Environmental Microbiology (2008) **10**(8), 2172–2178 doi:10.1111/j.1462-2920.2008.01620.x

Brief report

Microbial primary production on an Arctic glacier is insignificant in comparison with allochthonous organic carbon input

Marek Stibal,[1]* Martyn Tranter,[1] Liane G. Benning[2] and Josef Řehák[3]
[1]*Bristol Glaciology Centre, School of Geographical Sciences, University of Bristol, Bristol BS8 1SS, UK.*
[2]*Earth and Biosphere Institute, School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK.*
[3]*Speleo-Řehák, Semily, 513 01, Czech Republic.*

Summary

Cryoconite holes are unique freshwater environments on glacier surfaces, formed when solar-heated dark debris melts down into the ice. Active photoautotrophic microorganisms are abundant within the holes and fix inorganic carbon due to the availability of liquid water and solar radiation. Cryoconite holes are potentially important sources of organic carbon to the glacial ecosystem, but the relative magnitudes of autochthonous microbial primary production and wind-borne allochthonous organic matter brought are unknown. Here, we compare an estimate of annual microbial primary production in 2006 on Werenskioldbreen, a Svalbard glacier, with the organic carbon content of cryoconite debris. There is a great disparity between annual primary production (4.3 μg C g^{-1} $year^{-1}$) and the high content of organic carbon within the debris (1.7–4.5%, equivalent to 8500–22 000 μg C g^{-1} debris). Long-term accumulation of autochthonous organic matter is considered unlikely due to ablation dynamics and the surface hydrology of the glacier. Rather, it is more likely that the majority of the organic matter on Werenskioldbreen is allochthonous. Hence, although glacier surfaces can be a significant source of organic carbon for glacial environments on Svalbard, they may be reservoirs rather than oases of high productivity.

Received 17 September, 2007; accepted 27 February, 2008. *For correspondence. E-mail marek.stibal@bristol.ac.uk; Tel. +44 (0) 117 331 7313; Fax +44 (0) 117 928 7878.

Introduction

Glaciers and ice sheets cover approximately 10% of the Earth's land surface (Benn and Evans, 1998). They are now known to be highly dynamic systems whose physical and chemical conditions support thriving microbial communities (Hodson *et al*., 2008). Liquid water, essential for virtually all biological processes (Kennedy, 1993), is readily available on the surface of Arctic glaciers for several weeks to months each summer. Simultaneously, dark-coloured, mostly wind-borne debris deposited on glacier surfaces (cryoconite, i.e. 'ice dust') melts down into the ice when heated by solar radiation, creating small vertical, water-filled depressions called cryoconite holes (Wharton *et al*., 1985). The debris is a mixture of inorganic and organic particulates, including microbial propagules (Takeuchi *et al*., 2001), which provides the inoculum, substrate and some of the nutrient necessary for microbial growth and activity. The vast majority of active microbial life on glacier surfaces is contained within these unique freshwater environments (Stibal *et al*., 2006; Hodson *et al*., 2008). Water in cryoconite holes is recharged from upstream and drains down glacier, so transporting these constituents progressively down glacier.

It is not surprising that photoautotrophic microorganisms – cyanobacteria and microalgae – inhabit cryoconite holes on Svalbard glaciers (e.g. Säwström *et al*., 2002; Kaštovská *et al*., 2005), given the availability of solar radiation on glacier surfaces. Cyanobacteria dominate the phototrophic component of cryoconite hole communities (Stibal *et al*., 2006), consistent with the cyanobacterial dominance of most non-marine low-temperature environments on Earth and attributed to their relative simplicity and high resilience to environmental stresses (Vincent, 2000; Šabacká and Elster, 2006). It has been shown that cyanobacteria and other phototrophs in cryoconite holes have relatively slow rates of photosynthesis (Säwström *et al*., 2002; Stibal and Tranter, 2007). However, they are widely tolerant to the low ambient temperature and to pH perturbations connected to freezing events, during which cryoconite holes become isolated from the atmosphere by

ice lids (Tranter *et al*., 2004; Stibal and Tranter, 2007). Thus, photoautotrophs in cryoconite holes have the potential to serve as the base of glacial foodwebs and may represent an important source of carbon for the entire glacial ecosystem (Hodson *et al*., 2005; Mindl *et al*., 2007). Organic carbon in cryoconite debris is typically ~2–4% of dry weight (Takeuchi *et al*., 2001; Takeuchi, 2002; Stibal *et al*., 2006), and may be derived from both local (autochthonous) and distant (allochthonous) sources, as a component of the wind-borne debris. A comparison of the relative magnitudes of these sources has yet to be made. This comparison is of importance because if allochthonous sources dominate over autochthonous production, the glacier surface is a passive collector and reservoir of organic matter, rather than an oasis of productivity.

