents, and acts as an antiviral agent to enhanced the competitive and survival abilities in environmental stresses (Castro-Sowinski et al. 2007; Solano 2014). Melanin is a strong absorber of UV radiations and provides strong protective functions to microbes that's why extreme low temperature ecosystems are suitable habitats for microbial biosynthesis of melanin (Gessler et al. 2014).

In general, melanin pigment is insoluble both in organic and aqueous solvents, however, Kimura et al. (2015) isolated bacteria strain *Lysobacter oligotrophicus* from the Antarctic environment that produced water-soluble heteropolymer (Lo-melanin). Lo-melanin protects against UV radiation and scavenges ROS. Melanin is commonly present in polar dark septate hyphae, and guards hyphae against low temperatures and play a crucial role in their persistence (Robinson 2001).

Chyzhanska and Beregova (2009) isolated melanin from Antarctic yeasts. An Antarctic fungus, *Friedmanniomyces endolithicus* produces highly melanized thick-walled cells that protected cells from UV radiation (Onofri et al. 2004). Similarly, Rosa et al. (2009) isolated melanin-producing endophytic fungal strains from the leaves of *Deschampsia antarctica* and about 80% were black molds. In the Antarctic rocky deserts, rock-inhabiting fungi produce melanin pigments that protect the cells from extreme cold and heat, polychromatic UV radiations, extreme pH and osmotic conditions, and provides tolerance towards potentially toxic metals (Selbmann et al. 2015). Melanin was purified from cold-tolerant and oligotrophic bacterium *L. oligotrophicus* isolated from the Skarvsnes region, East Antarctica (Fukuda et al. 2013). UV-B radiations induced melanogenesis in *L. oligotrophicus* cells, that protected the suspensions of *E. coli* DH5 α cells from UV radiations by melanin solutions. In short, melanin biosynthesis by microorganisms can play crucial roles in low temperature environments such as to cope with low temperature, protection against UV radiations, freeze–thaw cycling and desiccation, scavenging ROS. These microbes could be a microbial model for exobiological/astrobiological studies.

Violacein

Violacein is violet or purple bisindole water-insoluble pigment and first reported from *Chromobacterium violaceum* from the Amazon River in Brazil (Durán et al. 1953). In nature, violacein protects cells from UV radiations (Füller et al. 2016). Several studies have reported the antibacterial, antiviral, anticancer, antiulcerogenic, antileishmanial, and enzymatic modulation activities of violacein pigments (Duran et al. 2007; Soliev et al. 2011). The maximum UV absorption capacity of violacein is $\lambda = 260$ nm, which suggests its crucial role in the protection of cells from visible and UV radiations (Marizcurrena et al. 2019). In nature, violacein is associated with biofilm production (Pantanella et al. 2007) and its production is regulated by quorum sensing thus acts as a marker of quorum sensing molecules (Burt et al. 2014). Violacein plays a vital role in protecting bacterial cells from predation (Choi et al. 2015). Apart from several other habitats, violacein has been reported from several low temperature environments. Lu et al. (2009) reported a novel psychrophilic bacterium from Xinjiang glaciers, China, capable of violacein production. Violacein producing psychrophilic *Janthinobacterium svalbardensis* bacterium was isolated from Glacier, Spirsbergen, Arctic region (Ambrožič et al. 2013). Kim et al. (2012) reported violacein producing psychrophilic bacterium *Janthinobacterium* sp. from alpine glacier cryoconite. Hakvag et al. (2009) reported violacein producing *Collimonas* sp. from Arctic coastal water in Trøndelag, Norway. Similarly, Nakamura et al. (2002) reported

Table 2 Types of pigments from cold-adapted microorganisms, their applications, and chemical structures

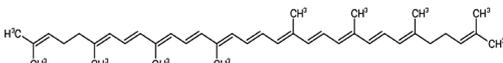
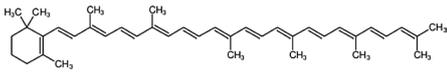
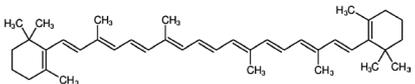
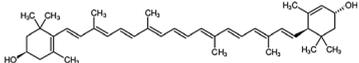
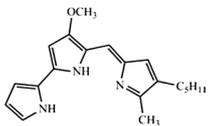
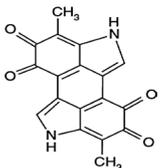
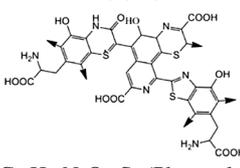
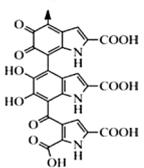
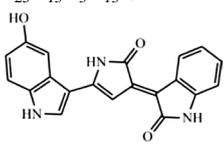
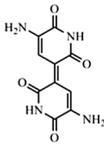
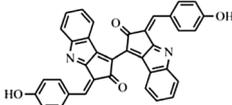
Pigments	Applications	Structures
Lycopene (all-E)-Lycopene)	Food additives, Antioxidant activities, Antimicrobial activities, and as Sun protector	 $C_{40}H_{56}$ (psi,psi-Carotene)
Torulene (Torulin)	Antioxidant activity, Cosmetics additives, Anti-cancerous activities, and Antimicrobial activities	 $C_{40}H_{54}$ (3',4'-Didehydro-beta,psi-carotene)
Beta-carotene (β-Carotene)	Food colorant, Antioxidant activity, and Precursor of vitamin A in food	 $C_{40}H_{56}$ (beta-Carotene)
Xanthophylls (lutein)	Feed additives, Protection against free radicals, and use in the pharmaceutical industry	 $C_{40}H_{56}O$ ((3R,3'R,6'R)-beta,epsilon-Carotene-3,3'-diol)
Prodigiosin	Dyeing agent in the textile industry, Coloring agents in the food industry, Antibacterial antiviral, and anticancer activities	 $C_{20}H_{25}N_3O$ (4-Methoxy-5-[(Z)-(5-methyl-4-pentyl-2H-pyrrol-2-ylidene)methyl]-1H,1'H-2,2'-bipyrrol)
Melanin	Antibacterial activity against antibiotic-resistant pathogens, Antioxidant activity, and cytotoxic activity	 $C_{18}H_{10}N_2O_4$ (6,14-dimethyl-4,12-diazapentacyclo[8.6.1.1 ^{2,5} .0 ^{13,17} .0 ^{9,18}]octadeca-1(17),2,5,9(18),10,13-hexaene-7,8,15,16-tetrone)
Pheomelanin	Markers in fossils, Antioxidant activity, Photoprotective effects	 $C_{34}H_{29}N_6O_{12}S_3$ (Pheomelanin)
Eumelanin	Antioxidant activity, Biomedical activities	 $C_{25}H_{13}N_3O_{13}$ (Eumelanin)
Violacein	Dyeing agent in the textile industry, Food industry, Antibacterial, fungicidal and antiviral activities, Antioxidant and cytotoxic activities, Use in cosmetics and medicine	 $C_{20}H_{13}N_3O_3$ (3-[2-hydroxy-5-(5-hydroxy-1H-indol-3-yl)-1H-pyrrol-3-yl]indol-2-one)

