

Adaptations, cultivation and commercial prospects of polar microalgae

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Abstract Polar microalgae are microscopic organisms adapted to survive in cold and extreme habitats such as sea-ice, glaciers, lakes and snow. These microorganisms provide an essential basis as primary food sources in polar ecosystems. Despite their ecological importance, polar microalgae remain relatively unexplored compared to their tropical and temperate counterparts, largely due to the practical challenges of obtaining and maintaining material from the harsh polar environments. However, interest has recently surged due to their specific adaptations and potential for utilization in various fields. This review explores the survival strategies of polar microalgae and their commercial applications in healthcare and other fields. We also consider the processes involved in processing polar microalgae, from cultivation to extraction of bioactive compounds. Our findings highlight a growing need for research in this rapidly evolving field to unlock the potential of polar microalgae in multiple fields.

Keywords polar microalgae, microalgal adaptations, microalgal processing, potential commercial applications

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1 Introduction

Microalgae are microscopic photosynthetic unicellular organisms which can be either eukaryotes or prokaryotes (cyanobacteria), ranging in size from several μm to a few hundred μm (Kukwa and Chetty, 2020). They are very complex and rather difficult to classify effectively, though they are broadly grouped according to their cell structure, pigmentation, habitat and temperature preferences. Microalgae are very hardy and adaptive organisms, and thrive in multiple ecological niches globally (Morais Junior et al., 2020). Polar microalgae are microorganisms uniquely adapted to the harsh habitats of the Arctic and Antarctic regions. They play a crucial role in polar ecosystems, providing the primary food source for many marine groups such as bacteria, protists, ctenophores, annelids, and crustaceans, and generating up to ~25% of total primary production in waters covered with seasonal ice and approximately 60% in Arctic waters covered with multiyear ice (Duncan and Petrou, 2022). Cold-adapted microalgae can have high levels of polyunsaturated and other essential fatty acids (FA), which are essential for zooplankton growth and reproduction. As temperatures warm during the early polar season, the melting of winter (annual) sea-ice releases huge quantities of microalgae into the water column, contributing to the seeding phytoplankton blooms. The released microalgae can also sink through the water column, with some being consumed by pelagic filter feeders, while those that reach the seafloor provide a vital food source for benthic invertebrates (Arrigo et al., 2014). Polar microalgae are also known for their role in global biogeochemical cycles, especially carbon cycling. As carbon dioxide (CO_2) has higher solubility in cooler

waters, the polar oceans sequester up to 30% of global carbon dioxide uptake despite covering only 10% Earth's total surface area. In addition, the breakdown of the phytoplankton metabolite dimethylsulfoniopropionate (DMSP) to a volatile gas, dimethylsulfide (DMS) introduces a large amount of biogenic sulfur to the atmosphere and when the sulphate molecules from DMS are oxidized subsequently, these particles aid in seeding clouds which can reduce global warming (Duncan and Petrou, 2022).

Most polar microalgae adapted to survive in low temperature environments are psychrotrophs that can tolerate temperatures below $15\text{ }^\circ\text{C}$ and exhibit optimum growth at temperature above $18\text{ }^\circ\text{C}$. Others are psychrophiles that exhibit optimum growth temperature at or below $15\text{ }^\circ\text{C}$ and a maximum growth temperature at $20\text{ }^\circ\text{C}$ (Lacour et al., 2017). Sympagic microalgae, also known as cryophiles, are microalgal communities adapted to survive in sea-ice, freshwater ice, glacial ice and snow. To date, 1027 sympagic protist taxa are known, of which diatoms are the most abundant group (71% of total identified taxa). Diatoms are mainly represented by Pennales, followed by dinoflagellates (Poulin et al., 2011; Zielinski et al., 2018). Other well-studied cold-adapted microalgae include species like *Nitzschia frigida*, which is capable of living in the pelagic environment, as well as *Navicula pelagica*, *Fragilariopsis cylindrus*, *F. oceanica* and *Pauliella taeniata*. In the Arctic, *Navicula frigida* is the most abundant diatom, while *F. cylindrus* is the most abundant diatom identified in Antarctica (Rózańska et al., 2009; Vancoppenolle et al., 2013). Polar microalgae are vastly diverse, and Table 1 provides a broad categorization of several well-studied species according to their characteristics.

Table 1 Categorization of microalgae based on specific characteristics

Microalgae species	Cell structure	Pigmentation	Habitat	Temperature preference	References
<i>Fragilariopsis cylindrus</i>	Eukaryotic	Ochrophyta	Antarctic sea ice, pelagic waters, and ice-edge zones	Psychrophile	Otte et al., 2023
<i>Chlamydomonas nivalis</i>	Eukaryotic	Chlorophyta	Arctic and Antarctic snowfields	Psychrophile	Zheng et al., 2020
<i>Nostoc commune</i>	Prokaryotic	Cyanophyta	Terrestrial habitats and freshwater in polar regions	Psychrotolerant	Pandey et al., 2004
<i>Polarella glacialis</i>	Eukaryotic	Dinophyta	Antarctic sea ice and brine channels	Psychrophile	Stephens et al., 2020
<i>Phaeocystis antarctica</i>	Eukaryotic	Haptophyta	Southern Ocean and Antarctic sea ice	Psychrophile	Delmont et al., 2014
<i>Mesotaenium berggrenii</i>	Eukaryotic	Charophyta	Freshwater streams and snowmelt pools in Arctic and Antarctic regions	Psychrophile	Holzinger and Pichrtová, 2016

Microalgae have long been recognized as a valuable target of interest for research as they are proven to be extremely useful in many fields (Saini et al., 2024; Su et al., 2023). For instance, they have been utilized in heavy metal and oil spill bioremediation, wastewater treatment and carbon sequestration as well as being cultivated in order to extract biofuels, pharmaceuticals, nutraceuticals, cosmetic products, and animal feed. However, compared to the relatively well studied tropical and temperate microalgae, polar microalgae have received limited research attention primarily due to the practical challenges of obtaining and

maintaining sample material from these harsh regions. Nonetheless, microalgae from cryogenic environments are rapidly increasing in research interest due to their unique adaptations and distinct biochemical composition, including the discovery of novel compounds. This review first focuses on the adaptations and mechanisms used by sympagic microalgae to enable them to survive and exploit extreme polar environments, and second briefly explores the processes involved in cultivating, harvesting and extracting them. The applications of polar microalgae and their bioactive compounds in several fields will also be discussed

in this article.

2 Unique adaptations of polar microalgae to extreme environments

In contrast with the relatively mild and stable conditions experienced by tropical and temperate microalgae, polar microalgae must cope with multiple challenges in polar environments, including low temperature, high salinity, varying daylight length and ultraviolet radiation exposure (Thomas and Dieckmann, 2002). To overcome these challenges, polar microalgae have developed many effective adaptations. Several reviews focused on the survival strategies employed by polar microalgae, however it is important to emphasize the association between their physiological responses and potential biotechnological applications, which shall be discussed in subsequent sections (Lauritano et al., 2020; Lyon and Mock, 2014; Mock and Thomas, 2008).

2.1 Low temperatures

The cold polar climate creates a low kinetic energy environment which leads to a decrease in the rate of enzyme-substrate interactions (Lyon and Mock, 2014). Increasing enzyme concentrations are characteristic of initial microalgal adaptation to cold temperatures, although a majority of upregulated enzymes are not cold-inducible, and this strategy most likely only contributes to short-term acclimatization (Wang et al., 2020). To better overcome these inhibiting effects, sympagic microalgae produce enzymes with active sites that require lower energy input for catalysis than the conventional induce-fit mechanism, thereby increasing the rate of reaction. These microorganisms also synthesize unique enzymes that are less susceptible to fluctuations in temperature or can achieve optimal activity at temperatures approaching 0 °C, for instance the enzymes responsible for the absorption of nitrate, ammonium, and carbon in cold-adapted diatoms (Priscu et al., 1989). In addition, Szyszka-Mroz et al. (2019) demonstrated that thylakoid protein kinases from *Chlamydomonas* sp. UWO241, an Antarctic green alga, are structurally altered to enable them to function optimally at low temperature. Another study demonstrated that the nitrate reductase (NR) and argininosuccinate lyase from an ice alga displayed optimal enzymatic activities at a colder temperature when compared to the corresponding enzymes of a mesophilic alga (Loppes et al., 1996). Studies on NR from cryophilic microalgae also reported that their enzymes function optimally at low temperatures (Di Martino Rigano et al., 2006; Vona et al., 2004). Notably, NR of ice microalgae are more versatile in electron donor selection as they can use both NADPH and NADH, in contrast with mesophilic microalgae which can utilize only NADH (Di Martino Rigano et al., 2006).

The polar microalgal community also needs to develop

strategies to protect against cold inactivation. In cold environments, unlike proteins which are susceptible to structural damage, DNA and RNA structures may exhibit increased stability, which causes difficulty in coiling and uncoiling thus affecting cell replication, transcription, and translation (Dasauni et al., 2022). To maintain normal cell processes at low temperatures, psychrophilic bacteria are reported to rely heavily on DEAD-box RNA helicase, overexpressing the associated gene for cold adaptation, and without DEAD-box RNA helicase, their growth and survival is severely affected (Jagessar and Jain, 2010; Lehnik-Habrink et al., 2013; Markkula et al., 2012; Pandiani et al., 2010). Similarly, DEAD-box RNA helicase was upregulated in psychrophilic microalgae when exposed to freezing condition. The number of RNA helicase genes upregulated in the microalgae also increased with the duration of cold stress up to 72 h, suggesting that early and late responses of the transcriptional mechanism of RNA helicase perform distinct roles in microalgal freezing acclimation (Liu and Huang, 2015). As protein misfolding triggered by cold stress is quite common, microalgae have been reported to upregulate genes responsible for post-translational modification in response to cold exposure (Liu et al., 2016).

