Chapter 4
Microbial Life in Supraglacial Environments

Arwyn Edwards and Karen A. Cameron

Abstract Supraglacial environments occupy 11% of Earth's surface area and represent a critical interface between climate and ice. This century has brought a renewed appreciation that glacier surfaces represent a collective of diverse microbial niches which occur wherever sufficient liquid water is available to support microbial activity: even at the microscopic scales of ice crystal boundaries within the crystalline matrices of snow or glacial ice. Within this chapter, we review the range of microbial habitats associated with snowpacks, the glacial ice photic zone, and phototrophic microbial biofilms formed by supraglacial algae or by the darkening of microbe–mineral aggregates known as cryoconite. In summary, glacier surfaces are home to surprisingly biodiverse and active microbial communities despite their low temperatures and austere conditions. Consequently, microbial communities and their processes are interposed between climate and ice and merit urgent consideration in the light of the effects of climate warming on Earth's supraglacial environments.

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4.1 Introduction

In the twenty-first century, approximately 198,000 glaciers and 2 ice sheets cover roughly 11% of Earth's surface area, sequestering 70% of Earth's freshwater (Shiklomanov 1993; Pfeffer et al. 2014). Within the recent geologic past, glacial ice covered ca. 30% of the Earth's surface during the last glacial maximum (Boyd et al. 2010), and the extent of ice is thought to have approached total coverage during so-called Snowball Earth events during the Cryogenian period 600–700 million years ago (Hoffman et al. 1998). However, within the near future, anthropogenic climate change will contribute to the decimation of Earth's glacial ice (Meier et al. 2007; Joughin et al. 2014; Pachauri et al. 2014). In the event of severe climate warming, the loss of up to 85% of mountain glaciers is predicted within this century (Pachauri et al. 2014). Moreover, climatic warming spurs the destabilization of Greenland's ice sheet and risks commitment to the loss of Antarctica's ice sheet (e.g., Joughin et al. 2014). Consequently, ice melt is set to be a major contributor to rising sea levels with impacts upon the habitability of coastal areas (FitzGerald et al. 2008) and the food and water security of densely populated regions nourished by glacial meltwaters (Edwards et al. 2014a; Hodson 2014). The importance of glaciers and ice sheets within the Earth system at both geologic timescales as well as the future of our contemporary society is therefore readily apparent and merits considerable investment in the study of both the fundamental properties of glacial systems and predictions of the rates and extents of their responses to climatic warming.

In contrast, a neglected facet of glacial systems is that they are also microbial habitats. In volumetric terms, glaciers and ice sheets represent Earth's largest freshwater ecosystem (Edwards et al. 2014a). Only in this century has the paradigm of glaciers and ice sheets as truly inhospitable environments been displaced as a result of experimental and conceptual advances spawning the field of glacier ecology, summarized in the seminal review of glacial ecosystems by Andrew Hodson and his colleagues in 2008 (Hodson et al. 2008). We now recognize that glacial systems represent both a deep frozen archive of microbial biodiversity (Bidle et al. 2007) and loci of globally significant biogeochemical processes mediated by microbes (Anesio et al. 2009; Boyd et al. 2010; Wadham et al. 2012; Hawkings et al. 2014), despite the unfavorable effects of their prevailing low temperatures (Rodrigues and Tiedje 2008). Indeed, microbial communities at the glacier–atmosphere interface constitute a supraglacial ecosystem and assume considerable importance as modulators of both biogeochemical cycling and glacial system response to melting (Anesio et al. 2009; Lutz et al. 2016b).

Within this chapter, we focus upon the microbial communities within the supraglacial ecosystem and their interactions within this habitat, addressing the key concepts, processes, and approaches relevant to the study of microbial life in supraglacial environments.

4.2 The Physical Properties of Glacial Systems

An understanding of the fundamental properties of glacial systems is an essential prerequisite to their consideration as microbial ecosystems. Readers from a non-glaciological background embarking upon the study of glacial ecosystems are advised to solicit the guidance offered by popular scholarly texts on the theory (e.g., Benn and Evans 2014) and practice (e.g., Hubbard and Glasser 2005) of glaciology to enrich their multidisciplinary endeavors. Within this section, we provide a synopsis of the properties of glacial systems pertinent to a discussion of supraglacial ecosystems.

As large persistent masses of ice, glaciers and ice sheets represent major features of the terrestrial cryosphere. These ice masses form where the prolonged accumulation of ice mass exceeds its loss by ablation, resulting in the metamorphosis of snow crystals to glacial ice. Glacial ice itself is a non-Newtonian fluid which is deformed under the pressure created by its own mass, resulting in the gravitational flow of glacial ice from higher to lower elevations once a critical thickness of glacial ice cover is achieved. Moreover, thick accumulations of glacial ice can sufficiently elevate pressures at the glacier bed to incur pressure-induced melting of glacial ice, resulting in an admixture of ice above its pressure melting point and influencing the *thermal regime* of a glacial system.

