Polar Biology
https://doi.org/10.1007/s00300-024-03296-z

REVIEW

# Sea ice as habitat for microalgae, bacteria, virus, fungi, meio- and macrofauna: A review of an extreme environment

**Lars Chresten Lund-Hansen**[1] · **Rolf Gradinger**[2] · **Brandon Hassett**[3] · **Sahan Jayasinghe**[4] · **Fraser Kennedy**[4] · **Andrew Martin**[5] · **Andrew McMinn**[4] · **Dorte H. Søgaard**[1,6] · **Brian K. Sorrell**[1]

Received: 3 August 2023 / Revised: 18 August 2024 / Accepted: 19 August 2024

**Abstract**

The novel concept of the review is a focus on the organisms living in the sea ice and what mechanisms they have developed for their existence. The review describes the physical environment of the sea ice and the microorganisms living there as microalgae, bacteria, virus, fungi, meio- and macrofauna where they inhabit the brine channels and exposed to low temperatures as down to −25 °C and high salinities—up to 300. Nutrients, $O_2$, $CO_2$, pH, light, and UV are also identified as stressors regarding the metabolism of the microorganisms. It is argued that sea ice must be recognized as an extreme environment as based on records of very high or very low concentrations or intensities of the stressors that living organisms in the ice are exposed to and able to endure. Each taxonomic group of organisms in the sea ice are dealt with in detail in terms of the explicit stressors the group is exposed to, and specifically what known mechanisms that the organisms have amended to secure existence and life. These mechanisms are known for some group of organisms as autotrophs, bacteria, meio- and macrofauna but less so for virus and fungi. The review concludes that sea ice is an extreme environment where the stressors vary significantly in both space and time, both in consort and solitary, classifying organisms living there as polyextremophiles and extremophiles. The review relates further to extraterrestrial moons covered with sea ice and these habitats and points toward sea ice on Earth for prospective studies until further technological advances.

**Keywords** Sea ice · Habitat · Microalgae · Bacteria · Virus · Fungi · Meio- and macrofauna · Extreme environment

## Introduction

There are reviews and papers on microorganisms inhabiting the cryosphere (Boetius et al. 2015), and specific sections of the cryosphere as glaciers and ice sheets (Garcia-Lopez and Cid 2017), ice shelves (Vincent and Mueller 2020), snow (Kilias et al. 2020), and sea ice (Thomas and Dieckmann 2002; Deming and Collins 2017). More detailed and thorough studies have focused on specific groups of microorganisms in sea ice as bacteria (Bowman 2015), microalgae (Arrigo 2017), virus (Paterson and Laybourn-Parry 2011), meio- and macrofauna (Gradinger 1999; Bluhm et al. 2017) with a focus on species compositions and distributions. There is, however, a clear tendency in the reviews to focus on specific groups of organisms with a brief summary of their physical conditions in the sea ice. Our concept in the present review is to treat all major groups of microorganisms living and thriving in sea ice with a specific on their specific physical conditions and what mechanisms they developed against the lethal stressors.

In first section of the review, we underline the significant physical features that characterize sea ice and compare these in the context of other extreme environments. Next is a section where sea ice stressors as salinity, temperature, pH, light, $O_2$, $CO_2$, and nutrients are outlined in detail, their interconnectedness, and variability in time and space. The

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✉ Lars Chresten Lund-Hansen
lund-hansen@bio.au.dk

[1] Department of Biology, Arctic Research Center, Aarhus University, Aarhus, Denmark

[2] UiT The Arctic University of Norway, Tromsø, Norway

[3] Texas A&M University, College Station, TX, USA

[4] Institute for Marine and Antarctic Studies, University of Tasmania, Battery Point, TAS, Australia

[5] School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

[6] Greenland Climate Research Centre, Greenland Institute of Resources, Kivioq 2, PO Box 570, 3900 Nuuk, Greenland

major section is devoted to the microorganisms as microalgae, bacteria, virus, fungi, viruses, meio- and macrofauna living and thriving inside the sea ice. Questions addressed are: What is the phylogenetic diversity in the group? How are they distributed in the sea ice? How did they get there? What are the main group specific stressors, and what biochemical mechanisms has each group developed to survive and withstand the extreme conditions? We focus especially on the acclimation to the abiotic factors, to gain insights into microbial, microalgae and metazoan responses to changing environments. A section on extraterrestrial sea ice environments is included for resemblance with sea ice conditions on Earth.

## Features of sea ice

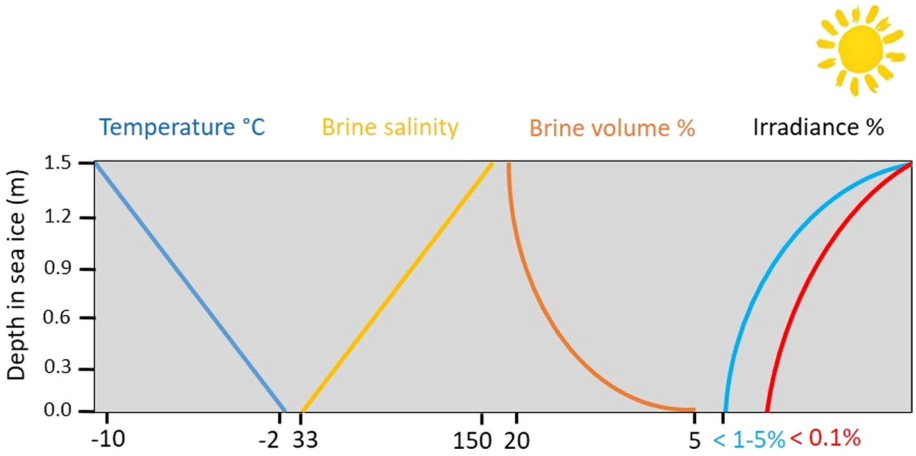
Sea ice is a characteristic and extremely important entity in Polar Regions, from both physical, chemical, biological, climatological, and geopolitical perspectives (Dieckmann and Hellmer 2010). Sea ice in the Arctic and Antarctic together cover about 10% of the world's oceans at its average winter maximum extent of 34 million km$^2$, an area larger than Africa (30.4 million km$^2$) (Lund-Hansen et al. 2020a, b). The Arctic sea ice extent varies from a minimum of 4.7 to 7.7 million km$^2$ and a maximum of 14.3 to 16.3 million km$^2$ (median values 1981–2010) (Cavalieri and Parkinson 2012). This seasonal difference between minimum and maximum sea ice extent of about 8 million km$^2$ compares to the total area of the USA (9.6 million km$^2$). Sea ice extent is an important indicator of climate change, as demonstrated by the recent large decrease in summer sea ice extent from *ca.* 7.5 million km$^2$ in 1979 to about 4.2 million km$^2$ in 2019 (Spreen et al. 2020). A central climatic feature of the sea ice is the high albedo of 0.5–0.6, giving that 50–60% of the incoming radiation is reflected back to space (Perovich 2017). More light and radiation will penetrate into the water column and get absorbed as albedo of water is very low (0.1) (Perovich and Polashenski 2012). This will increase the heating of the upper water column and enhance melting of the sea ice, leading to the so-called ice-ocean albedo feedback (Kashiwase et al. 2017). It is foreseen that there will be no summer sea ice in the Arctic Ocean in a few decades, except for certain areas north of Greenland (Howell et al. 2022).

Not only the extent of Arctic summer sea ice has decreased, but also sea ice thickness, as for the central Arctic Ocean where it decreased from *ca.* 3.6 m in 1975 to 1.3 m in 2012 (Lindsay and Schweiger 2015). Climate-driven atmospheric warming and increased inflow of warm Atlantic water to the Arctic Ocean has also decreased the thickness of Arctic sea ice (Polyakov et al. 2017). Furthermore, the ice-free period is now predicted to last for several weeks longer in autumn before waters re-freeze and sea ice again develops, which reduces the growth period of the sea ice, and thereby a reduced ice thickness (Kwok 2018). Anyhow, sea ice is biologically important for a microbial community that live and thrive in the brine channels or at the bottom of the ice (Deming and Collins 2017). For instance, the photosynthesis of sea ice-associated microalgae is estimated to account for 2–24% of the total carbon produced by primary production in sea ice-covered regions where the range indicates some uncertainty (Arrigo 2017). Critically, this production is the only carbon source as for the Arctic food webs during the ice-covered period (Kohlbach et al. 2016). In addition, a meiofauna community comprising nauplii, rotifers, nematodes, and polychaetes also inhabits the sea ice, but generally confined to its more porous lower sections. Macrofauna, such as larger copepods and amphipods, colonize the skeletal layer on the underside of the ice (Bluhm et al. 2017). Together, these microbial, meio- and macrofauna communities living inside or attached to the sea ice are defined as the sympagic biota (Ehrlich et al. 2020).

## The extreme conditions in sea ice

There are several well-defined extreme environments on earth, as deserts, hydrothermal vents, glaciers, the deep sea, and salt lakes a.o. (Merino et al. 2019). An extreme environment is defined as a habitat characterized by harsh environmental conditions, beyond the optimal range for the development of humans, for example, pH 2 or 11, −20 °C or 113 °C, saturating salt concentrations, high radiation, 200 bars of pressure as examples. Organisms that are able to live in extreme environments are known as extremophiles (Gomez 2015). Sea ice consists of a solid ice matrix with µm-mm wide brine channels where most of the microorganisms are located (Deming and Collins 2017). Brine channel diameters and the permeability in the ice decreases at lower temperatures, which, on the other hand, increases the brine salinity. Sea ice features temperatures as low as −25 °C, salinities as high as 300, high radiation on top of the ice, 24 h of perpetual light during summer, and no to very low light levels at the sea ice bottom during winter and spring (Hancke et al. 2018). This establishes a complex environment where several co-dependent parameters such as temperature and salinity strongly affect living conditions for the organisms in the ice. A significant feature of sea ice is the very strong vertical gradients parameters as for temperature from −10 ℃ at the surface to −2 ℃ at the bottom, brine volumes between 5 and 20%, and brine salinities between 33 and 150 over a distance of just 1.5 m (Fig. 1). Sea ice is accordingly an extreme environment as based on the definition above where groups of microorganisms have developed specific components to survive and thrive in this environment. However, pysical living conditions in the ice can change significantly in both space and time by which

**Fig. 1** A generalized Arctic sea ice depicting gradients of ice temperature, brine salinity, brine volume fraction, light distribution in the ice without snow (blue line) and with a snow cover (red line). (Adopted and modified from Eicken (1992) and Thomas and Dieckmann (2002))



sea ice differs from other extreme environments as deserts and deep oceans where the time-scale of changes is years or decades (Gomez 2015). In sea ice it can be down to hours following a sudden melt of a snow cover (Sorrell et al. 2021) whereby ice temperature decreased and light intensity in the ice increased significantly (Lund-Hansen et al. 2013; 2020a).

Conditions in sea ice are governed by the seasonality of temperature and light, which both vary on separate diurnal and seasonal scales, as from when sea ice is established during autumn freeze-up until the ice finally thaws (Stroeve and Notz 2018). All of the major stressors in sea ice, including temperature, salinity, pressure, light, UV radiation, pH, acidity, alkalinity, nutrients, and $O_2$ concentrations act on the microorganisms either separately or in concert. For instance, a change in temperature from −2 to −4 °C will change brine salinity from 36 to 68, and brine volume from 15 to 7% (Cox and Weeks 1983). This both strongly accentuates the interdependence between stressors, but also that the microorganisms are exposed to several stressors either simultaneously or separately which characterizes them as polyextremophiles (Seckbach et al. 2013; Martin and McMinn 2017). These organisms have evolved a variety of mechanisms, compounds, and solutes allowing them to survive and thrive in sea ice, for example cryoprotectants (Raymond and Knight 2003), osmoregulation (Torstensson et al. 2015), acclimation of pigment composition to high or low light (Galindo et al. 2017), and mycosporine like amino acids in high UV (Lund-Hansen et al. 2020a). The meio- and macrofauna, located at the bottom sections of the ice can be specified as extremophiles, coping with variations in one stressor—salinity, which here can vary between 5 and 60 (Gradinger 2001).

Microorganisms living in the brine channels are adapted to both a cold and saline environment, and the term halopsychrophile has been applied to these organisms, and specifies that organisms are adapted to and have the physiological ability to metabolize and thrive in a cold (psychrophile) or highly saline (halophile) environment (Gomez 2015; Merino et al. 2019). The term halopsychrophile specify the actual stressors, as compared the term polyextremophiles adapted here with no designation of the stressors. For further definitions and discussion we refer to Morita and Moyer (2001). Salinity and temperature are parameters that each define several extreme environments, but operate very differently in sea ice compared to other saline habitats (Chénard and Lauro 2017). The salinity in salt lakes or salt pans or the high temperatures of the water seeping out from hot springs on the ocean floor are relatively constant (Wharton 2002; Gomez 2015), compared to sea ice where significant changes in temperature and salinity can occur within hours. A level sea ice of 1.5 m thickness or less displays very steep gradients in temperature, brine salinity, brine volume, and irradiance (Fig. 1).

