

Dissolved gases in frozen basal water from the NGRIP borehole: implications for biogeochemical processes beneath the Greenland Ice Sheet

Brent C. Christner · Galena G. Montross ·
John C. Priscu

Received: 29 January 2012/Revised: 21 April 2012/Accepted: 7 May 2012
© Springer-Verlag 2012

Abstract Little information exists on biogeochemical transformations in aquatic ecosystems beneath polar ice sheets (i.e., water-saturated sediments, streams, rivers, and lakes) and their role in global elemental cycles. Subglacial environments may represent important sources of atmospheric CO₂ and/or CH₄ during deglaciation, thus acting as amplifiers in the climate system. However, the role of subglacial environments in global climate processes has been difficult to assess given the absence of biogeochemical data from the basal zones of inland polar ice sheets. Here, we report on the concentrations of CO₂, CH₄, and H₂ in samples of refrozen basal water recovered at a depth of ~3,042 meters below the surface during the North Greenland Ice Core Project (NGRIP). CH₄ and H₂ concentrations in the NGRIP samples were approximately 60- and 700-fold higher, respectively, relative to air-equilibrated water, whereas CO₂ was ~fivefold lower. Metabolic pathways such as (1) methanogenesis, (2) organic matter fermentation, carboxydrotrophic, and/or methylotrophic activity, and (3) CO₂ fixation provide plausible biotic explanations for the observed CH₄, H₂, and CO₂ concentrations, respectively.

Keywords Ice sheets · Subglacial environments · Greenland · Microbial biogeochemistry · Greenhouse gases

Introduction

Glaciological processes under ice sheets provide habitats for microbial metabolism via the production of liquid water and biogeochemical substrates through basal melting and the chemical weathering of sediments and comminuted bedrock (Skidmore 2011). Metabolic and chemical oxygen consumption in concert with the lack of ventilation would lead to anoxic conditions in subglacial environments (Wadham et al. 2010). Carbon cycling in subglacial systems will be affected by the relative contributions of species possessing autotrophic or heterotrophic metabolisms and the presence of oxygen. Anoxic conditions are compatible with microbial physiologies that use anaerobic respiration (e.g., nitrate, iron, and sulfate reduction or methanogenesis) or fermentation for their catabolism. In particular, methanogenesis has been demonstrated in subglacial sediments from alpine valley glaciers (Boyd et al. 2010) and may be significant beneath polar ice sheets (Wadham et al. 2008; Stibal et al. in press). Given the vast expanse of Earth's polar ice sheets and the rapid changes they are undergoing as climate warms (NRC 2011), an understanding of subglacial microbial processes is critical for accurately predicting the global ecosystem responses as climate fluctuates (Priscu et al. 2008).

Studies of glacial and basal ice from the Greenland Ice Sheet (GIS) indicate the presence of viable and novel bacteria (e.g., Miteva et al. 2004, 2009; Yde et al. 2010). Several studies have provided geochemical and isotopic evidence for a biogenic origin of the CH₄ in GISP2 basal ice and suggested that the excessively high CO₂ and CH₄

B. C. Christner (✉)
Department of Biological Sciences, Louisiana State University,
Baton Rouge, LA 70803, USA
e-mail: xner@lsu.edu

G. G. Montross · J. C. Priscu
Department of Land Resources and Environmental Science,
Montana State University, Bozeman, MT 59717, USA

Present Address:
G. G. Montross
Department of Geography, Queen's University,
Kingston, ON K7L 1N6, Canada

values were due to in situ microbial production by microorganisms within the basal ice (Tung et al. 2005; Miteva et al. 2006; Rohde et al. 2008). Pink-to-orange-colored basal water was encountered in 2003 by the North Greenland Ice Core Project (NGRIP) during basal drilling when sediment-laden subglacial water entered the borehole and raised the fluid level 45 m (Andersen et al. 2004). During the 2004 field season, portions of the 45-m long column of the frozen basal water (Fig. 1) were collected by the NGRIP consortium and cores were made available to various investigators for study. We examined samples from a section of this ice core and provide here a description of the physical, chemical, and biological parameters derived from analysis of the NGRIP basal water.