Typically, the distribution of ice mass across an elevational gradient incurs variation in the rates of ice accumulation and ablation as a consequence of altitudinal effects on local temperature from adiabatic cooling. Colder, higher elevations where the accumulation of ice mass directly from snowfall (or indirectly from wind-redistributed snow or avalanches) annually exceeds its ablation represent zones of net accumulation. Meanwhile, warmer lower elevations experience net ablation since the loss of ice mass (via sublimation, the generation of meltwater, or the direct loss of ice mass by the formation of icebergs) annually exceeds its accumulation. This property is known as the *mass balance gradient* of a glacial system and pivots upon an elevational contour known as the *equilibrium line altitude* where accumulation equals ablation on an annual basis. Glacial systems well-nourished by precipitation and residing in colder climates will tend towards the net accumulation of ice mass and consequently will advance as a result of their *positive mass balance* while glacial systems experiencing net ablation of ice mass will exhibit *negative mass balance* and exhibit recession. As such, glacial systems can be thought of as climatic thermometers and thermostats, and indeed the properties of ice within a glacial system can provide a proxy for the reconstruction of past climate (e.g., Petit et al. 1999).

Glacial systems take a range of forms. Glaciers are entities comprised of flowing glacial ice constrained by the topography of the landscape in which they reside while the accumulation of glacial ice present in ice sheets and ice caps override the underlying topography of their catchments. The division between ice caps and ice sheets is a function of their scale; ice sheets are defined as possessing surface areas greater than 50,000 km^2 (Benn and Evans 2014; Gokul et al. 2016) and presently include the ice sheet on Greenland and the Antarctic Ice Sheet which is divided into two sections, East and West, by the Transantarctic mountains. At the opposite end of the size spectrum, some glacial systems exhibit unconventional flow modes or, indeed, no detectable flow modes at all. These include ice patches, which are small, localized accumulations of glacial ice typically nourished by the wind-driven accumulation of snow (Andrews and MacKay 2012) and debris covered or buried ice masses (Franzetti et al. 2013). The scale of the ice mass and its relationship with the parent catchment has implications for cognate ecosystems in terms of the sources, residence time, and dynamics of microbiota.

Finally, glacial systems entrain both water and debris, affording resident microbes with solvent, nutritional solutes, habitats, and dispersal modes. In terms of debris accumulation transport, the burden of debris associated with glacial systems can be considerable, ranging from fine grained aeolian debris (McGee et al. 2010) to in extremis debris covered glaciers which are extensively covered in rocks, affording shelter and nutrition to lithotrophic microbial communities (Franzetti et al. 2013). Glacial melt can be stored and transported within glacial systems as water percolating in intercrystalline spaces (e.g., in water-saturated decomposing snowpacks, firn aquifers, the near-surface ice itself, or in saturated basal sediments); it can be captured by compartmentalized storage systems (e.g., in supraglacial lakes, englacial chambers, or subglacial lakes) or it can move rapidly though channelized drainage through surficial, englacial, or subglacial drainage networks. The interplay between glaciers and melt leading to the evolution of glacier hydraulic systems is multifaceted since multiple interactions that occur between mass balance and thermal regime (Irvine-Fynn et al. 2011b) complicate the evolution, storage, and flux of meltwater. Nevertheless, considering life's cardinal requirement is for liquid water, it is safe to conclude the relationship between melt and microbes is necessarily intimate within glacial systems.

The glacier surface itself represents the interface between the glacier and the atmosphere. Accordingly, there is a continual exchange of matter and energy, with the surface energy budget of a glacier being represented by Eq. (1) (Paterson 1994):

$$Q_{\mathrm{M}} + Q_{\mathrm{SW}} + Q_{\mathrm{LW}} + Q_{\mathrm{S}} + Q_{\mathrm{L}} + Q_{\mathrm{P}} + Q_{\mathrm{C}} = 0 \left(\mathrm{w\ m}^2\right) \tag{1}$$

where Q_{M} is the energy accessible for melting, Q_{SW} and Q_{LW} represent shortwave and longwave radiation, respectively, Q_{S} and Q_{L} are sensible and latent heat, while Q_{P} is energy from precipitation, and Q_{C} is energy conducted into the glacial system. Conditions at the supraglacial environment become most conducive for microbial life when the influx of energy, predominantly as shortwave radiation, is sufficient to incur melting. As a consequence, life can thrive at the glacier surface thanks to the genesis of liquid water and liberation of nutrients within snow and ice melt concomitant with the onslaught of photosynthetically available radiation (Anesio and Laybourn-Parry 2012) and elevated ambient temperatures.

4.3 Snow Habitats

Every glacier starts with a single snowflake. While the recognition of microbial processes in snow dates to Aristotle (Hell et al. 2013), and Van Leeuwenhoek found microbes within snowmelt among the first samples he viewed with a microscope (van Leewenhoeck 1677), the study of microbial life in supraglacial snow is a recent endeavor (Kol 1942). In spite of the low temperature and limited supply of nutrients typical of snow, microbial abundances in the range of 2×10^2 to 7.2×10^5 cells ml^{-1} of melted snow are reported from supraglacial snow (Carpenter et al. 2000; Amato et al. 2007; Irvine-Fynn et al. 2012). Considering that the 11% of Earth surface overridden by glacial ice is seasonally or perennially covered by snow, it is clear that supraglacial snowpacks represent globally extensive repositories of microbial assemblages, with considerable scope for variation in abundance, diversity, and activity. The abundance and activity of microbes within snow is influenced by their origins and the onset of melt (Xiang et al. 2009), so we consider distinct stages in the interactions between snow and its microbiota.