## Sea ice brine channels

Although gas and air bubbles can occur in both freshwater ice and in sea ice, presence of brine channels is a significant and important characteristic of sea ice alone (Cox and Weeks 1983). Brine channels are so-called because the salinity of the enclosed liquid can greatly exceed that of the underlying ocean water reaching salinities of 300 or more, in contrast to 32–35 of the seawater (*op. cit.*). Although much of the microalgae biomass is attached to the bottom of the ice, many microorganisms live in the brine channels, where surface areas can be as high as 0.6–4.0 m$^2$ kg$^{-1}$, depending on the ice temperature (Krembs et al. 2000). The volumes of brine channels are based on sea ice temperature, bulk salinity, and ice density Cox and Weeks 1983), and for sea ice temperatures > −2 °C the Leppäranta and Manninen (1988) relations for brine volume and brine salinities are applied. Brine channels may be inter-connected with free liquid flowing in the channels, or they are separated into solitary brine pockets, each with sympagic biota inclusions (Krembs et al. 2000). Different organisms can inhabit brine channels though brine channel diameters on the scale of μm-mm will to a large extent govern the type of organism inhabiting the channels (Krembs et al. 2000; Bluhm et al 2017). Brine channel connectivity is important for microalgae given their need for supply of nutrients from the water below the ice. Seawater with nutrients can enter the ice via the open and connected brine channels, but in case the ice turns colder the brine channels are disconnected and nutrients cannot be replenished. Whether interconnected or disconnected is known as the rule of five (Golden et al. 1998).

### Strong spatial and temporal scales

Examples from a typical land-fast sea ice from Kangerlussuaq, west Greenland (Fig. 2) show low (1–1.5%) air, gas, and brine volumes of 3–10% for a quite cold (20 March) and a warmer (26 March) ice (Fig. 2A). Gas volumes are in both cases quite low (< 2.0%), and only brine channels in the bottom ice (0–15 cm) are interconnected on 20 March, whereas the entire core is interconnected on 26 March (Fig. 2B). This increase in brine channel volume over just 6 days emphasizes that conditions can change quite rapidly. A change from a relatively cold to a warmer period will reduce the temperature of the ice and surpass the 5% brine volume where brine channels will reconnect and the brine, including nutrients, dissolved organic carbon (DOC), and other dissolved compounds, will vacate the ice (Lin et al. 2019). A brine drainage will accordingly affect the photosynthesizing organisms and reduce both photosynthesis and the heterotrophic activity, as lower primary production means less DOC available for heterotrophs. Accordingly, it must be assumed that brine drainage is more prevalent during late spring and summer with increasing air temperatures (Petrich and Eicken 2017). It is, on the other hand, unlikely that the entire microbial community will flow out with the brine, as both bacteria and microalgae can attach themselves to the walls of the brine channels using extracellular polysaccharides (EPS), which are organic rich compounds with cryoprotectant capacities (Collins et al. 2008).

## Stressors

### Temperatures in sea ice

Ice temperature is a profound, fundamental parameter of sea ice, controlling brine volume and brine salinity as outlined above, as well as the enzymatic activity of the brine channel microorganisms (Deming and Collins 2017). Despite the recent increase in Arctic air temperatures (Przybylak and Wyszyński 2019), they remain low in the Arctic and well below freezing point for several months of the year. Air temperature records from the Villum Research Station at 81°N in northernmost Greenland show temperatures above freezing for less than 2.5 months from mid-June to the end of August, with winter temperatures down to −35 °C. The period above freezing in southwest Greenland at a lower latitude of 64°N is about 5 months, from early May until early October. The transport of heat between ice and air, and thereby the cooling and temperature of the ice, is strongly modified by the snow cover with a high insulation capacity as snow grains are loosely packed with high air volumes (Sturm and Massom 2017). For instance, air temperatures ranged between −25 °C and −10 °C during April–May at Villum Research Station but sea ice temperatures below a 90 cm thick snow cover remained constant at −1.8 °C (Hancke et al. 2018).

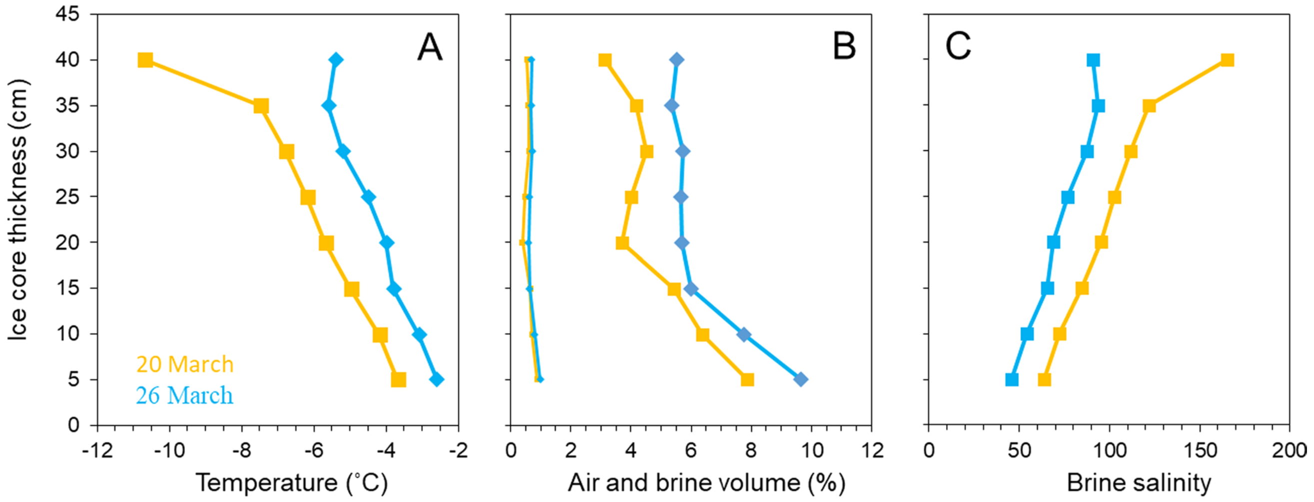


**Fig. 2** Temperature **A**, gas and brine volume **B**, and brine salinity in a sea ice core **C** on 20 and 26 March, Kangerlussuaq, West Greenland. (Modified from Lund-Hansen et al. 2013)

A yearlong time-series of a sea ice temperature profile in a 3.0–3.5 m thick multi-year ice floe, shows a characteristic pattern of strong temperature variations with depth and over time (Fig. 3)

Temperature variations are strongest at the ice surface, which is exposed to air temperatures that can range from −2.0 °C to −25.0 °C during the period of ice cover, whereas bottom temperatures at the ice-water interface remain nearly constant at −1.8 °C. A snow surface layer of about 0.5 m covered the ice from mid-November to about end-July but temperatures are still low in spite of the insulating effects of the snow.

## Salinity in the brine channels

The high saline brine developed during freezing of the ice is ejected into the underlying water column by gravity due to its high density (Cox and Weeks 1983), and by brine expulsion and flushing of the brine channels (Golden et al. 1998). Dissolved salts that remain in the brine channels develop into a highly saline liquid with a brine salinity ($S_b$) = (1-(54.11/T)$^{-1}$ 1000, with *T* as the ice temperature (Cox and Weeks 1983). The ice temperature dependency is illustrated by the brine salinity decrease of 30–35 related to a temperature rise in the ice of 2–3 °C between 20 and 26 March (Fig. 2A). Salinity of the brine was 165 in the upper part of the ice core and decreased gradually to 54 in the bottom section on 20 March.

However, conditions are significantly more extreme during this part of the year compared to late spring and summer conditions with a higher solar declination and higher air temperatures. For contrast, an ice core collected near the North Pole in August shows a vertical uniform temperature (−1.1 °C), and brine salinities between 18.2 and 23.5 (Fig. 5 in Lund-Hansen et al. 2013). Brine volume varies between 0.7% at top and 6.4% at the bottom of the core related to the low (0.4–1.4) bulk salinities (Cox and Weeks 1983) as desalination of the ice has been acting for a longer period in this multi-year ice, *i.e.,* ice which is > 1 year old (Petrich and Eicken 2017).

## Irradiance and UV

The range of wavelengths of electromagnetic radiation that reach the snow and ice surface is broad (310–2500 nm) with the photosynthetically active range between 400 and 700 nm termed PAR (Photosynthetic Active Radiation) (Kirk 1994). There are some distinct differences in annual distributions and intensities of PAR during a year between high and low Arctic (Fig. 4A–C), where high Arctic (81°N) Villum Research Station in North East Greenland resides in darkness from mid-October to early March with midnight sun lasting from early April to late August (Fig. 4A).

At the low Arctic (64°N) Kobbefjord in Greenland, there is in comparison no complete winter darkness but also no midnight sun (Lund-Hansen et al. 2020a, b). Sea ice is an opaque and low transparency medium with brine channels, air bubbles, solid and dissolved substances that scatters and absorbs the light (Perovich 2017). It is therefore a strong attenuator of light leaving less than a few percent of surface light at the bottom of the sea ice. Irradiance decreases exponentially through the ice from about 90% just below the ice surface to > 0.1% at the bottom of the 66 cm thick ice (Fig. 4E). A record low under ice PAR irradiance of 0.02% was measured in North East Greenland (Hancke et al. 2018). The most important parameter controlling under ice

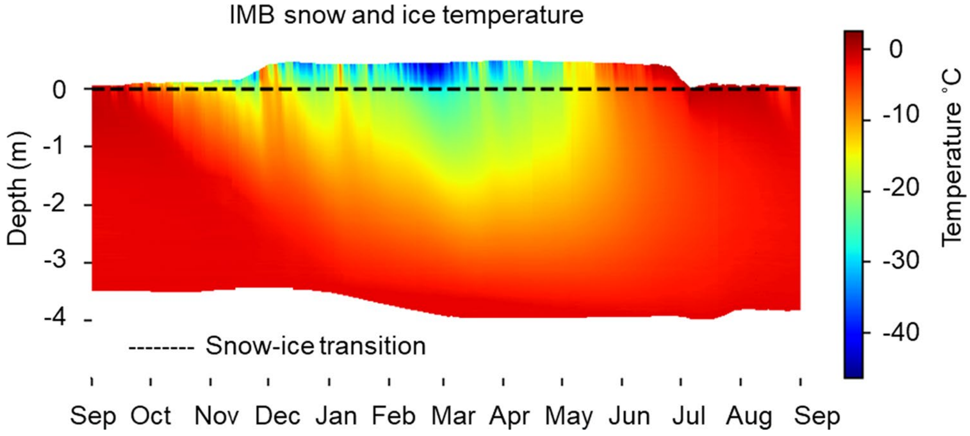


**Fig. 3** A one yearlong record of continuous sea ice temperature in multi-year ice from the Arctic Ocean from beginning September 2012 to September 2013. A thermistor string was positioned in the ice near the North Pole in mid-August 2012 and connected to a data-logger, with GPS, and satellite connection. The ice with instruments drifted southwards from around the North Pole to north of Greenland, where contact was lost in September 2013. Based on data from Gorm Dybkjær, Danish Meteorological Institute, Denmark. IMB is Ice Mass balance Buoy

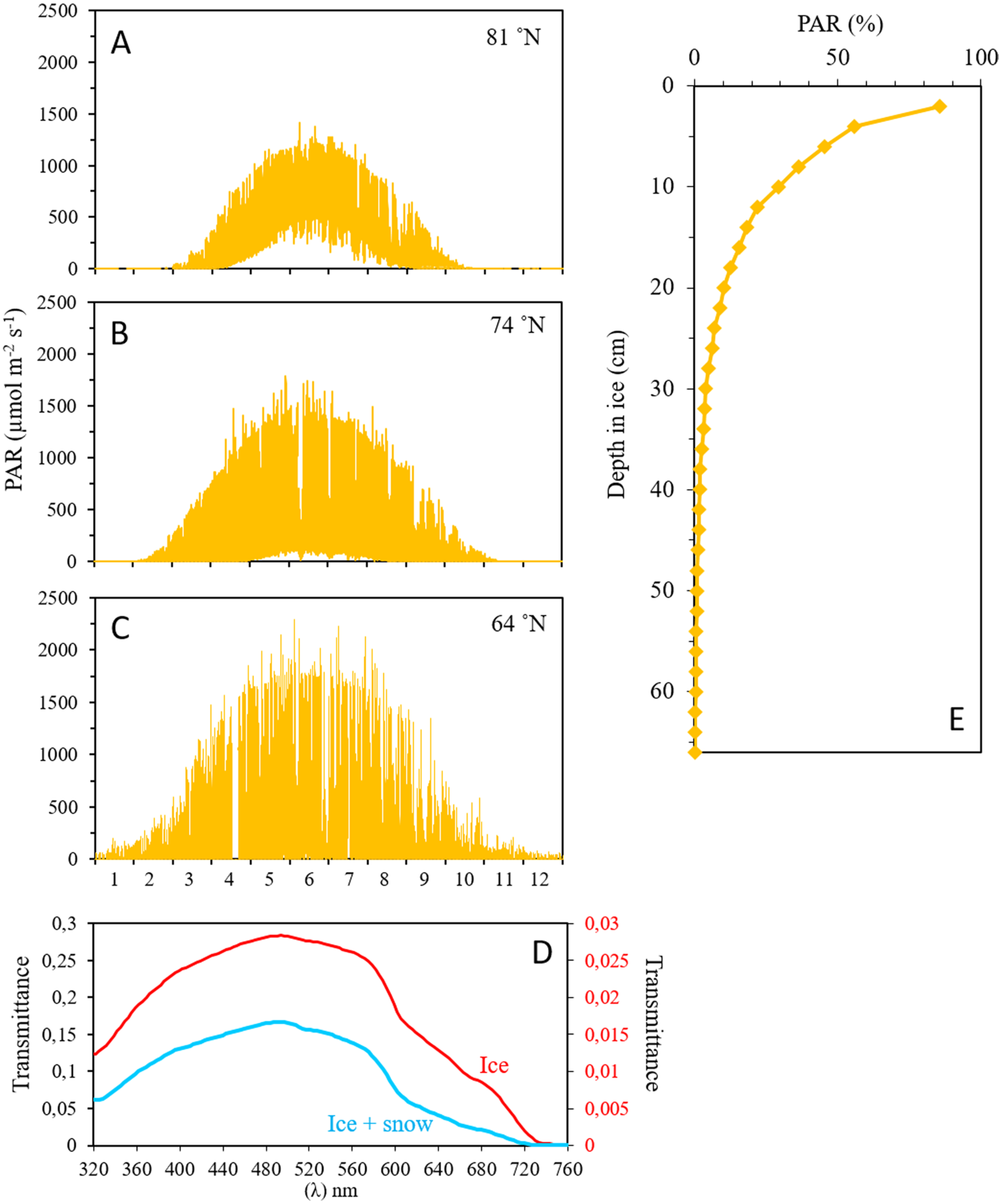


**Fig. 4** Comparison of incident photosynthetic active radiation (PAR) (400–700 nm) at three latitudes in Greenland during 12 months; **A** Villum Research Station (81°N), **B** Zackenberg (74°N), **C** Kobbefjord (64°N). **D** A comparison of spectrally resolved irradiance transmittance under sea ice with and without a snow cover, **E** attenuation of PAR through a 66 cm thick ice core in percent of surface radiation. **A**–**D** adapted from Lund-Hansen et al. (2020a, b) and **E** is based on unpublished data (Lund-Hansen, L.C.)

