CONCEPTS & SYNTHESIS
EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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GLACIAL ECOSYSTEMS

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Abstract. There is now compelling evidence that microbially mediated reactions impart a significant effect upon the dynamics, composition, and abundance of nutrients in glacial melt water. Consequently, we must now consider ice masses as ecosystem habitats in their own right and address their diversity, functional potential, and activity as part of alpine and polar environments. Although such research is already underway, its fragmentary nature provides little basis for developing modern concepts of glacier ecology. This paper therefore provides a much-needed framework for development by reviewing the physical, biogeochemical, and microbiological characteristics of microbial habitats that have been identified within glaciers and ice sheets. Two key glacial ecosystems emerge, one inhabiting the glacier surface (the supraglacial ecosystem) and one at the ice-bed interface (the subglacial ecosystem). The supraglacial ecosystem is characterized by a diverse consortium of microbes (usually bacteria, algae, phytoflagellates, fungi, viruses and occasional rotifers, tardigrades, and diatoms) within the snowpack, supraglacial streams, and melt pools (cryoconite holes). The subglacial system is dominated by aerobic/anaerobic bacteria and most probably viruses in basal ice/till mixtures and subglacial lakes. A third, so-called englacial ecosystem is also described, but it is demonstrated that conditions within glacier ice are sufficient to make metabolic activity and its impact upon nutrient dynamics negligible at the glacier scale.

Consideration of the surface and internal heat balances of the glacier show that all glacial ecosystems are sensitive to climate change, although at different timescales. Thus, while rapid, melt-driven habitat changes lead to melt-out, resuscitation, and redistribution of microorganisms in many supraglacial ecosystems, much slower climatic and glacial mass-balance processes effect such changes in the subglacial ecosystem. Paradoxically, it is shown that these forces have brought about net refreezing and the onset of cryostasis in the subglacial ecosystems of many Arctic glaciers subject to thinning in recent decades.

Key words: *biogeochemistry; geomicrobiology; glacier ecology; glaciology; ice ecology; snow ecology.*

Introduction

Castello and Rogers (2005) suggest that between 1×10^{17} and 1×10^{21} viable microorganisms are liberated each year by global glacier melt. These include extremophiles that are now known to exist in virtually all of the ice phases reported in glacial environments (Priscu and Christner 2004), such as atmospheric particles (Sattler et al. 2001), snow (e.g., Takeuchi et al. 1998, Hoham and Duval 1999, 2003), glacier ice (Abyzov 1993, Price 2000, 2007, Mader et al. 2006, Priscu et al. 2006), accretion ice (Priscu et al. 1999, 2006), and basal ice/till mixtures (Sharp et al. 1999, Skidmore et al. 2000, Foght et al. 2004). By far the most dominant microorganisms present are bacteria and eukarya. Interestingly, the reliable detection of archaea has (at the time of writing) been reported just twice: once upon an Alpine glacier (Battin et al. 2001) and once within a meltwater lake sediment sequence upon Ross Ice Shelf (Sjöling and Cowan 2003). Despite significant

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advances in our understanding of the distribution of the microbial groups that are present, via microscopic, culture-based, and most recently molecular analysis (e.g., Christner et al. 2001, 2003*a*, *b*, Deming 2002, Foght et al. 2004, Priscu et al. 2006), our understanding of ecosystem dynamics is poor. Thus, the most basic measurements of energy, water, and nutrient flows through glacial microbial habitats have only just begun to be collected (e.g., Hodson et al. 2005*b*, Hodson 2006), and their productivity and biomass remain almost unknown (e.g., Säwström et al. 2002).

The successful recovery of viable microorganisms in ice samples from several hundred meters beneath the surface of the East Antarctic Ice Sheet by Abyzov (1993) helped stimulate a significant research effort that now presents a case for an ecosystem characterized by microbial habitats on, within, and beneath glaciers (Price 2000, Christner et al. 2003*b*, Castello and Rogers 2005). These supraglacial, englacial, and subglacial environments may differ vastly in terms of their water content, nutrient abundance, redox potential, ionic strength, rock-water contact, pressure, solar radiation, and pH conditions. This remarkable physical diversity means that glaciers provide an ideal opportunity to draw the ecologies of ice in all its forms into one single field-scale system. The chief objective of this paper is therefore to outline this potential and to present the first glacier-scale perspective of the physical, biogeochemical, and microbiological characteristics of glacial ecosystems.

Water and Glacial Ecosystem Structure

Liquid water is vital for any ecosystem. In glacial environments, the distribution of water reflects the heat budget at given points within the ice and the hydraulic configuration of the drainage system that conveys water through it. The latter enables water to exist in glacial environments as discrete channels, water films, or veins and pockets at interstices or grain boundaries (Paterson 1994). Biological energy contributes little to the heat budget of melting ice (McIntyre 1984, Fogg 1998) and the major contribution is from physical controls such as solar radiation and air temperature. This section therefore presents a brief outline of how such physical processes govern the distribution of water in glaciers, from the ice crystal scale through to the whole glacier.

Surface heat budget of glacier ice

The heat budget at the air-ice/snow surface can be represented as follows (Paterson 1994):

$$Q_M + Q_{SW} + Q_{LW} + Q_S + Q_L + Q_P + Q_C = 0 \qquad (1)$$

where Q_M is energy available for melting, Q_{SW} is net shortwave radiation, Q_{LW} is net long-wave radiation, Q_S is sensible heat, Q_L is latent heat, Q_P is heat from precipitation, and Q_C is conduction into the glacier. For all terms in Eq. 1, the units are W/m^2.

Most often, net shortwave radiation accounts for 60–80% of the melt, while sensible and then latent heat sources contribute the rest (e.g., Rothlisberger and Lang 1987). During summer, when the ice on temperate glaciers is isothermal and at the melting point, the conduction term is essentially zero. In cold, polar conditions, latent heat, rather than melting, dominates ice ablation through the sublimation process (Paterson 1994).

Eq. 1 does not include any contributions from metabolic heat. Presently, direct assessment of biological heat as a source of energy for melting glacier ice is scarce in the literature. However, metabolic processes are known to be inefficient, especially in non-glacial, oligotrophic, aquatic ecosystems (Biddanda et al. 1994), where a large fraction of the carbon assimilated by bacteria (up to 99%) may be dissipated as respiration (Del Giorgio and Cole 1998). Therefore, metabolic heat may be important in certain icy habitats. For example, Gerdel and Drouet (1960) and McIntyre (1984) suggested metabolic heat may contribute to the thermodynamics of supraglacial habitats called cryoconite holes, perhaps providing as much as 10% of the heat used to melt their icy walls during the summer (McIntyre 1984). More measurements are almost certainly required before the magnitude and importance of metabolic activity in the heat budget of glacial habitats can be established with confidence. Such measurements might prove critical for understanding the duration and rate of metabolic activity in habitats close to or at the freezing point.

Another contribution of biologic material to the heat budget is through its effects on albedo of the ice surface. Aeolian dust certainly darkens a snow or ice surface, reducing its reflectivity, allowing for more shortwave radiation to be absorbed. The presence of organic matter on and/or in the sediment then significantly reduces the natural albedo of the sediment, increasing the effect further (Takeuchi et al. 2000). The presence of algae on snow, yielding red, green, and yellow colors can also decrease the albedo by half (Kohshima et al. 1993, Thomas and Duval 1995, Painter et al. 2001). Table 1 therefore presents typical albedos for glacial surface habitats and shows that the most absorbance (i.e., lowest albedo) is associated with organic sediments found on ice (or "cryoconite"), rather than with snow algal communities. Thus albedos as low as 2% are possible for wet cryoconite granules, although the values are higher (10–20%) when the material has been air dried. The lower albedos for cryoconite habitats compared to snow algae are probably caused by the presence of dark, humic substances (Takeuchi 2002).

The distribution of organic matter across glacier surfaces is heterogeneous, leading to differential absorbtion of shortwave radiation at a range of spatial scales. Fig. 1 shows such a surface in the melt zone of an Arctic glacier (Midtre Lovénbreen, Svalbard, Norway). Here the heterogeneous distribution of organic-rich debris

TABLE 1. Reflectance characteristics of debris matter in supraglacial habitats.

Habitat	Albedo	Reference
Glacier ice and cryoconite holes		
Tibet (three glaciers)	dried cryoconite: 14–17% at 450 nm, 39–52% at 900 nm	Takeuchi (2002)
Arctic (three glaciers)	dried cryoconite: 8–10% at 450 nm, 17–23% at 900 nm	Takeuchi (2002)
Nepal (three glaciers)	dried cryoconite: 9–12% at 450 nm, 17–23% at 900 nm	Takeuchi et al. (2000)
Nepal (Yala Glacier)	clean ice: 55% at 450 nm, 40% at 900 nm	Takeuchi (2002)
Tyndall Glacier, Patagonia	bare ice and cryoconite: 34–66% (mean 48%)	Takeuchi et al. (2001*c*)
Svalbard (Midtre Lovénbreen), Norway	bare ice and cryoconite: 12–13%; bare ice and cryoconite: 13–21%; bare ice: 17–44%; dried cryoconite: 9–10% at 450 nm, 13–15% at 900 nm; wet cryoconite: 1.5–1.8% at 450 nm, 3.2–3.3% at 900 nm	A. Hodson and T. Irvine-Fynn (*unpublished data*)
McMurdo Dry Valleys, Antarctica	cryoconite holes with ice lids: 60%	A. Fountain (*personal communication*)
Greenland Ice Sheet (Kronprins Christians Land, northeast Greenland)	large cryoconite deposits: 13% at 450 nm, 6% at 900 nm	Bøggild et al. (2006)
Snow and snow algae during bloom		
Sierra Nevada, USA	red snow: 41% at 450 nm, 50% at 900 nm; white snow: 85% at 450 nm, 60% at 900 nm	Thomas and Duval (1995), Painter et al. (2001)

results in the roughening of the ice surface: a process that enhances turbulent heat exchange across the atmospheric boundary layer–ice interface. Thus, if the air is warmer than the ice (as is the case in Fig. 1), then the melt rate of the glacier is further increased. The magnitude of this effect is unknown. Furthermore, there may be a feedback process whereby a roughening surface captures more sediment and organic matter, and so distinguishing cause and effect may be impossible.

Subsurface heat budget of ice

The heat budget at depth within the ice includes heat advected and conducted from elsewhere in the glacier (Q_C), geothermal heat from beneath the glacier (Q_G), and frictional heat (Q_{BS}) from sliding at the glacier bed. The amount of heat available for melting (Q_M) thus becomes

$$Q_M + Q_C + Q_G + Q_{BS} = 0. \quad (2)$$

The heat budget at the ice–bed interface is particularly important as it can govern the onset of basal melting, resulting in water-saturated ice and till, an ideal habitat for microbial life (e.g., Sharp et al. 1999). Christoffersen and Tulaczyk (2003) show that the temperature gradient under conduction-dominant conditions may be expressed in simple terms as

$$\frac{\partial T}{\partial z} K_t - \theta_b K_i + \tau_b U_b - \rho_i m L = 0 \quad (3)$$

where T is the temperature in the till layer, K_t its thermal conductivity, θ_b the basal temperature gradient of ice and K_i its thermal conductivity, τ_b is the basal shear stress, U_b the basal velocity, ρ_i the density of ice, m the melting rate, and L the latent heat of fusion of ice. The basal shear stress is

$$\tau_b = \rho_i \times g \times h \times \sin\alpha \quad (4)$$

where g is the gravitational constant, h is the ice thickness, and α is the slope of the ice surface. From Eqs. 3 and 4, one can see the dependence of m on h. Thus, ice thickness influences the heat conduction through the overlying ice (θ_b) and exerts a first-order control on the basal shear stress and basal velocity (not shown). The basal heat budget for polar glaciers is therefore sensitive to glacier thinning and so the potential for glacial mass balance change to induce ecosystem change through basal freezing/melting will be explored later. The sensitivity of the subglacial heat budget to glacier ice thickness is also important for understanding how thinner ice at the margins of polar glaciers can be frozen to the substrate, which reduces the spatial extent of saturated subglacial sediments with the capacity to support microbial activity. This heterogeneity is best understood using the concept of glacier thermal regimes, which is reviewed below and which ultimately provides a framework for understanding how the locus of significant microbial activity may vary from one glacier to another.

Glacier thermal regime and glacial ecosystem structure

Glacial thermal regimes are typically used to reflect the impact of the combined surface, internal, and basal heat budgets on the distribution of ice at the pressure melting point. This can vary from one glacier to another in accordance with variations in the relative importance of heat fluxes from below and above the glacier. Here, we introduce the contention that, since the distribution of favorable habitats can vary in accordance with these different thermal regimes, significant differences in ecosystem structure can also result from one glacier to another.

