

# High microbial activity on glaciers: importance to the global carbon cycle

ALEXANDRE M. ANESIO\*, ANDREW J. HODSON†, ANDREAS FRITZ‡, ROLAND PSENNER‡ and BIRGIT SATTLER‡

\*Bristol Glaciology Centre, School of Geographical Sciences, University of Bristol, Bristol, BS8 1SS, UK, †Department of Geography, University of Sheffield, Sheffield S10 2TN, UK, ‡Institute of Ecology, University of Innsbruck, Technikerstrasse 25, 6020 Innsbruck, Austria

## Abstract

Cryoconite holes, which can cover 0.1–10% of the surface area of glaciers, are small, water-filled depressions (typically <1 m in diameter and usually <0.5 m deep) that form on the surface of glaciers when solar-heated inorganic and organic debris melts into the ice. Recent studies show that cryoconites are colonized by a diverse range of microorganisms, including viruses, bacteria and algae. Whether microbial communities on the surface of glaciers are actively influencing biogeochemical cycles or are just present in a dormant state has been a matter of debate for long time. Here, we report primary production and community respiration of cryoconite holes upon glaciers in Svalbard, Greenland and the European Alps. Microbial activity in cryoconite holes is high despite maximum temperatures seldom exceeding 0.1 °C. *In situ* primary production and respiration in cryoconites during the summer is often comparable with that found in soils in warmer and nutrient richer regions. Considering only glacier areas outside Antarctica and a conservative average cryoconite distribution on glacial surfaces, we found that on a global basis cryoconite holes have the potential to fix as much as 64 Gg of carbon per year (i.e. 98 Gg of photosynthesis minus 34 Gg of community respiration). Most lakes and rivers are generally considered as heterotrophic systems, but our results suggest that glaciers, which contain 75% of the freshwater of the planet, are largely autotrophic systems.

*Keywords:* carbon cycle, CO<sub>2</sub> sequestration, cryoconites, DOC, glaciers, net metabolism, photosynthesis, respiration

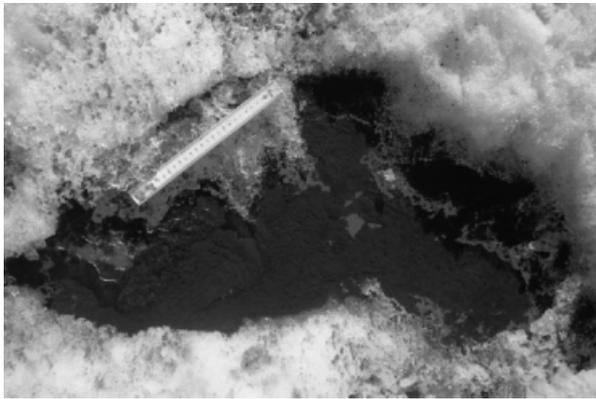
Received 25 February 2008; revised version received 29 July 2008 and accepted 30 July 2008

## Introduction

Cryoconite holes are water-filled depressions (typically <1 m in diameter and usually <0.5 m deep) that form on the surface of glaciers when solar-heated inorganic and organic debris melts into the ice (Fig. 1). There is increasing evidence from clone libraries and microscopy studies that a highly diverse microbial community can be found on the surface of glaciers in features called cryoconite ('ice dust') holes, including viruses, bacteria and algae (Mueller *et al.*, 2001; Christner *et al.*, 2003; Porazinska *et al.*, 2004; Kastovska *et al.*, 2005; Anesio *et al.*, 2007), and also – depending on the geographic region – other organisms, such as tardigrades,

rotifers, nematodes, protozoa, copepods and insect larvae (Kohshima, 1984; De Smet & van Rompu, 1994; Kikuchi, 1994; Gronggaard *et al.*, 1999). More recent investigations have suggested that glaciers, ice sheets and ice shelves are neither sterile nor abiotic repositories of dormant cells. In fact, they support a large number of active microbial communities which sequester nutrients from the atmosphere (Tranter *et al.*, 2004; Vincent *et al.*, 2004; Hodson *et al.*, 2005). Cryoconite holes are particularly considered 'hot spots' for biogeochemical cycling upon the surface of glaciers throughout the Earth's cryosphere (Sävström *et al.*, 2002; Tranter *et al.*, 2004; Hodson *et al.*, 2005). For instance, it has been shown that microbial sequestration of NH<sub>4</sub><sup>+</sup> is a major component of the annual nitrogen fluxes of the glacier surface, accounting for up to 50% of the atmospheric NH<sub>4</sub><sup>+</sup> deposited in the winter snowpack

