

Chapter 9

Arctic Ice Shelf Ecosystems

Anne D. Jungblut, Derek Mueller, and Warwick F. Vincent

Abstract Arctic ice shelves are microbial ecosystems with a rich biodiversity. Until recently, polar ice shelves were seen as mostly abiotic glaciological features, however they are oases for life, with snow, meltwater pools and sediments providing cryohabitats for microbiota. The biological communities are composed of diverse forms of microscopic life, including cyanobacteria, heterotrophic bacteria, viruses, algae, other protists and microfauna, and occupy a variety of habitats: supraglacial meltwater lakes, englacial microhabitats within the ice and snow and planktonic environments in ice-dammed, epishelf lakes. These habitats are defined by seasonal light availability, cold temperatures and nutrient poor conditions. In the supraglacial pools, production is dominated by benthic microbial mat assemblages that have diverse stress adaptation systems and that use internal nutrient recycling and scavenging strategies. Despite short growth periods and perennial low temperatures, biomass accumulations are considerable, with a striking diversity of light-harvesting, UV-protection and other accessory pigments. The chemical characteristics such as conductivity and origin of salts are defined by the underlying ice types, and microbial mat studies from adjacent habitats show a high resilience to solute concentration during freeze-up. The structural integrity of these cryoecosystems is dependent on ice, and they are therefore vulnerable to climate change. Many of these unique Arctic ecosystems have been lost by ice shelf collapse over the last two decades, and they are now on the brink of complete extinction.

A.D. Jungblut (✉)

Centre d'Études Nordiques (CEN), Institut de biologie intégrative et des systèmes (IBIS) and Département de Biologie, Laval University, Quebec City, QC, Canada

Life Sciences Department, The Natural History Museum, London, UK
e-mail: a.jungblut@nhm.ac.uk

D. Mueller

Department of Geography and Environmental Studies, Carleton University,
Ottawa, ON, Canada
e-mail: derek.mueller@carleton.ca

W.F. Vincent

Centre d'Études Nordiques (CEN), Takuvik Joint International Laboratory and Département de Biologie, Laval University, Quebec City, QC, Canada
e-mail: warwick.vincent@bio.ulaval.ca

Keywords Arctic ecosystems • Benthic • Biological production • Cryosphere • Ice shelf • Microbial biodiversity

9.1 Introduction

Polar ice including snow, glaciers, lake-ice and sea-ice is no longer considered an abiotic feature of the environment, but instead it is now realized to provide a broad suite of habitats for biological communities that survive and sometimes thrive in these extreme conditions (Prisco and Christner 2004; Boetius et al. 2015). Ice shelves have long been recognized as a compelling example of the biological richness of polar cryohabitats, as dynamic ecosystems that contain a remarkable diversity of life, most of it microscopic (Vincent 1988). Biological communities occur within and at the base of meltwater ponds (supraglacial ecosystems) and in meltwater microhabitats within the ice and snow (englacial ecosystems). Epishelf lakes are an additional ecosystem type that occur where ice shelves block the head of fiords and embayments, retaining a layer of freshwater (that has flowed in from terrestrial sources) over the marine water below. Given the complete dependence on ice for their structural integrity, each of these ecosystem types (supraglacial, englacial and epishelf) is highly vulnerable to climatic change.

The study of Arctic ice shelf ecology has been ongoing since the discovery of novel microbial communities on the Ward Hunt Ice Shelf in 1998 (Vincent and Howard-Williams 2000). In this chapter we review what has been learned to date about these ecosystems, and where scientific investigation has not yet occurred, we draw on literature from analogous environments (e.g., Arctic freshwater and marine ecosystems, Antarctic ice shelves and other cryoecosystems) to fill in these knowledge gaps. First, we introduce the general physical and chemical characteristics of the Canadian Arctic ice shelves as habitats for life. We review the biology of the supraglacial environments of ice shelves, from microscopic to macroscopic biota, and then describe the environmental and biological characteristics of epishelf lakes. We conclude this review by examining the significance of Arctic ice shelf ecosystems for insights into biological adaptation to environmental extremes, for an improved understanding of biotic-physical interactions in the cryosphere, and as ecosystems on the brink of extinction as a result of human induced climate warming.

9.2 Supraglacial Meltwater Lakes

9.2.1 *Physical Characteristics*

The surface of Arctic ice shelves is marked by an undulating topography or ‘rolls’ (Holdsworth 1987; Jeffries 2017), which created difficulty for travel by the early explorers to the region who referred to them as a ‘long fringe of large and

troublesome hummocks' (Nares 1878, cited in Vincent et al. 2001). In summer, the troughs between these hummocks fill with meltwater, and form long (1–15 km), narrow (10–100 m) and shallow (<3 m) lakes (Fig. 9.1). These Arctic supraglacial meltwater lakes are roughly parallel to each other and to the coastline, but become more chaotic in form and orientation behind any substantial obstruction (i.e., in fiords or behind islands). This parallel orientation has led some to conclude that these features are maintained by prevailing westerly winds (Holdsworth 1987). At times, lakes occupying bifurcating troughs have been observed to drain (or spill over) into each other. These long lakes can also drain completely if deep cracks form in the ice shelf and provide a conduit to the ocean below (e.g., during the 2002 Ward Hunt Ice Shelf break-up event; Mueller et al. 2003a).

Depressions in the ice surface, such as these long lakes, meltponds of variable size and small melt holes, termed cryoconite holes, collect sediment over time. This sediment is colonized by microbiota forming a matrix known as a microbial mat. Microbial mats on these ice shelves are dominated by cyanobacteria, vary greatly in their thickness and extent and may be emergent and exposed to the air, or covered by snow, ice or water (Mueller et al. 2006). Research on the physical and chemical aspects of supraglacial meltwater lakes, ponds and cryoconite holes has focused on variables likely to be of importance to the biology of the benthic microbial mats and, to a lesser extent, water column plankton.

Photosynthesis is the primary means of capturing energy within microbial mats, and *in situ* irradiance levels are therefore of critical importance for these consortia. The irradiance experienced by the mats may not increase until long after polar



Fig. 9.1 Elongated meltwater ponds on the Ward Hunt Ice Shelf in the Canadian High Arctic on July 18, 2003

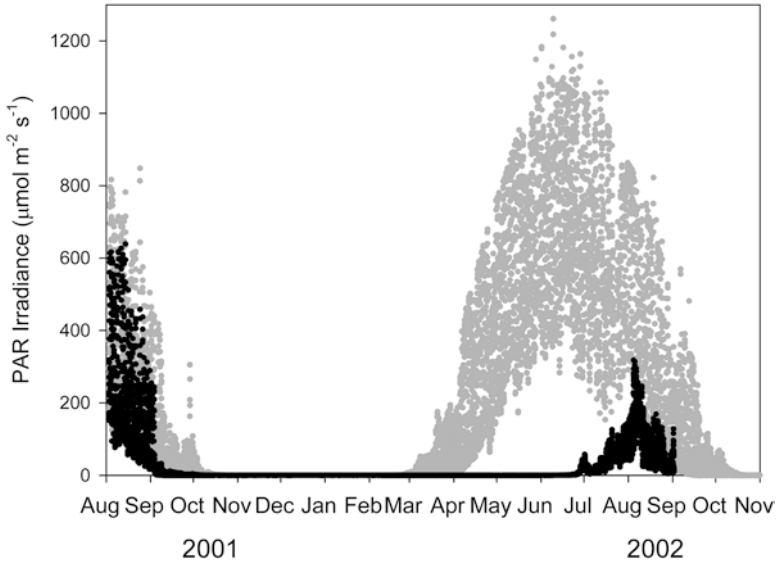


Fig. 9.2 Downwelling PAR irradiance (*grey*) from August 2002 to August 2003 on Ward Hunt Ice Shelf compared with irradiance 14 cm above the surface of a microbial mat (*black*) (From Mueller and Vincent (2006), © John Wiley & Sons. Ltd., used with permission)

dawn, once the snow and ice covering the lakes begins to melt (e.g., June or July, Fig. 9.2; Mueller and Vincent 2006). Solar energy is transmitted through the ice and absorbed by the microbial consortia and associated sediment, and the resultant heat begins to melt the ice above. The ice cover may persist throughout the entire melt season, but with a change in form from solid ice to vertically-oriented ice prisms ('candles') via preferential melting at the crystal boundaries. This ice candling contributes to light scattering and prevents much of the light from reaching the microbial mats (Fig. 9.2). At the height of the melt season, shading by the overlying ice and snow can reduce Photosynthetically Active Radiation (PAR) levels to 15% of ambient. However, this reduction in irradiance does not appear to affect the productivity of microbial mats, owing to their ability to acclimate to reduced irradiance (see Sect. 9.3.6; Mueller et al. 2005; Mueller and Vincent 2006; Hawes et al. 2008).

If the lake ice cover melts completely, then the downwelling irradiance is usually a little below ambient in-air values due to the albedo of the water surface and absorption of light in the water column. However, it is possible for the irradiance experienced by the benthic microbial mats to exceed atmospheric levels due to reflection from ice and snow that surround the lake. During a typical summer, a thin ice cover can form at any time on these lakes, and by late August or early-September the seasonal ice cover is re-established and thickens. In the presence of clear conglomeration ice, irradiance values at the lake bottom will drop somewhat, but if snow covers the ice, then light levels below will plummet further, long before the polar night begins.

Research on Arctic ice shelf biota has also characterized the temperatures that organisms are subjected to in their cryo-habitats. During the winter on the Ward Hunt Ice Shelf, the mean temperature in benthic mats in frozen ponds (-17°C ; Mueller and Vincent 2006) is typically higher than the mean temperature of the air (-26°C ; 01 September 2001 to 31 May 2002, Mueller unpublished). This relative warmth comes from the release of latent heat as the lake freezes and the insulation by snow from the colder air above. Some deep meltwater lakes on Antarctic ice shelves are even known retain a liquid core as a result of these effects (Hawes et al. 1999). Temperatures in the frozen microbial mats at the bottom of several ponds on the Ward Hunt Ice Shelf descended to an average minimum of -17°C in April after a long period of cumulative heat loss to the ice above and below (Mueller and Vincent 2006). Even at these temperatures, it is possible that metabolic activity can continue within the mats (Rivkina et al. 2000), albeit at a minimal rate (Price and Sowers 2004; see Sect. 9.3).

The snow and ice that insulates and protects benthic microbial mats from the Arctic winter air also retards their melt-out in the spring. For example, in one study, surface air temperatures on the Ward Hunt Ice Shelf exceeded 0°C in the first week of June 2002, yet several sub-nival microbial mat environments remained below 0°C until late June and early July (Mueller and Vincent 2006).

Due to their relatively low albedo, microbial mats begin to warm when solar radiation penetrates their overlying ice and snow cover. This can occur rapidly if the snow layer is removed, leaving only transparent ice between the microbial mat and the atmosphere. Once melted, the temperature of the microbial mats in the meltwater lakes and ponds does not rise appreciably above 0°C , since the absorbed solar energy and sensible heat flux are dissipated via melting of the surrounding ice. In contrast, microbial mats that are exposed on thick beds of sediment can warm to several degrees above freezing due to solar heating. Using temperature observations, an average growth season of 65 days was inferred for microbial mat communities on the Ward Hunt Ice Shelf in 2002 (Mueller and Vincent 2006, Fig. 9.3). This was slightly longer than the 61 days in 2002 when air temperature was above 0°C , likely due to enhanced absorption of solar radiation and meltwater production in the microbial mats. Temperatures in the microbial mats decrease below 0°C once the water column above freezes completely.

9.2.2 Conductivity and Origin of Salts

Arctic ice shelves are composed of two fundamental ice types: ice of marine origin and ice of meteoric origin (Mueller et al. 2006). Consequently, meltwater chemistry depends on which ice type is exposed at the ice shelf surface. For example, ice that is formed from melted and refrozen precipitation has a very low conductivity (on average $41 \mu\text{S cm}^{-1}$) in contrast to areas where ancient sea ice is exposed at the surface (on average $1260 \mu\text{S cm}^{-1}$; Mueller et al. 2006). The ionic composition of

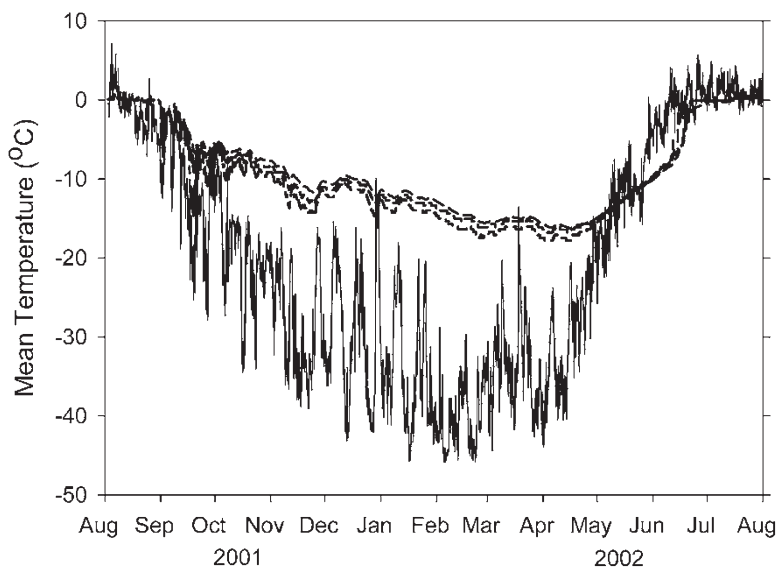


Fig. 9.3 Mean surface air and microbial mat temperatures on Ward Hunt Ice Shelf. Air temperature (*solid line*) versus the temperature within three microbial mats (*dashed line*) between August 2001 and August 2002 (From Mueller and Vincent (2006), © John Wiley & Sons, Ltd., used with permission)

surface meltwater can also be influenced by wind-blown sediments, which alters the relative concentration of ions (Mueller et al. 2006).