irradiance is the snow cover, with a high albedo up to 0.9 and a strong attenuation (Perovich et al. 1998, 2017). Transmittance, the ratio between under-ice and surface irradiance, is 0.016 for a 45 cm thick ice with 10 cm of snow and 0.28 with no snow cover at the specific wavelength of 500 nm (Fig. 4D), which gives that transmittance at this wave length was 16.5 times higher. PAR under ice irradiance with no snow was 174.9 µmol photons m$^{-2}$ s$^{-1}$ and decreased to 9.3 µmol photons m$^{-2}$ s$^{-1}$ with snow on the ice (Fig. 4D). There is a relatively strong attenuation in the red and near-infrared parts of the spectrum with a snow cover, whereas UV-A (400–320 nm) is readily transmitted through both the

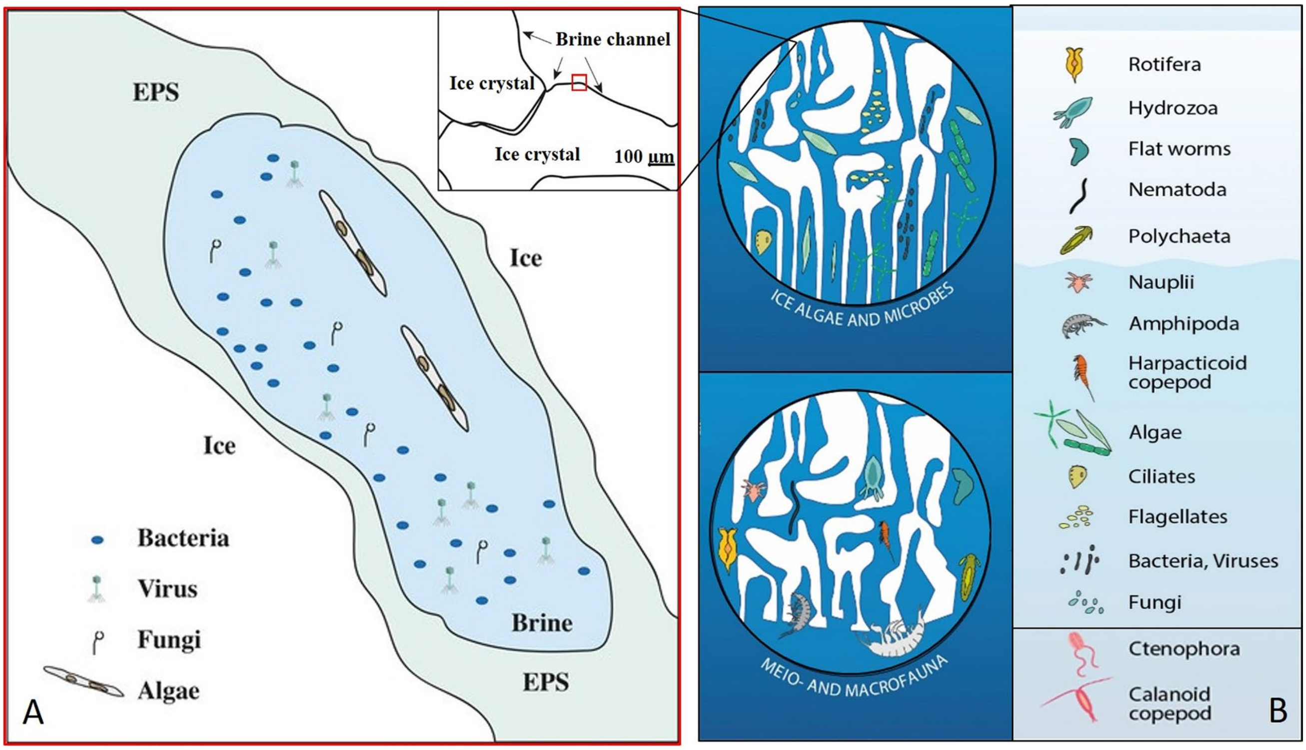


**Fig. 5** A brine channel lined with cryoprotective EPS between three ice crystals (insert) and two diatom cells with chloroplasts, bacteria, virus, and fungi **A**. Modified from Deming and Collins (2017). The sympagic biota and their location in the sea ice, where smaller organisms such as microalgae, bacteria, virus, and fungi dominate in areas of small and narrow channels in the upper section of the ice, compared to lower and bottom section inhabited by larger organisms **B**. Adapted with permission from https:/caff.is/

snow and ice as is UV-B (320–280 nm) with no clear comparable effects of the snow (Fig. 4D). Transmittance is not constant and can change within hours. For instance, a snowfall of 5 cm thickness on bare ice reduced transmittance from about 0.14 to 0.02 in parallel with the increase in albedo from 0.5 to 0.9 (Lund-Hansen et al. 2020a). The preceding gradual increase in transmittance was related to increasing air temperatures and snowmelt, concomitant with the albedo decrease. This emphasizes the dynamics and the short timescale of significant changes of irradiance conditions inside and at the bottom of the sea ice. The light environment in sea ice is also of importance for many non-photosynthetic sympagic organisms like phototrophic bacteria (Koh et al. 2011), mixotrophic ciliates (Olsen et al. 2019; Søgaard et al. 2021), but especially for the phototrophic microalgae as the first trophic level in the polar food chains (Kohlbach et al. 2016).

## Nutrients

Nutrients in sea ice come primarily from seawater, but also from flooding of the ice by seawater in Antarctica (Nomura et al. 2018) as well as from the atmosphere as shown for the Baltic Sea (Granskog et al. 2003). The supply of nutrients toward the ice is controlled by stratification and vertical advection, and reflects whether the water masses are nutrient-rich or nutrient-poor. This provides nutrients directly to the cells of the skeletal layer. Further up the ice column, they are concentrated into the brine by ice formation. Physical processes such as brine advection can control their availability, but biological assimilation and decomposition are the strongest drivers of their concentrations (Meiners and Michel 2017; Clark et al. 2020). Specifically, nitrogen along with silicate, as for diatoms to grow their silicate frustules (Ellegaard et al. 2016), are both essential in limiting algal growth. A recent study has demonstrated that a bloom of Dinoflagellates inside the sea ice was controlled and limited by nitrate (Lund-Hansen et al. 2024). However, all stressors are not equally important in this respect as especially light availability is a more profound parameter for photosynthesis (Kirk 1994). Nutrients can be considered as an extreme stress factor in sea ice, given that there is only a limited availability in the relatively small brine volume, and that the concentrations in under-ice water can be reduced by stratification and ice thaw (Ardyna et al. 2020; Søgaard et al. 2021). Nutrient concentrations in the sea ice brine channels are dynamic entities given by both a production from bacterial breakdown of organic matter and uptake by photosynthetic organisms, and whether production or uptake is given by a nutrient concentration relative to a dilution line (Søgaard et al. 2013).

### Dissolved oxygen, inorganic carbon, and pH

During the growth season, photosynthetic activity can raise the $O_2$ concentration of the brine to supersaturated values $> 30$ mg $O_2$ $L^{-1}$ (Gleitz and Thomas 1993). The limited volume of liquid brine in sea ice also allows large fluctuations in dissolved oxygen concentrations due to photosynthetic metabolism (McMinn et al. 2005). The low solubility of oxygen in water means that even a low rate of photosynthetic or respiratory activity can raise or lower the oxygen concentration several orders of magnitude. The concentration of oxygen in seawater with a salinity of 35, in equilibrium with the atmosphere, is *ca.* 320 µmol $O_2$ $L^{-1}$ at 4.0 °C (Breitburg et al. 2018). Mixing by winds and currents in open oceans ensure that surface waters are well mixed with the atmosphere whereby this concentration in water is largely constant. Oxygen conditions in sea ice are, however, quite different with considerable spatial and temporal variations (Rysgaard et al. 2007). Oxygen solubility decreases with increasing temperature and salinity, leading to periods of degassing and gas bubble nucleation (Tison et al. 2017). Subsequently, photosynthetic activity during the long diurnal periods of the polar growth season can elevate the concentration well above that which would develop by physical processes alone (*op. cit.*) Based on comparisons of $O_2$, $N_{2,}$ and argon (tracer gas) in brines, it was shown that the oxygen concentration in brines can be as high as 150–200% saturation relative to concentrations expected by physical processes alone (Papadimitriou et al. 2012). Even higher concentrations, up to partial pressures of 4.2 times higher than atmospheric equilibrium, have been recorded (McMinn et al. 2005).

While super-saturation is common during the growth season of active photosynthesis, autumn sea ice also undergoes brine drainage and thawing, which can result in degassing and oxygen depletion in the sea ice (Rysgaard and Glud 2004). These data show sea ice $O_2$ concentrations becoming under-saturated with $O_2$ later in the growth season, and development of full anoxia (*op. cit.*)

The concentrations of inorganic carbon species ($CO_2$, $HCO_3^-$, $CO_3^{2-}$) in sea ice are controlled by a complex of physical and biological processes (Tison et al. 2017). The relevant physical factors are ice temperature and permeability to gases, as the freezing and thawing processes drive dissolved gases in and out of the ice (Van der Linden et al. 2020). In addition to physical processes, photosynthetic and respiratory activity then deplete or enhance inorganic carbon concentrations, respectively. A consequence of the processes is a C-shaped pH profile in sea ice in which there is greatest inorganic carbon depletion in the brine channels near the ice interfaces (both top and bottom), with less or limited C availability for organisms here (Hare et al. 2013). The activity of photosynthetic autotrophs, which deplete the inorganic carbon and raise the pH due to their photosynthetic carbon assimilation, strongly affects conditions in the brine channels (Søgaard et al. 2011). The limited volume of sea ice brine can be rapidly depleted by prolonged photosynthetic activity in summer months (Søgaard et al. 2019). Another consequence of photosynthetic activity is an increase in pH. $CO_2$ assimilation itself raises pH somewhat, as removal of $CO_2$ from water drives the inorganic C equilibrium toward $HCO_3^-$ and $CO_3^{2-}$. Bicarbonate usage raises pH even more, as $HCO_3^-$ assimilation involves excretion of $OH^-$ ions from cells in order to maintain charge balance. $OH^-$ is a strong base, and very high pH values (pH 9–10) commonly occur where there are high concentrations of aquatic photoautotrophs (Brodersen et al. 2019) as also in sea ice.

## The sympagic biota

Sympagic refers to ice-associated organisms living attached to the bottom of the sea ice or inside the brine channels. The sympagic biota comprises a variety of taxa from different phyla, including microalgae, bacteria, archaea, viruses, fungi, and protozoa, all of which are microorganisms, and larger organisms such as macroinvertebrate grazers inhabit and forage at the bottom of the ice (Bluhm et al. 2017; Caron et al. 2017; Deming and Collins 2017) depicted in Fig. 5. Grazers consume autotrophic ice algae, bacteria, and fungi that break down organic matter, and viruses infect the bacteria forming a food web with a microbial loop inside the brine channels (Koh et al. 2012a, b) though details are still being debated (Bowman 2015).

The brine channels inhabited by the sympagic biota are comparatively small in diameter, with 50% of channels $< 41$ µm at −2.9 °C, increasing to 60% at −6.8 °C, and 78% and 82% for brine channel diameters $< 100$ µm at the same temperature (Krembs et al. 2000). This limits the size of the organisms that can actually live in the brine channels. The larger meiofauna is then confined to the bottom section of the ice where the brine volume is high and brine channels are interconnected (Bluhm et al. 2017). The vertical distribution of species with increasing organism sizes toward the bottom of sea ice is related to the parallel increase in brine channel size, in as much as organisms can adapt or develop mechanisms to cope with the very high salinities and the significant lower temperatures in the upper section of the sea ice (Fig. 1). Temperatures are higher and more constant near the ice-water interface, though salinity variations are more significant during brine drainage and melt of the sea ice, when high saline water is expelled from the ice and bottom-dwelling organisms have adapted osmoregulatory competences to endure the changes in salinity (Gradinger 2001; Kiko et al. 2009). Most of the microorganisms in the sea ice are not evenly distributed in the ice column as bacteria, which can show clear layering (Gosink et al. 1993). Specific intrusion layers, often prevalent in Antarctic pack ice (Leeuwe et al. 2022), show also clear layering of the biota in the ice column.

