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# Widespread bacterial populations at glacier beds and their relationship to rock weathering and carbon cycling

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## ABSTRACT

**Bacterial populations found in subglacial meltwaters and basal ice are comparable to those in the active layer of permafrost and orders of magnitude larger than those found in ice cores from large ice sheets. Populations increase with sediment concentration, and 5%–24% of the bacteria are dividing or have just divided, suggesting that the populations are active. These findings (1) support inferences from recent studies of basal ice and meltwater chemistry that microbially mediated redox reactions may be important at glacier beds, (2) challenge the view that chemical weathering in glacial environments arises from purely inorganic reactions, and (3) raise the possibilities that redox reactions are a major source of protons consumed in subglacial weathering and that these reactions may be the dominant proton source beneath ice sheets where meltwaters are isolated from an atmospheric source of $CO_2$. Microbial mediation may increase the rate of sulfide oxidation under subglacial conditions, a suggestion supported by the results of simple weathering experiments. If subglacial bacterial populations can oxidize and ferment organic carbon, it is important to reconsider the fate of soil organic carbon accumulated under interglacial conditions in areas subsequently overridden by Pleistocene ice sheets.**

## INTRODUCTION

Subglacial chemical weathering is usually attributed to purely inorganic reactions that take place within oxygenated environments (Raiswell, 1984; Chillrud et al., 1994). However, there is increasing evidence that redox reactions such as denitrification (Tranter et al., 1994) and the oxidation of organic carbon (Fairchild et al., 1993) occur at glacier beds, as does sulfide oxidation (Raiswell, 1984). Such reactions may be important proton sources for subglacial weathering and, in other environments, they are microbially mediated (Schlesinger, 1991). Little is known, however, about the size and characteristics of microbial populations at glacier beds. Although bacterial activity in general is inhibited by low temperatures, specialist bacteria (psychrophiles) are adapted for growth and activity at low temperatures. Some bacterial types are adapted to subfreezing temperatures (Wynn-Williams, 1990). Bacterial populations on the surface of ice caps and in cores from the Greenland and Antarctic Ice Sheets are very low (Jones et al., 1994; Catranis and Starmer, 1991; Abyzov, 1993). However, substantial populations (to $10^9$ cells per gram of sediment), which include nitrifiers, denitrifiers, sulfate reducers, and methanogenic archaeobacteria (Gilichinsky et al., 1995), occur in permafrost (D. Gilichinsky, 1997, personal commun.). It is therefore conceivable that such organisms could exist at glacier beds. To investigate this possibility, we determined bacterial populations in supraglacial, subglacial, and proglacial meltwaters, clean and debris-rich ice, and melt-out till at two Swiss glaciers.

## SAMPLING SITES

Samples were collected at Glacier de Tsanfleuron (46°19′N 7°15′E) and Haut Glacier d'Arolla (45°58′N 7°32′E), Switzerland. Glacier de Tsanfleuron is a 2.5 $km^2$ plateau glacier overlying impure carbonates. Basal ice containing abundant rock debris (Tison and Lorrain, 1987; Hubbard and Sharp, 1995) and melt-out tills derived from ablation of this ice were sampled at an elevation of 2500 m on the northern flank of the glacier (Table 1). Samples T1–T6 were collected within 5 m of each other at the glacier margin. Sample T7 was taken from two small mounds of meltwater-reworked sediment on the glacier surface, ~200 m to the east of the main sampling site. Haut Glacier d'Arolla is a 6.3 $km^2$ valley glacier underlain by schist, gneiss, and amphibolite. Samples were collected from the meltwater stream draining the glacier at daily minimum (A6; 2.6 $m^3 \cdot s^{-1}$) and maximum (A9; 4.4 $m^3 \cdot s^{-1}$) discharges, from three boreholes drilled to the glacier bed at an elevation of 2780 m on the eastern side of the glacier, and from two supraglacial streams located near the borehole array (A3, A7) (Table 1).

