Sea Ice Ecosystems

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Abstract

Polar sea ice is one of the largest ecosystems on Earth. The liquid brine
fraction of the ice matrix is home to a diverse array of organisms, rang-
ing from tiny archaea to larger fish and invertebrates. These organisms can
tolerate high brine salinity and low temperature but do best when condi-
tions are milder. Thriving ice algal communities, generally dominated by
diatoms, live at the ice/water interface and in recently flooded surface and
interior layers, especially during spring, when temperatures begin to rise.
Although protists dominate the sea ice biomass, heterotrophic bacteria are
also abundant. The sea ice ecosystem provides food for a host of animals,
with crustaceans being the most conspicuous. Uneaten organic matter from
the ice sinks through the water column and feeds benthic ecosystems. As sea
ice extent declines, ice algae likely contribute a shrinking fraction of the total
amount of organic matter produced in polar waters.

INTRODUCTION

A major speciation event in the Earth's history was the development of low-temperature surface ecosystems at the poles. Throughout the year, polar sea ice covers an area of between 15×10^6 and 22×10^6 km^2, equivalent to 3.9–4.3% of the total surface of the Earth or 4.1–6.1% of the area of the global ocean. This enormous area ranks sea ice as one of the most extensive habitats on Earth, one that is home to a diverse community of microalgae, bacteria, protists, and the occasional metazoan grazer within the numerous microhabitats that are formed during the lifetime of ice. Most of this ice is located in the Southern Hemisphere, where sea ice extent around Antarctica expands from a minimum of 3×10^6 km^2 in February to a maximum of 19×10^6 km^2 in September. Ice extent is lower and less seasonally variable in the Arctic, ranging from 5×10^6 km^2 in September to 15×10^6 km^2 in March. Ice extent is changing rapidly, however: The summer minimum ice extent in the Arctic has fallen by approximately 45% in the past three decades, from 7.0–7.5×10^6 km^2 in the 1980s to 3.5–4.5×10^6 km^2 between 2007 and 2012.

Associated with the reduction in Arctic sea ice extent is a corresponding drop in sea ice thickness, which is due mostly to a decrease in the proportion of thick multiyear ice over much of the central Arctic (Nghiem et al. 2007, Maslanik et al. 2011, Comiso 2012). This has resulted in an ice pack that is less ridged, has a thinner snow cover, contains more surface melt ponds, and reflects less incoming solar radiation (Nicolaus et al. 2012). In contrast, sea ice extent in the Antarctic has actually increased slightly over the past three-plus decades (Maksym et al. 2012), although the amount of multiyear ice has remained relatively constant. Furthermore, there is no clear evidence of a change over time in either snow or ice thickness, as there has been in the Arctic (Serreze et al. 2007, Stroeve et al. 2012).

Ongoing environmental changes might be expected to favor an increased proliferation of sea ice ecosystems in both the Arctic, owing to a higher proportion of more suitable annual (one year old or less) sea ice, and the Antarctic, owing to a greater area of sea ice habitat. However, factors other than sea ice extent and thickness also control the suitability of Arctic and Antarctic sea ice as a habitat for microorganisms. These include the proportion of deformed and rafted ice, the snow thickness distribution, the degree of surface flooding, the water column nutrient concentration, and the sea ice growth and melt rates. How these factors vary with the long-term changes in sea ice extent and thickness will determine the future suitability of sea ice as a microbial habitat and an important component of polar marine ecology and biogeochemistry.

This review assesses the current state of understanding of sea ice ecosystems in both the Arctic and the Antarctic. It covers the physical structure of sea ice and the characteristics that make it a good microbial habitat, the processes that facilitate the exchange of nutrients between the ice and the atmosphere and ocean, the factors that control the vertical distributions of temperature and salinity within the ice pack, and adaptations that allow different members of the microbial communities to thrive within the sea ice. It also includes important linkages between sea ice ecosystems and adjacent marine habitats, including processes such as trophic interactions and particle export. Finally, it assesses anticipated changes to sea ice ecosystems in response to an increasingly altered climate.

THE SEA ICE ENVIRONMENT

Sea Ice Structure

Sea ice that forms in shallow waters often has restricted motion owing to its direct connection to land. This land-fast ice can extend for tens of kilometers offshore. Ice that freezes farther offshore

and is free to drift with the winds and the currents is referred to as pack ice. Both types of ice can form in a variety of ways and exhibit a range of crystal structures.

Sea ice formation. In autumn, as atmospheric temperatures in polar regions drop below the freezing point of seawater, conditions become favorable for the formation of sea ice. Freezing of the ocean surface can begin in one of two ways, depending on whether the conditions are calm or turbulent. When atmospheric conditions are calm and the ocean surface is relatively undisturbed, ice crystals begin to form in the upper few millimeters of the ocean surface as the rate of heat extraction from the surface by the atmosphere exceeds the conductive heat flux from below (Maykut 1986). These ice crystals initially spread horizontally to form a continuous sheet across the ocean surface. However, as additional heat is extracted from the ocean, the ice crystals begin to extend vertically into the water column. Once the ice reaches a thickness of a few tens of millimeters, the downward-propagating ice margin is referred to as the skeletal layer (**Figure 1a**). This layer is composed of parallel ridges of ice crystals approximately 10–20 mm long and spaced <1 mm apart at their terminus, with essentially no space between crystals at their base (**Figure 2**). Although most salts are excluded from the crystal lattices as the ice crystals grow, small amounts of seawater may be trapped at the interfaces located between the bases of adjacent ridges (Cox & Weeks 1975). The faster the ice grows, the more seawater is trapped between the ice crystals. The skeletal layer remains at the base of the ice as long as the ice continues to grow. Ice that forms in this way is referred to as congelation ice, based on its regular crystal structure. This type of ice crystal structure dominates in land-fast ice (**Figure 1b**).

Sea ice can also form under more turbulent conditions. In deeper waters, strong winds promote vertical mixing, and cold atmospheric temperatures can rapidly extract enormous amounts of heat from the upper few tens of meters of the ocean. The surface ocean can then become supercooled, and small (<1 mm) ice crystals referred to as frazil ice nucleate throughout the mixed layer. These ice crystals remain distributed throughout the mixed layer until conditions calm, at which point they float to the sea surface, often scavenging particles such as microalgae as they rise. The floating ice crystals then coalesce into semiconsolidated grease ice and later into pancake ice (**Figure 3a**) (Garrison et al. 1983, 1990). Additional freezing eventually fuses the ice pancakes together to form a continuous ice sheet. The initial frazil ice layer can be relatively thick (>100 mm) depending on the conditions under which it formed, with greater turbulence leading to thicker layers. Subsequent vertical ice growth then proceeds as congelation ice crystals extend from the skeletal layer that forms at the lower frazil ice surface. Frazil ice is often a major component of pack ice that forms in offshore waters. Thus, in its early stages, pack ice is more porous and has a higher initial seawater content than newly formed congelation ice.

As sea ice continues to age and accumulate a snow cover, another type of sea ice can form through the metamorphosis of snow that has been infiltrated by seawater following a flooding event. Flooding is caused by two major processes. The accumulation of a thick snow cover can force the sea ice downward below the freeboard (sea ice floats partially above the sea, and the freeboard is the water line where the ice floe extends above the ocean surface). Alternatively, when adjacent ice floes converge, one floe can be forced over another, pushing the lower floe below the freeboard and flooding its surface. After the flooding event, most of the seawater drains from the snow, but some remains trapped between snow crystals, freezing them together to create snow/ice or slushy ice (Saenz & Arrigo 2012).