We conducted *in situ* primary production measurements in the summer of 2006 on Werenskioldbreen, a Svalbard glacier with a long and extensive research history (Řehák *et al*., 1990; 2007; Stibal *et al*., 2006; Kaštovská *et al*., 2007). These measurements were linked to hydrological and meteorological observations to gain an appreciation of the controls on primary production. Finally, the rate of microbial primary production in cryoconite holes was compared with the total organic carbon content of the debris in order to quantify the relative magnitude of autochthonous and allochthonous components.

Results and discussion

The first cryoconite holes on the surface of Werenskioldbreen appeared shortly after the beginning of ablation during the second week of July, when the surface was still mostly covered in snow. They melted out from beneath the snow, which suggests that the debris contained within them had accumulated on the glacier surface before it received the winter snow cover, either in autumn or as a relict of previous seasons. Debris was rapidly flushed from these shallow cryoconite holes by supraglacial meltwater, and new holes developed where the debris was entrapped by topographical barriers. Approximately 75% of supraglacial water was routed via moulins and crevasses to the glacier bed (Řehák *et al*., 2007), and a significant proportion of the debris was transported to the bed as a consequence.

The area of the ablation zone of Werenskioldbreen is ~19 km^2 (~70% of the glacier), as determined from field observations, the equilibrium line altitude in 2005 and 2006 (Řehák *et al*., 2007) and an ortophotographic map from 1990. The mean coverage of cryoconite holes in the ablation area was ~1.5% of the surface, and the wet weight of cryoconite debris was 12 ($\pm$ 21) g m^{-2}, as determined from measurements within random 1 m^2 sampling grids ($n = 50$) towards the end of the ablation season (4 August). Hence, cryoconite holes occupied an area of approximately 0.29 km^2 at the end of the season, and contained ~230 000 ($\pm$ 400 000) kg of debris. The great variation in the amount of debris per unit area is a result of the variable topography of the glacier surface. The absolute value of the total amount of debris must therefore be treated with caution, and may be underestimated.

The mineralogy of the debris is dominated by common silicates (quartz, chlorite, muscovite, albite and amphiboles), as determined by X-ray diffraction. Amorphous material was also present (Fig. 1). The total, inorganic and organic carbon content of the debris was determined by elemental analysis. Organic carbon (> 95%) dominates inorganic carbon, and was present in concentrations of 1.7–4.5% (dry weight). Direct observations and determinations of the elemental composition of three samples of cryoconite debris with SEM/EDS showed that organic carbon was almost exclusively associated with microbial cells and/or amorphous organic matter (Fig. 1, pie charts). The change in the organic and inorganic carbon content of the debris over the course of the season is shown in Fig. 2. Figure 2B shows a statistically significant decrease ($P < 0.01$) in the content of total carbon of ~70% during the season, without any significant change in the ratio of organic and inorganic carbon (Fig. 2A). This suggests that organic carbon was being removed from the cryoconite debris over time, and that the removal was more likely to be non-selective and physical (i.e. flushing) rather than biological (i.e. respiration).

The electrical conductivity (EC), a proxy of solute content, of supraglacial channel water was 6.1 $\pm$ 1.5 $\mu S\ cm^{-1}$ and did not show any significant trends throughout the season. In contrast, there was a significant decrease ($P < 0.001$; Pearson's correlation coefficient $r = 0.79$) in the EC of waters within cryoconite holes over the course of the season, from ~9 $\mu S\ cm^{-1}$ at the onset of ablation to values between 3 and 5 $\mu S\ cm^{-1}$ in the second half of the ablation season. This decrease can be explained by their constant flushing with supraglacial melt, which effectively removes solute derived from dissolution of cryoconite debris. Mean pH values and concentrations of dissolved carbon, nitrogen and phosphorus in surface waters on Werenskioldbreen and in its run-off can be seen in Table 1. The pH of waters in cryoconite holes was significantly higher than that of supraglacial channel water, consistent with active photosynthesis increasing the ambient pH (Tranter *et al*., 2004; Stibal and Tranter, 2007). No significant differences in nutrient concentrations between supraglacial and cryoconite waters were found, consistent with their intimate connectivity. Most of the dissolved carbon and nitrogen was present in their organic forms. The similarity between supraglacial waters and glacier run-off suggests that most organic