## METHODS

Samples were collected in clean, autoclaved bottles (acid-washed tops; glass containers heated at 450 °C overnight) containing sufficient 0.2-$\mu$m-filtered formaldehyde to produce a 4% concentration in the sample. Formaldehyde was used to ensure that there was no change in bacterial numbers during storage prior to counting. At Tsanfleuron, samples were taken with either an ice screw (ice), or a hammerhead (sediment). Immediately before use, sampling equipment was sterilized by alcohol treatment, followed by flaming with a portable gas burner. For each ice sample, outer and inner cores, each 6 cm long, were taken from the same hole. To avoid surface contamination, the top few millimeters of the ice surface were scraped off prior to sampling. Sample T5 consists of surface scrapings from clear glacier ice. At Arolla, stream samples were

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TABLE 1. RESULTS OF ANALYSES OF SAMPLES COLLECTED AT GLACIER DE TSANFLEURON (T) AND HAUT GLACIER D'AROLLA (A) IN 1993

| Site | Sample description | Log total bacteria ($mL^{-1}$) | Log growing bacteria * ($mL^{-1}$) | Sediment content ($g \cdot mL^{-1}$) | Organic carbon (%) |
|---|---|---|---|---|---|
| T1A | Clean ice - outer | 5.97 | 4.98 | 0.0001 | N.D.† |
| T1B | Clean ice - inner | 6.37 | 5.12 | 0.0004 | N.D. |
| T2A | Clean ice - outer | 6.40 | 5.15 | 0.0242 | N.D. |
| T2B | Clean ice - inner | 6.61 | 5.55 | 0.0002 | N.D. |
| T3A | Clean ice - outer | 6.87 | 5.85 | 0.0004 | N.D. |
| T3B | Clean ice - inner | 6.93 | 6.18 | 0.0136 | N.D. |
| T4A | Debris-rich ice - outer | 6.94 | 6.06 | 0.0372 | N.D. |
| T4B | Debris-rich ice - inner | 7.05 | 6.30 | 0.0476 | N.D. |
| T5 | Surface ice scraping | 7.68 | 6.79 | 0.5830 | N.D. |
| T6A | Melt-out till - surface | 7.21 | 6.18 | 1.1400 | 0.3 |
| T6B | Melt-out till - 5 cm below surface | 7.32 | 6.51 | 0.2620 | N.D. |
| T7A | Sandy supraglacial debris | 7.57 | 6.66 | 0.5300 | 0.35 |
| T7B | Flour-rich supraglacial debris | 7.77 | 7.08 | 0.6130 | 0.22 |
| A3 | Supraglacial runoff | 4.72 | 4.01 | 0.0001 | N.D. |
| A7 | Supraglacial runoff | 5.04 | 4.28 | 0.0006 | N.D. |
| A9 | Bulk runoff - maximum flow | 5.74 | 4.79 | 0.0014 | N.D. |
| A6 | Bulk runoff - minimum flow | 4.94 | 4.13 | 0.0002 | N.D. |
| A8 | Borehole A - surface | 5.18 | 4.48 | 0.0008 | N.D. |
| A2 | Borehole A - base | 6.09 | 5.08 | 0.0013 | N.D. |
| A1 | Borehole B - surface | 4.91 | 3.74 | 0.0002 | N.D. |
| A4 | Borehole B - base | 4.94 | 4.32 | 0.0001 | N.D. |
| A5 | Borehole C - surface | 5.12 | 3.79 | 0.0004 | N.D. |
| A10 | Borehole C - base | 6.26 | 5.31 | 0.0044 | N.D. |

*Growing bacteria were either in the process of dividing or had just divided.
†N.D. = not determined.

collected with a prerinsed bottle and transferred to a sterilized, 1 L glass bottle containing formaldehyde. Borehole samples were collected with a 250 mL borehole water sampler (which was rinsed by the flushing action of descending through the water column) and transferred immediately to sterile bottles containing formaldehyde. To minimize the risk of contamination of borehole samples with bacteria introduced during the drilling process, the hot water drill was operated at temperatures (80 to 150 °C) high enough to cause considerable bacterial lysis. Samples were collected approximately one month after boreholes were drilled and from boreholes that were actively connected to the subglacial drainage system and flushed daily by inputs of water derived from the glacier bed (Gordon et al., 1998). To allow comparison of bacterial populations between subglacially derived waters and waters that may have been contaminated by surface inflow, separate samples were collected from the top (A1, A5, A8) and base (A2, A4, A10) of the borehole water columns.

Total bacterial populations were determined by using acridine orange staining and microscopic counting (Fry, 1988). Fixed samples were vortex mixed, and a 4–10 $\mu$L subsample was added to 10 mL of 2% filter-sterilized (0.1 $\mu$m) formaldehyde in artificial seawater. Acridine orange (50 $\mu$L) was added to give a final concentration of 5 $mg \cdot dm^{-3}$. After 3 min, the solution was filtered through a 25-mm-diameter Nucleopore black polycarbonate membrane with 0.2 $\mu$m pore size. The filter was rinsed with a further 10 mL of 2% filter-sterilized formaldehyde in artificial seawater and mounted in paraffin oil under a coverslip. Three replicate filters were prepared from each sample to minimize the variance of the counts (Kirchman et al., 1982). Where 95% confidence limits of the mean count exceeded 0.5 $\log_{10}$ units, further replicate filters were prepared. At least 200 fields of view were counted.

