

Processes controlling carbon cycling in Antarctic glacier surface ecosystems

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Abstract

Glacier surface ecosystems, including cryoconite holes and cryolakes, are significant contributors to regional carbon cycles. Incubation experiments to determine the net production (NEP) of organic matter in cryoconite typically have durations of 6–24 hours, and produce a wide range of results, many of which indicate that the system is net heterotrophic. We employ longer term incubations to examine the temporal variation of NEP in cryoconite from the McMurdo Dry Valleys, Antarctica to examine the effect of sediment disturbance on system production, and to understand processes controlling production over the lifetimes of glacier surface ecosystems. The shorter-term incubations have durations of one week and show net heterotrophy. The longer term incubations of approximately one year show net autotrophy, but only after a period of about 40 days (~1000 hours). The control on net organic carbon production is a combination of the rate of diffusion of dissolved inorganic carbon from heterotrophic activity within cryoconite into the water, the rate of carbonate dissolution, and the saturation of carbonate in the water (which is a result of photosynthesis in a closed system). We demonstrate that sediment on glacier surfaces has the potential to accumulate carbon over timescales of months to years.

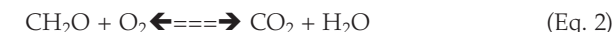
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Introduction

Glacier surface ecosystems are significant sites of biological production in an otherwise nutrient poor landscape (Bagshaw *et al.*, 2013). Meltwater flushed from glacier surfaces contains bioavailable carbon, which has the potential to stimulate production in downstream ecosystems (Lawson *et al.*, 2014). Glacier

surfaces in Antarctica host a variety of ecological niches, including cryoconite holes, cryolakes, and shallow supraglacial streams. The cryoconite holes and cryolakes are formed by rock debris on the surfaces melting into the ice as a consequence of solar heating. The debris is commonly fine-grained and aeolian transported, but can also be coarse material resulting from medial moraines or rock avalanches. Cryoconite holes are small (~1–50 cm diameter, sediment depth 0.5–5 cm), whereas cryolakes are larger (length scales ~2–20 m, sediment depth 0.5–10 cm; Bagshaw *et al.*, 2010). Antarctic cryolakes differ from larger and more commonly reported supraglacial lakes on Arctic glaciers by the presence of both a permanent layer of debris at the lake bottom and a persistent ice lid (Bagshaw *et al.*, 2012), which also differentiates Antarctic cryoconite holes from their Arctic counterparts (Fig. S-1). Antarctic cryoconite holes persist for at least several years (Fountain *et al.*, 2004) and host a variety of microorganisms, including cyanobacteria, tardigrades and rotifers (Christner *et al.*, 2003), likely inoculated by wind-blown fragments of algal mats and desiccated microorganisms (Nkem *et al.*, 2006). At shallow depths (<1 m) solar heating of the sediment melts the surrounding ice, so water is often present in these habitats, sealed beneath an ice cover of 3–20 cm, even when air temperatures are below 0 °C (Gribbon, 1979; Fountain *et al.*, 2004). Cryolakes are the largest reservoirs of liquid water in the typically frozen supraglacial environment (Fountain *et al.*, 2004). The organic carbon and nutrient stored can affect downstream ecosystems when organic compounds and nutrients are flushed from the glacier surface by periodic high melt rates (Bagshaw *et al.*, 2010), eventually supporting enhanced biological activity in glacier forefields, lakes and streams (Foreman *et al.*, 2004; Hood *et al.*, 2015).

The production of organic carbon on glacier surfaces has received considerable attention over the last decade (Anesio and Laybourn-Parry, 2012). New autochthonous organic carbon accumulates when production (P, Eq. 1) is greater than respiration (R, Eq. 2). Some studies find that P exceeds R in cryoconite holes (Anesio *et al.*, 2009), whilst others find that R exceeds P during the melt season (Stibal and Tranter, 2007; Bagshaw *et al.*, 2011).



