Glacial Water

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Microbial communities and nutrient dynamics in glaciers and ice sheets continuously change as the hydrological conditions within and on the ice change. Glaciers and ice sheets can be considered bioreactors as microbiomes transform nutrients that enter these icy systems and alter the meltwater chemistry. Global warming is increasing meltwater discharge, affecting nutrient and cell export, and altering proglacial systems.

glacial microorganisms glacier meltwater proglacial environment

1. Glacial Hydrology

1.1. Seasonal Variation

The presence of water in glaciers is highly seasonal, as the generation of glacial water depends on the energy available to melt snow and ice. Water input also comes from rain events. For most glaciers in the temperate and subpolar regions, mass accumulates during the accumulation season (e.g., winter), which is characterized by colder temperatures and snow accumulation [1]. By comparison, mass loss, including melt, occurs during the ablation season (i.e., summer), which is characterized by warmer air temperatures and greater solar radiation. During this season, the lower elevation ablation zone of a glacier is gradually exposed as the winter snow cover melts, revealing an ice surface. In the accumulation zone, located at a higher altitude on the glacier, only some of the accumulated snow melts, therefore accumulating and compacting it into firn (transition stage between snow and ice) and ultimately into ice. The amount of snow gained over winter minus the amount of snow and ice lost defines the glacial ice balance [1].

1.1.1. Ablation Season

In spring, the snowpack temperature increases through heat conduction from warm air and via refreezing of meltwater that percolates into the cold snow. Once the snowpack becomes isothermal at 0 °C, snow melt percolates into the entire seasonal snowpack. In the accumulation zone, the meltwater enters the firn, forming a firn aquifer that drains to nearby crevasses [2][3][4]. In the ablation zone, the water accumulates on the ice surface and also drains into nearby crevasses [5]. Once the snow melts off the ice in the ablation zone, a shallow weathering crust of porous ice forms, caused by penetration of solar radiation and enhanced by the flow of meltwater and potentially warm air [6]. The resulting weathering crust represents a photic zone a few centimeters to a few meters deep [6][7][8][9]. Both the weathering crust and the firn aquifers are active parts of the glacial hydrological system and contribute to accumulating, distributing, and regulating water discharge to the englacial system [2][3][4][6][8][10][11][12]. Cryoconite holes can also form on the ice surface as a result of the deposition of sediment and biological materials on the glacial surface. These patches of material melt into the ice faster than the surrounding ice, driven by increased heat absorption by the dark material [13][14][15]. Under the right circumstances, these holes can form glacial ponds and lakes (cryo-lakes) [16][17]. Thus the surface streams, weathering crust, cryoconite holes, and cryo-lakes form the complex surface hydrology of glaciers [18]. This supraglacial hydrology influences the drainage pattern and flux of meltwater into the glacial interior (i.e., englacial system) and bed and to proglacial systems [18].

The main pathways from the glacier surface and firn aquifers to the glacial interior are moulins and crevasses. Moulins constitute a direct connection to an englacial system of conduits, whereas crevasses drain water via a network of fractures thought to connect to englacial conduits [19][20][21]. The englacial system of conduits reaches the bottom of the glacier, where it flows along the ice-substrate interface and, if the substrate is sediment, through the sediment as well.

Most subglacial water originates from the glacier surface, although a small flux may originate englacially and subglacially due to frictional dissipation of heat generated by flowing water, ice deformation, or from geothermal heat at the bottom of the glacier [22][23][24]. The Antarctic ice sheet is a major exception, where the main source of subglacial water is basal melt [25]. Generally, subglacial water flows in two main types of systems: slow flow within a distributed network of linked cavities or confined groundwater flow within a layer of subglacial rock debris (i.e., subglacial till), or in a quick flow system composed of a network of subglacial channels [26][27]. Distributed systems are thought to be water-filled all year round, whereas channels are water-filled only at high meltwater discharge [10][28][29]. Under ice sheets, subglacial lakes may occur as stable subglacial water bodies that can be isolated or hydrologically connected to a subglacial flow system [30][31]. Regardless of its path and residence time within the glacier, water will eventually escape to proglacial systems via streams or groundwater flow.