In the first instance, the diversity of glacier thermal regime is best depicted using a simple continuum with the two end members: cold glaciers and temperate

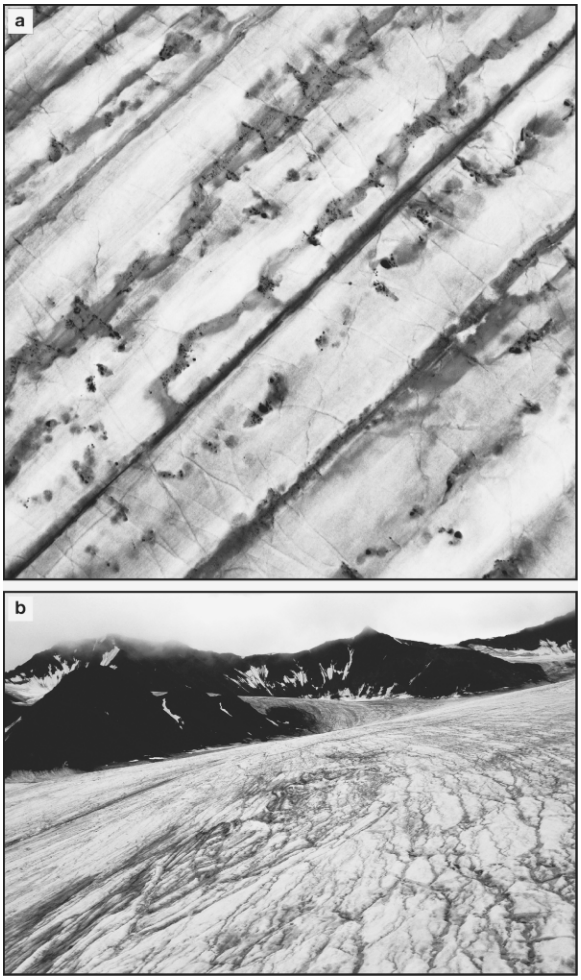

Fig. 1. The darkening of supraglacial ice by organic matter on Midtre Lovénbreen, Svalbard, Norway. (a) Aerial photograph covering an area approximately 100 m^2: cryoconite holes (clusters of small, dark circles) and cryoconite accumulation within streams (some of which follow linear, structural features upon the ice surface) are both discernable. (b) Oblique photograph of streams on the same part of the glacier: note the exceptionally dark accumulation of predominantly cyanobacteria in the central part of the image (deposits here are controlled by ice foliation patterns), giving way to the hydrologically controlled deposits to the right-hand side. Images are courtesy of HighSpy and are described further in Hodson et al. (*in press*).

glaciers (Fig. 2a, b, and e, respectively; developed from Blatter and Hutter 1991). Crudely speaking, the temperate glacier is represented by ice entirely at the pressure melting point, while the cold glacier is characterized by ice at temperatures below it. In both cases, the exception is a shallow surface ice layer (typically 15 m thick [Paterson 1994]) that undergoes seasonal temperature variations. For simplicity, thicker glaciers in the polar regions and also the great ice sheets of the last glacial cycle are perhaps best represented by an intermediate or polythermal category of thermal regime (Fowler and Larson 1978, Tranter 2005; Fig. 2c, d). These are more thermally complex because the location of the "warm" and "cold" ice may differ according to intrinsic and extrinsic controls upon the glacial heat balance (see Blatter and Hutter 1991, Paterson 1994). However, for the sake of the present paper, Fig. 2 is sufficient: the snowpack, glacier surface, and the glacier bed are therefore identified as key areas of potential melting and thus microbial activity. Advection of ice from these environments further into the glacier is also responsible for enabling the persistence of englacial ice at the pressure melting point (along with some internal strain heating). The ecological significance of surface and basal melting is even more obvious when their proximity to atmospheric and crustal nutrient sources is considered. However, far greater limitations on nutrient supply to englacial ice may be anticipated.

The interstitial water content of ice at the pressure melting point is vital for microbial life, and reaches 2% or more (e.g., Pettersson et al. 2004: Table 1), especially at grain intersections such as veins and ice lenses (Lliboutry 1996). Temporal variations at the seasonal scale can also occur when such water is in close proximity to major drainage features (Irvine-Fynn et al. 2006) or freezing fronts at the glacier surface. Elsewhere, in solid, cold ice, interstitial water is greatly restricted to solute-rich inclusions at small grain intersections, where the existence of the water phase is greatly dependent upon solution composition and its corresponding eutectic temperature (e.g., Barnes and Wolff 2005). Typical eutectic temperatures were reported by Price (2000) for common solutions. They include −43°C for HNO_3, −22°C for $NaCl{\cdot}2H_2O$, and −73°C for H_2SO_4. Exclusion of dissolved salts from the solid ice is therefore common, enabling nutrients to be sequestered from the aqueous phase at grain boundaries in most glaciers (Mader et al. 2006). It also means that nutrients are rejected during refreezing of snow melt at depth within cold snowpacks. Such events are common following snowmelt at the start of the summer season (Tranter and Jones 2001).

Despite the potential complexity of polythermal glaciers (see Blatter and Hutter 1991), many of them have at least part of the otherwise frozen glacier bed lying at the pressure melting point (Fig. 2c, d). The presence of pressure-melting-point ice at the glacier bed provides not only a basis for nutrient acquisition following rock–water contact (Tranter et al. 2005), but also an increased likelihood of crevassing due to enhanced basal sliding and subglacial till deformation (Paterson 1994). Importantly, crevassing enhances the flow of water, nutrients, and organisms from the surface of the glacier to its bed, resulting in the coupling of supraglacial and subglacial ecosystems by rapid, hydrological transfers if melting takes place (Fig. 2d, e). Fig. 2e thus shows that such coupling is most significant in Alpine type glaciers because the entire glacier lies at the pressure melting point (and because such glaciers typically have steeper surface slopes). However, great

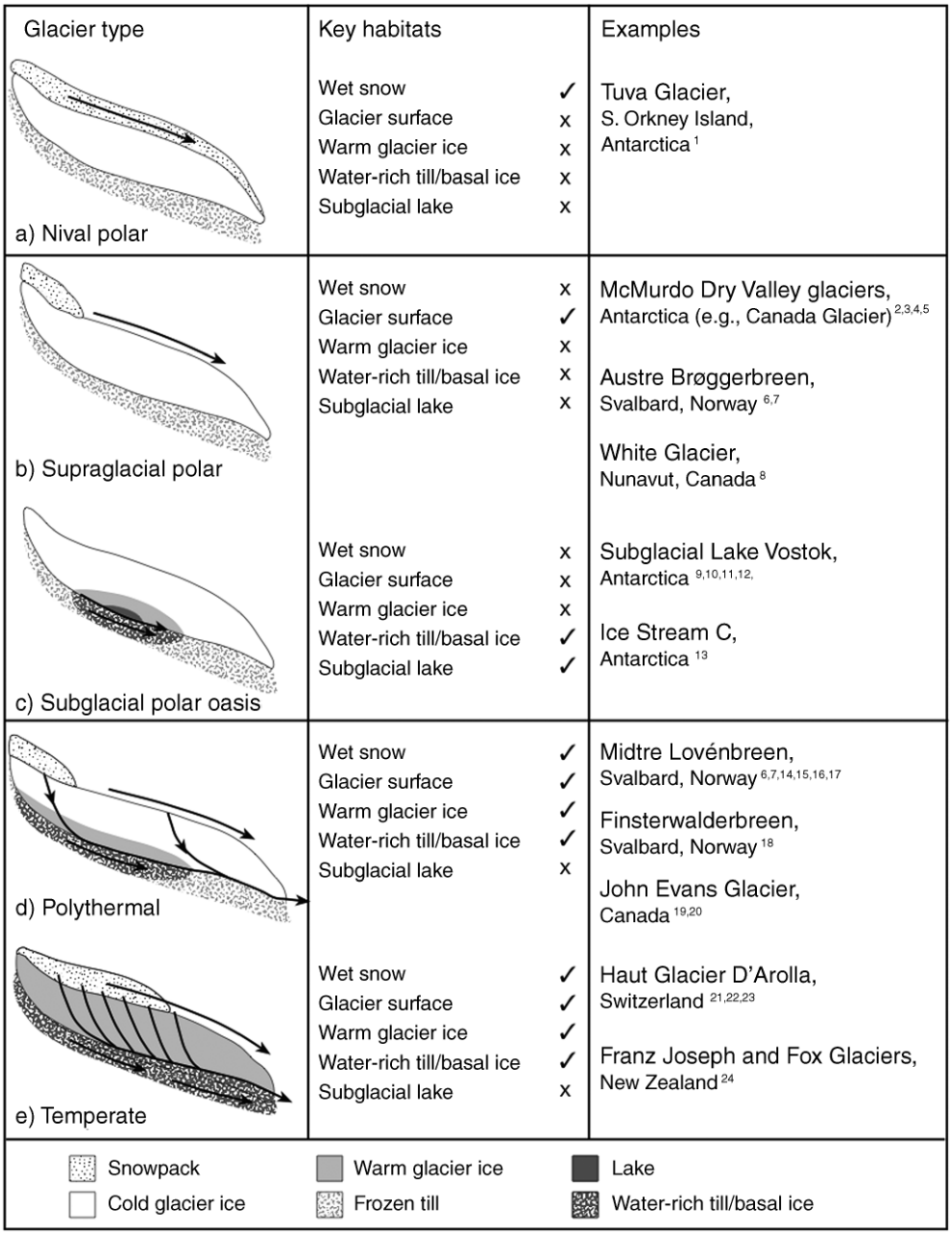

FIG. 2. Schematic representation of glacier thermal regimes and their most important microbial habitats. Hydrological transfers are shown by the arrows. Examples and key references for each type of habitat assemblage are given in the right-hand column and are as follows: 1, Hodson (2006); 2, Christner et al. (2003*b*); 3, Porazinska et al. (2002); 4, Tranter et al. (2004); 5, Wharton et al. (1981); 6, Kaštovská et al. (2005); 7, Hodson et al. (2005*a*); 8, Mueller and Pollard (2004); 9, Christner et al. (2001); 10, Karl et al. (1999); 11, Priscu et al. (1999); 12, Siegert et al. (2001); 13, Lanoil et al. (2004); 14, Anesio et al. (*in press*); 15, Mindl et al. (2007); 16, Säwström et al. (2002); 17, Wynn et al. (2006); 18, Wadham et al. (2004); 19, Bhatia et al. (2006); 20, Skidmore et al. (2000); 21, Bottrell and Tranter (2002); 22, Sharp et al. (1999); 23, Tranter et al. (2002); 24, Foght et al. (2004).

variations in such coupling may be demonstrated by polythermal glaciers because some are predominantly cold based, while others are dominated by pressure melting ice. The influence of subglacial till rheology also requires consideration in this context because even adjacent glaciers of comparable thickness and mass balance can demonstrate stark differences in the incidence and extent of crevassing. Fig. 3 shows such a contrast using adjacent polythermal glaciers in Svalbard, Norway.

Hydraulic conditions within glaciers

The hydraulic configuration of the glacial drainage system has the capacity to govern the distribution of

Fig. 3. The confluence of Kronebreen (left-hand side) and Kongsvegen (right-hand side) in Kongsfjord, Svalbard, Norway. The glacier on the left is highly crevassed, so the probability of surface melt reaching the glacier bed is near unity, and a much greater proportion of the glacier bed will receive these inputs than at Kongsvegen, where meltwaters enter the glacier at just a few locations. Photo credit: A. Hodson.

water and nutrients throughout the glacial ecosystem. Following the previous discussion, it also governs the efficacy of supraglacial–subglacial ecosystem coupling, as suggested by Tranter et al. (2005). It is the macro-scale structure of the glacial drainage network that is critical in this context, largely because the intra-granular permeability of ice is negligible (Lliboutry 1996). Thus the diffusion and advection transport of solutes along small-scale grain boundaries (see Barnes and Wolff 2004) are not important pathways for surface-derived nutrients to enter the glacier. However, diffusion might be significant for solute transport to the psychrophilic

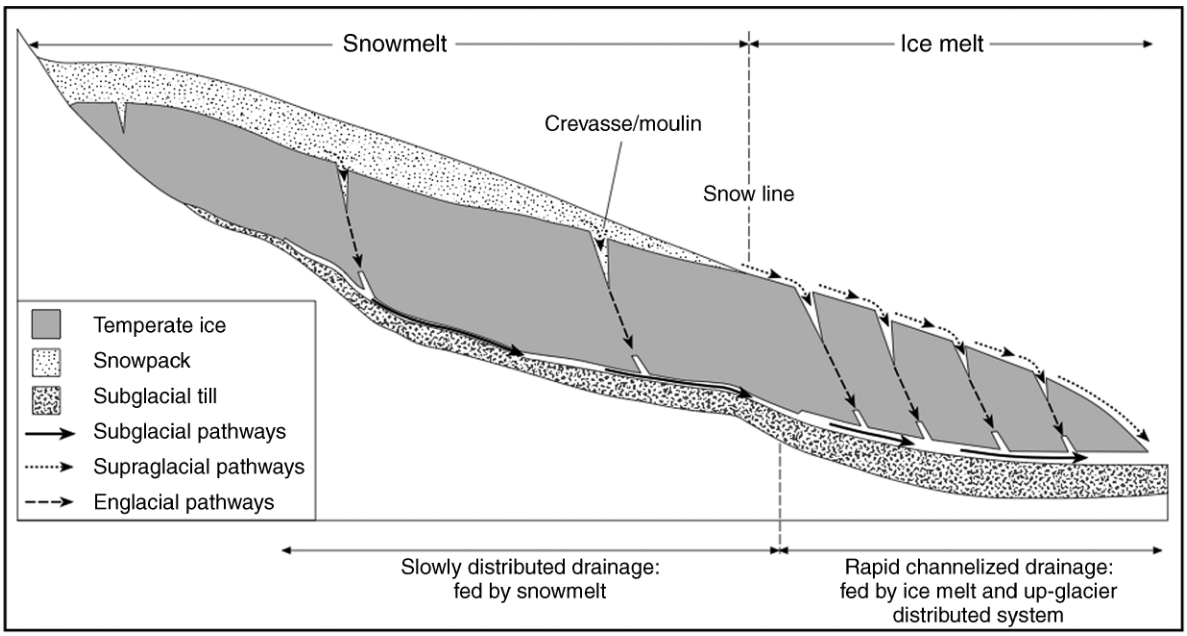

Fig. 4. Glacier drainage system structure (modified from Tranter et al. [1996]). Efficient channels or conduits lie beneath parts of the glacier bed that are ice-covered, while the subglacial drainage system beneath the snow-covered upper glacier is far less efficient and is distributed over broad areas of the glacier bed (offering more opportunities for the assimilation of nutrients derived from the snowpack and crustal sources).

bacteria purported to exist in deep englacial environments (Price 2000, Mader et al. 2006). Otherwise, the dominant fluxes of atmospheric nutrient inputs to glacial ecosystems during melting are most likely associated with snowmelt on glaciers subject to seasonal snow cover (e.g., Hodson 2006), or icemelt in colder, more continental environments (e.g., Fortner et al. 2005). Tranter et al. (2005) describe how these sources provide vital inputs to subglacial ecosystems following surface meltwater descent into the glacier via crevasses and vertical drainage shafts called "moulins" (Fig. 4).