In Antarctica, P is generally much lower in ice-lidded cryoconite holes than in their open Arctic counterparts (Hodson *et al.*, 2010b). Reported rates of P range from 1.3 (Bagshaw *et al.*, 2011) to 2.4 $\mu\text{g C g}^{-1} \text{d}^{-1}$ (Hodson *et al.*, 2010b), compared with 20.9 $\mu\text{g C g}^{-1} \text{d}^{-1}$ (Telling *et al.*, 2010) to 208 $\mu\text{g C L}^{-1} \text{d}^{-1}$ (Anesio *et al.*, 2009) in cryoconite on Svalbard glaciers. Telling *et al.* (2010) elaborate on some of the methodological differences between these experiments. A plausible explanation for these apparently contradictory findings is that the microbially-dominated communities within ice-lidded cryoconite holes self-organise to recycle and redistribute resources, to balance P and R over longer timescales and maintain the longevity of the ecosystem. In Arctic systems, individual cryoconite holes do not tend to persist for multiple ablation seasons because sediment is more frequently mobilised by supraglacial meltwaters (Hodson *et al.*, 2008). Instead,

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cryoconite granules form, which consist of polymer-bound sediment particles and microorganisms (Langford *et al.*, 2010; Takeuchi *et al.*, 2010) and likely maintain ecosystem longevity. Longer term trends in P and R are unlikely to be captured by traditional incubation techniques, which typically have durations of 24 hours. Incubations also disturb and/or mix the surface of the cm-deep sediment layer (Bagshaw *et al.*, 2013), where autotrophic microorganisms are concentrated, with deeper sediment in which heterotrophic microorganisms flourish. This is similar to observations in cryoconite granules, where photosynthetic organisms are concentrated on the exterior of polymer-bound particles and heterotrophs are found in the interior (Langford *et al.*, 2010; Takeuchi *et al.*, 2010). We contend that there is a need to conduct longer term incubations over periods more representative of the whole melt season in order to examine the interplay between autotrophic processes at the sediment surface and heterotrophic processes within the deeper sediment.

We report a combination of one week in-field incubations at Canada Glacier (77.6167 °S, 162.9833 °E), and longer term laboratory experiments, equivalent to two melt seasons, on cryolake sediments from Joyce Glacier (78.0243 °S, 163.7788 °E) (Fig. S-1), both in the McMurdo Dry Valleys, Antarctica. These incubations are much longer than those published to date, which are typically 24 hours in duration. Our aim is both to quantify the rates of P and R within cryolake sediment on these timescales, and to assess the interplay of microbial processes on the sediment surface and within the body of the sediment. We use these data to assess whether Antarctic cryolake ecosystems are in a state of net production or consumption of organic carbon.

Methods

Standard cryoconite incubation methods using oxygen microoptodes were employed (Hodson *et al.*, 2010b; Telling *et al.*, 2010; Bagshaw *et al.*, 2011), with experiment durations of one week for field incubations and 150 days for laboratory experiments. We equate dissolved oxygen concentration with carbon production (Telling *et al.*, 2010). Briefly, the field experiments were run *in situ* using cryolake sediment from Canada Glacier, and laboratory experiments with incubated cryolake sediment from Joyce Glacier in conditions which mimic the glacier surface in terms of temperature, light and gas exchange. Uniform sediment depth of 1 cm was employed in all incubations. Full details of methods, instruments and analyses are available in the Supplementary Information.

Results

The mean organic carbon (OC) and inorganic carbon (IC) content of the Joyce Glacier cryolake sediment were 0.12 ± 0.03 % ($n = 6$) and 0.34 ± 0.03 % ($n = 6$), respectively. For comparison, Canada Glacier cryoconite OC and IC were

0.18 ± 0.23 % ($n = 117$) and 0.07 ± 0.11 % ($n = 10$), respectively. The porosity of the sediment was 34 ± 11 % ($n = 117$). Heterotrophic processes (R) dominated throughout the 200 hour field experiment (Fig. 1). Oxygen decreased systematically over the first 100 hours in both the dark and light bottles. The absolute values of P, R and NEP are shown in Figure 1b, and are of the order of several $\mu\text{g C}$ per gram of wet sediment throughout the experiment. This is consistent with data reported by Hodson *et al.* (2010a) for incubations of cryoconite from Blue Ice in East Antarctica.