4.3.1 Depositional Modes

Snowflakes themselves, as the micro-scaled crystalline precipitates of water ice, represent microbial habitats (Sattler et al. 2001; Temkiv et al. 2011). While a detailed consideration of snow microbiology while aloft lies within the domain of atmospheric microbiology (see Chap. 3) and is thus beyond the scope of this chapter, the windborne redistribution of poorly consolidated supraglacial snow raises the potential for metabolic activity by microbes in ice precipitation (Temkiv et al. 2013). Moreover, microbial processes contribute to the nucleation of ice crystals, including fresh snowfall on glacier surfaces (Christner et al. 2008). Therefore, snow and ice precipitates both nourish the mass balance of glacial systems and inoculate glacial systems with microbiota (Harding et al. 2011; Cameron et al. 2014), representing *wet* modes of microbial deposition (Xiang et al. 2009). In contrast, *dry* modes of microbial deposition entail the passive sedimentation of airborne microbiota and in particular the co-deposition of microbial biomass with aeolian particulates (Xiang et al. 2009). Necessarily, the wet or dry mode of deposition will influence the origins, rates, viability, and composition of microbial inoculants to the snowpack (Hell et al. 2013; Cameron et al. 2014). Both locally derived material advected to the glacier surface (Hell et al. 2013) and (co-) deposition of microbiota following long-range transport from source environments are possible (Harding et al. 2011; Cameron et al. 2014; Nagatsuka et al. 2014; Wunderlin et al. 2016). As such, the supraglacial ecosystem can be connected with distant regions of the global cryosphere via atmospheric transport (Pearce et al. 2009) prompting the inoculation of globally ubiquitous microbial taxa (Darcy et al. 2011) to the supraglacial environment.

4.3.2 Microbial Life in the Dynamic Snowpack

Snowpacks represent complex habitats at the microbial scale. Although intrinsically defined by the presence of crystals of water ice, changes in the availability of water and impurities (including both nutrients and pollutants) are driven by the consolidation and melting of the snowpack, affecting the fundamental niches occupied by snow microbiota as the snowpack metamorphoses over time.

While dry, cold (i.e., subzero, non-melting) snowpacks are thought to represent a low end-member in the spectrum of activity and biomass associated with snow, they are not necessarily microbiologically inert. Initial evidence for in situ microbial activities in dry snow was offered (Carpenter et al. 2000) following low, but nonzero, rates of macromolecular synthesis via radioisotope inclusion in incubations of snow collected at the South Pole and incubated at temperatures representing in situ conditions. The validity of the inferences drawn from the experimental work was questioned within the literature (Warren and Hudson 2003) on the grounds of limited water availability and the eventual entombment of snow at depth, at temperatures of −50 °C. However, more recent work lends tacit support for the argument that microbes are active within dry polar snow. Firstly, sophisticated analyses of CRISPR repeat loci in shotgun metagenomic datasets of surface snow from the Antarctic plateau (Lopatina et al. 2016) infer a selection process is at play within the dry snow microbiota. While the stage (i.e., pre- or post-depositional) at which the selective pressures are manifest is less clear, the recovery of different community profiles from the sequencing of reverse-transcribed cDNA from 16S rRNA versus the sequencing of 16S rRNA genes from the same dry Antarctic snow samples (Lopatina et al. 2013) mitigates for the presence of translational machinery consistent with microbial activity (Blazewicz et al. 2013) in dry snow leading to interannual variability in communities within the snow (Lopatina et al. 2013). Moreover, Amoroso et al. (2009) concluded that microbial activities within dry, dark snowpacks must be responsible for nitrification occurring under conditions which do not permit abiotic photolysis of reactive nitrogen species. Considering the vast scale of dry, cold snowpacks, future work should examine these potential microbial habitats closely, since the cumulative effect of processes occurring at marginal rates across expansive habitats is nontrivial.

Seasonal melt transforms the snowpack habitat. Evidently, melt promotes the availability of liquid water. Furthermore, melt mobilizes of ionic impurities derived from aerosol deposits (e.g., from sea spray and atmospheric pollution) from the snowpack as they are rejected from decaying ice crystals (Davies et al. 1987; Kuhn 2001). Conservative, non-nutrient ions are eluted rapidly from the decaying snowpack, changing the boundary conditions for microbial life. Meanwhile, nutrient ions are sequestered within the snowpack, evidencing their biogeochemical transformations and identifying the melting snowpack as the locus of an active microbial ecosystem as well as the modulator of snowmelt composition, affecting nutrient availability in downstream habitats (Hodson et al. 2005).

The snowpack microbial community interacts closely with these complex changes in conditions (Larose et al. 2013; Maccario et al. 2014). In the first instance, the bacterial community of the snowpack has been shown to shift in its structure rapidly as melt progresses. Hell et al. (2013) examined the snowpack of a High Arctic glacier; in line with earlier studies, (Amato et al. 2007; Larose et al. 2010) a diverse bacterial community was identified in the snowpack. Notably, surface layers of snow harbor discrete communities of bacteria relative to melting snow and water-saturated snow (slush), indicating the role of post-depositional changes in community. While the class Betaproteobacteria retained its dominance of the community over the course of a week, the genus *Polaromonas* was able to adapt to the changing conditions. *Polaromonas* itself is ubiquitous within the global cryosphere (Darcy et al. 2011; Franzetti et al. 2013) and is characterized as a metabolically flexible genus, with the ability to degrade complex xenobiotics (Mattes et al. 2008). More recently, Franzetti et al. (2016) raised the prospect that supraglacial *Polaromonas* may act as anoxygenic phototrophs from the oxidation of carbon monoxide arising from photolytic degradation of supraglacial organic matter. While this study focused upon cryoconite environments, which are, at depth, attenuated in their exposure to high energy UV and possess an abundance of bioavailable organic carbon sources (Anesio et al. 2009), the potential for *Polaromonas*-mediated mixotrophy in the photochemically reactive (Amoroso et al. 2009) snowpack is unexplored.