For temperate glaciers, the subglacial drainage system apparently evolves rapidly from an inefficient network of pathways to an efficient channelized network following the input of large volumes of surface melt (Richards et al. 1966, Fountain and Walder 1998). Fig. 4 presents this conceptual hydrological model. Periodically high water pressures in glacial conduits have the capacity to recharge high rock–water contact environments in their immediate vicinity: a so-called channel marginal zone (Hubbard and Nienow 1997). Since such environments are more likely to harbor favorable substrates for microbial life (Sharp et al. 1999), there is some capacity for this recharge to bring important nutrients and inoculi from atmospheric or supraglacial sources. This model of drainage system structure, evolution, and its interaction with subglacial ecosystems was suggested by Tranter et al. (2005). However, it is unclear whether it can be applied to the polar regions because different hydraulic conditions result here due to a greater proportion of the glacier lying below the pressure melting point (e.g., Rippin et al. 2003, Fountain et al. 2005, Bingham et al. 2006, Irvine-Fynn et al. 2006; see also Fig. 2c, d). Further, the situation upon entirely cold polar glaciers (Fig. 2a, b) is even more different because the glacier bed remains frozen and thus penetration of surface-derived meltwaters is often restricted to either incised, meandering channels at the ice margins, or complex flows in near-surface channels (Fountain et al. 2004) and along fracture pathways (van der Veen 2007).

Turbulence

While the preceding discussion clearly emphasized the importance of hydraulic connections with respect to nutrient and water flows, consideration should also be given to the vast range of turbulence experienced in glacial drainage systems, both at the surface and at the glacier bed. Turbulence therefore exerts an important control upon the distribution of dark organic matter on melting glacier surfaces, influencing the formation of new habitats and the incidence of biofilm mobilization between them (a common feature early in the melt season near the snow line of many temperate and Arctic glaciers). Hydraulic turbulence will also influence organism motility more directly within individual habitats, and might even prevent the colonization of favorable habitats at various points within the system, especially in the case of larger supraglacial streams. When supraglacial waters have descended into the glacier, turbulence will then influence the erosion/sedimentation of channel marginal zone sediments, and the efficacy of nutrient exchange across its interface.

Synthesis

A basis for understanding the locus of viable microbial food webs has been established for glacial ecosystems (Fig. 2), in which the generation of water and its subsequent dispersal throughout the glacial drainage system are of critical importance (Fig. 4). This means that two key environments are most likely to be characterised by enhanced productivity: the glacier surface (including its snowpack) and the ice–bed interface. These habitats satisfy two key criteria: water may be abundant when ice is at the pressure melting point and new nutrients may be supplied from gases, precipitation, and/or debris such as crushed rock. It is argued that ecosystem productivity may be far greater here than in any englacial habitats, provided that flow turbulence, erosion and turbidity do not compromise niche stability, and that thermodynamic conditions (which vary both spatially and temporally) allow melting to occur. However, since the englacial ecosystem might be a source of inoculi for supraglacial and subglacial ecosystems, all three environments are considered below, where we review present understanding of their microbial ecology and biogeochemistry.

The Supraglacial Ecosystem

Important habitats in the supraglacial ecosystem include wet snow, cryoconite holes, streams, ponds, and moraines. Photosynthesis in these environments presents a fascinating opportunity for exploring feedbacks between physical and biological systems, not least because the absorption of solar radiation by low-albedo organic matter also causes melting to occur, furnishing vital water (see *Water and glacial ecosystem structure*). Thus, following melt, dark organic matter in sun cups upon snow, cryoconite holes, streams, and moraines are bathed in meltwater and begin sequestering nutrients from adjacent snow, ice, debris, and even directly from the atmosphere (e.g., Tranter et al. 2004). Presently, only the snowpack and the ice surface has received attention in this context and there are no accounts of supraglacial stream ecology, although Fortner et al. (2005) have shown that supraglacial stream hydrochemistry in the McMurdo Dry Valleys, Antarctica, bears the distinct traits of nitrogen uptake via microbial activity. The following discussion of supraglacial ecosystems therefore reflects this bias.

The ecology of supraglacial snow cover

Studies of the so-called snow algae (usually microalgae and/or phytoflagellates) are well developed in temperate environments subject to seasonal snow cover. A complete review of snow ecology in the context of the

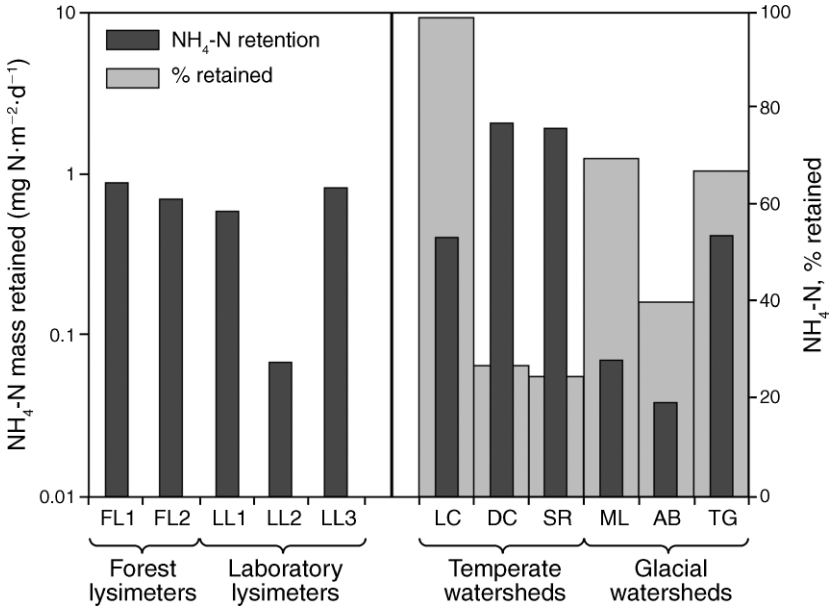

FIG. 5. Ammonium retention deduced from lysimeter experiments (left-hand vertical axis; log scale) and from catchment solute mass balances (right-hand vertical axis). Data are reported for field lysimeters (FL1 and FL2); laboratory lysimeters (LL1–LL3); high-altitude, snowmelt-driven, temperate watersheds (LC, Log Creek; DC, Deer Creek; SR, Snake River); and also for glacial watersheds (ML, Midtre Lovénbreen; AB, Austre Brøggerbreen; TG, Tuva Glacier). See Jones (1999) for the lysimeter studies, Williams and Melack (1997) for LC, Heuer et al. (1999) for DC and SR, Hodson et al. (2005*b*) for AB and ML, and Hodson (2006) for TG.

glacial ecosystem is thus unnecessary as there are excellent texts elsewhere (e.g., Jones et al. 2001). However, it should be appreciated that the snowpack will provide an important supply of inoculi, nutrients and water that will cascade through the glacial ecosystem (Fig. 2). The snowpack also exerts a critical control upon the development of the subglacial drainage system (Fountain 1996, Richards et al. 1996, Tranter et al. 1996; Fig. 4) and so it governs, to some extent at least, the degree of interconnectivity in the integrated glacial ecosystem.

Studies of glacial snowpack biogeochemistry and ecology are few in number compared to those undertaken in non-glacial environments (see Vincent 1988, Jones 1999, and Jones et al. 2001 for reviews). However, Hodson et al. (2005*b*), Hodson (2006), and Jones (1999) have shown that nitrogen cycling is important in melting polar glacial snowpacks, although it tends to take place at rates far slower than in seasonal snowpacks in temperate catchments. Rates of inorganic nitrogen retention inferred from solute mass-balance studies are therefore shown for glacial and non-glacial environments in Fig. 5 (after Jones 1999, Hodson 2006). Low rates in the glacial environments (especially Midtre Lovénbreen and Austre Brøggerbreen) most probably indicate a lack of litter and other debris, which has been shown to greatly enhance microbial processes in forest snowpacks (Jones and DeBlois 1987, Jones 1999). Otherwise, the assimilation of NH_4^+ observed at Tuva Glacier basin in the maritime Antarctic was significantly higher and comparable to high altitude temperate watersheds in the United States. This reflects the influence of atmospheric nutrient inputs from downwind penguin colonies upon the productivity of the snowpack ecosystem at this site (Hodson 2006).

The retention of inorganic nitrogen and also PO_4^{3-} (see Hodson 2006) in all the glacier data sets may be easily explained by phototrophic activity owing to the abundance of snow algae and cyanobacteria in snowpacks worldwide. However, heterotrophic activity in snow is difficult to assess owing to a paucity of data. Amato et al. (2007) used molecular methods (16S rRNA gene sequencing) to demonstrate the presence of a diverse consortium of bacteria upon Kongsvegen, a polythermal glacier in West Svalbard, Norway (Fig. 3, right-hand side). Here $1–4 \times 10^4$ cells/mL were found in young snow that were dominated by *Proteobacteria* (α, β, and γ), *Firmicutes*, and *Actinobacteria* and able to degrade organic compounds common in Arctic snow (propionate, acetate, and formate). The dearth of studies like this therefore means that the balance of phototrophic and heterotrophic activity is not at all understood and the impact of snow biota upon the carbon cycle of glacial ecosystems is unknown. Jones (1999) suggested that the balance may vary in response to changing meteorological conditions. For example, frequent snow flurries will suppress photosynthesis by burial, resulting in rather different microbial impacts on carbon (and nutrient) transfers into and out of the system than would have otherwise been the case if

photosynthesis dominated. This potential cause of interannual variability in supraglacial biogeochemistry remains unexplored at the time of writing.

In some cases, the biota of glacial snowpacks has been compared to that established on bare glacier ice surfaces, a necessary exercise given the transient nature of the snow line during the summer in many parts of the glacial cryosphere. Thus Takeuchi et al. (1998) and Yoshimura et al. (1997) have shown that snow algal biomass and species composition change markedly along glacier mass balance gradients in the Himalayas. Here, "snow specialists" (*Trochiscia* sp.) dominated at altitude in the accumulation area, but were only moderately competitive near the equilibrium line and soon usurped by "ice environment specialists" (*Cylindrocystis brébissonii*) in the higher biomass ablation area. Generalist species included *Mesotaenium berggrenii* and were most successful in the zone of maximum species diversity in the vicinity of the equilibrium line altitude (Yoshimura et al. 1997). A glacier with a low accumulation rate was not found to be characterised by dominant snow specialists, allowing Takeuchi et al. (1998) to speculate that the algal community structure is perhaps indicative of the glacier's mass balance status, at least in the Central Asian area.

Snow algae upon glaciers in the maritime Antarctic have also been given particular attention in the past, dating back to Fritsch (1912, in Vincent 1988). Here the blue, green, and red algal blooms are most noteworthy and often develop following melt and fertilization from ornithogenic emissions that volatilize from penguin and other bird guano (Hodson 2006). On Signy Island, cell numbers ranging from 5×10^3 cells/mm^3 for colored snow to just 1–2 cells/mm^3 in "clean" snow have been reported. Most algae were found concentrated in the upper centimeter of snow unless burial occurred, although motile green algae were also found some distance beneath red snow patches (Fogg 1967 in Vincent 1988). Fogg (1967) showed that rates of photosynthesis at 0°C in these Signy Island snowpacks gave rise to areal fixation rates of ~10 mg C·m^{-2}·d^{-1}, significantly lower than those typical of sea ice ecosystems (Vincent 1988). Such low rates of photosynthesis are commensurate with the low rates of NH_4^+ assimilation (0.4 mg NH_4-N·m^{-2}·d^{-1}) estimated from snowpack chemistry on the same island by Hodson (2006; see Fig. 5), which produce a C fixation rate of 2.3 mg C·m^{-2}·d^{-1} assuming Redfield stoichiometry.

The ecology of supraglacial ice

Algae and phytoflagellates have also been reported upon bare glacier ice within cryoconite holes and even distinct mats, especially in the ice shelf ecosystems of Markham Ice Shelf in the High Arctic (e.g., Vincent et al. 2004) and the McMurdo/Ross Ice shelves (e.g., Hawes et al. 1993). In the Arctic, Vincent et al. (2000, 2004) show that these ice shelves can be very productive, and support algal mats where photosynthesis rates approach those of productive marine waters in the polar oceans (i.e., 200–1200 mg C·m^{-2}·d^{-1} (Vincent et al. 2000)). In Antarctica, the ice shelves may be fertilized by marine benthic debris following basal refreezing and surface sublimation, or by mirabilite and other mineral phases precipitated following the injection and freezing of sea water via pressure ridges: both processes making them rather unique glacial ecosystems (e.g., Brady and Batts 1981, Howard-Williams et al. 1990, Hawes et al. 1993). Here productivity can easily match that observed upon the Markham Ice Shelf, especially where fertilization from marine fauna (usually penguins and seals) can be anticipated.

