Viral impacts on bacterial communities in Arctic cryoconite

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Abstract
The surfaces of glaciers are extreme ecosystems dominated by microbial communities. Viruses are found in abundance here, with a high frequency of bacteria displaying visible virus infection. In this study, viral and bacterial production was measured in Arctic cryoconite holes to address the control that viruses play in these highly truncated ecosystems. Mean bacterial carbon production in the sediments of cryoconite holes was found to be 57.8 ± 12.9 ng C g⁻¹ dry wt. h⁻¹, which predicted a mean of 1.89–5.41 × 10⁶ cells g⁻¹ dry wt. h⁻¹ based on a range of conversion factors. Relative to this, virus production was found to be high, up to 8.98 × 10⁷ virus like particles g⁻¹ dry wt. h⁻¹ were produced, which is comparable to virus production in sediments around the globe. The virus burst size was assessed by transmission electron microscopy and found to be amongst the lowest recorded in the literature (mean 2.4). Hence, to account for the measured virus production, the viral induced bacterial mortality was calculated to be more than capable of accounting for the mortality of all bacterial production. The data presented here, therefore, suggests that viral induced mortality is a dominant process for the release and recycling of carbon and nutrients in supraglacial ecosystems.

Keywords: virus, bacteriophage, cryoconite, glacier, DOM

Non-standard abbreviations

| Abbreviation | Description |
|--------------|-------------|
| BDC          | Bacterial direct counts |
| BCP          | Bacterial carbon production |
| Bₜ           | Burst size |
| CC           | Carbon content (cell⁻¹) |
| FVIC         | Frequency of visibly infected cells |
| GrIS         | Greenland ice sheet |
| NCP          | New cell production |
| VBR          | Virus to bacteria ratio |
| VIBM         | Virus induced bacterial mortality (VMM ÷ NCP × 100) |
| VLP          | Virus like particles |
| VMM          | Virus mediated mortality (VP ÷ Bₜ) |
| VP           | Virus production |
| VT           | Virus turnover (VP ÷ VLP) |

1. Introduction

Sedimentary ecosystems contain highly abundant virus communities which require high rates of new virus production to be maintained (Danovaro et al 2008a). In freshwater and marine sediments around the globe, virus production rates
of $0.2–19.8 \times 10^7$ virus like particles (VLP) $g^{-1} h^{-1}$ have been reported (Danovaro et al. 2008a, 2008b). Such large scale virus production comes at a significant cost to heterotrophic bacterial hosts, as viral release from infected cells is generally via lysis. Lysis also releases cellular carbon and nutrients back into the dissolved and bioavailable particulate phase, effectively diverting the flow of carbon away from higher trophic levels, whilst maintaining its availability for the remaining microbial community (Wilhelm and Suttle 1999). Viruses play a significant role in the carbon and nutrient transformations in sedimentary ecosystems. Between 10% and 100% of all bacterial carbon production is channelled through viral processes (Danovaro et al. 2008a and references therein).

The surfaces of glaciers are extreme environments, characterized by persistent low temperatures, yet they harbour abundant communities of microorganisms which cycle carbon and nutrients (Stibal et al. 2012a). The most abundant and active microbial communities are found in the small, water filled depressions known as cryoconite holes (Hodson et al. 2008). Cryoconite is dark material on glacial ice that may arise from the surrounding moraines, tundra, bed of the glacier (Wharton et al. 1985, Fountain et al. 2004, Hodson et al. 2010), or may even be produced in situ by carbon fixation (Anesio et al. 2009). The dark colouration of the material causes it to melt into the ice maintaining a pool of water above. Cryoconite holes are typically tens of cm wide and deep, with water temperatures relatively constant at $\sim 0.1 ^\circ C$ (Säwström et al. 2002). Cyanobacteria account for the majority of carbon fixation (Stibal et al. 2006) and primary production is approximately balanced by respiration rates, depending on sediment depth (Telling et al. 2012). However, bacterial production only accounts for $<10\%$ of the respiration values (Hodson et al. 2007, Anesio et al. 2010). In a previous study, bacterial production was not correlated to bacterial biomass, suggesting a strong top-down control on heterotrophic microbial abundances in cryoconite holes (Anesio et al. 2010). Grazers, such as ciliates and tardigrades, are present (Sømme 1996, Porazinska et al. 2004), but their abundances are relatively low (Säwström et al. 2002), suggesting an alternative control on bacterial abundances.