Considering that multiple studies indicate the bacterial community is responsive to melt at week- to seasonal timescales (Hell et al. 2013; Maccario et al. 2014), the impacts of contemporary climate change on the timing, rate, duration, spatial extent, and hydrological flowpaths of seasonal snowmelt and the cognate bacterial community must be considered (Fig. 4.1). Spatially expansive yet transient melting

Fig. 4.1 Liquid water saturating a shallow firn core in the accumulation zone of the Greenland Ice Sheet (Photo credit: Sara Penrhyn-Jones)

episodes have been observed already, most notably during August 2012 ca. 97% of the surface area of the Greenland Ice Sheet (GrIS) exhibited melting, albeit for a duration of less than a week (Nghiem et al. 2012). While Betaproteobacteria may respond and influence the cycling of nitrogen pollutants deposited in the snowpack at such timescales on valley glaciers (Hell et al. 2013), whether the microbiota of the GrIS snowpack (Cameron et al. 2014) responded to this event is open to question. Stibal et al. (2015a) identified elevated microbial cell concentrations present in the refrozen 2012 melt layer relative to un-melted layers of the snowpack at a site high upon the GrIS, but the limited numbers of samples available precluded further detailed investigation. Moreover, whether the percolative redistribution of snowmelt into the perennial, near-surface firn aquifer of the GrIS accumulation zone (Forster et al. 2013) permits microbial community activities in a potential habitat four times the size of Wales is entirely unknown. While the empirical evidence for bacterial activities of biogeochemical significance in melting snowpacks is clear, it is evident that there are significant lacunae in our understanding of these processes in the context of rapid changes in the cryosphere.

Beyond the bacterial community, the snowpack is home to other types of microbiota. The presence of Archaea is variable, notably absent in some studies (Hell et al. 2013; Lazzaro et al. 2015) but detected independently by others (Cameron et al. 2014; Lutz et al. 2015). Over 30 Archaeal taxa were identified (Choudhari et al. 2013) in avalanche debris cone snow, paralleling an average number of 30 Archaeal taxa per sample across GrIS snow samples (Cameron et al. 2014). Archaea from the class Nitrosphaerales, associated with ammonia oxidation, predominate in both GrIS and Icelandic snow samples harboring Archaea (Cameron et al. 2014; Lutz et al. 2015), implying a potential role for Archaea in supraglacial nitrification, although further evidence for archaeal contributions to nitrogen cycling in glacial habitats is limited (Boyd et al. 2011).

In contrast to the enigmatic Archaea, the microeukaryotic component of the snowpack is readily apparent in the form of charismatic snow algae. Typically described as *Chlamydomonas nivalis,* snow algae are comprised of several algal lineages within the Chlorophyceae, in particular the Chlamydomonadaceae genera *Chloromonas, Chlamydomonas,* and *Raphidonema* (Spijkerman et al. 2012; Lutz et al. 2016a). Characteristic of these algae are the presence of unicellular motile cells within the isothermal snowpack, which form either green snow or red snow dependent upon reaching a quiescent phase in which the cells accumulate carotenoid pigments such as astaxanthin (Remias et al. 2005) as a means of photoprotection from high levels of UV penetrating the atrophied snowpack later in the melting season. Algal communities in red snow are apparent upon glaciers worldwide (Kol 1942; Yoshimura et al. 1997; Lutz et al. 2016b), and the community composition of red snow is remarkably uniform at the interspecific level across the European and Greenlandic Arctic (Lutz et al. 2016b). Interestingly, within defined, regional-scale catchments, patches of red snow appear exclusively dominated by differing single haplotypes (Brown et al. 2016) consistent with dispersal limitation incurred ecological priority effects. As such, reconciling these contrasts in the biogeography of glacial colonization by algae remains a challenge. Similarly, blooms of snow algae are associated with a diverse community of microbial heterotrophs, including bacteria, algae, and fungi (Weiss 1983; Lutz et al. 2015, 2016a). While some bacteria are intimately associated with snow algae (Weiss 1983), whether co-occurring microbes in general simply share a habitat with the algae or whether algal colonization facilitates their presence via the transfer of autochthonous carbon (Brown et al. 2015) is open to question; bacterial communities in algal blooms appear structured by locally varying lithological factors (Lutz et al. 2016a). If the translocation of carbon from algal photosynthesis itself is not pivotal to the assembly of snow algae associated communities, it may be that the evolution of meltwater from algal-mediated albedo depression (Lutz et al. 2016b) promotes the development of the cognate assemblage of microbes within snow algal blooms.

4.4 Supraglacial Ice and Meltwater Habitats

Within this section, we focus upon supraglacial ice and meltwater as active microbial habitats; discrete biofilms found in association with bare ice zones will be discussed in Sect. 4.5.