A final type of sea ice found almost exclusively in Antarctica is platelet ice, a semiconsolidated layer of ice commonly observed beneath sea ice in regions adjacent to floating ice shelves (Dayton et al. 1969, Sullivan & Palmisano 1984, Garrison et al. 1986, Smetacek et al. 1992). As ocean currents force seawater beneath floating ice shelves, the increased pressure causes the water
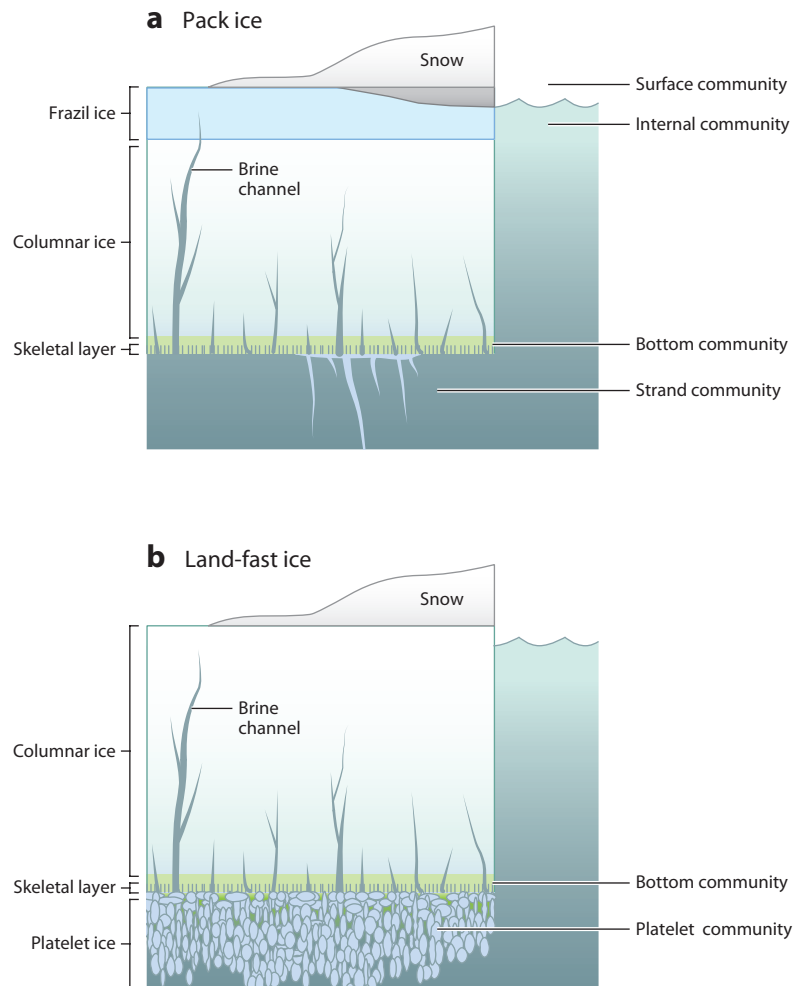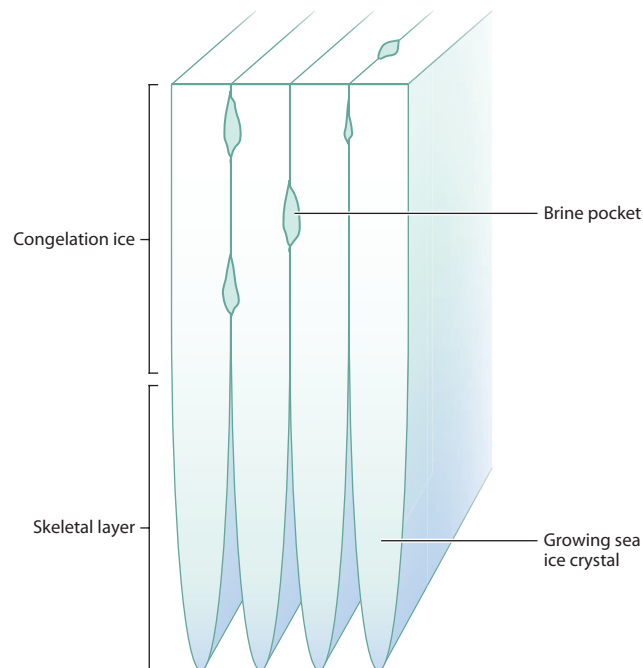
Figure 1

Schematic diagrams of (*a*) pack ice and (*b*) land-fast ice, including typical positions of different ice types of sea ice and sea ice communities as well as the brine drainage system.

to warm adiabatically, and the excess heat is conducted away by the ice shelf until the water reaches thermal equilibrium. Once this water exits from beneath the shelf, it rises again and becomes supercooled adiabatically as the pressure is reduced. This supercooled water nucleates ice crystals that can grow to 0.10 m in diameter and 2–3 mm in thickness. Eventually, these platelet ice crystals rise to the surface, where they become trapped beneath the sea ice cover, eventually producing a semirigid layer of flat, randomly oriented, disk-shaped ice crystals ranging in thickness from approximately 0.1 to 2.0 m. Platelet ice is the most permeable type of sea ice, being composed of approximately 20% ice and 80% seawater by volume (Bunt 1964).

Brine drainage system. Frazil ice and slushy ice, and to a lesser extent rapidly growing congelation ice, initially have a relatively high seawater fraction and a high brine volume

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Figure 2

Close-up view of a cross section of the skeletal layer located at the base of actively growing congelation ice. Seawater, including salts, nutrients, gases, and biogenic material, is often trapped as brine pockets between ice crystal boundaries as they extend downward.

(the proportion of bulk ice volume that is in the liquid phase). As the ice continues to freeze, much of this brine is rejected into the water column through brine channels and tubes that develop within the growing ice (**Figure 1**). Brine drainage continues as long as the brine volume is large enough to ensure connectivity of the brine channels, eventually reducing the bulk salinity of first-year ice to approximately 5–8. Older, multiyear ice can be even fresher because of the additional time available for desalination, with bulk salinities commonly falling to 1. However, once the brine volume drops below 5%, brine tubes become isolated from one another, and desalination due to brine rejection from the ice slows considerably (Golden et al. 1998). Brine rejection can also slow when concentrations of exopolysaccharides (EPSs) produced by microbial communities are sufficient to impede the flow of brine through brine tubes (Krembs et al. 2011).

The salinity of these isolated brine tubes and smaller brine pockets is controlled by the local temperature of the sea ice. Because salts can reduce the freezing point of sea ice, a brine pocket that is saltier than its equilibrium value at a given temperature melts the sides of the brine pocket, thereby increasing the size and lowering the salinity of the pocket until equilibrium is reached. Near the ice surface, where temperatures can be very cold (<20°C), brine salinity within these brine pockets and tubes can exceed 150; near the ice/water interface, where temperatures are warmer (−1.5°C), brine salinity is near that of the underlying seawater (∼35). Because brine volume is controlled by both bulk ice salinity and temperature, as temperatures warm in spring, the brine volume of the ice can increase beyond the 5% threshold required for brine tube connectivity, and desalination can begin again (Golden et al. 1998).

Figure 3

Photographs of (*a*) pancake ice from Antarctica (courtesy of Christopher Peterson), (*b*) ice with melt ponds in the Arctic Ocean (courtesy of Gert van Dijken), and (*c*) old rafted and ridged sea ice in the Antarctic (courtesy of Christopher Peterson).