Methods

The NGRIP site (75.1°N, 42.3°W) is located near the Greenland ice divide at an elevation of 2,930 m above sea level. Although radar profiles provided no evidence for basal water at NGRIP, measurements of the borehole temperature during drilling operations indicated that the basal geothermal heat flow was higher than anticipated and the base was at or near the pressure melting point (Andersen et al. 2004; Buchardt and Dahl-Jensen 2007). When the drill reached bedrock at a depth of 3,085 m on 17 July 2003, basal water entered the deepest 45 m of the borehole and “approximately 10 kg of reddish, bubbly frozen basal water” was recovered on the surface of the drill (Dahl-Jensen et al. 2003). An ice core of the frozen basal water recovered during drilling in 2004 at a depth of ~3,042 mbs (core designation ‘NGRIP BC-2004 Main bag, Bag# 10’) was sampled to document variation of

chemical and biological analytes within different portions of the ice (Fig. 1). Chemical and biological contamination on surfaces of the ice core samples was removed using protocols demonstrated effective in eliminating cells, nucleic acids, and hydrocarbon-based drilling fluids from ice core exteriors (Christner et al. 2005). The concentration of SYBR Gold™ (Molecular Probes, Inc.)—stained cells and major inorganic ions were determined as described by Christner et al. (2006). Meltwater pH was estimated using EMD colorpHast* pH strips (pH range 4–7).

Nuclear magnetic resonance (NMR) spectroscopy (Bruker DRX500 NMR spectrometer) was used to determine the concentration and composition of hydrocarbons present at a proton frequency of 500.13 MHz. Each sample (0.5 mL) was amended with 0.05 mL of D₂O, and proton spectra were collected using a 1 s presaturation pulse for water signal suppression. Scanning electron microscopy (SEM) and energy-dispersive spectrometry (EDS) were performed as described by Christner et al. (2006).

Samples of the ice were melted (33 mL water equivalent) in sealed glass serum bottles (71 mL capacity) capped with butyl rubber septa, the bottles were shaken for at least 1 h to facilitate the equilibration of dissolved gas species with the air-filled headspace, and the concentrations of CO₂, CH₄, and H₂ in the headspace were quantified using gas chromatography (GC). For each measurement, 1.5 mL of the headspace gas was collected using an air-tight syringe and injected into a Varian CP 4900 gas chromatograph (Varian, Palo Alto, CA, USA). All gas species were analyzed using a thermal conductivity detector, CH₄ and CO₂ were analyzed with helium as the carrier gas and a molecular sieve separator, and H₂ was analyzed using ultra-high purity argon as the carrier gas and a Poraplot-Q column (Varian). The detection limits for CO₂, CH₄, and

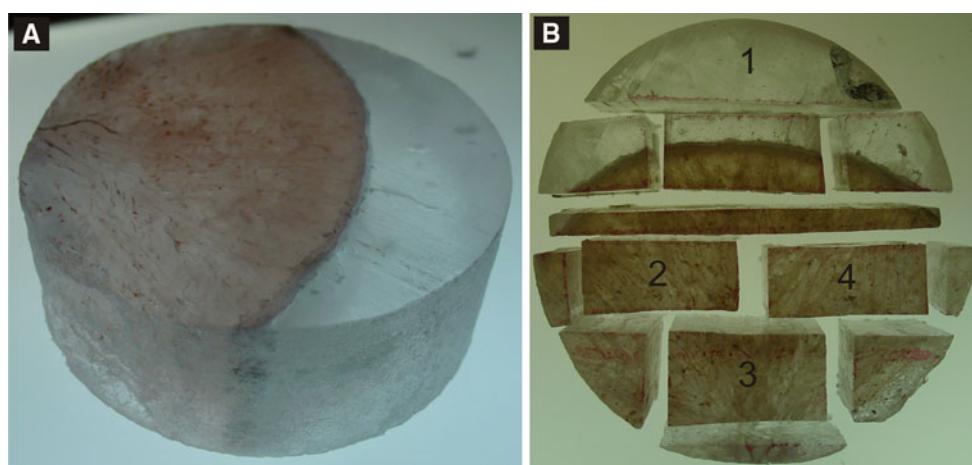


Fig. 1 **a** Cross-sectional sample of the NGRIP ice core showing the frozen, orange-colored basal water and the half-moon shaped portion of relatively clear Eemian-age meteoric ice. **b** Cut plan strategy used to analyze the biological and chemical components found in horizons of

the recovered NGRIP samples. The cut samples shown were used for determining the cell concentration (1 and 3), SEM (1 and 4), and NMR (1–4). The ice samples used for the gas analysis were sampled using a similar cut strategy. The core diameter was 9.7 cm (color figure online)

H₂ were 2, 1, and 0.8 ppmv, respectively. Dissolved gas concentrations in the melted ice samples were determined using a mass balance approach and the temperature-dependent Henry's Law constant to define the proportion of gas species between headspace and liquid, expressed as follows: $C_{\text{total}}V_{\text{total}} = C_HV_H + C_LV_L$; where C_{total} is the sum of headspace and dissolved aqueous gas concentrations, V is the volume, and H and L subscripts designate either the gas concentration or volume associated with the headspace and liquid, respectively.