## How did microorganisms get there?

With an extended amount of microorganism in sea ice the question is how they got there and which has been a research focus since the early 1980s (Ackley and Sullivan 1994; Spindler 1994; Gradinger and Ikävalko 1998). Particle scavenging is considered the main process for accumulating particles in growing sea ice (Garrison et al. 1983; Reimnitz et al. 1993). During the first stages of ice formation, individual frazil ice crystals are suspended in the water column, mixed to several meters' depth by advection and turbulence (Różańska et al. 2008). While suspended, they come into contact with other suspended particles in the water column. The particles with sticky surfaces as several microalgae and bacteria attach to the frazil ice crystals and rise with the crystals to the surface of the ocean, where further freezing occurs (Riedel et al. 2007). This initial process leads to a considerable concentration of microalgae in the ice. During late fall to early spring, phytoplankton concentrations in the oceans are typically relatively low, but abundances of, *e.g.,* bacteria (Riedel et al. 2007), virus (Maranger et al. 1994), and microalgae (Arrigo et al. 2014a, b) within the ice can exceed those in the water column by orders of magnitude. The highest enrichment factors have been observed for diatoms, which are well known to have sticky cell surfaces due to their coating of extracellular polymeric substances (Santschi et al. 2020). Bacterial enrichment can be attributed to their own stickiness and also through their attachment to microalgae.

The enrichment is well documented both experimentally (Garrison et al. 1983) and in several field studies (Ikävalko and Gradinger 1997; Różańska et al. 2008). Once incorporated, the unique sea ice properties will lead to selection processes reshaping the initial plankton community driven patterns. In Antarctica, for example, sea ice bacterial production increases over short time scales in the newly formed ice with fast growth rates of up to 0.6 $d^{-1}$ exceeding microalgal growth (Grossmann 1994; Grossmann and Dieckmann 1994). For viruses, information so far is limited, but initial work by Maranger et al. (1994) also indicates efficient enrichment.

When frazil ice crystals have consolidated at the surface and nilas or pancake ice have formed, wave field pumping may additionally contribute to organism incorporation (Spindler 1994). Here wave fields pump water into and out of the ice brine channel system in nilas/pancake and young ice where particles and organisms within the pumped water can remain within the ice. However, this process appears to be less effective compared to suspension freezing, likely because the total interactions between ice surface and water is less than with floating frazil ice crystals in the water column. For example, Weissenberger and Grossmann (1998) detected Chlorophyll *a* (Chl *a*) enrichments of up to 54 for suspension freezing, but only 8 for a propagating wave field experimental approach. Together, suspension freezing and wave pumping are the two major processes in the initial stages of ice formation. Once established, active organism migration into the ice becomes relevant, specifically for larger metazoan (Kiko et al. 2008). In shallow waters, larvae and juveniles of benthic biota can seasonally inhabit the ice, likely actively swimming into the ice matrix present and feeding on the rich spring ice biota (McConnell et al. 2012). Settlement by microalgae at the sea ice bottom can also occur and be promoted by the development of a skeletal layer at ice-water interface (Lund-Hansen et al. 2016). Pelagic biota can also seasonally migrate into the ice-water boundary to feed on ice algae. The Arctic copepod *Calanus glacialis* females use the lipid-rich ice algal food to fuel their maturation and reproduction (Søreide et al. 2010) while Antarctic sea ice is an important overwintering habitat for larval and juvenile Antarctic krill (Veytia et al. 2021; Fraser et al. 2023). In areas with older ice floes, *i.e.*, second-year or multi-year ice, these older ice floes might act as seed banks to populate younger ice stages with typical ice biota (Olsen et al. 2017) and potentially also for ice-endemic taxa like Arctic under-ice amphipods.

## The autotrophs

Sea ice is home to a wide range of photoautotrophic eukaryotes (Arrigo 2017). Although their activity naturally follows seasonal irradiance cycles, their presence and abundance is also controlled by the freeze–thaw cycles, temperature and salinity regimes in the brine channels, carbon, and nutrient availability (Leeuwe et al. 2018). They exist as spores in the under-ice water and ice during the winter darkness, and begin colonizing and growing on the underside of the ice at polar first light, even at extreme low irradiances $< 0.17$ µmol photons $m^{-2}$ $s^{-1}$ (Hancke et al. 2018). This extreme shade adaptation allows them to bloom earlier in the season than phytoplankton, making important contributions to food webs when no other autotrophic production occurs being the only carbon source in late winter/early spring (Kohlbach et al. 2017). The annual production cycle of ice algae relative to respiratory activity of non-autotrophic organisms determines whether sea ice is net autotrophic or net heterotrophic, and the amount of organic carbon the sea ice ecosystem delivers into the pelagic food web (Arrigo et al. 2014a).

## Phylogenetic diversity and distributions

The most common taxonomic groups are flagellates, dinoflagellates, and diatoms, with cryptophytes, euglenophytes, and ciliates regularly present (Engberg et al. 2018). They are the sole organisms in the sea ice that utilizes the light for photosynthesis, compared to the other heterotrophic groups (Raven 1991). Cyanobacteria are apparently absent from sea ice, despite being ubiquitous in other polar marine and ice habitats (Koh et al. 2012a). The most dominant taxa are pennate diatoms (Arrigo 2017), which appear to have the shade adaptation characteristics most suitable for the low-light environment of the skeletal layer at the ice-water interface. Their motility, allowing them to move vertically in brine channels, may also be an important survival attribute, helping them avoid the most extreme conditions (Aumack et al. 2014). Centric diatoms, as another group of diatoms are in comparison much less motile (Leeuwe et al. 2018). Most ice algal biomass is usually concentrated in the skeletal layer at the bottom of the ice, where conditions are relatively benign (Meiners and Michel 2017) at temperatures close to the freezing point of −1.8 °C and larger brine volumes (Fig. 1). Higher in the ice, microalgae biomass is reduced as brine channel volume restricts available habitat and algae are subject to increasingly high salinity, lower temperatures, and reduced carbon availability. Often only traces ($<0.001$ mg Chl *a* $m^{-2}$) (Hancke et al. 2018) of ice algae are found in the upper sections of the ice, though some observations from Nuup Kangerlua, Greenland, have shown nearly uniform biomass distributions with depth in the ice core (Lund-Hansen et al. 2021). There is a specific development in the species compositions at the bottom ice starting with very small flagellates that are gradually replaced by larger-celled taxa, culminating in the diatom-dominated communities characteristic of most sea ice (Leu et al. 2015). This progression of the diatom-dominated community of the skeletal layer follows the increasing seasonal irradiance, with larger cells with higher light demands increasingly prevalent over time (Kauko et al. 2018).

## Light as stressor—strategies and adaptations

Sea ice algae are strongly shade-adapted due to the extensive light attenuation through the snow and ice cover, with photosynthetic light responses that saturate at a fraction of full sunlight (Falkowski and Raven 2007). In periods of stable weather with relatively constant snow and ice cover and a predictable light climate, the daily excess illumination is managed by non-photosynthetic quenching (NPQ) processes as the diadinoxanthin-diatinoxanthin cycle (Kvernik et al. 2021). Diadinoxanthin and diatinoxanthin are specific pigments, also called sunscreen pigments, which the ice algae develop for protection of the cells in periods of high light. Mycosporine-like amino acids (MMA's) is another compound developed by the algae for light protection and specifically for UV protection (Piiparinen et al. 2015). We refer to Lund-Hansen et al. (2020a) for a detailed time-series study of changes in photosynthetic parameters, ice algae biomass, pigment composition, and MMA's at increased irradiances.

Extreme light environments are caused by excursions beyond these predictable limits, where cells experience photon fluxes beyond that to which NPQ is acclimated. Extreme conditions can prevail in the form of variable photon fluxes that can rapidly overwhelm the chloroplast's light harvesting capacity, especially when irradiance suddenly increases after a snow loss event (Lund-Hansen et al. 2013; Sorrell et al. 2021). These features of sea ice suggest photoinhibition and protein damage in algal photosystems, even at intermediate $O_2$ concentrations, although the degree of damage could be ameliorated by periods of normal $O_2$ (McMinn et al. 2005). The fact that sea ice algae are exposed to prolonged irradiance during summer with no nocturnal alleviation of the hyperoxia is suggestive of their being subject to especially deleterious interactions of high irradiance and high $O_2$ (Kvernik et al. 2021), in contrast to more temperate phototrophs that can recover at night (Oliver et al. 2003). This phenomenon emphasizes how sea ice is a much more extreme environment for photoautotrophs than seawater, as even Arctic phytoplankton are available to avoid high $O_2$ during photosynthesis as they are periodically mixed to deeper water and low irradiance throughout the photic season (Kvernik et al. 2021).

## Salinity

There are no extreme hypersaline or hyposaline conditions at the ice-water interface during most of the ice-covered season (Notz and Worster 2009), though studies show that higher than seawater salinities in the brine channels strongly inhibit photosynthesis (Zhang et al. 1999; Søgaard et al. 2011). The photosynthetic stress experienced by microalgae subject to hypo- or hypersaline conditions is characterized by parameters as $\mathrm{rETR}_{\mathrm{max}}$ and $F_v/F_m$, which are derived by Pulse Amplitude-Modulated fluorometry (Ralph and Gademann 2005). The $F_v/F_m$ is maximum fluorescence yield of Photosystem II, and an indicator of "how good are they at doing photosynthesis" (Hawes et al. 2012), with $\mathrm{rETR}_{\mathrm{max}}$ as the maximum relative electron transfer rate in photosynthetic chain. $F_v/F_m$ is particularly sensitive to salinity stress (Fig. 6), which demonstrates that the ice algae have a photosynthetic optimum in salinity between 30 and 65 from where it decreases at higher brine salinities.

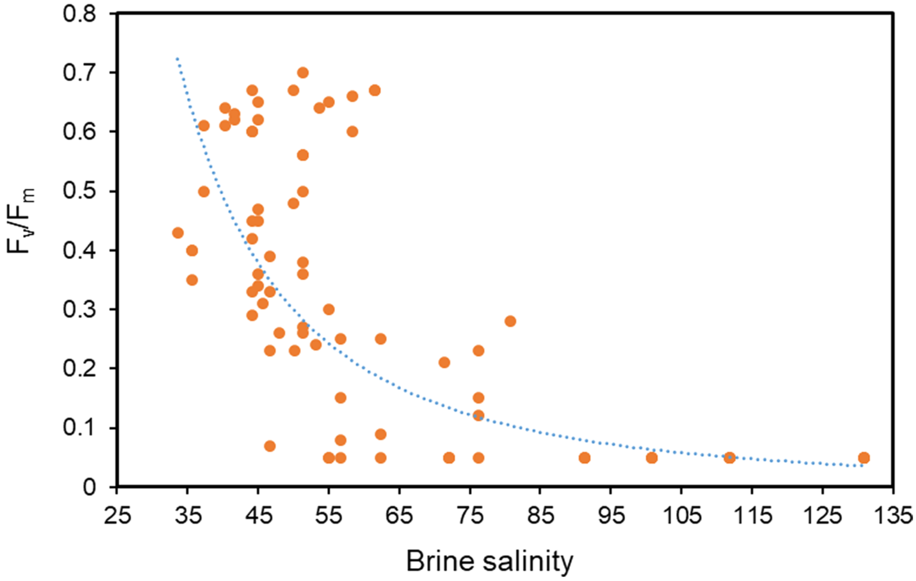


**Fig. 6** Relationship between ice algal $F_v/F_m$, the maximum dark-adapted yield of photosynthesis, and brine channel salinity in land fast first-year ice from Nuup Kangerlua Fjord, Greenland. Compilation of data from four seasons from 2017 to 2020. Power function regression: $y = 1759.5\ x^{-2.21}$ ($p < 0.001$). Modified from Sorrell et al. (2024)

Ralph et al. (2007) documented a significant decrease in $rETR_{max}$ over several hours of exposure to high (51 and 64) salinities in a mixed sample of the pennate diatoms *Nitzschia stellata* and *Fragillariopsis curta*. This study emphasizes that photosynthesis in these species has a narrow window of optimum salinities around 30–35. A study of salinity tolerances of the diatom *Fragilariaopsis nana* and the green algae *Chlamydomonas sp.* showed similarly an optimum growth rate, based on the increase in cell numbers day$^{-1}$ at a salinity of 33, and negative growth rates at a salinity of 150 (Søgaard et al. 2011). Growth rates were here significantly lower in *Chlamydomonas* at higher salinities compared to *F. nana*. Photosynthetic performance given by rETRmax and $F_v/F_m$ decreased significantly with reduced salinities for the diatoms *Fragilariopsis curta* and *Entomoneis kjellmanii* (Ryan et al. 2004). A comparable study encompassing growth rates of seven species of the pennate diatom *Nitzschia* sp. samples from the bottom of an ice floe in the Greenland Sea also showed decreasing and lower growth rates at higher salinities (~90) (Zhang et al.1999). Different ice algae respond differently to ionic and osmotic stress, and some species such as *Entomoneis kjellmanii* can maintain photosynthetic activities over a wide range of salinities (Ralph et al. 2007). On the other hand, a study from Antarctica showed that some chrysophytes and dinoflagellates were capable of active photosynthesis in the upper section of the ice core even at a salinity of 129 (Stoecker et al. 1997). Hence, these other phototrophs are able to cope with these very high salinities by release or production of solutes where glycine betaine was shown to be important in osmoprotection of Antarctic diatoms (Torstensson et al. 2019), and similar for other diatom associated compounds as proline and homarine (Boroujerdi et al. 2012; Dawson et al. 2020).