Table 2 (continued)

Pigments	Applications	Structures
Indigoidine	As bioindicator, Antimicrobial activities, and the Textile industry as a dyeing agent	 <p>$C_{10}H_8N_4O_4$ (3-(5-amino-2-hydroxy-6-oxo-1H-pyridin-3-yl)-5-iminopyridine-2,6-dione)</p>
Scytonemin	Anti-inflammatory and Anti-proliferative drugs, Antioxidant agents, Use in cosmetics	 <p>$C_{36}H_{20}N_2O_4$ (3E,3'E)-3,3'-Bis(4-hydroxybenzyliden)-1,1'-bicyclopenta[b]indol-2,2'(3H,3'H)-dion</p>

violet pigment-producing psychrotrophic bacterium from the water tank keeping rainbow and exploited its pigment for antibacterial potential. Shivaji et al. (1991) isolated the bacterium of *Janthinobacterium* genus that produced violacein and further Durán et al. (2007) evaluated the pigments for several therapeutic activities. Mojib et al. (2010) extracted violacein-like purple violet pigment from *Janthinobacterium* sp. reported from Proglacial Lake Podprudnoye, Schirmacher Oasis, Antarctica that inhibited the growth of *Mycobacterium smegmatis* and *Mycobacterium tuberculosis*. At low doses, the same pigment showed activity against methicillin-resistant and multiple drug-resistant clinical strains of *Staphylococcus aureus* (Huang et al. 2012).

Indigoidine

Indigoidine is a brilliant blue, water-soluble pigment synthesized by very few microorganisms (Sutthiwong et al. 2014) namely *Erwinia chrysanthemi* (Reverchon et al. 2002), *Phaeobacter* sp. (Cude et al. 2012), *Streptomyces chromofuscus* (Yu et al. 2013) and *Vogesella indigofera* (Day et al. 2017), and the biological and environmental role of indigoidine is unclear, however, it has been described that this pigment could protect against oxidative stress (Reverchon et al. 2002). Indigoidine also possesses antimicrobial activities as stated in *Leisingera* isolates (Gromek et al. 2016). Consequently, microbes producing indigoidine could have advantage of competition in the environment due to the antibiotic and antioxidant properties of indigoidine. Furthermore, indigoidine acts as intracellular signaling molecules related to motility (Reverchon et al. 2002; Cude et al. 2012). Additionally, indigoidine provides adaptability to microbial cells such as *Vogesella* sp. reported from Andean Patagonia in iron-rich environments (Day et al. 2017). Several isolates of Antarctic genus *Arthrobacter* were reported to produce indigoidine (Sutthiwong et al. 2014). *Arthrobacter* genus (family Micrococcaceae) are more common in Antarctic

surroundings such as sediments and soils (Reddy et al. 2003; Dsouza et al. 2015). Bacteria belong to this genus produce different pigments including blue indigoidine (Sutthiwong et al. 2014). Kobayashi et al. (2007) reported indigoidine production from *Shewanella violacea* DSS12 a piezophilic and psychrophilic bacterial strain isolated from deep-sea sediments of the Ryukyu Trench. Liao et al. (2019) studied the multipartite genomes and sRNome of Arctic *Pseudoalteromonas fuliginea* BSW20308 and reported upregulated genes encoding indigoidine biosynthetic.

Scytonemin

Scytonemin is a secondary metabolite of small hydrophobic alkaloids having yellowish-brown color (Table 2). Cyanobacteria when get exposed to UVA-blue wavelengths, scytonemin was produced (Fleming and Castenholz 2007). Scytonemin and its methoxylated and methylated derivatives are mostly reported in the upper portion of the microbial mats; that could protect the cells from extreme environments, which makes this pigment a potential biomarker molecule for studying the presumed exobiology habitats. Exposure of cyanobacteria to UV radiation produces scytonemin along with several other protective metabolites (Sinha et al. 1998). Therefore, these molecules might have performed a crucial role in Antarctica during the initial life stages on this planet (Dillon and Castenholz 1999). The palaeolimnological investigation that was carried out in 62 east Antarctic lakes revealed that the composition of pigments was different in different depths of lakes and higher scytonemin was reported in shallow lakes. Since cyanobacteria regulate their pigment production, this difference of pigment contents could be due to the light-harvesting ability of pigments at different depths (Sabbe et al. 2004). Several Antarctic cyanobacterial genera that are capable to produce scytonemin are reported in Table 1.