1.1.2. Seasonal Evolution

During summers with plenty of meltwater, surface streams flow over the ablation zone, and the weathering crust, including cryoconite holes, is full of water [1]. Surface water that accumulates in weathering crust and cryoconite holes drains into crevasses and moulins, and water in surface streams commonly pours into moulins. Compared to supraglacial systems, water accumulated in firn aquifers is less connected to the rest of the glacial system, and it occasionally drains into nearby crevasses [5]. Englacial and subglacial channels (quick flow) are thought to be filled when water discharge reaches its daily maximum and are less full early the following morning when the air temperature is the coolest, and the sun is just beginning to warm the snow and ice [32][33]. The subglacial distributed systems are thought to be continually water filled [28]. In addition to daily cycles of glacial runoff, longer variations occur with the occurrence of warm and cool weather systems [32][33]. Episodic floods may also occur due to the sudden release of ponded water within the glacier or to the sudden drainage of glacier-dammed lakes [34][35][36].

At summer's end and the beginning of winter's accumulation season, much less water is present in the glacial system due to the low air temperatures and reduced solar radiation, which largely eliminates surface melt, and while precipitation falls mostly as snow [1]. Some water may remain unfrozen over winter in subsurface weathering crust and firn aquifer due to the insulating effects of a deep snow cover [15]. Over winter, the englacial and subglacial channels collapse due to ice pressure and the absence of a counteracting pressure from flowing water [10][37][38]. However, due to a decrease in water flow, water pockets may form within the englacial or subglacial system [39][40]. Glacial streamflow also often continues through the winter, albeit at very low discharge. This may be due to the drainage of water resident in the glacier as well as meltwater produced by geothermal heat and by deformation within the ice [5][32].

1.2. Hydrological Residence Times

The residence time of water in various parts of the glacial hydrological system varies and influences in situ geochemical processes [41]. The extent to which microbial communities can develop and contribute to geochemical modification depends both on microbial doubling times [9][42] and on how long they can reside in a specific glacial compartment (i.e., water residence time). Furthermore, different residence times create a variety of conditions for microbial metabolism [43][44]. For example, the lower the residence time, the better ventilated a system is with the consequent creation of oxic waters. Oxic waters will promote aerobic or facultative anaerobic microbial metabolism, such as nitrification and iron oxidation, whereas anoxic waters will promote the growth of anaerobic organisms, such as methanogens and sulfate-reducing bacteria and archaea [45].

The residence times of water in a glacier depend on the glacier's size, where the bigger the glacier, the longer the water takes to flow through the system because of longer routing pathways [46]. Meltwater residence in ice sheets is, therefore, generally higher than in glaciers [32][47]. In the photic zone on and just below the glacier surface, water residence times in the weathering crust are at least several days during the ablation season [9][12]; weathering crust can store some water in winter if covered with a thick snowpack [6]. Ice-lidded cryoconite holes found on ice sheets and polar glaciers store water from days to months, and isolated cryoconite holes that melt within the ice and refreeze annually without connecting to the surface or subsurface hydrologic system may store water for more than a decade [13][48][49]. Open cryoconite holes on temperate and polythermal glaciers are connected to the supraglacial hydrological system and may have residence times of a few minutes to hours [15][16]. Water residence times in supraglacial lakes and ponds vary similarly to those of cryoconite holes [13][17][18]. Supraglacial streams are usually fast water-flowing systems where water fluxes vary based on the glacial system state [18].

Below the photic zone, within the firn aquifer of the ablation zone, water residence times can range from hours to days [5][50]; perennial firn aquifers have also been observed [2][3][51][52][53][54]. Within the englacial realm, two very different water-flowing systems exist. A quick flow system of conduits may have residence times of hours and perhaps up to a day [39][55][56]. A very slow system exists along the boundaries of the ice crystals, where three or more crystals meet, creating a small flow passage (i.e., ice vein) [57]. In ice veins, water flows at very slow rates and is easily blocked by air bubbles. However, these veins can host viable microorganisms [58]. Residence time in these veins is unknown. At the bottom of the glacier, channels residence time can be hours, whereas, in slow-flow distributed subglacial systems, it can be days to months [59][60][61], reaching estimated water permanence times of millions of years in subglacial lakes under ice sheets [30][31][62].