## Temperature

Most autotrophic organisms have temperature optima for photosynthesis and growth that are close to mean temperatures experienced during their growth season (Dusenge et al. 2018) which is around −1.8 °C in the skeletal layer (Lund-Hansen et al 2013). Ralph et al. (2005) studied temperature effects on photosynthetic performance of incubated diatoms from the Antarctic surface pack ice at three temperatures (−1.8, −5.0, and −10.0 °C) and a range of growth irradiances (0–375 µmol photons $m^{-2}\ s^{-1}$). Photosynthetic performance given by $rETR_{max,}$ was lowest at −10.0 °C and highest at −1.8 °C, and also increased at higher growth irradiances (up to 175 µmol photons $m^{-2}\ s^{-1}$). However, even at −10.0 °C $rETR_{max}$ did not reach zero and a low photosynthetic rate was maintained. Laboratory experiments with the chlorophyte *Chlamydomonas* from Chukchi sea ice showed positive growth rates down to −5 °C, but maximum rates at + 5 °C (Eddie et al. 2008). Teoh et al. (2004) also found maximum rates at 5–10 °C in laboratory studies with *Chlamdymonas*, an extensively used model organism (Harris 2001). Sea ice algae nutrient uptake rates reached a maximum at temperatures of 0.5–2.0 °C for $NO_3^-$ and 2.0–3.0 °C $NH_4^+$, which were quite similar to the temperature range (2.5–3.0 °C) of maximum photosynthesis (Priscu et al. 1998). Ice algae can upregulate galactolipids, which can increase the tolerance to high salinities (Wang et al. 2014; Young and Schmidt 2020), as well as downregulate the compound at lower temperatures as to increase cell membrane fluidity.

## Nutrients

Light is the main factor limiting ice algal productivity for much of the growth season but nutrients become limiting in mid-summer when long days provide adequate light, and continued growth can deplete brine nutrients (Petrou et al. 2010). Nitrate most often becomes limiting and which falls to low concentrations, close to exhaustion in brine channels with Redfield ratios indicating strong N-limitation (Duprat et al. 2020). The degree of nutrient limitation often increases with increasing distance from the ice-water interface (McMinn et al. 1999). However, even the skeletal layer can become nitrate limited when vertical advection cannot deliver sufficient nitrate to sustain large biomass as in platelet ice (Robinson et al. 1997). Nitrate limitation is a feature of ice algae in both the Arctic (Gosselin et al. 1990; Smith and Clement 1990) and Antarctic (McMinn et al. 1999). Given the importance of diatoms in the ice algal community, silicic acid has also been found to be limiting (Gosselin et al. 1990; Robinson et al. 1997). The general iron depletion of the Southern Ocean (Bazzani et al. 2023) has also been shown to limit sea ice algae photosynthesis in Antarctic sea ice (Yoshida et al. 2021).

## Inorganic carbon $CO_2$

Sea ice algae photosynthesis is also based on the enzyme Rubisco (Sage et al. 2008). Rubisco is inefficient in modern organisms because it reacts with both $CO_2$ and $O_2$, and the reaction with $O_2$ (photorespiration) competes with C assimilation by the $CO_2$ reaction (photosynthesis), limiting the amount of C that can be fixed (McMinn et al. 2005). The degree of photorespiratory loss depends on the ratio of $CO_2$:$O_2$ present and temperature, *i.e.,* the oxygenation reaction has a higher $Q_{10}$ than carboxylation, so photorespiration increases with raised temperatures (Launay et al. 2020). The low temperature of sea ice will provide a carboxylation-friendly environment whereas the prolonged daylight and limited water volume in sea ice likely result in a very low $CO_2$:$O_2$ ratio, as the season progresses (Raven et al. 2014). This will enhance photorespiration at the expense of photosynthesis, depending on the contribution of carbon-concentrating mechanisms (*op.cit.*). Sea ice microalgae have carbon-concentrating mechanisms (CCMs) to avoid photorespiration (Goldman et al. 1982; Reinfelder 2011), and the CCMs are active in processes that enhance photosynthesis over photorespiration by concentrating $CO_2$ around Rubisco against prevailing $CO_2$ concentration gradients.

The CCM involves bicarbonate usage in eukaryotic algae, in which bicarbonate ions are actively pumped into the cell where they are converted to $CO_2$ by the enzyme carbonic anhydrase, concentrating $CO_2$ around Rubisco in the chloroplast (Falkowski and Raven 2007). Although CCMs are energetically unfavorable in C assimilation, compared to direct $CO_2$ fixation, which requires no energy, they are beneficial by enhancing the pool of inorganic C that can be assimilated. Common sea ice taxa such as *Nitzschia frigida* (Mitchell and Beardall 1996) and *Phaeocystis antarctica* (Tortell et al. 2012) show a high capacity for $HCO_3^-$ usage and exudation of extracellular carbonic anhydrase, both of which afford effective C-concentration. These mechanisms are widely documented in the diatom species that dominate sea ice biota (McMinn et al. 2014), whereas photosynthesis regarding protists, dinoflagellates, and chlorophytes which are much smaller but important for sea ice biodiversity (Hegseth and Quillfeldt 2022), is poorly understood and needs further attention.

The large ice algal biomasses commonly seen colonizing the underside skeletal layer of sea ice are less likely to experience C limitation than those occurring in the brine channels, as they have access to seawater. CCMs are still important here, as seawater itself has a pH of 8.2, at which the dissolved inorganic carbon occurs primarily in the form of $HCO_3^-$ rather than $CO_2$ (Beardall and Raven 2020), but bottom ice diatom communities are unlikely to be C-limited during the growth season. However, they may become C-limited later during the ice melting phases, when expulsion of C-depleted brine and thawing of ice can dilute the under-ice water and reduce the availability of both inorganic carbon and nutrients (Lavoie et al. 2005; Van der Linden et al. 2020).

The high $O_2$ concentrations in sea ice brine can enhance photorespiration in autotrophs, although this is not usually a major problem for taxa with carbon-concentrating mechanisms (*e.g.*, bicarbonate usage), including most diatoms and chlorophytes (Beardall and Raven 2020). What are the implications of such high $O_2$ concentrations for sea ice biota? For photosynthetic organisms, extreme high oxygen concentrations are detrimental for photosynthesis. In taxa that fix $CO_2$ solely by C3 photosynthesis using Rubisco, such concentrations would lead to high rates of photorespiration at the expense of photosynthesis, especially if there is inorganic carbon depletion (Kazbar et al. 2019). As the ratio of oxygenase:carboxylation activity in Rubisco is temperature-dependent, this would not normally be a problem at sea ice temperatures in a non-carbon limited system. However, the extreme drawdown of $CO_2$ in sea ice by photosynthesis coupled with the super-saturation of $O_2$ (Meiners et al. 2009) is definitely favorable to photorespiration, even at low polar temperatures.

Photorespiration may be an avoidable problem for many taxa due to CCMs, whereas toxic effects of high $O_2$ concentrations are less easily managed. High $O_2$ can also generate reactive oxygen compounds, which can exacerbate the effects of photoinhibition (Kazbar et al. 2019) and a more probable stress experienced by ice algae in the brine. The generation of reactive oxygen compounds as superoxide ($O_2^-$), hydrogen peroxide ($H_2O_2$), singlet oxygen ($^1O_2$), and hydroxyl ($^\bullet OH$) radicals (Foyer et al. 1994) is well-documented in photosynthetic organisms under hyperoxia (Raven 1991; Raven et al. 1994). These are highly damaging compounds that destroy cell membranes, photosynthetic proteins and DNA, and increase susceptibility to excess irradiance and UV radiation (Raven 1991). High $O_2$ reduced growth rates, maximum quantum yield, relative maximum electron transport rate, and photosynthetic efficiency as shown for a wide range of Antarctic and Arctic sea ice algae as *Fragilariopsis cylindrus*, *Pseudonitzschia* sp., *Fragilariopsis curta*, *Porosira glacialis*, *Entomoneis kjellmannii* and *Nitzschia frigida* (McMinn et al. 2005).

### Dissolved oxygen $O_2$ and pH

Low $O_2$ concentrations in the brine channels are also an issue for sea ice algae, and depends on minimum $O_2$ concentrations to being a stress factor (Falkowski and Raven 2007). The enzyme cytochrome oxidase, used in cellular respiratory $O_2$ consumption, has a very high affinity for $O_2$, and will therefore not become inhibited unless concentrations are anoxic or close to it (Nikkanen et al. 2021). Large biomasses of algae could nevertheless suffer $O_2$ deprivation at higher ambient concentrations, as their respiratory demand may cause localized cellular anoxia, as seen nocturnally in many biofilms (Hancke et al. 2014). Oxygen depletion in sea ice is also likely to be a problem to the heterotrophic community, as many microfauna are susceptible to $O_2$ deprivation (Dıaz and Rosenberg 1995). Due to their ability to use $HCO_3^-$ in photosynthesis, low dissolved $CO_2$ concentrations are not usually a major stress factor in themselves for microalgae. High pH is more stressful for brine algae, with pH values $> 8.5$ reducing photosynthetic activity of *Fragilariopsis* spp., whereas chlorophytes such as *Chlamydomonas* are more tolerant of high pH (Søgaard et al. 2011). This is consistent with the diatom dominance of the skeletal layer community where high pH and high $O_2$ concentrations are less common, compared to the chlorophyte-flagellate dominance of the brine with its more extreme conditions.

Sea ice algae can tolerate pH ranges of 7–9 without significant decreases in production (McMinn 2017). High pH values impair metabolic processes due to disruption of cell transport processes (Goldman et al. 1982; Boatman et al. 2018). The damage to cell metabolism caused by high pH is as likely to be experienced by the sea ice bacteria as well as the ice algae (Lizotte 2003). Decreases in pH, as occur during melting of sea ice, can also be a stress factor due to increases in concentration of $H^+$ ions (Castrisios et al. 2018). Optimum ice algal growth is generally found at *ca.* pH 8.0, with pH $< 7.2$ leading to ca. 50% less growth due to increasing concentrations of $H^+$ (McMinn et al. 2014). The internal minima in pH described above for the C-shaped pH profiles (Hare et al. 2013) are in this range. The on-going acidification of the oceans (Doney et al. 2009) is likely to lower pH further and exacerbate this stress (McMinn et al. 2014).

## The bacteria

Evidence that bacteria actively grow on and within sea ice dates back to the 1970s (Kaneko et al 1978). Diverse bacterial communities that exhibit similar patterns of biomass, production, and growth rates to that of sea ice algae (Søgaard et al. 2010; Deming and Collins 2017) have now been described from both Polar Regions. However, the number of sequenced isolates remains constrained and connecting bacterial community structure with biogeochemical function remains a significant challenge (Bowman 2015). While the bacterial fraction of the sea ice microbial community is thought to play a key role in secondary production mediated via a microbial loop (Sullivan and Palmisano 1984) this dynamic remains equivocal because of the inherent spatiotemporal variability of the sea ice matrix (Stewart and Fritsen 2004; Martin et al. 2012; Piontek et al. 2020) as described above. Trophic interactions are further complicated by the fact that ice-associated bacteria and algae are likely to interact both synergistically and antagonistically in response to nutrient availability and the steep physicochemical gradients that define the habitat (Thomas and Dieckmann 2002). Equally ambiguous is the notion that bacterial respiration maintains a balance of oxygen concentration within the ice microenvironment and that bacteria are involved in ice nucleation during the initial stages of sea ice formation (Sullivan 1985).

### Phylogenic diversity and distributions

Molecular-based surveys of the 16S rRNA taxonomic marker gene in sea ice bacteria have historically revealed psychrophilic and halotolerant members of the Proteobacteria, Bacteroidetes (previously known as the Cytophaga-Flavobacteria-Bacteroides (CFB) cluster) and Gram-positive bacteria (*e.g.,* Brinkmeyer et al. 2003; Martin et al. 2011; Deming and Collins 2017). In 2015, a much-needed meta-analysis of the available data from both poles (20 studies, comprising both Sanger and deep sequencing studies) provided an important consensus regarding these earlier findings (Bowman 2015). Ice-associated bacteria comprise 13 major taxonomic divisions primarily dominated by members of the Gammaproteobacteria and Bacteriodetes and secondarily by the Alphaproteobacteria and members of the phyla Actinobacteria and Verrucomicrobia. However, given the general paucity of data, there remains a significant disconnect in linking phylogenetic diversity with community respiration rates and biogeochemical function. Importantly, the rate of in situ bacterial heterotrophic activity can exceed algal-derived oxygen production, which infers that bacterial metabolism is not restricted to $O_2$ as an electron acceptor (Bowman 2015; Eronen-Rasimus et al. 2017). Additional pathways of potential ecological interest have only recently been inferred from sea ice 16S rRNA gene libraries (Bowman and Ducklow 2015). In addition to aerobic anoxygenic photosynthesis (Koh et al. 2011) and rhodopsin-driven metabolism (Burr et al. 2017), sea ice bacteria may well exhibit a wide range of metabolic capabilities, including nitrogen fixation, denitrification, sulfate reduction, sulfite oxidation, mercury conversion, halocarbon degradation, glycine betaine production, choline degradation, and C1 metabolism (Bowman and Ducklow 2015).