4.4.1 Life in Glacial Ice

As the snowline of a glacier recedes to higher elevations in summer, the extent of bare glacial ice increases in its prominence within the supraglacial environment. Glacial ice is typically considered as an archive of microbial biomass (Willerslev et al. 1999; Biddle et al. 2007; Castello and Rogers 2005) which may serve to seed the re-emergent glacial ice surface and downstream fluvial habitats with its microbiota. While this source of microbiota may be particularly important for environments characterized by low dust fluxes and limited surface melting, for example, blue ice ecosystems within the Antarctic (Hodson et al. 2013), microbial biomass in supraglacial ice is also sourced from both wet and dry deposition and the translocation of cells from the supraglacial snowpack itself (Irvine-Fynn et al. 2012; Hell et al. 2013; Björkman et al. 2014). Furthermore, arguments that englacial ice itself represents active microbial habitats within intercrystalline vein junctions, ice–mineral interfaces and even intracrystalline spaces have been advanced (Mader et al. 2006; Rohde and Price 2007). Therefore, while glacial ice may archive microbial biomass, the immured assemblage of microbiota is likely subject to post-depositional changes (Xiang et al. 2009; Liu et al. 2016) occurring over prolonged residence times (10^2–10^4 years).

4.4.2 Life in the Glacial Photic Zone

Bare ice itself represents an active microbial habitat. The glacial ice extent exposed by seasonal melting (excepting Antarctica) is estimated at a maximum of 7.5×10^5 km^2 (Anesio et al. 2009; Irvine-Fynn and Edwards 2013). The microbial communities of bare ice vary spatially, likely the result of localized inoculation sources and the physicochemical conditions presented to them (Edwards et al. 2013c; Cameron et al. 2014; Stibal et al. 2015a). Similarly, the total abundance of microbiota on surface ice is spatially variable and has been reported to range from 10^3 cells ml^{-1} in the zone of accumulation to 10^6 cells ml^{-1} in the ablation zone (Irvine-Fynn et al. 2012; Stibal et al. 2015a).

The physical processes of ice melt make it a viable microbial habitat. Incident shortwave radiation, which affects glacier surface energy balance (Eq. 1), penetrates ablating glacial ice to incur subsurface melt. The depth of subsurface melt is influenced by the extinction coefficient of the ice matrix, which will vary but can reach 2–20 m in optically clear ice (Hodson et al. 2013). Dissipation of incident radiation penetrating the surface ice incurs subsurface melt, decaying ice crystal structure and expanding interstitial spaces. This genesis of near-surface melt and its subsequent percolation at very low velocities further perpetuates the evolution of a highly porous near-surface ice layer, termed the weathering crust which stores meltwater in a perched aquifer atop nonporous englacial ice (Müller and Keeler 1969). As such, glacial ice surfaces in receipt of solar shortwave radiation represent a meteorologically controlled, seasonally evolving three-dimensional porous ice matrix which harbors a trifecta of decaying ice crystals, the percolative interstitial transfer of melt, and a decay gradient of incident radiation, all occurring to a depth which is delimited by the transmission of incident radiation and the corresponding inversely increasing density of ice (Cook et al. 2015b). Irvine-Fynn and Edwards (2013) recognized that these physical parameters amount to a glacial ice photic zone in which the liberation of melt commingled with nutrient, cell, and particulate mobilization and the availability of photosynthetically available radiation distributed in its intensity across a spectrum of photosynthetic optima promotes biological activity. Empirical support for a glacial ice photic zone is derived from the flow cytometric quantification of cell and particulate budgets of the weathering crust of a Svalbard glacier (Irvine-Fynn et al. 2012). When the rates of microbial biomass aeolian input, storage within ice, and fluvial release are considered, considerable microbial biomass is accumulated within the glacial ice photic zone under typical melting conditions (Irvine-Fynn et al. 2012) and thus the perched aquifer of the weathering crust modulates the fluvial delivery of cells to proglacial habitats.

The potential for physical redistribution and substantial concentration of cells in the interstitial spaces of the ice matrix (Mader et al. 2006; Irvine-Fynn et al. 2012) is coupled with the in situ activities of the microbial community. While the overall abundance of cells discharged from the weathering crust was consistent, specific subpopulations (Irvine-Fynn et al. 2012) were seasonally eluted, indicating a temporal shift in the microbial community's structure. Moreover, measurements of bacterial and abundance carbon production (Rassner et al. 2016) indicate the potential community doubling time in the weathering crust is considerably briefer than the hydrological residence time of cells within percolating melt. Finally, Irvine-Fynn et al. (2012) identified nucleic acid bearing cell populations with a median size of 0.5 μm as well as smaller nucleic acid-rich particles consistent with virus-like particles. Rassner et al. (2016) amended meltwater with organic carbon and nutrients to observe the interactions of supraglacial meltwater bacteria and their viruses, finding a community dominated by the Betaproteobacteria genus *Janthinobacterium* which was resilient to viral predation. Therefore, it appears likely that the glacial ice photic zone presents a locus of microbial interactions.

The implications of a glacial ice photic zone for glacial systems and their biogeochemistry are threefold. Firstly, it appears to be an extensive yet poorly characterized habitat. Irvine-Fynn and Edwards (2013) extrapolated measurements of the cellular concentrations within glacial ice photic zones with the potential scale of the glacial ice photic zone on ablating glacial ice. Excluding Antarctic ice, the calculations suggest 1×10^{21} to 1×10^{26} cells reside within the global glacial ice photic zone. This is comparable to the abundance of Archaea and Bacteria within the global oceanic photic zone (4×10^{25} cells; Whitman et al. 1998) which is both greater in surface area and volume (reaching 200 m deep) than the glacial ice photic zone. The pivotal role of marine microbes within the global carbon cycle and biosphere function is well known (Fuhrman and Steele 2008); what, therefore, constrains the impact of microbes from the enigmatic glacial ice photic zone? At present we do not know.