As with meltwater discharge, water residence times change seasonally, with the shortest residence time being in the summer [41]. In winter, after the system closes down and various components are no longer linked due to the lack of water flow, the freezing of passageways or ductile closure of passageways causes residence times to increase [41].

2. Hydrology Influences on Glacial Nutrients and Microbial Communities

2.1. Deposition of Nutrients and Microorganisms on Glacial Surfaces

Dry and wet deposition of atmospheric aerosols transports diverse chemistry and biology to the glacier surface [63][64][65][66][67]. Their chemistry and concentration depend on patterns of atmospheric circulation, distance to source regions, and type of source emissions [68][69][70]. The distribution of chemical compounds across a glacier can be heterogeneous due to variable aeolian deposition [71]. For example, mineral dust is more highly concentrated at the margins of a glacier due to its proximity to bare rock and soils [72].

Bioaerosols (particulates containing microorganisms) may inoculate glacier surfaces, and subsequent microbial community development depends on the surface environment and microbial adaptations [73][74][75]. Such microbial communities typically include both endemic and cosmopolitan microorganisms [76][77][78][79][80][81]. Considering the dynamic and ever-shifting nature of glacial ice sheet systems, these communities will experience a broad range of icy micro-environments and will shift accordingly as they transit through the system [82][83].

2.2. Microbial and Geochemical Dynamics during the Ablation Season

2.2.1. Supraglacial Realm

In the supraglacial environment, organic and inorganic nutrients and carbon are often available in dissolved forms released by the biochemical weathering of deposited particles [84][85]. With the onset of the ablation season, nutrients and carbon deposited during the accumulation season progressively percolate through the snowpack into the weathering crust, cryoconite holes, and glacial ponds (ablation zone) [6][44], and microorganisms are able to resume metabolic activity shortly after thawing [86].

In the photic layer of the weathering crust, UV- and visible-light-driven chemical transformations lead to the dissolution of iron oxide and silicates in mineral particles and Fe^{3+} reduction in ice-hosted sediment particles [6][84][87]. Nutrient concentrations, particularly dissolved organic nitrogen (DON) and P are generally higher in weathering crust compared to supraglacial streams and cryoconite holes [88]. Cryoconite holes are widely recognized as hotspots of microbial activity [15][48][89][90]. The waters are generally oxic environments, and ice-lidded cryoconite holes in Antarctica can be supersaturated in O_2 [49][91]. However, within thick cryoconite granules (aggregates of microorganisms and organic and inorganic nutrients present in both open and ice-lidded cryoconite holes), the environment can become anoxic [92]. The oxidation state of cryoconite holes is important as it dictates the oxidation state of key nutrients. For example, the most common Fe ions, Fe^{2+} and Fe^{3+}, are soluble only within certain pH and dO_2 conditions, affecting their capacity to associate with other ions (e.g., chloride and hydroxide ions) or to adsorb onto ice crystal surfaces [84].

With the onset of the ablation season, during which the primary nutrient input is from snowmelt, the exposed component of the supraglacial environment (e.g., weathering crust) is dominated by prokaryotic photoautotrophs (e.g., Cyanobacteria in cryoconite holes) and ice algae (e.g., *Ancylonema nordenskiöldii*, and *Mesotaenium berggrenii* on the surface of the ice/weathering crust) [67][93]. These organisms can directly affect melt rates and surface morphology (Box 2) and play an important role in fixing atmospheric CO_2 and N_2 when nitrogen-fixing cyanobacteria, such as *Nostoc* and *Anabaena*, are present [94][95]. Microbial activity changes as the ablation season progresses. For example, during initial phases of snowmelt early in the ablation, excess concentrations of inorganic nitrogen (NO_3^- and NH_4^+) flush from the snowpack and are utilized by microbial communities, while later in the season (after the inorganic flush and when concentrations are low) microbial activity switches to dinitrogen fixation [96][97][98]. Phototrophic communities help to produce dissolved organic nutrients (i.e., dissolved organic carbon, nitrogen, and phosphorous), enriching the glacial surface with organic and inorganic nutrients that would be otherwise limiting factors for heterotrophic microbial activity [80][88][99]. Phosphorous is typically sourced from supraglacial particles via geochemical and physical processes and from microbial necromass via biological activity [99][100]. Microbial exudates and necromass on the glacial surface are essential for the functioning of the heterotrophic component of the microbial community. In this context, it has also been observed that different exudates are differentially utilized by microorganisms [101][102] within a complex glacial microbiome where heterotrophic organisms present a wide range of metabolisms [102][103][104]. Bradley et al. (2023) observed that more than 50% of bacterial cells (dominated by Actinomycetota, Pseudomonadota, and Planctomycetota) are translationally active on glacial surfaces [86]. Most of the deposited and transformed nutrients in the supraglacial realm are then exported to the rest of the glacial system [42][83]. With the development of warmer conditions due to the progression of the ablation season, weathering crust and cryoconite holes contribute nutrients and microbial cells to the rest of the glacier [9][105][106][107].