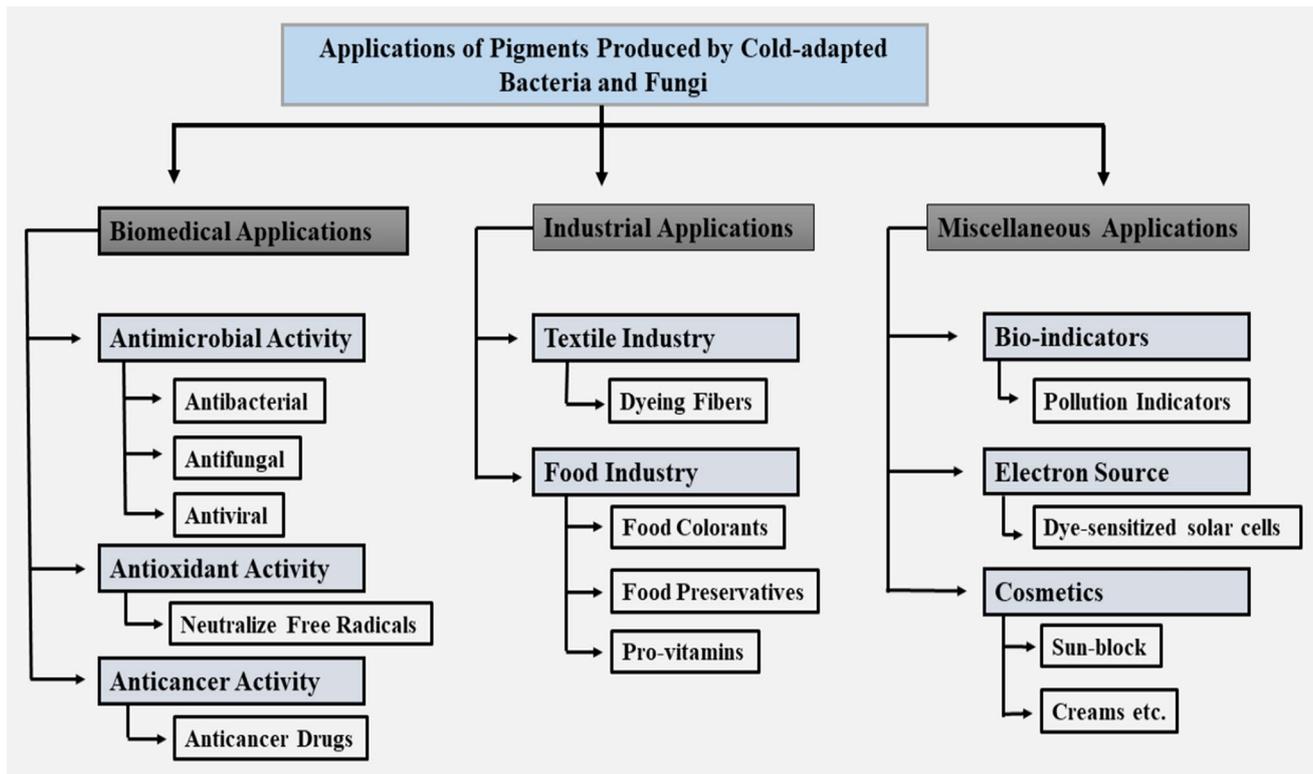


Fig. 2 Schematic representation of the pigments applications obtained from cold-adapted microbes

Applications of microbial pigments

Versatile pigments produced by microorganisms are more focused during present research due to their extensively observed applications in textile industries, food industries, and biomedical purposes. Global trade of naturally derived pigments has been increased by 29% and reached 600 million USD from 2007 to 2011 (Tuli et al. 2015). This indicates that the pigments produced by microorganisms would dominate the organic market and pigment industries very soon (Ramesh et al. 2019). Such economic growth and vast applications of pigments rationalize the exploration of new sources of natural pigments. Cryospheric environments might provide the best source for the exploration of novel pigments producing microorganisms. Biotechnological applications of psychrophilic microorganisms remained a dream for decades. However, in the early 1990s researchers started focusing their possible usefulness in genetic bioengineering, food and mining industries (Gounot 1991). Currently, several of these expectations are being confirmed, since psychrophilic microorganisms and their secondary metabolites are now acting as sustainable and priceless resources for biotechnological development. Among other invaluable products, pigments produced by these psychrophilic microorganisms are the

center of focus in modern research. Table 1 illustrates the microorganisms isolated from cryospheric environments producing pigments of potential applications in industries (Fig. 2). General applications of microbial pigments are as following.

Industrial applications

Textile industry

Textile industries use 1.3 million tons of synthetic dyes and precursors (worth of 23 billion USD) 15% of which leak as effluents during their use (Venil et al. 2013; Chequer et al. 2013). Unluckily, enough portion of these dyes escape the conventional processes of wastewater treatment and exist as a potentially toxic environmental pollutant with adversities on public health and environment (Ogugbue and Sawidis 2011). Consequently, a great concern exists to replace the synthetic dyes in the textile industry with environmentally friendly dyes. Pigments obtained from microorganisms are environmentally friendly that is considered appropriate for the textile industry (Chadni et al. 2017). Violacein, a multipurpose pigment extracted from *C. violaceum* is capable of dyeing both natural and synthetic fibers and has gained increasing importance in textiles (Wan et al. 2014; Venil

et al. 2016). Prodigiosin a bright red pigment from *Vibrio* sp. is suitable for dyeing a range of fibers including nylon, acrylics, wool, and silk (Alihosseini et al. 2008). Similarly, prodigiosin reported from *Serratia* sp. BTW J8 was demonstrated to color various fabric types such as chiffon, cotton, pure silk, poplene, century cotton, organdi, dupoil silk, terrycotton, polyester, and nylon (Krishna 2008). The blue pigment indigoidine produced by fungal host *Rhodospiridium toruloides* possesses potential applications in the dye industry (Wehrs et al. 2019). Pigment extracted from *J. lividum* shows a bluish-purple color tone on cotton, silk, and wool, while with vinylon and nylon it appears dark blue (Shirata et al. 2000). Likewise, the yellow pigment extracted from *Thermomyces* exhibited a higher dyeing affinity for silk fabric compared to other fabrics (Poorniammal et al. 2013). Similarly, red and deep blue pigments reported from *Streptomyces* strains NP2 and NP4 exhibited substantial variations in dyeing ability depending upon fabric materials. For instance, acrylic and polyamide fibers were vibrantly stained, however, cellulose and cotton fibers were weakly stained (Kramar et al. 2014). In the view of such extensive use of microbial pigments in the textile industry could increase their market value; therefore, new microbial sources are crucial to explore for pigment production and cryosphere inhabit broad microbial diversity capable of pigment production.