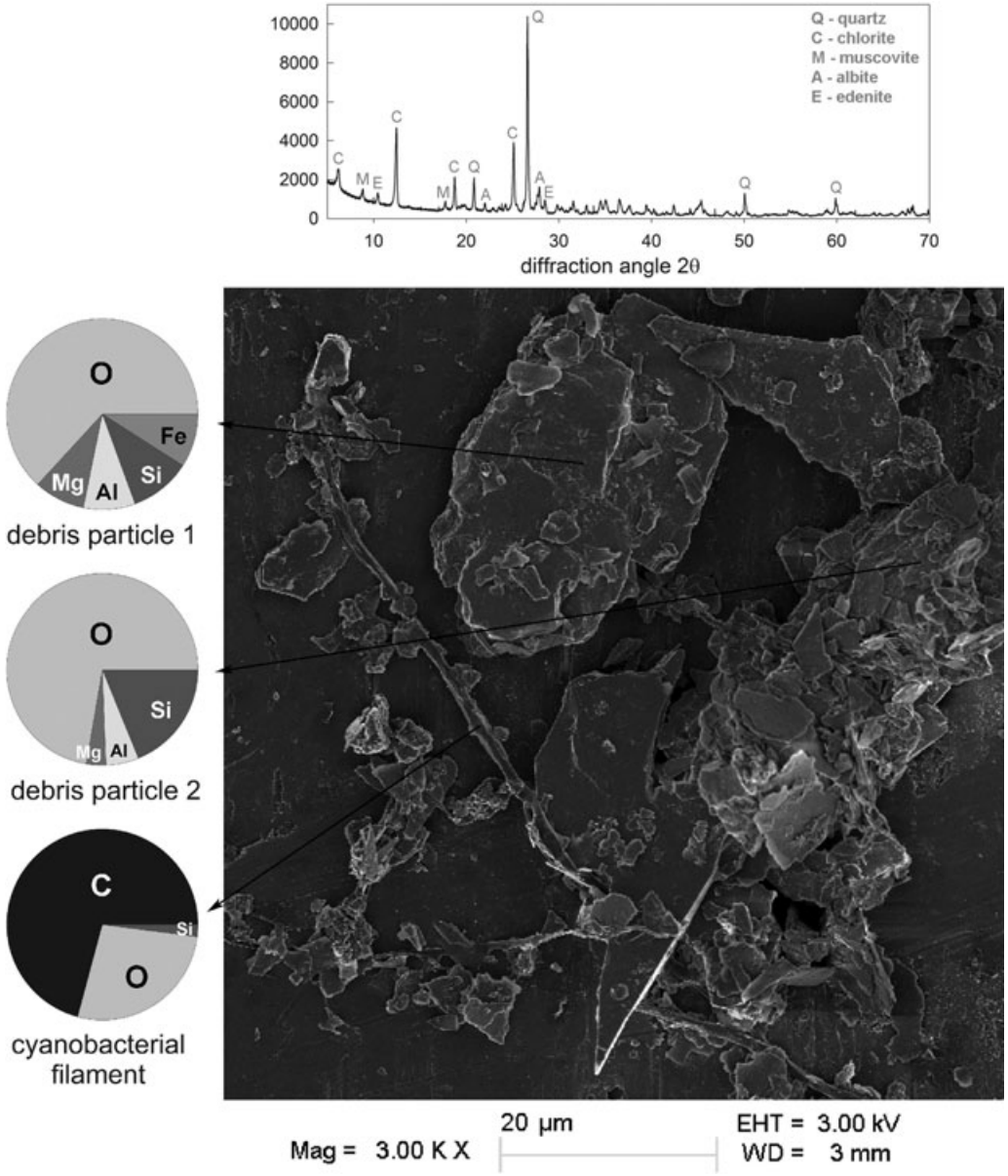

Fig. 1. Scanning electron microscopy image of cryoconite debris showing individual particles with attached cyanobacteria. The sample (~10 mg) was thawed and directly deposited onto an Al-stub and coated with 3 nm of platinum. The image shows microbial filaments and various mineral phases. The cyanobacterial filament in the image is probably *Leptolyngbya* sp. An associated bulk XRD trace of the same sample (top of picture) revealed the main mineral phases to be chlorite, muscovite, quartz, feldspars and amphiboles (edenite); the high background under the main peaks between ~18 and 35 degrees 2θ indicates amorphous materials, most probably representing amorphous organic matter. Images were recorded at 3 kV and a working distance of 3 mm, while elemental distributions (pie charts at left) were determined on various particles (15–20 spectra per sample) by energy dispersive X-ray spectroscopy at 20 kV and the working distance of 8 mm.

carbon and virtually all nitrogen in the run-off came from the glacier surface (Table 1).