Another low temperature challenge faced by cryophilic microalgae is that of maintaining membrane fluidity, which is important for efficient uptake of nutrients and elimination of wastes as well as the proper functioning of cellular membrane-associated processes such as energy generation, cell division and photosynthesis. As opposed to mesophilic microalgae, where the cell membrane is exposed to relatively higher heat, resulting in the development of mechanisms to keep the membrane intact, polar microalgae modify the lipid composition of the phospholipid bilayer membrane, for instance, by incorporating more polyunsaturated fatty acids (PUFAs) to prevent membrane rigidification (Morgan-Kiss et al., 2006). Recent research has highlighted the importance of PUFAs in the polar microalga, *Chlamydomonas malina*, which produced the highest amount of PUFAs in a low temperature environment (4 °C), while the total contents of carbohydrate and lipid were higher when the microalgae were stressed at temperatures higher than 8 °C (Morales-Sánchez et al., 2020a). Indeed, lipid metabolism, especially unsaturated FA biosynthesis, is extremely important for the survival of ice microalgae in the polar environment. For instance, *Coccomyxa subellipsoidea* was reported to overrepresent genes coding for FA synthase, FA elongase, FA ligase and particularly FA desaturase, which is also identified as one of the highly expressed genes in *Chlamydomonas* sp. (Blanc et al., 2012; Zhang et al., 2020). Elevated amounts of lipids are also found in chloroplast membranes, increasing thylakoid membrane fluidity for optimal photosynthesis in sympagic microalgae (Morgan-Kiss et al., 2006). Most of the photosynthetic apparatus protein is bound to specific lipids known as galactolipids which

consist of monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG). MGDG is formed when a single galactose molecule is attached to a glycerol backbone, while DGDG consists of two galactose molecules bonded to the same backbone (Riccio et al., 2020). Other than preserving the functionality of photosynthesis, high amounts of unsaturated lipids in the chloroplast membrane serve to protect the photosynthetic apparatus against photoinhibition induced by cold stress (Kugler et al., 2019). A recent study revealed several mechanisms that the psychrotolerant microalga, *Coccomyxa subellipsoidea* has developed to acclimatize to low temperature. They were shown to produce and accumulate lipids and soluble sugars when they were exposed to cold stress which enable them to adjust the osmotic pressure of the cytosol and maintain membrane fluidity (Kania et al., 2023).

Cold environment microalgae produce various cryoprotectants to protect against freezing damage and desiccation due to intracellular and extracellular ice formation (Lauritano et al., 2020). Compatible solutes are low molecular weight osmolytes that primarily play a role in osmoregulation. However, some have cryoprotective properties that confer cold tolerance in microalgae through lowering the intracellular freezing point, thereby maintaining

intracellular fluidity and stabilizing enzyme structures to maintain enzyme function (Dawson et al., 2023). The amino acid proline is one such compatible solute that is very well represented in the expressed sequence tags cold library in *F. cylindrus* (Lauritano et al., 2020). The importance of proline as cryoprotectant has also been highlighted in psychrophilic bacteria, where the gene involved in expressing proline is upregulated in response to cold stress (Bergholz et al., 2009), as well as playing analogous roles in multicellular organisms as has been well studied in polar terrestrial invertebrates (e.g., see syntheses of Convey (1996) and Denlinger and Lee (2010)). Other common compatible solutes such as polyhydroxy compounds, betaine, DMSP, glycine, ectoine, and trehalose also offer cryoprotection to both cryophilic microalgae and bacteria (Table 2). Late embryogenesis abundant (LEA) proteins also play an important role as cryoprotectants for polar microalgae. A cold-adapted *Chlorella vulgaris* strain expressed more abundant LEA proteins when compared to its counterpart mesophilic strain (Wang et al., 2020). Other than microalgae, LEA proteins can confer cold tolerance in plants, fungi, bacteria, and some invertebrates, and they are suggested to protect enzymes against denaturation and preserve protein structures (Sasaki et al., 2014).

Table 2 Compounds synthesized by polar microalgae for adaptation to cold environments

Compound type	Examples	Function	References
Enzymes	NR and DEAD-box RNA helicase	Performing optimally at low temperature	Di Martino Rigano et al., 2006; Liu and Huang, 2015
Lipids	PUFAs	Maintaining membrane fluidity at low temperatures	Morales-Sánchez et al., 2020b
Compatible solutes	Proline, glycine, betaine and trehalose	Helping with osmotic balance and stress tolerance	Lyon and Mock, 2014
IBP	AFP, INP and IA	Preventing ice crystal formation and recrystallization	Bialkowska et al., 2020
EPS	Alginate and xanthan gum	Forming protective biofilms, shielding against ice formation, and aiding in adhesion to surfaces	Nagar et al., 2021

In addition to cryoprotectants, cryophilic microalgae also secrete ice-binding proteins (IBP) as well as extracellular polymeric substances (EPS) to mitigate freezing damage due to extracellular ice formation or to prevent ice formation altogether. IBPs are proteins secreted by an organism that can bind to ice surfaces and manipulate growth of ice (Voets, 2017). It is an umbrella term that includes proteins such as antifreeze proteins (AFP), ice-nucleating proteins (INP) and ice adhesin (IA). AFPs are proteins with low thermal hysteresis activity that can lower the freezing point of bodily fluids in an organism by preventing further growth of existing ice crystals or secondary nucleation events occurring, while IAs allow the host organism to adhere to the ice surface to facilitate the exchange of air and nutrients (Ekpo et al., 2022; Gharib et al., 2022). INPs promote the formation of ice at a relatively high sub-zero freezing temperature in supercooled liquids, thereby allowing greater control of the ice formation process, and are conversely also utilized by pathogens to induce freezing damage to plants and fruits in order to

release nutrients for their use (Hartmann et al., 2022). INPs also offer cold protection to certain plants through extracellular freezing. Other known actions of IBPs to improve the survival in freezing habitat are the inhibition of ice recrystallisation as well as the organizing of ice structure to create a liquid environment for microorganisms.

Microalgae depend on IBPs for survival in sub-zero environments, as possession of multiple genes encoding for IBPs has been confirmed in multiple species of microalgae from different cold habitats (Cho et al., 2019; Gálvez et al., 2021; Gwak et al., 2014; Jung et al., 2016; Kondo et al., 2018; Liu et al., 2016; Raymond and Morgan-Kiss, 2017). It has been suggested that microalgae originally acquired the IBP gene through horizontal gene transfer from cold-adapted prokaryotic organisms (Raymond and Remias, 2019). However, compared to the single IBP gene in prokaryotes, microalgae with multiple IBP genes may survive better under various ice exposure conditions (Raymond and Morgan-Kiss, 2017). Microalgal IBP genes are cold-inducible and highly expressed. Microalgae secrete

IBPs extracellularly into the environment to inhibit ice recrystallisation and manipulate the growth of surrounding ice in order to maintain a liquid environment (Jung et al., 2016; Raymond and Morgan-Kiss, 2017; Raymond et al., 2009). In contrast to microalgae that thrive in sea ice, the marine diatom, *Chaetoceros neogracile*, retains IBPs intracellularly, possibly thereby protecting against freezing damage, suggesting that secretion of IBPs varies between species and habitats (Gwak et al., 2014). Transgenic plant with IBP genes inserted from Arctic microalgae also showed improved cold tolerance, highlighting the potential for agricultural applications of IBP in promoting cold adaptation in crop species (Cho et al., 2019).

EPS are high molecular weight biopolymers that are found loosely or tightly attached to microorganisms or secreted into their environment. The major components of EPS are polysaccharides and proteins, but other molecules such as nucleic acids, lipids and humic substances can also be included within EPS. Microalgae secrete EPS into their surroundings in order to form aggregates that have various functions such as facilitating nutrient uptake, assisting in energy production, and conferring mechanical support and protection against external stress (Xiao and Zheng, 2016). Different microorganisms generate EPS with diverse chemical compositions and structures by altering the length of sugar chain, branching, sugar constitution, types of sugar connection and incorporating additional chemical groups (Ewert and Deming, 2013). EPS can also play a role in cold acclimatization of microalgae, with production increasing in response to freezing stress, and by acting as a cryoprotectant for microalgae through the inhibition of ice formation (Aslam et al., 2012). Aslam et al. (2018) reported that the genes involved in EPS production, mainly carbohydrate-active enzymes, were upregulated in cold conditions and that the microalgae could adapt to a changing environment by reconstructing their EPS production pathway, essentially altering the characteristics of EPS to suit the environment.