Viruses are likely to be important entities in cryoconite holes, responsible for a significant portion of heterotrophic bacterial mortality (Säwström et al. 2007, Anesio et al. 2007). The viral induced destruction of host cells and the release of cellular carbon and nutrients may be important for the continued production of the non-infected microbial community. Whether microbial communities and organic carbon build up on glaciers or are washed out to hydrologically connected ecosystems remains an important question. DOC in supraglacial runoff is believed to be derived, in part, from in situ microbial processes (Hood et al. 2009). As a significant proportion of organic carbon may flow through viral mediated processes, there is a pressing need to investigate the impact of viruses on microbial communities and their potential to influence carbon cycling in these environments. In this study, the viral communities in the sediment of cryoconite holes are addressed. Here, virus abundances have been shown to be over an order of magnitude higher than the overlying waters (Anesio et al. 2007) and the vast majority of microbial activity on a glacier takes place here. For the first time, rates of virus production are calculated and related to bacterial activity, allowing for the impact of viruses on the heterotrophic bacterial community to be estimated.

2. Methods

2.1. Study area and sample collection

This study addressed viral dynamics in cryoconite holes over two consecutive field seasons in Svalbard and Greenland. The Svalbard study centred on two valley glaciers, Midtre Lovénbreen (ML) and Austre Brøggerbreen (AB), near Ny-Ålesund (78°55’N 11°55’W, figure 1). Virus and bacterial production was measured in incubation experiments on the 25 July 2009 on sediment sampled from cryoconite holes at point ML, and on the 4 August 2009 from site AB.
(figure 1). Between June and August 2010, sampling and activity measurements were conducted on the western margin of the Greenland ice sheet (GrIS) around Kangerlussuaq. The study sites for activity measurements were approximately 1 km from the ice margin on the Russell Glacier (RG) at approximately 67°09’39.7”N, 50°05’52.7”W (figure 1). Viral production was measured in two independent cryoconite holes at RG1 on 15 June 2010 and three independent cryoconite holes on 27 July 2010 at RG2 (figure 1 and table 1). A transect was also conducted via helicopter on 2 August 2010 to measure virus and bacterial abundances throughout the entire ablation zone of the GrIS (sample points 5–42 km); (figure 1). These points represented elevations of ~550 m above sea level at point RG1 to 1186 m above sea level at 42 km.

2.2. Virus and bacterial counts

For enumeration of viruses and bacteria, 1 ml of cryoconite was sampled with a large pipette and transferred into a sterile 15 ml centrifuge tube. The sample was mixed with 9 ml of 30 kDa glacial ultraltrate which had a virus concentration of at least four orders of magnitude lower than the sediment and is hence referred to as virus-free water. This was shaken vigorously for 2 min. Fifteen seconds after cessation of shaking, 100 µl of supernatant was sampled and fixed with glutaraldehyde (2% final conc.), which allowed us to detect viruses at concentrations of 10⁶ VLP g⁻¹ or greater in this instance. Samples were filtered onto 0.02 µm Anodisc filters (Whatman) within 24 h, stained with SYBR gold (Invitrogen) and counted using epifluorescence microscopy filters (Whatman) within 24 h, stained with SYBR gold (Invitrogen) and counted using epifluorescence microscopy (Anesio et al 2007). Bacterial biovolume was also calculated by measuring approximately 2000 individual bacteria from six cryoconite holes (three from RG1, two from ML, one from AB) using an F-view II CCD (Olympus) and digitally measuring the length (L) and width (W) using Cell^f^ software (Olympus) of bacteria in three fields of view per cryoconite. Cell biovolume (V) was calculated by using the formula \( V = (\pi/4)W^2 (L - \frac{W}{2}) \). The mean biovolume from the six cryoconite holes was used in further calculations. Biovolume (µm³) was subsequently converted to carbon content (CC; fg cell⁻¹) by using a range of suitable conversion factors in the literature. Based on a review by Posch et al (2001) we chose CC conversion factors that are in common use in the literature. Because ultrafiltration is the usual method to pellet both virus and host and host to TEM grids (Bettarel et al 2006). In this study, the low speed centrifugation used to pellet bacteria, but not viruses, greatly reduced the free viruses. This allowed use of a lower detection limit of two phages per cell in a similar fashion to Säwström et al (2007). The frequency of infected cells (FVIC) and burst size (Bc) were calculated from the mean and standard deviation of the six cryoconite holes.