The microbial abundances within the debris determined by epifluorescence microscopy are shown in Fig. 3A. The abundance of heterotrophic bacteria ranged from 10×10^3 to 50×10^3 cells per mg (wet weight) of debris. It was very variable even within a single sample, which is probably a result of the heterogeneity of the cryoconite debris. The abundance of photoautotrophic microbes was lower, between 0.25×10^3 and 8.0×10^3 cells mg^{-1}. Filamentous cyanobacteria, mostly *Leptolyngbya* and *Phormidium* species, made up 90–99% of all phototrophic cells. A more detailed description of the phototrophic community in cryoconite holes on Werenskioldbreen can be found in previous papers (Stibal *et al.*, 2006; Stibal and Tranter, 2007). The high heterogeneity of the debris and subse-

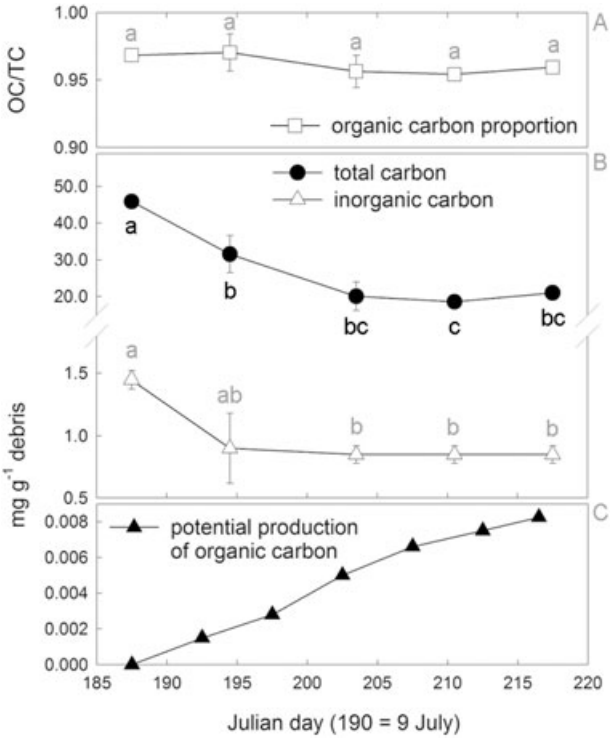

Fig. 2. Variations in total, inorganic and organic carbon content, and the potential organic carbon production in cryoconite debris on Werenskioldbreen over summer 2006.
A. Proportion of organic carbon (OC) to total carbon (TC).
B. Total and inorganic carbon in mg C g^{-1} debris.
C. Potential carbon production over time calculated using the inorganic carbon uptake rates shown in Fig. 3D.
Note the marked difference in the scale in (B). Dissolved inorganic carbon uptake rates in μg C g^{-1} debris h^{-1} here are equal to uptake rates in μg C l^{-1} h^{-1}/200, as the *in situ* incubation ratio of cryoconite debris : water was set to be ~200:1 (g : l) after Stibal and Tranter (2007). Total carbon was determined using a EuroVector EA3000 Elemental Analyser, and inorganic carbon on a Strohlein Coulomat 702 analyser adapted for the purpose. Points with the same letter are not significantly different at $P = 0.01$ (one-way ANOVA with Tukey's honest significant difference test).

quent variability in the microbial abundance makes an assessment of the changes in microbial abundance over time very difficult. The peaks in both heterotrophic and photoautotrophic abundances in the sample from 30 July are more likely the result of a very fine-grained sample, rather than of an actual peak in the natural microbial population. The content of chlorophyll *a* in the debris is therefore shown in Fig. 3B for comparison, as > 100× more debris was used for the extractions than for the epifluorescence enumerations of cells. This shows a decrease over time from ~15 to ~11 μg chlorophyll *a* g^{-1}. The estimated amount of carbon present in living microbial cells, calculated after Bratbak (1985), was 0.04–0.08 mg C per gram of cryoconite debris, which represents only 0.2% of all organic carbon in the cryoconite. The remainder of the organic carbon probably consists of amorphous organic matter and the residue of dead microbial cells, which are not detected by epifluorescence microscopy.