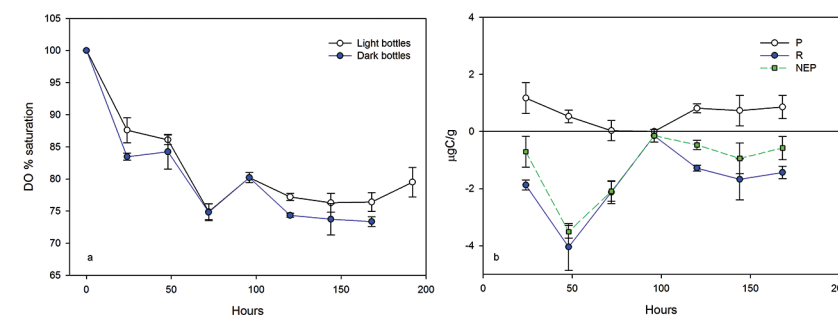


Figure 1 (a) Oxygen concentrations in dark and light bottles during the 200 hr incubation of cryolake sediment from Canada Glacier with (b) corresponding values of P, R and NEP.

Dissolved oxygen (DO) variations in the long-term laboratory incubations of cryolake sediment from Joyce Glacier also show net heterotrophy during the first week (200 hr, Fig. 2), and DO concentrations in the light and dark bottles again show strong similarity. The DO concentrations begin to diverge after 380 hr (16 d), with the light bottles eventually becoming supersaturated after 1000 hr (40 d). The DO concentrations in the light bottles increase to 140 % saturation after 250 hr, a value that has been observed in cryoconite holes on Canada Glacier (Tranter *et al.*, 2004; Bagshaw *et al.*, 2011). The dark bottles become increasingly undersaturated, falling to values of 23 %.

The overall NEP in these long term incubations is $110 \mu\text{g C}$. The dissolved inorganic carbon (DIC) content in the deionised water at the start of the experiment was $\sim 32.2 \mu\text{eq L}^{-1}$, or $39 \mu\text{g C}$, as calculated by PHREEQC assuming that the 100 ml water is at 0°C and in equilibrium with an atmospheric CO_2 concentration of 380 ppm. Since the OC content of the sediment was 0.12 %, the ~ 25 g of wet sediment contained $\sim 20 \text{ mg C}$ (water content of 34 %). These calculations demonstrate that the initial water does not contain sufficient DIC to account for all the new organic matter fixed on the surface, and suggests that carbon must be transferred via respiration in the sediment body to the surface to make up the shortfall in available DIC.



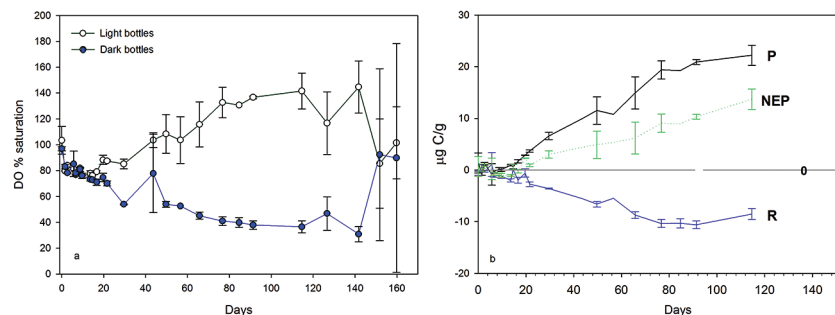


Figure 2 (a) Oxygen concentrations in dark and light bottles during the long term (one year) incubation of cryolake sediment from Joyce Glacier. **(b)** Corresponding values of P, R and NEP.