Correspondence: Alexandre Magno Anesio, tel. + 44 117 331 4157, fax + 44 117 928 7878, e-mail: a.m.anesio@bristol.ac.uk



**Fig. 1** A cryoconite hole on the Vestre Brøggerbreen glacier in Svalbard.

(Hodson *et al.*, 2005). Further, there is an additional  $\text{NO}_3^-$  source in the nitrogen budget which strongly suggests that cyanobacteria in cryoconite holes are able to fix nitrogen directly from the atmosphere once they have been exposed to the atmosphere in the summer (Hodson *et al.*, 2005). A consortium of nitrifiers within cryoconite holes may also be important in the conversion of  $\text{NH}_4^+$  to  $\text{NO}_3^-$ , but further studies need to be conducted to quantify their relative importance in supraglacial ecosystems (Hodson *et al.*, 2008). Further, at present, there are no quantitative studies about carbon fluxes through the microbial communities in cryoconite holes. Primary production has only been measured on one occasion in cryoconites (Sävström *et al.*, 2002) and these results revealed high levels of photosynthesis comparable with warmer eutrophic lakes (Daniel *et al.*, 2005). Considering that the cryosphere covers 10% of the landmass of our planet, it is startling that biomass and productivity of these environments have not yet been estimated at the ecosystem scale. Here, we provide the first simultaneous quantitative measurements of primary production and respiration in cryoconite holes on different glaciers of the Earth, followed by a simplified upscaling approach in order to consider its global importance for the very first time.

Primary production and respiration are the main components of the carbon cycle in aquatic ecosystems and net heterotrophy (i.e. where the community respiration exceeds primary production) is often used to infer  $\text{CO}_2$  export to the atmosphere (Cole & Caraco, 2001). It was found that net primary production values below  $100 \mu\text{g CL}^{-1} \text{day}^{-1}$  indicate a threshold below which aquatic ecosystems are usually heterotrophic (del Giorgio *et al.*, 1997). In fact, most freshwaters around the globe are net heterotrophic systems characterized by oligotrophic (i.e. nutrient poor) conditions and a heterotrophic community biomass that is

typically higher than that of the autotrophs (del Giorgio *et al.*, 1999). In contrast, considering (i) the high primary production found in cryoconite holes (Sävström *et al.*, 2002), (ii) the level of nutrient deposition and potential for nitrogen fixation (Hodson *et al.*, 2005) and (iii) the abundance of cryoconites on glaciers (Fountain *et al.*, 2004), we speculate that the surface of glaciers are net autotrophic ecosystems (i.e. where primary production is higher than total respiration) of global importance.

## Materials and methods

In this study, we measured primary production (using  $^{14}\text{C}$  incorporation) and community respiration (through oxygen consumption in dark incubations) from cryoconite holes of various glaciers in Svalbard, Greenland and the Austrian Alps. We used  $^{14}\text{C}$  incorporation for measuring primary production rather than oxygen production due to the better sensitivity of the former method and in order to have an independent measurement of microbial activity in cryoconite holes. Three valley glaciers in the Kongsfjord region of northwest Spitsbergen ( $78^\circ 53'\text{N}$  and  $12^\circ 04'\text{E}$ ) were investigated; Midtre Lovénbreen, Austre Brøggerbreen and Vestre Brøggerbreen. The glaciers range from ca. 50 m above sea level (a.s.l.) at their terminus to ca. 600 m at the head wall. The valley glacier Frøya is located at  $74^\circ 24'\text{N}$  and  $20^\circ 50'\text{W}$  in East Greenland at an altitude between 0 and 500 m a.s.l., and an area of  $6.3 \text{ km}^2$  (Ahlmann, 1942). As an example of a high altitude temperate glacier, Stubacher Sonnblickkees, ranging from 2500 to 2780 m a.s.l., has also been sampled ( $47^\circ 03'\text{N}$  and  $12^\circ 00'\text{W}$ ). In total, 53 cryoconite holes in five glaciers were individually investigated for measurements of primary production and community respiration. Sixteen cryoconites were sampled in Austre Brøggerbreen, 10 in Midtre Lovénbreen, 6 in Vestre Brøggerbreen, 10 in Stubacher Sonnblickkees, and 11 in Frøya Glacier. Because of logistical difficulties, only primary production was investigated in Frøya Glacier.