Although sea ice bacteria are known to exhibit seasonally elevated metabolic activity within the sea ice matrix (*e.g.,* Junge et al. 2004; Martin et al. 2008; Bowman 2015), few authors have examined their adaptation to the physicochemical extremes of this environment or provided mechanistic insights into their biogeochemical functions (but see Kottmeier and Sullivan 1988; Nichols et al. 1999, 2000; Martin et al. 2011; Torstensson et al. 2015). Dominant species of sea ice bacteria can also vary through the season where a progression occurs from a dominance of pelagic taxa like Alphaproteobacteria in young ice to typical sea ice taxa like Gammaproteobacteria in older ice (Eronen-Rasimus et al. 2015). Stressful environments require lifeforms to generate additional cellular energy to acclimate to changing, potentially deleterious conditions. Whether sea ice bacteria exhibit species-specific environmental tolerances, and how this relates to the availability of growth substrates, remains unknown. Importantly, bacteria can exhibit a range of physiological states including being viable, non-culturable, dormant, and active. The incorporation of microbial observations into numerical ecosystem models is clearly warranted, but to date only one study has modeled the relationship between the physiological traits of ice-associated bacteria and their link with the key ecosystem functions (Kim et al. 2022). Relative to the autotrophic biomass, descriptions of the distribution and relative abundance of bacteria in the Arctic and Antarctic remain fragmentary (but see Helmke and Weyland 1995; Archer et al. 1996; Mock et al. 1997; Junge et al. 2002; 2004; Brinkmeyer et al. 2003). Most studies have focused on annual land fast ice that only constitutes 1–5% of the seasonal ice cover in Polar Regions. However, the majority of sea ice is pack ice, and while this supports microbes concentrated within both interstitial and surface layers (Ackley and Sullivan 1994), there is much less known about the diversity, distribution or abundance of these communities because of limited accessibility. Despite this regional sampling bias, bacteria are present in significant numbers throughout the ice, irrespective of age, thickness, or season (Deming 2007). The depth-integrated biomass of bacteria sampled from extracted ice cores can exceed the algal biomass during both the polar winter and summer bloom seasons (Deming and Collins 2017). The density of bacteria, when scaled to ice volume, typically ranges from $4 \times 10^3$ mL$^{-1}$ in upper ice horizons of Arctic winter ice, to bi-polar estimates of $3 \times 10^7$ mL$^{-1}$ in summer following the in situ ice algal bloom (Collins et al. 2008). Importantly, this upper endpoint rivals or exceeds the maxima found in most aquatic environments at any latitude on Earth (Gradinger and Zhang 1997; Deming and Collins 2017).

## Light as stressor

In contrast to microalgae, adaptive strategies in bacteria to UV-B appear to be limited; in controlled experiments that mimic the rapid exposure associated with ice melt, cell health decreased significantly in Antarctic bacteria (Martin et al. 2009). With respect to energy flux, research to date has confirmed that some sea ice bacteria are capable of phototrophic metabolism, most likely as a supplement to an otherwise heterotrophic lifestyle (Koh et al. 2011; Koh et al. 2012a, b). Although the specific physiological roles and adaptive strategies of phototrophic bacteria have yet to be elucidated, it is likely that phototrophy provides an important competitive advantage. This was first demonstrated by Koh et al. (2010) who documented the presence of proteorhodopsin (PR) from diverse locations in the Ross Sea region of Antarctica. Analysis of bacterial RNA revealed PR transcripts, indicating that these cells were transcribing PR genes and were metabolically active. In addition, two forms of PR were identified: blue-light-absorbing PR, which was common in the middle of the ice, and green-light-absorbing PR, at the bottom. This distribution implies 'spectral tuning,' whereby bacteria specialize in generating energy from different light wavelengths and may occupy discrete microniches within the ice. The utilization of proteorhodopsin as an accessory metabolic pathway may also be beneficial for survival at low temperatures. Photon-based energy acquisition is less thermally sensitive than catabolic processes (Morgan-Kiss et al. 2006). Thus, during periods of extremes in temperature when the activation energy required for the catabolic breakdown of organic carbon is unfavorable, the supplementation via accessory pathways would confer a competitive advantage. While, marine diatoms are known to apply PR for osmotic protection (Marchetti et al. 2015) they do not seem to appear in sea ice diatoms.

## Temperature

The ability to detect temperature change is equally important for ice-associated microbes (Margesin and Miteva 2011). Most bacteria in Polar Regions are psychrophilic or cold-loving (fastest growth at ≤ 15 °C; growth not possible > 20 °C) (Morita and Moyer 2001). Metabolic plasticity in these organisms facilitates acclimation to sub-zero temperatures via membrane fluidity, production of cold-adapted enzymes, and regulation of extracellular compounds (Feller and Gerday 2003; Gerday 2013). Membrane fluidity relates to cell membranes controlling the transport of nutrients and metabolic waste products in and out of the cell, as the ability to retain a functional lipid bilayer is a critical low-temperature requirement. Bacteria use a combination of changes in fatty acid composition, including polyunsaturated, short-chain, branched, or cyclic fatty acids to maintain fluidity (Mock and Thomas 2005). A second mechanism is production of cold-adapted enzymes, which are produced with relatively minor changes in amino acid sequences, but they can be up to 10 times more active at low temperature. For example, the cold-adapted proteases produced by *Colwellia psychrerythraea* 34H (Huston et al. 2000) do not appear to correlate with a unique set of genes (Methé et al. 2005). Some psychrophiles produce antifreeze or ice-binding proteins termed cryoprotectants that effectively modify ice crystal structure and inhibit recrystallization of ice within the cell (Gilbert et al. 2004; Maayer et al. 2014).The behavior of microbial exudates in solution is complex, and different taxa produce extracellular compounds with different physical and chemical structures (Krembs et al. 2011). In general, these exudates improve the habitability of the ice by preventing freeze-induced injury, trapping and protecting saline water within brine channels, and potentially aiding in both motility and the attachment of cells to adjacent ice crystals (Dolev et al. 2016; Giudice et al. 2020).

### Salinity

Heterotrophic physiological activity is challenged by both hyper- and hypo-salinity and this reflects the dynamic flux between temperature and interstitial brine volume which can vary over timescales of a few hours to several days (Ewert and Deming 2014). Saline stress can significantly impair protein function in sea ice bacteria or lead to dehydration and a reduction in cell volume (Ewert and Deming 2013). In general, sea ice bacteria appear to be tolerant of ambient salt concentrations, given that sustained metabolic activity has been observed at salinities of 20–70 at an incubation temperature of −1.8 °C (Martin et al. 2009). This likely reflects the production of osmolytes, including inorganic ions and organic solutes (*e.g.,* proline, mannitol, and glycine betaine) that are accumulated or synthesized within the cell in response to localized hypersaline conditions (Thomas and Dieckmann 2002; Ewert and Deming 2014). The accumulation of compatible solutes assists with the maintenance of turgor pressure, cell volume, and intracellular electrolytes (Mahajan and Tuteja 2005). Conversely, hyposaline shock can be alleviated by releasing osmolytes to the external environment. These mechanisms are energetically expensive and the disturbance of cellular homeostasis due to the influx or efflux of ions can result in a temporary decline in both growth rate and cell division (Feng et al. 2013; Ewert and Deming 2014). For Baltic sea ice bacteria Kaartokallio et al. (2005; 2008) demonstrated considerably less salinity stress for ice compared to pelagic bacteria indicating better adaptation of this community.

### Nutrients

In general, nutrient concentrations within sea ice are seldom growth-limiting for biological assemblages (Fritsen et al. 2001; Thomas and Papadimitriou 2003). In the strict absence of microbial activity, the concentration of nutrients is proportional to brine salinity and can therefore be exceptionally high in the coldest regions that are found near the upper surface of the ice (Werner et al. 2007). This is significant, because bacteria appear to be unable to sequester inorganic substrates or organic compounds with decreasing temperature because of lowered substrate affinity (Nedwell 1999; Pomeroy and Wiebe 2001). Importantly, the degree to which substrate affinity restricts the in situ exchange of metabolites between bacteria and algae remains unclear. In spite of some progress there is still a need for a better understanding of seasonal growth dynamics and microbial driven nutrient regeneration (Bowman 2008; 2015), as to determine whether sea ice represents a seasonal net source or sink for important macronutrients (*e.g.,* phosphate, nitrogen) and micronutrients (*e.g.,* iron, vitamin B12).

### Dissolved oxygen, inorganic carbon, and pH

Carbonate chemistry dynamics within sea ice are influenced by seasonal microbial activity, and this significantly also influences the in situ concentration of dissolved gases ($O_2$, $CO_2$) and also pH. Resolving this variability at the required millimeter scale to validate ‘ice acidification’ remains an outstanding challenge, but the available data describe a trend of very low $pCO_2$ (< 100 μatm) and high pH (> 8.6) during spring months (Bates et al. 2014). Although pH may be the primary physicochemical parameter controlling in situ bacterial community development, the available data is limited to just one study (Nichols et al. 1999).

## The fungi

The eufungi are generally characterized as prolific osmotrophic degraders of vascular plant materials (Cragg et al. 2015) and as their pathogens (Perfect and Green 2001). Sea ice harbors large quantities of algae (Gradinger et al.

1999; Arrigo et al. 2014a), whose growth is stimulated by the returning spring light in sea ice with high early-spring concentrations of inorganic carbon and nutrients that support algal growth (Matrai and Apollonio 2013; Leu et al. 2015). As the algal bloom progresses and ocean inorganics are depleted while photon flux density increases, both scenarios can lead to algal stress (Manes and Gradinger 2009; Lund-Hansen et al. 2013; 2020a), predisposing algae to parasitism (Scholthof 2006). During this developing window of rapid algal growth and the onset of abiotic stress, the eufungal community becomes topical and of relevance to biological processes in sea ice.

## Phylogentic diversity and distributions

The characterization of eufungal ecology in the Arctic marine environment has been greatly aided by recent molecular taxonomy employed by mycologists. They have established the phylogenetic limits of eufungal phyla and their subclades, including many of the non-mycelial forming members of the zoosporic eufungi (Karpov et al. 2014; Grossart et al. 2016). Their morphology is superficially congruent with many eufungal-like protists that would traditionally be included among the heterotrophic nanoflagellates. The near-concurrent application of high-throughput sequencing to recover millions of DNA sequences from environmental samples, quite rapidly revealed diverse and abundant eufungal communities throughout the marine world (Li et al. 2016; Picard 2017), including Arctic marine ice ecosystems (Terrado et al. 2011; Rämä et al. 2014; Hassett and Gradinger 2016).

Algal pathogens belonging to the flagellated Chytridiomycota were morphologically identified in the Arctic Ocean as early as 1973 (Sparrow 1973) and noted to be members of sea ice biological communities parasitizing diatoms (Horner and Schrader 1982). Molecular surveys of Arctic marine fungal communities have consistently revealed a preponderance of Chytridiomycota (Hassett et al. 2017; Perini et al. 2019; Kilias et al. 2020), many directly parasitizing diatoms in sea ice (Hassett and Gradinger 2016; Hassett et al. 2016, 2019a, b). Other studies report statistically significant co-occurrence of DNA sequences classified as diatoms and Chytridiomycota in the pelagic realm (Kilias et al. 2020). The Chytriodinium occurred in relatively high abundances in a dinoflagellate dominated sea ice bloom as shown in a recent study (Lund-Hansen et al. 2024). The parasitism is apparently tied to light stress, and is governed in ice by snow cover (Hassett and Gradinger 2016), and occurs in polynyas (Terrado et al. 2011), where ice algae are seeded into the pelagic realm and exposed to high light intensities. The ecological relevance of Chytridiomycota remains to be fully elucidated in the Arctic Ocean, as the species diversity, likely representing novel genera, remains uncharacterized (Comeau et al. 2012; Hassett et al. 2017), despite novel discoveries in lower latitudes (Reñé et al. 2022). However, these Chytridiomycota and their associated parasitic activity presumably aids, as is documented in other ecosystems, in the temporal succession of algal communities (Donk 1989). They also contribute to the nutrient pool via lysis of algal cells (Klawonn et al. 2021), and serve as a carbon bridge by converting large colonial algae, whose size restricts zooplankton feeding, into smaller zoospores of an accessible size class via the mycoloop (Kagami et al. 2014). Evidence of the mycoloop in sea ice-covered ecosystems is emerging (Cleary et al. 2017). The flagellated reproductive zoospores of Chytridiomycota have been identified in sea ice (Hassett et al. 2019a, b) and are hypothesized to comprise a sizable fraction of the heterotrophic nanoflagellate pool, as has been described elsewhere (Sherr et al. 2003).

The eufungal community of sea ice is also represented by a diverse community of other eufungal phyla, including many hyphae-forming molds in the Ascomycota and Basidiomycota, as reported in various molecular surveys cited above. Hundreds of operational taxonomic units classified as eufungi have been detected from single substrates in the Arctic Ocean (Rämä et al. 2017; Amend et al. 2019). These Arctic marine eufungi encode genes that aid in cycling carbon and nitrogen (Hassett et al. 2019a), which they presumably do in sea ice as in other marine environments (Gutiérrez et al. 2020; Chrismas and Cunliffe 2020). However, in the absence of morphological observations or RNA data to definitively demonstrate activity, it is exceptionally challenging to discern DNA signatures derived from latent fungal propagules sourced from terrestrial environments in the Arctic (Fu et al. 2013; Yu et al. 2013) or from fungal DNA sourced from ecologically relevant eufungi facilitating biological turnover. With that said, there is an average of 3.59 mg C $m^{-3}$ of eufungi carbon in sea ice that includes many catalytic genes responsible for carbon turnover and degradation of recalcitrant molecules (Hassett et al. 2019a). It is presumed that this diverse community of sea ice fungi work in concert with bacteria and heterotrophic eukaryotic microbes to facilitate nutrient cycling in sea ice brine channels, as has been implied from other Arctic marine substrate (Rämä et al. 2014).