2.2 High salinity

Polar microalgae can also face high salinity, especially in brine channels within the sea-ice where salinity can reach more than $200 \text{ g}\cdot\text{kg}^{-1}$ as compared to seawater ($\sim 35 \text{ g}\cdot\text{kg}^{-1}$) (Wittek et al., 2020). As the temperature drops, the salinity increases further due to more salt being forced out of the developing ice into the brine channel, creating a hypersaline liquid environment that is more resistant to freezing. Microalgae exposed to salt stress have a reduced rate of cell

division, smaller size, decreased motility and may even enter a temporary palmelloid stage to protect themselves (Shetty et al., 2019). As with cold tolerance adaptations, psychrophilic microalgae produce and accumulate compatible solutes such as glycerol, proline, dimethylsulfoxide (DMSO) and DMSP to balance the osmotic stress between the external environment and the cytosol (Figure 1). Glycerol is a highly soluble and non-toxic end-product metabolite, formed mainly through the degradation of starch, which accumulates in microalgae exposed to high salinity environments (Ng et al., 2014). Similarly, production of proline, which has a low molecular weight, neutral charge and is highly soluble, increases in microalgae exposed to salinity stress (Shetty et al., 2019). Proline synthesis genes were highly represented in the salt stress EST library of *F. cylindrus*, and a proteomics study showed that among the 36 proteins with an increase in relative abundance under high salinity, seven were specifically related to the proline synthesis pathway (Lyon and Mock, 2014). Antarctic bacteria and algae have also been reported to accumulate proline under freezing and high salinity conditions (Dawson et al., 2023). DMSO and DMSP are also involved in the osmoregulation of microalgae, with their concentrations increasing in response to high salinity, although when exposed to the highest salinities, microalgal mortality was higher and DMSO and DMSP concentrations dropped drastically (Wittek et al., 2020). Other osmolytes such as trehalose, betaine, sorbitol and mannitol are also involved in osmoregulation in cryophilic microalgae (Lauritano et al., 2020).

2.3 Fluctuating daylength

The Earth's polar regions are characterized by extreme fluctuation in daylength over the annual cycle, which affects the rate of photosynthesis of microalgae to the point of inducing oxidative stress and photoinhibition in summer or makes photosynthesis impossible in winter. Heavy seasonal snowfall and ice formation can also reduce incident solar radiation (Lauritano et al., 2020). Algae in these regions have evolved light harvesting mechanisms that are efficient and robust under both low and high light conditions, and polar microalgae have adapted to survive in condition with limited light exposure. *F. cylindrus* cultured under low light conditions exhibited higher amounts of chloroplast-specific PUFAs, likely improving the fluidity of the thylakoid membrane and enhancing photosynthetic efficiency (Mock and Kroon, 2002). Furthermore, pigment concentrations, particularly chlorophyll *a*, chlorophyll *c* and fucoxanthin

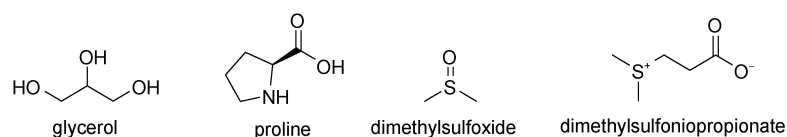


Figure 1 Chemical structures of compounds produced and accumulated by psychrophilic microalgae to mitigate osmotic stress: glycerol, proline, dimethylsulfoxide (DMSO), and dimethylsulfoniopropionate (DMSP). These compounds help maintain osmotic balance between the external environment and the cytosol.

increased significantly in low light when compared to higher irradiance. Carbohydrate concentration was also reduced in microalgae under low light conditions, consistent with them utilizing carbohydrates as an alternative energy source to compensate energy deficiency. Two genes encoding for fucoxanthin chlorophyll *a/c*-binding protein (FCP), a light harvester that is distinct from the light-harvesting complexes of higher plants, were up-regulated to enhance light-harvesting efficiency (Mock and Valentin, 2004). The Antarctic microalga *Chlamydomonas raudensis* shows adaptation to a low irradiance environment by having a high photosystem II (PS II) to photosystem I (PS I) ratio and producing pigments that specifically absorb in the blue light region (Lauritano et al., 2020). It is also possible for ice microalgae to acquire organic matter through mixotrophy when light availability is limiting (Morgan-Kiss et al., 2006). A separate strategy for overwinter survival is through the formation of spores (Duncan et al., 2024). This dormant state allows the organism to withstand the environmental challenges due to its extremely low metabolism and reserve of essential biological materials. Spore formation may only take 8 to 10 h under unfavorable conditions and, when the spores are exposed to light, they can reactivate after some days (Pelusi et al., 2019). A similar mechanism is also employed by some polar microalgae to tolerate freezing temperatures (Hejduková and Nedbalová, 2021). However, the role of such mechanisms in the field requires further investigation as the experimental conditions applied in the laboratory do not necessarily reflect the natural polar environment in which the microalgae were sampled.

In the polar summer high light intensity environment, microalgae employ several mechanisms to dissipate excess light energy to avoid phototoxicity and photodamage primarily caused by reactive oxidative stress (Kennedy et al., 2020). Most of the polar microalgae species such as *Chaetoceros neogracilis* were able to maintain its growth and photosynthesis rate which are unaffected by higher irradiances (Lacour et al., 2022). Non-photochemical quenching (NPQ) as well as the concentrations of the pigments diadinoxanthin and diatoxanthin increased in *C. neogracilis* exposed to high light conditions, dissipating excess light energy and preventing photoinhibition (Lacour et al., 2022). NPQ is also employed by other cold environment microalgal species for photoprotection against high levels of light (Petrou et al., 2011; Yoshida et al., 2020). Another mechanism utilized by sympagic microalgae to counter high irradiance is to down-regulate genes involved in PS II and carbon fixation. Chaperones and genes encoding plastid protein synthesis and turnover are conversely up-regulated, implying that this process may be involved in repairing photodamage (Mock and Valentin, 2004). FCP which plays a role in harvesting light, is also involved in light energy dissipation. FCP exposed to high light levels showed not only rapid energy quenching, but also possible alterations in the energy-transfer pathways

(Nagao et al., 2021).

Formation of plastoglobules, as observed in the red snow alga, *Sanguina nivaloides*, but not in the orange snow alga *S. aurantia*, may also contribute to photoprotection (Procházková et al., 2021). Indeed, plastoglobules which are globular lipid droplets integrated with proteins present in the thylakoid membrane, participate in photoprotection, especially with the Fibrillin2 protein being highly expressed under high light intensity (Kim et al., 2022). Several snow and permafrost microalgae were also shown to accumulate secondary carotenoids and α -tocopherols under intense irradiation, suggesting the photoprotective function of these compounds (Leya et al., 2009). Unlike primary carotenoids that are linked to photosynthetic apparatus, secondary carotenoids are compounds inducible by adverse environmental conditions with functions such as photoprotection, antioxidants and energy storage. This ability of carotenogenesis may be the key survival strategy to the abundant carotenogenic microalgae in the Arctic White Sea coastal region (Chekanov et al., 2020). However, as secondary carotenoids only absorb wavelengths between 390 and 600 nm, they are unable to protect the microalgae against excessive ultraviolet (UV) radiation.

2.4 UV radiation exposure

During the polar summer and autumn, microalgae are exposed to high levels of UV radiation, and this exposure may increase further due to seasonal thinning of the ozone layer, especially in the early season in Antarctic. UV radiation includes three regions, UV-A, UV-B and UV-C, each including progressively shorter and more energetic and biologically damaging wavelengths. UV-A makes up about 90% of total UV radiation and can penetrate the atmosphere to ground level, but its relatively lower energy does not usually cause severe damage, and it even plays beneficial roles in pigment repair processes in photosynthetic organisms. In contrast, the higher energy UV-C is far more damaging to biological structures, compounds and processes, it does not penetrate the atmosphere to ground level. Marine microorganisms, including microalgae, are especially vulnerable to UVB, as while the majority is absorbed by the stratospheric ozone later, it can penetrate to the ocean surface where it can cause DNA damage, induce oxidative damage, trigger formation of cyclobutene pyrimidine dimers and inhibit photosynthesis and growth (Araújo et al., 2022; Fal et al., 2022; Kennedy et al., 2020).

Psychrophilic microalgae have remarkably powerful antioxidant mechanisms enabling them to tolerate UV-induced damage and are reported to be more resistant to UV-B exposure than tropical and temperate species (Wong et al., 2007). In addition to responding to exposure to intense light levels, LHC genes in Antarctic microalgae are upregulated when exposed to UV-B radiation, suggesting a role in UV photoprotection (Mou et al., 2012). The same microalgal species show an increase in transcription of a photolyase gene under UV-B radiation treatment (An et al.,

2018). Photolyase is a light-activated enzyme that can repair DNA damage induced by UV radiation through photoreactivation. Transformed *Escherichia coli* expressing the photolyase gene extracted from this microalga demonstrated improved survival relative to the control *E. coli* without the inserted gene after UVB irradiation. Photolyase activity had been evaluated using animal studies involving mice, where topical application of the photolyase in the form of nanoliposomes successfully conferred protection against UVB-induced erythema, alterations in epidermal thickness and the formation of wrinkles (Qu et al., 2022).

Cold environment microalgae can utilize a wide range of enzymatic antioxidants, for example catalase, superoxide dismutase, ascorbate peroxidase and glutathione reductase, to protect themselves against oxidative damage (Lyon and Mock, 2014). Polar microalgae also produce non-enzymatic antioxidants, primarily carotenoids and flavonoids that can disrupt the reactive oxygen species (ROS) chain reactions (Gauthier et al., 2020). Flavonoids are strong antioxidants that can chelate metal ions to prevent the formation of ROS, while carotenoids are pigments that can broaden the light spectrum for photosynthesis. Carotenoids such as zeaxanthin, lutein, astaxanthin and β -carotene, commonly produced by microalgae, can also provide photoprotection in high light environments. Other non-enzymatic antioxidants

produced include mycosporine-like amino acids (MAAs), polyphenols, proline and tocopherols. MAAs are strongly associated with UV photoprotection as they are small metabolites that can absorb ultraviolet radiation between 310 and 362 nm wavelength, thereby acting as natural sunscreen for microorganisms, although they are also involved in other protective and regulatory roles (Gerald and Pinto, 2021). Cold environment microalgae also synthesize the extracellular pigment scytonemin and its degradation by-product, scytonemin-red, which screen UV radiation and allow improved survival (Morgan-Kiss et al., 2006).