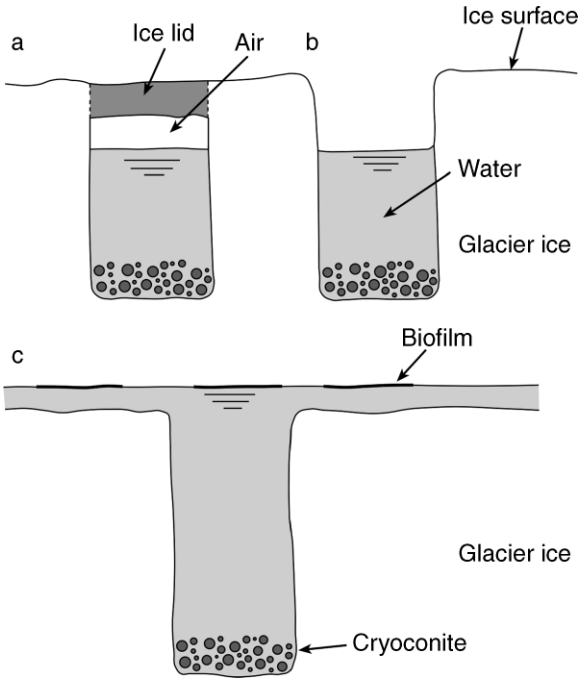

FIG. 6. Anatomy of a cryoconite hole, showing (a) closed, (b) open, and (c) submerged morphologies.

Cryoconite holes and other cryoconite habitats

Cryoconite holes represent probably the most active microbial habitat upon snow-free, melting ice, and so this section is entirely dedicated to this particular habitat. Cryoconite holes are common to all glacial environments where surface melting occurs, but are usually restricted to the ice surface of the glacier ablation zone. The cryoconite, defined as "cold dust," often has a distinct granular appearance (Takeuchi et al. 2001*b*) that forms following deposition onto the glacier surface by aeolian, fluvial, mass movement and/or melt-out processes. The cryoconite then preferentially melts into the ice due to its lower reflectance than the surrounding ice (Table 1) forming a hole that becomes filled with its own meltwater. However, it should be noted that the holes are unstable and so in parts of the glacial cryosphere where melt rates are high, the cryoconite may be washed into streams and accumulate

TABLE 2. Morphology and composition of cryoconite ecosystems.

Site	Diameters (cm)	Depths (cm)	Description
Commonwealth, Canada, Howard, Hughes and Taylor Glaciers, McMurdo Dry Valleys, Antarctica	mean 18.1–41.0	4–56 cm	circular holes, covering 3.4–6.4% of glacier; ice lids of up to 30 cm typically exist all year
Midre Lovénbreen, Svalbard	mean 6.3 (0.8–35)	mean 8.3 (3.6–17.0)	circular holes, no ice lids persist during summer; granules of ~2 mm typically observed
Hyrnebreen, Svalbard	nd	nd	nd
Yala Glacier, Nepal	nd	nd	granules 0.1–3.0 mm
Manatee Glacier, British Columbia	nd	2–10	sample of 125 holes, many D-shaped
Sermikavasak, Greenland	nd	2–23	sample of 158 holes in superimposed ice from 10 locations
Devon Island and Penny Ice caps, Canadian Arctic	nd	nd	organic matter in the debris 0.8–13%; granules 0.09–1.7 mm

Note: Entries of "nd" indicate that there are no data.

in new deposits (Fig. 1) that often result in the formation of new holes (Takeuchi et al. 1998). Three types of cryoconite hole exist: open holes, submerged holes, and closed holes (Fig. 6). The formation of these different types results from the surface heat balance and presence of surface water. The physical processes governing their formation and maintenance can be found in Gribbon (1979), McIntyre (1984), Podgorny and Grenfell (1996), and Fountain et al. (2004). The closed cryoconite holes of the McMurdo Dry Valleys and other cold Antarctic environments are particularly interesting because they may be entombed by lids up to 30 cm thick that persist for 10 years or more (Fountain et al. 2004). This feature greatly restricts CO_2 and N_2 gas exchanges between the atmosphere and the water, yet allows photoautotrophic processes to continue, resulting in some rather extreme conditions as a result of the isolation (Tranter et al. 2004).

Cryoconite holes have been found to harbor a greater diversity of life (Table 2) than the snowpack and are typically dominated by bacteria (mainly cyanobacteria, phytoflagellates), algae, and fungi (Steinbock 1936, Wharton et al. 1981, 1985, Vincent 1988, Takeuchi et al. 2000, Porazinska et al. 2002, Säwström et al. 2002, Christner et al. 2003*a*, Kaštovská et al. 2005). Diatoms may also be present in holes where the inoculi are sourced from ice-marginal lakes (e.g., Porazinska et al. 2002). Tardigrades, rotifers, and nematodes have also been observed (De Smet and Van Rompu 1994, Shain et al. 2001) and viruses are present (Säwström et al. 2007; Anesio et al., *in press*). The composition of cyanobacterial, algal, and phytoflagellate communities within open and closed cryoconite holes has been shown to differ as assessed by cell microscopy by Mueller and Pollard (2004). In their study, gradient analysis between community characteristics and environmental variables (largely physical and chemical attributes of the holes and the climate of the sites) was undertaken for Canada Glacier (McMurdo Dry Valleys, Antarctica) and White Glacier (Axel Heiberg Island, Nanavut, Canada). This showed that variability in the community structure was dependent upon the environmental conditions at Canada Glacier, while on White Glacier, continuous flushing by meltwater was thought to continually reset the community structure present within the holes. Thus it is assumed that inter-hole mixing leads to a more homogeneous ecosystem in the Arctic, while isolation leads to more optimized communities in areas of different environmental pressures in the colder Antarctic system. Molecular analysis of bacterial communities present within cryoconite holes on Midtre Lovénbreen, Svalbard, Norway (where melting is significant at ~1–2 m/yr) has also found that these communities show considerable homogeneity between holes (A. M. Osborn, K. A. Cameron, M. Killion, and A. J. Hodson, *unpublished data*).

A key finding in the most recent studies of cryoconite holes has been that rates of photosynthesis in open cryoconite holes can be surprisingly significant and thus warrant further study in a range of environments. Measurements in several Svalbard cryoconite holes using ^{14}C uptake have therefore reported values between 0.24 and 10.56 μg $C \cdot L^{-1} \cdot h^{-1}$ (Säwström et al. 2002) in the water of cryoconites upon Midtre Lovénbreen and 0.63–156.9 μg $C \cdot L^{-1} \cdot h^{-1}$ in the bottom sediment: all at 0.1°C. These rates of carbon fixation are comparable to Arctic lakes, where temperatures can reach 15°C in summer (Laybourn-Parry 2003). Light levels are high on the glacier surface during the melt season (Säwström et al. 2002) and so photosynthetic elements (e.g., cyanobacteria and snow algae) appear well adapted and may be less susceptible to photo-inhibition than most other aquatic phototrophs.

When activity in the water and sediment of the cryoconites studied by Säwström et al. (2002) are combined, areal rates of carbon fixation by phototrophic activity become ~10 mg $C \cdot m^{-2} \cdot d^{-1}$, and thus broadly equivalent to those of the red algal blooms in snows adjacent to penguin colonies of the maritime Antarctic (Fogg 1967). It is not yet known how the rates

TABLE 2. Extended.

Who's there?	References
cyanobacteria and algal cells, diatoms, protozoans (especially ciliates), rotifers, and tardigrades	Wharton et al. (1981), Porazinska et al. (2002), Fountain et al. (2004)
cyanobacteria and algal cells, especially nanoflagellates (heterotrophic and autotrophic); viruses and some ciliates in the benthos	Säwström et al. (2002), Kaštovská et al. (2005); Anesio et al. (*in press*); A. Hodson (*unpublished data*)
cyanobacteria and algal cells, rotifera, tardigrada, and minor ciliates	De Smet and Van Rompu (1994)
algal cells, cyanobacteria (including oscillatoriaceans), and other bacteria.	Yoshimura et al. (1997), Takeuchi et al. (2000)
nd	McIntyre (1984)
nd	Gribbon (1979)
cyanobacteria and algal cells, including seven taxa of snow algae	Takeuchi et al. (2001*a*)

of photosynthesis in the entombed holes typical of Antarctica compare to these high rates in the Arctic. However, striking changes in the geochemistry of their dissolved inorganic carbon, dissolved organic carbon, and nutrient pools clearly indicate that the process is important (Tranter et al. 2004). In order to demonstrate these changes and show how biogeochemical conditions in closed cryoconite holes evolves from those of open holes, Fig. 7 uses a Cl^- index as a qualitative assessment of the duration of hole entombment. The Cl^- concentration factor is therefore defined as

$$CF_{Cl} = Cl_{hole}/Cl_{ice} \quad (5)$$

where Cl_{hole} denotes the concentration of the solution in the hole, while Cl_{ice} denotes the concentration of the ice wall surrounding the hole. The ratio is a crude indicator because Cl_{hole} in shallow waters will vary seasonally as the holes freeze and thaw out again. Nevertheless, for open holes, CF_{Cl} approaches 1 if the holes are flushed out by ice melt, and progressively increases if an ice lid forms and persists. This is because scavenging of solute from ice takes place beneath the lid during the annual melt of the holes. The solute, in this case Cl^-, then accumulates in the solution while pure vapor freezes onto the underside of the lid: a process driven by sublimation loss from its upper surface (Fountain et al. 2004, Tranter et al. 2004). Fig. 7 presents the different geochemistries of Svalbard and McMurdo Dry Valley cryoconite holes. The open Svalbard holes have CF_{Cl} values close to unity and show $p(CO_2)$ and pH conditions close to atmospheric equilibrium for dilute water ($1 \times 10^{-3.5}$ bar [32 Pa] and pH 5.6). The chemistry of open Svalbard holes therefore reflects the continuous bathing that they receive during ice melt, and the short residence time of these meltwaters within the ecosystem. By contrast, the extremely high pH, low $p(CO_2)$ solutions (pH = 11, $p(CO_2) = 1 \times 10^{-7}$ bar [0.01 Pa]) reported by Tranter et al. (2004) develop with increasing CF_{Cl}, suggesting that photosynthesis continues during prolonged entombment. Where entombment is most prolonged, nutrient limitation also clearly becomes significant (Tranter et al. 2004), necessitating the recycling of the organic nutrient pool and resulting in very high dissolved organic nitrogen to total dissolved nitrogen ratios (up to 100%).

Following the above discussion, primary production within cryoconite holes appears readily capable of sustaining bacterial production in a wide range of glacial environments during the melt season. However, there are simply insufficient data to assess whether these cryoconite ecosystems, like many other aquatic ecosystems (e.g., del Giorgio and Cole 1998, Duarte and Prairie 2005), demonstrate net heterotrophy and thus net biological CO_2 export to the atmosphere. What is becoming clear is that while measurements of microbial activity (i.e., primary and bacterial production) in the open waters of arctic and alpine cryoconite holes indicate that they are typically oligotrophic, the same measurements in the debris are much higher and closer

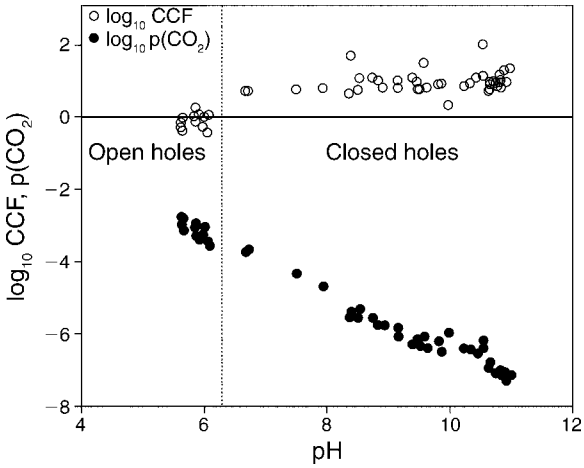

FIG. 7. Geochemical conditions inside open and closed cryoconite holes (A. Hodson, *unpublished data* from Svalbard, Norway [labeled "open holes"], and data of Tranter et al. [2004] from the McMurdo Dry Valleys, Antarctica ["closed holes"]). The dotted vertical line separates the two types. Abbreviations are: CCF, chloride concentration factor; $p(CO_2)$, the partial pressure of CO_2 in the remaining solution.

FIG. 8. A cryoconite mantle upon Midtre Lovénbreen, Svalbard, Norway (foreground). The cracked, hummocky surface results in the formation of distinct blocks whose cores are anoxic. Felix Ng for scale. Photo credit: A. Hodson.

to those found in nutrient-rich environments (e.g., Antarctic soils [Tibbles and Harris 1996]). For example, an average of 98% and 99% of total community respiration (65.2 ± 23.0 μg $C \cdot L^{-1} \cdot h^{-1}$ [mean ± SD]) and bacterial production (0.04 ± 0.019 μg $C \cdot L^{-1} \cdot h^{-1}$), respectively, was attributed to the debris layer in 8 cryoconite holes upon the Midtre Lovénbreen glacier (Svalbard, Norway) according to Hodson et al. (*in press*). However, the methods used for measuring bacterial production in this investigation (i.e., tritiated leucine incorporation) should also account for some of the production due to activity of cyanobacteria (Kamjunke and Jähnichen 2000). Thus the further characterization of autotrophy and heterotrophy in this habitat is required to better understand the differences between the aquatic (pelagic) and solid (benthic) phases of cryoconite, and also between autotrophic and heterotrophic bacterial production. Such measurements should consider adaptation to a wide range of carbon substrates, since Margesin et al. (2002) reported utilization of lignin, cellulose, proteins, carbohydrates, and fat by Stubaier Glacier cryoconite in Austria. Investigation of a wider range of supraglacial habitats is also required, and should ideally include entombed cryoconite holes, the slush zones at the base of melting snowpacks, and deposits of cryoconite debris that develop sufficient thickness to enable warm, anaerobic conditions to develop (Fig. 8). The latter can be found upon almost any Svalbard glacier and enable respiration to occur under quite different redox and hydrological conditions to those observed in the oxic, open, cryoconite holes and streams reported above. Further, high rates of respiration can be anticipated here on account of the insulation provided by the thick layers of dark organic matter that can form. Quite unlike cryoconite holes, this insulating layer suppresses the ablation rate of the underlying ice and results in a characteristically hummocky, cracked surface. When these cracks form, they allow the ingress of atmospheric gases that rapidly oxidize the edge of the cryoconite debris block (Fig. 8). Such thick accumulations of cryoconite debris are analogous to the thick mats that may become established on ice shelves (e.g., Vincent et al. 2004), although they are relatively uncommon upon steeper glaciers and have yet to be reported upon larger ice sheets. However, they clearly serve to demonstrate that respiration takes place in a range of supraglacial habitats.