The mounted membrane filters were viewed under incident illumination with a Zeiss Axioskop microscope fitted with a 50 W mercury-vapor lamp, a wide-band interference filter set for blue excitation, a 100 × (numerical aperture = 1.3) Plan Neofluar objective lens, and 10 × eyepieces. Bacterially shaped green- and red-fluorescing objects were counted. Cells on or off particles were counted separately, and the numbers of those on particles were doubled in the final calculations to account for cells hidden from view by particles (Goulder, 1977). Dividing cells (those with a clear invagination) and divided cells (pairs of cells of identical morphology) were also counted. The proportion of cells which are dividing or divided is related to bacterial growth in sediment slurries (Getliff et al., 1992) and correlates well with an independent measure of bacterial growth, thymidine incorporation, in near-surface sediments (Wellsbury et al., 1996). It is therefore used here as an index of bacterial growth.

To investigate the possibility that bacteria from the basal ice mediate the oxidation of sulfide minerals, ice from sample T4 was kept frozen for 21 months and then subdivided into 2 samples (A and B), each representing a particular layer of basal ice, and allowed to melt. One aliquot of each sample was filtered immediately for sulfate determination by ion chromatography, and replicates were incubated for 1 week and 2 months, at 4 °C, before being analyzed again for sulfate. Direct bacterial populations were determined on the samples incubated for two months. To determine the rate of sulfate release from sulfide oxidation at low temperatures, three aliquots of a suspension of debris from Glacier de Tsanfleuron were incubated at 3 °C for 1 week, after which sulfate yields were determined by ion chromatography. This debris contained a mean of 4% pyrite by weight in the 0.45–20 $\mu$m fraction, but there was no pyrite visible in the <2 $\mu$m fraction.

## RESULTS

All samples contained significant bacterial populations (Table 1). Numbers were generally higher in Tsanfleuron ice and sediments (mean $9.6 \times 10^6$ $mL^{-1}$, range $9.3 \times 10^5$ to $5.9 \times 10^7$ $mL^{-1}$) than in Arolla meltwaters (mean $2 \times 10^5$ $mL^{-1}$, range $5.3 \times 10^4$ $mL^{-1}$ to $1.8 \times 10^6$ $mL^{-1}$), suggesting that populations in ice were not simply entrained during the freezing of subglacial meltwaters. Between 5% and 24% of the cells counted were dividing or had just divided, suggesting that part of the population was active. Even if the populations from basal ice were entrained when the ice was formed, the proportion of dividing or recently divided cells provides an index of bacterial growth in the subglacial environment from which the source waters were derived. Population sizes in inner and outer ice cores were very similar, but they were about five times lower than in surface ice and sediments. This argues against surface-derived contamination of the ice-core samples. Populations from the surface of borehole water columns were comparable to those in supraglacial meltwaters (which were used as drill fluid and which can drain into open boreholes), but much lower than those in more sediment-rich waters from the bases of boreholes. Two arguments suggest that bacteria from borehole bases are representative of in situ subglacial populations and not derived from populations introduced during drilling: (1) boreholes were flushed daily with subglacially derived waters, and (2) because bacterial populations in samples from borehole bases were higher than those in surface-derived waters, they cannot have been introduced during drilling unless they increased by an order of magnitude during the month between drilling and sampling. If this occurred, it underlines the ability of bacteria to be active and grow in the subglacial environment and suggests that natural flow of supraglacial meltwater to the glacier bed via crevasses could be one means of establishing subglacial bacterial populations.