A collection of aerosolized eukaryotic communities north of Svalbard has demonstrated that Eufungi are present in air samples, comprising as much as 33% of the entire community (Hassett, unpublished data). Eufungal communities are dominated by conidia-forming Dikarya in the Ascomycota and Basidiomycota that have evolved for aerial dispersal (James et al. 2006), many of which have adapted for survival in high-latitude (Robinson 2001). The observations are a stark contrast to the, flagellated Chytridiomycota that are known to generally dominate Arctic marine fungal communities. Many of the eufungal taxa detected, including the Sporidiobolaceae and the rust fungi belonging to the Melampsoraceae, are exclusively terrestrial, yet they can be the most abundant eufungal group detected. This detection of streptophytes and members of Ebridea (cercozoans that are exclusively marine taxa) in aerosolized communities underscores that both marine and terrestrial organisms are aerosolized and likely transported above the Arctic Ocean. For euryhaline organisms, such as the eufungi, the effects of marine-sourced eufungi on terrestrial eufungal biodiversity and associated processes remains unknown. It is clear that terrestrial eufungi are sourced into the marine environment, and their presence challenges the earlier paradigms of marine eufungal data. This is in line with the observation of comparatively higher fungal colony forming units in glacier ice, which acts as a trap for aerosolized fungal spores (Gunde-Cimerman et al. 2003).

In addition to the eufungal community, the ecological fungi make up large fractions of the sea ice community, also assisting the eufungi and bacteria in biological turnover of nutrients. The ecological fungi are eukaryotic microbial osmostrophs that possess several morphological features of the eufungi through convergent evolutionary processes but are actually phylogenetically quite distinct. The diversity of these organisms is extraordinarily underexplored; however, inventories from across the Arctic (Poulin et al. 2010), supplemented by surveys of eufungal-like organisms, including the Oomycetes (Hassett et al. 2019a, b) and thraustochytrids (Naganuma et al. 2006), underscore that these organisms are hyper-abundant. They are associated with sea ice algae and sinking particulates in the Arctic Ocean (Rapp et al. 2018; Hassett 2020) and likely comprise as much biomass as other organisms generally considered essential to maintaining Arctic ecosystem structure, as has been reported in other ecosystems (Bochdansky et al. 2017). The true relevance of these organisms in the Arctic is far from being fully understood and integrated into sea ice ecosystem modeling efforts, and appears to be more a function of human efforts and interests than a question of their existence in substantial quantities in Arctic marine ecosystems. There are only few studies of fungi adaptations to the sea ice as for Gunde-Cimerman et al. (2003) in a comparative study showed that certain groups of fungi were well adapted to high salt concentrations, though without specifying the mechanisms. Antarctic soil and lake sediment fungi reproduced at −1 ℃, and contained high concentrations of unsaturated fatty acids as to maintain membrane fluidity (Tsuji et al. 2013). Fungi cold tolerance comprises production trehalose, antifreeze proteins and compatible solutes (Robinson 2001) and some have developed mechanism against UV-A and UV-B (Rastogi et al. 2010; Rafiq et al. 2019).

## The viruses

### Phylogenetic diversity and distributions

Initially thought to primarily infect bacteria, viruses are now known to also infect all major phytoplankton algal groups (Short and Suttle 2002; Yau and Seth-Pasricha 2019). Virus infection rates in marine ecosystems have been thought to be largely host density-mediated, *i.e.,* the more abundant a species becomes the more likely it is that it will interact with a virus, become infected and then suffer cell lysis. Thus, viruses were thought to have the ability to control species succession and maintain maximum biodiversity; this became known as the ‘kill the winner’ scenario (Thingstad 2000). However, rather than always causing cell lysis, some viruses transfer their DNA into the host’s genome without killing it, a process known as lysogeny. This mechanism, which enables the virus to coexist with a rare host over many generations, is thought to be increasingly important in oligotrophic environments (Thingstad and Bratbak 2016). Furthermore, it has been shown that as host cell densities increase, some viruses integrate themselves into their host. These viruses replicate more slowly but also avoid competing with other viruses and their own host’s immune system; this includes a switch between a lytic and lysogenic mode (also referred to as ‘temperate’), a process termed ‘Piggyback the Winner’ (Knowles et al. 2016; Silveira and Rohwer 2016). The first virus to be isolated from polar sea ice infected the typical sea ice bacteria genera *Paraglaciecola* and *Octadecabacter* (Luhtanen et al. 2018), although phage-host systems had earlier been isolated and characterized from Baltic Sea ice (Luhtanen et al. 2013). Viruses occur generally in much higher numbers than bacteria, as expressed by the virus:bacteria ratio (VBR), which can be as high as 2800 in Arctic sea ice (Collins and Deming 2011). Large viruses, *i.e.,* those thought likely to infect eukaryotes, were first recorded from sea ice by Gowing et al. (2002; Gowing 2003). These viruses, which in Gowing (2003) comprised up to 18% of the virus community, occurred at abundances of 106–108 $mL^{-1}$ and were strongly correlated with the Chl *a* concentration. However, in spite of the large number (> 10,000) of eukaryote cells examined, no diatoms were infected, although other microeukaryotes, such as *Pyramimonas* and *Cryothecomonas*, were (Gowing 2003). It has recently been shown that the release of dissolved organic matter (DOM) caused by viruses and cell lysis is an important component of the microbial loop in oceans (Zhao et al. 2019) and might also be in the sea ice. Although viruses are now known to be the most abundant lifeform in the oceans, with global numbers of ~$10^{30}$, their role, function and importance in marine microbial ecosystems was only identified in the late 1980s (Bergh et al. 1989). Bacteriophages, *i.e.,* viruses infecting bacteria, were reported from sea ice as early as 1994 (Maranger et al. 1994), and from both the Arctic (Maranger and Bird 1994) and the Antarctic (Maranger et al. 1994; Paterson and Laybourn-Parry 2011; Luhtanen et al. 2018). Viruses occur in sea ice in Antarctica (Gowing et al. 2004; Paterson and Laybourn-Parry 2011) and in the Arctic in numbers up to $1.7 \times 10^9$ viruses $mL^{-1}$ of sea ice (Collins and Deming 2011). Time series have shown a close correlation between numbers of viruses and bacteria, which again is related to the microalgae biomass expressed as Chl *a* (Maranger et al. 1994). The studies have not shown any specific distribution of number of viruses with depth in the bottom section of the ice cores (Maranger et al. 1994a; Gowing et al. 2002) or between surface slush layer and solid ice (Paterson and Laybourn-Parry 2011). In a study of the seasonal dynamics of viruses in Antarctic sea ice no seasonal dynamics could be detected, and there was no seasonal pattern in the abundance of viruses or bacteria, although the relationship between season and VBR (0.2–20.8) was significantly lower in winter (Paterson and Laybourn-Parry (2011).

Relatively higher VBR ratios of 10–72 have been reported from Arctic sea ice (Maranger et al. 1994) with no correlation between viruses and bacterial numbers, but a positive such for Chl *a* concentration Gowing et al. (2004). A study showed between 40 and 50% of bacteria cells were infected with viruses (Patterson and Laybourn-Parry 2011).

It has been shown that there were 10–100 times more viruses in the underlying water than in the sea ice Maranger et al. (1994) although Paterson and Laybourn-Parry (2011) found the reverse. A strong association between viruses and Antarctic ice edge phytoplankton blooms has also been noted (Han et al. 2022a, b), and while bacteriophage taxa predominate, viral taxa associated with phytoplankton were also present. For most of the year, the dominant algal group in sea ice is diatoms, and yet most sea ice studies have found that virus infection by diatoms or even the presence of diatom viruses is very low or non-existent. These studies have mostly only examined DNA viruses. Recent research has demonstrated that diatoms are far more likely to be infected by RNA viruses. Our most recent research on sea ice from McMurdo Sound showed diatom RNA viruses to be common (McMinn unpublished data).

Recent studies have demonstrated the existence of fatty acid desaturase genes (FAD) in viruses in high saline brines in sea ice (Zhong et al. 2023), which enhance cell membrane fluidity when being exposed to low temperatures and high salinities (Beney Gervais 2001). Genes of epsG encoded by viruses were recently identified in high saline brine and sea ice (Zhong et al. 2023), and is a variant of extracellular polysaccharides EPS that microalgae and bacteria in sea ice apply as cryoprotectants (Collins et al. 2008).

## The heterotrophic protists and metazoa

### Phylogenetic diversity

As outlined in the previous chapters, sea ice provides an environment rich at times in microalgal food and bacterial biomass, while at the same time challenging its inhabitants through its unique environmental settings. Consequently, a wide range of partially unique pico-, nano-, micro-, and meiofauna taxa inhabit the brine channel systems, feeding on different components of the brine channel bound food web. Studies on sea ice heterotrophs date back to the earliest Arctic and Antarctic scientific exploration. Nansen (1906) for example described protozoans living on top of Arctic sea ice floes in summer in freshwater melt ponds.

The overall taxonomic composition in Arctic and Antarctic sea ice is remarkably similar at higher taxonomic levels but with some distinct differences. Typical heterotrophic unicellular eukaryotes range from small, hard to identify bacterial feeding picoflagellates to relatively large herbivorous Euglenophyceae (*e.g., Anisonema* spp., *Peranema* spp.) (Ikävalko and Gradinger 1997). DNA analysis approaches (Stecher et al. 2016) have greatly extended the knowledge of, *e.g.,* dinoflagellates and choanoflagellates in sea ice. High abundances of the typically pelagic foraminifera such as *Neogloboquadrina pachyderma* are commonly found alive in all stages of sea ice from newly formed ice to first-year ice (Dieckmann et al. 1991) in Antarctica, but only rarely in the Arctic. Ciliophora occur at both poles in high abundances, at times dominating the sea ice fauna composition (Ehrlich et al. 2020). Taxonomic studies have led to the discovery of previously unknown genera and species (Agatha et al. 1993; Song and Wilbert 2000), as for the euglenophytes or *Rhynchomonas nasuta*, surface-crawling species such as *Euplotes* spp., distinctly different from dominant oligotrich taxa in the planktonic realm, dominate in the sea ice system.

Sea ice metazoans mainly fall into the meiofauna size range, usually defined as > 62 µm, when the upper size is restricted by the brine channel diameter. In both the Arctic and Antarctic, flatworms and crustaceans often dominate (Gradinger et al. 1999; Granata et al. 2022). Unique to the Arctic is the high frequency of partially endemic Nematoda, Rotifera and one cnidarian (*Sympagohydra tuuli*) (Bluhm et al. 2017), while Antarctic sea ice has distinct contributions by the nudibranch *Tergipes antarcticus* and the ctenophore *Euplokamis* sp. (Kiko et al. 2008, Kiko et al. 2009). In both Polar Regions juvenile stages of pelagic crustaceans can seasonally occur in high abundances (Schnack-Schiel et al. 1995). Furthermore, in shallow Arctic seas larvae and juveniles of benthic biota may enter the ice brine channels, which provides both protection against larger grazers and ample food supply in spring to fall (McConnell et al. 2012). Initially food web interactions were considered rather simple with meiofauna being mainly herbivorous but the view has changed. Stable isotope analyses have revealed different trophic positions for major Arctic meiofauna taxa, with the carnivorous Cnidaria likely at the top of the pyramid (Gradinger and Bluhm 2020), while dissolved organic matter and bacteria provide alternative carbon pathways for, *e.g.,* Nematoda and Rotifera.

## Distribution and abundances

The sea ice brine channel network presents a highly structured habitat for sea ice metazoans. The spatial dimensions of the brine channels play a significant role in determining the diversity and distribution of metazoans in sea ice. A large fraction of sea ice meiofauna taxa have body width < 200 µm while flexible species like turbellaria can exceed this size (Patrohay et al. 2022).The sea ice meiofauna taxa are capable to using the narrow channel system due to their elongated (nematoda) or flexible (turbellaria, rotifers) bodies. Krembs et al. (2000) observed that rotifers were able to pass narrow passages of only 57% of their typical body width, with a 60% value for turbellarians. Interestingly they also demonstrated that increasing salinities caused a shrinkage in body size of the turbellarians at a time when brine volume fraction and channel diameters would decrease. The size limitation explains the absence within the brine channels of typical larger pelagic taxa like large copepods or euphausiids that often dominate in the pelagic realm of polar systems. However, small larvae and juveniles of pelagic or benthic animals (*e.g.,* Grainger and Hsiao 1990) can seasonally explore the ice system to feed on the abundant food supply within the ice (McConnell et al. 2012), while retreating at a later stage of the seasonal cycle to the water column or sea floor. Consequently, sea ice brine channel geometry is a major factor shaping the seasonality and diversity of sea ice meiofauna. See Bluhm et al. (2018) for a review on spatial meiofauna distributions in the Arctic.