Given the diversity and activity of microorganisms reported above, it is unsurprising that cryoconite holes are thought to exert a major influence upon the biogeochemical cycling of key nutrients in glacial ecosystems, especially NH_4^+ (Tranter et al. 2004, Hodson et al. 2005*b*) and PO_4^{3-} (Säwström et al., *in press*). As seen in many different types of freshwaters in tropical and temperate regions (e.g., Farjalla et al. 2002), bacterial activity in cryoconite holes is primarily limited by P (Mindl et al. 2007; Säwström et al., *in press*), although temperature limitation also appears significant (Margesin et al. 2002; Säwström et al., *in press*). Thus Säwström et al. (*in press*) showed that additions of P alone in water samples from Svalbard cryoconite holes stimulated bacterial production, while no stimulation was detected by addition of either N or C alone. Results from their study also suggested that bacteria in the water phase of cryoconite holes may be colimited by temperature, since stimulation by P was only seen when water temperature increased from the typical 0.1°C to 12°C. The lack of limitation by inorganic nitrogen in these

experiments suggests that bacteria involved in nitrogen cycling must also occupy an important niche in cryoconite holes. Fortner et al. (2005) also suggest that NO_3^- uptake may occur in the cryoconite ecosystems of the McMurdo Dry Valleys, a finding that contrasts with other studies of NO_3^- abundance in the maritime Antarctic and European High Arctic (Hodson et al. 2005*b*, Hodson 2006). In the latter cases, NO_3^- production was observed, and attributed to either nitrification (in moraines) or mineralization following N_2 fixation by cyanobacteria (Wynn 2004, Hodson et al. 2005*b*, Hodson 2006; Wynn et al. 2007). Of these, the latter appears most likely upon the glacier surface due to the abundance and diversity of cyanobacteria in supraglacial habitats (Table 2; Kaštovská et al. 2005). Experiments using treatments applied in water to snowpack lysimeters have also failed to detect nitrification (Williams et al. 1996; P. Wynn, *unpublished data*), although the process almost certainly takes place at rates equivalent to $\sim$1 g $N \cdot m^{-2} \cdot yr^{-1}$ in the ponds of Antarctic ice shelves (Fernández-Valiente et al. 2001). The different NO_3^- dynamics of the McMurdo Dry Valley glaciers (i.e., net NO_3^- depletion) when compared to the Svalbard glaciers (net NO_3^- production) might therefore indicate another impact of the ice lid upon microbial functioning: this time inhibiting N_2 transfer to cyanobacteria. If this is the case, then here exists another interesting example of the tight coupling of physical (thermal), chemical, and biological processes in these fascinating habitats.

Viruses and the supraglacial ecosystem

Viruses are the most abundant and dynamic members of aquatic microbial communities (Bratbak et al. 1990, Maranger et al. 1994, Anesio et al. 2004). Further, viral lysis can contribute substantially to bacterial mortality and in so doing stimulate the release of nutrients and organic matter into many aquatic food webs (Fuhrman 1999). Cryoconite holes are no exception, and recent work has shown high abundance and activity of viruses in Svalbard (Säwström et al. 2007; Anesio et al., *in press*). Viral abundances of $\sim 0.6 \times 10^6$ viruses/mL and 20×10^6 viruses/mL in water and sediment respectively have been found in cryoconite holes upon the Midtre Lovénbreen glacier (Anesio et al., *in press*). From ultra-oligotrophic freshwaters in Antarctica and cryoconite holes in Svalbard, Säwström et al. (2007) have also found that viral burst sizes (i.e., the number of viruses released upon lysis from of a single bacterial cell) are substantially lower (i.e., an average of three) when compared to temperate freshwaters (e.g., an average of 26). However, the frequency of visibly infected cells (i.e., the percentage of visible virus-infected bacteria in the population) has been found to be substantially higher in Svalbard cryoconite holes (i.e., average of 13%) when compared to temperate freshwaters (typically 2% [Säwström et al. 2007]). The truncated nature of microbial food webs in glacial ecosystems may therefore mean that viruses play a more important role in controlling bacterial processes than in other temperate, open freshwater ecosystems (Laybourn-Parry et al. 2001) and so their activity requires further investigation.

The extent to which supraglacial ecosystems support viruses resuscitated by melt-out from glacier ice also requires attention, not least because there has been speculation over the release of pathogenic human viruses previously isolated at depth within glaciers and ice sheets (Smith et al. 2004). Rogers et al. (2004) report that pathogenic microbes with the capacity to survive the freeze–thaw process typical of glacial environments include influenza viruses, polioviruses, caliciviruses, and tobamoviruses. Further, their entombment within englacial ice can occur over periods long enough to overcome resistance mechanisms and thus enhance the infection of host cells after their liberation by the melt process. This hypothesis was developed further into a genome recycling concept by Rogers et al. (2004), who argue that disease cycles might be intricately linked to glacial cycles owing to pathogen storage within glaciers and ice sheets (see also Smith et al. 2004). A particularly exciting aspect of the genome recycling concept is its capacity to influence the process of evolution (Rogers et al. 2004). This is caused by the impact of prolonged, cold storage upon metabolic processes, growth and thus nucleotide change. The view that englacial ice therefore serves as a "museum" (Priscu et al. 2006) serves well to introduce the contention that low rates of activity can be anticipated in the englacial ecosystem, as is considered in the following section.

The Englacial Ecosystem

Englacial habitats not only include deep, entombed environments, but also the vertical walls of crevasses and moulins, which can convey water, nutrients, atmospheric gases, and biota into the glacier. However, since observations from the latter are understandably lacking, the following discussion only considers the entombed habitats typical of ice cores. Here some of the most extreme conditions found in the entire glacial biome may be anticipated due to the high pressure, low temperature, darkness, and acidity found there (see Price 2000, 2007; Priscu et al., *in press*). Unlike good ice core sites, however, conditions within englacial ice lying at the pressure melting point are far more favourable for metabolism due to increased temperatures and water availability. However, even here conditions are difficult because Lliboutry (1996) has shown that no ingress of surface water, nutrients, and biota can be anticipated on account of the micro-scale permeability of temperate ice. This impermeability results from clogging of ice veins by debris and bubbles, the tortuosity and continuity of veins and the hydraulic conditions within the vein network itself (see Lliboutry 1996).

Data provided by Abyzov (1993) provided the earliest insights into the viable microorganisms that may be entrapped within ice cores, indicating that supraglacial,

englacial, and subglacial ecosystems may be coupled by the extremely slow transfer of microorganisms by firn burial and glacier ice flow. Since this study, a wealth of literature has further characterized the viable microorganisms that may be recovered from ice cores (e.g., Castello and Rogers 2005, Price 2007; Priscu et al., *in press*). However, in-situ activity is poorly understood and most probably dominated by a limited range of (chemoautotrophic and heterotrophic) bacterial and viral processes, of which the former has received most attention. Bacterial metabolism is most likely at grain boundaries and other interstices, which Price (2000) and Mader et al. (2006) have shown can easily incorporate motile bacteria, even at depths in excess of 3000 m. Mader et al.'s (2006) experimental work further characterized these niches by showing how solute rejection generates concentrated brines at subfreezing temperatures (3.5 mol/L and −10°C, respectively), and results in significant partitioning of cell counts across the grain-interstice boundary (i.e., bacterial cell counts of 1×10^2 to 1×10^3 cells/mL in the solid ice and 1×10^6 to 1×10^8 cells/mL in the vein fluid). More recently, Price (2007) has also considered the so-called "hydration distance" at the surface of solid impurities as a further viable habitat. Here, an unfrozen layer of temperature-dependent thickness (≥10 nm at 0°C) can exist upon the surface of hydrophilic mineral substrates such as clay particles (Price 2007), providing a substrate, nutrients, and a supply of water for microorganisms, including chemoautotrophs, in silty, englacial ice such as that observed in the Greenland ice cores.

Active englacial bacteria most likely use simple carbon substrates such as methanesulfonic acid (MSA), formic acid and acetic acid (e.g., Eqs. 6 and 7 [after Price 2000]). Other organic substrates may also be metabolized by heterotrophic bacteria, for example solubilized products following the rupture of pollen cells, invertebrates, and other microorganisms, perhaps by viral lysis. However, little is known of the composition of dissolved organic matter in the glacial system and so its systematic characterization is much needed in order to better understand the range of carbon substrates and organic nutrients that may be available. In many cases, dissolved SO_4^{2-} and NO_3^- are the most likely terminal electron acceptors, as both solutes are sufficiently abundant in glacial ice (see Legrand 1997, Röthlisberger et al. 2002):

MSA:

$$CH_3SO_3^- \Rightarrow HS^- + HCO_3^- + H^+ \quad (6)$$

Formic acid:

$$4CHOO^- + 5H^+ + SO_4^{2-} \Rightarrow HS^- + 4H_2O + 4CO_2. \quad (7)$$

At great depth within ice cores (but not necessarily at their base), the removal of atmospheric oxygen as clathrates might mean that anaerobic respiration can take place (see Tung et al. 2005, Price 2007). For example, Price (2007) reviewed work undertaken down the GISP2 ice core and, with coworkers, has presented to a compelling case for active methanogenesis following the advection of ancient methanogens from up-glacier subglacial sources. In this way, the problematic survival of methanogens during burial in the aerated firn layer of the ice sheet is not required. Although it is difficult to assess how widely englacial methanogens are likely to be distributed throughout the cryosphere, the work described here clearly demonstrates the need to be aware of potentially active microorganisms before interpreting the ice core record. What is clear, however, is that methanogens are far more likely to be active in the subglacial ecosystems of many worldwide glaciers.

An increasing awareness that vast numbers of viable microorganisms are entombed within glacial ice makes it tempting to propose that the englacial ecosystem contributes significantly to carbon and nutrient cycling within glaciers and ice sheets. This is made even more appealing when studies of sea ice and permafrost microbial activity at temperatures of −20°C and below are considered (Junge et al. 2004, Panikov and Sizova 2006). However, environmental conditions in deep, englacial ice are more extreme than those encountered in cold near-surface habitats such as sea ice and permafrost. Very low metabolic rates are therefore almost certain to dominate within glaciers and ice sheets, such that much of the nutrients and energy that become available are likely to be expended in just the repair of molecular damage (Price 2007). Thus, while this strategy enables some microorganisms to remain viable for perhaps millions of years (e.g., in permafrost), it almost certainly means that englacial microorganisms play only a minor role in the overall biogeochemical cycles of glaciers, especially those where surface and basal melting takes place.

The Subglacial Ecosystem

Microbial processes within subglacial habitats have been the subject of significant interest during the last 10 years. Over this interval, microorganisms have been shown to impart a strong signature on the chemistry of subglacial meltwater (e.g., Bottrell and Tranter 2002, Tranter et al. 2002, 2005, Wadham et al. 2004, Skidmore et al. 2005, Wynn et al. 2006). Such research has had a significant impact in its field, causing inorganic models of rock–water interaction at the glacier bed (Raiswell 1984, Tranter et al. 1993) to be usurped by ones that demand an appreciation of microbial activity (e.g., Sharp et al. 1999, Tranter et al. 2002, Skidmore et al. 2005). This paradigm shift can be witnessed by comparing two interpretations of detailed geochemical data sets from a single field site: the first in 1993 presents the inorganic model (Tranter et al. 1993), while the second, almost 10 years later, includes important microbial processes (Tranter et al. 2002).