Food industry

One important goal in the food industry is to develop foods having an attractive appearance that has been achieved with synthetic dyes. Progressively, food industries are now using natural food colorants, since certain synthetic food colorants have demonstrated adverse health problems after consumption. Due to the shortage of natural food additives resources, their demand is increasing particularly in the food industry (Aberoumand 2011). This demand can be fulfilled by providing a more natural and healthy means of food colors offering a clean and safe tag declaration. Scientists have isolated food-grade pigments from bacterial strains that might provide a natural food colorant having tremendous stability, health safety profile and also act as antioxidants and preservatives (Nigam and Luke 2016). Pigment approval as food color and nutritional supplements greatly depend upon the health safety of consumers and product freshness. Thus, the use of pigmented molecules in food, cosmetics, medicine, and other medical devices is under the control of the Federal Food, Drug, and Cosmetic Act (Chapter VII, Sect. 721) and authorization should be taken before use for the specific time (<https://www.fda.gov/>).

Several microbial pigments like astaxanthin from *Xanthophyllomyces dendrorhous*, a red pigment obtained from *Monascus* sp., β -carotene produced by *Blakeslea trispora*,

lycopene from *Fusarium sporotrichioides* and *Erwinia uredovora*, riboflavin reported from *Ashbya gossypii*, and Arpink red™ from *Penicillium oxalicum* were supplemented in different food items to enhance its appeal (Dharmaraj et al. 2009). For instance, carotenoids obtained from bacteria are used in feed as pro-vitamins and coloring agent in food industries (Nelis and De Leenheer 1991). Carotenoids are studied to be used as coloring agents for soft drinks, cooked sausages, and baked items (Konuray and Erginkaya 2015). It can also protect food from intense light and maintain the food quality by acting as a sunscreen (Chattopadhyay et al. 2008). Spray-dried prodigiosin from *S. marcescens* has been applied effectively as a coloring agent in milk, yogurt, and carbonated drinks (Namazkar and Ahmed 2013). Violacein obtained from bacterial sources has been successfully used in food industries (Dufosse 2018). Canthaxanthin is used in food items such as fish, candy, cheese, fruits, meat, snacks, beverages, wine, and beer. Currently, several pigments obtained from microorganisms are approved and used in foods for several purposes (Nigam and Luke 2016).

Biomedical applications

Antimicrobial activities

Infectious diseases are the second major reason for global human deaths and third in developed countries after non-contagious diseases (WHO 2018). In the recent few decades, new drug entry in the market has been decreased and microbial resistance against antibiotics is increasing. This increasing trend of microbial antibiotic resistance amplified the demand for novel antimicrobial agents. As an alternative to antibiotics, several microbial pigments have been successfully evaluated for antimicrobial activities. Umadevi and Krishnaveni (2013) studied pigments extracted from *Micrococcus luteus* that exhibited inhibitory potential against wound pathogens such as *Pseudomonas* sp. *Klebsiella* sp. and *Staphylococcus* sp. Carotenoids extracted from *Holomonas* sp. exhibited antimicrobial potential against antibiotic-resistant *S. aureus*, *Klebsiella* sp., and *Pseudomonas aeruginosa*, and ophthalmic *S. aureus*, *Streptococcus pyogenes*, and *E. coli* (Ravikumar et al. 2016). Vasanthabharathi et al. (2011) studied the inhibitory potential of crude melanin obtained from *Streptomyces* against *E. coli*. Pigment extracted from *Streptomyces hygroscopicus* was effective against pathogens such as vancomycin and methicillin-resistant *S. aureus*, β -lactamase producing *E. coli*, *P. aeruginosa* and *Klebsiella* sp. (Berlanga et al. 2000; Selvameenal et al. 2009). Violacein obtained from *C. violaceum* and *J. lividum* showed promising antibacterial activities (Durán et al. 2007). Violacein reported from *C. violaceum* ATCC 12472 showed tremendous antimicrobial activity against *S. aureus* and inhibition of its biofilm formation (Batista and da Silva

Neto 2017). Similarly, *Antarctic* bacterial violacein in lower concentrations showed activity against avirulent *M. tuberculosis* (Mojib et al. 2010). A combination of violacein with antibiotics such as kanamycin and cefadroxil minimize the inhibitory concentration of drugs against *S. aureus* (Subramaniam et al. 2014). Additionally, violacein extracted from *J. lividum* exhibited fungicidal activity against white root rot causing *Rosellinia necatrix* (Shirata et al. 1997). Prodigiosin obtained from *Vibrio ruber* DSM 14,379 exhibited bacteriostatic activity against *E. coli* and *Bacillus subtilis* (Danevčič et al. 2016). Furthermore, prodigiosin intracellularly produced by *S. marcescens* IBRL USM 84 inhibited the growth of tested bacteria (Ibrahim 2008). Prodigiosin revealed promising antibacterial activity against pathogens such as *S. aureus*, *S. pyogenes*, *P. aeruginosa* and *Klebsiella pneumoniae* (Nwankwo et al. 2017). Pigments extracted from endophytic fungi *Monodictyocystis astaneae* demonstrated antibacterial activity against *Vibrio cholera*, *K. pneumoniae*, and *S. aureus* (Visalakshi and Muthumary 2010). Suryawan-shi et al. (2017) studied the strong antimicrobial activity of prodigiosin against *E. coli*, *S. aureus*, and *Candida albicans*. Similarly, several prodiginine compounds are reported having fungicidal activities against fungi such as *Penicillium*, *Aspergillus*, *Candida*, and *Cryptococcus* sp. (Stankovic et al. 2014).