3 Overview of polar microalgal cultivation, harvest, and metabolite extraction

Successful laboratory research on polar microalgae, as well as any subsequent developments towards industrial application require careful planning and execution of sampling, isolation, cultivation, harvesting, extraction and characterization (Figure 2). The various methodologies involved in this stepwise process will require optimization in relation to multiple factors. Particularly, the process of algae cultivation, harvest, and bioactive compounds extraction are crucial for the commercialization and industrial scalability of polar microalgae.

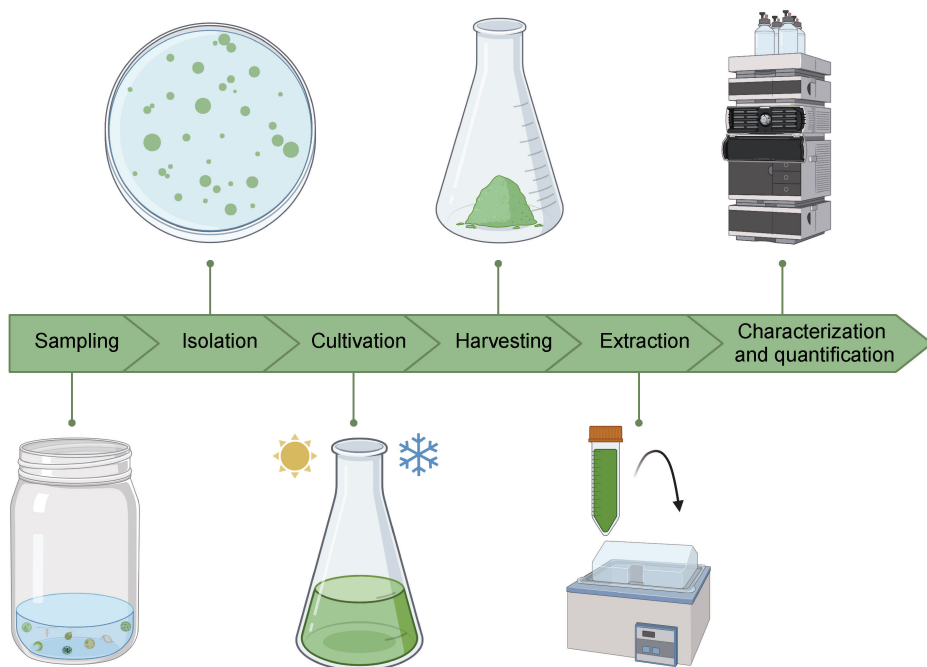


Figure 2 General flow chart on the processing of microalgae depicting the stepwise procedure of sampling, cultivation and metabolite extraction.

3.1 Cultivation

Cultivation of polar microalgae is generally carried out in a way that mimics their natural habitat. Growth-limiting factors such as temperature, salinity, humidity, light

intensity, pH, nutrient content and even snow cover should be considered when culturing specific cold-adapted microalgal strains (Gatamaneni et al., 2018; Rysgaard et al., 2001). Many polar microalgae experiments were carried out in Erlenmeyer flasks in a controlled environment (Boelen et

al., 2013; Canora et al., 2022; Urme et al., 2025), while others utilized various types of PBR (thin-layer, glass columnar and lab scale) to grow microalgae with high efficiency (Kvíděrová and Lukavský, 2023; Lim et al., 2023; Morales-Sánchez et al., 2020a). Various well-established media are available with specific nutrient composition, such as Blue Green-11 (BG-11) medium, modified Bristol medium (MBM), Seewasser Erddekokt Salze (SWES) medium, modified Zarrouk medium (MZM) and Bold's Basal Medium (BBM) (Carvalho et al., 2019). Most polar microalgae cultivation techniques involve BBM, tris-acetate-phosphate (TAP) and *f/2* medium (Lim et al., 2023; Morales-Sánchez et al., 2020a; Suzuki et al., 2019).

Cultivation temperature used for polar microalgae commonly ranges from 4 to 10 °C, although some taxa are eurythermic and can grow at temperatures up to 30 °C (Teoh et al., 2004). Cold environment microalgae commonly grow well in media with pH of 6 to 8. Salinity requirements can vary widely across different microalgal taxa, with an obvious relationship between these requirements and their source habitat (marine, freshwater, terrestrial, etc.) (Canora et al., 2022; Koppel et al., 2021; Suzuki et al., 2019; Zamree et al., 2023). Cool, white, fluorescent light is commonly used to provide artificial lighting in a 12:12 h light:dark cycle, although other illumination regimes can be used (İnan et al., 2023a). Thus far, cultivation of polar microalgae has been occurring mainly in laboratory settings to elucidate their physiological responses and potential biotechnological applications. Hence, further research to determine the balance between growth and metabolite production, similar to the study by Figueroa-Torres et al. (2021), should be undertaken.

Unlike tropical and temperate microalgae which are widely cultivated for food and bioactive compounds production, mass cultivation of polar microalgae are still in the early phase (Kvíděrová et al., 2017). Cultivation system plays an important role in industrial upscaling of microalgae commercialization and open cultivation is the most used culturing system for mass production of microalgae. Open cultivation, also referred to as open pond, have benefits including structural simplicity, mass culture potential, and minimized operational and maintenance costs. Circular pond is the main open pond used for mass accumulation of microalgal biomass, attached with a rotating arm to mix the microalgae (Qin et al., 2023). The design of circular open limits its size to approximately 10000 m² because an even mixing is unattainable beyond that. Circulation cascades, a high cell-density cultivation system emerged as a better alternative, boosting productivities of microalgae biomass of *Chlorella* sp. and *Scenedesmus obliquus* up to 20 g (DW)·m⁻²·d⁻¹ (Chuka-ogwude et al., 2021; De Marchin et al., 2015). However, open ponds have clear disadvantages including risk of microbial contamination, water loss through evaporation, limited diffusion of atmospheric carbon dioxide, necessity of extensive land area and low productivity (Singh et al., 2015).

Closed photobioreactors (PBRs) have been designed to overcome the drawbacks of open ponds, including features such as artificial lighting, controlled gas exchange and agitation of media that address many microalgal growth limiting factors. Vertical-column PBRs are commonly used in a seed culture in microalgal cultivation plant while tubular PBRs are utilized commercially for biomass production (Qin et al., 2023). A two-plane tubular PBR was able to produce 30 g (DW)·m⁻²·d⁻¹. Newer PBR design were successful in raising the productivity of microalgal biomass with the ultra-thin flat PBRs producing a maximum of 1.34 g·m⁻²·h⁻¹ of *C. sorokiniana* and 2.8 g·L⁻¹ *S. obliquus* biomass (Deprá et al., 2019). PBRs' major disadvantages are their high installation and operation/ maintenance costs. Hence, PBRs are usually used to produce high value microalgal products. As cultivating polar microalgae have different requirements, optimization of the conditions for large-scale farming is equally important for the potential commercialization of polar microalgae, as discussed in a review by Novoveská et al. (2023).

3.2 Harvesting

After a predetermined culture period or when sufficient biomass of microalgae is accumulated, microalgae harvesting, which may take up to 20% to 30% of the total cost of microalgae downstream processes, can take place (Okoro et al., 2019). This stage focuses on removing as much culture medium as possible from the microalgal concentrate using techniques such as sedimentation, centrifugation, filtration, flotation and flocculation. It is important that this process does not alter the microalgae (Muylaert et al., 2017). Microalgae harvesting methods have been extensively reviewed in previous literature (Barros et al., 2015; Deepa et al., 2023; Roy and Mohanty, 2019; Singh and Patidar, 2018; Tan et al., 2020) and harvesting polar microalgae utilized similar methods.

Sedimentation is a passive process, whereby microalgal cells settle at the bottom of the culture container through gravity, and only applicable to microalgae that sink easily (Tan et al., 2020). Sedimentation is the most economical method of harvesting microalgae as little to no energy is consumed during the process, though it may not be the most time-effective technique. As the disadvantages outweigh the advantages of this technique, it is not widely applied for large-scale harvesting. Centrifugation may be the most common technique, with almost 100% efficiency in harvesting microalgae. Almost all polar microalgae studies utilized centrifugation to harvest the biomass due to high recovery rate and rapid processing. However, its disadvantages include a high upfront capital cost and large energy requirements (Okoro et al., 2019). Disc stack centrifuge and decanter centrifuges are two typical industrial centrifuges with extensive energy consumption of 1.4 and 8 kWh·m⁻³, respectively, limiting their usage in harvesting and extracting high-valued microalgal products (Milledge and Heaven, 2013). A study found that the

centrifugation technique is the most costly but also the most effective harvesting technique compared to three other harvesting methods: filtration, flocculation and sedimentation (approximately 2.18 \$·kg⁻¹ of microalgal oil produced) (Najjar and Abu-Shamleh, 2020). Fully utilizing the entire microalgae content, rather than focusing on extracting one specific compound, could make this technique more feasible in upscaling to lower the net processing cost.

Filtration results in a high yield and can be used to harvest microalgae that are susceptible to shearing damage, as well as able to recollect used water. Most microalgae ranged between 2 and 30 µm in size, hence microfiltration is sufficient for harvesting (Milledge and Heaven, 2013). A major drawback for this technique is that it is prone to clogging and may require frequent filter replacement thereby increasing maintenance cost. Development of effective yet inexpensive anti-fouling mechanisms is the key for large-scale applications of filtration to harvest microalgae.