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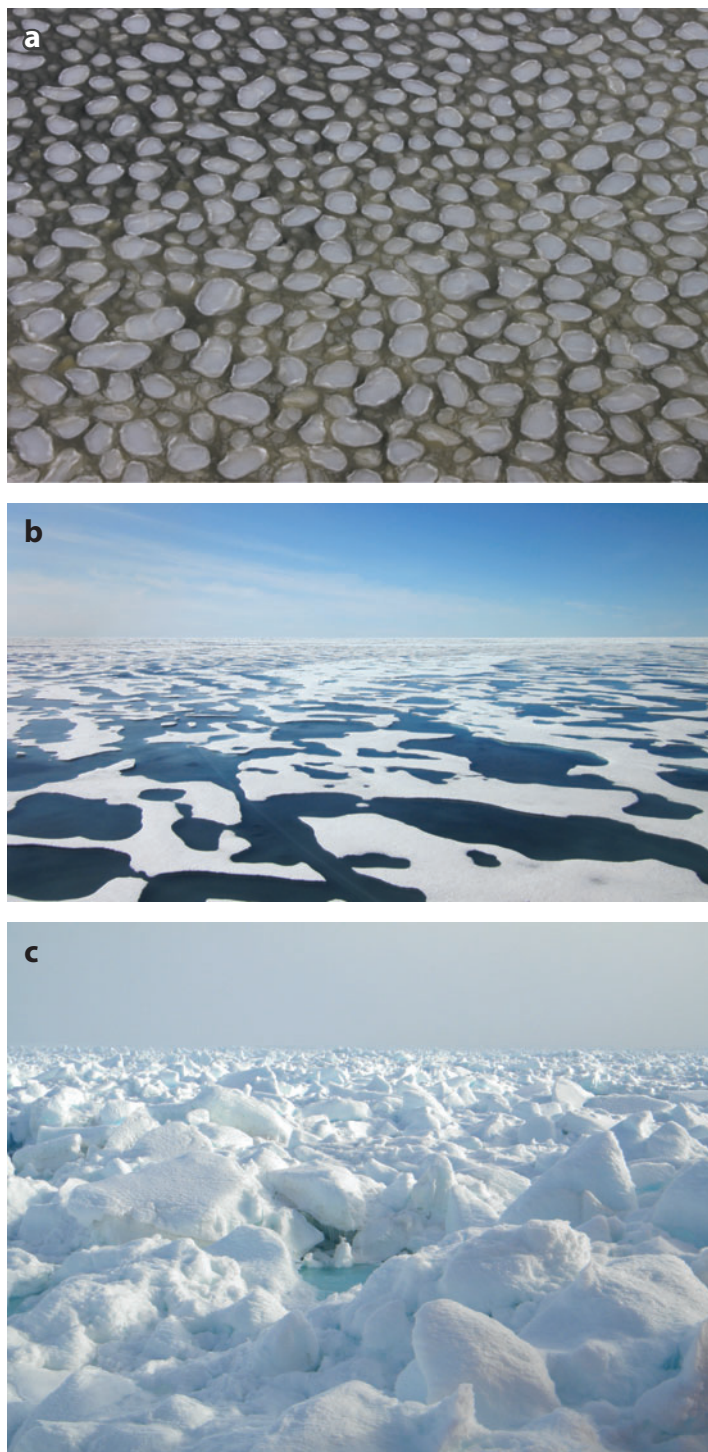
Sea Ice Physicochemistry

Conditions within sea ice are controlled from above by atmospheric forcing and from below by the physical, chemical, and biological environment of the ocean from which the ice is derived.

Temperature. In the simplest case, the temperature gradient within a uniformly flat slab of snow-free ice is controlled by the temperatures of the ocean below and the atmosphere above. At thermal equilibrium, the lower ice surface will be at its freezing point and the upper ice surface will be near the atmospheric temperature, with a linear temperature gradient in between (Maykut 1986). Although this simple case has been observed in nature, the situation is usually more complicated. For example, because the ocean is almost always warmer than the air when ice is present, there is a conductive flux of heat through the ice that generally keeps the surface of the ice warmer than the atmosphere. This reduces the temperature gradient in the ice. Adding an insulating cover of snow allows this conductive heat flux to warm the sea ice even more; the thicker the snow cover is, the smaller the temperature gradient through the ice will be. A snow cover also increases the time required for the ice to reach thermal equilibrium with the atmosphere, with thick, dry snow having a larger impact than thin, wet snow. Snow-covered ice rarely exhibits a simple linear vertical temperature gradient, because atmospheric temperatures change rapidly, and the snow cover slows the rate at which these temperature variations propagate to the ice surface. Flooding events can also perturb the temperature distribution in the ice, because the warm seawater adds a great deal of heat to the ice surface (Fritsen et al. 1994). This heat is eventually conducted away, but the time required depends on the severity and longevity of the flooding event. Finally, rafting of two ice floes initially results in a greatly modified temperature profile for both, although thermal equilibrium can be reached within a week or two under the right conditions.

Nutrients. Processes that trap seawater within the sea ice matrix during initial ice formation also trap dissolved nutrients such as nitrate, phosphate, silicate, and trace metals like iron. In the absence of biological activity, nutrient concentrations in the brine are proportional to brine salinity (Granskog et al. 2003, Melnikov et al. 2003). As a result, whereas bulk nutrient concentrations in the ice are low compared with those in seawater, concentrations in the brine fraction of the ice can be very high when the ice is cold (Werner et al. 2007). However, nutrient assimilation by microalgae and degradation of organic matter by bacteria can markedly alter the nutrient:salinity relationship in brines (Melnikov et al. 2002, Krell et al. 2003, Riedel et al. 2007).

Nutrients can also be brought into the sea ice after the ice has formed. As dense brine flows out of the ice through brine tubes and channels and from between skeletal-layer ridges during the desalination process, it is replaced by an approximately equivalent volume of seawater, with its complement of fresh nutrients (Wakatsuchi & Ono 1983). Surface flooding, which impacts 15–30% of the Antarctic ice pack (Wadhams et al. 1987), also brings new nutrients to the surface layer of the ice (Granskog et al. 2003) that eventually percolate down to lower layers of the floe. If temperatures are low and the ice surface is covered with snow, the flooded snow freezes and rejects salts as the freezing front propagates downward. The resulting convective overturning in the slush layer can replace brine several times before freezing is complete, enhancing microbial growth (Fritsen et al. 1994, Saenz & Arrigo 2012). In addition, once sea ice becomes nearly isothermal in spring, its brine volume increases dramatically, and nutrients are easily flushed through the porous ice structure by tidal currents and other advective processes (Cota & Horne 1989). Finally, dust deposited on the surface of the ice, either directly or transported with snow, contains relatively small amounts of macronutrients but relatively large amounts of trace metals such as iron. These

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nutrients may become available to the sea ice community or to the pelagic ecosystem after the ice has melted (Sedwick et al. 2000, Lannuzel et al. 2007, Aguilar-Islas et al. 2008, Smith et al. 2012).

Contaminants and trace gases. Sea ice frequently contains nonnutrient compounds, including contaminants and trace gases, whose roles are not well understood. Hexachlorocyclohexane, a by-product of insecticide production, has been found to be highly enriched, relative to seawater concentrations, in sea ice of the Canadian Arctic (Pucko et al. 2010), although its origin and impact on the sea ice community are not yet well known. Halocarbons are often enhanced in sea ice, presumably through biogenic production (Sturges et al. 1992, Mattson et al. 2012). The most abundant trace gas in sea ice is dimethylsulfide (DMS), a bacterial breakdown product of dimethyl-sulfoniopropionate (DMSP). This compound is produced by ice algae for use as an osmolyte, a cryoprotectant, or an antifreeze, and can be found in high concentrations within sea ice (Levasseur et al. 1994, Trevena et al. 2003, Trevena & Jones 2006, Delille et al. 2007, Asher et al. 2011).

Sea ice optics. Light is an essential resource for sea ice microbial ecosystems, and its propagation through sea ice has been reasonably well characterized. Snow is a highly scattering medium, and snow-covered ice frequently has an albedo of >80%, although this value declines rapidly for wet snow (Perovich 1990). Light attenuation by snow due to both scattering and absorption is approximately an order of magnitude greater than that of the underlying sea ice, which in turn is approximately an order of magnitude greater than that of seawater (Perovich 1990). Consequently, snow-covered ice transmits very little light to depths more than 1 m below the snow surface (Palmisano et al. 1987, Arrigo et al. 1991, Zvalinsky et al. 2010) and supports very little microbial biomass (Arrigo et al. 2003, Mundy et al. 2005). Even under snow-free conditions, the growth of photoautotrophic organisms living in the ice can be limited by light availability, particularly early in spring, when nutrients are still abundant in the ice brines (Arrigo & Sullivan 1994). However, ice and snow also strongly attenuate harmful UV radiation (Perovich 1993, 1995), particularly UVB (280–320 nm), which is beneficial for algae living at the bottom of the sea ice (Lazzara et al. 2007) and invertebrate larvae living in the water column below (Lister et al. 2010).