Throughout human history, several viral outbreaks occurred and still occurring such as the Western African Ebola virus epidemic and the recent Coronavirus pandemic COVID-19 accompanied with moderate to high mortality rate. This urge that the discovery of novel antiviral drugs is critically important as many viral infections lack vaccines and effective treatments. Researches showed some initial successes using microbial pigments as antiviral agents. Violacein possesses antiviral potentials against poliovirus, simian rotavirus SA II, and herpes simplex virus (HSV) (Durán et al. 2007). In vitro effects of violacein are also evaluated against Acquired Immuno Deficiency Syndrome (AIDS) related lymphoma (Duran et al. 1996). Andrighetti-Fröhner et al. (2003) studied the antiviral activities of bacterial extracted violacein and inhibition of HSV-1 and Poliovirus-2 (PV-2) replication was observed. Similarly, an in-silico examination of prodigiosin by targeting proteins of Human Immunodeficiency Virus (HIV), Hepatitis B virus (HBV), influenza A virus (H1N1) and Hepatitis C virus (HCV) was performed (Suba et al. 2013). The outcome proposed potential antiviral activities of prodigiosin pigment against all tested viruses excluding HCV, where no binding interactions with active sites were reported. Moreover, compounds of quinone such as naphthoquinones, anthraquinones, and benzoquinones possess strong antiviral potential (Koyama 2006; Gessler et al. 2013). Several compounds obtained from Phoma species exhibited the inhibition of HIV integrase (Rai 2009).

Phenazine compounds extracted from *Streptomyces* and *Pseudomonas* species have been demonstrated promising antiviral activities (Schneemann et al. 2011). Therefore, microbial pigments are potential agents to administered as a novel source of medications against pathogens.

Antioxidants activity

The rise of free radicals inside the body increases the risks of chronic diseases such as diabetes, autoimmune disorders, and cancer (Phaniendra et al. 2015). To evade this, antioxidant compounds are used which donate electrons to free radicals and neutralize them to protect cellular damage (Lobo et al. 2010). Antioxidants are obtained either from natural or synthetic sources, however, synthetic antioxidants are losing demand due to possible side effects on the human body (Ahmed et al. 2013). Therefore, microbial-based antioxidants are gaining ground in the pharmaceutical industry. Pigments from microorganisms such as carotenoid, xanthomonadin, and naphthaquinone showed antioxidant potential (Tuli et al. 2015). Carotenoids extracted from Antarctic bacterium *Pedobacter* exhibited solid antioxidant activity with protection against oxidative harm (Correa-Llantén et al. 2012). Osawa et al. (2010) demonstrated promising antioxidant abilities of rare C-50 carotenoids such as sarcinaxanthin monoglucoside, sarcinaxanthin diglucoside, and sarcinaxanthin, reported from a halophilic bacterium *Micrococcus yunnanensis*. Moreover, Shindo and Misawa. (2014) extracted rare and new carotenoids from the novel bacterial isolates and these pigments exhibited strong antioxidant activities. Similarly, flexirubin (red carotenoid), obtained from *Fontibacter flavus* showed antioxidant activity against 2, 2-diphenyl-1-picryl-hydrazyl-hydrate (DPPH), nitric oxide, hydroxyl radical, and inhibition of lipid peroxidation (Prabhu et al. 2013). Additionally, melanin reported from fungal isolate *Streptomyces glaucescens* (El-Naggar and El-Ewasy 2017) and anthraquinones obtained from endophytic *Stemphylium lycopersici* (Li et al. 2017) were characterized as antioxidants. Another valuable bacterial pigment violacein obtained from *C. violaceum* exhibited antioxidant protection in gastric ulceration (Antoniamy and Ignacimuthu 2010). Violacein can also safeguard the cellular lipid membranes from peroxidation due to hydroxyl radicals (Stafsnes and Bruheim 2013). Several studies reported melanin obtained from *Pseudomonas* sp, *S. glaucescens* NEAE-H, and *Bifidobacterium infantis* were found antioxidant agents (Huang et al. 2011; Tarangini and Mishra 2014; Zerrad et al. 2014). These reports recommend that pigments obtained from microorganisms could be used as antioxidant agents to prevent several chronic diseases.

Anticancer activity

Cancer is one of the most lethal diseases in human history. Till now, several anticancer medicines have been designed and are in the stage of the clinical trial. However, success limitations, adverse effects, and resistance towards treatments are the major challenges in cancer treatment (Foo and Michor 2014). Therefore, search for novel and effective anticancer agents with least or no side effects is of great interest. Several kinds of research conducted on microbial pigments as anticancer agents exhibited promising results. One such study on novel red pigment extracted from *Athrobacter* sp. G20 exhibited anticancer potential against the oesophageal cancer cell line (KYSE30) (Afra et al. 2017). A yellow pigment reported from *Streptomyces griseoaurantiacus* demonstrated strong cytotoxic activity against cervical cancer cells (HeLa) and HepG2 and resulted in a lower number of viable cells (Prashanthi et al. 2015). Carotenoid extracted from *Kocuria* sp. QWT-12 revealed anticancer potential against breast cancer cell lines and lung cancer cells (Rezaeeyan et al. 2017). Similarly, carotenoids from *Haloferax volcanii* killed 53.52% of human liver carcinoma cell lines (Sikkandar et al. 2013). Black melanin extracted from *S. glaucescens* exhibited significant cytotoxic activity against the HFB4 skin cancer cell line (El-Naggar et al. 2017). Dihydroxyphenylalanine melanin obtained from *Streptomyces* sp. MVCS6 exhibited dose–response anticancer activity against the cervical cancer cell line (Sivaperumal et al. 2015). Wang et al. (2012) studied prodigiosin obtained from *Pseudoalteromonas* sp. having a cytotoxic effect against U937 leukemia cells. Strong anticancer activity of prodigiosin obtained from *S. marcescens* is reported against human cervical cancer cells and laryngeal cancer cells (Maheswarappa et al. 2013). Cheng et al. (2017) evaluated the influence of prodigiosin reported from *Vibrio* sp. against human oral squamous carcinoma cells (OSCC) and found that the prodigiosin arrests their cell cycle. Recently, prodigiosin showed a reduction of the intracellular signaling pathway during the cell cycle and induced apoptosis in lung cancer cells and also showed in vivo tumoricidal activity (Chiu et al. 2018). Interestingly, a combination of natural compounds with chemotherapy drugs enhance its efficacy and reduce their toxicity. Prodigiosin when combined with paclitaxel against MCF7 breast cancer cells (Ho et al. 2009) and doxorubicin (Dox) against OSCC cell lines (Lin and Weng 2018) an efficient synergistic effect was reported. Violacein obtained from *C. violaceum* induced cytotoxicity and apoptosis activity in Chinese hamster lung fibroblast V79 cells (Melo et al. 2000) and leukemia cell lines (Melo et al. 2003; Ferreira et al. 2004). Additionally, violacein also increased apoptosis in colon cancer cells (Kodach et al. 2017) and human breast cancer cells (Alshatwi et al. 2016). Several anthraquinone derivatives from marine-derived

fungi are capable of tumor cell inhibition (Fouillaud et al. 2016). Anthraquinone derivatives from fungus *Alternaria* sp. have been studied for anticancer activity against human breast cancer cell lines (Huang et al. 2011). In light of the above studies, the microbial pigment could be potential chemotherapeutic agents for cancer treatment.