Population sizes reported here are similar to those in Weddell Sea pack ice (to $2.8 \times 10^6$ $mL^{-1}$; Grossman and Dieckmann, 1994) and to 10 orders of magnitude higher than recorded in Antarctic ice cores ($10^{-3}$ $mL^{-1}$; Abyzov, 1993). Populations per gram of sediment ranged from $1.5 \times 10^7$ $g^{-1}$ to $2.1 \times 10^8$ $g^{-1}$ in Arolla meltwaters and from $1.3 \times 10^6$ $g^{-1}$ to $1.8 \times 10^9$ $g^{-1}$ in Tsan-

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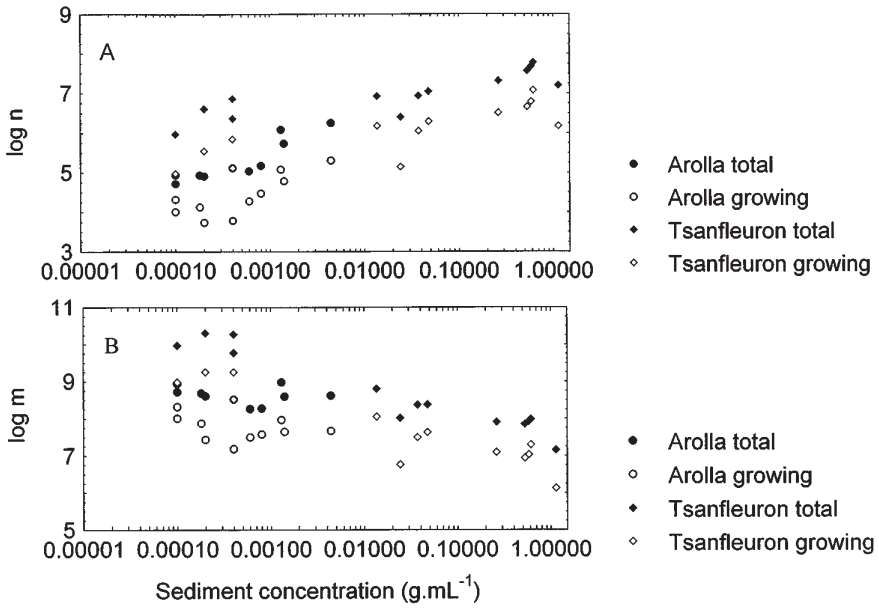


**Figure 1. Relationship between bacterial population size and sediment concentration in samples from Glacier de Tsanfleuron and Haut Glacier d'Arolla. A: Populations per milliliter sample (*n*). B: Populations per gram of sediment (*m*).**

fleuron ice and sediments. These values are similar to the highest populations recorded in permafrost ($10^7 - 10^9$ $g^{-1}$; D. Gilichinsky, 1997, personal commun.).

Bacterial populations ($n$; $mL^{-1}$) were positively correlated with sediment concentrations ($C$; $g \cdot mL^{-1}$) in ice and meltwater samples ($\log n = 7.67 + 0.59 \log C$, $r^2 = 0.68$, $p < 0.001$; Fig. 1A). This suggests that the abundance of sediment substrate helps to make the subglacial environment relatively favorable for microbial growth. However, populations per gram of sediment ($m$) decreased with increasing sediment concentration ($\log m = 7.67 - 0.41 \log C$, $r^2 = 0.5$, $p < 0.001$; Fig. 1B), probably because the most sediment-rich samples also contained the greatest proportions of coarse sediment, which is less favorable than fine sediment as a microbial substrate (Gilichinsky et al., 1995).

The relationship between population size and sediment availability suggests that part of the population may derive energy from the oxidation of either reduced minerals or organic carbon within the sediments. When basal ice was melted and incubated in the laboratory for two months at 4 °C, considerable sulfate was produced (Table 2). Over the same period, bacterial populations increased four fold to six fold, indicating that they are active at temperatures close to freezing. It is therefore likely that microbially mediated pyrite oxidation contributed to the observed sulfate release. Microbial activity can increase the rate of oxidation of ferrous iron to ferric iron by as much as $10^6$ times (Singer and Stumm, 1970). Because this is often the rate limiting step in sulfide oxidation, the sulfide oxidation rate is also increased. To investigate whether this effect may be important under subglacial conditions, the mean sulfate yield from the three suspensions incubated for 1 week at 3 °C (4 meq sulfate per gram of pyrite) was compared with calculations of the yield expected from "inorganic" oxidation of pyrite under equivalent temperature and pH conditions (7.6 to 8.4). The "expected" yield was estimated from experimental data of Nicholson et al. (1988), assuming a mean grain size of 5 μm for pyrite (estimated from microscope measurements). The resulting value (0.05 meq sulfate per week per gram of pyrite) is two orders of magnitude less than the observed yield. This finding provides further evidence that microbial mediation may play a role in subglacial sulfide oxidation.