Meltwater ponds on the Arctic ice shelves have conductivities that typically range from 50–5700 $\mu\text{S cm}^{-1}$, with bottom water conductivities that can reach up to 10,200 $\mu\text{S cm}^{-1}$, based on measurements on the Ward Hunt and Markham ice shelves (Mueller et al. 2005; Mueller and Vincent 2006). However, these values are much lower than conductivities found on the McMurdo Ice Shelf in Antarctica which range from 100–50,000 $\mu\text{S cm}^{-1}$ (Howard-Williams et al. 1990). Similar to the McMurdo Ice Shelf, the ratio of potassium to chloride in meltwater from certain regions of the Ward Hunt Ice Shelf indicates a marine origin, while the sulphate to chloride ratio is much higher; this is consistent with the redissolution of mirabilite precipitated during the freezing of seawater (de Mora et al. 1994; Vincent et al. 2000). A marine origin of parts of the Ward Hunt and Markham ice shelves is further supported by the presence of marine sediments and remains of sponges, molluscs and benthic crustaceans on the surface of the ice shelves, due to the freeze-on of these materials to the bottom of the ice shelf followed by eventual release at the surface of the ice shelf following many years of surface ablation (Vincent et al. 2000, 2004).

The presence of an ice cover on these lakes and ponds determines to a great extent whether their water columns will be mixed. Even when a lake itself mixes, water in cryoconite holes on the lake bottom may remain stratified, with conditions at the sediment/water interface being vastly different than the lake in general. This

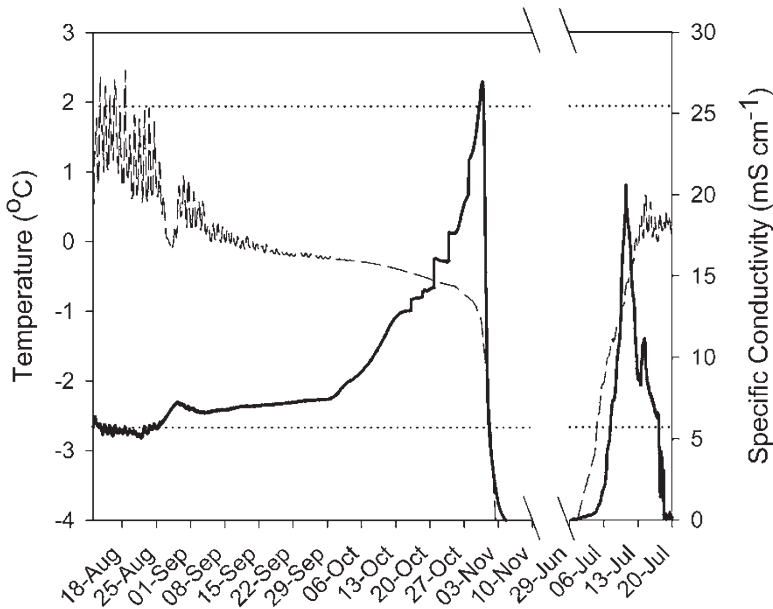


Fig. 9.4 Freeze-up and thaw of a meltwater pond on the Ward Hunt Ice Shelf. Specific conductivity (solid line) and temperature (dashed line) measured at the bottom of a 9.4 m³ meltwater lake. Horizontal dotted lines indicate the mean of half-hourly observations for temperature (upper line) and specific conductivity (lower line) during open-water conditions (23 July to 10 August 2002) (From Mueller and Vincent (2006), © John Wiley & Sons, Ltd., used with permission)

discrepancy is more pronounced in areas where marine ice underlies the lakes and provides a source of salts, which promotes density stratification (Mueller and Vincent 2006).

As meltwater lakes freeze, solutes in the water are rejected from the freezing front and concentrate in the water column below. In one study lake on the Ward Hunt Ice Shelf, this phenomenon increased the conductivity of the remaining water over time, which caused a slight freezing point depression (-1.3°C) before the phase change occurred (Mueller and Vincent 2006; Fig. 9.4). This increase in salinity is a function of the subjacent ice type (marine or meteoric), freezing rate and elevation relative to sea level of the lake in question. In the case of one 9.4 m³ pond, the bottom froze at the end of October 2002, 52 days after the air temperature went below freezing (Mueller and Vincent 2006). The conductivity near the microbial mats increased fourfold (from 5700 to 27,000 $\mu\text{S cm}^{-1}$) during freeze-up which suggests that salinity is not only spatially heterogeneous in the ice shelf cryo-ecosystem but also varies substantially with time (Mueller and Vincent 2006). Studies on microbial mats in the nearby Ward Hunt Lake have shown that the photosynthetic communities are highly resistant to the major increases in salinity that may be associated with solute concentration during freeze-up (Lionard et al. 2012).

9.2.3 *Nutrients and Organic Matter*

Polar freshwater ecosystems are usually considered to be ultra-oligotrophic, with the phytoplankton community biomass severely constrained by limited nutrients (Vézina and Vincent 1997). However, the microbial mat communities may escape this constraint because nutrients may become trapped over time within the diffusion-limited mat matrix and made available through decomposition of dead biomass (Vincent et al. 1993; Bonilla et al. 2005). In addition to recycling nutrients, there is evidence based on $\delta^{15}\text{N}$ signatures that nitrogen may be fixed by the benthic heterocyst-forming cyanobacteria that exist within these mats (Mueller and Vincent 2006).

Analysis of nutrient concentrations within the microbial mats illustrates how the mat microenvironment is dissimilar from the rest of the ice shelf habitats. Studies of Ward Hunt and Markham ice shelf mats on northern Ellesmere Island show they have two to five orders of magnitude more dissolved inorganic carbon (DIC) and ammonium-N than found in the overlying water column (Mueller and Vincent 2006). Other nutrients, such as dissolved organic carbon (DOC), total dissolved nitrogen, nitrate, nitrite, total dissolved phosphorus and soluble reactive phosphorus are two orders of magnitude more concentrated in the microbial mat than in the overlying water. A metagenomic analysis of microbial mats from the Ward Hunt and Markham ice shelves (Varin et al. 2010) showed that they contained diverse nutrient scavenging systems including genes for transport proteins and enzymes converting larger molecules into more readily assimilated inorganic forms (allantoin degradation, cyanate hydrolysis, exophosphatases, phosphonases). These molecular results underscored the capability of ice shelf mats to retain and recycle nutrients in the benthic microenvironment.

Analysis of nutrient concentrations in the water column of ponds of the Markham Ice Shelf showed that dissolved reactive phosphorus levels were high enough to exclude P-limitation, however inorganic nitrogen concentrations were relatively low and the supply of nitrogenous nutrients may have limited phytoplankton biomass (Mueller and Vincent 2006; Mueller et al. 2006). Thus ice shelf supraglacial ponds contain two disparate communities that differ in nutrient status: nutrient-limited plankton and the nutrient-replete benthic mats, consistent with observations on land-based water bodies in the High Arctic (Bonilla et al. 2005).

In one study, coloured dissolved organic matter (CDOM) in the benthic mat pore water was similar in composition to that in the overlying water, based on the McKnight ratio (fluorescence index, McKnight et al. 2001). The CDOM was composed of complex molecules likely derived from terrestrial vegetation debris, such as *Salix arctica* leaves, that have occasionally been observed within the ice shelf microbial mats. The presence of other water-soluble compounds, such as exopolymeric substances (EPS) and oligosaccharide mycosporine-like amino acids (MAAs), may have also been responsible for such a low McKnight ratio (Mueller et al. 2005).

CDOM strongly absorbs in the ultraviolet (UV) region of the solar spectrum and in the process undergoes photochemical degradation to products that can have both positive (e.g., increased C, N, P and Fe availability to microbiota), and negative effects (e.g., production of reactive oxygen species such as peroxides) on aquatic communities (Vincent and Neale 2000). Photochemical reactions may also promote the loss of carbon from these ecosystems via photochemical degradation of DOC to CO₂ and CO during continuous summer daylight and subsequent evasion (transfer from the water to the atmosphere) of these gases. The implications of stratospheric ozone depletion for surface water photochemistry are of particular interest for northern lake environments given the potential for increased levels of UV-B in this region (ACIA 2005).

9.3 Biological Properties of Supraglacial Lakes

9.3.1 Habitat Distribution

Until summer 2005, the six largest remnant ice shelves in the Canadian High Arctic totaled 1043 km² and 8% of their surface area provided sediment cryohabitats for microbiota (Fig. 9.5; Mueller et al. 2006; Copland et al. 2007). Ecological studies to date have focused primarily on the Markham and Ward Hunt ice shelves with Markham Ice Shelf being the richest in biomass per unit area of all Arctic ice

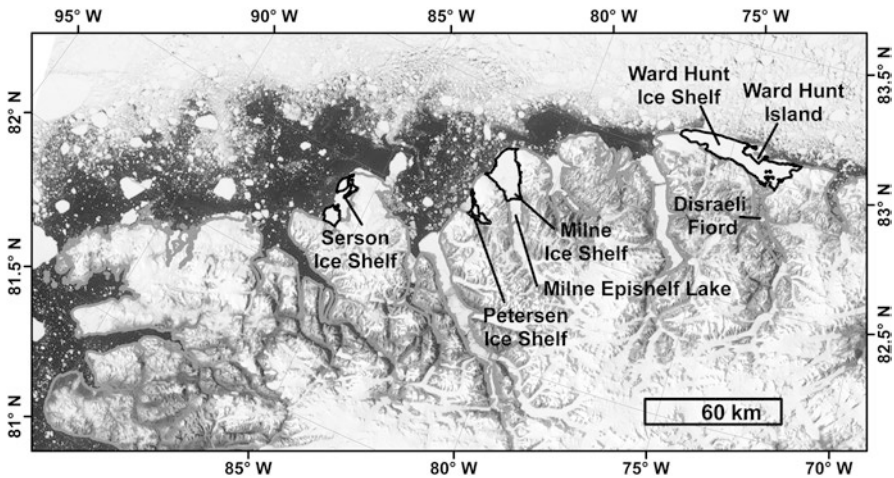


Fig. 9.5 Open water stretching along the northwest coast of Ellesmere Island for 250 km at the end of August, 2008. This unusually wide (up to 55 km) region of ice-free water began to form in the third week of July 2008, at the same time as the ice shelves began to calve. The ice shelves are outlined in *black* and the coast is outlined in *grey* (MODIS image acquired on 2008-08-29 at 19:55 UTC, from the Rapid Response Project at NASA/GSFC)

shelves, until it broke up completely in the summer of 2008 (Mueller et al. 2008; Vincent et al. 2009).

On the Ward Hunt and Markham ice shelves 10% and 44%, respectively, of their surface areas were covered with sediments and microbial mat communities (Mueller et al. 2006). Meltwater ponds on the ice shelves are dominated by benthic communities that represent most of the biomass. A total of 34 Gg of organic matter was estimated for the entire Canadian Ellesmere ice shelves' ecosystem with average per unit area productivities ($129 \text{ mg C m}^{-2} \text{ d}^{-1}$) that are well above values in the Central Arctic pack ice (Mueller et al. 2006).

Arctic ice shelf cryohabitats are heterogeneous at the sub-ice shelf scale with sediments and associated microbial mats distributed in patches. However, species richness and diversity among ice shelves and habitat patches does not differ significantly. Therefore, it is plausible that there is considerable connectivity and dispersal between the individual ice shelves as well as between habitat patches, likely in the direction of the prevailing wind (Mueller et al. 2006). Most of the organisms found in ice shelf mats are present in nearby microbial mats from terrestrial ponds (Villeneuve et al. 2001) and glacial cryohabitats (Mueller et al. 2001), which serve as sources of organisms for ice shelf cryo-ecosystems.

9.3.2 *Benthic Biology*

The abundance of microbial mats is highly variable across the surface of Arctic ice shelves, ranging from lakes with a continuous layer of thick accumulated benthic microbial biomass and sediment (e.g., Markham Ice Shelf; Fig. 9.6), to lakes with little or no microbial mats, containing only small patches of mats or sparse cryoconite holes. In the latter case, the cryoconite holes seem to be preferentially distributed along the strand line or former strand lines (high water mark), parallel to the lake edge (Mueller, personal observations). Microbial mats may also be found in the numerous water-filled caverns and ice interstices that occur within the ice shelves (Mueller, personal observations).