Results and discussion

Annual layers at depths >2,900 m in the NGRIP ice core are ~1 cm thick, which is in contrast to the much thinner annual layers typically observed near the bed of cold-based glaciers or in the GRIP core (Andersen et al. 2004). The excellent resolution observed in deep horizons of the NGRIP record is attributed to the continual melting of ice from the base, which reduces flow-induced disturbances that thin annual layers due to plastic deformation (Paterson 1994). Estimates of the melt rate and geothermal heat flow at NGRIP are 6.1 mm year⁻¹ and 129 mW m⁻² (Buchardt and Dahl-Jensen 2007), respectively, which are values higher than those estimated for the ~4-km deep subglacial environment at Vostok Station, Antarctica (4 mm year⁻¹ and 46 mW m⁻²; Siegert et al. 2001) and Greenland's continental background (57 mW m⁻²; Fahnestock et al. 2001). The presence of basal water beneath the ice sheet at NGRIP and NEEM (http://neem.dk/field_diaries_folder/uk_diaries_2011/2011-07-08/) has confirmed that wet-based conditions exist at certain locations at the bed and suggests liquid water may be more prevalent beneath the GIS than previously thought. Little is known about the subglacial environment beneath the GIS, but the presence of subglacial water beneath the NGRIP borehole implies that either melting is occurring beneath portions of the GIS or that there is ponding of water derived from moulin's. The frozen basal material recovered at NGRIP has provided the first opportunity to explore the range of microbial biogeochemical reactions that may be occurring beneath the GIS.

The concentration of major ions (i.e., Ca²⁺, Mg²⁺, K⁺, Na⁺, SO₄²⁻, Cl⁻, and HCO₃⁻), sampled in bulk from a single horizon of the NGRIP basal ice core, was ~30 times higher than that found in the adjacent glacial ice ($\sum_{\text{ions}} 465$ and 14.5 $\mu\text{eq L}^{-1}$, respectively; Table 1; Royston-Bishop 2006). Solute partitioning into the liquid phase during freezing would be expected as a concentrating mechanism; however, with the bulk sampling technique used, the samples were effectively homogenized. If freezing occurred from the top of the water column down and from

Table 1 Biogeochemical data obtained from the NGRIP refrozen water recovered at ~3,042 m

Constituent	Results obtained
Cell concentration (cells mL ⁻¹)	1.6 ± 0.38 × 10 ³
SEM-EDS	K-feldspar and biotite minerals with iron oxide coatings; particles observed were 1–5 μm in diameter and composed of siliceous minerals
Gas chromatography (nmol L ⁻¹)	
CH ₄	70–79
H ₂	200–550
CO ₂	1,000–4,100
pH	5.0–5.3
NMR	Ethanol, ethylene glycol, and aromatic and other hydrocarbons present
Major ions (mg L ⁻¹) ^a	
Na ⁺	1.1
K ⁺	0.44
Mg ²⁺	0.23
Ca ²⁺	3.1
Cl ⁻	0.070
NO ₃ ⁻	0.021
SO ₄ ²⁻	0.073

^a Data from Royston-Bishop (2006)