More recently, several additional approaches have further constrained subglacial ecological processes,

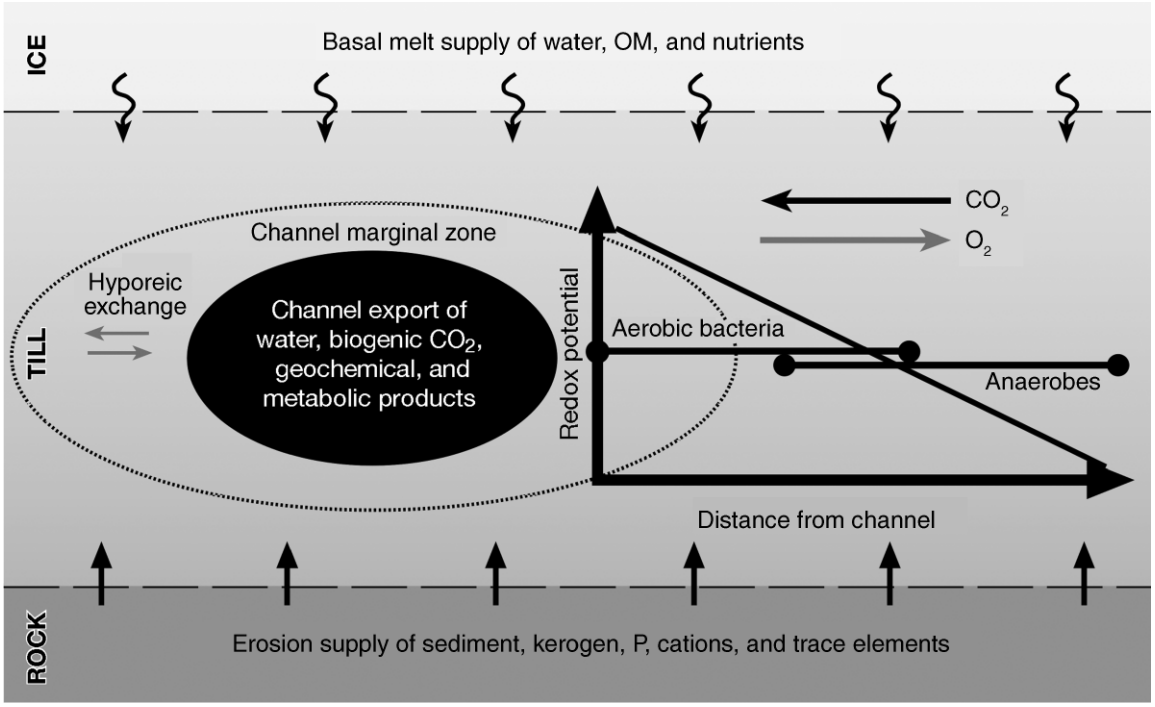

FIG. 9. Conceptual model of the relationship between hydraulic conditions at the glacier bed, the biogeochemical transfers that take place, and the broad types of bacterial activity. In the channel marginal zone (CMZ), regular (diurnally fluctuating) exchanges take place between pore waters in the till and channel waters otherwise in transit. "OM" is organic matter.

including the in-situ sampling/incubation of bore-hole water–sediment mixtures (e.g., Sharp et al. 1999, Tranter et al. 2002; R. Palma-Alvarez and B. D. Lanoil, *public communication*), incubations of bacteria from subglacial sediments sampled at the ice margin (e.g., Sharp et al. 1999, Skidmore et al. 2000, 2005, Foght et al. 2004) and characterization of microorganisms entrapped at the bottom of ice cores (e.g., Priscu et al. 1999, Christner et al. 2001, 2006, Miteva et al. 2004). Thus major ion chemistry, isotope geochemistry, and both traditional and molecular microbiological methods are the sophisticated tools now being adopted to characterize community structure and functioning. These tools are being applied to a range of Arctic, temperate, and Antarctic glacier beds, although it is the former that is presently the best known. Despite this research effort, rates of microbial activity are proving very difficult to constrain from field measurements. For example, Wadham et al. (2004) speculated that rates of sulfide oxidation (deduced from stable isotopic measurements in subglacial outlflow) are anything between 10 and 1000 $mmol \cdot L^{-1} \cdot m^{-2} \cdot yr^{-1}$ beneath the polythermal Finsterwalderbreen, Svalbard, Norway (or about 1.2–1200 $mg\ C \cdot m^{-2} \cdot d^{-1}$). Otherwise, field-derived, quantitative data are greatly lacking and, more importantly, there are major unresolved issues concerning the provenance of nitrogen (e.g., Wynn 2004, Hodson et al. 2005*b*) and organic carbon substrates (e.g., Wadham et al. 2004) involved in bacterial activity.

Redox conditions and subglacial bacterial activity

Tranter et al. (2005) speculate that a strong coupling is likely to exist between the hydraulic conditions at the glacier bed and the bacterial processes that take place. Fig. 4 shows that there are likely to be aerated sedimentary environments in close proximity to major drainage features (or channels) near the glacier terminus, and poorly aerated environments with long residence times, a distributed type of drainage system and high rock : water ratios over much of the rest of the glacier bed. Clearly, the latter provide a more viable habitat for anaerobic bacteria, because the ingress of aerated, surface-derived waters is far less likely, especially during the winter when basal melting will dominate the supply of water. Fig. 9 therefore shows a conceptual model of how bacterial function is likely to change from largely aerobic processes in the sediments that flank such channels to sub-oxic/anaerobic processes such as denitrification, $Fe_{III}/MnIV/SO_4^{2-}$ reduction, and eventually methanogenesis at increasing distances away from them (see Tranter et al. 2005). Eqs. 8–13 also show the principal bacterially mediated reactions that take place along such a redox gradient:

Sulfide oxidation:

$$FeS_{2(s)} + 14Fe^{3+}{}_{(aq)} + 8H_2O_{(l)} = 15Fe^{2+}{}_{(aq)} + 2SO_4^{2-}{}_{(aq)} + 16H^+{}_{(a)} \quad (8)$$

TABLE 3. Subglacial microbial abundance, composition, and respiration activity from two New Zealand glaciers (data are from Foght et al. [2004]).

Glacier and fraction	Total cell count (cells/g)	Count of culturable bacteria: Aerobic heterotrophs	N_2 fixers	NO_3 reducers	Fe_{III} reducers	Respiration
Fox Glacier						
Subglacial sediments	2.3×10^6	6.1×10^5 CFU/g	200 MPN/g	1.9×10^5 MPN/g	55 MPN/g	35–40%
Basal ice	na	<70 CFU/mL				<1%
Franz Josef Glacier						
Subglacial sediments	7.4×10^6	6.5×10^5 CFU/g		2.9×10^5 MPN/g	1.2×10^2 MPN/g	35–40%
Basal ice	na	$1.5 \times$ CFU/mL		3.4 MPN/mL		35–40%

Notes: Key to abbreviations: na, not assessed; CFU, colony-forming unit; MPN, maximum probable number. Bacteria were incubated at 4°C for 105 days. Respiration was measured as the percentage of ^{14}C-labeled (15 μmol/L) acetate recovered after 60 days at 8°C.

Dentrification:

$$5CH_2O_{(aq)} + 4NO_3^-{}_{(aq)} = 2N_{2(g)} + 5HCO_3^-{}_{(aq)} + H^+{}_{(aq)} + 2H_2O_{(l)} \quad (9)$$

Manganese(IV) reduction:

$$CH_2O_{(aq)} + 2MnO_{2(s)} + 3H^+{}_{(aq)} = 2Mn^{2+}{}_{(aq)} + HCO_3^-{}_{(aq)}2H_2O_{(l)} \quad (10)$$

Iron(III) reduction:

$$CH_2O_{(aq)} + 4Fe(OH)_{3(s)} + 7H^+{}_{(aq)} = 4Fe^{2+}{}_{(aq)} + HCO_3^-{}_{(aq)}10H_2O_{(l)} \quad (11)$$

Sulfate reduction:

$$2CH_2O_{(aq)} + SO_4^{2-}{}_{(aq)} = HS^-{}_{(aq)} + 2HCO_3^-{}_{(aq)} + H^+{}_{(aq)} \quad (12)$$

Methane fermentation:

$$2CH_2O_{(aq)} + H_2O_{(l)} = CH_{4(g)} + HCO_3^-{}_{(aq)} + H^+{}_{(aq)}. \quad (13)$$

So far, only manganese has yet to be invoked as an electron acceptor during the oxidation of organic carbon (shown here as a basic carbohydrate), although the recent reports of sudden increases in the abundance of Mn^{2+} concentrations at the base of Ice Stream C might change this (B. Lanoil, M. Skidmore, S. Han, W. Foo, D. Bui, *public communication*). Importantly, the transgression from aerated to anoxic conditions is likely to be characterised by anoxic microenvironments of increasing size. Such isolated microenvironments are necessary to explain the cyclic oxidation–reduction inferred from isotopic data (e.g., Wadham et al. 2004, Wynn et al. 2006) and the perhaps the syntrophic associations proposed between facultative anaerobes (in this case *Marinobacter* sp.) and sulfate reducing bacteria (*Desulfovibrio oxyclinae*) by Grasby et al. (2003). However, challenging in situ observations from the ice–bed interface are required to better understand the importance of such microscale niches, although studies of subglacial tills revealed at the ice margin by fast retreating glaciers might provide a more accessible environment (e.g., Bhatia et al. 2006).

Culturable and non-culturable bacteria in subglacial samples

Tables 3, 4, and 5 show that bacterial function may be additionally constrained from the incubation of subglacial samples. Microscopy-based enumeration of the bacteria suggests that total cell counts of 1×10^6 to 1×10^7 cells/g and 1×10^2 to 1×10^4 cells/mL are typical for subglacial sediments and waters, respectively. Culturable bacteria observed in such samples include NO_3^-, Fe(III), and SO_4^{2-} reducers in a range of glacial environments, confirming that the above conceptual model of bacterial function is reasonable (e.g., Skidmore et al. 2000, Foght et al. 2004). Further, they also demonstrate N_2-fixing bacteria in some cases and a range of aerobic heterotrophic bacteria capable of respiration at 0.3°C, but not at −4.8° and −1.8°C, according to Skidmore et al. (2005). This suggests respiration is negligible beneath cold-based parts of the glacier bed, in spite of interstitial water being present at temperatures below the freezing point. This might explain the exceptional preservation of fossil soils and plants that is sometimes observed in subglacial sediments beneath cold-based glaciers (e.g., Humlum et al. 2005).

It is now well recognized that a large proportion of viable subglacial bacteria might not be culturable (Skidmore et al. 2005) and so there have been recent attempts to characterize the total microbial communities, including the hitherto unculturable organisms, using molecular methods based on isolation of DNA directly from the environmental sample of interest. Thus Willerslev et al. (1999), Grasby et al. (2003), Foght et al. (2004), Skidmore et al. (2005), Bhatia et al. (2006), Christner et al. (2006), and Cheng and Foght (2007), among others, have described the subsequent application

TABLE 4. Subglacial microbial abundance and activity measurements from John Evans Glacier, Canada (data are from Skidmore et al. [2000]).

Glacial fraction	Total cell count†	Activity measurements			
		Respiration‡	Nitrate reduction§	Sulfate reduction§	Methanogenesis
Subglacial sediments	$>1 \times 10^6$ CFU/mL				
Basal ice	nd	~20%	100% depletion of NO_3 (5 mmol/L) after 25 d	50% depletion of SO_4 (14 mmol/L) after 60 d	16 000 ppmv CH4 in the 68–80 mL headspace of a 50-mL sample incubated in R2A medium

† After static incubation in the dark at 4°C with $0.1 \times$ R2A medium; $>1 \times 10^3$ for unamended water. Key to abbreviations: CFU, colony-forming unit; nd, not determined.

‡ Percentage of ^{14}C-labeled (<50 μmol/L) acetate recovered after 100 days of static incubation with 30 mL basal ice melt at 4°C without R2A medium.

§ Static anaerobic incubation in the dark at 4°C for 90 days with NO_3, SO_4, N_2, and R2A media; 5 g basal ice or 45 mL basal ice meltwater.

of polymerase chain reaction (PCR) methods to amplify ribosomal RNA genes from environmental DNA to enable the characterization of the total microbial community. For example, Christner et al. (2006) using 16S rRNA sequencing identified four key phyla in the accretion ice above subglacial Lake Vostok. These included 16S rRNA gene sequences that were related to α, β, and γ *Proteobacteria* such as aerobic methylotrophic genera (*Methylobacillus* and *Methylophilius*), chemolithotrophic acidophiles (*Acidothiobacillus ferrooxidans*), and chemoautotrophic sulfur oxidizers; as well as better known aerobic and anaerobic bacteria with metabolisms based upon the oxidation or respiration of SO_4^{2-}, S^0, Fe(III), and Mn(IV). These molecular studies of glacial microbial communities are fast growing in number and are clearly beginning to demonstrate that there are many diverse phylogenetically distinct bacterial taxa present in subglacial ecosystems, and they appear to include a mixture of psychrotolerant and psychrophilic species. Skidmore et al. (2005) suggest that this is pattern most likely reflects their tolerance of physical (rather than geochemical) conditions at the glacier bed (namely, oligotrophic, dark, constant cold temperature, and high mineral substrate availability).

Carbon and nitrogen substrates for bacterial activity

Other bacterially mediated processes in subglacial (and ice-marginal) environments most probably include nitrification (Eq. 14), because "excess NO_3^-" has been identified in Arctic, alpine, and Antarctic glacial meltwaters (Tockner et al. 2002, Hodson et al. 2005*b*, Hodson 2006):

$$NH_3 + O_2 \rightarrow NO_2^- + 3H^+ + 2e^-$$

$$NO_2^- + H_2O \rightarrow NO_3^- + 2H^+ + 2e^-. \qquad (14)$$

Wynn (2004) and Wynn et al. (2007) show that for Midtre Lovénbreen in Svalbard, Norway, the additional NO_3^- is isotopically enriched with respect to snowpack and atmospheric ^{15}N and ^{18}O, which is almost certainly the result of bacterial processes occurring in subglacial sediments. Here, bacterial NO_3^- production is most pronounced following the displacement of sub-oxic or "old" water from the glacier bed in early summer (Hodson et al. 2005*a*, Wynn et al. 2006). Thus, since the

TABLE 5. Subglacial microbial abundance in various glaciers.

Glacier	Reference	Fraction	Total cell counts
Haut Glacier, D'Arolla, Switzerland	Sharp et al. (1999)	subglacial (borehole) water	8.7×10^4 to 1.8×10^6 cells/mL
Glacier de Tsanfleuron, Switzerland	Sharp et al. (1999)	basal ice	8.7×10^6 to 1.1×10^7 cells/mL
Midtre Levénbreen, Svalbard, Norway	C. Säwström (*unpublished data*)	subglacial water	2.2×10^3 to 8.0×10^3 cells/mL
Krieger Mountains, Ellesmere Island, Canada	Grasby et al. (2003)	subglacial spring water	1.9×10^4 to 2.9×10^4 cells/mL
Ice Stream C, Antarctica†	Lanoil et al. (2004)	subglacial sediments	1.0×10^7 cells/g
Bench Glacier, Alaska	Skidmore et al. (2005)	snowmelt, ice-marginal/ subglacial streams, borehole waters	6.6×10^4 to 3.7×10^5 cells/mL
Grimsvotn subglacial (volcanic crater) lake, Iceland‡	Gaidos et al. (2004)	lake water	$21 \times 10^3 \pm 5.7\ 10^3$ cells/mL
Grimsvotn subglacial (volcanic crater) lake, Iceland	Gaidos et al. (2004)	lake sediment (tephra)	$38 \times 10^6 \pm 7.6 \times 10^6$ cells/g

Note: Respiration, nitrate reduction, sulfate reduction, and methanogenesis were not determined for these glaciers.