Microbial mats on the Canadian Arctic ice shelves have been macroscopically classified into three categories: "orange", "matlet" and "sediment" mat (Mueller et al. 2006). Orange mats are luxuriant, thick ($>0.5 \text{ cm}$) loosely cohesive mats with a thin surface layer containing orange pigmentation (Fig. 9.7a). The "matlet" type mats are 1- to 2- mm wide flakes that lie loosely on the ice but can accumulate to a thickness of 3 cm, and the "sediment" mats have no visible biological aggregate and occur in a fine to coarse sediment (Mueller et al. 2006). These mats differ greatly from benthic communities in nearby lakes such as Ward Hunt Lake (on Ward Hunt Island) and Antoniades Pond (northern Ellesmere Island), where the mats are more cohesive with a macroscopic stratification of different pigment groupings (Bonilla et al. 2005, Jungblut et al. 2010). Arctic ice shelf mats are less diverse in their macrostructure than similar assemblages on Antarctic ice shelves, such as the McMurdo Ice Shelf. This could be due the greater range of physical and chemical properties



Fig. 9.6 Sampling a meltwater lake on the Markham Ice Shelf, Canadian High Arctic (Date: 12 July 2007; Photograph: W.F. Vincent)

present in the meltwater ponds of the McMurdo Ice Shelf (Howard-Williams et al. 1990) where higher variability of pond size, depth and conductivity likely supports a higher phenotypic and genotypic diversity and hence, mat macrostructure.

The mat-containing sediments of the Markham Ice Shelf occurred on raised mounds of ice and also at the base of meltwater ponds and lakes that occupied the parallel troughs that are characteristic of all of the Canadian High Arctic ice shelves. The microbial mats on Markham Ice Shelf could be separated into two layers with the lower layer being directly in contact with the ice. Algal counts (protists and cyanobacteria) identified slightly different abundances in these layers with 4.58×10^5 and 2.51×10^5 cells cm^{-2} in the upper and lower layer respectively (Vincent et al. 2004). Microbial mats on the Ward Hunt Ice Shelf do not have macroscopic strata, with the exception of an orange surface layer up to 220 μm thick. Total standing stock of microbial mats on the Markham Ice Shelf in 2001 was estimated to be 16.5 Gg of organic matter, about 50% of the total estimated organic matter on the Ellesmere Ice Shelves at that time (34 Gg; Mueller et al. 2006).

The biomass of the aquatic ecosystems on Arctic ice shelves is dominated by benthic assemblages, whereas the planktonic assemblages in the overlying oligotrophic water occur in dilute concentrations. Chlorophyll *a* in the water ranges from 0.02–0.68 $\mu\text{g L}^{-1}$ indicating a sparse phytoplankton communities and limited resuspension of benthic communities (Vincent et al. 2004). In comparison, chlorophyll *a*

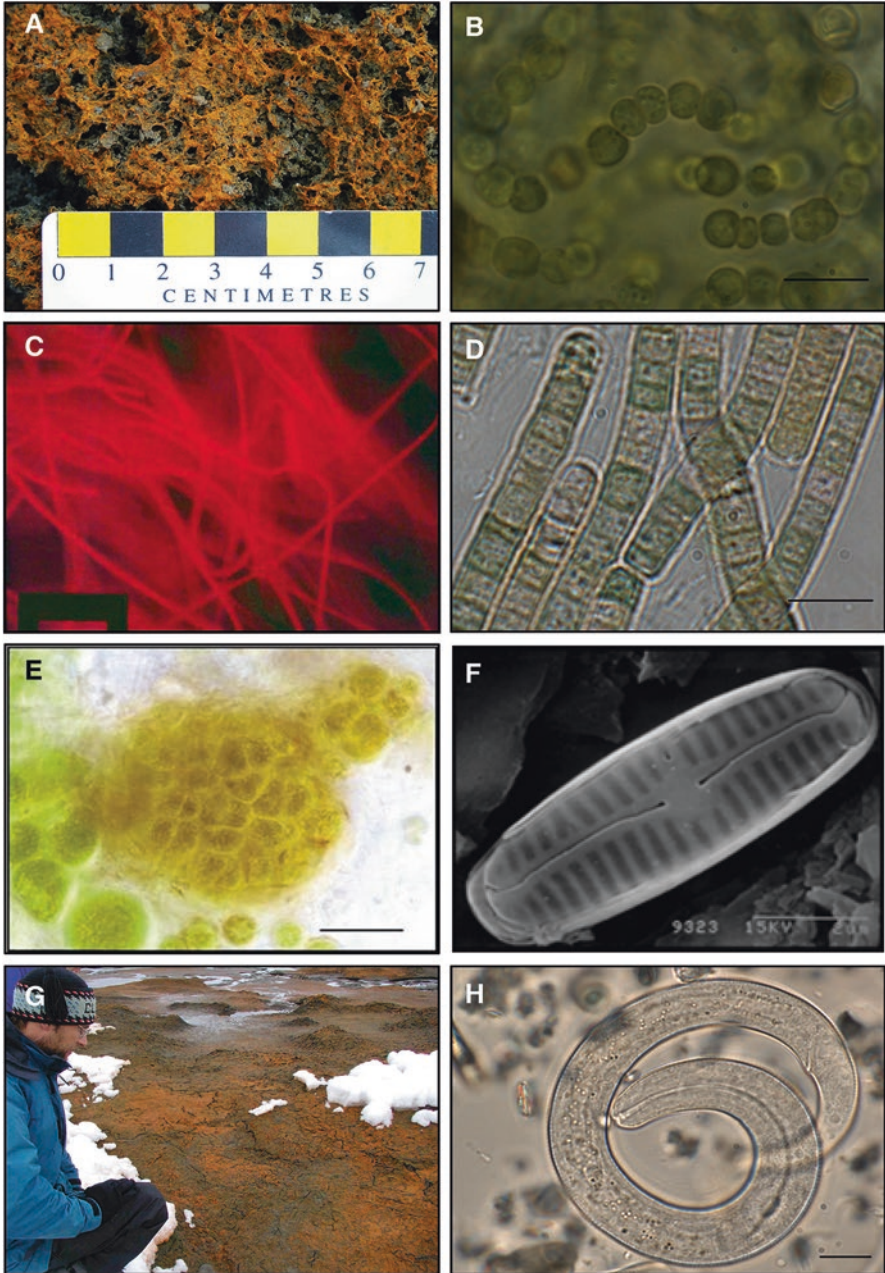


Fig. 9.7 Microbial mat diversity on Ward Hunt and Markham ice shelves. (a) “Orange” mat (>0.5 cm thick) with characteristic thin layer of orange pigmentation (Photograph: D. Sarrazin). (b) N_2 -fixing filamentous cyanobacterium *Nostoc* sp.; the scale bar represents 10 μ m (Photograph: A.D. Jungblut). (c) Epifluorescence micrograph of filamentous cyanobacteria (Oscillatoriales); the scale bar represents 10 μ m (Photograph: V. Villeneuve). (d) Filamentous cyanobacterium

concentrations in the benthic communities ranges from 5.4 to 448 chl *a* mg m⁻² with an average of 147 chl *a* mg m⁻², while carotenoid levels range from 18–6460 mg m⁻² with an average of 1307 mg m⁻² (Vincent et al. 2004; Mueller et al. 2005). However, benthic chlorophyll *a* concentrations can vary greatly among meltwater ponds due to the patchy distribution of mats (Vincent et al. 2004; Mueller et al. 2005).

Benthic microbial mat consortia are often characterized by vertical physical and biochemical stratification including gradients in variables such as irradiance, redox potential, pH, and concentrations of dissolved oxygen, carbon dioxide, methane and nutrients (Stal 2000). These gradients are generated in part by external physical factors such as light, sediment composition and water characteristics, but also through the zonation of metabolic activities such as sulphate-reduction and oxidation, photosynthesis, respiration, nitrification, denitrification, nitrogen fixation, fermentation and methanogenesis (Stal 2000), which arise from the functionally diverse microbial consortia. These gradients have received little attention in the ice shelf mats and more research should be undertaken to understand them.

9.3.3 Prokaryotic Diversity

9.3.3.1 Cyanobacterial Diversity

Cyanobacteria dominate the autotrophic biomass of the Arctic ice shelf mats, comprising at least 88% of total algal cell counts (Vincent et al. 2004). Cyanobacteria are important for mat cohesion and structure due to their production of exopolymeric substances (EPS) and the filamentous morphology of the dominant taxa, which intertwine to form the mats. Commonly found genera are *Nostoc* (Fig. 9.7b), *Phormidium*, *Oscillatoria* (Fig. 9.7c, d), *Leptolyngbya* and *Gloeocapsa* as revealed by microscopy on the Markham and Ward Hunt ice shelves (Mueller et al. 2006). However, further molecular investigations such as 16S rRNA gene analysis are needed to fully understand their diversity, distribution between sites and their biogeographic relationship to cyanobacterial communities elsewhere in the Arctic, or Antarctic shelves such as the McMurdo Ice Shelf (Jungblut et al. 2005) The first molecular analyses of this type on the Ellesmere Island ice shelves indicated the presence of cyanobacterial ecotypes that are distributed throughout the cold biosphere, including Antarctica (Jungblut et al. 2010). A subsequent detailed meta-analysis has corroborated these findings, but also draws attention to the urgent need for full genomic analysis of cold-tolerant cyanobacteria (Christmas et al. 2015).

←
Fig 9.7 (continued) (Oscillatoriales) isolated from Markham Ice Shelf mats; the scale bar represents 10 μm (Photograph: A.D. Jungblut). (e) Mat algae from Markham Ice Shelf; the scale bar represents 10 μm (Photograph: S. Bonilla). (f) Electron micrograph of a mat diatom; the scale bar represents 2 μm (Photograph: V. Villeneuve). (g) Highly pigmented microbial mats on the Markham Ice Shelf (Photograph: W.F. Vincent). (h) Nematode, common in Arctic ice shelf mats; the scale bar represents 20 μm (Photograph: A.D. Jungblut)

Cyanobacteria dominate the benthic communities of many polar freshwater ecosystems due to multiple factors, including low grazing-pressure and their ability to tolerate the extreme conditions found in these environments (Vincent 2007, 2009). Tang et al. (1997) showed that many high latitude mat-forming cyanobacteria tend to be psychrotrophs (cold-tolerant microorganisms) not psychrophiles (cold-loving microorganisms). This strategy of general tolerance to a broader range of temperatures allows a faster acclimatization in the presence of frequent freeze-thawing cycles, rapid changes in temperatures and high UV radiation despite suboptimal growth under low temperatures. For example, freeze-dried cyanobacterial mats from Antarctic ice shelves can resume photosynthesis within minutes to hours after thawing and rehydration, which is important in an ecosystem with a limited growing season (Vincent 1988; Hawes et al. 1999).

Cyanobacteria have also developed an array of mechanisms to ensure cell integrity during freezing such as the synthesis of extracellular compounds to reduce ice nucleation around the cells (Vincent 1988). Furthermore, polyunsaturated fatty acids are incorporated into membranes to retain fluidity at low temperatures (Laybourn-Parry 2002) and compatible solutes such as trehalose are produced to reduce the freezing point of intracellular fluids (Oren 2000). Some of these organic osmolytes including glycine betaine can also be used as a long-term strategy to balance extracellular ions at higher salinities, as found in some Arctic ice shelf waters and particularly during freeze-up.

High UV radiation is another major stress factor for microorganisms in Arctic aquatic ecosystems (Roos and Vincent 1998). In cyanobacteria, it can lead to photo-inhibition, phycobiliprotein degradation and chlorophyll-bleaching (Castenholz 1992; Ehling-Schulz and Scherer 1999). Furthermore, exposure of DNA to UVB radiation can lead to DNA lesions and mutagenesis, including dimerisation of adjacent pyrimidine bases (Vincent and Neale 2000, and references therein). However, cyanobacteria have evolved a variety of DNA repair mechanisms, such as excision repair and photo-reactivation, to cope with UV induced DNA damage (Garcia-Pichel and Castenholz 1991). Another strategy observed in motile cyanobacteria is migration to deeper layers within the microbial mats to avoid radiation (Vincent et al. 1993; Quesada and Vincent 1997). Cyanobacteria are also able to synthesize a variety of pigments such as carotenoids, scytonemin, and MAAs for protection against UV radiation (Hodgson et al. 2004b; Squier et al. 2004).

9.3.3.2 Heterotrophic Bacterial, Archaeal and Viral Diversity

Other bacterial phyla are also well represented in Arctic ice shelf communities, and studies using epifluorescence microscopy showed the presence of viruses and heterotrophic bacteria, with abundances of $2.3\text{--}16.5 \times 10^7$ viruses and $0.7\text{--}7.5 \times 10^7$ bacteria per square centimetre in mat systems on the Ward Hunt Ice Shelf (Vincent 2000a). Bottos et al. (2008) identified heterotrophic bacterial communities that were dominated by the Bacteroidetes, Proteobacteria (α -, β -, δ - and γ -) and Actinobacteria on the Markham and Ward Hunt ice shelves using 16S rRNA gene analysis. They

also found Firmicutes, Verrucomicrobia and Gemmatimonadetes on the Markham Ice Shelf and Fibrobacteres on Ward Hunt Ice Shelf, albeit in lower abundances. Interestingly, no community differences were noted between upper and lower layers in ice shelf microbial mats using Denaturing Gradient Gel Electrophoresis (DGGE) analyses. The presence of both α - and β -Proteobacteria implies a community with some marine affinities (β -Proteobacteria usually occur more frequently in marine plankton) as well as a strong freshwater influence (β -Proteobacteria are found in freshwater). Most of the archaeal taxa found within the ice shelf mats grouped within the phyla Euryarchaeota and Crenarchaeota (Bottos et al. 2008; Varin et al. 2010). The microbial abundances of these bacterial communities are similar to those reported in microbial mats from Antarctic ice shelves communities (Van Trappen et al. 2002; Sjöling and Cowan 2003; Archer et al. 2015). In addition, Archer et al. (2014) identified that bacterioplankton is influenced by geochemical characteristics of Antarctic meltwater ponds, and that distinct populations can be present in the upper and lower part of highly stratified water columns of meltwater ponds on the McMurdo Ice Shelf based on ARISA finger print (Automated Ribosomal Intergenic Spacer Analysis). Further analyses are required of Arctic bacterioplankton to determine if similar heterotrophic bacterial communities are dominating meltwater ponds, however they will likely lack stratification as Arctic meltwater ponds are usually shallow and more edaphic than McMurdo Ice shelf aquatic ecosystems.