Light attenuation within the ice is further enhanced by particle absorption (Arrigo et al. 1991, Fritsen et al. 2011), particularly by sediments in nearshore areas (Lee et al. 2010) and pigment-containing microalgae growing at the bottom of the ice (Arrigo et al. 1991, Ehn et al. 2008). Because these communities can reach high densities, they are able to absorb almost all of the available light; in doing so, they can warm the bottom of the ice, causing it to melt prematurely (Grossi et al. 1987, Zeebe et al. 1996), especially when the ice is free of snow (Mundy et al. 2005).

Sea Ice Habitats

Because of the relative complexity and variability in the structure of polar sea ice, there are a variety of quite different habitats within the ice that are suitable for microbial community development. These include surface melt ponds, internal ice layers, internal spaces within deformed and/or rafted ice, bottom ice (the skeletal layer), platelet ice, and strand communities. The most desirable of these habitats are those that provide ready access to seawater nutrients and receive sufficient light for net photosynthesis by microalgae.

Melt ponds. Melt ponds are common features on Arctic sea ice; they are much less so in the Antarctic. Melt ponds typically form in the Arctic and Antarctic when snowmelt collects on the surface of relatively flat ice into discrete freshwater ponds (**Figure 3b**). They usually contain relatively little biomass owing to their low nutrient concentrations (Garrison et al. 2003). However,

in recent years, increased Arctic temperatures have produced surface ponds that melt completely through the ice, greatly increasing the exchange of nutrients with the underlying water column (Lee et al. 2011). Consequently, these brackish ponds can have significantly higher microbial biomass than the underlying water column (Mundy et al. 2011). Although microbial activity in melt ponds is not as high as it is in other sea ice habitats, it has been proposed that microbes provide an important food source for metazoans before the onset of winter (Lee et al. 2011).

Interior sea ice. Probably the most inhospitable habitat for microbial life in sea ice is in the internal layers of relatively solid, undeformed ice. Although these layers can receive sufficient light for net photosynthesis, they are often very cold and characterized by brine salinities that are too high to support microalgal growth (Arrigo & Sullivan 1992). In addition, the low brine volumes of these internal layers restrict nutrient exchange with the water column below (Golden et al. 1998, 2007). Only after temperatures warm in spring do brine salinities decline and brine volumes increase to the point that nutrient exchange and net microalgal growth in these layers are possible (Garrison et al. 2003, Mundy et al. 2011). However, near the edges and adjacent to cracks in the ice floe, seawater can often infiltrate the internal layers of the ice and create a nutrient-replete gap layer at the freeboard depth (sometimes called an infiltration community), which promotes the development of a rich microbial community inside the ice (Garrison 1991, Kennedy et al. 2002, Kattner et al. 2004). Internal microbial communities can also develop in the void spaces that invariably form when ice floes converge during the rafting/ridging process (Hegseth & Von Quillfeldt 2002). These habitats are common in the Antarctic (**Figure 3c**) and can persist for a few weeks before they eventually melt.

Bottom ice. Bottom ice is often the most biologically productive sea ice habitat owing to its ubiquity, proximity to seawater nutrients, and mild temperature and salinity gradients. Algal biomass accumulations are greatest within the bottom 0.05–0.10 m of the ice, primarily in the skeletal layer, where ice accretion and salt rejection in actively growing sea ice drive convection currents that keep this layer supplied with nutrients. Farther from the ice/water interface, microbial communities become concentrated in and around the numerous brine tubes (500–1,000 m^{-2}) and channels that drain salts from the upper ice and provide light, nutrients, and space for microbial growth (Mundy et al. 2007).

Platelet ice. Because platelet ice is the most porous type of sea ice, facilitating relatively free nutrient exchange with the underlying seawater, it harbors some of the largest microbial accumulations ever measured in sea ice (Arrigo et al. 1993). Algal concentrations tend to be highest in the upper layers of the platelet ice, just below the congelation ice, owing to increased light availability. This is especially true at the peak of the ice algal bloom, when concentrations of chlorophyll *a* (Chl *a*) can climb to >1,000 mg m^{-3} (Arrigo et al. 2010), high enough to attenuate much of the available light and shade populations below. Because of their unusual mode of formation, these highly productive ecosystems are found only in nearshore environments adjacent to floating ice shelves, so they have a limited range in the Antarctic and are virtually absent from the Arctic.

Strand communities. Some species of colonial diatoms (e.g., *Melosira arctica* in the Arctic and *Berkeleya antarctica* in the Antarctic) encase themselves in mucilaginous tubes that are attached to the bottom of the sea ice and suspended into the upper ocean. Rather than consuming nutrients from within the sea ice, these algae take up nutrients directly from the water column, allowing them to accumulate large amounts of biomass and reach lengths of 1 m or more

(Melnikov & Bondarchuk 1987). When the ice melts, large aggregates of these algae sink rapidly to the bottom and provide food for the benthic habitat (Ambrose et al. 2005, Boetius et al. 2013).

Exopolysaccharide Production

EPSs are produced and utilized by many members of the sea ice microbial community, and concentrations in sea ice are much higher than those in the water column below (Meiners et al. 2003, Riedel et al. 2006). EPSs alter sea ice morphology by reducing rates of brine drainage (thereby increasing bulk salinity) and by increasing brine pocket complexity (Krembs et al. 2011). The net result is a sea ice structure that is more suitable for microbial communities. Sea ice diatoms can also take up EPSs in both light and dark (Palmisano & Garrison 1993), an advantage under conditions of light limitation or during overwinter survival.

The rate of EPS production by diatoms (as a fraction of primary production) in sea ice appears to be high (Gosselin et al. 1997, Meiners et al. 2003). The proportion of photosynthate excreted as EPS increases under high light stress because of photorespiration, in which high intracellular oxygen favors RuBisCO oxidation (rather than carboxylation) of carbon-cycle intermediates. Products of photorespiration include low-molecular-weight compounds such as glycolate. Not surprisingly, EPS concentrations in sea ice are variable and positively correlated with concentrations of particulate organic carbon and Chl a (Meiners et al. 2003; Riedel et al. 2006, 2007; Van der Merwe et al. 2009).

Localized concentrations of EPS in sea ice harbor high concentrations of metabolically active bacteria, which use it as an energy source (Meiners et al. 2008). In this way, the presence of EPSs may enhance biogeochemical cycling and nutrient regeneration within the ice (Krembs et al. 2002, Riedel et al. 2007, Meiners et al. 2008). Bacteria also produce EPSs as a way to adhere to solid surfaces and to survive adverse conditions (Poli et al. 2010).

SEA ICE INHABITANTS

Microalgae

The most conspicuous members of the sea ice microbial community are the single-celled microalgae that form the base of the food web and give heavily colonized sea ice its distinctive brown color.

Diversity. Autotrophic communities in sea ice can be diverse (**Figure 4**), and their composition is controlled largely by species-specific responses to temperature, salinity, light, and nutrients (Petrou & Ralph 2011). The most abundant microalgal taxa in sea ice in both the Arctic and Antarctic are the diatoms (Bacillariophyceae). More than 550 diatom species have been identified in the Arctic alone (Il'iash & Zhitina 2009), including 446 pennate (longer in one axis) and 122 centric forms. Individual sea ice communities usually harbor 30–170 different diatom species (Melnikov et al. 2003, Riaux-Gobin et al. 2003, Werner et al. 2007). Pennate forms (e.g., species of the genera *Nitzschia*, *Fragilariopsis*, *Entomoneis*, and *Navicula*) are common in bottom ice (Fiala et al. 2006), particularly in land-fast ice (Ratkova & Wassmann 2005), but also have been noted in surface ice (Whitaker & Richardson 1980, Lizotte & Sullivan 1992, Ryan et al. 2006), infiltration communities (Garrison 1991), and platelet ice (Arrigo et al. 1995), and many form chains of cells. Unicellular forms tend to be large; thus, as either cells or chains, the sea ice diatoms are large (>20 μm) compared with oceanic phytoplankton.