Bio-indicators

Bioindicator bacteria are bacteria that can monitor environmental health and reveal the qualitative status of the environment by changing their behavior and specific physiological characteristics (Parmar et al. 2016). One such change is the production and/or alteration of certain pigments in pigmented bacteria that could be effectively used as bioindicators. For instance, violet pigmented bacteria along with *Sporocytophaga* and *Flexibacter* species were bioindicators of polluted drinking water (Schindler and Metz 1989). Indigoidine production by *Vogesella indigofera* is suppressed by Cr^{6+} in a concentration-dependent manner which is an indication of chromium concentration and toxicity in the environment (Gu and Cheung 2001). The existence of carotenoid in *Lecanoraceae lichens* has been confirmed to depend upon the pollution level in the atmosphere of the surrounding environment, where they reside by analyzing the carotenoid content of fungi acting as bioindicator (Ibarrondo et al. 2016). Using the gene clusters encoding prodigiosin biosynthesis in *S. marcescens* and violacein biosynthesis from *C. violaceum* demonstrate the implementation of reporter systems for the signal of biosynthetic gene expression (Domröse et al. 2017). The participation of melanin pigments in protection from environmental stress like UV radiation and potentially toxic metals is regarded as a bioindicator due to its overproduction in adverse conditions (Egorova et al. 2011). Similarly, cyanobacteria naturally present in water sources could act as excellent bioindicators for heavy metals, since in the presence of heavy metals, the carotenoids content in these cyanobacteria reduces (Wong and Teo 2014).

Miscellaneous applications

Pigment-producing microbes in cryospheric environments could act as a potential source of electrons and may be employed for developing dye-sensitized solar cells (DSSC) that would be a potential alternative of conventional photovoltaic-silicon cells based. Consequently, DSSC might signify a remarkable alternative that could somewhat solve the energy requirement at Antarctic regions. For instance, the orange-xanthophyll pigment extracted from UVC-resistant *Hymenobacter* sp. (Marizcurrena et al. 2017) was exploited for DSSC development (Órdenes-Aenishanslins

et al. 2016; Montagni et al. 2018). Similarly, Pezzella et al. (2019) studied the eumelanin and graphene integration and observed improved electrical conductivity which shows the scope of eumelanin in bioelectronics. Bacterial pigments can be used as biodegradable ink on plastic materials. The hue and chroma values are observed in red and violet color suggestive of prodigiosin and violacein pigments isolated from *S. marcescens* and *C. violaceum*, respectively (Venil et al. 2017). Astaxanthin from radioresistant *Deinococcus* sp. exhibiting radio-protective and antioxidant activities can be incorporated in cosmetics including sunblock and sunscreen (Sajjad et al. 2017). The bacterial pigments prodigiosin and violacein exhibiting antioxidant and antimicrobial activities represent a new paradigm for sunscreens that utilize substances of biological origin (Suryawanshi et al. 2015). These pigments can be a potential ingredient in a range of commercial sunscreen products. Indigoidine can be used as an organic semiconductor with numerous applications in carbon dioxide capture devices, electrochemical cells, super capacitors, batteries, etc. (Yumusak et al. 2019).

Conditions optimization for pigment production

Microbial survival depends upon a wide range of nutrients and physicochemical factors that further control the production of metabolites illustrated in Fig. 3. In general, microbes could adapt three routes for metabolites production. These routes are; natural production of metabolites; metabolites production under strained environmental conditions; and stimulation of metabolites production by supplementing certain nutritional requirements along with physiological parameters (Ramesh et al. 2019). Detail description of pigment extraction has been reviewed from microalgae (Amaro et al. 2016), yeast (Yurkova et al. 2008), fungi (Rai 2009; Ahmad et al. 2015), and bacteria (Stafsnes and Bruheim 2013). Psychrophilic microorganisms produce several pigments to cope with the life-endanger challenges in the cryosphere. Cold-adapted algae are extensively studied for pigment production, however, little is known about the pigment production potential of cold-adapted bacteria and fungi due to several reasons such as their unique physiological and nutritional requirements, slow and unseen growth in the environment, and less exploration in axenic form. To obtain pigments from cold-adapted microorganisms identifying suitable substrates and evaluation of physicochemical factors are essential for better growth and higher pigment yield.

Pigment production takes place intracellular or/and extracellular depending on pH, temperature, light, several media constituents (Buck et al. 1974), sampling sites and cultivation conditions (Stafsnes and Bruheim 2013). Under laboratory conditions, the microbial pigment production