Flotation is a simple procedure that greatly improves harvesting efficiency and screening throughput. Conventionally, dissolved air flotation is applied for harvesting microalgae, and a recent study demonstrated that dissolved air flotation is very effective in separating marine microalgae when compared to sedimentation (Tyagi et al., 2024). However, dissolved air flotation is energy-intensive and requires a space-consuming compressor and saturator to create microbubbles, thus alternatives such as dispersed air flotation and electroflotation have emerged. Dispersed air flotation does not need energy to pressurize the culture medium, instead it generates bubbles by injecting compressed air through a diffuser with pores diameter between 60 to 655 µm (Alhattab and Brooks, 2017). The use of surfactants was proved to improve the effectiveness of this technique by conferring positive charge to the bubbles to aid in the binding of microalgae to bubbles and the cost of foam flotation is estimated at 0.11 \$·kg⁻¹ DW accounting for its harvesting efficiency (Zhang and Zhang, 2019).

Flocculation may be the most efficient harvesting method among known techniques (Okoro et al., 2019; Vasistha et al., 2021). Chemical flocculants are cheap but may become toxic environment pollutants and contaminate the biomass collected. Kumar et al (2024) highlighted the enormous potential of magnetic nanoparticles in flocculation that necessitates lower doses, unlike conventional chemical flocculants. The nanoparticles are simple to recover and retain high efficiency even after several cycles, suggesting the sustainability of magnetic flocculation for industrial applications. Although this method requires high initial capital cost, with proper planning and suitable design, the cost can be minimized to 0.07–0.16 \$·kg⁻¹ of microalgal biomass (Zhu et al., 2024). Bio-flocculants are not only environmentally friendly and do not require a pre-treatment processes, but they also allow the recycling of culture medium (Chen et al., 2018).

Electroflocculation is a simple alternative but it requires a frequent change of electrodes and hence a cost-saving substitution of the metal electrodes with non-sacrificial carbon electrodes have been explored (Guldhe et al., 2016; Hou et al., 2022).

It is common to utilize a combination of these techniques to further increase the efficiency of harvesting; for example, gravity sedimentation or flotation is frequently carried out in combination with flocculation when harvesting microalgae (Ajala and Alexander, 2020; Besson et al., 2019). Similarly, large-scale microalgae harvesting often involves multiple harvesting methods in a two-step process, namely thickening and dewatering, to greatly reduce harvesting costs and save time. Electroflocculation-electroflotation (ECF) is an integrated process performed in thickening microalgae. A study employed ECF to harvest microalgae with a 98% efficiency and a low cost of 2.48 \$·kg⁻¹, strongly suggesting its feasibility (Nageshwari et al., 2022). Dewatering techniques typically utilized are centrifugation and filtration to reduce the slurry content to 15%–25% solid matter. Dewatering is followed by drying, another energy-intensive process to concentrate the biomass up to 90%–95% solid, with spray drying, drum drying, freeze drying or sun drying (Sharma et al., 2013). Solar drying may be the most cost-effective method, but it requires massive land space for industrial operation.

3.3 Extraction of bioactive compounds

Microalgae are extremely valued for their health-beneficial bioactive compounds. However, many of these useful molecules are confined within the microalgal cells. The extraction of bioactive substances from microalgae, first involves the disruption of cell wall to release the cell and its contents for further processing (Tan et al., 2020). The cell wall can be disrupted mechanically, physically, enzymatically or chemically. Mechanical extraction applies shear forces to break the cell wall using techniques such as grinding in a mortar and pestle, use of a blender, bead beating and ultrasonication. Physical methods can involve heat, electrical discharges, exposure to freeze-thaw cycles or osmotic shock. Enzymes such as trypsin are commonly applied to digest the cell wall. Polar and non-polar solvents can be used to chemically extract the intracellular contents (Rahman et al., 2022). Solvents such as hexane, chloroform, ethyl acetate, ethanol and methanol are used in a Soxhlet apparatus (Bhuvana et al., 2019; İnan et al., 2023b; Martins et al., 2018; McMinn et al., 2012). It is also common to use variable ratios of different polarity of solvents in solvent extractions, or a combination of different extraction methods to enhance the efficiency of extraction and increase the yield of the compounds of interest (Li et al., 2019; Yi et al., 2021). Following solvent extraction, the extracts obtained are dried under a stream of nitrogen gas, by freeze drying or evaporation using a rotary evaporator or vacuum pump to remove the solvents and avoid them

interfering with subsequent processes.

Many studies focused on extracting lipids with chloroform and methanol, while others utilize DMSO or dichloromethane (DCM) in combination with methanol for lipid extractions (Boelen et al., 2013; Gao et al., 2023; Morales-Sánchez et al., 2020a). Svenning et al. (2020) concluded that DCM/methanol is a more suitable choice due to the highest amount of lipids extracted from *Porosira glacialis* and an additional step of extraction increases the lipid yield significantly. The effects of sonification on the lipid extraction on *P. glacialis* were minimal in contrast to other mass-cultivated algae species, suggesting that this is a viable option for lipid production. However, the lipids extracted are mostly for biofuel production and are unsafe for consumption due to the use of toxic solvents. Hence, safe, feasible and sustainable alternatives should be developed for large scale extraction. Acetone or methanol is typically used for pigment extraction to obtain chlorophyll and carotenoids from microalgae, although a study

suggested that dimethylformamide is a more appropriate solvent in conserving the stability of the pigments (Leya et al., 2009). Table 3 summarizes the techniques currently utilized to extract bioactive compounds from polar microalgae.

Though there had been attempts to develop protein and carbohydrate production methods in polar microalgae, there is very limited data on the sole extraction of proteins or carbohydrates (Morales-Sánchez et al., 2020a, 2020b; Zhu et al., 1997). Thus, protein and carbohydrate extraction protocols from studies on non-polar microalgae and seaweed may be explored to elucidate novel bioactive metabolites from polar species (Eilam et al., 2023; Sarkar et al., 2024). Particularly, green techniques such as switchable solvents, microwave-assisted extraction and compressed fluid extractions should be implemented to obtain high-value polar microalgal products with an effective and economic sense (Imbimbo et al., 2020).

Table 3 The methods employed to extract different target compounds from selected polar microalgae species

Polar microalgae species	Extraction method	Solvents used	Target molecules	References
<i>Porosira glacialis</i>	Modified Folch method, assisted with shaking or sonication	DCM-methanol (2:1), hexane-isopropanol (2:1) or hexane	Lipids	Dalheim et al., 2021; Svenning et al., 2020
<i>Sanguina nivaloides</i> , <i>Sanguina aurantia</i> , <i>Chloromonas hindakii</i> , <i>Chlamydomonas</i> sp., <i>Chlorella</i> sp., <i>Stichococcus</i> sp., <i>Klebsormidium</i> sp., <i>Navicula</i> sp. and <i>Scenedesmus</i> sp.	Bligh and Dyer method	Chloroform-methanol-water (1.0:2.0:0.8)	Lipids	Barati et al., 2018; Chen et al., 2012; Procházková et al., 2021, 2019; Teoh et al., 2004; Wong et al., 2007
<i>Chlamydomonas malina</i> , <i>Chlamydomonas klinobasis</i> , <i>Chlamydomonas pulsatilla</i> , <i>Chloromonas platystigma</i> , <i>Raphidonema sempervirens</i> and <i>Macrochloris rubroleum</i>	Solvent extraction assisted with bead mill and sonication	Chloroform-methanol (2.0:2.5)	Lipids	Hulatt et al., 2017; Morales-Sánchez et al., 2020a, 2020b; Urme et al., 2025
<i>Coccinodiscus concinnus</i> , <i>Porosira glacialis</i> , and <i>Chaetoceros socialis</i>	Solvent extraction assisted with bead mill and sonication	DCM-methanol (1:1)	Lipids	Artamonova et al., 2017
<i>Chlamydomonas</i> sp.	Solvent extraction assisted with sonication	Chloroform-methanol (1:2)	Lipids	Kim et al., 2020
<i>Coccomyxa subellipsoidea</i>	Soxhlet extraction	Hexane	Lipids	Kania et al., 2023
<i>Chlamydomonas</i> sp.	Sasser method	Hexane-methyl tert-butyl ether (1:1)	Fatty acids methyl esters	Kim et al., 2016
<i>Chaetoceros brevis</i> and <i>Pyramimonas</i> sp.	Klein Breteler method	DCM	Fatty acids	Boelen et al., 2013
	Solvent extraction	90% (aqueous) acetone	Pigment	
<i>Chlorella</i> sp.	Solvent extraction	Acetone	Pigment	Barati et al., 2018; Wong et al., 2023
<i>Chloromonas nivalis</i> , <i>Chlorococcum</i> sp., <i>Chlamydocapsa</i> sp. and <i>Raphidonema nivale</i>	Solvent extraction assisted with bead mill and sonication	Dimethylformamide	Pigment	Leya et al., 2009
<i>Koliella antarctica</i>	Solvent extraction	N-dimethylformamide	Pigment	Vona et al., 2018
<i>Haematococcus lacustris</i> , <i>Haematococcus rubicundus</i> , <i>Coelastrrella aeroterrestica</i> and <i>Bracteacoccus aggregatus</i>	Folch method	Chloroform-methanol (2:1)	Pigment	Chekanov et al., 2020
<i>Sanguina nivaloides</i> and <i>Sanguina aurantia</i>	Solvent extraction	Methyl tert-butyl	Pigment	Procházková et al., 2021
<i>Chloromonas hindakii</i>	Solvent extraction	Chloroform-DCM (2:1)	Pigment	Procházková et al., 2019
<i>Chlorella variabilis</i> and <i>Auxenochlorella pyrenoidosa</i>	Soxhlet extraction	Ethanol	Crude extract	İnan et al., 2023b

Continued

Polar microalgae species	Extraction method	Solvents used	Target molecules	References
<i>Botrydiopsidaceae</i> sp., <i>Chloromonas</i> sp. and <i>Micractinium</i> sp.	Solvent extraction assisted with shaking	Ethanol	Crude extract	Suh et al., 2017a, 2017b, 2018
<i>Chlorella</i> sp.	Solvent extraction assisted with sonication	Methanol	Crude extract	Wong et al., 2023
<i>Micractinium</i> sp., <i>Chlamydomonas</i> sp. and <i>Chlorococcum</i> sp.	Solvent extraction assisted with shaking	80% methanol	Crude extract	Lim et al., 2023

4 Potential commercial applications

4.1 Health product-related applications

Microalgae are highly valuable natural resources, providing applications in multiple fields spanning, for instance, education, environment, industry, food security and healthcare (Susanti and Taufikurahman, 2021) (Figure 3). Polar microalgal adaptations, enabling their survival in cold harsh environments, have led to a unique biochemical composition when compared with other microalgae species. Compounds synthesized by these microalgae are now generating considerable attention from industrial and pharmaceutical practitioners, in particular, as they have been shown to exhibit diverse health benefits in numerous studies (Table 4).