the outside to the inside of the borehole, the highest concentration of salts and microbial cells would be expected in the middle and deepest portion of the core. As such, the horizontal concentration of ions and cells would not follow typical freeze back patterns. Nevertheless, the lower concentration of Cl⁻ observed in the NGRIP basal water (1.99 $\mu\text{eq L}^{-1}$) compared to the glacial ice (2.75 $\mu\text{eq L}^{-1}$) does not support basal freezing as a process responsible for solute concentration. Therefore, the additional solutes observed in the NGRIP basal water are likely to have a crustal provenance (Royston-Bishop 2006). This interpretation of the major ion geochemistry agrees with geophysical data supporting melting as the overriding phase change process at the ice sheet bed (Buchardt and Dahl-Jensen 2007). Macroscopic particles were present in the NGRIP refrozen water imparting an orange color to the ice (Fig. 1), and visually, the material appeared similar to the iron oxide deposits formed in the subglacial outflow of Blood Falls (Taylor Glacier, Antarctica; Mikucki et al. 2009). Indeed, much of the orange material in the NGRIP basal water was acid soluble, and SEM-EDS analysis indicated the presence of K-feldspar and biotite minerals with iron oxide coatings. Most of the particles observed in the NGRIP basal water were 1–5 μm in diameter and composed of primary rock forming siliceous minerals, consistent with expectations for a subglacial till (Fig. 2).

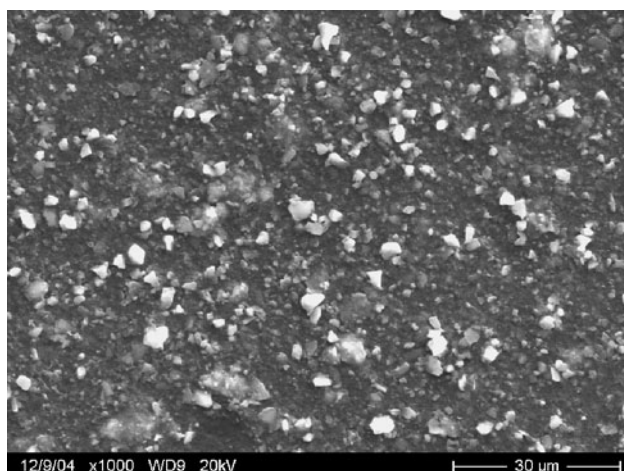


Fig. 2 Scanning electron microscopy (SEM) of particles present in samples of the frozen NGRIP basal water recovered at a depth of $\sim 3,042$ mbs. The image was obtained by cryogenic SEM (JEOL-6100 SEM with an Oxford instruments cryogenic preparation stage) on particles captured by $0.2 \mu\text{m}$ filtration of melted ice

Surface decontaminated samples of the NGRIP refrozen basal water recovered at 3,042 m contained $1.6 \pm 0.38 \times 10^3$ DNA-containing cells mL^{-1} of melt water (mean \pm SD), which was tenfold higher than that observed in an adjacent horizon of the Eemian glacial ice (Fig. 1; $1.6 \pm 0.19 \times 10^2$ cells mL^{-1} , Table 1). Bulat et al. (2005) reported the successful amplification of bacterial 16S rRNA gene sequences from DNA extracted from the refrozen NGRIP water recovered at depths of 3,039 m and 3,045 m, but they were only able to amplify archaeal 16S rRNA from the former depth and did not quantify the total number of cells in their samples. These authors also reported that the ice samples from 3,039 m appeared to have more ‘reddish’ sediment and mixed heavily with the drilling fluid, compared with the sample analyzed from 3,045 m, which was composed of a cleaner ice containing sediment inclusions. Based on these observations and the vigorous manner in which the basal water entered the borehole, it is possible that microbial cells present in the drilling fluid may have contaminated the basal water before freezing. The drilling fluid at NGRIP is 67% Exxsol D60 and 33% Frigen 141B (densifier) but also contains traces of Solkane 123, n-butyl acetate, Frigen 113, Invarol (aviation lubricant), ethylene glycol, and ethanol (J. P. Steffensen, pers. comm.). These fluids were not sterilized or filtered previous to use, and it has been shown that hydrocarbon-based ice core drilling fluids contain significant quantities of microbial cells (Christner et al. 2005; Alekhina et al. 2007).

NMR was used to determine whether hydrocarbons and other compounds in the drilling fluid were incorporated into the basal water before freezing. Our analyses revealed that known components of the drilling fluid were present in

the interior portions of all the basal samples examined (Table 1). While NMR is not an analytical approach ideally suited for the high-precision quantification of hydrocarbons and other compounds, signals obtained in the resonance regions for ethanol were strong enough to estimate its concentration in some samples of the NGRIP basal material at concentrations as high as $\sim 0.02 \text{ mol L}^{-1}$ (~ 900 ppm). These results indicated that the unfrozen basal water had mixed with the drilling fluid during entry of the water into the borehole before freezing. Based on the extent of drilling fluid contamination and its potential to contain microbial cells, we were unable to produce unequivocal data on the microbiological properties of the NGRIP basal material. Since the drilling fluid is hydrophobic and the ions are polar, salts would not dissolve in the drilling fluid. However, if the water and drilling fluid were an emulsion and the ions were excluded from the hydrophobic drilling fluid, then their concentrations in the basal water would be underestimated because the volume containing ions would be lower than the bulk volume. This would not be the case for gases, which are soluble in the drilling fluid.