is ephemeral in nature. However, higher yield could be obtained if several factors such as medium components and environmental parameters are optimized in an understandable way (Ramesh et al. 2019). Such as a study conducted by Pandey et al. (2018) stated that additional supplementation of maltose as a source of carbon in potato dextrose broth boosted the orange pigment production by a psychrophilic strain of *Penicillium* sp. followed by fructose and glucose, however, supplementation of lactose inhibited this production. Pandey et al. (2018) found that extra nitrogen source could not enhance the pigment production, however, minerals salts like $MgSO_4$ and KH_2PO_4 can enhance the production of pigment. Maximum pigment production was observed in *Monascus* sp. supplemented with maltose (Omamor et al. 2008). Pradeep and Pradeep (2013) reported maximum pigment production from *Fusarium moniliforme* by supplementing glucose in the medium. In the case of filamentous fungi, Carbon/Nitrogen (C/N) ratio is extremely essential in pigment production (Gmoser et al. 2017). A decrease in pigment production was reported by Cho et al. (2002) and Gunasekaran and Poorniammal (2008) during a higher C/N ratio. Similarly, high phosphate concentration and acidity caused the reduction of pigment production and a trace amount of sulfate vitiate pigment production (Reichenbach et al. 1974). Singgih et al. (2015) studied *Neurospora intermedia* N-1 for carotenoid production in the presence of maltose (2% w/v) as a carbon source. Moreover, minerals salts having different cations were found to improve the production of pigments (Pradeep and Pradeep 2013). Organic acid produced by *Monascus ruber* inhibits pigment production (Hajjaj et al. 2000). The addition of certain substrates such as wheat, rice meals, and light stimulation enhanced carotenoid production in yeasts and fungi (De Carvalho et al. 2014). ZoBell and Upham (1944) reported an increase in pigment production when bacteria were cultured in seawater supplemented with neopeptone, bacto-tryptone, and beef extract at 4 °C. Ghosh et al. (2007) reported that methanol acted as a sole carbon source induced the production of pink pigment in *Acinetobacter wofii*. The yellow–green pigment was produced by *Pseudomonas fluorescens* supplemented with succinate as a sole carbon source, while this production was stopped by the addition of malic and citric acids as substrate (Margalith 1992). Moreover, the influence of light and dark on pigment production was studied and *Myxococcus xanthus*, *Mycobacterium marinum*, *Rhodotorula glutinis*, and *Dacryopinax spathularia* produced carotenoids during the presence of light. *S. marcescens* produced red pigment on solid peptone-glycerol agar plates, and unable to produce pigment in liquid medium except when supplemented with silica gel (Yamashita et al. 2001). Chen et al. (2013) reported that the prodigiosin production was enhanced when peptone and starch were supplemented as a source of carbon and calcium alginate beads were added as

a porous carrier. Similarly, Lu et al. (2009) reported sucrose and casein as best carbon and nitrogen sources, respectively, for violacein production by *J. lividum* XT1 bacteria reported from the glacier in Xinjiang China.

To obtain higher pigment yield, pH and temperature optimization are essential as they affect the metabolic growth and physical activities of microorganisms. Being cold-adapted organisms, the temperature is a vital factor to be optimized for pigment production. Pandey et al. (2018) reported maximum pigment production at low temperature (15 °C) and acidic condition (pH 5) by *Penicillium* sp. Chattopadhyay et al. (1997) studied Antarctic psychrotrophic bacterium *M. roseus* that produced higher carotenoid pigment at 5 °C compared to 25 °C. Similarly, Lu et al. (2009) reported an optimal temperature of 15 °C for violacein production by psychrotrophic bacteria. *M. tuberculosis* produced carotenoid pigments under acidic stress (pH 5–6) (Saviola 2014), and different pigment production was reported in other *Mycobacterium* species (Robledo et al. 2011). Overproduction of pigment at lower temperatures shows the phenomenon of ecological resilience among cold-adapted microorganisms that combat the deadly environmental conditions. Similarly, enhancement of pigment production below optimum temperature range could be an adapting reaction that compensates the downregulation of metabolic processes at low temperatures (Gmoser et al. 2017). Several genes are responsible for the biosynthesis

of pigments in microorganisms. To enhance the pigment production mutagens such as UV light, 1-methyl-3-nitro-1-nitrosoguanidine, and ethyl methanesulfonate were used in *Haematococcus pluvialis* and microwave in *S. marcescens* (Nigam and Luke 2016), which shows these mutagens could enhance the pigment yield when used precisely. In addition, alteration in genes (knockout or promotion of genes) and mutagenesis practices can increase the pigment production (Venil et al. 2014). Different substrates such as tryptophan, phenylalanine, tyrosine, and several physicochemical parameters can efficiently stimulate pigment production by microorganisms.

Essential pigments from fungal strains can be obtained under optimum growth conditions by solid, semi-solid, and submerged fermentation (Vendruscolo et al. 2010; Akilandeswari and Pradeep 2016) using a diverse range of sustainable substrates (Gupta and Aggarwal. 2014). However, parameters such as pH, temperature, agitation, aeration, and culture medium directly influence the production of pigment and should be kept at an optimized level (Medentsev et al. 2005). Moreover, several solvents such as acetone, chloroform, cyclohexane, acetonitrile, ethanol, dichloromethane, pyridine, hexane, and water are used to extract fungal pigments. The solvent choice is crucial for pigment extraction and depends upon the polarity of the studied molecules. After extraction and purification of pigments, it should be handled carefully and must be kept under optimum