4.1.1 Crude extracts

Crude extracts from members of the Antarctic microalgal group *Botrydiopsidaceae* have been shown to exert anti-cancer effects on several cancer cell lines (Suh et

al., 2017a, 2017b). The ethanolic extracts inhibited proliferation and induced apoptosis in cancer cells but displayed minimal effects on normal cells. In addition, the treated tumor cells demonstrated suppressed invasion and migration which could contribute to controlling cancer metastasis. The extracts also exhibited antioxidant activities, with better radical scavenging at higher concentrations. Conversely, methanolic extracts from two polar *Chlorella* species demonstrated much lower antioxidant activities, although one of these species displayed the higher activity in comparison with tropical counterparts (Wong et al., 2023). A recent study further highlighted the potential of encapsulating microalgal extracts to protect their anti-cancer activities against oxidation and enhance cancer selectivity (İnan et al., 2023b). The extracts from two microalgae species, *C. variabilis* and *C. pyrenoidosa* encapsulated in nanoparticles showed significant anti-tumor activities against two cancer cells lines, and it is noteworthy that their encapsulated counterparts required higher concentrations to achieve the same effects. The encapsulated extracts were also slightly less toxic to normal cells compared to unencapsulated ones which indicated better cancer selectivity (İnan et al., 2023b).

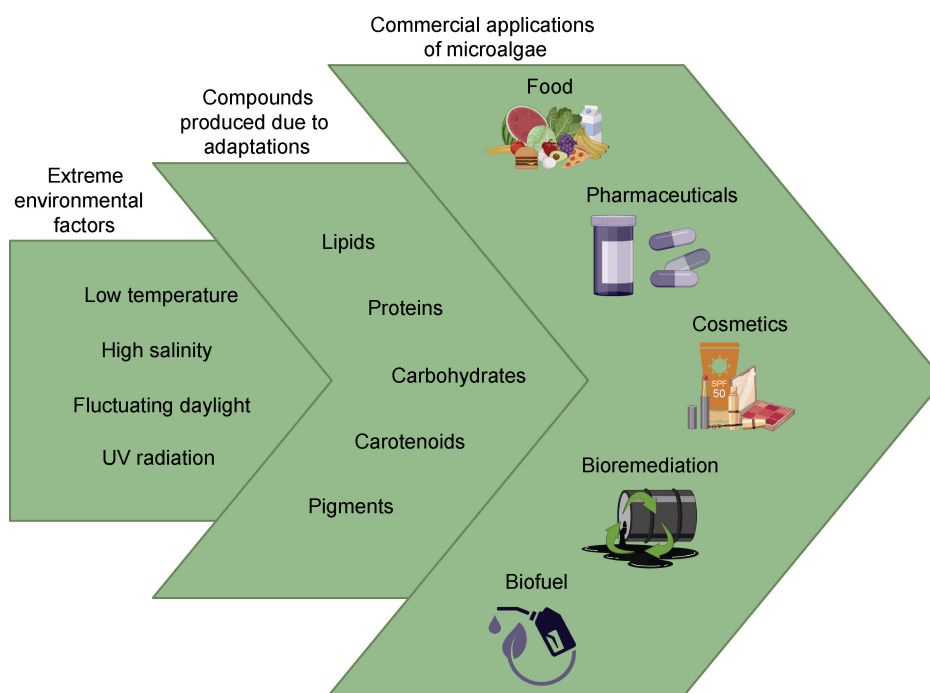


Figure 3 The environmental factors which stimulated the production of beneficial bioactive compounds with commercial value.

Table 4 Potential commercialization of polar microalgal bioactive compounds with health benefits and cosmetic properties

Microalgae genus/species	Bioactive compound	Health/cosmetic benefit	References
Botrydiopsidaceae, <i>Chloromonas</i> sp.	Crude extracts	Anti-cancer and antioxidant	Suh et al., 2017a, 2017b
<i>Chloromonas reticulata</i>	Crude extracts	Anti-cancer and anti-inflammatory	Suh et al., 2018, 2019
<i>Micractinium</i> sp.	Crude extracts	Antioxidant	Wong et al., 2023
<i>Chlorella</i> sp.	Crude extracts	Anti-cancer	İnan et al., 2023b
<i>Chlorella variabilis</i>	Crude extracts	Anti-aging and anti-inflammatory	Chae et al., 2021
<i>Chlorella pyrenoidosa</i>	Crude extracts	Anti-psoriatic and photoprotective effects	Lim et al., 2023
<i>Micractinium simplicissimum</i>	Crude extracts	Anti-inflammatory	Min et al., 2020
<i>Micractinium</i> sp.	Chlorophyll, carotenoids, phenolic compounds	Antioxidant and anti-inflammatory	León-Vaz et al., 2023; Leya et al., 2009
<i>Chlamydomonas</i> sp.	Polysaccharides	Antioxidant	Yi et al., 2021
<i>Chlorococcum</i> sp.			
<i>Desmodesmus opoliensis</i>			
<i>Haematococcus pluvialis</i>			
<i>Scenedesmus</i> sp. <i>Chlamydocapsa</i> sp.			
<i>Raphidonema</i> spp.			
<i>Chlamydomonas</i> sp.			
<i>Chlamydomonas</i> spp.			
<i>Raphidonema sempervirens</i>			
<i>Macrochloris rubroleum</i> <i>Chlamydomonas malina</i>			
<i>Koliella antarctica</i>	PUFAs	Anti-inflammation and antioxidant	Artamonova et al., 2017; Hong et al., 2015; Hulatt et al., 2017; Morales-Sánchez et al., 2020b; Shukla et al., 2013; Suzuki et al., 2019
<i>Chaetoceros brevis</i>			
<i>Pyramimonas</i> sp. <i>Coscinodiscus concinnus</i>			
<i>Porosira glacialis</i> <i>Chaetoceros socialis</i> <i>Chlorella mirabilis</i> <i>Micractinium</i> sp.			
<i>Phaeocystis antarctica</i> <i>Porosira pseudodenticulata</i>	MAAs	Photoprotective effects	Hernando et al., 2002; Riegger and Robinson, 1997
<i>Thalassiosira</i> sp.			
<i>Ramalina terebrata</i>	Ramalin, usnic acid, usimine A, usimine B, usimine C	Anti-bacterial, antioxidant, anti-cancer and anti-allergy	Chang et al., 2012; Jang and Pyo, 2015; Lee et al., 2016; Paudel et al., 2010, 2011
<i>Stereocaulon alpinum</i>	Lobaric acid, lobarstin	Anti-cancer, antimicrobial and antipyretic	Hong et al., 2018

Polar microalgal extracts from *Chloromonas reticulata* have also demonstrated anti-inflammatory activity on macrophages exposed to lipopolysaccharides (LPS) to induce inflammation. During the inflammatory reaction, nitrogen oxide (NO) production, inflammatory mediators such as cyclooxygenase-2 (COX-2), inducible nitric oxide synthase (iNOS) and proinflammatory mediators such as tumor necrosis factor alpha (TNF- α) and interleukin-6 (IL-6) are upregulated, which is also seen in LPS-induced inflammation (Suh et al., 2019). When the LPS-exposed macrophages were treated with microalgal extracts, transcriptional expression levels of COX-2, iNOS, TNF- α and IL-6 as well as NO production were reduced. Extracts from another microalgal species *Micractinium* also displayed comparable outcomes, suggesting that Antarctic microalgal extracts may have more general effectiveness in managing inflammation (Suh et al., 2018). In addition to their anti-inflammatory properties, extracts from the same Antarctic microalgae showed potential as anti-aging treatment, suppressing the production of metalloproteinase-1 (MMP-1), an enzyme involved in collagen fragmentation and an important mediator in dermal aging (Chae et al., 2021). Other studies have demonstrated protective effects on skin cells faced with oxidative stress induced by UVB radiation and psoriasis agents. Polar microalgal extracts enhanced the survival of UV-irradiated keratinocytes and

the extract-treated skin cells maintained their barrier integrity when exposed to psoriatic cytokines. The extracts also exhibited restorative activities on psoriatic skin cells as their normal cellular functions were regained. Similarly, microalgal extracts also attenuated psoriatic inflammation and dermal infiltration of inflammatory immune cells in treated psoriatic mice (Lim et al., 2023). Studies have also reported anti-bacterial, anti-cancer, antioxidant, and anti-diabetic potential in extracts from phytoplankton, including from several species of Arctic microalgae (Lauritano et al., 2016). However, more detailed research is required to clarify the bioactivities induced by extracts from different microalgal species (Ingebrigtsen et al., 2017). Ingebrigtsen et al. (2016) also confirmed that some Arctic diatoms demonstrated anti-bacterial, anti-cancer, anti-diabetes, anti-inflammatory and antioxidant properties.