Net primary production both in water and debris was measured by incorporation of  $\text{NaH}^{14}\text{CO}_3$ . For the liquid compartment, 50 mL of supernatant in the cryoconite hole has been collected into a 80 mL Whirlpak™ (Nasco, Fort Atkinson, WI, USA) with a syringe, and  $10 \mu\text{L}$  of  $^{14}\text{C}$  ( $10 \mu\text{Ci}$ ) was added to three replicates for light samples and two parallels as dark controls which were thoroughly wrapped with aluminium foil. Two mL of debris has been collected from the bottom of the cryoconite hole and treated as described above. All arctic samples were incubated at *in situ* conditions for 24 h in the polar sun. Samples from the Alps have been incubated for 4 h during the zenith of the sun. Incubations were not open to the atmosphere. After recollection of

bags and immediate transport to the lab, the whole amount of sample has been filtered onto Whatman glass fibre filters (47 mm diameter), acidified with HCl and dried overnight. Filters with sediments have been weighed for calculation of gross primary production on weight base. The filtrates from both liquid and sediments samples were further filtered through HTPP filters (Millipore, 0.22 µm pore size, 25 mm diameter, Bedford, MA, USA) in order to estimate photosynthetic <sup>14</sup>C fixation, extracellular release of dissolved organic carbon (DOC). Samples were counted with a LS6000IC scintillation counter with internal quench curve. Dissolved inorganic carbon at the beginning of the incubations was calculated according to titration of alkalinity and validated with data from ion concentration.

Community respiration was monitored by measurements of dissolved oxygen consumption using a dissolved oxygen meter (YSI 550a) with a 0.01 mg L<sup>-1</sup> resolution. Water (with and without sediments) were taken from the cryoconite holes and distributed into triplicate Pyrex glass bottles (100 mL) with ground glass stoppers. Initial dissolved oxygen concentration was measured immediately and the bottles were incubated in the dark at *in situ* temperature for 20 h. Oxygen consumption was converted to carbon, using a respiratory quotient of 1.

## Results and discussion

Primary production and respiration in the water phase of cryoconites were low (Table 1) but in the same order

**Table 1** Primary production and community respiration in the water and debris of cryoconite holes

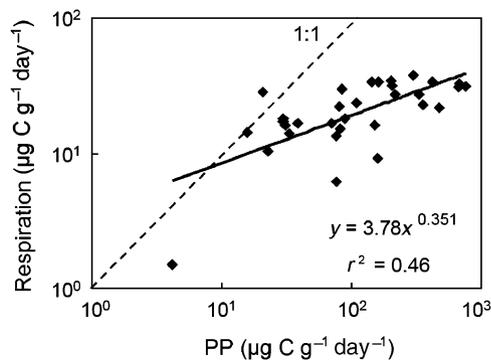
Primary production (water)	µg C L <sup>-1</sup> day <sup>-1</sup>
Midtre Lovénbreen	79.8 ± 75.9 (5.38–234)
Austre Brøggerbreen	87.5 ± 56.0 (24.8–158)
Vestre Brøggerbreen	94.6 ± 58.0 (41.9–190)
Frøya Glacier	53.5 ± 59.7 (7.97–183)
Community respiration (water)	µg C L <sup>-1</sup> day <sup>-1</sup>
Austre Brøggerbreen	72.9 ± 29.8
Stubacher Sonnblickkees	86.7 ± 17.9
Primary Production (debris)	µg C g <sup>-1</sup> day <sup>-1</sup>
Midtre Lovénbreen	353 ± 248 (72.2–756)
Austre Brøggerbreen	48.0 ± 35.9 (11.2–125)
Vestre Brøggerbreen	208 ± 106 (101–368)
Frøya Glacier	115 ± 56.3 (35.5–205)
Stubacher Sonnblickkees	147 ± 78.3 (2.83–2059)
Community respiration (debris)	µg C g <sup>-1</sup> day <sup>-1</sup>
Midtre Lovénbreen	28.2 ± 4.37 (21.9–34.6)
Austre Brøggerbreen	15.3 ± 5.02 (6.23–28.6)
Vestre Brøggerbreen	34.3 ± 2.18 (32.0–37.9)
Stubacher Sonnblickkees	42.1 ± 7.91 (29.7–44.8)