It is difficult to infer metabolic functionality based solely on current 16S rRNA gene analyses, therefore further metagenomic analysis is required for a better understanding of functional ecology. The first application of this approach to microbial mats from the Ward Hunt and Markham ice shelves revealed a large functional as well as taxonomic diversity, with proteobacteria contributing the largest number of gene sequences (Varin et al. 2010). This proteobacterial diversity in Arctic ice shelf mats would facilitate a broad suite of aerobic and anaerobic processes, including sulphur-reduction activities as observed in Antarctic microbial mats communities from the McMurdo Ice Shelf (Mountfort et al. 1999; Mountfort et al. 2003). A variety of stress tolerance strategies has been identified from subsequent metagenomic analysis of Arctic ice shelf mats, with similarities but also certain differences relative to Antarctic ice shelf mats (Varin et al. 2012).

9.3.4 Eukaryotic Diversity

To date, the study of eukaryotes in Arctic ice shelf mats is mostly limited to morphological identification and enumeration. Eukaryotic algae are commonly found within the matrix of cyanobacteria. In Ward Hunt Ice Shelf mats, these include the Chlorophytes *Palmellopsis*, *Chlorosarcinopsis*, *Pleurastrum*, *Chlamydomonas*, *Chlamydocapsa*, *Chlorella*, *Chlorococcum*, *Klebsormidium*, *Palmellopsis*, cf. *Chlorokybus* and solitary cells of *Bracteacoccus* (Vincent 2000a; Mueller et al. 2006). On Markham Ice Shelf similar groups of mainly terrestrial and subaerial

palmelloid chlorophyte genera occur (Fig. 9.7e; Vincent et al. 2004). Phylogenetic analysis of 18S rRNA genes grouping within Chlorophyceae suggested that sequences from Arctic ice shelf microbial mat cluster together with ripotypes that had been previously been reported to be endemic to Antarctica (Jungblut et al. 2012).

Benthic and aerophilic diatom communities on the Ward Hunt Ice Shelf are dominated by *Chamaepinnularia begeri* (Krasske) Lange-Bertalot (syn. *Navicula begeri* Krasske) accounting for 90% of frustules (Fig. 9.7f; Vincent et al. 2000). Mats from this ice shelf also contain *Nitzschia palea* (Kützing) W. Smith (2.3%), *Navicula phylleptosoma* Lange-Bertalot (1%), *C. krookii* (Grunow) Lange-Bertalot, *C. gandrpii* (Petersen) Lange-Bertalot and Krammer, *Pinnularia borealis* Ehrenberg, *Luticola palaeartica* (Hustedt) Mann, *Achnanthes petersenii* Hustedt and *Nitzschia cf. pusilla* Grunow (all <1%). In comparison, Antarctic mats from the McMurdo Ice Shelf similarly contain coccoid chlorophytes and a diatom assemblage dominated by the genera *Navicula*, *Nitzschia*, *Pinnularia* and *Achnanthes* (Howard-Williams et al. 1990). Chrysophyte cysts are also present in Ward Hunt Ice Shelf mats (Vincent et al. 2000, 2004), but are not found on the McMurdo Ice Shelf.

The first 18S rRNA gene assessment of the microbial eukaryote diversity in microbial mats of High Arctic ice shelves such as the Ward Hunt and Markham ice shelves highlighted that their assemblages do not only contain various microalgae and ciliates but also but also fungi including Ascomycota, Basidiomycetes and Chytridiomycota, as well as rhizaria such as Cercozoa with many having the highest similarity to uncultured environmental sequences (Jungblut et al. 2012). Although the study was only preliminary due to incomplete sampling, it is still noteworthy a limit overlap was found between microbial eukaryote composition in microbial mats from ice- and land-based aquatic ecosystems.

9.3.5 Primary and Heterotrophic Productivity

On the Ward Hunt Ice Shelf, maximum photosynthesis rates range from 0.059 to 0.17 g C g chl $a^{-1} h^{-1}$ (27.3–105 mg C $m^{-2} h^{-1}$), whereas bacterial productivity is three orders of magnitude lower, ranging from 0.085 to 0.38 μg C g biomass $^{-1} h^{-1}$ (0.037–0.21 mg C $m^{-2} h^{-1}$). The measured chlorophyll-specific primary productivity in Ward Hunt Ice Shelf mats, as well as the heterotrophic bacterial production lie within the range of polar microbial ice mat literature such as the McMurdo Ice Shelf (Vincent and Howard-Williams 1989). However primary productivity on a per unit area basis is much higher in the Arctic mats, due to the large standing stocks of photosynthetic pigments (Mueller et al. 2005).

Using the above productivity rates and based on a growing season of ~70 days, the annual primary production of the communities on the Ward Hunt Ice Shelf is approximately 108 g C m^{-2} . Of this, bacterial heterotrophy would recycle an estimated 4.3 g m^{-2} of biomass (or approximately 2.15 g C m^{-2}) within the microbial mats given an average efficiency of 30% (Mueller et al. 2005). This further reflects

the overwhelming dominance of autotrophic biomass relative to heterotrophic bacteria in the mats (Mueller et al. 2005), and indicates the tendency of the mats to accumulate rather than fully degrade.

Primary productivity assays of Ward Hunt Ice Shelf mats identified broad tolerances optima outside the ambient range of key stressors such as salinity, irradiance and temperatures in the autotrophic community. This tolerance was related to their diverse suite of pigments (see Sect. 9.3.6; Mueller et al. 2005), which can assist the organisms to acclimatize to changing conditions. Experimental manipulation of salinity had only limited effects on primary productivity, which also suggests a broad growth optimum between 3000 and 29,000 $\mu\text{S cm}^{-1}$ for these Arctic ice-mat autotrophs (Mueller et al. 2005). Similarly, in their studies on Antarctic microbial mats, Hawes et al. (1999) found no change in photosynthetic rates (relative to control) up to 20,000 $\mu\text{S cm}^{-1}$.

Heterotrophic bacterial productivity on Ward Hunt Ice Shelf does not appear to respond favourably to increased salinity and temperature (Mueller et al. 2005), and physiological studies on community isolates from Ward Hunt and Markham Ice Shelves showed that most of them were cold adapted, with growth at temperatures as low as -10°C (Bottos et al. 2008). Therefore, in contrast to the broad tolerance of the autotrophic community, Arctic ice shelf heterotrophic bacterial communities appeared to be extremophilic (specifically adapted to the 'extreme' ambient conditions in their habitat; Mueller et al. 2005). The large concentrations of viruses found in these mats (Vincent et al. 2000) and the diverse viral sequences in the metagenomic analysis of ice shelf mats (Varin et al. 2010) suggest that phage attacks may limit the standing stock of bacterial biomass, and thereby also limit the extent of bacterial decomposition processes.

9.3.6 Pigment Content and Photoprotection

A striking feature of Arctic ice shelf communities is their richness and diversity of pigments (Fig. 9.7g). These pigments can be classed into screening compounds (e.g., MAAs and scytonemins that absorb UV-A and UV-B radiation), light harvesting and accessory pigments (chlorophylls, phycobiliproteins and certain carotenoids), and anti-oxidants (other carotenoids and perhaps MAAs).

High Arctic planktonic and benthic communities exist in shallow waters with low concentrations of UV-filtering coloured dissolved organic matter (CDOM), and must therefore contend with a high UV exposure (Bonilla et al. 2009). The pigment assemblage suggests that these microbial communities can spectrally modify their environment for both photo-protection, and photosynthetic efficiency (Vincent et al. 2004; Mueller et al. 2005; Bonilla et al. 2009). On ice shelves, planktonic communities apparently use a different strategy to counter the effects of high UV radiation than benthic microbial mat communities. A study of pigments in Arctic lakes and ponds at several locations showed that planktonic communities favour quenching reactive oxygen species with carotenoids, particularly under high UV

radiation and at low temperatures while benthic consortia employ a screening approach using scytonemin and reduced scytonemin, which accumulate in high concentrations (Bonilla et al. 2009).

Chlorophyll *a* levels in mats in high biomass areas of the Ward Hunt and Markham ice shelves are higher relative to microbial mats from many ponds and lakes throughout the polar regions, including meltwater ponds on the McMurdo Ice Shelf, Antarctica. For example, on Markham Ice Shelf mean chl *a* biomass value for microbial mats was 147 mg chl *a* m⁻² while concentrations in the Ward Hunt Ice Shelf mats range from 5.6–31 mg chl *a* m⁻². A possible explanation for extremely high values might be the enhanced preservation of pigments due to the inhibitory effects of low temperatures on bacterial processes. McMurdo Ice Shelf microbial mats often lie atop relatively thick sediment, which likely warm to temperatures not experienced on the northern ice shelves (Mueller et al. 2005; Mueller and Vincent 2006).

Similar to land-based Arctic freshwater systems, the cyanobacterial-dominated mats on ice shelves are structured with respect to their pigment characteristics. The upper layer of mats may be optimized to filter out UV wavelengths and/or quench reactive oxygen species in response to the photo-oxidative stress imposed by the large cumulative UV dose in summer (Quesada et al. 1999). In Markham Ice Shelf mats, the carotenoid/chlorophyll *a* ratio was found to be twice as high in the surface layer than in the bottom, even with chl *a* and chl *b* concentrations being higher in the upper layer than at the bottom of the mat (Vincent et al. 2004). These results underscore the use of carotenoids as anti-oxidants in the microbial mats, whereas the high concentrations of scytonemin and presence of MAAs indicate the importance of screening deleterious radiation from the microbial consortia throughout the mat (Mueller et al. 2005). However, the high concentration of screening pigments and the low concentration of light-harvesting pigments deeper within the mat may also represent pigment accumulation and the relatively slow degradation of dead cells in this cold environment (Vincent et al. 2004).

9.3.7 *Invertebrates and Other Animals*

Observations of the faunal composition of meltwater lakes on Arctic ice shelves are very limited, and most records are based on anecdotal reports rather than detailed studies. Fish, such as the slimy sculpin (*Cottus cognatus*), and amphipods, such as gammaridae, have been observed in sections of the ice shelves which have some connection to the sea (Jungblut, personal observations). However, chironomid larvae and fairy shrimp that are regularly found in nearby lakes on Ward Hunt and Ellesmere islands have not been observed in meltwater ponds of the ice shelves. Metazoan diversity is commonly limited to nematodes (Fig. 9.7h), rotifers and tardigrades, which compares with findings from the McMurdo Ice Shelf, Antarctica. For example, one of the only molecular studies of eukaryotic diversity on ice shelves showed that Arctic ice shelf tardigrades had the highest 18S rRNA gene similarity

to *Isohypsibius granulifer* (99%), a species with a cosmopolitan distribution (Jungblut et al. 2012). However, platyhelminth worms have also been found in microbial mats on the Ward Hunt Ice Shelf, but have not been found to date on Antarctic ice shelves (Vincent et al. 2000).

9.4 Other Biota Associated with Ice Shelves

9.4.1 Macrobiology of the Ice Shelves

Knowledge of the macrobiota inhabiting Arctic ice shelves is very limited, and records are based on anecdotal reports rather than detailed studies. However, it can be assumed that Arctic ice shelves are infrequently visited by animals and birds due to the limited food sources there. Arctic foxes (*Vulpes lagopus*) and polar bear (*Ursus maritimus*) tracks have been reported on the Ward Hunt Ice Shelf and polar bear, Arctic fox, ermine (*Mustela erminea*) and lemming (*Dicrostonyx greenlandicus*) tracks have been observed on the Milne Ice Shelf. Seals have been observed at the seaward edge and within fractures on the Ward Hunt and Milne ice shelves. Arctic hares (*Lepus arcticus*) and Peary caribou (*Rangifer tarandus pearyi*) inhabit the northern part of Ellesmere Island and could potentially cross the ice shelves. Muskox (*Ovibos moschatus*) excrement has been found on the Ward Hunt Ice Shelf (Mueller and Stern, personal observations) near Ward Hunt Island and caribou antlers were recovered from the Ice Island T-3 (Jeffries 1992). On Ellesmere Island approximately 34 different species of birds can be seen, with 21 confirmed to nest on the island (Parks Canada, unpublished data). Birds such as Brant geese, short tail jaegers, snow buntings, red-throated loons, red knots, gulls (species not identified) and shorebirds such as ruddy turnstone have been observed (Sarrazin, personal communication) flying over Ward Hunt Island and Ward Hunt Ice Shelf during summer. Ivory gulls have been spotted over Milne Ice Shelf on several occasions. Red-throated loons (*Gavia stellata*) have been found nesting and feeding on fish in the lakes with open water in the summer at the northern tip of Ellesmere Island (Jungblut, personal observation), however it is not known if they use the ice shelves as habitats as well. Recent changes in climate and ecosystem structure such as the opening of polynyas near the edge of the ice shelves due to sea ice melt and reduction of ice shelf size may redefine the role of the remaining ice shelves as habitats for Arctic macrobiota if they can gain access to the ocean from the ice edge.