Lichens are unique organisms resulting from symbiosis between a fungus (mycobiont) and a microalga or cyanobacterium (photobiont) (Duran-Nebreda and Valverde, 2023). The mycobiont primarily contributes protection against harsh environmental conditions while the photobiont provides a carbon (energy) source through photosynthesis. Methanolic extract of the Antarctic lichen species, *Lecania gerlachei* displayed remarkable anti-inflammatory effects on murine macrophage cells, reducing the production of NO and down-regulating iNOS,

several pro-inflammatory interleukins and TNF- α (Min et al., 2020).

4.1.2 Bioactive compounds

Various studies have attempted to isolate the bioactive compounds produced by polar microalgae to determine their health benefits. These microalgae produce pigments such as chlorophyll *a*, chlorophyll *b* and carotenoids as well as phenolic compounds (León-Vaz et al., 2023). Carotenoids and phenolic compounds are well-known for their antioxidant properties (Cichoński and Chrzanowski, 2022). Additionally, carotenoids also offer other health benefits such as anti-cardiovascular, anti-inflammatory, anti-cancer and provitamin properties. They also have industrial application as colorants, contributing to their high commercial interest. Abiotic stress, such as high light can stimulate production of carotenoids and phenolic compounds, and it is well established that higher levels of these compounds are correlated with increased antioxidant properties. Similar stress conditions were also found to induce the production of secondary carotenoids such as astaxanthin and canthaxanthin in several snow and permafrost algae (Leya et al., 2009). However, some microalgal species display high antioxidant activity despite having lower contents of carotenoids and phenolic compounds, suggesting the presence of other potent antioxidants that are yet to be discovered (León-Vaz et al., 2023). One of the isoforms of vitamin E, α -tocopherol was inducible in two polar microalgae species, suggesting the potential large-scale production of the compound (Leya et al., 2009). α -tocopherol is a phenolic compound with many health-promoting properties such as antioxidant, anti-inflammatory and wound healing enhancement (Gamna and Spriano, 2021).

Polysaccharides produced by cold environment microalgae can also offer positive impacts on health when consumed. For instance, a cocktail of sugars was extracted from microalgae which included mannitol, ribose, anhydrous glucose, xylose and fucose, when fed to *in vivo* models, inhibited oxidative damage caused by D-galactose (Yi et al., 2021).

Cold environment microalgae also synthesize large amounts of fatty acids, particularly PUFA, which have high commercial value. For instance, five species of Arctic snow/soil microalgae significantly accumulated monounsaturated fatty acids (MUFA) and PUFA when cultivated in photobioreactors (Hulatt et al., 2017). MUFAs are reported to have anti-inflammatory effects, although higher levels of MUFAs do not automatically translate to positive impacts on inflammation (Ravaut et al., 2021). PUFA can be classified into 18 carbon atoms and long chain PUFAs with more than 18 carbons, are known to enhance metabolism, to regulate blood pressure and blood sugar level and reduce the risk of certain diseases including cancer. Well-known PUFAs with beneficial health effects include eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), linoleic acid (LA)

and arachidonic acid (AA) (Santin et al., 2021). Cold environment microalgae can also produce significant amounts of EPA and DHA which are essential omega-3 fatty acids for human consumption. Notably, an Antarctic species of microalga produced the highest amount of EPA among several species studied, including temperate microalgae (Boelen et al., 2013). Similarly, another study reported that cold-adapted Arctic microalgae produced high amounts of EPA (Artamonova et al., 2017). EPA and DHA are recognized for their importance in fetal development, lowering the risk of cardiovascular diseases and mitigating cognitive decline (Djuricic and Calder, 2021; Swanson et al., 2012). Other than that, *Chlorella mirabilis*, a cold-adapted microalga was suggested to be a promising source of LA, as glycerol treatment in mass cultivation increased the production of LA (Shukla et al., 2013). In addition, several Antarctic *Micractinium* algae strains were found to synthesize high amount of LA (Hong et al., 2015). LA is an essential fatty acid that plays a role in growth, reproduction, and healthy development in animal diets, as it can be esterified to form neutral and polar lipids (Whelan and Fritsche, 2013).

Another bioactive compound, MAA, derived from polar microalgae has application in the cosmeceutical industry. Cold environment microalgae synthesize MAA that can absorb UV radiation and protect against oxidative damage, making these compounds suitable candidates to be incorporated into sunscreens. Three MAAs (porphyra-334, mycosporine-glycine and shinorine) were identified in a single Antarctic microalga, *Porosira pseudodenticulata*, while other tested diatoms generally produced only two types of MAAs. The production of MAAs in algae was inducible through exposure to blue or UV light, which suggests a possibility of mass production (Hernando et al., 2002; Riegger and Robinson, 1997). There was a patent regarding the MAAs isolated from polar microalgae for the potential application as sunscreen, however much research is needed to realize the true value of MAAs (Kviderová et al., 2017).

The Antarctic lichen, *Ramalina terebrata* is capable of synthesizing ramalin, a bioactive substance with multiple health benefits. Ramalin, along with other compounds extracted from the lichen such as usnic acid, usimine A, usimine B and usimine C, demonstrated anti-bacterial activity towards *Bacillus subtilis*, while the crude extracts and usnic acid additionally showed anti-bacterial activity against *Staphylococcus aureus* (Paudel et al., 2010). Ramalin was also reported to have antioxidant effects while showing little to no adverse impacts on normal skin cells and fibroblasts. *In vivo* testing involving murine macrophage Raw264.7 cells showed that ROS induced by LPS was significantly diminished by the application of ramalin (Paudel et al., 2011). Other studies have revealed that ramalin has anti-cancer and anti-allergen activities (Jang and Pyo, 2015; Lee et al., 2016). Furthermore, ramalin also holds promise in the cosmetics industry

because it inhibits the production of melanin in a melanocyte cell line as the application of a ramalin formulation in a clinical study improved the skin brightness of human participants with no side effects reported (Chang et al., 2012). Lobaric acid and lobarstin extracted from another Antarctic lichen species, *Stereocaulon alpinum*, exhibited anti-cancer effects on cervix adenocarcinoma and colon cancer cells through mechanisms such as cell cycle arrest and induction of apoptosis (Hong et al., 2018). In addition to antitumor activities, the two bioactive compounds demonstrated potent antimicrobial and antipyretic properties (Bhattarai et al., 2013; Seo et al., 2009).

4.2 Other industrial applications

Besides pharmaceutical and cosmetic applications, polar microalgae are valued for their usefulness in other fields as well. Cold strains marine microalgae had shown promise as a potential food source and nutritional supplement due to their ability to produce high levels of protein and fatty acids (Schulze et al., 2019). Jo et al. (2020) also demonstrated the high protein content of polar *Chlorella vulgaris*, achieving almost 40% of total weight when grown in 10 °C. Microalgae cultivation can alleviate the pressure of catching wild fish for their oils. However, storage for these algae as food is a challenge as their fatty acids are prone to oxidation. A study explored several storage methods and concluded that heat-treated algal biomass stored at 4 °C is the best way to preserve the integrity of PUFAs (Dalheim et al., 2021). The study also mentioned that lipid degradation mainly stems from endogenous enzymatic reactions instead of external microorganisms, thus future research should focus on overcoming this for more feasible preservation methods.

Aside from human consumption, polar microalgae appear to be a viable option for making animal feed. A study found that salmon feed supplemented with Arctic diatom biomass displayed a reduction in lice infestation, likely due to the production lice-deterring bioactive compounds (Eilertsen et al., 2021). The modified feed not only supported the robust growth of the salmon, but there were also no side effects observed on the fish health as well. This greatly implies the potential of culturing polar microalgae for animal feedstock. A review by Saadaoui et al. (2021) demonstrated the potential of microalgae-based feed for livestock and poultry, highlighting the various benefits of microalgal feed particularly in improving the yield and quality of animal products while discussing the challenges in manufacturing animal feed with microalgae.

Various bioactive compounds extracted from cryophilic microalgae, for instance AFP that can minimize or prevent freezing damage, were identified and characterized by several studies (Jung et al., 2014; Kim et al., 2017). This property of AFP can be utilized for various purpose such as cell preservation as AFP was able to improve the survival rate of preserved mammalian cells, tissues and even organs (Lauritano and Coppola, 2023;

Sreter et al., 2022; Yamauchi et al., 2021). Other applications of AFP include enhancing the freezing and liquefying properties of food and improving ice cream texture, and cryosurgery. Other than AFP, cold-adapted enzymes from polar microalgae may be exploited for detergent production. Cold-tolerance genes in particular can be introduced into crops to confer cold protection to improve survivability. In addition, robust light-harvesting genes and UV-tolerance genes may be potentially introduced into susceptible crops to improve yield and stress-tolerance against harsh agricultural conditions.