Data is expressed as average ± SD (minimum–maximum).

of magnitude as oligotrophic aquatic ecosystems elsewhere (del Giorgio *et al.*, 1997). On the other hand, microbial activity (both primary production and respiration) in the sediments of cryoconite holes was typical of soils in warmer climates and mesotrophic sediments (Rutigliano *et al.*, 2004; Fierer *et al.*, 2006). We calculated the microbial activity associated with the debris on a volume basis, in order to compare it with the results from Sävström *et al.* (2002), and we found values that were within the range of their study (data not shown). Further, ca. 90% of the respiration and primary production in a typical cryoconite hole were found associated with the debris. An average of 10% (± 9% SD) of the <sup>14</sup>C fixed was released as DOC, suggesting that an important fraction of the photosynthesis on glacial surfaces can be flushed as DOC and exported to proglacial ecosystem and coastal waters.

In general, lakes and rivers have respiration rates higher than photosynthesis which indicates that they receive inputs of organic matter from the terrestrial catchment (Cole *et al.*, 2007). The comparison of net primary production and community respiration in the cryoconite holes indicated, however, that they are autotrophic (Fig. 2). These findings have a number of consequences. Firstly, our results indicate that the combined activity of primary producers and bacteria in cryoconite holes results in the accumulation of dark-coloured organic matter, which may contribute to further absorption of solar radiation and thus enhance glacial melting. This is in agreement with previous studies that revealed that microorganisms contribute to the formation of the dark colour of the cryoconite (Takeuchi *et al.*, 2001b). Secondly, the excess organic matter can be exported during the summer melt season to other ecosystems, including the oceans, and thus sustaining life elsewhere. Most interesting, however, is the contention that because photosynthesis exceeds respiration, biological activity in glacial ecosystems can fix CO<sub>2</sub> from the atmosphere.

For global calculations, we preferred to exclude Antarctic cryoconites, despite the fact that more than 90% of the ice sheets of the planet are situated there. Cryoconite holes in continental Antarctica have ice lids which can keep them isolated from the atmosphere for years (Tranter *et al.*, 2004; Foreman *et al.*, 2007). Nevertheless, chemical measurements under these extreme conditions also indicated that Antarctic cryoconites are autotrophic ecosystems. High pH and O<sub>2</sub> concentrations and low pCO<sub>2</sub> suggest that photosynthesis continues during prolonged isolation with the atmosphere (Tranter *et al.*, 2004). Further, we have only considered data of microbial activity associated with the debris as most of the microbial activity is there. We considered an average



**Fig. 2** Community respiration as a function of primary production in cryoconite holes from Svalbard. Each point is averaged per cryoconite hole (10 cryoconites from Midtre Lovénbreen, 16 from Austre Brøggerbreen and 6 from Vestre Brøggerbreen). The dashed line is the 1:1 ratio between primary production and respiration. Points on the right side of the 1:1 line indicate net autotrophy, whereas points on the left side of the 1:1 line indicate net heterotrophy. In del Giorgio *et al.* (1997), the threshold where there is a switch between net heterotrophy and net autotrophy (i.e. when the regression line intersects the 1:1 line) occurs when net primary productivity exceeds ca.  $100 \mu\text{g CL}^{-1} \text{day}^{-1}$ . If our data of primary production per mass of cryoconite is converted to a volume basis, the average primary production in cryoconite holes would be  $1971 \pm 1365 \mu\text{g CL}^{-1} \text{day}^{-1}$  (SD), which is within the range of primary production in cryoconite holes found by Sävström *et al.* (2002) and indicative of a highly net autotrophic ecosystem.