Discussion

Conceptual model. The initial stages of the longer term incubations (Fig. 2) are similar to the shorter term incubations (Fig. 1), in that both sets of incubations show unequivocal net heterotrophy over timescales of ~8 days. This is consistent with other studies which use 24 hr incubation of cryoconite from Antarctica (Hodson *et al.*, 2010a,b; Bagshaw *et al.*, 2011; Hodson *et al.*, 2013). However, the longer term incubations suggest that more complex interactions control the overall C balance, with net heterotrophy shifting to net autotrophy over timescales of >~20 days. Phototrophs in the sediment only fix organic carbon in the illuminated zone, often forming mat-like features (Hodson *et al.*, 2010b). The phototrophs were physically disturbed during transfer of the sediment into the incubation bottles at the start of the experiment, so we hypothesise that they can only begin to colonise the surface layer after the experiment begins. Consistent with this were the green-coloured algal mats and granules, visible on the sediment surface by the end of our longer light incubation, which have occasionally been observed in the field. By contrast, the heterotrophic community is less sensitive to physical disturbance and may even be stimulated by the burial of fresh surface organic matter, so it is unsurprising that the incubations show net heterotrophy during the initial stages.

A simple conceptual model of O_2 and DIC fluxes into and out of the sediment accounts for the observed changes in NEP. Figures 2 and 3(d-f) show that during the first days of the incubation (<50 hr) in the light bottles, rates of heterotrophic activity in the sediment are greater than the rate of photosynthesis in the surface layer. Hence, oxygen concentrations become lower in the sediment, and consequently there is net diffusion of oxygen from the overlying water into the sediment. Simultaneously, the relatively high rate of heterotrophic activity in the sediment results in elevated concentrations of DIC, and so there is diffusion of DIC from the sediment into the overlying water. Gradually, the phototrophs

increase in biomass, and start to elevate O_2 concentrations in the water, utilising DIC diffusing up through the sediment. Continued heterotrophic activity deeper in the sediment further depletes sediment O_2 . The rate of heterotrophic activity is likely to diminish over time at depth, as more labile organic matter sources are exhausted and DO concentrations diminish. Near surface layers, in closer diffusive contact with O_2 production, maintain higher DO concentrations. In the dark bottles, there are no phototrophic processes, and so concentrations of DO decrease continuously in both the water and sediment (Fig. 3a-c).

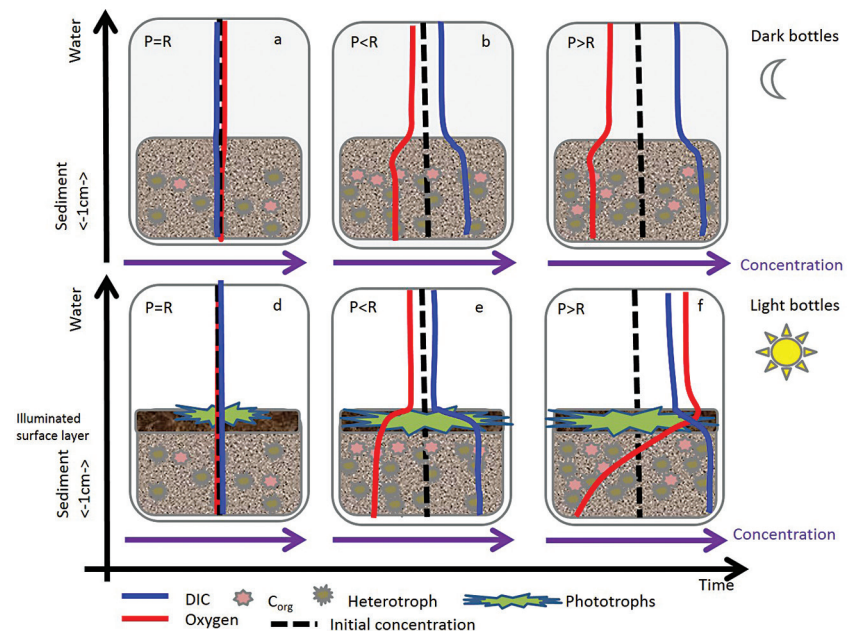
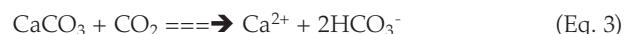