9.4.2 Microbial Biota of Snow

Microbial diversity of snow on Arctic ice shelves is likely enhanced by propagules from the rich microbial mat communities and sediment on the ice shelf, as well as from meltwater lakes and terrestrial soil. Long-range aeolian dispersal of microbes

could connect ice shelf ecosystems with not only other Arctic ecosystems but other cold environments such as temperate alpine regions and Antarctica (Christner et al. 2008). Snow microbial communities are often dominated by highly adapted and relatively fast growing biota such as heterotrophs and protists, whereas cyanobacteria are typically found in low abundances. For example, the snowpack in Spitsbergen, Svalbard was found to contain α -Proteobacteria, β -Proteobacteria and δ -Proteobacteria, Firmicutes and Actinobacteria using 16S rRNA gene analysis (Amato et al. 2007). Snow algae have been studied in detail in the Antarctic and genera such as *Chlamydomonas*, *Ochromonas*, *Raphidonema* and *Chlorosphaera* are found at different locations there (Vincent 1988). Taxa such as *Chlamydomonas* spp. and *Chloromonas* spp. are also reported from Spitsbergen at such high concentrations that they visibly coloured the snow owing to their pigmentation (Müller et al. 1998). This ‘watermelon snow’ has not been found on Arctic ice shelves and the abundance of these red pigmented snow algae is likely to be low. However, blooms of *Ancyclonema nordenskiöldii* have been noted in the weathering crust (a slushy mixture of canded ice and snow) of the Ward Hunt Ice Rise during August 2002 (Mueller, unpublished data).

A molecular microbiological analysis of snow on the Ward Hunt Ice Shelf along with other sites in the northern Ellesmere Island region was undertaken by Harding et al. (2011). This revealed a diverse microbiota of bacteria and eukaryotes, including taxa found in the Arctic Ocean and in freshwater microbial mat environments, implying the importance of local aerial processes for microbial dispersion. Some sequences were most similar to those found outside the Canadian Arctic but previously reported in snow, lake ice, sea ice, glaciers and permafrost, alpine regions, Antarctica, and elsewhere in the Arctic, supporting the view that certain microbial ecotypes are globally distributed throughout the cold biosphere. As noted in Pointing et al. (2015), further evaluation of this view and of the contrary likelihood of a certain degree of microbial endemism in the polar regions will require more detailed genomic analysis of isolates in the future.

9.4.3 *Microbial Life Within the Ice*

Diverse microbial consortia are found in meltwater lakes on Arctic ice shelves and they also likely inhabit the ice itself. Arctic ice shelf ice has not yet been analyzed for microbial life, however the presence of microbes is plausible based on the availability of space, nutrients and liquid water. In systems such as the ice-covers of perennially frozen lakes in the Dry Valleys of Antarctica, pockets of liquid water that support microbial ecosystems form during the warmer months in ice where dark-coloured material has been incorporated into the ice (Paerl and Pinckney 1996; Fritsen and Priscu 1998; Hawes et al. 2008). These pockets of sediment are known to occur within the ice shelf, both near the surface (‘buried’ cryoconite holes) and at great depths within the ice (Crary et al. 1955). However, microbes that are not associated with sediments could also be buried within the ice shelf. Molecular analysis

of ice shelf cryoconite holes are lacking by several sequencing surveys of glacial cryoconite communities in the Arctic and Antarctica have now shown that they contain diverse communities of cyanobacteria, bacteria, archaea and microbial eukaryotes and that both environmental variables and geography play role in shaping these cryospheric communities (Cameron et al. 2012; Edwards et al. 2013; Webster-Brown et al. 2015).

Microbes can survive unfavourable conditions in a dormant state for extended periods of time or, if they are surrounded by even minute quantities of water (such as in brine channels, veins or pore spaces in the ice), they can theoretically maintain metabolic activity (Price and Sowers 2004). Microorganisms could potentially survive at crystal boundaries in pure polycrystalline ice by using water and nutrients provided by aqueous ionic solutions (Price 2007). These organisms would have to be small enough to fit into a network of veins with diameters in the micron range, which form during freezing processes through solute and salt exclusion from the freezing front (Mader et al. 2006). Other microhabitats within ice include the surface of ice-entrained mineral grains covered with thin films of unfrozen water. Others studies were able to isolate aerobic bacteria grouping belonging to high-G + C gram-positives, low-G + C gram-positives, *Proteobacteria*, and *Cytophaga-Flavobacterium-Bacteroides* groups (Miteva et al. 2004), from a silty ice core obtained from Greenland that included metabolically active cells. Similarly, Brinkmeyer et al. (2003) identified a diverse assemblage of bacteria dominated by α -, β -*Proteobacteria* and *Cytophaga-Flavobacterium* group from Arctic and Antarctic pack ice. Based on the physical properties of the ice shelf ice and the high microbial diversity and activities present on the surface of the ice, bacterial assemblages are also expected to be present within the ice.

9.5 Epishelf Lakes

9.5.1 Physical Properties

Epishelf lakes are ice-dependent stratified ecosystems that form between an ice shelf and land with an upper freshwater layer, derived from ice and snow melt that is dammed behind an ice shelf (Gibson and Andersen 2002). The depth of the freshwater layer is constrained by the minimum draft of the ice shelf (Keys 1978) and the mixing of the freshwater and marine layer is prevented through strong density stratification and the lack of wind-induced turbulence due to a perennial ice-cover. The saline bottom waters are hydrologically connected to the ocean and therefore the entire water column is influenced by tidal forces (Veillette et al. 2008, and references therein).

The last remaining deep epishelf lake in the Arctic (as of July 2016) is located behind Milne Ice Shelf in Milne Fiord. This is a large reduction from the 17 deep epishelf lakes that may have formerly existed behind the “Ellesmere Ice Shelf”,

which up until the early twentieth century fringed the northern coast of Ellesmere Island from Cape Colan to Nansen Sound. These deep freshwater ecosystems were most likely lost following calving or draining through cracks in the former ice shelf. This latter case was documented for the Disraeli Fiord epishelf lake, where the freshwater layer drained through a fracture in the adjacent Ward Hunt Ice Shelf between 1999 and 2002 (Vincent et al. 2001; Mueller et al. 2003a, b), although the ice shelf remained in place. In contrast, numerous deep epishelf lakes exist in Antarctica such as at the edge of the Amery Ice Shelf (Beaver Lake; Laybourn-Parry et al. 2006), adjacent to the Shackleton Ice Shelf in the Bunger Hills Oasis, East Antarctica (including White Smoke Lake; Doran et al. 2000; Gibson and Andersen 2002) and between George VI Ice Shelf and Alexander Island on the western side of the Antarctic Peninsula (Ablation Lake and Moutonnée Lake; Heywood 1977; Hodgson et al. 2004a; Smith et al. 2006).

Shallow 'ice-dammed' lakes, with a freshwater layer of less than 5 m depth, also exist along the northern coast of Ellesmere Island and are intermediate systems between deep epishelf lakes with a complete ice shelf dam and open fiords without any ice dam. Some of the shallow ice-dammed lakes including Taconite Inlet, Ayles Fiord and the Serson ice-dammed lake, cannot accumulate a thick freshwater layer because their ice shelf dam is incomplete and/or they are impounded by relatively thin, multiyear landfast sea ice. A total of eight of these lakes were still present along the northern coast of Ellesmere Island as detected by RADARSAT-1 synthetic aperture radar imagery in the winter of 2007 (Veillette et al. 2008).

The epishelf lake in Milne Fiord is characterized by a 16 m thick freshwater layer overlying the marine layer beneath (Fig. 9.8). It is dammed by the Milne Ice Shelf, the second largest of the Ellesmere ice shelves with a length of 20 km. The central unit of this ice shelf is influenced by glacial ice and has been estimated in the past to be up to 100 m thick (Narod et al. 1988). However, measurements of the depth of the epishelf lake behind this ice shelf, suggest the Milne Ice Shelf has a minimum draft of 16 m. The persistence of the Milne Ice Shelf and its epishelf lake is likely aided by the long, protected fiord in which the ice shelf is located. Furthermore, the ice shelf is glacially thickened by inflowing ice from both sides, which keeps the ice shelf pinned in place (Veillette et al. 2008).

Profiling of Milne Fiord epishelf lake and several shallow ice-dammed systems in the Arctic shows that there is inter-annual variation in their freshwater layers, with slight differences in upper layer thickness and salinity. Salinities in the freshwater layers of these ice dammed lakes ranges from 0.6–3 ppt, and seasonal variations, as seen in Markham and Ayles Fiord, likely reflect ice melt and runoff during the summers, whereas salinities below the halocline are constant and match Arctic Ocean values (Ludlam 1996; Veillette et al. 2008).

Temperatures in the seawater layer of the water column range from -1.5°C to 0.3°C whereas the freshwater layer temperature varies from 0°C to 3.6°C . Summer temperature profiles are often complex with two temperature maxima. The first maximum is located below the ice cover as result of heating by solar radiation. The second, less pronounced temperature peak is found just above the thermocline and is caused by heat released by the formation of frazil ice in supercooled water at the bottom of the freshwater layer. This frazil ice then floats up and contributes to the ice cover of

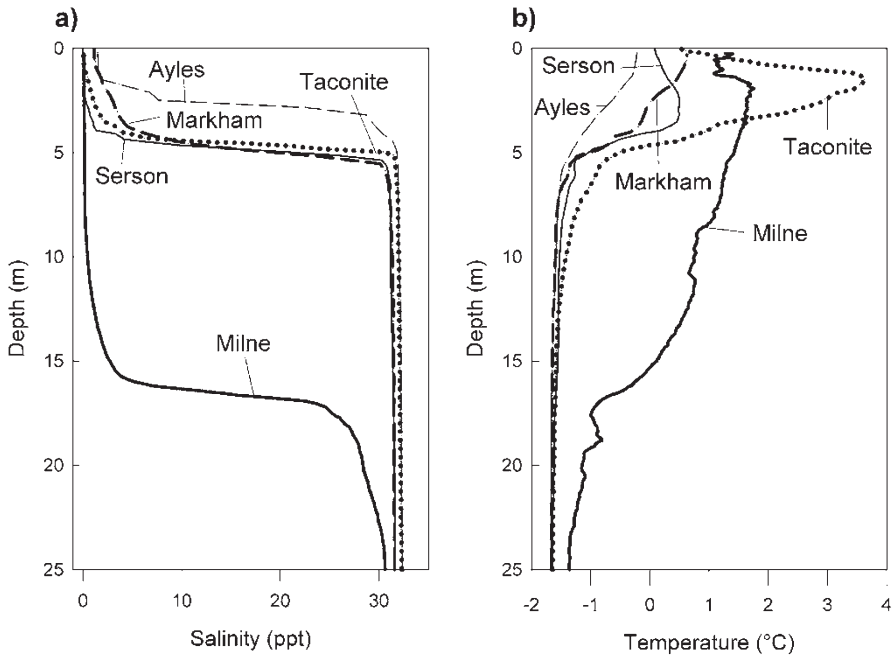


Fig. 9.8 Stratification of the Milne Fiord epishelf lake and ice-dammed lakes in Serson Bay, Taconite Inlet, Ayles Fiord and Markham Fiord. (a) Salinity profiles; (b) temperature profiles. Profiles were taken between 2004 and 2007 (From Veillette et al. (2008), Copyright 2008 American Geophysical Union. Reproduced with permission of American Geophysical Union)

the epishelf lake (Keys 1977). The correspondence between halocline and thermocline depths in Milne Fiord, as well as Serson Bay, Taconite Inlet and Ayles and Markham fiords is linked to the presence of cooler seawater (Keys 1977) that acts as a heat sink and prevents the freshwater layer from reaching higher temperatures.

In the long-term, ice-dammed lake ecosystems of Ellesmere Island could regain their original size and depths via a thickening of multiyear landfast sea ice; however, this is not likely to occur as Arctic ice shelf and multiyear landfast sea ice loss appear to be irreversible for the foreseeable future (Copland et al. 2007; Mueller et al. 2008; White et al. 2015). Therefore, epishelf lakes are highly vulnerable to climate change and can serve as sentinel ecosystems for the monitoring of regional and global climate change because their presence is entirely dependent on ice shelf integrity and their depths provide a proxy measure of the minimum draft of their ice dam.