community respiration and primary production of 0.95 and  $7.35 \mu\text{g C g}^{-1} \text{h}^{-1}$ , respectively, in cryoconite holes. Unfortunately, whilst the occurrence of cryoconite upon these glaciers is widely reported, it is seldom quantified. However, about  $0.25 \times 10^6 \text{ km}^2$  of bare glacier ice is exposed at the end of the summer along the margins of the Greenland Ice Sheet (Hanna *et al.*, 2005), and cryoconite is common here (Bøggild *et al.*, 1994). Elsewhere outside Antarctica, about  $0.48 \times 10^6 \text{ km}^2$  of glacier ice, and ice caps are exposed (Dyrgerov, 2002) and thus likely to have cryoconite holes according to observations from Central Asia, North and South America, Europe and Svalbard (McIntyre, 1984; Takeuchi *et al.*, 2000, 2001a,c; Sävström *et al.*, 2002). Together, they represent a maximum potential ice area of  $0.73 \times 10^6 \text{ km}^2$  for colonization by cryoconite ecosystems outside Antarctica. Observations of the spatial extent of cryoconite upon these melt zones are scarce, but the extent is between 1.2% and 3.5%, according to glacier-wide surveys undertaken by the authors in Svalbard and the European Alps (A. Hodson *et al.*, 2007; unpublished data). Other estimates in the literature tend to be higher, for example 4–6% in the McMurdo Dry Valleys (Fountain *et al.*, 2004), but have not resulted from extensive, glacier-wide surveys. Thus 2% is a

reasonable and conservative estimate of the cryoconite cover outside Antarctica, producing a global extent of ca.  $14.6 \times 10^3 \text{ km}^2$  (i.e. the equivalent of 6% of the total area of the United Kingdom). On Svalbard glaciers, we found on average  $1250 \pm 0.005$  (SD) grams of debris per  $\text{m}^2$  of cryoconite hole (Hodson *et al.*, 2007). Considering that 2% of the surface of glaciers is covered by cryoconites, we calculate  $\sim 25 \text{ g debris m}^{-2}$ . This is a conservative loading estimate, because deep cryoconite holes can effectively 'fill up' and yield over  $1500 \text{ g m}^{-2}$  upon parts of the Greenland Ice Sheet margin (C. Bøggild, unpublished data) and up to  $4400 \text{ g m}^{-2}$  upon the Canadian Arctic ice caps that lie further west (Takeuchi *et al.*, 2001a). Further,  $50\text{--}900 \text{ g m}^{-2}$  of cryoconite were estimated on a Himalayan glacier known for high rates of dust deposition (Takeuchi *et al.*, 2000). However, these high values represent local maxima upon the ice masses concerned and it is not yet clear how the cryoconite is distributed over large ice caps and ice sheets. A glacier-wide survey of cryoconite debris has been produced (Hodson *et al.*, 2007), which indicated that loading of  $0.8\text{--}36.7 \text{ g m}^{-2}$  (average  $11 \text{ g m}^{-2}$ ) is typical for West Svalbard glaciers. These figures compare favourably with the only other estimates of mass loading that have been published at the time of writing, namely  $14\text{--}71 \text{ g m}^{-2}$  for a Patagonian glacier (Takeuchi *et al.*, 2001c).

An average photosynthesis period of 744 h per summer across this area is reasonable due to snowpack, diurnal and seasonal controls upon light receipt, producing a global photosynthesis rate of  $98 \text{ Gg C yr}^{-1}$  ( $\pm 65$  SD, minimum = 27 and maximum = 198). The corresponding annual respiration rate is harder to estimate, because bacterial activity is possible in the dark and also beneath wet snowpacks close to the snowline. However, if these factors double the duration of respiration relative to photosynthesis, then the corresponding fluxes using our data would be ca.  $34 \text{ Gg C yr}^{-1}$  ( $\pm 13$  SD, minimum = 17 and maximum = 47). These figures generate an annual net carbon fixation from biological activity of  $64 \text{ Gg of C}$  by cryoconite holes outside Antarctica. The net carbon fixation by cryoconite ecosystems worldwide outside Antarctica is therefore far from trivial. Considering that ca. 10% of C fixation is released as DOC (our data), then DOC produced by primary production in cryoconite holes outside Antarctica is about  $10 \text{ Gg C yr}^{-1}$  ( $\pm 6.5$  SD, minimum = 2.7 and maximum = 19.8). Although covering an average of just 2% of the glacier surface, cryoconites may be responsible for a substantial fraction of the DOC exported to the oceans during ablation [between 39 and  $259 \text{ Gg C yr}^{-1}$  considering the average DOC value in the cryosphere to be  $0.11 \text{ mg CL}^{-1}$  (Prisco & Christner, 2004), and the average glacial runoff outside