Visual observation of the approximately 10 kg of sediment-laden frozen water recovered in the drill’s inner core barrel during drilling in 2003 revealed that the ice retrieved was unconsolidated, indicating possible degassing of the water as the core was brought to the surface. The composition of gases that were present the drilling fluid was not measured and is assumed here to have been atmospheric in origin and composition. An expected source of gases beneath NGRIP is basal melting, which continually introduces water and ice-entrapped atmospheric gases that became captured during bubble close-off in the metamorphosis of firn to glacial ice. Hence, analysis of the gases entrapped in the refrozen subglacial water provided a means to investigate the range of biogeochemical reactions that may be occurring beneath the GIS. Based on analysis of 4 samples from a single horizon of the recovered NGRIP basal profile, the dissolved concentration of CH_4 , H_2 , and CO_2 ranged between 70–79, 200–550, and 1,000–4,100 nmol L^{-1} , respectively (Table 1). Owing to gas exclusion during freezing of the water in the borehole, the gas content at a particular depth or portion of the core will not precisely reflect the actual subglacial water gas content, as revealed by the variation observed in the concentrations of gases in samples from different sections of the same horizon. When the gas data for the NGRIP basal water are compared to predictions for air-equilibrated freshwater at 25°C and 1 atm, the CH_4 and H_2 concentrations were approximately 60- and 700-fold higher, respectively, whereas the CO_2 concentration was approximately fivefold lower (Fig. 3). The pH of the melt water ranged from 5.0 to 5.3 (Table 1), which is similar to values observed in samples of the

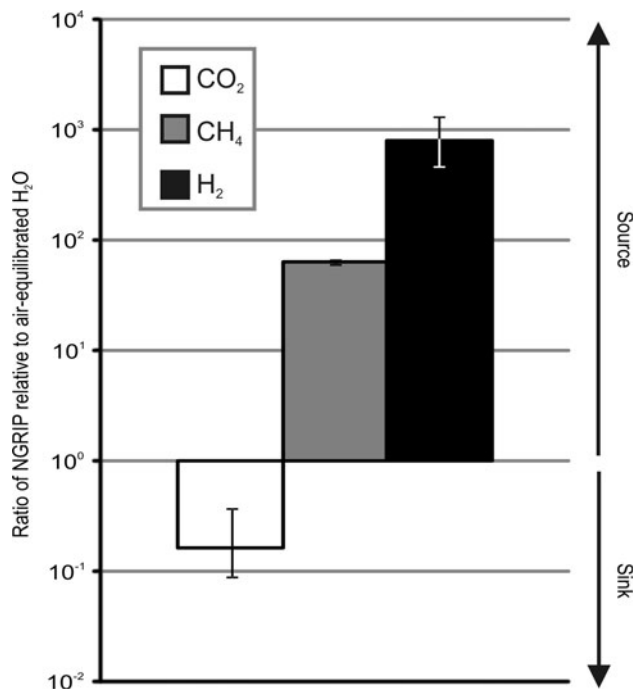


Fig. 3 The average ratio of dissolved CO₂, CH₄, and H₂ in frozen NGRIP basal water relative to air-equilibrated water. Measurements and calculations were as described in the text and based on the ideal behavior of gases at 298 K and 1 atm. Bars indicate ratio values based on the minimum and maximum concentration of gases observed in the NGRIP samples

accreted ice from Subglacial Lake Vostok (pH 5.2–5.8; Royston-Bishop 2006). It is important to note that acidic conditions would be expected to enhance carbonate dissolution and other chemical reactions that produce CO₂. Thus, the initial dissolved CO₂ concentration in the NGRIP basal water was probably lower than that determined by our wet extraction technique. As such, our measurements essentially represent the total dissolved inorganic carbon concentration in the basal water.