The rate of dissolved inorganic carbon (DIC) uptake by microorganisms in cryoconite holes on Werenskioldbreen ranged from 0.4 to 2 μg C l^{-1} h^{-1}, as determined from *in situ* incubations of 24 h duration, conducted every 5 days. Photosynthesis accounted for 82–96% of the total uptake, while dark uptake accounted for 3–12%. The total DIC uptake changed over the season (Fig. 3D), with a mid-season peak followed by a decline towards the end of the season, when the rates decreased below 1 μg C l^{-1} h^{-1}. The mean proportion of dark (non-photosynthetic) DIC uptake was constant around 5% until the beginning of August, when it briefly increased to ~9%. No significant correlations were found between DIC concentration, microbial abundance and the chlorophyll content with DIC uptake (Fig. 3). Overcast skies occurred on most days of the sampling period, during which the incident radiation reaching the glacier surface seldom exceeded 250 μmol photons m^{-2} s^{-1} (Stibal *et al.*, 2007). However, the peak in the inorganic carbon fixation coincided with a short period of clear skies, and thus of high irradiation of the glacier surface.

The rates of DIC uptake were at the lower end of the range documented for the same community in the laboratory (0.6–15 μg C l^{-1} h^{-1}; Stibal and Tranter, 2007), as well as of those recorded by Säwström and colleagues (2002) on another Svalbard glacier (0.6–160 μg C l^{-1} h^{-1}). This may be explained by higher temperatures and irra-

Table 1. Concentrations of dissolved inorganic and organic carbon (DIC; DOC), nitrogen (DIN; DON) and soluble reactive phosphorus (SRP) in surface waters and run-off from Werenskioldbreen over summer 2006 (mean ± SD; C in mg l^{-1}, N and P in μg l^{-1}).

	n	pH	DIC	DOC	DIN	DON	SRP
Supraglacial channel	27	5.1 ± 0.27a	1.3 ± 0.52a	1.8 ± 1.2a	48 ± 17a	130 ± 87a	0.91 ± 0.80a
Cryoconite holes	48	5.4 ± 0.19b	1.3 ± 0.93a	2.1 ± 1.6a	49 ± 22a	130 ± 95a	0.75 ± 0.47a
Glacier run-off	27	6.9 ± 0.33c	4.1 ± 0.57b	3.4 ± 3.5a	55 ± 15a	180 ± 130a	0.80 ± 0.83a

Values of pH are also presented. Water samples were collected every day where possible. Total carbon (TC), DOC and total nitrogen (TN) concentrations were determined with a Shimadzu TOC-V analyser, NH_4^+, NO_2^-, $NO_3^-$and SRP concentrations were analysed colorimetrically by an AutoAnalyser 3. Dissolved inorganic carbon was calculated as [TC] – [DOC], DON as [TN] – [NH_4^+] – [NO_2^-] – [NO_3^-]. Values with the same letter are not significantly different at $P = 0.01$ (one-way ANOVA with Tukey's honest significant difference test).