**Table 2** Annual primary production (PP) and respiration from different freshwaters and marine habitats

	PP g C m <sup>-2</sup> yr <sup>-1</sup>	Respiration g C m <sup>-2</sup> yr <sup>-1</sup>	Reference
<b>Freshwaters</b>			
Glaciers* – only debris covered areas, considering 1250 g of sediment per m <sup>2</sup>	1.87–79.9 (6.97)	0.62–3.80 (2.02)	This study
Glaciers† – whole surface (debris and nondebris covered areas), considering 25 g of sediment per m <sup>2</sup>	0.04–1.60 (0.14)	0.01–0.07 (0.04)	This study
21 boreal lakes in Sweden	0.03–0.15 (0.08)	0.63–5.05 (2.25)	Algesten <i>et al.</i> (2003)
32 streams from in Eastern United States‡	10.95–1084 (233.1)	94.90–2222 (658.2)	McTammany <i>et al.</i> (2003)
Lake Hoare (whole lake with benthic mats) – Dry Valleys, Antarctica	0.47–4.11 (1.97)	–	Moorhead <i>et al.</i> (2005)
4 Arctic lakes	14.04–38.88 (25.23)§	6.72–51.24 (31.17)	Ramlal <i>et al.</i> (1994)
<b>Marine</b>			
Wadden Sea (shallow productive coastal basin)	146	50	Loebl <i>et al.</i> (2007)
Ocean¶			Behrenfeld & Falkowski (1997)
Oligotrophic	54.5	–	
Mesotrophic	155.3	–	
Eutrophic	442.5	–	

Data are expressed either as minimum–maximum (average) or as average only.

\*Activity in the water was also considered in the calculations using an average cryoconite hole depth of 5 cm.

†Activity in the water was also considered in the calculations considering that 1 m of ice melts during summer (Tranter, 2006).

‡Annual data obtained by multiplying daily rates by 365.

§Primary production taking into account phytoplankton, benthic and macrophyte contribution.

¶From the vertically generalized production model described in Behrenfeld & Falkowski (1997).

Antarctica to be between 0.348 and  $2.356 \times 10^{12} \text{ m}^3 \text{ yr}^{-1}$  (Tranter, 2006). Our data, therefore, suggest that global productivity in the glacial ecosystem ought to be considered in greater detail, especially as vast numbers of glaciers are now experiencing longer melt periods that will provide vital water for microbial activity on their surfaces. Annual estimates of net primary production and respiration on glaciers on an areal basis are comparable with many freshwaters around the globe (Table 2) and, considering that glaciers cover 15% of the landmass of the planet, could have global implications. Further, the surplus of autochthonous organic matter from cryoconite holes may give an important bioavailable contribution of dissolved organic matter for proglacial and marine ecosystems, at least on an ecosystem scale. Although primary production in cryoconites can be considered a significant sink for CO<sub>2</sub> (although DOC will be exported to aquatic ecosystems downstream), particulate organic carbon accumulation in cryoconite holes may ultimately contribute to further absorption of solar radiation and glacial melting.

### Acknowledgements

We are grateful to Martyn Tranter for critical comments on the manuscript. Two anonymous reviewers greatly improved this manuscript. We are grateful to the staff of the Arctic NERC

Research Station in Ny-Ålesund for their help in making this project possible. This work was supported by a grant from the Natural Environmental Research Council to A. M. A. and A. H. while A. F. was supported by the Austrian Ministry of Science and Education as well as the Austrian Academy of Sciences (ÖAW). B. S. was supported by ÖAW and Planetary Studies Foundation.