While there are caveats in using the refrozen NGRIP ice core samples to infer the composition and concentration of gases present in the basal water, our data imply that the

subglacial environment beneath NGRIP is a source for CH₄ and H₂, and a sink for CO₂ (Fig. 3). Potential sources and sinks for CO₂, CH₄, and H₂ in the subglacial system are summarized in Table 2. Methane and H₂ are produced abiotically in hydrothermal systems and physical processes in cold debris-laden ice may concentrate and redistribute atmospheric gases during basal freezing (i.e., Samyn et al. 2005). Currently, there is no evidence for active hydrothermal systems beneath the GIS, and the geothermal heat flow at NGRIP indicates net losses of basal ice due to melting (Buchardt and Dahl-Jensen 2007). Serpentinization of ultramafic rocks in subsurface environments beneath the oceans and in continental crust produces H₂, CH₄, and a variety of other low molecular weight hydrocarbons (Sleep et al. 2004). It is currently not known whether the geological conditions beneath the GIS are appropriate for serpentinization to occur in groundwater systems, but this process could supply reducing agents to support a subsurface microbial community, as has been observed in oceanic crust environments (Mason et al. 2010; Schrenk et al. 2010). An alternative cause of the elevated CH₄ and H₂ concentrations in the NGRIP basal water can be explained by microbial activity, with CH₄ being produced by methanogenesis and H₂ as a product of organic matter fermentation, carboxydrotrophic, and/or methylotrophic activity. If the bedrock is comprised of calcite-containing limestone and/or there are alkaline conditions (e.g., a serpentinizing system), carbonate precipitation is a plausible abiotic sink for CO₂; however, these scenarios are not compatible with the slightly acidic pH of the basal water (Table 1). Biotic sinks for CO₂ include its methanogenic reduction to CH₄ and consumption by autotrophic pathways (i.e., CO₂ fixation). A key point about CO₂ fixation is that in the absence of sunlight, chemolithoautotrophic activity would be ecologically important for the production of organic carbon beneath the ice sheet. Chemolithotrophically produced organic carbon could also be advected to downstream environments and drive heterotrophic biogeochemical processes in oxic ice-marginal and marine settings.

Table 2 Potential sources and sinks for CO₂, CH₄, and H₂ in the subsurface beneath the GIS

Gas	Biotic		Abiotic	
	Sources	Sinks	Sources	Sinks
CO ₂	Respiration and fermentation	<i>Autotrophy and as an e-acceptor^b</i>	Carbonate dissolution	<i>Carbonate precipitation; freeze concentration^a</i>
CH ₄	<i>Methanogenesis</i>	Methanotrophy	<i>Hydrothermal; serpentinization</i>	Freeze concentration ^a
H ₂	<i>Fermentation, methylotrophy, and carboxydrotrophy</i>	Lithotrophy	<i>Hydrothermal; serpentinization; freeze concentration^a</i>	?

Italics denote processes required to produce the gas data observed in Fig. 3

^a Following the arguments of Samyn et al. (2005) for selective gas redistribution in cold debris-laden ice

^b i.e., in H₂-based methanogenesis

Microorganisms inhabiting water and sediments at the bed of glaciers and ice sheets are thought to represent a globally significant reservoir of biomass and biological diversity (Christner et al. 2008; Priscu et al. 2008; Lanoil et al. 2009). The biogeochemical activities of subglacial microbial communities are known to drive chemical weathering and influence meltwater chemistry (Sharp et al. 1999; Skidmore et al. 2005; Mikucki et al. 2009). Recent work has also shown that solute fluxes from beneath ice sheets rival those of the largest rivers (Wadham et al. 2010) and microbially-derived dissolved organic matter and iron from glacial systems can positively influence marine productivity (Statham et al. 2008; Hood et al. 2009). While there are no other biogeochemical datasets from inland polar ice sheets with which to compare our results, the metabolic activities we have inferred are consistent with those predicted for other sub-ice sheet environments (Siegert et al. 2001; Wadham et al. 2010). Our analysis of the NGRIP basal water indicates that biogeochemical cycling of carbon and other elements occurs beneath the GIS and supports the notion that microbiological processes beneath Pleistocene mid-latitude ice sheets could act as climate amplifiers during periods of deglaciation (e.g., Wadham et al. 2008). Based on our results, we contend that microbial transformations beneath the Earth's polar ice sheets have a significant role in global biogeochemical cycles, which can influence atmospheric greenhouse gases.