9.5.2 *Biology of Epishelf Lakes*

Scientific knowledge of Arctic epishelf and ice-dammed lake biology is limited to only a few published studies. Nutrient concentrations in the former freshwater layer of Disraeli Fiord and Taconite Inlet were oligotrophic to ultra-oligotrophic based on

total phosphorus, and values in the deeper layer seawater layer were also in the oligotrophic range (Van Hove et al. 2006). DIC increased from 10 mg L⁻¹ in the freshwater layer of Disraeli Fiord to concentrations of 25 mg L⁻¹ in the marine layer, whereas DOC concentrations remained low (0.3–0.8 mg L⁻¹) throughout the entire water column (Van Hove et al. 2001). A chlorophyll *a* maximum of 0.3 µg L⁻¹ was found in the upper section of the freshwater layer of Disraeli Fiord, prior to its loss in 2002. This peak corresponded with the sub-ice temperature maximum and is comparable with the lower limit of chlorophyll *a* concentration measured in the central Arctic Ocean (Wheeler et al. 1996). The highest abundance of picocyanobacteria corresponded with the chlorophyll *a* maximum in Disraeli Fiord and Taconite Inlet with concentrations of up to 18 × 10³ cells ml⁻¹ and 6 × 10³ cells ml⁻¹, respectively (Van Hove et al. 2008).

Initial 16S rRNA gene analyses of picocyanobacterial communities in Taconite Inlet and Disraeli Fiord identified one phylogenetic group (referred to in the molecular ecology literature as an Operational Taxonomic Unit, OTU), related to *Synechococcus*. This OTU was also identified in freshwater ecosystems in nearby lakes such as lakes A, C1, C2 and C3 and is characteristic of water layers around or under the oxycline of the different High Arctic lakes, which could mean that it is a microbial generalist with microaerophilic and halotolerant characteristics (Van Hove et al. 2008). In a phylogenetic analysis, this OTU clustered with strains of temperate origin and OTUs from the Beaufort Sea that had been attributed to riverine inputs.

A more detailed analysis of the microbiota in an epishelf lake was undertaken in the Milne Fiord system (Veillette et al. 2011). Pigment profiles showed that there were pronounced floristic differences in the phytoplankton through its highly stratified water column, with chlorophytes dominating in the freshwater layer, prasino-phytes in the halocline, and mainly fucoxanthin groups in the bottom marine layer. Detailed microscopy analysis of their freshwater layer at 5 m identified Chlorophyceae (e.g. *Chlamydomonas*), Cryptophyceae (cf. *Rhodomonas*), Dinophyceae (*Gymnodinium*, *Peridinium*) Choanoflagellates (cf. *Monosiga*) as well as various other unidentified autotrophs and heterotrophs. In the work by Veillette et al. (2011) it was also possible to retrieve 18S rRNA gene sequences from the freshwater layer of Milne Fiord, which had highest similarities to ciliates, stramenophiles, euglenozoa, and fungi. Eukaryotes in the upper layer were freshwater taxa while only marine Archaea were retrieved from below the halocline. Bacteria belonging to Alpha-, Beta, and Gammaproteobacteria as well as Actinobacteria, Bacteroidetes, and Planctomycetes were identified in the epishelf lake. Many of these bacterial taxa were characteristic of cold, freshwater environments, while bacterial genotypes known from the Pacific and Arctic oceans were found in the marine layer. Similarly, molecular analyses of T-4 like bacteriophages showed completely different viral assemblages in the upper and lower layers, further indicating the biologically diverse, highly stratified nature of epishelf lake ecosystems.

The zooplankton assemblages in the freshwater layer of Disraeli Fiord contained different growth stages for the species *Limnocalanus macrurus*, *Drepanopus bungei*, *Oithano similis* and *Oncaea borealis* (Van Hove et al. 2001). However, the genus

Calanus, which generally dominates zooplankton assemblages in the Arctic Ocean and has been found in nearby Nansen Sound (Cairns 1967; Thibault et al. 1999), was absent from the Disraeli Fiord sample. Due to the presence of *L. macrurus* and *D. bungei*, which are common in High Arctic lakes such as Lake A on Ellesmere Island, and the absence of *Calanus*, the Disraeli Fiord epishelf lake ecosystem provides an intermediate state between freshwater and marine zooplankton assemblages. Additional research efforts are needed to fully understand the significance of this unique ecosystem type, before it is lost due to the continued breakup of Arctic ice shelves.

9.6 Wider Applications of the Study of Ice Shelf Ecosystems

9.6.1 Astrobiology

The widespread distribution of microbial communities in cold habitats such as ice shelf ecosystems makes them of great interest for the reconstruction of microbial life and diversification on early Earth (Vincent and Howard-Williams 2000; Vincent et al. 2004). Polar microbes, including cyanobacteria, are also of interest to astrobiologists studying the prospects for life beyond our planet as ice-based ecosystems have been proposed as an analogue to an early stage of the development of Mars and Jupiter's frozen moon Europa. On Mars, where liquid water occurred long ago, it is proposed that life could have evolved at a similar time to the development of cyanobacteria on early Earth (Friedmann 1986). An understanding of conditions required for life to originate and evolve in the cryosphere assists in interpreting biogeochemical "fingerprints of life" in the study of life beyond Earth.

There is also evidence that the Precambrian biosphere experienced extreme low temperature conditions several times during the Paelo- and Neoproterozoic. Ice-based habitats with their sustainable microbial communities are thought to be potential analogues for biotopes present during these major glaciation events, such as the hypothesized "Snowball Earth" (Vincent and Howard-Williams 2000; Vincent et al. 2004). Fossil records suggest that cyanobacteria, in particular oscillatorian taxa, were present throughout these Proterozoic events, and perhaps during earlier periods of global cooling (Schopf and Walter 1982). The cold tolerance combined with growth optima at higher temperatures found in polar oscillatorian cyanobacteria would present ideal characteristics to survive global "ice house/hothouse" cycles during the Proterozoic (Tang et al. 1997). Furthermore, cyanobacteria and other microorganisms are able to maintain prolonged dormancy under freeze-up conditions as well as have a variety of adaptive mechanisms to withstand high UV radiation, desiccation and hypersaline conditions (Vincent 2009; Zakhia et al. 2008). Therefore, cyanobacteria-dominated mats in supraglacial cryoconite holes and other ice-based ecosystems would have presented a potential refuge for survival, growth and diversification for a variety of organisms, including multicellular eukaryotes with protection from the extreme low temperature conditions provided

by the vertical stratification (Vincent and Howard-Williams 1989; Vincent 2000b; Vincent et al. 2004; Hoffman 2016). Furthermore, due to the large micro- and nanoscale variations in microhabitat properties, these ecosystems could have been conducive to evolutionary diversification due to inter- and intra-species interaction such as competition for resources and communication as well as homologous and heterologous gene transfer.

9.6.2 Biotic-Physical Interactions in the Cryosphere

Arctic ice shelves, with their surface marked by microbial mats covering vast areas or in more patchy distributions (Mueller et al. 2006), provide an intriguing opportunity to evaluate the influence of microorganisms on their physical environment as well as the reverse. Diverse life tolerates and even thrives in the environmental conditions found on Arctic ice shelves but the presence of these microbiota also impacts the ice shelf surface geomorphology. One example of this biotic-physical coupling is the effect microbial mats have on the inversion of topography in certain areas of the ice shelf (Fig. 9.8). Where microbial mat cover is extensive and meltwater ponds are less regularly shaped, there is a progression of the relative surface elevation due to differences in albedo between mats, water, ice and snow (Schraeder 1968). Frozen meltwater ponds with benthic microbial mats accumulate snow preferentially due to their lower relative elevation via wind re-distribution. In spring and summer, the lower albedo of the surrounding ice causes melting of the more exposed and higher ‘icescape’ features, leading to a plateau of snow and canded ice (the former meltwater pond) and new meltwater ponds in place of the former shoreline (Mueller and Vincent 2006). Microbial mats contain exopolymeric substances (EPS), a type of mucilage that enhances their cohesion (Stal 2003). They then tend to slide down-slope *en masse* from the plateau areas towards the meltwater ponds. This cycle, known as ‘inversion of relief’ (Smith 1961), appears to repeat itself although not necessarily on an annual basis. This geomorphological process affects the surface ablation of the shelf in areas where it occurs and it is doubtful that it would continue without the cohesive qualities provided by the ice shelf microbial mats (Mueller and Vincent 2006). Similarly, Yallop et al. (2012) identified an ice algae community that grew directly on the bare ice of the Greenland Ice Sheet that appeared to affect the melting of the ice due to their highly pigmented biomass.

9.6.3 Ecosystems on the Brink of Extinction

The ice shelf surface where microbial mats are found and the epishelf lakes that harbour freshwater microbial and zooplankton communities are ice-dependent ecosystems. These habitats are being extirpated due to the loss of Arctic ice shelves (Mueller et al. 2008). The scientific exploration of these ecosystems is in its infancy

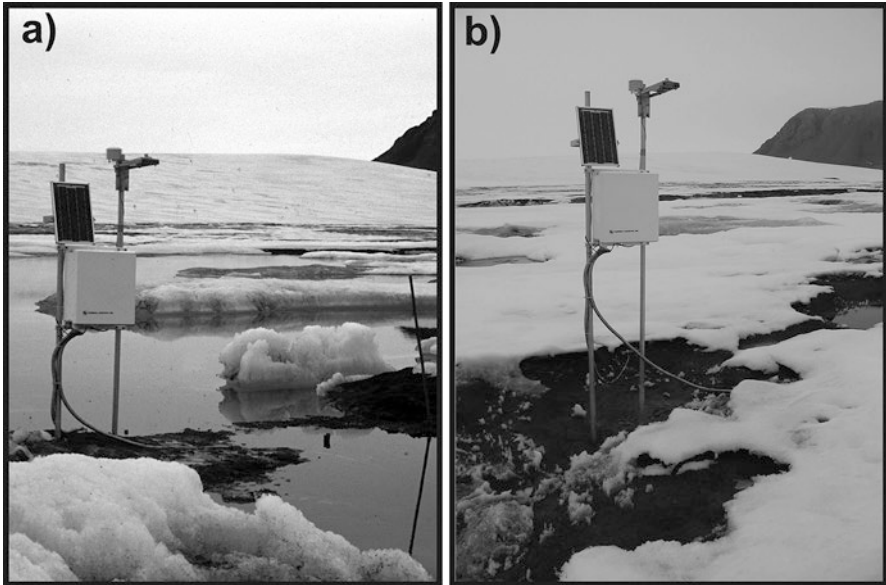


Fig. 9.9 Microbial mat-mediated ‘inversion of relief’ on the Ward Hunt Ice Shelf. The photographs taken in: (a) August 2001 and (b) July 2002 show a change in surface cover (from microbial mat to snow and vice versa) and relative elevation over time (Modified from Mueller and Vincent (2006), © John Wiley & Sons. Ltd., used with permission)

and therefore it is not possible to fully gauge the implications of their imminent loss. To date, no endemic organisms have been described in these habitats, but these environments are unique and so this possibility cannot be ruled out. Each taxon found in the microbial mats and epishelf lakes has also been found in analogous habitats in the region (Van Hove et al. 2001; Mueller et al. 2006; Bottos et al. 2008); however, the consortia that are found on the ice shelf surface appear to be unique to Arctic ice shelves (Vincent et al. 2000). Habitat fragmentation does not appear to influence the biodiversity of algal taxa in ice shelf microbial mats (Mueller et al. 2006), but the ongoing loss of ice shelf habitat is leading to the extinction these cryo-ecosystems along with their unique microbial consortia. Given the high tolerance to cold and light stresses in these microbiota and the suite of pigments and other compounds that they can synthesize (Mueller et al. 2005), including bioactive compounds, the loss of their cryo-habitat could also have implications for bioprospecting for the biotechnology and biomedical industries (Prisco and Christner 2004). As analogues for life on Snowball Earth (Vincent et al. 2000; Vincent and Howard-Williams 2000) and model systems for investigating physical-biotic interactions, the extinction of these ecosystems also represents loss of potential scientific knowledge.

In a changing environment, some ecosystems may be eliminated, but others are created. Over recent summers (2005, 2007 and 2008) there have been extensive open water areas for periods of up to five weeks along the northern coast of Ellesmere Island (Fig. 9.9; Copland et al. 2007; Mueller et al. unpublished). Little is known

about the characteristics of this novel habitat or the implications of its recent expansion. The North Water Polynya (in northern Baffin Bay) is the nearest permanent open water area to the northern coast of Ellesmere. This is an exceedingly productive area and may be, in a limited sense, an analogue for the nascent flaw lead polynya north of Ellesmere Island. These open water areas also facilitate the calving of ice shelves by removing the ice pressure that kept potentially broken pieces of ice shelf in place (Mueller et al. 2008; Copland et al. 2017). The development of new open water ecosystems along the northern coast of Ellesmere Island will likely impact coastal environment such as ice push from pack ice, disruption and thawing of permafrost, and wave-induced coastal erosion.

9.7 Conclusions

Until recently, Arctic ice shelves were seen as mostly abiotic glaciological features. However, in recent years it has become clear that their aquatic ecosystems are oases for life. Arctic ice shelves are now seen as dynamic structures that harbour a range of ecosystems with diverse biology. They contain ecosystems with different physical and chemical properties located on the surface and within the ice shelves. Based on current knowledge, much of the biomass is dominated by microbial assemblages, with the microbiota attaining biomass stocks comparable to lakes in temperate climatic zones. They represent analogues for the survival, growth and diversification of life on early Earth, and models for understanding properties of life beyond Earth. All the ice shelf ecosystems reviewed here are completely dependent on the continuous presence of ice, and are therefore highly vulnerable to ongoing climate change. With the accelerated break-up and loss of Arctic ice shelves (Mueller et al. 2008; Vincent et al. 2009), there may be little time left to explore their remarkable biology.