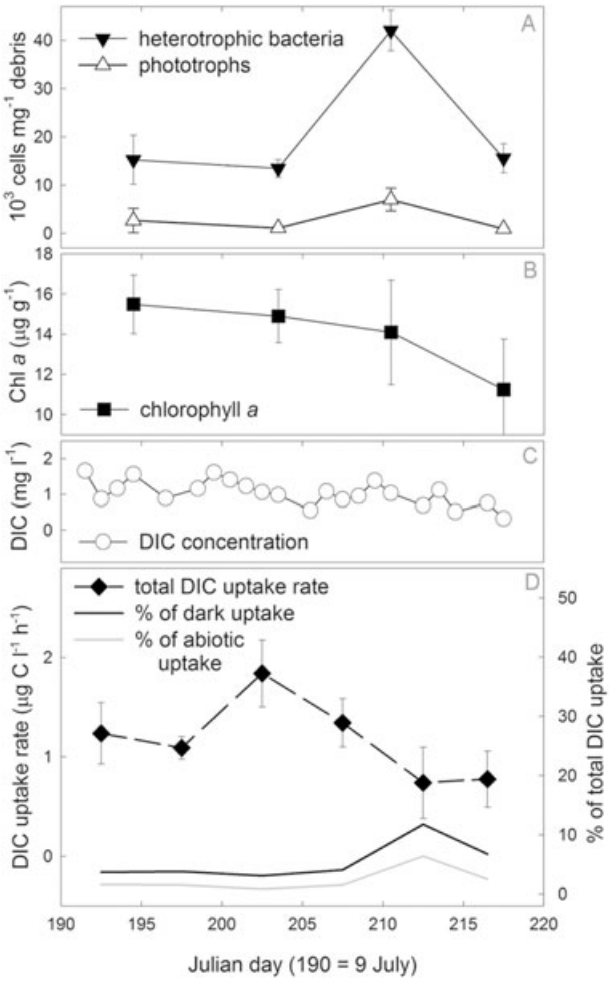

Fig. 3. Microbial abundance and inorganic carbon uptake rates in cryoconite holes on Werenskioldbreen over summer 2006.
A. Microbial abundance determined by epifluorescence microscopy with 450–490 nm excitation, using both chlorophyll autofluorescence and staining with DNA-binding SYTO 9/propidium iodide.
B. Chlorophyll *a* (Chl *a*) content in the debris, determined spectrophotometrically after extraction of the debris in 90% acetone at 5°C in the dark.
C. Dissolved inorganic carbon (DIC) concentrations in cryoconite water.
D. Dissolved inorganic carbon uptake rates based on *in situ* measurements of ^{14}C-labelled bicarbonate uptake: 2 ml of water and 0.4 g of debris were placed into a scintillation vial, spiked with $NaH^{14}CO_3$, and the sample was incubated for 24 h within the hole. Formalin-killed sediment provided a control without any life, and darkened vials a non-photosynthesis control. Incubations were terminated by adding 120 μl of 3 M HCl and 120 μl of 37% formalin. The vials were opened after *c.* 2 h and left open overnight. Scintillation cocktail (10 ml) was added and the vials were counted in a scintillation counter. Isotopic equilibration of C between the water and the headspace during the incubations might have resulted in underestimations of the DIC uptake. The real values could potentially be up to ~3 times as high.

diance values in the former study, which may have represented a more favourable environment for microbial activity. In the latter case, the community was also exposed to higher irradiance. Hence, we believe that the rates of photosynthesis in cryoconite holes on Werenskioldbreen measured in this study are likely to be low due to light limitation. The high DIC uptake peak during the brief period of a high incident radiation supports this assertion.

The annual primary production per gram of wet debris can be estimated as the product of the mean DIC uptake rate (1.2 μg C l^{-1} h^{-1}; Fig. 3D) and the duration of the ablation season (assumed to be 72 h; Fig. 2C). The potential primary production is estimated to be ~4.3 μg C per gram of wet debris. This is three orders of magnitude lower than the total organic carbon content of the debris (8500–22 000 μg C g^{-1} debris). This simple calculation and comparison suggests that the organic carbon present in the debris could not be produced *in situ* during the typical lifetime of cryoconite holes on Werenskioldbreen, which is one or a small number of years due to the high dynamics of the glacier surface (Řehák *et al.*, 2007). We do not believe that the organic carbon content of the debris was unusually high, as similar values have been found in other seasons (Stibal *et al.*, 2006; Kaštovská *et al.*, 2007) or on other glaciers (Takeuchi *et al.*, 2001; Takeuchi, 2002; Kaštovská *et al.*, 2005). We acknowledge that the measured DIC uptake rates may have been underestimated up to ~3 times due to C equilibrium between the headspace in the vial and the solution during the incubations. They could also be lower than usual, due to the relatively low light levels. Other factors, such as high viral infection of bacteria in Arctic cryoconite holes (Säwström *et al.*, 2007a), are also likely to have a detrimental effect on the microbial primary production on glacier surfaces (Anesio *et al.*, 2007). The single highest DIC uptake rate recorded for the supraglacial environment is 160 μg C l^{-1} h^{-1} (Säwström *et al.*, 2002). Even when we apply this value to Werenskioldbreen, the total annual carbon fixation would be ~580 μg C g^{-1} debris over the season, and the required time for accumulation of organic matter in the cryoconite hole debris would be ~15–40 years. This is still an order of magnitude higher than the lifetime of the cryoconite holes on Werenskioldbreen. The low annual carbon fixation relative to the total amount of organic carbon in the cryoconite holes is accentuated by microbial respiration (Hodson *et al.*, 2007). For example, it has been suggested that respiration may even exceed primary production in other environments with low productivities (< 3–5 μg C l^{-1} h^{-1}; del Giorgio *et al.*, 1997), comparable to cryoconite holes on Werenskioldbreen. Hence, we conclude that most organic carbon in the cryoconite debris is not likely to be autochthonous, and comes from another source.