Acknowledgments The ice cores in this study were recovered during the NGRIP ice core project, which was directed by the Ice and Climate Research Group at the Niels Bohr Institute, University of Copenhagen and funded by agencies in Denmark (FNU), Belgium (FNRS-CFB), France (IPEV and INSU/CNRS), Germany (AWI), Iceland (RannIs), Japan (MEXT), Sweden (SPRS), Switzerland (SNF), and the USA (NSF, Office of Polar Programs). We especially acknowledge NGRIP project leader Dorthe Dahl-Jensen for organizing the NGRIP basal ice working group and providing ice core samples for analysis. We also thank D. Mogk and M. Skidmore for assistance with SEM-EDS, S. Busse for assistance with the NMR measurements and interpretation, and G. King for discussion. Travel funding for Brent C. Christner to visit the University of Copenhagen was provided by the Arctic Natural Sciences Program of the NSF. This study was partially supported by NSF grants OPP-0636828, OPP-0838941, and OPP-1023233 awarded to Brent C. Christner, and OPP-0838933, OPP-0839075, OPP-1027284 and NASA NAI5-0021 awarded to John C. Priscu.

References

- Alekhina IA, Marie D, Petit JR, Lukin VV, Zubkov VM, Bulat SA (2007) Molecular analysis of bacterial diversity in kerosene-based drilling fluid from the deep ice borehole at Vostok, East Antarctica. *FEMS Microbiol Ecol* 59:289–299
- Andersen KK et al (2004) High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* 431:47–51
- Boyd ES, Skidmore M, Bakermans C, Mitchell A, Peters JW (2010) Methanogenesis in subglacial sediments. *Environ Microbiol Rep* 2:685–692
- Buchardt SL, Dahl-Jensen D (2007) Estimating the basal melt rate at NorthGRIP using a Monte Carlo technique. *Ann Glaciol* 45:137–142
- Bulat S, Alekhina I, Petit J-R, Steffensen JP, Dahl-Jensen D (2005) Bacteria and archaea under Greenland Ice Sheet: NGRIP 'red' ice issue. *Geophys Res Abstr* 7:05298
- Christner BC, Mikucki JA, Foreman CM, Denson J, Priscu JC (2005) Glacial ice cores: a model system for developing extraterrestrial decontamination protocols. *Icarus* 174:572–584
- Christner BC, Royston-Bishop G, Foreman CF, Arnold BR, Tranter M, Welch KA, Lyons WB, Tsapin AI, Studinger M, Priscu JC (2006) Limnological conditions in Subglacial Lake Vostok, Antarctica. *Limnol Oceanogr* 51:2485–2501
- Christner BC, Skidmore ML, Priscu JC, Tranter M, Foreman CM (2008) Bacteria in subglacial environments. In: Margesin R, Schinner F, Marx J-C, Gerday C (eds) *Psychrophiles: from biodiversity to biotechnology*. Springer, New York, pp 51–71
- Dahl-Jensen D, Johnsen S, Willerslev E, Miller H, Thorsteinsson T (2003) Basal water at the NorthGRIP drill site. In: Third mars polar science conference, 13–17 October 2003, Alberta, Canada
- Fahnestock M, Abdalati W, Joughin I, Brozena J, Gogineni P (2001) High geothermal heat flow, basal melt, and the origin of rapid ice flow in central Greenland. *Science* 294:2338–2342
- Hood E, Fellman J, Spencer RGM, Hernes PJ, Edwards R, D'Amore D, Scott D (2009) Glaciers as a source of ancient and labile organic matter to the marine environment. *Nature* 462:1044–1047
- Lanoil B, Skidmore M, Priscu JC, Han S, Foo W, Vogel SW, Tulaczyk S, Engelhardt H (2009) Bacteria beneath the West Antarctic Ice Sheet. *Environ Microbiol* 11:609–615
- Mason OU, Nakagawa T, Rosner M, Van Nostrand JD, Zhou J et al (2010) First investigation of the microbiology of the deepest layer of ocean crust. *PLoS ONE* 5:e15399. doi: 10.1371/journal.pone.0015399
- Mikucki JA, Pearson A, Johnston DT, Turchyn AV, Farquhar J, Schrag DP, Anbar AD, Priscu JC, Lee PA (2009) A contemporary microbial maintained subglacial ferrous "ocean". *Science* 324:397–400
- Miteva VI, Sheridan PP, Brenchley JB (2004) Phylogenetic and physiological diversity of microorganisms isolated from a deep Greenland ice core. *Appl Environ Microbiol* 70:202–213
- Miteva V, Sowers T, Olsen C, Brenchley J (2006) Geochemical and molecular data support a biogenic origin of methane in the basal Greenland ice. *ISME 11 Vienna, Austria* A371
- Miteva V, Teacher C, Sowers T, Brenchley J (2009) Comparison of the microbial diversity at different depths of the GISP2 Greenland ice core in relationship to deposition climates. *Environ Microbiol* 11:640–656
- National Research Council (2011) *Frontiers in understanding climate change and polar ecosystems*. National Academies Press, Washington, DC
- Paterson WSB (1994) *The physics of glaciers*. Butterworth-Heinemann, Oxford
- Priscu JC, Tulaczyk S, Studinger M, Kennicutt MC II, Christner BC, Foreman CM (2008) Antarctic subglacial water: origin, evolution and ecology. In: Vincent W, Laybourn-Parry J (eds) *Polar lakes and rivers*. Oxford University Press, Oxford, pp 119–135
- Rohde RA, Price PB, Bay RC, Bramall NE (2008) In situ microbial metabolism as a cause of gas anomalies in ice. *Proc Natl Acad Sci USA* 105:8672–8687
- Royston-Bishop GW (2006) *The hydrochemistry of Subglacial Lake Vostok, Antarctica*. Dissertation, Bristol Glaciology Centre, University of Bristol