Secondly, the net accumulation of microbes, noncellular, and inorganic particulates within the glacial ice photic zone is enhanced at high melt rates. Indeed, Irvine-Fynn et al. (2012) observed an inverse nonlinear relationship between melt discharge and the accumulation of microbial biomass. As such, this prompts a positive feedback in which the contact rates between the glacial ice photic zone microbiota and inorganic particulates are promoted. Moreover, noting the tendency for *Janthinobacterium* as a dominant taxon within the glacial ice photic zone (Rassner et al. 2016) to exude biofilms and extracellular material (Pantanella et al. 2007), it is likely that cell–mineral aggregates are initiated within the glacial ice photic zone (e.g., Simon et al. 2009) further accelerating near-surface melt. Irvine-Fynn et al. (2012) identified this retention of biomass and its confection with inorganic particulates as a mechanism for the “biological darkening” of ice surfaces, accelerating ice melt.

Finally, the evolution of the glacial ice photic zone and its ability to modulate the flux of melt, biomass, and particulate matter influences the properties of proximal and downstream ecosystems. Cook et al. (2015b) used cryoconite holes (discussed below; Sect. 4.5.2) as naturally occurring piezometers dwelling within the weathering crust to explore the hydrology of the glacial ice photic zone of a second Svalbard glacier. Diurnal fluctuations in the storage and transmission of meltwater were identified, corresponding to changes in the porosity of the weathering crust. While the porosity of the crust is insufficient to permit the mobility of microbe–mineral aggregates, the crust permits the interconnection of supraglacial microbial habitats, buffering against local variations in soluble nutrient availability. Moreover, microbial productivity contributes to the organic carbon budget of glacial systems (Hood et al. 2015). The porous ice of the glacial ice photic zone permits the connection of supraglacial loci of productivity with downstream habitats by the transmission of runoff to supraglacial channels, releasing bioavailable carbon (Lawson et al. 2014; Feng et al. 2016), nutrients, and microbiota to depauperate proglacial habitats including proglacial streams, glacial forefields, and coastal oceans (Hood et al. 2009; Singer et al. 2012; Wilhelm et al. 2013, 2014; Hood et al. 2015).

4.5 From Bioalbedo to Biocryomorphology: Microbial Biofilms on the Ice Surface

Each year, as winter turns to summer, snow cover on lower altitude glacial surfaces melts away as a result of elevated air temperatures and solar irradiation. This event exposes bare ice surfaces and brings about notable changes in the physical, chemical, and biological properties of supraglacial ecosystems. This area is extensive (Anesio et al. 2009; Irvine-Fynn and Edwards 2013) and growing in scale. On the GrIS, the maximum area of snow-free ice that is exposed each year has increased steadily since passive microwave satellite observations began in 1979 (Fettweis et al. 2007), one of many indicators that this region is responding to changes in climate. Bare ice has a higher spectral absorption (Warren et al. 2006) and is denser than snow, and impurities within the ice help to contribute towards a topographically uneven surface (Irvine-Fynn et al. 2014). The melting of snow gives rise to a pulse of nutrient release, including SO_4^{2-}, NH_4^+, NO_3^-, Ca^{2+}, Cl^-, and Na^+ (reviewed in Kuhn 2001). Bioavailable nitrogen, in the form of ammonia, may be sequestered and mineralized within the sediment material of cryoconite holes (Wynn et al. 2007). However, the remaining nutrients released from melting snowpacks are likely evacuated from the surface ice environment by supraglacial meltwater rivers. Therefore, the chemistry of ice is predominantly dependant on the era and location in which it was laid down as snow, a feature that can be used when analyzing ice cores to recreate historical records of atmospheric chemistry.

4.5.1 Algal Biofilms

The most visually notable biological feature of bare ice surfaces is that they are plastered with Zygnematophyceae green algae. In addition to the lutein, violaxanthin, chlorophyll a and b, and β-carotene primary pigments that these cells contain, they also carry pigment-filled vacuoles, which are responsible for coloring the cells into shades of dark brown and purple (Uetake et al. 2010; Remias et al. 2012b; Yallop et al. 2012). Populations of these cells are so dense that they darken glacial surfaces: a “bloom” phenomenon which can be observed both on the ground with the naked eye (Fig. 4.2) and from space in satellite imagery. Surface ice algal abundance has been reported in the range of 10^5 cells ml^{-1} (Yallop et al. 2012); however, as these cells coat the exposed solid ice crystals of this crusty surface, expressing abundance as a liquid concentration is an experimentally and conceptually challenging task. Three ice algae species have been found to dominate polar and alpine glaciers: *Cylindrocystis brébissonii*, *Mesotaenium berggrenii*, and *Ancylonema nordenskiöldii* (Remias et al. 2009, 2012a, b; Remias 2012; Yallop et al. 2012). Analysis of vacuole pigments from Alpine *M. berggrenii* reveals the

Fig. 4.2 The ablation zone of the Greenland Ice Sheet. Surface ice is darkened by Zygnematophyceae green algae, in contrast to englacial ice, as highlighted by the crevasse opening (Photo credit: Sara Penrhyn-Jones)

presence of a phenolic compound called purpurogallin carboxylic acid-6-O-β-D-glucopyranoside. This compound likely functions as an ultraviolet and visible radiation photoprotectant, due to its broad spectral absorbance capacity. In addition, it has been suggested that these vacuoles may act as chemical deterrents against grazers or as energy sinks when temperature or nutrient availability limits cell function (Remias et al. 2012b). While little is known about the specific ecological activities of these communities, their darkening of glacial surfaces, and therefore their ability to reduce solar reflectance and consequently enhance surface melt through bioalbedo reduction (Yallop et al. 2012; Lutz et al. 2014), has become a key consideration for glacial surface mass balance studies in recent years (Tedesco et al. 2016).