2.2.2. Englacial Realm

Snowmelt also enters into the firn aquifer. No studies reporting biological processes in firn aquifers are available. However, there are indications of microbial activity: Holland et al. (2022) observed similar NO_3^- concentrations between the ice-snow interface meltwater and the snowpack [88]. However, DON and NH_4^+ concentrations were variable, possibly indicating microbial activity at the ice-snow interface. The chemical composition of the meltwater that enters the englacial system varies across the ablation season. Whereas meltwater at the beginning of the ablation season is likely to reflect the chemical composition of the snow, microbial processes and particle weathering ensure that meltwater that enters the englacial system later in the season is enriched with carbon, macronutrients (e.g., N, P, and Si) and ions such the dissolved inorganic forms of sulfur (e.g., SO_4^{2+}) [108][109]. The englacial realm, with its network of water pathways, transfers cells and nutrients within the glacial system. It is unclear whether the englacial realm also has a role in nutrient and carbon transformation and is characterized by a microbial community specific to englacial pathways conditions [110]. Microbial nutrient cycling observed in fast-flowing supraglacial streams [104] suggests that microbial processes may be significant in fast-flowing englacial conduits. In addition, ice cores collected from englacial systems indicate that microorganisms are not quiescent but maintain an active metabolism [111]. These active metabolisms could be ascribed to chemoautotrophic organisms [111] or could rely on simple carbon substrates (e.g., acetic and formic acids) using NO_3^- and SO_4^{2+}, which are abundant in meltwater deriving from supraglacial systems, as terminal acceptors [45].

In addition to englacial conduits, ice veins, with their high nutrient concentrations, offer a favorable habitat for microbial activity [58][112][113][114], and high cell concentrations have been measured in this environment [115]. Liquid flow in veins has long residence times, suggesting low oxygen concentrations and anaerobic metabolism [112][116], which can be mediated by methanogens such as *Methanosphaerula* and *Methanococcus* [117]. Despite the high nutrient concentrations and favorable conditions for active communities, microbial structure and function in the englacial realm are poorly understood [110][111].

2.2.3. Subglacial Realm

In subglacial systems, meltwater contacts bedrock (and subglacial till) and is consequently enriched in compounds released by rock comminution and dissolution (e.g., H_2 and FeS_2), creating environments where redox conditions may vary widely [118][119]. Chemical compositions of subglacial water highly vary due to (i) supraglacial and englacial hydrology, which controls the pattern, discharge, and biogeochemistry of meltwaters reaching the bottom of the glacier; (ii) subglacial hydrology, which controls the discharge and residence time of waters along the bed and influences patterns of erosion and regelation; and (iii) the geology of the subglacial substrate [28][41][77][106][120].

Depending on the mineral composition of the glacier and ice sheet beds, subsurface meltwater can be influenced by the weathering of pyrite (i.e., pyrite oxidation) and/or carbonates (i.e., carbonate dissolution) [121][122]. The dissolution of pyrite releases protons, and the dissolution of carbonate rocks releases dissolved inorganic carbon (e.g., CO_2), which then creates carbonic acid in aqueous environments [123]. Pyrite oxidation is the prevalent form of mineral weathering in subglacial environments and has been observed to drive subglacial microbial metabolism [120][123]. The acidic environment resulting from pyrite oxidation also drives carbonate and silicate weathering [124]. The presence of subglacial tills also influences meltwater chemical compositions [10][125][126], and glacial beds can also be connected via aquifers to subterranean water sources [127]. All these factors further influence meltwater chemical composition and shape microbial community input to the subglacial environment [28][127][128].