- Samyn D, Fitzsimons S, Lorrain R (2005) Strain induced changes within cold basal ice from Taylor Glacier (Antarctica) as indicated by gas and microstructural analyses. *J Glaciol* 51:611–619
- Sharp M, Parkes J, Cragg B, Fairchild IJ, Lamb H, Tranter M (1999) Widespread bacterial populations at glacier beds and their relationship to rock weathering and carbon cycling. *Geology* 27:107–110
- Schrenk MO, Huber JA, Edwards KJ (2010) Microbial provinces in the subseafloor. *Annu Rev Mar Sci* 2:279–304
- Siegert MJ, Ellis-Evans JC, Tranter M, Mayer C, Petit J-R, Salamatin A, Prisco JC (2001) Physical, chemical and biological processes in Lake Vostok and other Antarctic subglacial lakes. *Nature* 414:603–609
- Skidmore M (2011) Microbial communities in Antarctic subglacial aquatic environments. In: Siegert MJ, Bindschadler R, Kennicutt MC (eds) *Exploration and study of Antarctic subglacial aquatic environments*. AGU Press, Washington, DC, pp 61–82
- Skidmore M, Anderson SP, Sharp M, Foght J, Lanoil BD (2005) Comparison of microbial community compositions of two subglacial environments reveals a possible role for microbes in chemical weathering processes. *Appl Environ Microbiol* 71:6986–6997
- Sleep NH, Meibom A, Fridriksson T, Coleman RG, Bird DK (2004) H₂-rich fluids from serpentinization: geochemical and biotic implications. *Proc Natl Acad Sci USA* 101:12818–12823
- Statham PJ, Skidmore ML, Tranter M (2008) Inputs of glacially derived dissolved and colloidal iron to the coastal ocean and implications for primary productivity. *Glob Biogeochem Cycle* 22:GB3013. doi:10.1029/2007GB003106
- Stibal M, Wadham JL et al (in press) Methanogenic potential of Arctic and Antarctic subglacial environments with contrasting organic carbon sources. *Glob Chang Biol*
- Tung HC, Bramall NE, Price BP (2005) Microbial origin of excess of methane in glacial ice and implications for life on Mars. *Proc Natl Acad Sci USA* 102:18292–18296
- Wadham JL, Tranter M, Tulaczyk S, Sharp M (2008) Subglacial methanogenesis: a potential climatic amplifier? *Glob Biogeochem Cycle* 22:1–16
- Wadham JL, Tranter M, Skidmore M, Hodson AJ, Prisco JC, Lyons WB, Sharp M, Wynn P, Jackson M (2010) Biogeochemical weathering under ice: size matters. *Glob Biogeochem Cycle* 24:GB3025. doi:10.1029/2009GB003688
- Yde JC, Finster KW, Raiswell R, Steffensen JP, Heinemeier J, Osen J, Gunnlaugsson HP, Nielsen OB (2010) Basal ice microbiology at the margin of the Greenland Ice Sheet. *Ann Glaciol* 51:71–79