### References

- Ahlmann HW (1942) Studies in northeast Greenland. III. Accumulation and ablation on the Frøya Glacier; its regime in 1938–39 and 1939–40. *Geografiska Annaler*, **24**, 1–22.
- Algesten G, Sobek S, Bergström A-K, Gren A, Tranvik LJ, Jansson M (2003) Role of lakes for organic carbon cycling in the boreal zone. *Global Change Biology*, **10**, 141–147.
- Anesio AM, Mindl B, Laybourn-Parry J, Hodson AJ, Sattler B (2007) Viral dynamics in cryoconite holes on a high Arctic glacier (Svalbard). *Journal of Geophysical Research*, **112**, G04S31, doi: 10.1029/2006JG000350.
- Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, **42**, 1–20.
- Bøggild CE, Reeh N, Oerter H (1994) Modelling ablation and mass-balance sensitivity to climate-change of Storstrommen, Northeast Greenland. *Global and Planetary Change*, **9**, 79–90.
- Christner BC, Kvitko BH, Reeve JN (2003) Molecular identification of bacteria and eukarya inhabiting an Antarctic cryoconite hole. *Extremophiles*, **7**, 177–183.

- Cole JJ, Caraco NF (2001) Carbon in catchments: connecting terrestrial carbon losses with aquatic metabolism. *Marine and Freshwater Research*, **52**, 101–110.
- Cole JJ, Prairie YT, Caraco NF *et al.* (2007) Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems*, **10**, 171–184.
- Daniel C, Gutseit K, Anesio AM, Granéli W (2005) Microbial food webs in the dark: independence of lake plankton from recent algal production. *Aquatic Microbial Ecology*, **38**, 113–123.
- del Giorgio PA, Cole JJ, Caraco NF, Peters RH (1999) Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology*, **80**, 1422–1431.
- del Giorgio PA, Cole JJ, Cimleris A (1997) Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic ecosystems. *Nature*, **385**, 148–151.
- De Smet WH, Van Rompu EA (1994) Rotifera and Tardigrada from some cryoconite holes on a Spitsbergen (Svalbard) glacier. *Belgium Journal of Zoology*, **124**, 27–37.
- Dyrugerov M (2002) Glacier mass balance and regime: data of measurements and analysis. In: *INSTAAR/OP-55* (eds Meier M, Armstrong R), p. 275. INSTAAR and NSIDC, Boulder, CO, USA.
- Fierer N, Colman BP, Schimel JP, Jackson RB (2006) Predicting the temperature dependence of microbial respiration in soil: a continental-scale analysis. *Global Biogeochemical Cycles*, **20**, GB3026, doi: 10.1029/2005GB002644.
- Foreman CF, Sattler B, Mickuchi JA, Porazinska DL, Priscu JC (2007) Metabolic activity and diversity of cryoconites in the Taylor Valley, Antarctica, 2007. *Journal of Geophysical Research*, **112**, G04S32, doi: 10.1029/2006JG000358.
- Fountain AG, Tranter M, Nysten TH, Lewis KJ, Mueller DR (2004) Evolution of cryoconite holes and their contribution to meltwater runoff from glaciers in the McMurdo Dry Valleys, Antarctica. *Journal of Glaciology*, **50**, 35–45.
- Grongaard A, Pugh PJA, McInnes SJ (1999) Tardigrades and other cryoconite biota on the Greenland Ice Sheet. *Zoologischer Anzeiger*, **238**, 211–214.
- Hanna E, Huybrechts P, Janssens I, Cappelen J, Steffen K, Stephens A (2005) Runoff and mass balance of the Greenland ice sheet: 1958–2003. *Journal of Geophysical Research*, **110**, D13108, doi: 10.1029/2004JD005641.
- Hodson A, Anesio AM, Ng F *et al.* (2007) A glacier respire: quantifying the distribution and respiration CO<sub>2</sub> flux of cryoconite across an entire Arctic supraglacial ecosystem. *Journal of Geophysical Research*, **112**, G04S36, doi: 10.1029/2007JG000452.
- Hodson A, Anesio AM, Tranter M *et al.* (2008) Glacial ecosystems. *Ecological Monographs*, **78**, 41–67.
- Hodson AJ, Mumford PN, Kohler J, Wynn PM (2005) The High Arctic ecosystem: new insights from nutrient budgets. *Biogeochemistry*, **72**, 233–256.