Figure 3 Conceptual model of the exchange of oxygen and DIC between the water column, heterotrophs in the deeper sediment layers and phototrophs concentrated at the sediment surface, during early (a,d) middle (b,e) and later (c,f) stages of the long-term incubation in the dark (a-c) and light (d-f) bottles. The panels are ordered left to right by time into the experiment, and the x-axis of each panel represents DIC and O_2 concentrations relative to starting values (dotted line).

Geochemical balancing. Heterotrophic activity in the sediment generates CO_2 , which is used in photosynthesis, but also dissolves carbonate minerals (Eq. 3). The chemical composition of the final dark and light bottles is consistent with this assertion, since both Ca^{2+} and HCO_3^- have increased. The final DIC concentrations are 761 and 241 $\mu\text{eq L}^{-1}$ respectively, and this presents, superficially, a problem with the calculation of P and R from DIC changes. If all the DIC was derived from heterotrophic reactions in the sediment, and the initial DIC concentration of the water was 32.2 $\mu\text{mol L}^{-1}$, then R would be equivalent



to 913 $\mu\text{g C}$, and P equivalent to 289 $\mu\text{g C}$. This implies that the incubation is net heterotrophic, and that 624 $\mu\text{g C}$ net of organic matter has been assimilated within the sediment, which is at odds with the conclusions reached based upon changes in DO alone.



The large discrepancy with the net autotrophy suggested by the DO changes (+110 $\mu\text{g C}$ vs -624 $\mu\text{g C}$), can be resolved by considering the geochemical balance of the incubation. Heterotrophic activity in the sediment produces CO_2 which chemically weathers carbonate and silicate minerals in the sediment. This causes an increase in Ca^{2+} , Mg^{2+} , K^+ and HCO_3^- in the sediment pore waters, which diffuse into the overlying waters. However, the concentration of these species is very different between the final light and dark bottles (Table 1). Photosynthesis in a closed aquatic system increases the pH of the solution and causes increasing saturation with aragonite and calcite (Table 1; Tranter *et al.*, 2004). It is notable that Table 1 shows that water is approximately saturated with calcite and aragonite in the light bottles, but is under-saturated in the dark bottles. Hence, as heterotrophic activity within the sediment causes Ca^{2+} and HCO_3^- to diffuse through the illuminated sediment surface into the overlying water, photosynthesis, predominantly at the sediment-water interface, saturates the waters and causes carbonate precipitation (Eq. 4). The latter prevents high accumulation of DIC in the light bottles, in contrast to the dark bottles. The actual concentration of Ca^{2+} and DIC found in solution is thus a kinetic balance between the rate of diffusion of Ca^{2+} and DIC from the sediment and the rate of photosynthesis. This is a similar scenario to that found at the seafloor (Wilson *et al.*, 1985).



The oxygen depletion in the dark bottle is $\sim 340 \mu\text{eq L}^{-1}$. The measured increase in DIC in the dark bottles is $\sim 730 \mu\text{eq L}^{-1}$, over double that inferred from the oxygen measurements. This suggests that carbonate minerals are being dissolved in the sediment, rather than silicate minerals, since one mole of rock DIC is liberated for each mole of CO_2 generated from oxidation of organic matter. This supports our assertion that carbonate dissolution supplies the additional DIC for the positive NEP that was measured.