In the Arctic, *Fragilaria*, *Cylindrotheca*, and *Achnanthes* are relatively common unicellular diatom genera, whereas in the Antarctic, large species of *Amphiprora*, *Pinnularia*, *Pleurosigma*, *Synedra*, and *Tropidoneis* are commonly reported, especially in land-fast ice. Centric diatoms (e.g.,
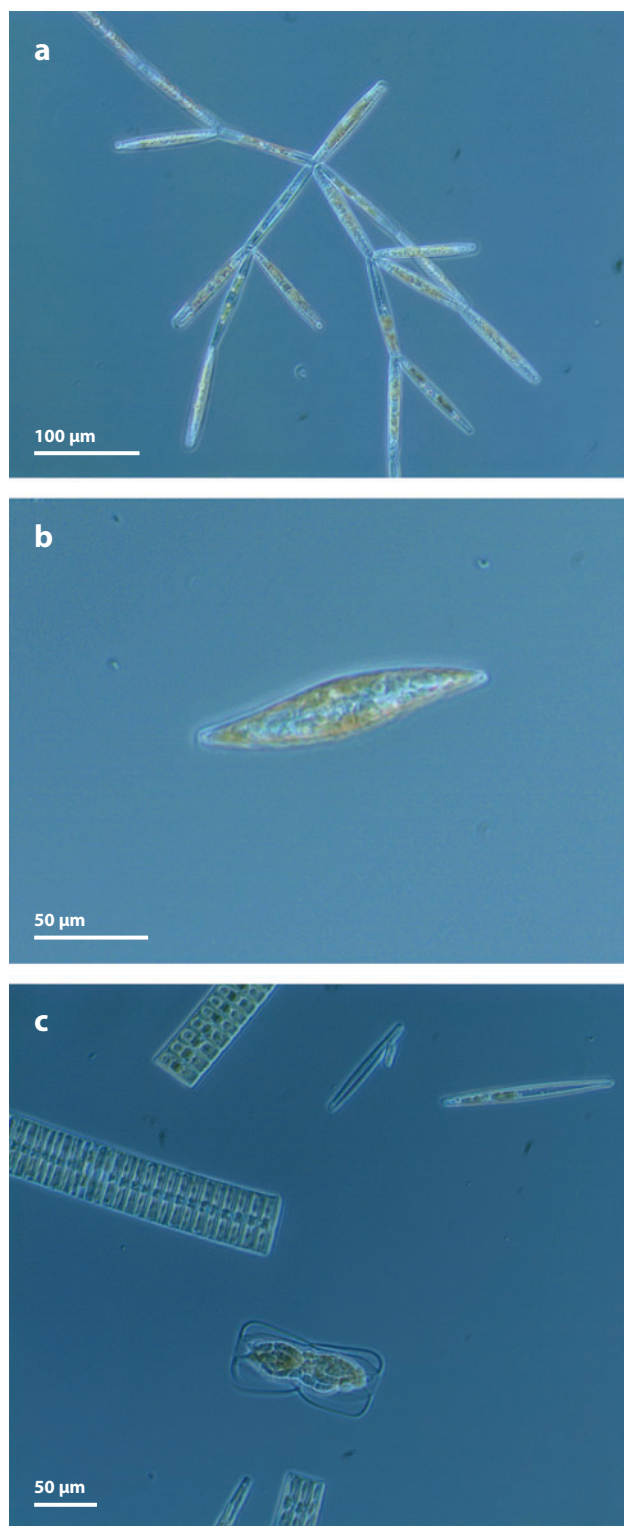
Figure 4

Examples of algae commonly found in sea ice: (*a*) *Synedropsis* sp., (*b*) *Pleurosigma* sp., and (*c*) *Amphiprora* sp. (the bow tie–shaped single cell) and *Fragilariopsis* sp. (the two long chains of cells) (photographs courtesy of Rebecca Gast).

Thalassiosira, *Porosira*, and *Chaetoceros*) are also found in sea ice but generally dominate in recently formed ice or in platelet ice habitats in the Antarctic (Lizotte & Sullivan 1992, Smetacek et al. 1992, Riaux-Gobin et al. 2003).

A few diatom species are associated with the strand communities that grow beneath sea ice, making use of extensive extracellular matrix material that can extend centimeters to meters below the ice bottom. In the Arctic, colonies of the centric diatom *Melosira arctica* can reach lengths of several meters below the ice (Melnikov 1997, Ambrose et al. 2005, Boetius et al. 2013). In the Antarctic, the most common strand-forming species are from the genus *Berkeleya* (Ryan et al. 2006), which can reach lengths of up to 15 cm (McConville & Wetherbee 1983).

Although not as numerous as diatoms, autotrophic flagellates are also found in sea ice from both poles; these include prymnesiophytes (*Phaeocystis*), dinoflagellates (*Gymnodinium* and *Karenia/Karlodium*), prasinophytes (*Mantoniella* and *Pyramimonas*), chlorophytes (*Monoraphidium* and *Chlamydomonas*), silicoflagellates (*Dictyocha*), chrysophytes, and cryptophytes (Arrigo et al. 2003, Gast et al. 2006, Ichinomiya et al. 2007, Eddie et al. 2010, Bachy et al. 2011). Evidence suggests that they may be more common in pack ice than in land-fast ice (Ratkova & Wassmann 2005).

Abundance. Microalgal densities can be very high in sea ice, although the greatest densities are usually restricted to relatively thin layers owing to high light attenuation by ice and self-shading by high concentrations of algal pigments (Arrigo et al. 1991, Lazzara et al. 2007). Algae are most abundant in first-year ice (Fiala et al. 2006), in bottom ice (Garrison et al. 2003), in gap layers and ice cavities within the sea ice interior (Hegseth & Von Quillfeldt 2002, Kattner et al. 2004), in platelet ice (Arrigo et al. 1993), and in strand communities, where access to nutrients is greatest (Melnikov et al. 2002, Michel et al. 2003). Volumetric Chl *a* concentrations range from 3 to 800 mg m^{-3} in the Arctic and from 3 to 10,100 mg m^{-3} in the Antarctic (Arrigo et al. 2010). The depth-integrated biomass per unit area ranges from 1 to 340 mg Chl *a* m^{-2} in the Arctic and from <1 to 1,090 mg Chl *a* m^{-2} in the Antarctic (Arrigo et al. 2010). However, algal abundances in most areas are at the lower end of this range, usually <100 mg Chl *a* m^{-2} (table 8.1 in Arrigo et al. 2010).

Microalgal blooms in sea ice are generally fairly short lived. Algal biomass is usually low in winter (Krell et al. 2003, Ratkova et al. 2004, Werner et al. 2007) owing to insufficient light, low temperature, and high sea ice brine salinity. Concentrations of algae increase rapidly in spring as light and temperature increase and salinity drops (Delille et al. 2002, Riaux-Gobin et al. 2003, Mundy et al. 2005). Given that sea ice may start with only minimal algal biomass from seawater (∼0.01 mg m^{-3}), algal abundance can increase by five to seven orders of magnitude during the bloom. To accumulate this biomass from algal growth via cell division requires 16–20 generations within a growth season of a few months. Blooms often peak in late spring or early summer, just prior to ice melt and subsequent breakup, when the ice is nearly isothermal and increased brine volume allows for enhanced nutrient exchange (Arrigo & Sullivan 1994, Garrison et al. 2005, He et al. 2005). Summer declines in ice algal abundance are related primarily to losses from melting sea ice (Grossi et al. 1987) but also to nutrient limitation and increased grazing pressure (Hegseth & Von Quillfeldt 2002, Elliott et al. 2012). A secondary ice algal bloom may develop in autumn as the ice pack begins to re-form. However, these blooms are usually short lived and accumulate little biomass before environmental conditions become too harsh to support algal growth (Kennedy et al. 2002; Meiners et al. 2003; Garrison et al. 2003, 2005).

Distributions of algal biomass can be very patchy, owing primarily to variations in surface snow cover (Rysgaard et al. 2001, Granskog et al. 2005), because even small differences in snow thickness can have large impacts on light transmission to the ice below (Perovich 1990, Arrigo et al. 1991). However, other factors can also impact patchiness, including ice thickness (Granskog et al. 2005); structural heterogeneities related to ice rafting (Babko et al. 2002); gap-layer formation

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(Kattner et al. 2004); surface flooding (Fritsen et al. 1994); and, in the Arctic, low surface salinity resulting from proximity to rivers (Rysgaard et al. 2001, Kaartokallio et al. 2007).