A likely allochthonous source of organic matter is wind-borne material deposited on the glacier surface. The ultimate sources of this organic matter include the proglacial and coastal wetlands and soils, which have high abundances of organic matter and microbial cells (Kaštovská *et al*., 2007). Strong winds occur on a regular basis in autumn, when temperatures have dropped below freezing and desiccated surface debris, including organic matter, can be lifted and transported onto glaciers (Marshall and Chalmers, 1997), where it is deposited, and can be re-mobilized during the following ablation season. This is consistent with field observations of high surface dust falls in the autumn (J. Řehák, unpubl. data).

This study has potentially important implications for carbon and nutrient export to downstream ecosystems. Our crude estimate is that there was ~230 000 kg of cryoconite debris on Werenskioldbreen at the end of the season, containing ~2300 kg of organic carbon (Fig. 2A and B). This is only ~30% of the initial OC present in the debris (Fig. 2B), so we can infer a significant loss of OC from the surface over the ablation season. Some ~75% of supraglacial water flows to the glacier bed during the ablation season (Řehák *et al*., 2007), so it is likely that a substantial quantity of organic carbon, of the order of ~1 tonne, was supplied to the subglacial environments during the ablation season. This may represent an important annual source for subglacial heterotrophic microorganisms that have been found at the bed of Werenskioldbreen (Kaštovská *et al*., 2007) and other Svalbard glaciers (Wadham *et al*., 2004; Hodson *et al*., 2008). Ultraoligotrophic nutrient-limited proglacial freshwater ecosystems, such as lakes (Säwström *et al*., 2007b), may also receive significant carbon and nutrient inputs from stores on the glacier surface, as has been documented in Antarctica (Foreman *et al*., 2004).

It is evident that microbial processes, including inorganic carbon fixation and primary production, occur in cryoconite holes, and that significant amounts of carbon and nutrients are contained within them. However, on Werenskioldbreen, there is a considerable difference between the low DIC uptake rates and the high organic carbon content of the debris, making long-term accumulation of organic matter as a consequence of local primary production unlikely. Instead, we believe that most of the organic matter may be allochthonous and originates from production sites elsewhere. The glacier surface of Werenskioldbreen seems to be a reservoir rather than an oasis of productivity. This need not be the case on other glaciers, and further studies would be highly desirable in order to better define the production potential of the glacial ecosystem and its significance to local, regional and global carbon cycling.

Acknowledgements

This work was supported by BIOTRACS, an EU-funded EST fellowship for M.S. We thank Alexandre Anesio and Marie Šabacká for comments on an earlier draft of the manuscript. Three anonymous reviewers stimulated a major revision of the manuscript.

References

Anesio, A.M., Mindl, B., Laybourn-Parry, J., Hodson, A.J., and Sattler, B. (2007) Viral dynamics in cryoconite holes on a high Arctic glacier (Svalbard). *J Geophys Res* **112:** G04S31. doi:10.1029/2006JG000350.

Benn, D.I., and Evans, D.J.A. (1998) *Glaciers and Glaciation*. London, UK: Arnold.

Bratbak, G. (1985) Bacterial biovolume and biomass estimations. *Appl Environ Microbiol* **49:** 1488–1493.

Foreman, C.M., Wolf, C.F., and Priscu, J.C. (2004) Impact of episodic warming events on the physical, chemical and biological relationships of lakes in the McMurdo Dry Valleys, Antarctica. *Aquat Geochem* **10:** 239–268.

del Giorgio, P.A., Cole, J.J., and Cimbleris, A. (1997) Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* **385:** 148–151.

Hodson, A.J., Mumford, P.N., Kohler, J., and Wynn, P.M. (2005) The High Arctic glacial ecosystem: new insights from nutrient budgets. *Biogeochemistry* **72:** 233–256.

Hodson, A., Anesio, A.M., Ng, F., Watson, R., Quirk, J., Irvine-Fynn, T., *et al.* (2007) A glacier respires: quantifying the distribution and respiration CO_2 flux of cryoconite across an entire Arctic supraglacial ecosystem. *J Geophys Res* **112:** G04S36. doi:10.1029/2007JG000452.

Hodson, A.J., Anesio, A.M., Tranter, M., Fountain, A.G., Osborn, M., Priscu, J., *et al.* (2008) Glacial ecosystems. *Ecol Monogr* **78:** 41–67.

Kaštovská, K., Elster, J., Stibal, M., and Šantrůčková, H. (2005) Microbial assemblages in soil microbial succession after glacial retreat in Svalbard (High Arctic). *Microb Ecol* **50:** 396–407.

Kaštovská, K., Stibal, M., Šabacká, M., Černá, B., Šantrùèková, H., and Elster, J. (2007) Microbial community structure and ecology of subglacial sediments in two polythermal Svalbard glaciers characterized by the epifluorescence microscopy and PLFA. *Polar Biol* **30:** 277–287.