Significance for carbon budgets. These results demonstrate that glacier surface ecosystems such as cryolakes and cryoconite holes can exist in a state of net production. Processes of carbon cycling have long been documented in cryoconite holes (Tranter *et al.*, 2004; Bagshaw *et al.*, 2007; Foreman *et al.*, 2007; Stibal and Tranter, 2007), but the extent of the dependence of photosynthetic organisms concentrated at the surface of the sediment layer on heterotrophic processes deeper in the sediment has not been fully discussed in the literature to date. This inter-dependence may also help explain the link between sediment depth and P:R balance previously observed in short term (6-24 hr) cryoconite incubations (Telling *et al.*, 2012). The heterotrophic activity in the deeper sediment serves to relocate organic matter, fixed as CO_2 , from the deeper layers to the surface of the sediment, and to dissolve carbonate minerals. Should the carbonate minerals be

ancient, then the new organic matter fixed from their dissolved DIC will be old in radiocarbon terms. It follows that extracellular exudates and the contents of lysed and partially degraded cells this otherwise new, yet radiocarbon old, organic matter, will produce radiocarbon old dissolved OC (DOC). This combination of processes may help to explain why labile DOC in supraglacial runoff is radiocarbon old (Lawson *et al.*, 2014; Hood *et al.*, 2015). Microbes on glacier surfaces may utilise this ancient DOC in their metabolic processes and augment it with organic matter fixed from the dissolution of ancient carbonates.

Table 1 Initial deionised water (DIW) concentration and final concentrations of major ions, DO (% saturation), pH and the Saturation Index (SI) of calcite and aragonite in incubation waters after 360 days. Mean concentration ($\mu\text{eq L}^{-1}$ minus blanks) of each bottle type is reported. DIC* and SI were calculated from mean concentrations by PHREEQC (phreeqc.dat database), assuming that $T = 0^\circ\text{C}$, and that $\text{Cl}^- = \text{Na}^+$ in the calculation of DIC. *P* values for one-tailed paired student's t-tests show variance of: initial conditions vs. final dark and final light; and final light vs. final dark bottles.

Sample	Cl^-	NO_3^-	SO_4^{2-}	K^+	Mg^{2+}	Ca^{2+}	DO	pH	DIC*	SI _{aragonite}	SI _{calcite}
DIW (initial)	0	0	0	0	0	0	100	5.55	32.2	n/a	n/a
Light (final)	4.11	0	23.3	37.1	0.25	290	122	9.97	241	-0.08	+0.09
<i>St dev.</i>	0.01	0.04	8.84	0.50	8.34	68.7	8.06	0.49	n/a	n/a	n/a
T-Test (initial vs. light)	0.00	0.00	0.08	0.00	0.49	0.05	0.07	0.06	0.15	n/a	n/a
Dark (final)	4.84	61.9	24.9	71.1	48.6	735	22.5	8.66	761	-0.24	-0.40
<i>St dev.</i>	1.02	11.75	6.18	8.32	9.54	131	16.4	0.01	n/a	n/a	n/a
T-Test (initial vs. dark)	0.05	0.04	0.06	0.03	0.04	0.04	0.05	0.00	0.02	n/a	n/a
T-Test (light vs. dark)	0.25	0.04	0.45	0.06	0.01	0.10	0.05	0.08	0.01	n/a	n/a

Conclusions

Short-term field and longer-term laboratory incubations demonstrate that autotrophic and heterotrophic processes in glacier surface sediments are closely linked. In the short term, carbon consumption equals or exceeds production if the initial DIC concentrations in the waters are low. This is particularly the case when the sediment depth is sufficient to eliminate light beyond surface layers. If, however, there are sufficient carbonate minerals in the sediment which dissolve to provide additional DIC for fixing, net heterotrophy may eventually give rise to net autotrophy. The rate at which this occurs depends on dissolution of carbonate minerals and diffusion of DIC through the sediment into the surface; hence there is a relationship between primary production in cryoconite and sediment depth, as has previously been reported. We hypothesise that fixation of DIC from carbonate dissolution and the consequence recycling of organic matter has the



potential to form radiocarbon old DOC from otherwise young organic matter. These results demonstrate that microbial communities on glacier surfaces do have the potential to accumulate carbon on timescales of months to years.

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Additional Information

Supplementary Information accompanies this letter at www.geochemicalperspectivesletters.org/article1605

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