TABLE 2. RESULTS FROM A SIMPLE WEATHERING EXPERIMENT CONDUCTED AT 4 °C ON MELTED SUBSAMPLES OF DEBRIS-RICH BASAL ICE FROM GLACIER DE TSANFLEURON

| Sample | Initial sulfate ($\mu eq \cdot L^{-1}$) | Log total bacteria ($mL^{-1}$) | Growing bacteria* (%) | 1 week sulfate ($\mu eq \cdot L^{-1}$) | 2 month sulfate ($\mu eq \cdot L^{-1}$) | 2 month log total bacteria ($mL^{-1}$) | 2 month growing bacteria * (%) |
|---|---|---|---|---|---|---|---|
| A | 43 | 7 | 15 | 760 | 3190 | 7.8 | 14 |
| B | 32 | 7 | 15 | 91 | 520 | 7.6 | 9 |

Note: Sediment concentrations in the two samples were 39.8 and 28.2 $g \cdot L^{-1}$, respectively.
*Growing bacteria were either in the process of dividing or had just divided.

## DISCUSSION

Several factors combine to make subglacial environments viable microbial habitats. Glacier beds are insulated by overlying ice from temperature fluctuations across the freezing point. When mean subglacial temperatures reach the pressure melting point, water is present in subglacial sediments, in the grain-boundary network in basal ice (Nye and Frank, 1973), and in larger subglacial and englacial water pockets. Water acts as a cryoprotector (Gilichinsky et al., 1995) and a source of nutrients and thus provides a favorable microbial habitat. Basal and surface melting replenish these waters, and may supply nutrients, dissolved gases, and particulate material (organic and inorganic) to the subglacial environment, thereby sustaining conditions that allow microbial populations to remain viable. Surface-derived meltwaters may be a source of nitrate and ammonium, especially during spring snow melt, whereas basally derived meltwaters supply potentially limiting nutrients such as Fe and Si. Iron hydroxides, precipitated as a byproduct of sulfide oxidation, may be a source of colloidal Fe. Organic carbon, which provides a substrate for heterotrophic respiration, may be derived from bedrock, soils, or plant material overridden during glacial advance (Röthlisberger and Schneebeli, 1979) and from inwashing from the glacier surface (Table 1). Fine-grained rock flour may provide a favorable substrate for microbial activity. As microorganisms can survive in a viable state for as long as $10^6$ yr at subfreezing temperatures in permafrost (Gilichinsky et al., 1995), thawing of permafrost beneath ice sheets may reactivate microbial populations and allow them to become established in the subglacial environment.

Microbially mediated oxidation of sulfides and organic carbon could be the dominant source of protons that drive chemical weathering beneath glaciers and ice sheets. This possibility is significant because many workers have argued that chemical weathering beneath ice sheets may be limited by the lack of an atmospheric $CO_2$ source (Gibbs and Kump, 1994; Hallet et al., 1996; Kump and Alley, 1994). Microbial mediation of proton-supplying reactions implies that rates of subglacial chemical weathering cannot be predicted from thermodynamic or kinetic considerations alone, since the weathering rates may be strongly affected by microbial population dynamics.

## POSSIBLE IMPLICATIONS

If there are large, active microbial populations at temperate glacier beds, they might play an important role in carbon cycling on glacial-inter-

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glacial time scales. Some $400 \times 10^{15}$ g of carbon (equivalent to ~25% of the world's soil organic carbon pool and >50% of the carbon in the atmosphere) are now stored in soils in areas that were ice covered at the last glacial maximum (Schlesinger, 1991, p. 138). If a similar carbon pool existed in this area during the last interglacial, at least part of it was probably overridden by ice sheets during the last glaciation. The fate of this organic carbon needs to be understood because the mass involved is large enough to reconcile the discrepancy ($150–430 \times 10^{15}$ g of carbon; Crowley, 1995) between estimates of the glacial-interglacial change in terrestrial carbon storage derived from paleovegetation reconstructions and from analyses of $\delta^{13}C$ of oceanic carbon. Estimates based on paleovegetation reconstructions assume that all glacially overridden carbon was released to the atmosphere prior to the last glacial maximum (Adams et al., 1990; Van Campo et al., 1993), whereas those estimates based on oceanic $\delta^{13}C$ suggest that it might not have been. Some of this carbon may have been oxidized or fermented beneath warm-based sectors of Pleistocene ice sheets. $CO_2$ and $CH_4$ produced by these processes may have been dissolved in meltwaters. Alternatively, they may have accumulated in the basal layers of ice sheets (Souchez et al., 1995) or in subglacial sediments, and been released to the atmosphere following deglaciation. In cold-based sectors, however, carbon may simply have been stored beneath the ice sheets and made available for oxidation following deglaciation.

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