- Kastovska K, Elster J, Stibal M, Santruckova H (2005) Microbial assemblages in soil microbial succession after glacial retreat in Svalbard (high Arctic). *Microbial Ecology*, **50**, 396–407.
- Kikuchi Y (1994) *Glaciella*, a new genus of freshwater *Canthyocammyidae* (Copepoda Harpacticoida) from a glacier in Nepal, Himalayas. *Hydrobiologia*, **292/293**, 59–66.
- Kohshima S (1984) A novel cold-tolerant insect found in a Himalayan glacier. *Nature*, **310**, 225–227.
- Loebl M, Dolch T, van Beusekom JEE (2007) Annual dynamics of pelagic primary production and respiration in a shallow coastal basin. *Journal of Sea Research*, **58**, 269–282.
- McIntyre NF (1984) Cryoconite hole thermodynamics. *Canadian Journal of Earth Sciences*, **21**, 152–156.
- McTammany ME, Webster JR, Benfield EF, Neatrou MA (2003) Patterns of metabolism in a Southern Appalachian river. *Journal of the North American Benthological Society*, **22**, 359–370.
- Moorhead D, Schmeling J, Hawes I (2005) Modelling the contribution of benthic microbial mats to net primary production in Lake Hoare, McMurdo Dry Valleys. *Antarctic Science*, **17**, 33–45.
- Mueller DR, Vincent WF, Pollard WH, Fritsen CH (2001) Glacial cryoconite ecosystems: a bipolar comparison of algal communities and habitats. *Nova Hedwigia*, **123**, 173–197.
- Porazinska DL, Fountain AG, Nysten TH, Tranter M, Virginia RA, Wall DH (2004) The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley glaciers, Antarctica. *Arctic, Antarctic and Alpine Research*, **36**, 84–91.
- Priscu JC, Christner BC (2004) Earth's icy biosphere. In: *Microbial Diversity and Bioprospecting* (ed. Bull AT), ASM Press, Washington, DC, USA.
- Ramlal PS, Hesslein RH, Hecky RE, Fee EJ, Rudd JWM, Guildford SJ (1994) The organic carbon budget of a shallow Arctic tundra lake on the Tuktoyaktuk Peninsula, N.W.T., Canada. *Biogeochemistry*, **24**, 145–172.
- Rutigliano FA, D'Ascoli R, De Santo AV (2004) Soil microbial metabolism and nutrient status in a Mediterranean area as affected by plant cover. *Soil Biology and Biochemistry*, **36**, 1719–1729.
- Sävström C, Mumford P, Marshall W, Hodson A, Laybourn-Parry J (2002) The microbial communities and primary productivity of cryoconite holes in Arctic glaciers (Svalbard 79°N). *Polar Biology*, **25**, 591–596.
- Takeuchi N, Kohshima S, Goto-Azuma K, Korner RM (2001a) Biological characteristics of dark coloured material (cryoconite) on Canadian Arctic glaciers (Devon and Penny Ice Cap). *Memoirs of the National Institute of Polar Research Special Issue*, **54**, 495–505.
- Takeuchi N, Kohshima S, Seko K (2001b) Structure, formation, and darkening process of albedo-reducing material (cryoconite) on a Himalayan glacier: granular algal mat growing on the glacier. *Arctic, Antarctic and Alpine Research*, **33**, 115–122.
- Takeuchi N, Kohshima S, Shiraiwa T, Kubota K (2001c) Characteristics of cryoconite (surface dust on glaciers) and surface albedo of a Patagonian glacier, Tyndall Glacier, Southern Patagonia Icefield. *Japanese Bulletin of Glaciological Research*, **18**, 65–69.
- Takeuchi N, Kohshima S, Yoshimura Y, Seko K, Fujita K (2000) Characteristics of cryoconite holes on a Himalayan glacier, Yala Glacier Central Nepal. *Bulletin of Glaciological Research*, **17**, 51–59.
- Tranter M (2006) Glacial chemical weathering, runoff composition and solute fluxes. In: *Glacier Science and Environmental Change* (ed. Knight PG), Blackwell, Australia.
- Tranter M, Fountain AG, Fritsen CH, Lyons WB, Priscu JC, Statham PJ, Welch KA (2004) Extreme hydrochemical conditions in natural microcosms entombed within Antarctic ice. *Hydrological Processes*, **18**, 379–387.
- Vincent WF, Mueller DR, Bonilla S (2004) Ecosystems on ice: the microbial ecology of Markham Ice Shelf in the high Arctic. *Cryobiology*, **48**, 103–112.