Kennedy, A.D. (1993) Water as a limiting factor in the Antarctic terrestrial environment – a biographical synthesis. *Arct Alp Res* **25:** 308–315.

Marshall, W.A., and Chalmers, M.O. (1997) Airborne dispersal of Antarctic algae and cyanobacteria. *Ecography* **20:** 585–594.

Mindl, B., Anesio, A.M., Meirer, K., Hodson, A.J., Laybourn-Parry, J., Sommaruga, R., and Sattler, B. (2007) Factors influencing bacterial dynamics along a transect from supraglacial runoff to proglacial lakes of a high Arctic glacier. *FEMS Microbiol Ecol* **59:** 307–317.

Řehák, J., Ouhrabka, V., and Braun, M. (1990) New information about the interior drainage of a subpolar glacier and the structures of medial moraines of the Southwest Spitsbergen. *Stud Carsol* **1:** 15–56.

Řehák, J., Řehák, S., Stibal, M., Řeháková, K., Šabacká, M., and Kostka, S. (2007) Glacier caves and drainage systems of the northern part of Hornsund area, southwest Spitsbergen, Svalbard. *8th GLACKIPR Symposium*, Sosnowiec, Poland, p. 111.

Šabacká, M., and Elster, J. (2006) Response of cyanobacteria and algae from Antarctic wetland habitats to freezing and desiccation stress. *Polar Biol* **30:** 31–37.

Säwström, C., Mumford, P., Marshall, W., Hodson, A., and Laybourn-Parry, J. (2002) The microbial communities and primary productivity of cryoconite holes in an Arctic glacier (Svalbard 79°N). *Polar Biol* **25:** 591–596.

Säwström, C., Granéli, W., Laybourn-Parry, J., and Anesio, A.M. (2007a) High viral infection rates in Antarctic and Arctic bacterioplankton. *Environ Microbiol* **9:** 250–255.

Säwström, C., Laybourn-Parry, J., Granéli, W., and Anesio, A.M. (2007b) Heterotrophic bacterial and viral dynamics in Arctic freshwaters: results from a field study and nutrient-temperature manipulation experiments. *Polar Biol* **30:** 1407–1415.

Stibal, M., and Tranter, M. (2007) Laboratory investigation of inorganic carbon uptake by cryoconite debris from Werenskioldbreen, Svalbard. *J Geophys Res* **112:** G04S33. doi:10.1029/2007JG000429.

Stibal, M., Šabacká, M., and Kaštovská, K. (2006) Microbial communities on glacier surfaces in Svalbard: impact of physical and chemical properties on abundance and structure of cyanobacteria and algae. *Microb Ecol* **52:** 644–654.

Stibal, M., Elster, J., Šabacká, M., and Kaštovská, K. (2007) Seasonal and diel changes in photosynthetic activity of the snow alga *Chlamydomonas nivalis* (*Chlorophyceae*) from Svalbard determined by pulse amplitude modulation fluorometry. *FEMS Microbiol Ecol* **59:** 265–273.

Takeuchi, N. (2002) Optical characteristics of cryoconite (surface dust) on glaciers: the relationship between light absorbency and the property of organic matter contained in the cryoconite. *Ann Glaciol* **34:** 409–414.

Takeuchi, N., Kohshima, S., and Seko, K. (2001) Structure, formation, and darkening process of albedo-reducing material (cryoconite) on a Himalayan glacier: a granular algal mat growing on the glacier. *Arct Antarct Alp Res* **33:** 115–122.

Tranter, M., Fountain, A.G., Fritsen, C.H., Lyons, W.B., Priscu, J.C., Statham, P.J., and Welch, K.A. (2004) Extreme hydrochemical conditions in natural microcosms entombed within Antarctic ice. *Hydrol Process* **18:** 379–387.

Vincent, W.F. (2000) Cyanobacterial dominance in the polar regions. In *The Ecology of Cyanobacteria*. Whitton, B.A., and Potts, M. (eds). Dordrecht, the Netherlands: Kluwer, pp. 321–340.

Wadham, J.L., Bottrell, S., Tranter, M., and Raiswell, R. (2004) Stable isotope evidence for microbial sulphate reduction at the bed of a polythermal high Arctic glacier. *Earth Planet Sci Lett* **219:** 341–355.

Wharton, R.A., Jr, McKay, C.P., Simmons, G.M., Jr, and Parker, B.C. (1985) Cryoconite holes on glaciers. *Bioscience* **35:** 499–503.