As cold-adapted microalgae were known for their high concentration of lipids, industry practitioners are keen to extract the lipids to produce biofuels. The discovery and generation of biofuels such as bioethanol, biodiesel, biomethane, and biobutanol has always been a hot topic for research as they are renewable and environmentally friendly energy resources, unlike conventional fossil fuel. An Antarctic freshwater microalga was demonstrated to be a suitable candidate for biodiesel production due to high level of neutral lipids (Chen et al., 2012). Nitrogen starvation triggered the algae to possess higher neutral lipids due to hydrolysis of phospholipids and glycolipids. Neutral lipids are preferred over phospholipids and glycolipids because it is easier to convert the neutral lipids to biodiesel through transesterification, while more steps are required to process phospholipids and glycolipids that translate into higher cost. Kim et al. (2016) found that an Arctic *Chlamydomonas* microalgae species exhibited optimal growth at a low temperature (4 °C) and produced PUFA at higher levels than the percentage of saturated fatty acids synthesized, suggesting a favorable source for biofuel production. A later study by the same research team was able to synthesize biodiesel and bioethanol through performing and comparing several fatty acid methyl ester extraction methods on psychrophilic microalgae (Kim et al., 2020). Due to the usefulness of polar microalgae lipids especially in the biofuel production, a few studies have optimized the conditions for culturing the several species of cold-adapted microalgae to maximize their growth and the production of PUFAs (Kim et al., 2022; Morales-Sánchez et al., 2020b; Suzuki et al., 2019).

Bioplastics can be produced using polar microalgae as feedstock. A recent review highlighted the feasibility of microalgae-based bioplastics due to several advantages such as sustainability, reduced toxicity and significant degradability (Roy Chong et al., 2022). Although polar microalgae have yet to be introduced to bioplastic industries, it is likely that they will receive attention due to their high lipid content, which is a source of bioplastics. Other components of polar microalgae such as cellulose and lactic acid are also raw materials for bioplastics. The feasibility of bioplastic production can be further improved by processing the residual biomass into bioplastics after high-valued bioactive compounds are extracted (Moreno-Garcia et al., 2017).

Bioremediation, a process of introducing microorganisms to consume and break down pollutants in the environment, is also one of the potential applications of algae. The release of agriculture effluents into the environment is known to cause eutrophication and affect water quality. Even when substantial management is applied, the effluents will still contain micronutrients that would induce toxic algal bloom and affect the aquatic food chain. An Arctic microalgae strain was able to steadily proliferate in the hydroponic effluents released from greenhouses while efficiently bioremediating the hydroponic effluents through nutrient removal (Salazar et al., 2021). In addition, northern microalgae were confirmed to have the ability to remove pharmaceuticals from their surroundings (Gojkovic et al., 2019). Most microalgae strains utilized in the study grew well and were able to effectively uptake lipophilic compounds from the environment although hydrophilic compounds were more persistent. The majority of the algae were found to bioremediate and accumulate the pharmaceuticals in their biomass, but two species had little compound accumulation despite highly efficient removal of pharmaceuticals suggesting the possibility of repeated applications. As polar microalgae are able to efficiently fix carbon dioxide, they can be employed to sequester excess carbon for instance processing flue gas from factories (Ekendahl et al., 2018). Besides, a study showed that an Antarctic microalga can bioremediate diesel through biodegradation and biosorption while potentially stimulating the production of lipid at the same time (Lim et al., 2023). A recent study collected and analyzed some microalgae from Arctic beaches and discovered that they possessed hydrocarbon degradation genes (Freyria et al., 2024). Although bacteria were found to be the major hydrocarbon degraders and only a small portion of microalgae were identified to have these genes, this confirms that these Arctic microorganisms are capable of carrying out biodegradation. However, microalgae recovery may pose a challenge after the remediation. A recent study addressed the issue by immobilizing the microalgae onto coral fleece fabrics, which not only eased the biomass recovery but also enhanced the algae's ability to remove nitrogen from the wastewater (Wang et al., 2025).

4.3 Navigating the journey from potential to profitability

The burgeoning literature on polar microalgae has shed a positive light on their enormous commercial potential, allowing them to compete in the bioactive compound market currently dominated by artificial molecules or compounds extracted from animals and plants. *Spirulina* sp., a microscopic blue-green algae traditionally consumed as food, stands out as one of the successful cases of commercialization. Its journey, from scientific discovery in the 1960s to its global recognition as a superfood in the late

1970s, highlights the various obstacles and hurdles along the way in achieving widespread acceptance (AlFadhly et al., 2022; Soni et al., 2017). Similarly, polar microalgae research, which is still at its infancy, faces several challenges before achieving commercialization and industrial scale up.

One major challenge is that polar microalgae have low production of biomass and slower growth rate particularly when compared to tropical and temperate microalgae when cultivated at their respective optimum conditions (Barati et al., 2018; Lacour et al., 2017; Lee et al., 2018). Polar microalgae have lower growth efficiencies, likely due to the various innate photoprotective mechanisms and alternative electron pathways for photosynthesis (Lacour et al., 2017). Various factors can affect the growth of microalgae (Okoro et al., 2019). Hence, improving the efficiency of photobioreactors will boost the growth rate of polar microalgae. Parameters such as nutrient availability, light intensity and temperature should be manipulated to optimize the algal growth rate. A study investigated the use of artificial night LED lights to simulate the condition of a polar day in a photobioreactor (Kvíděrová and Lukavský, 2023). This improves the feasibility of polar algae farming in places where natural polar day is unavailable. Another study provided some insights into scalability of Arctic diatom cultivation with their uniquely designed PBR (Eilertsen et al., 2022). Larger diatoms were found to grow quicker due to lower self-shadowing and fully utilizing the light energy, having an average production rate of $0.22 \text{ g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ in the 300 m^3 PBR. Agitation can raise growth rates by preventing nutrient saturation and significantly increase biomass accumulation (Nurhidayati et al., 2020). Vona et al. (2018) also indicated that indoor or outdoor conditions may affect the growth of psychrophilic microalgae. *Koliella antarctica*, a microalga isolated from Antarctica, yielded higher growth rates when grown outdoors – a less expensive setup when compared to high-maintenance indoor conditions.

Another known challenge in polar microalgae cultivation is the requirement of cold conditions which may increase the production cost, unlike most other microalgae species which prefer an optimum temperature of between 20 and 30 °C (Singh and Singh, 2015). Most polar microalgae species grow best at temperatures lower than 5 °C and stop growing beyond 10 °C (Lacour et al., 2017). Although this disadvantage can be easily managed if microalgae cultivation is performed in naturally cold places all year round, it is essential to explore the possibilities of cultivating polar microalgae in temperate/tropical climates. A study by Morales-Sánchez et al. (2020a) demonstrated that polar microalga had the most rapid growth rate at 4 °C as compared to the same alga species cultivated at 8 and 15 °C, though the microalgae cultivated at higher temperatures contained higher lipids and carbohydrates content likely as a response to stress, which can be beneficial for biofuel production. However, Lee et al. (2018)

discovered that polar *Chlorella* species was able to tolerate wider range of temperatures, from 4 to 33 °C as well as exhibiting higher growth rate at 20 °C, a temperature higher than their ambient temperature (4 °C), which signifies *Chlorella* being a psychrotolerant algae. Other studies on polar *Chlorella* species also displayed similar trend whereby the algae grew better at 25 °C, instead of its ambient cold temperature, suggesting the possibility of non-cold cultivation of polar microalgae (Barati et al., 2018; Jo et al., 2020). Another Antarctic microalgae, *Micractinium* sp., is also a suitable option to cultivate under non-cold temperatures to produce LA (Hong et al., 2015).

Furthermore, polar microalgae generally have high resource requirements. Compared to the animal and plant industry which uses more resources, the microalgae industry still appears to be a more sustainable and cheaper alternative. Nevertheless, this issue remained to be addressed. Cultivating polar microalgae in wastewater appears to be a solution to improve economic feasibility, as demonstrated by Nordic microalgae sustaining themselves in greenhouse effluent (Salazar et al., 2021). Ekendahl et al. (2018) have explored the possibility of using flue gas and waste heat from a pulp and paper mill as carbon source to cultivate microalgae in cold climates. This approach not only can save valuable resources but at the same time, sequester carbon. Although there is limited research on utilizing wastewater to cultivate polar microalgae, this sustainable approach should be explored as it is widely applied to culture other microalgae for valuable bioproducts (Kong et al., 2024). Another study has proposed potato peel as an alternative carbon source for polar microalgae (Urme et al., 2025). Under mixotrophic conditions, the polar microalgae grew in the potato peel hydrolysates and had higher lipid accumulation. This signifies potential improvement to economic feasibility by using food waste, although the growth of algae was significantly affected.

5 Conclusion

Polar microalgae are hardy microorganisms that reside in the harsh environments of the Antarctic and Arctic regions. Compared with tropical microalgae species, cold-adapted microalgae developed unique mechanisms and adaptations for enhanced survival in highly challenging habitats, thereby attracting interest from researchers and industry practitioners alike. While the extensive processes leading up to the extraction of bioactive compounds are meticulous and time-consuming, several studies have proposed specific optimization steps to increase biomass and improve the yield of beneficial bioactive substances. Current research has focused on the distribution and speciation of polar microalgae, as well as determination of their role in various habitats and the effects of climate change. However, the applications of polar microalgae and their bioactive molecules remain untapped, and only a small fraction of their tremendous potential in various fields has

been demonstrated.

Moving forward, a key priority should be to conduct rigorous qualitative and quantitative analyses of polar microalgae crude extracts and their isolated bioactive compounds. This will not only advance our fundamental scientific understanding, but also enable the development of innovative applications in fields such as pharmaceuticals, nutraceuticals, and biotechnology. By leveraging the tremendous but underexplored potential of polar microalgae, researchers across diverse disciplines can contribute to addressing pressing global challenges and unlocking new avenues for sustainable innovation.

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