Acknowledgements This work has been supported by the Natural Sciences and Engineering Research Council of Canada, the Canada Research Chair program, le Fonds québécois de la recherche sur la nature et les technologies, the Northern Scientific Training Program, and the Network of Centre of Excellence program ArcticNet, with logistics support from the Polar Continental Shelf Program and Parks Canada. We thank Dominic Hodgson and an anonymous reviewer for their insightful comments on the manuscript.

References

- ACIA. (2005). *Arctic climate impact assessment* (pp. 1042). Cambridge: Cambridge University Press.
- Amato, P., Hennebelle, R. I., Maganda, O., Sancelme, M., Delort, A.-M., Barbante, C., Boutron, C., & Ferrari, C. (2007). Bacterial characterization of the snow cover at Spitzberg, Svalbard. *FEMS Microbiology Ecology*, 59, 255–264.

- Archer, S., McDonald, I., Herbold, C., & Cary, S. (2014). Characterization of bacterioplankton communities in the meltwater ponds of Bratina Island, Victoria Land, Antarctica. *FEMS Microbiology Ecology*, *89*, 451–464.
- Archer, D. J., McDonald, I. R., Herbold, C. W., Lee, C. K., & Cary, C. S. (2015). Benthic microbial communities of coastal terrestrial and ice shelf Antarctic meltwater ponds. *Frontiers in Microbiology*, *6*, 485. doi:[10.3389/fmicb.2015.00485](https://doi.org/10.3389/fmicb.2015.00485).
- Boetius, A., Anesio, A. M., Deming, J. W., Mikucki, J. A., & Rapp, J. Z. (2015). Microbial ecology of the cryosphere: Sea ice and glacial habitats. *Nature Reviews Microbiology*, *13*, 677–690.
- Bonilla, S., Villeneuve, V., & Vincent, W. F. (2005). Benthic and planktonic algal communities in a High Arctic lake: Pigment structure and contrasting responses to nutrient enrichment. *Journal of Phycology*, *41*, 1120–1130.
- Bonilla, S., Rautio, M., & Vincent, W. F. (2009). Phytoplankton and phyto-benthos pigment strategies: Implications for algal survival in the changing Arctic. *Polar Biology*, *28*, 846–861.
- Bottos, E. M., Vincent, W. F., Greer, C. W., & Whyte, L. G. (2008). Prokaryotic diversity of arctic ice shelf microbial mats. *Environmental Microbiology*, *10*, 950–966.
- Brinkmeyer, R., Knittel, K., Jürgens, J., Weyland, H., Amann, R., & Helmke, E. (2003). Diversity and structure of bacterial communities in Arctic versus Antarctic pack ice. *Applied and Environmental Microbiology*, *69*, 6610–6619.
- Cairns, A. A. (1967). The zooplankton of Tanquary Fjord, Ellesmere Island, with special reference to calanoid copepods. *Journal of Fisheries Research Board of Canada*, *24*, 555–568.
- Cameron, K. A., Hodson, A. J., & Osborn, A. M. (2012). Structure and diversity of bacterial, eukaryotic and archaean communities in glacial cryoconite holes from the Arctic and the Antarctic. *FEMS Microbiology Ecology*, *82*, 254–267.
- Castenholz, R. W. (1992). Species usage, concept, and evolution in the cyanobacteria (blue-green algae). *Journal of Phycology*, *28*, 737–745.
- Christmas, N. A. M., Anesio, A. M., & Sánchez-Baracaldo, P. (2015). Multiple adaptations to polar and alpine environments within cyanobacteria: A phylogenomic and Bayesian approach. *Frontiers in Microbiology*, *6*, 1070.
- Christner, B. C., Cai, R., Morris, C., McCarter, K. S., Foreman, C. M., Skidmore, M. L., Montross, S. N., & Sands, D. C. (2008). Geographic, seasonal, and precipitation chemistry influence on the abundance and activity of biological ice nucleators in rain and snow. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 18854–18859.
- Copland, L., Mueller, D. R., & Weir, L. (2007). Rapid loss of the Ayles Ice Shelf, Ellesmere Island, Canada. *Geophysical Research Letters*, *34*, L21501.
- Copland, L., Mortimer, C., White, A., Richer McCallum, M., & Mueller, D. (2017). Factors contributing to recent Arctic ice shelf losses. In L. Copland & D. Mueller (Eds.), *Arctic ice shelves and ice islands* (p. 263–285). Dordrecht: Springer. doi:[10.1007/978-94-024-1101-0_10](https://doi.org/10.1007/978-94-024-1101-0_10).
- Cary, A. P., Kulp, J. L., & Marshall, E. W. (1955). Evidences of climatic change from ice island studies. *Science*, *122*, 1171–1173.
- de Mora, S. J., Whitehead, R. F., & Gregory, M. (1994). The chemical composition of glacial melt water ponds on the McMurdo Ice Shelf, Antarctica. *Antarctic Science*, *6*, 17–27.
- Doran, P. T., Wharton Jr., R. A., Lyons, J. B., Des Marais, D. J., & Andersen, D. T. (2000). Sedimentology and geochemistry of a perennially ice-covered epishelf lake in Bunger Hills Oasis, East Antarctica. *Antarctic Science*, *11*, 131–140.
- Edwards, A., Douglas, B., Anesio, A. M., Rassner, S. M., Irvine-Flynn, T. D. L., Sattler, B., & Griffith, F. W. (2013). A distinctive fungal community inhabiting cryoconite holes on glaciers in Svalbard. *Fungal Ecology*, *6*(2), 168–176.
- Ehling-Schulz, M., & Scherer, S. (1999). UV protection in cyanobacteria. *European Journal of Phycology*, *34*, 329–338.
- Friedmann, E. I. (1986). The Antarctic cold desert and the search for traces of life on Mars. *Advances in Space Research*, *6*, 265–268.

- Fritsen, C. H., & Priscu, J. C. (1998). Cyanobacterial assemblages in permanent ice covers on Antarctic lakes: Distribution, growth rate, and temperature response of photosynthesis. *Journal of Phycology*, *34*, 587–597.
- Garcia-Pichel, F., & Castenholz, R. W. (1991). Characterization and biological implications of scytonemin, a cyanobacterial sheath pigment. *Journal of Phycology*, *27*, 395–409.
- Gibson, J. A. E., & Andersen, D. T. (2002). Physical structure of epishelf lakes of the southern Bunge Hills, East Antarctica. *Antarctic Science*, *14*, 253–261.
- Harding, T., Jungblut, A. D., Lovejoy, C., & Vincent, W. F. (2011). Microbes in high Arctic snow and implications for the cold biosphere. *Applied and Environmental Microbiology*, *77*, 3234–3243.
- Hawes, I., Smith, R., Howard-Williams, C., & Schwarz, A. M. (1999). Environmental conditions during freezing, and response of microbial mats in ponds of the McMurdo Ice Shelf, Antarctica. *Antarctic Science*, *11*, 198–208.
- Hawes, I., Howard-Williams, C., & Fountain, A. G. (2008). Ice-based freshwater ecosystems. In W. F. Vincent & J. Laybourn-Parry (Eds.), *Polar lakes and rivers – limnology of Arctic and Antarctic aquatic ecosystems* (p. 103–118). Oxford: Oxford University Press.
- Heywood, R. B. (1977). A limnological survey of the ablation point area, Alexander Island, Antarctica. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *279*, 39–54.
- Hodgson, D., Gibson, J., & Doran, P. T. (2004a). Antarctic paleolimnology. In R. Pienitz, M. S. V. Douglas, & J. P. Smol (Eds.), *Long-term environmental change in Arctic and Antarctic lakes* (p. 419–474). Dordrecht: Springer.
- Hodgson, D., Vyverman, W., Verleyen, E., Sabbe, K., Leavitt, P., Taton, A., Squier, A., & Keely, B. (2004b). Environmental factors influencing the pigment composition of in situ benthic microbial communities in East Antarctic lakes. *Aquatic Microbial Ecology*, *37*, 247–263.
- Hoffman, P. F. (2016). Cryoconite pans on snowball earth: Supraglacial oases for Cryogenian eukaryotes? *Geobiology*, *14*, 531–542.
- Holdsworth, G. (1987). The surface waveforms on the Ellesmere Island ice shelves and ice islands. In *Workshop on Extreme Ice Features, Banff, Alberta, November 3–5, 1986, National Research Council of Canada* (p. 385–403).
- Howard-Williams, C., Pridmore, R. D., Broady, P. A., & Vincent, W. F. (1990). Environmental and biological variability in the McMurdo Ice Shelf ecosystem. In K. R. Kerry & G. Hempel (Eds.), *Antarctic ecosystems: Ecological change and conservation* (p. 23–31). Berlin: Springer.
- Jeffries, M. O. (1992). Arctic ice shelves and ice islands: Origin, growth and disintegration, physical characteristics, structural-stratigraphic variability, and dynamics. *Reviews of Geophysics*, *30*, 245–267.
- Jeffries, M. O. (2017). The Ellesmere ice shelves, Nunavut, Canada. In L. Copland & D. Mueller (Eds.), *Arctic ice shelves and ice islands* (p. 23–54). Dordrecht: Springer. doi:10.1007/978-94-024-1101-0_2.
- Jungblut, A., Hawes, I., Mountfort, D., Hitzfeld, B., Dietrich, D., Burns, B., & Neilan, B. (2005). Diversity within cyanobacterial mat communities in variable salinity meltwater ponds of McMurdo Ice Shelf, Antarctica. *Environmental Microbiology*, *7*, 519–529.
- Jungblut, A., Lovejoy, C., & Vincent, W. F. (2010). Global distribution of cyanobacterial ecotypes in the cold biosphere. *The ISME Journal*, *4*, 191–202.
- Jungblut, A. D., Vincent, W. F., & Lovejoy, C. (2012). Eukaryotes in Arctic and Antarctic cyanobacterial mats. *FEMS Microbiology Ecology*, *82*, 416–428.
- Keys J. E. (1977). *Water regime of ice-covered fiords and lakes*. Ph.D. Thesis, Marine Sciences Centre, McGill University, Montreal, pp. 75
- Keys J. E. (1978). *Water regime of Disraeli Fiord, Ellesmere Island Report Number 792*. Ottawa: Defence Research Establishment Ottawa, pp. 58
- Laybourn-Parry, J. (2002). Survival mechanisms in Antarctica lakes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*, 863–869.

- Laybourn-Parry, J., Madan, N. J., Marshall, W. A., Marchant, H. J., & Wright, S. W. (2006). Carbon dynamics in an ultra-oligotrophic epishelf lake (Beaver Lake, Antarctica) in summer. *Freshwater Biology*, *51*, 1116–1130.
- Lionard, M., Péquin, B., Lovejoy, C., & Vincent, W. F. (2012). Benthic cyanobacterial mats in the high Arctic: Multi-layer structure and fluorescence responses to osmotic stress. *Frontiers in Aquatic Microbiology*, *3*, 140. doi:10.3389/fmicb.2012.00140.
- Ludlam, S. D. (1996). Stratification patterns in Taconite Inlet, Ellesmere Island, N.W.T. *Journal of Paleolimnology*, *16*, 205–215.
- Mader, H. M., Pettitt, M., Wadham, J. L., Wolff, E., & Parkes, J. (2006). Subsurface ice as a microbial habitat. *Geology*, *34*, 169–172.
- McKnight, D. M., Boyer, E. W., Westerhoff, P. K., Doran, P. T., Kulbe, T., & Andersen, D. T. (2001). Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. *Limnology and Oceanography*, *46*, 38–48.
- Miteva, V. I., Sheridan, P. P., & Brenchley, J. E. (2004). Phylogenetic and physiological diversity of microorganisms isolated from a deep Greenland glacier ice core. *Applied and Environmental Microbiology*, *70*, 202–213.
- Mountfort, D., Kaspar, H. F., Downes, M. T., & Asher, R. (1999). Partitioning effects during terminal carbon and electron flow in sediments of a low-salinity meltwater pond near Bratina Island, McMurdo Ice Shelf, Antarctica. *Applied and Environmental Microbiology*, *65*, 5493–5499.
- Mountfort, D., Kaspar, H., Asher, R., & Sutherland, D. (2003). Influences of pond geochemistry, temperature, and freeze-thaw on terminal anaerobic processes occurring in sediments of six ponds of the McMurdo Ice Shelf, near Bratina Island, Antarctica. *Applied and Environmental Microbiology*, *69*, 583–592.
- Mueller, D. R., & Vincent, W. F. (2006). Microbial habitat dynamics and ablation control on the Ward Hunt Ice Shelf. *Hydrological Processes*, *20*, 857–876.
- Mueller, D. R., Vincent, W. F., Pollard, W. H., & Fritsen, C. H. (2001). Glacial cryoconite ecosystems: A bipolar comparison of algal communities and habitats. *Nova Hedwigia, Beiheft*, *123*, 173–197.
- Mueller, D. R., Jeffries, M. O., & Vincent, W. F. (2003a). Ice shelf break-up and ecosystem loss in the Canadian High Arctic. *Eos, Transactions of the American Geophysical Union*, *84*, 548,552.
- Mueller, D. R., Vincent, W. F., & Jeffries, M. O. (2003b). Break-up of the largest Arctic ice shelf and associated loss of an epishelf lake. *Geophysical Research Letters*, *30*, 2031.
- Mueller, D. R., Vincent, W. F., Bonilla, S., & Laurion, I. (2005). Extremotrophs, extremophiles and broadband pigmentation strategies in a high Arctic ice shelf ecosystem. *FEMS Microbiology Ecology*, *53*, 73–87.
- Mueller, D. R., Vincent, W. F., & Jeffries, M. O. (2006). Environmental gradients, fragmented habitats and microbiota of a northern ice shelf cryoecosystem, Ellesmere Island, Canada. *Arctic, Antarctic, and Alpine Research*, *38*, 593–607.
- Mueller, D. R., Copland, L., Hamilton, A., & Stern, D. R. (2008). Examining Arctic ice shelves prior to 2008 breakup. *Eos, Transactions of the American Geophysical Union*, *89*, 502–503.
- Müller, T., Bleiß, W., Martin, C.-D., Rogaschewski, S., & Fuhr, G. (1998). Snow algae from Northwest Svalbard: Their identification, distribution, pigment and nutrient content. *Polar Biology*, *20*, 14–23.
- Narod, B. B., Clarke, G. K. C., & Prager, B. T. (1988). Airborne UHF radar sounding of glaciers and ice shelves, northern Ellesmere Island, Arctic Canada. *Canadian Journal of Earth Sciences*, *25*, 95–105.
- Oren, A. (2000). Salt and brines. In B. A. Whitton & M. Potts (Eds.), *The ecology of cyanobacteria: Their diversity in time and space* (p. 281–306). Dordrecht: Kluwer Academic Publishers.
- Pearl, H. W., & Pinckney, J. L. (1996). A mini-review of microbial consortia: Their role in aquatic production and biogeochemical cycling. *Microbial Ecology*, *31*, 225–247.