4.5.2 Cryoconite Ecosystems

While algal populations may bloom on bare ice, the ice surface is also home to more stable microbial habitats. Key among these are cryoconite ecosystems, formed as microbial communities biofilm aeolian dusts and organic matter (e.g., wind-blown material from proximal habitats or surficial algal necromass) (see the recent review by Cook et al. (2016a) and references therein). The ensuing microbial–mineral aggregate is termed cryoconite, which darkens the ice surface through localized reduction of the albedo through the accumulation of dark humic substances (Takeuchi et al. 2001a, b; Takeuchi 2002). This contributes to the evolution and storage of surface meltwater and the formation of quasi-circular holes within the ice surface (Wharton et al. 1985). The thermodynamic evolution of so-called cryoconite holes occurs in three dimensions. Firstly, depth evolution proceeds until an equilibrium depth is maintained, at which the melting rate of ice in contact with the dark cryoconite debris is equivalent to the melting rate of the adjacent bare ice (Gribbon 1979). Secondly, lateral re-equilibration of cryoconite debris and hence cryoconite hole morphology can occur as sediment loads shift as the result of coalescence or evacuation of cryoconite holes as the ablation season proceeds. In this case, thick layers of cryoconite are redistributed to laterally widen the cryoconite hole (Cook et al. 2016b). In milder climates typical of Arctic and mountain glacial surfaces, cryoconite holes are typically open (or at least transiently lidded by a thin layer of ice on a diurnal cycle) to the atmosphere and reside within the porous ice of the glacial ice photic zone (Cook et al. 2015b) which likely permits hydraulic connectivity of cryoconite ecosystems within the same supraglacial catchments (Edwards et al. 2011). However, in the colder climate of Antarctica, attainment of equilibrium depth may mean the cryoconite hole is sufficiently deep to permit re-freezing of its surface, isolating the cryoconite hole from the exchange of biomass, gases and nutrients for extended periods, up to a decade (Tranter et al. 2004). In the most extreme conditions of Antarctica, where strong winds scour bare ice clean to form areas of blue ice, it is thought that the entombed cryoconite holes can only be colonized by microbes liberated from the melt-out of ancient ice and entrapped dusts (Hodson et al. 2013). As such cryoconite ecosystems occupy glacial ice surfaces across the world and endure conditions over an extended gradient of climatic and geochemical conditions. It is thought cryoconite ecosystems may have contributed to the demise (Abbot and Pierrehumbert 2010) of the pervasive Neoproterozoic glaciation ("Snowball Earth"; Hoffman et al. 1998) and the survival of microbial eukaryotes despite (near-)global ice cover (Hoffman 2016).

Indeed, cryoconite holes (Fig. 4.3) are considered "ice-cold hot spots" of microbial activity and diversity on contemporary ice surfaces (Edwards et al. 2013b, 2014b). It appears the principal agent in the formation of cryoconite is the action of filamentous microbial phototrophs, typically cyanobacteria such as *Phormidesmis pristleyi* (Edwards et al. 2011; Chrismas et al. 2015, 2016; Gokul et al. 2016) which exude photosynthetic carbon as extracellular polymeric substances which aggregate biomass and particulate matter (Hodson et al. 2010; Langford et al. 2010, 2014). Consequently, cyanobacteria are thought of as "ecosystem engineers" of the cryoconite ecosystem (Edwards et al. 2014b). As a result of such activity, cryoconite is a locus of carbon and macronutrient biogeochemical cycling on glacial ice the world over (Smith et al. 2016) exhibiting surprisingly high rates of net carbon fixation during the melt season (Anesio et al. 2009), as well as the cycling of nitrogen (Cameron et al. 2012a) through fixation (Telling et al. 2011, 2012b) and both nitrification and denitrification (Segawa et al. 2014). Where