As in the supraglacial and englacial realms, subglacial microbial communities are largely composed of heterotrophic microorganisms. However, contrary to the supraglacial realm, the primary producers of subglacial communities are chemolithotrophs. These organisms rely on nutrients transported from the glacial surface but also those released by rock weathering, and they accelerate mineral weathering of the glacial bed and chemical transformations within the subglacial system [84]. Biotic pyrite (FeS_2) dissolution is rapid both in oxic and anoxic conditions [84][129], where O_2 and Fe^{3+} can be used as sulfide oxidants [119]. Sulphide oxidation in oxic conditions uses pyrite, oxygen, and water to produce H^+, $Fe(OH)_3$ (iron (oxyhydr)oxides), and SO_4^{2}. $Fe(OH)_3$ dissociates to Fe^{3+} in the acidic subglacial environment (created by a high concentration of H^+ due to rock dissolution) [84]. Anoxic pyrite dissociation can then occur: pyrite, Fe^{3+}, and water react to form Fe^{2+}, SO_4^{2-}, and H^+. Anoxic pyrite dissociation is faster than oxic dissociation because of the higher H^+ production, which accelerates rock dissolution and weathering [84][130]. These weathering reactions are mediated by iron/sulfur-oxidizing bacteria, such as *Thiobacillus* and *Sideroxydans* species, and iron-reducing bacteria, such as *Desulfosporosinus*, *Geobacter* and *Rhodoferax* species [120][123][130][131]. Other microbial-mediated processes in the subsurface environment include denitrification, Mn^{4+} reduction, SO_4^{2-} reduction, methanogenesis, and nitrification [45][64][132][133][134]. In this environment, complex microbial interactions occur where, under anaerobic conditions, SO_4^{2-} reducing bacteria compete with methanogens for carbon substrates [135].

While meltwater that reaches subglacial systems is mostly oxygenated, as it is sourced from well-ventilated environments (e.g., supraglacial streams, moulins, and fast-flowing englacial conduits), oxygen levels in the subglacial environment can significantly vary based on the morphological characteristics of the system and, consequently, on water residence times [28][124]; whereas channelized subglacial systems are characterized by oxic waters thanks to their fast-flowing waters [28], anoxia and higher rock dissolution rates are observed with longer water permanence times and typically indicate higher rates of microbial activity and respiration [28][124]. In distributed drainage systems, there is a progressive development of anoxic conditions due to slow water flow, which creates favorable conditions for the uptake and use of organic matter by heterotrophic organisms via oxidative cellular respiration [46]. Despite these shifts in water oxygen levels, in general, microbial metabolism is thought to be driven by the mineralization of organic carbon and nitrogen under oxic conditions [45], whereas microbial communities performing sulfate reduction and methanogenesis prevail with the development of anoxic conditions [136].

2.3. Microbial and Geochemical Dynamics during the Accumulation Season

Most of the studies on glacial microbial communities take place during the summer ablation season at temperate and polythermal glaciers, where geochemical and microbial processes are most active due to the presence of meltwater and nutrients in the system [137]. Consequently, little information is available on microbial processes during winter.

Even in winter, water in ice veins, englacial pockets, and subglacial regions [28][45][112] may retain sufficiently high solute concentrations to sustain basal microbial metabolism (e.g., DNA repair mechanisms) [138] or even microbial growth. During the accumulation season, the prevalent microbial metabolism is likely to be chemoautotrophy in all glacial environments; the newly secreted nutrients and remnant nutrients from ablation seasons could also sustain metabolism in heterotrophic organisms. Active microbial communities have been identified in systems that are only minimally influenced by ablation/accumulation seasonal differences, such as subglacial lakes in ice sheets [139][140][141]. Furthermore, in glaciers during the accumulation season (when nutrient input from the surface is largely absent), nutrients can be sourced from glacial bedrock where H_2 is released abiotically from rock comminution and can be oxidized in both aerobic and anaerobic conditions, fueling microbial chemolithotrophy [118][142][143][144]. Thus, even during the accumulation season, glaciers can harbor biogeochemical transformations thanks to microbial-mediated processes. This is also supported by observations of active heterotrophic communities in snowpacks incubated in cold and dark conditions [145].

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