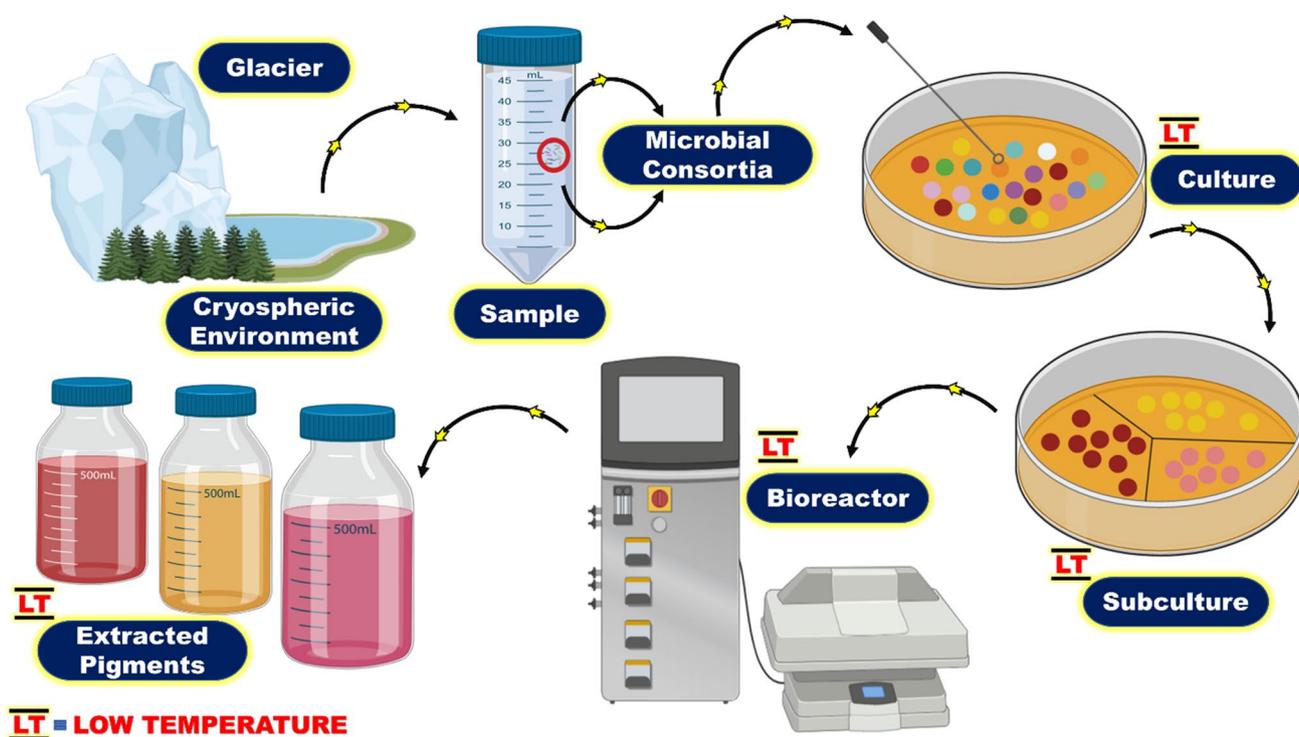


Fig. 3 Schematic representation of pigment extraction from cold-adapted microbes at low temperature

temperature, and pH to preserve its original colorimetric characteristics. Pigment storage in dry powder form is more preferable because of its higher stability and low water activity (De Carvalho et al. 2014).

Challenges in pigments obtained from psychrophiles

Antarctic region and the adjacent Southern Ocean is the rich source of psychrophilic microorganisms capable of pigment production. However, in 2014 the bioprospection is defined during XXXVII Antarctic Treaty Consultative Meeting held in Brasilia. According to this definition, bioprospection is “any activity of search, identification, description, collection, survey, monitoring, cultivation, replication, or any other scientific investigation processes, performed on indigenous biological species with the initial intention to consider potential industrial or commercial derived products or applications, notably through the development of patentable material or process.” According to this definition, research curiosity on the biological resources of Antarctica is growing for commercial use. However, several reports highlighted that due to the lack of clear governing and ownership rules for these resources causes appropriation by those who discover it and subsequently develop patent (UNU-UNEP 2009; Jabour 2010; UNEP 2012; Puig-Marcó 2014). In 2008, Antarctic Treaty Committee launched an online database for bioprospecting in Antarctica that provides up-to-date information about bioprospecting in Antarctica. This database also provides information about commercialized products obtained from biological samples indigenous to Antarctica. The records in the database contained many patents related to microbial metabolites having potential biotechnological applications (UNEP Report 2012). The increase in patents shows that Antarctic microorganisms are a precious source of marvelous potential profits. However, one of the leading challenges is the assurance of sustainable exploitation of indigenous biological resources of Antarctica which is yet to decide that how positive benefits of bioprospecting could achieve without inducing major damage to the indigenous environment. Since the uncontrolled prospecting actions that would include logistical labors to reach the biological resources and their definite outcomes could make the process unsustainable and compromise the indigenous microbial diversity (Hughes et al. 2015). In addition, the commercial based research activities and their secrecy could compromise the main pillar of the Antarctic Treaty System (Article III), viz., the unrestricted cooperation and free exchange of information among all parties (Yarzabal et al. 2016). Furthermore, the emerging profitable interest in biological resources raised several key policies, moral and ethical queries: Who would be the owner of these

biological resources? How should they be exploited and used? And whom should be benefited and to what extent? Although, few of these questions are included in the 2014 SCAR1-sponsored Antarctic and Southern Ocean Horizon Scan (Kennicutt et al. 2014, 2015). However, several current uncertainty and absence of policies for these biological resources should be addressed to the territorial and commercial sensitivities to agree upon common agreement to protect the local environment. For instance, the Nagoya protocol that entered into force in October 2014 by over 70 countries under international law for the fair and equitable sharing of benefits derived from the utilization of genetic resources (Smith et al. 2017). Like Nagoya protocol, countries should be placed under an obligation to establish legislative, administrative and/or political measures regarding the access to common cold reservoirs such as Arctic and Antarctic. This will aim to provide equal chances of obtaining common cold resources for commercial or academic development by a country or organization. Moreover, to commercialize any kind of microbial pigments, huge investment along with research work for characterization, optimization processes, possible toxicological testing, regulatory approval, and penchant by the consumers are greatly essential (Ahmad et al. 2015; Dufossé et al. 2016; Carvalho et al. 2016). Similarly, optimized fermentation conditions, design and type of bioreactor to achieve desired productivity of microbial pigments (Venil et al. 2014) along with the downstream processing of product purification are quite essential to be considered especially for microorganisms from unusual environments such as cryosphere. Therefore, widespread research is essential to convey the microbial pigments from laboratories to markets, since its demand is higher than supply.

Conclusion

The demand for natural pigments obtained from microorganisms is now increasing due to the adverse effects causing by synthetic dyes. Therefore, new potential sources are crucial to explore for pigment-producing microorganisms. One such environment is the cryosphere which inhabits microorganisms that produce natural pigments as a protective shield against life-endangered ecological stresses. Exploration of these microorganisms would certainly provide promising sources of novel pigmented molecules having wider biotechnological applications. These unexplored microbes especially novel species could be the potential source for pigments that could be used to develop novel drug compounds as well as in the textile and food industries. Efforts should be done to produce cost-effective production of pigments from these microbes by optimization, and strain improvement through genetic engineering to get rid of toxic synthetic dyes. Sustainable exploitation of these biological

resources from the cryosphere should be focused to prevent environmental disruption. Several cryospheric environments such as Antarctica should be considered a common legacy for mankind and the international community should declare a clear ethical and moral policy for certain questions including possession of these resources. It is obvious that due to unique qualities, the applications of these pigments obtained from cold-adapted microorganisms would be broader and will start many newer domains in biotechnology.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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