† Total anaerobic bacteria were measured at 3.63×10^5 CFU/mL in subglacial sediments; no anaerobic bacteria were detected.

‡ In lake water, C fixation, measured as initial ^{14}C-radiolabeled bicarbonate incorporation at 4°C in the dark (compared to 2–3 $nmol \cdot L^{-1} \cdot d^{-1}$ in snow and borehole water), was 3.2 ± 0.5 $nmol \cdot L^{-1} \cdot d^{-1}$.

subglacial drainage system is supplied by snowmelt for much of the summer at Midtre Lovénbreen, nitrification of snowpack NH_4^+ to NO_3^- most conveniently explains Wynn et al.'s stable isotopic data. However, a supply of NH_4^+ from crushed rock is also conceivable, which could be nitrified by bacteria or even (theoretically) oxidized abiotically by MnO_2 (Luther et al. 1997). Finally, mineralization of organic N to NO_3^- at the glacier bed is also a distinct possibility. Despite uncertainty over these additional processes, it is clear that the biogeochemistry of nitrogen in glacial meltwaters is far more complex than hitherto expected, and that microorganisms are certainly responsible for at least some of this complexity.

Perhaps the most vital, unresolved problem with our understanding of bacterial functioning in subglacial environments involves the fact that the precise carbon substrates used have yet to be determined in a range of glacial environments (Wadham et al. 2004). Eqs. 9–13 show a simple carbohydrate substrate, despite a virtual absence of data reporting carbohydrate abundance in the glacial ecosystem. However, better known are the concentrations of total dissolved organic carbon in meltwaters, which usually lie in the range of 0–10 mg/L (Skidmore et al. 2005, Christner et al. 2006). Grasby et al. (2003) and Wadham et al. (2004) speculate that the organic-rich shales beneath glaciers in the Canadian and European High Arctic, respectively, might also provide sufficient kerogen to sustain bacterial activity, while elsewhere necromass and the in-wash of surface-derived young organic carbon are considered important (e.g., Tranter et al. 2005). In this context, the hydraulic coupling between the surface and the bed again appears to be critical (Figs. 2, 4, and 9), as it will govern the efficacy of the carbon flux into subglacial habitats. More studies of organic carbon provenance are urgently required as key questions regarding the role of subglacial respiration in the oxidation of carbon stored in terrestrial ecosystems (and subsequently overridden by ice sheets) are unanswered (see Sharp et al. 1999, Skidmore et al. 2000, Tranter et al. 2005). For example, the discussion in *Water and glacial ecosystem structure* and *The supraglacial ecosystem* present the distinct possibility that viral lysis is important in the provision of younger organic carbon to/from bacterial cells. It has been shown that the role of viruses in the recycling of DOC is even more relevant during dark conditions, as demonstrated in a recent seasonal study in two large ultra-oligotrophic freshwater lakes in the Vestfold Hills, Eastern Antarctica (Säwström et al., *in press*). Here, more than 60% of the carbon supplied to the DOC pool during winter originated from virus-mediated lysis of bacteria. It is also important that more attention is also given to the role of chemoautotrophic and/or chemolithoautotrophic bacteria in the provision of organic carbon substrates at the glacier bed, as these clearly provide a basis for sustaining viral and bacterial biomass in the most remote and extreme of subglacial habitats (see Fig. 2c) such as Lake Vostok (e.g., Lavire et al. 2006). This would appear particularly relevant in the cases where subglacial environments are subject to geothermal activity, the best known example being the Grimsvötn caldera beneath Vatnajökul in Iceland, where Gaidos et al. (2004) have described autotrophy within a bacterial community that is distinct from that in the overlying glacier. More recently, Mikucki and Priscu (2007) have described chemoautotrophic (sulfur-oxidizing) bacteria in another distinct subglacial ecosystem: that beneath Taylor Glacier in the McMurdo Dry Valleys, Antarctica. Here Mikucki and Priscu (2007) found many clones closely related to an obligate chemoautotroph (*Thiomicrospira arctica*) that fixed CO_2 under dark conditions at rates similar to those reported by Gaidos et al. (2004) in the Icelandic subglacial lake.

Subglacial lakes

Subglacial lakes are perhaps the least understood ecosystem within the glacial biome. To date, there has been just one lake that has been explored (the Grímsvötn caldera; see Gaidos et al. 2005), while another, Lake Vostok, has been the focus of intense research activity, but has yet to be penetrated and sampled. The review below therefore reflects this bias and considers first the vast Lake Vostok and its potential importance before considering the Grímsvötn volcanic caldera in Iceland.

There has been considerable interest in the subglacial lakes of Antarctica following the discovery of subglacial Lake Vostok (Kapitsa et al. 1996, Siegert et al. 2001). This not only reflects the possibility that subglacial lakes host unique microbial life-forms, but also that they hold detailed sedimentary records of past climate change. Further, at least 145 subglacial lakes are known to lie beneath the Antarctic Ice Sheet (Siegert et al. 2005), and there are good reasons to hypothesize that they also existed beneath the former Laurentide and Scandinavian ice sheets (C. Clark, *personal communication*). In Antarctica, there is new evidence that some of these lakes are interconnected, and so there is some kind of drainage system beneath warm-based sectors of the ice sheet (Clarke 2006, Wingham et al. 2006). An ecosystem involving microorganisms with novel redox couples for the production of energy, adaptations to extremes of temperature, pressure, ionic strength, and pH, as well as potentially unique strategies for withstanding starvation, is therefore anticipated (Madigan and Marrs 1997, Rothschild and Mancinelli 2001).

The reconnaissance of Lake Vostok has involved ice coring and geophysical exploration, revealing that it is one of the largest freshwater lakes on Earth and the largest of the Antarctic subglacial lakes identified to date (14 000 km^2 and ~5400 km^3 according to Siegert et al. 2005 and Studinger et al. 2003). Both the geochemical composition of the Vostok ice core and the geophysical data have revealed that a significant layer of accreted ice has formed at the base of the ice sheet following the

refreezing of lake water. The freshwater that has formed this layer, and which therefore fills the lake, is also produced from the overlying ice sheet, which melts near the shoreline and at the northern ice–water interface of the lake (Seigert et al. 2000, Studinger et al. 2003). Accretion to the base of the ice sheet occurs in the central and southern regions (within a shallow embayment [Bell et al. 2002]) and continues as the ice flows into deeper water, removing water from the lake (Siegert et al. 2000). Microbiological and molecular-based studies of the accretion ice have indicated low but detectable amounts of prokaryotic cells and DNA (Karl et al. 1999, Priscu et al. 1999, Christner et al. 2001), which have been shown to be metabolically active in the laboratory when exposed to liquid water and organic electron donors (Karl et al. 1999, Christner et al. 2001). Molecular identification of microbes within the accretion ice described earlier showed close agreement with present-day surface microbiota within the bacterial phyla *Proteobacteria* (α, β, and γ), *Firmicutes*, *Actinobacteria*, and *Bacteroidetes* (Priscu et al. 1999, Christner et al. 2001, Bulat et al. 2004). It is anticipated that viruses will also occur alongside these bacteria in Lake Vostok, since an enormous diversity of viral particles has been detected in Antarctic surface lakes (Kepner et al. 1998), and preliminary results from electron microscopy have indicated the presence of viruses in Vostok glacial and accretion ice (Priscu et al. 2006). Further, since the sediments of most aquatic ecosystems contain higher densities of microbial populations than the water column, it is also likely that the sediments of Lake Vostok contain microbial life, given the presence of life in the water column (Siegert et al. 2001).

The accretion ice above Lake Vostok is essentially gas-free relative to the overlying glacial ice (Jouzel et al. 1999), and so the lake water is thought to have a high dissolved gas content (2.5 L/kg water [McKay et al. 2003]) supplied from air hydrates released as glacial ice melts into the lake. The dissolved oxygen concentration has therefore been predicted to be ~50 times higher than air-equilibrated water (McKay et al. 2003). Although these oxygen estimates assume no biogenic alteration within the lake, it has been hypothesized that aerobic conditions in the upper portion of the water column could support autotrophic and heterotrophic metabolic lifestyles, while deeper portions of the lake and sediment are likely to be anoxic if biotic and abiotic O_2 sinks exist (Siegert et al. 2003). The heterotrophic potential of the lake is supported by measurable dissolved organic carbon concentrations in the accretion ice (Karl et al. 1999, Priscu et al. 1999), together with microbial respiration of organic substrate in melted ice samples (Karl et al. 1999). Priscu et al. (1999) estimated a DOC level of 1200 μg/L, which is adequate to support heterotrophic growth. Karl et al. (1999) also reported total nitrogen levels in accretion ice ranging from 14 to 36 μg/L, which would fuel a well developed microbial assemblage within the lake and therefore supporting the estimates of 1×10^6 cells/mL in the Vostok water column made by Priscu et al. (1999).

As with all subsurface glacial habitats, a permanent absence of incident radiation means that substantial biomass and a diversity of microorganisms need to be supported by either geothermal energy and/or a readily available supply of reduced compounds. Helium isotope data (Jean-Baptiste et al. 2001) indicate that hydrothermal activity is unlikely in Lake Vostok, suggesting that adaptation to a low energy flux environment is most likely. However, there has been speculation about geothermal energy input into the lake from seismotectonic activity (Bulat et al. 2004) leading Bulat et al. (2004) to suggest that fault activity could sustain thermophilic chemolithoautotrophic microbial communities, an assertion that is consistent with small subunit rRNA gene sequences found in accretion ice samples (Christner et al. 2001, Bulat et al. 2004, Lavire et al. 2006) and minor tectonic activity detected near the Lake Vostok basin (Studinger et al. 2003). If this emerging picture is correct, the deep waters of Lake Vostok could harbor an ecosystem fueled by geochemical energy, much like that observed in deep-sea hydrothermal vent systems (Parkes et al. 2000).

A second possibility for sustaining life in Lake Vostok is the existence of a supplemental microbial food web based simply upon chemolithotrophic primary production as a consequence of simple glaciological processes that enable a range of reduced compounds (e.g., HS^-, S^0, and Fe^{2+}; see Siegert et al. [2003] for a comprehensive inventory) to be available for biogeochemical reactions in the lake (see Eqs. 8–13). As described earlier, oxidants can be readily supplied by the ice sheet (O_2 and NO_3^-) following melt and its chemical alteration of bedrock and sediment (e.g., SO_4^{2-} from sulfide oxidation). Basal ice continually melts into Lake Vostok and could thus fuel such processes. Further, several of the small subunit rRNA gene sequences recovered by Christner et al. (2006) are most closely related to species with these metabolic lifestyles. A key point about this basis for sustaining a chemolithotrophic-based ecosystem in subglacial lakes is that known glacial processes supply the energy source and there is no necessity to invoke geothermal inputs to fuel bacterial activity within the lake environment.

Unlike Lake Vostok, work undertaken at Grímsvötn caldera documents life in habitats fashioned by the direct interaction of glacial and volcanic processes. Gaidos et al. (2005) sampled the subglacial lake via boreholes about 4 years after the most recent eruption and found a 20 m deep, cold lake of modest ionic strength and of glacial meltwaters acidified (to ~pH 5) by volcanic CO_2. Particulate organic carbon in the lake water was of the order of 0.33 mg/L, and comparable to that in the overlying glacier ice and snowpack (0.22 and 0.58 mg/L, respectively). Modest numbers of microorganisms were found in these ice and water samples (4.1×10^3 to 3.8×10^4 cells/mL), yet far greater abundance was recorded in the lake tephra sediments (3.8×10^7 cells/g).

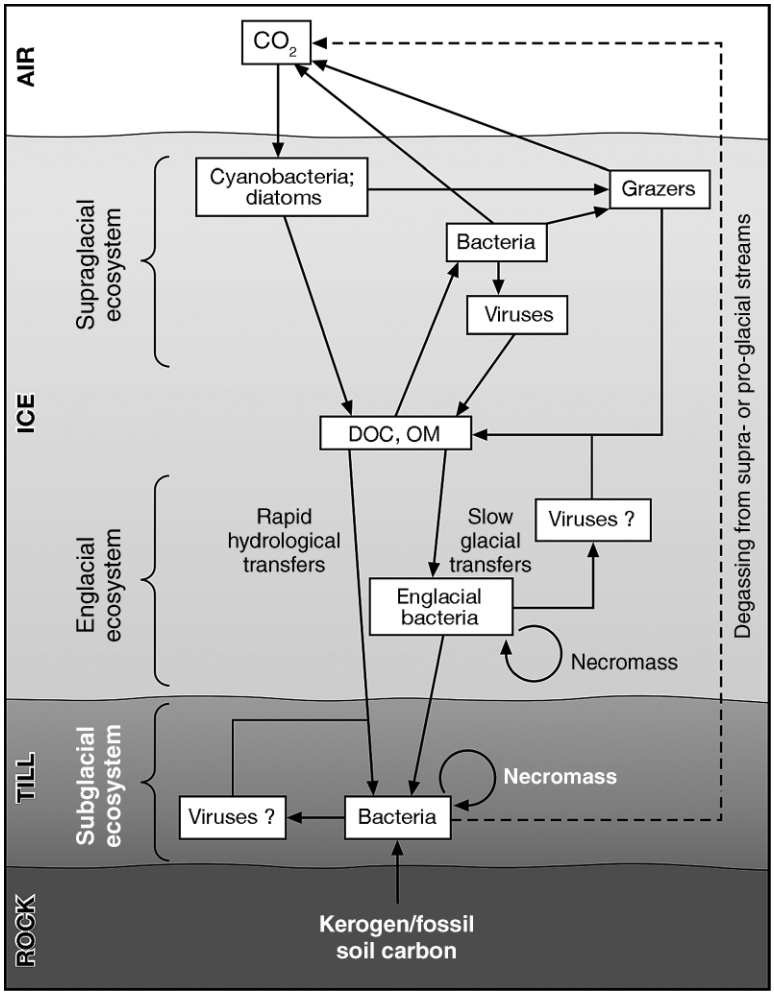

FIG. 10. Carbon flows through glacial food webs. "DOC" is dissolved organic carbon, "OM" is organic matter, and "Necromass" refers to OM produced from in situ bacteria.