## Salinity

Not all incorporated planktonic organisms can tolerate the associated environmental changes including salinity change during freezing (Werner and Auel 2004). Selection of the typical sea ice biota during freezing decreases overall diversity, with those bacteria and protists with high salinity acclimation potential and ability to grow at low temperatures dominating (see chapters above). For Arctic protists there is a decrease in diversity as new ice proceeds to later stages of ice formation indicating selection processes occurring immediately following organism incorporation, comparable to the succession in dominant bacteria mentioned earlier (Eronen-Rasimus et al. 2015). For sea ice meiofauna, the same shift from pelagic species with good swimming abilities in young ice like rotifers or turbellaria to more unique sea ice meiofauna taxa (harpacticoid copepods and nematodes) in older Arctic sea ice was observed (Kiko et al. 2017). The responses of organisms incorporated into sea ice have been sporadically studied in the Arctic and Antarctic mainly regarding shifting biodiversity aspects. However, the physiological response on scales of hours to days to weeks appears to be still an open field for research, and specifically for sea ice meiofauna, the information of changes in biodiversity during ice formation and salinity are limited (Bluhm et al. 2017). Taxa typically occurring in sea ice show a much wider range of salinity acclimation potential compared to dominant pelagic taxa, pointing toward an evolutionary adaptation. For instance, sea ice copepods like *Tisbe furcata* demonstrate a much wider range of salinity tolerance up to 70 compared to pelagic taxa up to 50 (Grainger and Mohammed 1990). The two dominant Antarctic planktonic copepods (*Calanus propinquus* and *Metridia gerlachei*) could not survive the typical salinity increases related to life in sea ice, while sea ice turbellarians survived salinities up to 75 (Gradinger and Schnack-Schiel 1998). Interestingly, sea ice meiofauna and also under-ice amphipods (*e.g.,* Kiko et al. 2008, Kiko et al. 2009) appear to adjust their internal hemolymph concentrations to stay iso-osmotic over salinity ranges of ca. 25 to 45 or 55 (Kiko 2009). However, sea ice meiofauna taxa must also be able to tolerate low brine salinities during the summer melt season. For example, based on the vertical distribution within ice floes, sea ice rotifers lived at brine salinities below 20 (Friedrich and de Smet 2000). However, Arctic meiofauna abundances in summer level sea ice with low brine salinities were lower compared to those in associated pressure ridges with higher brine salinities (Gradiner et al. 2010).

## Temperature

The wide range of sea ice temperatures will directly impact sea ice meiofauna physiology, diversity and distribution in addition to the above mentioned impacts on sea ice habitat structure and brine salinity. However, little experimental knowledge is available regarding the physiological response or survival over a wide range of temperatures for sea ice meiofauna. Generally, temperature has a major impact on the physiology of marine invertebrates and many rate processes like respiration, excretion or feeding are related to habitat temperature (Torres et al. 2021). For instance, thermal hysteresis has been proven for several Antarctic crustaceans likely to avoid ice formation within the bodies, and it is likely that they inherited this ability through lateral gene transfer from bacteria (Kiko 2009). Empirical relationships (Moloney and Field 1989) have been used to estimate the ingestion of prey by sea ice meiofauna assuming a Q10 value of 2 (Gradinger and Bluhm 2020). The Q10 value describes the change of a physiological rate due to temperature changes, and has been experimentally determined to be around 2 for herbivorous meiofauna (*e.g.,* Price and Warwicj 1980) and for a sea ice inhabiting polychaete (McConnell et al. 2012). However, Price and Warwicj (1980) found that the Q10 value differed between taxa as also for marine phytoplankton (Anderson et al. 2021).

Sporadic experimental evidence indicates that sea ice meiofauna can tolerate temperatures well below the freezing point of seawater. The sea ice endemic hydrozoan *Sympagohydra tuuli* survived temperatures of −4.6 ℃ (Siebert et al. 2009). In summer, low abundances of rotifers have been observed in the warmer upper parts of the ice floes, while abundances were highest in the colder bottom layers of the ice floes (Friedrich and de Smet 2000). However, such field data provide limited direct evidence of temperature effects, as brine channel structure including volume, and brine salinity will co-vary with temperature. Due to the lack of consistent physiological studies on sea ice meiofauna considering the combined effect of these factors, improved knowledge on temperature and salinity tolerance of sea ice fauna at high taxonomic resolution would be a major step to understand the occurrence of meiofauna in sea ice, as also to incorporate sea ice meiofauna in ecosystem model studies.

## Extraterrestrial sea ice environments

The search for habitable extraterrestrial worlds has been driven by the presence of liquid water (Hays 2015). Water has a fundamental influence on determining planetary habitability by controlling geological and evolutionary processes by moderating thermodynamics and acting as an initiator for chemical reactions that ultimately result in the creation and liberation of energy (Korenaga et al. 2017). Water is essential for performing the internal cellular functions of all known life (Jones and Lineweaver 2010), and is significantly abundant in the outer solar system in the form of ice but less so as liquid on planetary objects (Nimmo and Pappalardo 2016). Due to the vast distance from the Sun, temperatures in the outer Solar system are significantly colder than the inner solar system which causes water methane and ammonia to solidify as 'ices' and accumulate during planetary formation (Grasset et al. 2017). Planetary evolution and geological processes over millions of years cause these ices to evolve into the liquid states present today (Soderlund 2019). The two ice giant planets Uranus and Neptune contain the largest volumes of water in the solar system (Frelikh and Murray-Clay 2017). Both planets have similar elemental composition and internal structure, with oceans composed of hot dense water intermixed with ammonia and methane ices beneath a thick gaseous outer layer (Atreya et al. 2019; 2020). A liquid ocean with an abundance of biomolecules would seemingly satisfy the requirements for life, but it is highly unlikely any life could survive the extreme atmospheric pressures and temperatures present on either planet (Madhusudhan et al. 2016; Hofstadter et al. 2017).

In contrast, the icy environments on a number of smaller celestial objects in the outer solar system present potentially more habitable locales for life to exist as for the dwarf planets Ceres and Pluto. These smaller bodies have the fundamental requirements for life: liquid water, suitable temperature and physicochemical conditions, an energy source, biologically relevant elements—carbon, hydrogen, nitrogen, oxygen, phosphate and silicate—and additional elements likely to be specific for each organism (Lammer et al. 2009). Intracellular biochemical reactions require a solvent to act as an internal fluid medium to dissolve molecules and to facilitate enzymatic activity (Chyba et al. 2000), and the only solvent used for this purpose is water (Cockell et al. 2016).

### Exomoons—the icy ocean worlds

The two most studied and arguably most favorable candidate worlds for habitability in the outer Solar System are Jupiter's moon Europa and Saturn's moon Enceladus (Martin and McMinn 2017) These two moons, classified as 'icy ocean worlds,' meet the requisite criteria for life, and have several potentially habitable and ecologically viable niches (Cottin et al. 2017; Hand et al. 2020). Due to the action of tidal heating both moons have developed clearly defined stratifications of rock and ice to form layers of ocean and ice (Schubert et al. 2010). The outer icy shells are a large multifaceted environment probably containing brine channels, pockets, cracks, fissures, and fractures that penetrate throughout the icy shell to form 'fracture networks' that span for kilometers in all directions. The network is possibly connecting the exterior surface to the subsurface ocean and facilitating the active exchange of chemical materials between seafloor and outer ice exterior (Greeley et al. 1998; Chyba and Phillips 2001). This creates localized habitats throughout the ice shell that could potentially support life. The exact measurements of the thickness of Europa's icy outer shell and the depth of the underlying ocean remains unknown, with estimates ranging from < 1 km to 30 km for the icy exterior (Hussmann 2002; Billings and Kattenhorn 2005) and up to 100 km for the subsurface ocean (Hussmann et al. 2006). The total combined ice shell and ocean thickness is estimated to be between 80 and 170 km (Anderson et al. 1998; Hand and Chyba 2007). Enceladus' icy exterior is thought to be 21–30 km thick (Parkinson et al. 2006) but recent data suggests the existence of an ocean that is

26–31 km deep (Thomas et al. 2016). The most favorable region for potential life in either Europa or Enceladus is likely at the ice/water interface (Martin and McMinn 2017). The ice/water interface on these moons would likely be subject to localized physicochemical properties with pressure and temperature thought to range between 84 and 205 MPa and −20 °C and 4 °C, respectively. These are within the known tolerance thresholds for microbial lifeforms. If the modeled pressure and temperature parameters are accurate, the habitable area of the Europan ice shell could extend 5 km upward into the overlying ice layer from the ice/water interface. Beyond this area, it is likely temperatures decrease below the low temperature biological threshold. Modeling of temperature gradients through the ice shell suggests a temperature increase in the ice shell from −230 °C at the surface to −78 °C at 10 km depth (Kalousová et al. 2017). Such extremely low temperatures could preserve microbial cells for long periods, inducing a state of suspended animation. Terrestrial microbes have been revived from deep-freezing in the last millennia, but their temperature exposure only dropped down to −130 °C (Houseknecht et al. 2011). The range of the physicochemical parameters as temperature in the icy shell of both moons are extreme by any definition and would exert substantial physiological demands on any potential microbial consortia to survive.

## Using earth's sea ice as a tool to explore extraterrestrial habitability

Although there are no environments on Earth that have conditions that fully replicate extraterrestrial systems, microbial communities surviving in extreme habitats can be used to establish the thresholds for life to exist. The sea ice environment is analogous to some extraterrestrial habitats on icy ocean worlds (Léveillé 2010; Martin and McMinn 2017). Earth's cryosphere is inhabited by microorganisms of all three domains of life. Within the sea ice matrix, psychrophiles have to tolerate a challenging physiochemical environment as outlined in previous chapters. The response of polyextremophiles to multiple physiological stressors currently impedes the search for extra-terrestrial life because there is a lack of a mechanistic framework that links the capacity for biological adaptation with environmental variability (Martin and McMinn 2017). We need to characterize the theoretical limits to support biological processes that are distinct from the limits imposed on terrestrial analogues. An important step will be to undertake experimental work across multiple physicochemical extremes and couple this with research that contrasts the limits of Earth's biosphere with extraterrestrial environments of interest. The icy environments on the moons of Jupiter and Saturn have led astrobiologists to view sea ice terrestrial environments and its polyextremophiles in a new light. This in turn provokes new questions to be asked about the concept of habitability and the physical limitations for life and has raised the probability that the first discovery of extraterrestrial life could be from with our Solar System (Priscu and Hand 2012). Several spacecraft missions are planned to address the shortcomings of the current biogeochemical datasets on potential habitable worlds. The missions will gather data to validate the habitability by aiming at the presence composition and concentration of large biomolecules and organic compounds along with surveys of the physical parameters of potential niches as the sea ice or oceans below. The field of astrobiology given the long time frame of the missions will remain transient requiring continued research utilizing poly- and extremophile sea ice microorganisms to develop hypotheses for potential life beyond Earth.

## Main findings

- The review has shown that sea ice is an extreme environment in line with deep-sea hydrothermal vents, deserts salt lakes, and glaciers as for the high salinities reached in the brine channels governed by the temperature of the ice. Nutrient depletion increased levels of pH lowered levels of $O_2$ increased light and UV in the upper section of the ice. Here organisms are characterized as polyextremophiles, considering their adaptation to more than one stressor. Conditions are relatively more stable at the bottom of the ice considering the temperature around −1.8 °C, whereas strong variations in salinity can occur here due to brine drainage and/or flushing of brine channels.
- Autotrophic organisms occur generally at the bottom of the sea ice, but also in the upper sections of the ice exposed to more extreme conditions being mainly extremophile in the bottom sections and clearly polyextremophiles in the upper section. The organism's adaptations to the extreme environment implied a variety of functions and mechanisms to endure conditions as light harvesting and sunscreen pigments, down- and upregulation of photosynthetic capacity, development of MMA's (mycosporine amino-like acids) for UV protection and cryoprotectants (EPS).
- Bacteria occur in the entire section of the ice and endure concurrently very low temperatures and high salinities. The bacteria are able to adjust cell membrane fluidity, develop cold-adapted enzymes, antifreeze ice-binding proteins to cope with the low temperatures. Production of osmolytes, inorganic, and organic solutes are mechanisms applied to protect the cells at high and increased salinities.
- Fungi occur likewise in the entire section of the ice, but there are currently no studies of specific adaptations to the physical conditions in sea ice.

- Virus also occur in the entire section of the ice and very recent studies have shown viral development of compounds for both osmo- and cryoprotection.
- Meio- and macrofauna occur both at the water–ice interface and inside the brine channels, as determined in concert by the diameter of the organism and the diameter of the brine channel. Salinity in brine channels varies during expulsion of high saline brine, on one side, and low saline conditions during melt of the ice, and organisms have accordingly developed osmoregulatory mechanisms. Salinity is the main driver of changes here and the fauna is here classified as extremophiles.
- Until further advances in the future, sea ice environments on Earth are still proficient for models and studies of living conditions in sea ice covering extraterrestrial planets and moons.

## Conclusion and outlook

There has been a distinctive focus on microalgae in sea ice, and specifically their photosynthesis being a primary producer, and an important so in the Arctic. Less research has been devoted to the other microorganisms in sea ice as the bacteria, virus and fungi and their abilities to survive and thrive in this extreme environment. Are there any unknown mechanisms in cryoprotection, for instance, which could be exploited in other contexts? What are the effects for these organisms with less and less summer sea ice and thereby loss of habitat? There is still winter sea ice, but spring and early summer are the periods of highest biological activity. What are the specific ecological roles of the bacteria, the viruses, and the fungi in microbial loop in the sea ice? What are the interconnections between the groups in order to quantify the pathways of energy and matter in a space confined by the most extreme conditions, established by stressors as temperature, salinity, light, $O_2$, pH, nutrients, and UV as outlined here.

**Acknowledgements** Aarhus University Research Foundation (AUFF) is acknowledged for housing and logistical support during preparations of the manuscript. The manuscript was conceived and developed as part of the EU funded project FACE-IT (The Future of Arctic Coastal Systems—Identifying Transitions in Fjord Systems and Adjacent Coastal Areas). FACE-IT has received funding from European Union's Horizon 2020 research and innovation program under grant number agreement No 869154.

**Author contributions** LCLH and BS conceived and designed the outline of the review, and the entire author team LCLH, BS, RG, BH, SJ, FK, AM, AMc and DS contributed equally, wrote and edited the manuscript. All authors read and have approved the manuscript.

**Funding** This study was supported by HORIZON EUROPE European Innovation Ecosystems, 869154.

## Declarations

**Competing interests** The authors declare no competing interests.

**Ethical approval** No ethical aspects to be considered here.

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