Activity. The physiological activity of sea ice microalgae is sensitive to ambient salt concentrations, with reductions in photosynthetic efficiency, photosynthetic capacity, and growth rate as salinity diverges from seawater values (Bunt 1964, Grant & Horner 1976, Bates & Cota 1986, Vargo et al. 1986, Kottmeier & Sullivan 1988, Ryan et al. 2004, Krell et al. 2007, Ralph et al. 2007, Eddie et al. 2008). Experiments have indicated that the growth and photosynthesis rates of sea ice algae are reduced to virtually zero at salinities below 5 and above 100, with maximum rates occurring at salinities near 30 (Arrigo & Sullivan 1992, Ryan et al. 2004, Ralph et al. 2007, Eddie et al. 2008). However, acclimation to high or low salinity is possible over both the short term (minutes) (Bates & Cota 1986) and long term (weeks) (Grant & Horner 1976, Vargo et al. 1986).

Sea ice microalgae can acclimate to changes in external salinity within a limited range by altering their internal osmolyte concentration. A widely used osmolyte is DMSP, produced copiously by sea ice diatoms, with concentrations in ice reaching up to 2,910 nM (Trevena et al. 2003, Trevena & Jones 2006). Because sea ice is likely a large source of DMSP and DMS to the surrounding ocean and atmosphere (Trevena & Jones 2006, Delille et al. 2007, Asher et al. 2011), changes in sea ice distributions, and in populations of ice algae acclimating to suboptimal salinity via production of DMSP, can exert important feedbacks on the climate system via the production of sulfate aerosols, which are important cloud nucleation surfaces (Charlson et al. 1987).

Metabolic rates of psychrophilic (cold-loving) algae increase with temperature up to the point where macromolecules become denatured. These rates include those of critical processes like growth (Werner et al. 2007, Eddie et al. 2008), photosynthesis (Mock & Hoch 2005; Ralph et al. 2005, 2007), protein metabolism (Mock et al. 2006), xanthophyll cycling (Mock & Hoch 2005), and nitrogen assimilation (Priscu et al. 1989). The metabolic rate changes with temperature are often quantified in terms of the Q_{10}, which is defined as the ratio of the metabolic rates at temperatures $T°C$ and $T + 10°C$. The photosynthetic Q_{10} for ice algae has been reported to range from 1.0 to 6.0 (Palmisano et al. 1987, Kottmeier & Sullivan 1988, Arrigo & Sullivan 1992) and is generally higher than those observed for temperate phytoplankton, which generally range from 1.9 to 2.3 (Talling 1955, Ichimura & Aruga 1964, Williams & Murdoch 1966, Eppley 1972). Heat- and cold-shock proteins are also produced in response to the stress involved in rapid or dramatic temperature changes (Allen & Ort 2001). Given sufficient time, these metabolic changes allow polar microalgae to acclimate to a wide range of polar temperatures (Mock & Hoch 2005).

Freezing becomes a problem when temperatures drop too low. Ice algae cope with freezing temperatures by producing macromolecules that can inhibit ice crystallization (Raymond & Knight 2003). These molecules often include ice-binding proteins that resemble antifreeze proteins found in other cold-tolerant organisms (Janech et al. 2006). In addition, EPSs secreted primarily by ice diatoms (Meiners et al. 2003; Riedel et al. 2006, 2007) have been measured at very high concentrations in sea ice and also may serve as a cryoprotectant (Krembs et al. 2002).

Sea ice algae can be exposed to a wide variety of light conditions, ranging from extremely low irradiance in bottom ice to physiologically damaging doses of both visible and UV radiation near the sea ice surface. Thus, ice algae have evolved efficient mechanisms for dealing with both extremes (McMinn & Hattori 2006, Rintala et al. 2006). Low light stress is more common (Long et al. 2012), and acclimation can be accomplished on a timescale of hours (McMinn et al. 2003) by increasing light-harvesting potential and photosynthetic efficiency (the amount of carbon fixed per unit light absorbed) (Palmisano et al. 1985, 1986, 1987; Arrigo et al. 1993; Robinson et al. 1995; Lazzara et al. 2007). Light harvesting is enhanced by both increasing intracellular pigment concentrations to expand the absorption cross section of the cell and by producing

accessory photosynthetic pigments (e.g., fucoxanthin and Chl c for diatoms) that absorb light at wavelengths most effective at penetrating the ice and snow (e.g., blue-green light that Chl a is less efficient at absorbing). Photosynthetic efficiency is increased at low light by increasing quantum yields to near the theoretical maximum (0.1 moles of carbon fixed per mole of photons absorbed), assuming sufficient nutrients are available to maximize electron transport (Mock & Kroon 2002a,b; McMinn & Hegseth 2004; Rintala et al. 2006). Electron transport is also enhanced by increasing the proportion of monogalactosyldiacylglycerols, fatty acids that support the fluidity of the thylakoid membrane at low temperature and maintain the velocity of electron flow (Mock & Kroon 2002a,b).

High levels of visible light and UV inhibit photosynthesis in sea ice diatoms by diminishing photosystem II performance and photosynthetic rates (Juhl & Krembs 2010) and increasing DNA damage (Karentz & Spero 1995), which impacts the recovery of the photosynthetic apparatus. High light responses include alternative electron cycling and reduced electron transport (Petrou & Ralph 2011). The response of sea ice diatoms to enhanced UV includes increasing concentrations of photoprotective pigments and mycosporine-like amino acids (Karentz 1994, Ryan et al. 2002) to reduce UV exposure. UV-damaged photosystems can also produce oxygen radicals that can damage other cellular machinery. Ice algae minimize this damage by producing antioxidants such as malondialdehyde, superoxide dismutase, catalase, and peroxidase when UV levels are high (Wang et al. 2009).

Nutrient limitation of ice algal growth is common in habitats that have restricted exchange with the underlying water column. In these interior habitats, growth is often reduced by low temperatures and high salinities. In sea ice habitats where nutrients exchange freely and algal biomass accumulates, regeneration processes can result in nutrient concentrations that are much higher than would be expected given a conservative relationship with salinity (Arrigo et al. 2003, Werner et al. 2007, Meiners et al. 2011). However, nutrients can occasionally fall to growth-limiting levels (Kuosa & Kaartokallio 2006, Lee et al. 2010), especially when external supplies to a previously productive site are cut off. Silicic acid is often cited as the macronutrient most likely to limit algal growth (Gosselin et al. 1990), owing to its low rate of recycling within sea ice relative to nitrogen (Gleitz et al. 1995, Arrigo et al. 2002). However, nitrate uptake is reduced at low temperatures because of reduced rates of active transport (Priscu & Sullivan 1998, Reay et al. 1999). Consequently, nitrogen occasionally becomes limiting in sea ice (Smith et al. 1987, Lizotte & Sullivan 1992), often leading to high rates of fatty acid synthesis by diatoms (Gleitz et al. 1996, McMinn et al. 1999). Micronutrients such as iron are generally in ample supply, as they are generally concentrated in sea ice because of both atmospheric deposition onto the ice surface and high incorporation rates during sea ice formation (Sedwick et al. 2000; Lannuzel et al. 2007, 2008).

Estimates of annual sea ice primary production from direct measurements of ^{14}C uptake are uncommon. A limited number of studies have indicated that annual production is similar in the Arctic and Antarctic, ranging from 2 to 15 g C m^{-2} y^{-1} and from 0.3 to 38 g C m^{-2} y^{-1}, respectively (Arrigo et al. 2010). These rates are consistent with biomass accumulation data from the two regions that represent a minimum estimate of annual production. Melt ponds likely contribute <10% to this total (Lee et al. 2012), with bottom ice responsible for the rest (McMinn et al. 2007). Despite the limited data and high spatial variability (Mock et al. 2003, McMinn & Hegseth 2007), it is likely that even in the most productive sea ice habitats, annual production is <40 g C m^{-2} y^{-1}, similar in magnitude to production in the oligotrophic central gyres of the open oceans. Productivity in most areas is lower than this, equivalent to approximately 1% of annual production in the pelagic environment of polar waters (Arrigo et al. 1997, 1998, 2010; Rysgaard et al. 2001).