The cell count for the subglacial tephra therefore represents the upper limit of microbial abundance observed in other subglacial sediments (see Table 5).

Gaidos et al. (2005) also demonstrated that chemoautotrophic activity can take place in dark, subglacial ecosystems by documenting ^{14}C radiolabeled bicarbonate uptake following incubation at 4°C (Table 5). Significant rates of carbon fixation can therefore take place in the subglacial lake. Further, small sub-unit rRNA gene DGGE band patterns and cloned fragment sequences showed that the microorganisms within the lake were distinct from those in the overlying snow and ice. Importantly, they were also distinct from known thermophilic bacteria found elsewhere in Iceland and appeared to be dominated by β proteobacteria typical of oligotrophic, oxygenated lakes and the other subglacial habitats described above. Thus the now cold Grímsvötn caldera is occupied by an ecosystem dominated by psychrotolerant species, especially in the lake tephra sediments. Demonstration of their chemoautotrophy is therefore a key finding, because their non-thermophilic behavior suggests such bacteria should also be functioning in other subglacial lakes and habitats.

FOOD WEB STRUCTURE IN THE GLACIAL ECOSYSTEM

Food webs for glacial ecosystems were first proposed by Vincent (1988), who argued that simple trophic structures are most likely in snowpacks, where low rates of photosynthesis and respiration are achieved by just a few species of phototrophs, bacteria, and fungi. Vincent (1988) suggested that more complexity may be expected in the aqueous ecosystems, such as cryoconite holes, which is certainly the case given the range of microorganisms revealed by more recent work. Most important in this context is the need to place greater emphasis upon bacteria and even viruses, especially in cryoconite habitats (i.e., holes and streams), which are clearly some of the most important habitats in the supraglacial ecosystem. Thus, it might be pertinent to consider a more complex microbial food web of the sort proposed

in Fig. 10 for the supraglacial ecosystem. Similarly, more complex subglacial community structures than hitherto realized are becoming apparent, a finding that has resulted in the new paradigm whereby bacteria govern highly variable redox conditions and play a significant role in the cycling of Fe, S, N, and P.

The hypothetical food web of Fig. 10 therefore presents an early attempt to constrain the complexity of supraglacial, englacial and subglacial ecosystems by showing the principal carbon transfers within and between them. More work is clearly necessary in order to better define the importance of viruses and bacteria (especially chemoautotrophs) in englacial and subglacial habitats. Further, the rates of the carbon transfers identified remain virtually unknown, and must also form the basis of future investigation.

Glacial Ecosystems and Climate Change

A framework for understanding the locus and nature of microbial life upon, within, and beneath a variety of glaciers has now been presented. This section therefore presents preliminary observations on the sensitivity of these glacial ecosystems to climate change. Emphasis is given to the changes as revealed over the last 50 years by glacier mass balance measurements (Haeberli et al. 1999, Braithwaite 2002, Dyurgerov et al. 2002, Meier et al. 2003), especially in the polar regions, where some of the most extreme climate change has occurred. It should be noted however, that reliable data are lacking for the Antarctic and Greenland ice sheets. The mass balance of the smaller glaciers have been largely negative over the last century, and typically show increasing mass turnover due to rising rates of accumulation and ablation (Meier et al. 2003). However, regional differences are important (Braithwaite 2002). For example, in the European High Arctic the mass turnover is relatively low, there are virtually no trends in the accumulation and ablation series, and the net mass balance of the glaciers monitored is nearly always negative (Hagen et al. 2003). In the case of Svalbard glaciers, the end of summer snowlines can therefore be exceptionally high, such that the annual accumulation area represents less than 10% of the total glacier area. In the McMurdo Dry Valleys of Antarctica, the glaciers are in equilibrium with no significant trends (Fountain et al. 2006), although the Dry Valleys have been cooling for the past two decades (Doran et al. 2002), which might reflect the strengthening of the Antarctic Oscillation (Thompson and Solomon 2002).

In the following discussion, we therefore identify the impacts of increased summer ablation upon the glacial ecosystem and assume that this is not offset by an increase in winter snow accumulation. By doing this, we are clearly focusing upon the worst case scenario in terms of glacial net mass balance change (i.e., glacier volume reduction) in a style that is typical of many Arctic glaciers and at least certain parts of the maritime Antarctic. If such conditions are sustained, then concomitant changes in the glacier thermal structure may be anticipated, which has the potential for marked impacts upon the subglacial ecosystem of the polythermal glaciers that are found here.

Impacts upon the supraglacial ecosystem

More melting will enhance snowpack productivity, but the effects will still most likely depend upon the relative importance of snow and rain during summer.—Longer melt seasons will almost certainly enhance the water and nutrient supply to nival biota (unless the snowpack is completely ablated). However, it is unclear how this will influence the balance of phototrophic and heterotrophic activity. For example, Jones (1999) suggested that fewer snowfalls mean less burial of phototrophs and thus primary productivity can be high relative to heterotrophic activity. Such conditions are a major feature in westernmost Svalbard in the European High Arctic, where stable July and August air temperatures rarely drop below the freezing point and rainfall dominates snowfall at altitudes below 500 m (e.g., Hodson et al. 2005*a*). However, these conditions are in direct contrast to the synoptic warming phases described in a maritime Antarctic glacial ecosystem by Hodson (2006), where regular cyclonic activity brought warmer air masses and snow flurries. The melting of regular snow flurries on Tuva Glacier, Signy Island, during 2003 supplied water and nutrient to a significant snowpack ecosystem, but at the same time completely masked the algal blooms that formed on the surface of the snowpack between these events. It is therefore possible that under these conditions, heterotrophic processes will benefit in the first instance, because phototrophic activity will be reduced following burial after the snow flurry. More studies of algal and bacterial productivity under changing climate are therefore required before these changes can be better understood (see Jones 1999).

Higher end-of-summer snowlines place greater emphasis upon cryoconite habitats than snowpack habitats, although niche stability is threatened.—A major feature of temperate and Arctic glaciers is that summer snowpack retreat yields large snow-free expanses of glacier ice that are partly covered by cryoconites within holes and streams. In West Svalbard, low winter accumulation means that these environments have usurped the snowpack as the most important habitat in the supraglacial ecosystem. Here, glaciers included in the mass balance monitoring program (Austre Brøggerbreen and Midtre Lovénbreen) have melt rates equivalent to ~1 m/yr water equivalent (Hagen et al. 2003), which effectively swamp cryoconite habitats with water, causing their dynamic redistribution throughout the summer (Fig. 1). Since the frequency of redistribution is vital for understanding ecosystem stability, plot and glacier scale observations of these changes are urgently required. Further, the slow rate of biomass accumulation means that it is the frequency of redistribution that governs the impact of biological

activity upon glacier melting. This is because redistribution causes new holes to continuously form across the glacier surface, while stable holes melt to a certain depth until the enhanced absorption of radiation becomes negligible.

Surface melt-out and resuscitation of englacial and near-surface microorganisms will enhance productivity in the supraglacial ecosystem.—The assertion that $\sim 1 \times 10^{19}$ microorganisms melt out of ice each year (Castello and Rogers 2005) suggests that their resuscitation might be a major contributor to changing productivity in the supraglacial ecosystem. However, there are no data with which to assess this process and so it is again clear that plot and glacier scale observations are required in order to establish ecosystem dynamics and biomass (re)distribution.

In the McMurdo Dry Valleys, warmer summers mean an increased incidence of ice lid ablation. Thus greater exchange between the hole and the atmosphere is made possible, resulting in different rates of CO_2 and N_2 transfers and also greater likelihood of the in-wash of microbes, organic/inorganic debris, water, and nutrients. Presently, these "warm events" may be limited to just one or two summers in every decade (Fountain et al. 2004, Tranter et al. 2004). It is currently unclear as to how an increased incidence of melting will impact upon the cryoconite habitats found here, although the clear differences between open and closed holes suggest that changes in activity may also be accompanied by changes in species diversity and composition (Porazinska et al. 2002, Mueller and Pollard 2004, Tranter et al. 2004). It is therefore not unreasonable to expect major changes in the structure and function of the microbial communities within these habitats if the frequency of ice lid ablation increases markedly.

Impacts upon the englacial and subglacial ecosystems

Recent mass balance changes indicate net freezing at the beds of certain High Arctic valley glaciers, leading to isolation and probable cryostasis in subglacial habitats.—The response of glacier thermal regime to climate change is a critical control upon ecosystems in englacial and subglacial environments. Net mass loss throughout the 20th century has been coupled with changing ice dynamics, causing widespread refreezing at the bed of certain valley glaciers (Glasser and Hambrey 2001), some of which have become entirely cold-based (e.g., Hodgkins et al. 1999). This change effectively ceases the interaction between surface-derived melt and the glacier bed. The implications of such changes are fascinating, as gradual isolation and onset of cryostasis in subglacial sediments is very likely to have occurred, causing the ecology of such glaciers to shift toward a system dominated by the supraglacial ecosystem. Further, Hodson et al. (2000, 2004, 2005*b*) have shown that such a shift in the basal thermal regime of Austre Brøggerbreen in Svalbard is most likely responsible for major changes in the chemistry of its outflow waters. These included reduced runoff yields of S and P, but increased yields of N, specifically as NO_3^-. Thus the greatly reduced importance of subglacial rock–water contact and its microbially mediated reactions might be very significant artefacts of this change.

Elsewhere, increased melt fluxes might enhance the coupling between supraglacial, subglacial and ice-marginal ecosystems.—In stark contrast to the above scenario, there are polythermal glaciers in which the volume of ice below the pressure melting point is actually decreasing in response to climate change (e.g., Storglaciären; see Pettersson et al. 2004). Here the onset of basal refreezing is clearly difficult to invoke and a more likely response will involve enhanced coupling between the subglacial and supraglacial environments. A similar effect is likely in temperate glaciers, leading to greater fluxes of water, biota, and nutrients being conveyed from the glacier surface, through to the glacier bed. However, more research is required to determine the efficacy of any subsequent exchanges that may take place, especially as larger, melt-induced fluxes appear to be associated with more rapid transit times through the glacier (e.g., Nienow et al. 1996). However, it is quite possible that these conditions could improve the oxygenation of the glacier bed during the summer melt period, a change that would favor aerobic bacterial processes in stable habitats.

Synthesis and conclusion

Glaciers support fascinating, microbially dominated, food webs that have the capacity to thrive wherever there is liquid water and crushed rock. Since there is a ready supply of meltwater during summer across much of the glacial cryosphere, microorganisms soon become active in cryoconite holes, supraglacial streams, moraines, and snowpacks. In most cases, this supraglacial ecosystem is probably dominated by cyanobacteria in cryoconite habitats, although it should be noted that microalgae and diatoms can be important, along with other bacteria, fungi, and viruses. This food web provides an excellent basis for considering Gaia-type hypotheses, because the cryoconite hole (a major habitat on bare ice surfaces) exists as such by virtue of the fact that dark organic matter preferentially absorbs incident radiation, and thus melts into the glacier to create its own niche. When perturbed, the cryoconite is able to form new holes following dispersal, a process that also enhances the melt rate of the glacier surface and thus provides a further critical feedback within the ecosystem. As well as representing ideal model ecosystems, cryoconite holes are also the locus of significant rates of primary and secondary productivity and thus might represent a globally significant carbon reservoir. Observations are in their infancy in this context, but clearly show that supraglacial bacteria can be active at rates equivalent to other aquatic ecosystems in warmer climes. However, the balance of primary productivity vs. respiration remains unknown, and so we are not yet in

a position to identify whether the supraglacial ecosystem is a net source or sink of CO_2 to the atmosphere.

At depth within the ice, and in particular along its bed, there exists the potential for a broad range of chemoautotrophic and heterotrophic bacteria to occupy niches that include ice interstices and, most importantly, water-rich subglacial sediments. Here, redox gradients vary significantly from the well aerated sediments adjacent to major arterial drainage features that convey surface-derived meltwater through the glacier, to anoxic pore spaces in remote subglacial environments conducive to methanogenesis. All of these habitats are notoriously difficult to constrain in terms of activity and so most previous research has instead focused upon simple enumeration of culturable microorganisms. Molecular microbial ecology methods now afford the opportunity to further investigate these communities in terms of both the potential and activity of particular functional guilds. Nevertheless, the analysis of these communities undertaken to date has, importantly, confirmed that bacteria are indeed the culprits responsible for major changes in the biogeochemistry of runoff that have been identified following the emergence of ice and snow melt from the glacier bed. Thus an ecosystem dominated by aerobic and anaerobic bacteria with metabolisms based upon the oxidation or respiration of DOC, NO_3^-, SO_4^{2-}, S^0, Fe(III), and Mn(IV) is likely to exist. Understanding the provision of DOC for much of these bacteria presents a major research need, as the relative importance of in-washed DOC, in situ necromass and/or kerogen, and "fossil" DOC acquisition from bedrock and over-ridden soils respectively is not yet known. Of equal importance is also the provision of organic carbon by subglacial chemoautotrophs, enabling the efficient recycling of necromass in a truly isolated ecosystem such subglacial Lake Vostok in Antarctica.

Glacial ecosystems represent not only vital refugia for microorganisms during the onset of cold, glacial conditions, but also potential moderators of the ecosystems that begin to develop following the onset of deglaciation. The resuscitation of microorganisms entombed in englacial ice and also in subglacial sediments is a distinct possibility once such conditions become established in response to a warming climate. At present it seems we are in an ideal situation to study this process.

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