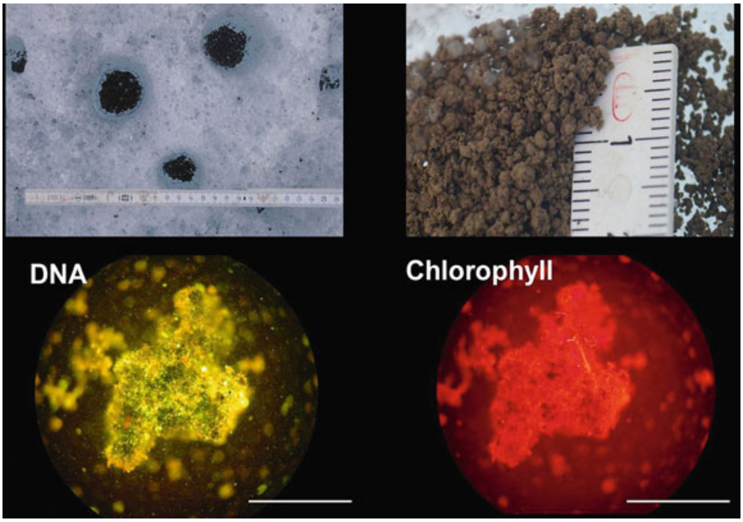

Fig. 4.3 Cryoconite and cryoconite holes: *Top panel*: A cryoconite hole in plan view (*left*), with close up on granular cryoconite typical of Arctic cryoconite sediments (*right*). *Lower panel*: Epifluorescence microscopy of individual cryoconite granules reveals the abundance of microbial life stained for nucleic acid with SYBR Gold (*left*) and chlorophyll *red* autofluorescence (*right*). Scale bars = 200 μm (Top panel photo credit: Nozomu Takeuchi; Lower panel photo credit: Arwyn Edwards)

cryoconite ecosystems are hydraulically connected to proximal habitats or open to the atmosphere the impacts of these supraglacial "bioreactors" can be disseminated further, fertilizing downstream environments (Feng et al. 2016).

The biogeochemical activities of cryoconite are the concerted activity of a diverse, microbially dominated biotic community which ranges from viruses to meiofauna. Along with the cyanobacterial ecosystem engineers, other microbial phototrophs include green algae and diatoms (Stibal et al. 2006; Yallop and Anesio 2010; Stanish et al. 2013; Vonnahme et al. 2015). Conglomeration of cryoconite and moss can result in the development of moss-dominated surface aggregates (Uetake et al. 2014). Notable cryoconite heterotrophs include bacteria, protozoal grazers, fungi and meiofauna such as tardigrades and rotifers (Desmet and Vanrompus 1994; Säwström et al. 2002; Edwards et al. 2013a); Archaea appear to be a minor and variable component of the cryoconite community, but more prevalent within Antarctic and some alpine cryoconite (Cameron et al. 2012b; Hamilton et al. 2013). Perhaps most is known of the bacterial community of cryoconite, which is typically dominated by Proteobacteria, with an apparent divide between Alphaproteobacteria in the Arctic and Betaproteobacteria within alpine cryoconite (Edwards et al. 2014b). Other notable groups include the Actinobacteria, in the form of taxa associated with soil humus (Gokul et al. 2016), Bacteroidetes (Edwards et al. 2013b) and Fibrobacteres (Ransom-Jones et al. 2014) associated with the cycling of complex carbohydrates. The composition of the cryoconite bacterial community is regionally variable at a range of scales from the local (Gokul et al. 2016), to ice sheet (Stibal et al. 2015b) and between global regions (Cameron et al. 2012b; Edwards et al. 2014b). While lithological and hydrologic factors are relevant (Edwards et al. 2011; Lutz et al. 2016a) the ability of the cryoconite community to sequester organic matter (Edwards et al. 2011, 2014b) is closely coupled to the structure and function of the bacterial community.

Accordingly, cryoconite ecosystems represent microbial habitats where the range and rate of microbial processes and the taxa present interact closely within the habitable confines of the cryoconite holes. The receipt and transfer of solar energy as both photosynthetically available radiation and heat for melting is pivotal. The equilibrium depth of seasonally open cryoconite holes coincides with the photosynthetic maxima of phototrophs resident within the cryoconite; as such the flux of photosynthetically available radiation is maintained at optimal levels (Cook et al. 2010, 2012, 2016b). As noted above, the thickening of cryoconite sediments as the consequence of the overloading of cryoconite holes incurs the lateral redistribution of sediments towards single-granule layers and expansion of the cryoconite hole's profile. Since thicker sediment layers of cryoconite tend towards net heterotrophy through the self-shading of cryoconite granules (Cook et al. 2010; Telling et al. 2012a) this restores net autotrophy (Cook et al. 2016a). Disturbing this process artificially incurs a profound metabolomic stress response and impact upon carbon cycling (Cook et al. 2016b). As such the floors of cryoconite holes are sensitively adjusted in three dimensions to provide optimal conditions for the accumulation of organic matter within cryoconite, which in turn enhances the melting of ice and the shaping of the cryoconite hole. Cook et al.

(2015a) defined this multi-lateral network of interactions between cryoconite biota and the ice surface as “biocryomorphology.” Considering the ubiquity and mobility of cryoconite holes (Irvine-Fynn et al. 2011a), the potential for microbial processes to shape the ice surface topography by modulating micro- to meso-scale roughness and further influence surface melt rates is raised (Cook et al. 2015a). Understanding how the concerted actions of microbial players within the varied range of biofilms on ice surfaces—from algal blooms to cryoconite holes—influence glacier processes from bioalbedo to biocryomorphology therefore presents a vital research priority.

4.6 Conclusions

Glacier surfaces are a tripwire for climate change since their response to climatic warming is to form meltwater which contributes to sea level rise. They also represent a spatially expansive collective of microbial habitats where life finds niches in the voids between ice crystals or forms biofilms which promote the melting of the ice. As always, the abundance and activity of life is closely intertwined with liquid water, and glacier surfaces are no exception in this regard. In turn glacial microbial processes accelerate melting and are exported in meltwater. Given the contemporary trends for climate warming and consequent wastage of glacial ice, the interactions between life and the surfaces of Earth’s glacier ice will continue to merit close study by scientists at the interface of microbiology and glaciology.

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