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Bacteria and Archaea

Other than viruses, about which little is known in sea ice, the smallest members of the sea ice microbial community are the bacteria and archaea. They are also the most numerically abundant.

Diversity.   Populations of Arctic and Antarctic bacteria are taxonomically similar, showing few signs of the endemism that might be expected given the large geographic distance between the two poles. In some cases, Arctic and Antarctic isolates exhibited 100% similarity (Junge et al. 2002). Most of the bacteria found in ice are heterotrophic, and they include numerous genera of Proteobacteria (Alpha-, Beta-, and Gammaproteobacteria), green nonsulfur bacteria, and even Planctomycetes, the group known for anammox metabolism (Rysgaard & Glud 2004). However, photosynthetic prokaryotes, probably of terrestrial freshwater origin, have also been observed occasionally in Arctic ice; these include cyanobacteria (Ikävalko & Thomsen 1997) and purple sulfur bacteria (Petri & Imhoff 2001). The scant evidence that exists (from 16S rRNA) suggests that archaea make up <10% of the sea ice prokaryotic community (Cowie et al. 2011). In Antarctic sea ice, ∼90% of archaeal clones are close relatives of ammonia-oxidizing Thaumarchaeota, and the rest are aligned with Euryarchaeota (Cowie et al. 2011).

Abundance.   Whereas bacteria are ubiquitous in sea ice, observed at all depths within the ice and in all seasons investigated (Deming 2010), archaea are far less common, having been identified in only a handful of studies (Cowie et al. 2011). Bacterial numbers can range over four orders of magnitude, with small populations ($\sim10^3$ mL^{-1}) in old land-fast ice and cold winter ice and much larger assemblages (10^7 mL^{-1}) and higher turnover rates near the ice/water interface of first-year ice in spring (Thomas et al. 2001, Kuparinen et al. 2007). Cell densities can be high in new ice because of scavenging from the water column during sea ice formation, with enrichment factors of >10 being relatively common (Sullivan & Palmisano 1984). Populations tend to be smallest in winter (Stewart & Fritsen 2004) and increase dramatically through spring (Delille et al. 2002, Kaartokallio et al. 2008) and summer (Delille et al. 2002, He et al. 2005) in response to increasing organic carbon supplies made available by the developing ice algal bloom. This carbon is eventually transferred from bacteria to phages and protists, especially at higher sea ice melt rates (Boras et al. 2010). Protists seem to play a particularly important role in controlling bacterial populations (Delille et al. 2002) and transferring carbon to higher trophic levels (Boras et al. 2010).

Activity.   Unlike most marine bacteria, sea ice bacteria are highly culturable (>60%) and readily grow in artificial media (Junge et al. 2002). In addition, a higher fraction of the cells in sea ice are metabolically active, indicating that sea ice is a more favorable bacterial habitat than the water column (Martin et al. 2010).

Bacterial respiration can be highly variable in sea ice (2–22 mg C m^{-3} d^{-1}), and despite their low abundance relative to autotrophs in spring (Kaartokallio et al. 2008), bacteria are capable of consuming a substantial fraction of sea ice primary production (Nguyen & Maranger 2011), particularly in summer, when they can make up the bulk of the microbial biomass (He et al. 2005). In doing so, bacteria also remineralize organic nitrogen and phosphorus into NH$_4$ and PO$_4$, often resulting in extremely high concentrations within the sea ice matrix (Arrigo et al. 2003). High respiration rates in sea ice can reduce ambient O$_2$ concentrations and favor denitrification and anammox (Rysgaard et al. 2008), possibly resulting in significant production of N$_2$ gas (Rysgaard et al. 2004) and losses of fixed nitrogen. Bacterial metabolism may also be augmented by proteorhodopsins, which have been observed in active bacterial cells within the classes

Figure 5

Examples of heterotrophic protists commonly found in sea ice: (*a*) unidentified scuticociliate, (*b*) *Polykrikos* sp., and (*c*) *Myrionecta* sp. (photographs courtesy of Rebecca Gast).

Alphaproteobacteria, Gammaproteobacteria, and Flavobacteria (Koh et al. 2010). The molecules are used as proton pumps that maintain the pH gradients required to make the ATP used to fuel cell metabolism.

Although most bacteria are free living, some epiphytic bacteria live in a mutualistic relationship with sea ice diatoms and contribute significantly to the diatoms' antioxidant defenses. These bacteria produce enzymes (catalase, superoxide dismutase, and glutathione reductase) that help to eliminate the reactive oxygen species produced by diatoms. In turn, these bacteria consume organic substances secreted by diatoms (Hünken et al. 2008). This interspecies H_2O_2 reduction might benefit diatom growth under high light stress, where most of the H_2O_2 is being produced.

Heterotrophic Protists

Protists are the main consumers of microalgae, bacteria, and archaea in sea ice. They come in a variety of forms, and many are unique to the sea ice environment (**Figure 5**).

Diversity. Although comprehensive estimates of the diversity of heterotrophic protists are currently lacking, a wide variety have been observed in sea ice (Caron & Gast 2010). Some of these taxa are endemic to polar regions, whereas others can be found in adjacent seas (Lovejoy et al. 2006). A high degree of similarity in protist assemblages has been observed at both large spatial scales (Thomson et al. 2006) and throughout the year (Garrison et al. 2005). Gast et al. (2004) showed that there is a high degree of endemism among the protistan assemblages within different microhabitats of sea ice and between sea ice and seawater. The primary source of sea ice protists is the underlying water column, but Gast et al. (2004) showed that either there are major shifts in the dominance of species after incorporation into the ice, or morphologically similar but genetically distinct strains are present.

Among the most conspicuous heterotrophic protists in sea ice are the ciliates (Delille et al. 2002, Garrison et al. 2005, Fiala et al. 2006), which include the filter-feeding tintinnids and strombidiids (Garrison 1991); the particle-associated spirotrichs, heterotrichs, and hypotrichs; and the bactivorous oligohymenophoreans (Petz et al. 1995, Song & Wilbert 2000). Flagellates are also common in sea ice (Ratkova et al. 2004, He et al. 2005); this group includes heterotrophic and kleptoplastidic dinoflagellates (Garrison 1991, Stoecker et al. 1993, Sime-Ngando et al. 1997,

Michel et al. 2002, Thomson et al. 2006) [the latter with chloroplasts that have been preserved from its cryptophyte food (Park et al. 2006)], choanoflagellates (Lovejoy et al. 2006), cercozoans (Garrison & Buck 1989), and euglenoids (Caron & Gast 2010). Finally, amoeboid protists are also found in sea ice, although the naked forms (Gymnamoebae) are often difficult to isolate. Easier to identify are the more conspicuous skeleton-forming foraminifera, acantharia, and radiolarians.

Abundance. As is the case for autotrophs and prokaryotes, the abundance of heterotrophic protists can be orders of magnitude higher in sea ice than in the surrounding seawater (Garrison 1991, Sime-Ngando et al. 1997). After initial incorporation, the abundance of protists in ice appears to be correlated with the abundance of bacteria and algae, their primary food sources (Delille et al. 2002, He et al. 2005, Fiala et al. 2006, Ichinomiya et al. 2007).

Activity. Heterotrophic protists appear to be capable of growing at salinities ranging from nearly freshwater to triple seawater concentrations (Thomson et al. 2006). In contrast, feeding and growth rates of heterotrophic sea ice protists tend to be reduced at low temperature (Rose & Caron 2007). However, the effects of temperature on gross growth efficiency are unclear, so the net ecological impact of this growth rate reduction is unclear (Caron & Gast 2010). Microbial food webs in sea ice appear to be complex, with heterotrophic protists employing a wide range of nutritional strategies, including mixotrophy (Moorthi et al. 2009), grazing on ice algae (Michel et al. 2002), bactivory (Laurion et al. 1995), and predation on other protists (Gowing & Garrison 1992).

Metazoans

Because sea ice provides a solid substrate at the ocean surface, it harbors some species that are unique to the ice, some that normally live in the benthos, and pelagic species that enter the ice to either feed or find refuge from predation.