- Pointing, S. B., Büdel, B., Convey, P., Gillman, L., Körner, C., Leuzinger, S., & Vincent, W. F. (2015). Biogeography of photoautotrophs in the high polar biome. *Frontiers in Plant Science*, *6*, 692. doi:10.3389/fpls.2015.00692.
- Price, P. B. (2007). Microbial life in glacial ice and implications for a cold origin of life. *FEMS Microbiology Ecology*, *59*, 217–231.
- Price, P. B., & Sowers, T. (2004). Temperature dependence of metabolic rates for microbial growth, maintenance, and survival. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 4631–4636.
- Priscu, J. C., & Christner, B. C. (2004). Earth's icy biosphere. In A. Bull (Ed.), *Microbial diversity and bioprospecting* (p. 130–145). Washington, DC: American Society for Microbiology.
- Quesada, A., & Vincent, W. F. (1997). Strategies of adaptation by Antarctic cyanobacteria to ultraviolet radiation. *European Journal of Phycology*, *32*, 335–342.
- Quesada, A., Vincent, W. F., & Lean, D. R. S. (1999). Community and pigment structure of Arctic cyanobacterial assemblages: The occurrence and distribution of UV-absorbing compounds. *FEMS Microbiology Ecology*, *28*, 315–323.
- Rivkina, E. M., Friedmann, E. I., McKay, C. P., & Gilichinsky, D. A. (2000). Metabolic activity of permafrost bacteria below the freezing point. *Applied and Environmental Microbiology*, *66*, 3230–3233.
- Roos, J. C., & Vincent, W. F. (1998). Temperature dependence of UV radiation effects on Antarctic cyanobacteria. *Journal of Phycology*, *34*, 118–125.
- Schopf, J. W., & Walter, M. R. (1982). Origin and early evolution of cyanobacteria: The geological evidence. In G. Carr & B. A. Whitton (Eds.), *The biology of cyanobacteria* (p. 543–564). Oxford: Blackwell Scientific Publisher.
- Schraeder, R. L. (1968). *Ablation of Ice Island ARLIS II, 1961*. M.Sc. Thesis, Department of Geology, University of Alaska, College, Fairbanks, pp. 59
- Sjöling, S., & Cowan, D. A. (2003). High 16S rDNA bacterial diversity in glacial meltwater lake sediment, Bratina Island, Antarctica. *Extremophiles*, *7*, 275–282.
- Smith, D. D. (1961). Sequential development of surface morphology on Fletcher's Ice Island, T-3. In G. O. Raasch (Ed.), *Geology of the Arctic* (p. 896–914). Toronto: University of Toronto Press.
- Smith, J. A., Hodgson, D., Bentley, M. J., Verleyen, E., Leng, M. J., & Roberts, S. J. (2006). Limnology of two Antarctic epishelf lakes and their potential to record periods of ice shelf loss. *Journal of Paleolimnology*, *35*, 373–394.
- Squier, A. H., Airs, R. L., Hodgson, D. A., & Keely, B. J. (2004). Atmospheric pressure chemical ionisation liquid chromatography/mass spectrometry of the ultraviolet screening pigment scytonemin: Characteristic fragmentations. *Rapid Communications in Mass Spectrometry*, *18*, 2934–2938.
- Stal, L. (2000). Cyanobacterial mats and stromatolites. In B. A. Whitton & M. Potts (Eds.), *The ecology of cyanobacteria: Their diversity in time and space* (p. 61–120). Dordrecht: Kluwer Academic Press.
- Stal, L. (2003). Microphytobenthos, their extracellular polymeric substances, and the morphogenesis of intertidal sediments. *Geomicrobiology Journal*, *20*, 463–478.
- Tang, E. P. Y., Tremblay, R., & Vincent, W. F. (1997). Cyanobacteria dominance of polar freshwater ecosystems: Are high-latitude mat-formers adapted to low temperature? *Journal of Phycology*, *33*, 171–181.
- Thibault, D., Head, E. J. H., & Wheeler, P. A. (1999). Mesozooplankton in the Arctic Ocean in summer. *Deep Sea Research: Part I - Oceanographic Research Papers*, *46*, 1391–1415.
- Van Hove, P., Swadling, K., Gibson, J. A. E., Belzile, C., & Vincent, W. F. (2001). Farthest north lake and fjord populations of calanoid copepods *Limnocalanus macrurus* and *Drepanopus bungei* in the Canadian High Arctic. *Polar Biology*, *24*, 303–307.
- Van Hove, P., Belzile, C., Gibson, J. A. E., & Vincent, W. F. (2006). Coupled landscape-lake evolution in the coastal High Arctic. *Canadian Journal of Earth Sciences*, *43*, 533–546.

- Van Hove, P., Vincent, W. F., Galand, P. E., & Wilmotte, A. (2008). Abundance and diversity of picocyanobacteria in High Arctic lakes and fjords. *Algological Studies*, 126, 209–227.
- Van Trappen, S., Mergaert, J., Van Eygen, S., Dawyndt, P., Cnockaert, M. C., & Swings, J. (2002). Diversity of 746 heterotrophic bacteria isolated from microbial mats from ten Antarctic lakes. *Systematic and Applied Microbiology*, 25, 603–610.
- Varin, T., Lovejoy, C., Jungblut, A. D., Vincent, W. F., & Corbeil, J. (2010). Metagenomic profiling of Arctic microbial mat communities as nutrient scavenging and recycling systems. *Limnology and Oceanography*, 55, 1901–1911.
- Varin, T., Lovejoy, C., Jungblut, A. D., Vincent, W. F., & Corbeil, J. (2012). Metagenomic analysis of stress genes in microbial mat communities from extreme Arctic and Antarctic environments. *Applied and Environmental Microbiology*, 78, 549–559.
- Veillette, J., Mueller, D. R., Antoniadis, D., & Vincent, W. F. (2008). Arctic epishelf lakes as sentinel ecosystems: Past, present and future. *Journal of Geophysical Research - Biogeosciences*, 113, G04014.
- Veillette, J., Lovejoy, C., Potvin, M., Harding, T., Jungblut, A. D., Antoniadis, D., Chénard, C., Suttle, C. A., & Vincent, W. F. (2011). Milne Fiord epishelf lake: A coastal Arctic ecosystem vulnerable to climate change. *Ecoscience*, 18, 304–316.
- Vézina, S., & Vincent, W. F. (1997). Arctic cyanobacteria and limnological properties of their environment: Bylot Island, Northwest Territories, Canada (73°N, 80°W). *Polar Biology*, 17, 523–534.
- Villeneuve, V., Vincent, W. F., & Komárek, J. (2001). Community structure and microhabitat characteristics of cyanobacterial mats in an extreme high Arctic environment: Ward Hunt Lake. *Nova Hedwigia, Beiheft*, 123, 199–224.
- Vincent, W. F. (1988). *Microbial ecosystems of Antarctica* (304 pp). Cambridge: Cambridge University Press.
- Vincent, W. F. (2000a). Evolutionary origins of Antarctic microbiota: Invasion, detection and endemism. *Antarctic Science*, 12, 374–386.
- Vincent, W. F. (2000b). Cyanobacterial dominance in the polar regions. In B. A. Whitton & M. Potts (Eds.), *The ecology of cyanobacteria: Their diversity in time and space* (p. 321–340). Dordrecht: Kluwer Academic Press.
- Vincent, W. F. (2007). Cold tolerance in cyanobacteria and life in the cryosphere. In J. Seckbach (Ed.), *Algae and cyanobacteria in extreme environments* (p. 287–301). Heidelberg: Springer.
- Vincent, W. F. (2009). Cyanobacteria. In G. E. Likens (Ed.), *Encyclopedia of inland waters* (Vol. 3, p. 55–60). Oxford: Elsevier.
- Vincent, W. F., & Howard-Williams, C. (1989). Microbial communities in southern Victoria Land streams (Antarctica). 2. The effects of low temperature. *Hydrobiologia*, 172, 39–49.
- Vincent, W. F., & Howard-Williams, C. (2000). Life on snowball earth. *Science*, 287, 2421.
- Vincent, W. F., & Neale, P. J. (2000). Mechanisms of UV damage to aquatic organisms. In S. J. de Mora, S. Demers, & M. Vernet (Eds.), *The effects of UV radiation in the marine environment* (p. 149–176). Cambridge: Cambridge University Press.
- Vincent, W. F., Castenholz, R. W., Downes, M. T., & Howard-Williams, C. (1993). Antarctic cyanobacteria: Light, nutrients, and photosynthesis in the microbial mat environment. *Journal of Phycology*, 29, 745–755.
- Vincent, W. F., Gibson, J. A., Pienitz, R., Villeneuve, V., Broady, P. A., Hamilton, P. B., & Howard-Williams, C. (2000). Ice shelf microbial ecosystems in the high Arctic and implications for life on snowball earth. *Naturwissenschaften*, 87, 137–141.
- Vincent, W. F., Gibson, J. A. E., & Jeffries, M. O. (2001). Ice shelf collapse, climate change, and habitat loss in the Canadian High Arctic. *Polar Record*, 37, 133–142.
- Vincent, W. F., Mueller, D. R., & Bonilla, S. (2004). Ecosystems on ice: The microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology*, 48, 103–112.
- Vincent, W. F., Whyte, L. G., Lovejoy, C., Greer, C. W., Laurion, I., Suttle, C. A., Corbeil, J., & Mueller, D. R. (2009). Arctic microbial ecosystems and impacts of extreme warming during the International Polar Year. *Polar Science*, 3, 171–180.

- Webster-Brown, J. G., Hawes, I., Jungblut, A. D., Wood, S. A., & Christenson, H. K. (2015). The effects of entombment on water chemistry and bacterial assemblages in closed cryoconite holes on Antarctic glaciers. *FEMS Microbiology Ecology*, *91*(12). doi:[10.1093/femsec/fiv144](https://doi.org/10.1093/femsec/fiv144).
- Wheeler, P. A., Gosselin, N., Sherr, E., Thibault, D., Kirchman, D. L., Benner, R., & Whiteledge, T. E. (1996). Active cycling of organic carbon in the Central Arctic Ocean. *Nature*, *380*, 697–699.
- White, A., Mueller, D., & Copland, L. (2015). Reconstructing hydrographic change in Petersen Bay, Ellesmere Island, Canada, inferred from SAR imagery. *Remote Sensing of Environment*, *165*, 1–13.
- Yallop, M. L., Anesio, A. M., Perkins, R. G., Cook, J., Telling, J., Fagan, D., MacFarlane, J., Stibal, M., Barker, G., Bellas, C., Hodson, A., Tranter, M., Wadham, J., & Roberts, N. W. (2012). Photophysiology and albedo-changing potential of the ice algal communities on the surface of the Greenland Ice Sheet. *The ISME Journal*, *6*, 2302–2313.
- Zakhia, F., Jungblut, A. D., Taton, A., Vincent, W. F., & Wilmotte, A. (2008). Cyanobacteria in cold environments. In R. Margesin, F. Schinner, J. C. Marx, & C. Gerday (Eds.), *Psychrophiles: From biodiversity to biotechnology* (p. 121–135). Heidelberg: Springer.