Diversity. A relatively small number of metazoans have been found in association with sea ice. Most of these inhabit the water column near the ice/water interface, but some live within the sea ice matrix. Among the gelatinous zooplankton, cnidarians have been observed in Arctic ice (Bluhm et al. 2007, Piraino et al. 2008), and ctenophores have been seen in the Antarctic (Kiko et al. 2008). A few species of rotifers (Friedrich & De Smet 2000) and nematode worms have been found in sea ice (Reimann & Sime-Ngando 1997), mostly in the Arctic. The only mollusk representatives in sea ice are the occasional nudibranch and the larvae of gastropods (Gradinger & Bluhm 2005). Among the annelids, both turbellarians and polychaetes live in sea ice (Gradinger & Bluhm 2005). Arthropods living in the ice include amphipods and harpacticoid, cyclopoid, and calanoid copepods (Guglielmo et al. 2007, Schnack-Schiel et al. 2008).

The ice/water interface is home to a more diverse array of crustaceans (Conover et al. 1986, Bluhm et al. 2010), especially copepods, amphipods, and euphasiids, as well as small fish. Turbellarians and numerous planktonic forms of invertebrate larvae are also found there (Conover et al. 1990).

Abundance. Metazoan abundance can be patchy as a result of the highly variable ice and snow cover and corresponding variability in the sea ice microbial community. Owing to the life history strategies of the different metazoan inhabitants of the ice, temporal variability can also be high, with population increases of one to four orders of magnitude between spring and summer (Gradinger & Bluhm 2005). Arthropods tend to be the most abundant metazoan group in sea ice. The largest

changes are often associated with larval forms of polychaetes and crustaceans, which can occasionally account for >90% of the metazoan population in sea ice (Schunemann & Werner 2005).

Activity. Some metazoans are occasional visitors to the sea ice, grazing on sea ice biota opportunistically when food concentrations are high. These include the gelatinous zooplankton (Bluhm et al. 2007, Kiko et al. 2008, Piraino et al. 2008) and larval molluscs (Gradinger & Bluhm 2005). Other forms, such as annelids and crustaceans, are more permanent residents (Gradinger & Bluhm 2005, Guglielmo et al. 2007, Schnack-Schiel et al. 2008).

Because of the patchy distribution of most metazoans, there seems to be little top-down control of microbial populations. Some are effective predators, yet their numbers are too low until late in the season to have a substantial impact on algal populations (Gradinger & Bluhm 2005). It is still unclear to what degree metazoans feeding on the ice transfer this energy to the pelagic or benthic ecosystems.

RELATIONSHIP BETWEEN SEA ICE AND THE PELAGIC ENVIRONMENT

Because sea ice is located at the interface of the ocean and atmosphere, its presence affects a variety of important processes, including exchange of heat and gases, transmission of light to the upper ocean, and fluxes of freshwater. The fact that it also often harbors a highly concentrated biological community at the ocean surface has important implications for the much more dilute water column below.

When sea ice algal communities reach their seasonal peak in spring, their associated pigment concentrations can absorb a large fraction of the available light, thereby reducing the amount of light available to the upper water column (SooHoo et al. 1987, Arrigo et al. 1991). Consequently, water column blooms of phytoplankton are delayed until after the ice algal bloom has subsided, even in situations where sea ice has become thin enough to transmit sufficient light for net phytoplankton growth in the waters below (Arrigo et al. 2012). Thus, the timing of sea ice algal blooms often controls the timing of the subsequent phytoplankton bloom.

Once the sea ice has begun to melt, the bottom ice algal community is often released into surface waters rapidly and in a large pulse (Grossi et al. 1987, Suzuki et al. 2001, Juul-Pedersen et al. 2008). Some of the algal cells remain in the surface waters and provide seed stock for the phytoplankton blooms that frequently form at the receding ice edge (Haecky et al. 1998, Mangoni et al. 2009). The effectiveness of this seeding process depends on the ability of the ice algae to resist sinking (Riebesell et al. 1991) and to acclimate to the much higher light levels in the ice-free surface ocean (Mundy et al. 2011, Palmer et al. 2011). Generally, small diatoms are the most common microalgal forms in both the sea ice and the ice edge bloom (Arrigo et al. 2003).

Some of the ice algae that do not remain suspended in surface waters are eaten by pelagic grazers as they sink through the water column. Ice algae have recently been identified in the diets of zooplankton by their unique lipid composition, which includes the 25-carbon lipid IP25 (where IP stands for ice proxy). Recently, IP25 concentrations in pelagic zooplankton were shown to be greatest when ice algae are released from the melting sea ice, indicating a relatively high fraction of sea ice diatoms in their diet (Brown & Belt 2012). This is consistent with historical observations of high krill densities beneath the ice throughout the year (Flores et al. 2011, 2012). Ice algal food is also important because it is rich in polyunsaturated (Søreide et al. 2010) and other essential fatty acids (McMahon et al. 2006) that are produced exclusively by algae and are required for successful zooplankton growth and reproduction. Søreide et al. (2010) found that female copepods (*Calanus glacialis*) utilize these high-quality ice algae to fuel early maturation

and reproduction, and their resulting offspring have access to ample high-quality food during the subsequent phytoplankton bloom.

Algae not eaten during their descent through the water column settle on the seafloor (Ratkova & Wassmann 2005). *Melosira* colonies can sink rapidly and have been observed on the seafloor thousands of meters below the surface virtually intact and being actively consumed by benthic invertebrates (Boetius et al. 2013). Ice algae can also be recognized in the sediment by the presence of IP25, which constitutes a useful proxy for reconstructing historical sea ice extent (Vare et al. 2010, Brown et al. 2011). Ice algae tend to be enriched in ^{13}C relative to pelagic phytoplankton (Rau et al. 1991), and their unique ^{13}C signatures have been used to show that the diet of benthic invertebrates living below sea ice can consist of 5–100% sea ice algae (Wing et al. 2012). These benthic fauna can respond rapidly to the episodic deposition of sea ice algae to the seafloor, showing signs of feeding within a few hours (McMahon et al. 2006) and fully consuming the food pulse in 7–19 days (McMahon et al. 2006, Sun et al. 2007).

SEA ICE ECOSYSTEMS AND CLIMATE CHANGE

Climate change has resulted in a dramatic loss of sea ice in the Arctic and a redistribution of sea ice in the Antarctic, with losses in the Weddell Sea and increases in the Ross Sea (Stammerjohn et al. 2012). These changes in sea ice cover are sure to impact ice algal communities via changes in physical forcing and biogeochemical cycling as well as alterations in trophic interactions due to loss of habitat (Melnikov 2005, Aguilar-Islas et al. 2008, Nishi & Tabeta 2008, Boras et al. 2010, Hendry et al. 2010, Johannessen & Miles 2011, Fountain et al. 2012).

Model results suggest that mild climate change might actually increase ice algal production while reducing phytoplankton productivity through increased stratification (Tedesco et al. 2012). However, higher temperatures could intensify heterotrophic processes in sea ice, increasing rates of grazing and nutrient regeneration (Melnikov et al. 2009). There are limits, however, and despite possible short-term increases in ice algal production (Melnikov et al. 2009), shrinking sea ice cover will eventually decrease the relative proportion of annual production contributed by sea ice to Arctic marine ecosystems (Johannessen & Miles 2011).

Earlier melting of the highly reflective snow cover could also accelerate the timing of ice algal blooms (Wassmann & Reigstad 2011). The impacts of an earlier bloom season are hard to predict, but a timing mismatch between the production of high-quality food and the reproductive cycle of key Arctic grazers may have negative consequences for the entire lipid-driven Arctic marine ecosystem (Søreide et al. 2010). In the Antarctic, a loss of sea ice and its associated algal community will likely reduce the survival of postlarval krill, a critical food source for many upper-trophic-level organisms, such as fish, seals, and baleen whales (Nicol et al. 2008). Thus, the importance of sea ice algae as a winter food source indicates that a loss of sea ice would likely have profound ecological ramifications throughout the Antarctic food web (Flores et al. 2012).

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