2.4. Virus production

Virus production (VP) was determined in cryoconite sediment samples using the dilution method (Mei and Danovaro 2004). A 1:10 sediment: virus-free water dilution was achieved for each of three sub-replicates per cryoconite hole in three holes from Svalbard and five from Greenland. Virus-free water (13.5 ml) was added to 1.5 ml cryoconite sediment to significantly reduce encounter rates and new virus infections. Each incubation was conducted for 24 h in the dark at in situ temperatures. To determine the virus increase, subsamples of 100 µl were removed at approximately 4 h intervals and immediately fixed with 0.02 µm-filtered glutaraldehyde (2% final conc.) before slide preparation and viral counts by epifluorescence microscopy as above. VLP were counted at each time point. VP was calculated by plotting a first order regression of VLP against time during the first increase in VLP numbers in each of the three sub-replicates. To confirm viruses were not simply detaching from the sediment and influencing counts, a killed control incubation was performed by adding glutaraldehyde (2% final conc.) to an extra replicate from each sample location and treated as above. All counts were normalized to dry weight by desiccation at 105°C for 24 h.

To determine the significance of lysogeny in cryoconite holes, the induction agent mitomycin C was added to triplicate cellulose ester filter (SSWP Millipore). To further separate the bacteria from the sediment matrix, a 200 µl aliquot of the filtered sediment extract was centrifuged onto a 70% sucrose cushion at 10 000 × g for 10 min. The top layer of this mixture, plus 100 µl from the top of the sucrose cushion, were removed and made up to 2 ml with 2% glutaraldehyde. This mixture was then pelleted at 10 000 × g for 5 min. The supernatant was removed and discarded before the pellet was resuspended in 1 ml 2% glutaraldehyde. The dilution step and further pelleting served to reduce the background level of viruses which remained in the supernatant. 5 µl of each sample was placed onto a carbon coated 400-mesh Cu grid resting on filter paper. Grids were left overnight to dry, before being negatively stained for one minute with 2% uranyl acetate and then rinsed with deionized distilled water. Two grids per cryoconite were examined for visibly infected bacterial cells at 80 kV and 20 000–40 000× magnification. A cell was considered infected when two or more viruses were visualized inside a cell based on a dark staining and a clearly recognizable round or hexagonal capsid structure. Normally, counting cells with such low numbers of virus particles inside increases the risk of counting cells that are simply resting on top of viruses as infected bacteria. This is because ultrafiltration is the usual method to pellet both virus and host to TEM grids (Bettarel et al 2006). In this study, the low speed centrifugation used to pellet bacteria, but not viruses, greatly reduced the free viruses. This allowed use of a lower detection limit of two phages per cell in a similar fashion to Säwström et al (2007). The frequency of infected cells (FVIC) and burst size (Bc) were calculated from the mean and standard deviation of the six cryoconite holes.
Table 1. Mean virus and bacterial abundances and activity measurements calculated in cryoconite hole sediments from Svalbard and Greenland. (Note: all values are per g dry wt. sediment ± standard deviation of independent cryoconite holes except AB which is ± standard deviation of three replicates from the same cryoconite. VBR—virus to bacteria ratio; VBM—virus induced bacterial mortality; VMM—virus mediated mortality).

| Glacier | Position | Code | n Date | Viruses (10^3 VLP g⁻¹) | Bacteria (10⁶ cells g⁻¹) | VBR | Virus production (10⁴ VLP g⁻¹ h⁻¹) | Virus turnover (ng C g⁻¹ h⁻¹) | Bacterial productiona (10⁶ Cells g⁻¹ h⁻¹) | Bacterial turnovera (d⁻¹) | VMMb (10⁶ g⁻¹ h⁻¹) | VBM ab (%) |
|---------|----------|------|--------|-------------------------|--------------------------|-----|-------------------------------|-----------------------------|--------------------------------|----------------|----------------|-------------|
| Midtre  | 78°53′25.57″N 12°3′16.32″E | ML   | 2 25/07/09 | 6.26 ± 0.90 | 3.99 ± 0.29 | 1.6 | 8.84 ± 0.20 | 0.134 ± 0.024 | 45.6 ± 14.36 | 1.49–4.27 | 0.089–0.255 | 36.8 | 911–2606 |
| Austre  | 78°53′51.29″N 11°49′33.71″E | AB   | 1 01/08/09 | 7.52 ± 4.23 | 3.79 ± 0.27 | 2.0 | 8.17 ± 2.72 | 0.109 ± 0.071 | 48.6 ± 14.1 | 1.59–4.55 | 0.101–0.288 | 34.0 | 748–2139 |
| Russell | 67°9′39.71″N 50°0′52.66″W | RG1  | 1 15/06/10 | 13.5 ± 2.58 | 3.35 ± 0.23 | 4.0 | 6.38 ± 0.11 | 0.048 ± 0.004 | 72.7 ± 0.53 | 2.38–6.81 | 0.171–0.489 | 26.6 | 390–1115 |
| Russell | 67°9′39.20″N 50°0′52.76″W | RG2  | 3 27/07/10 | 8.23 ± 2.79 | 2.68 ± 0.00 | 3.1 | 4.87 ± 0.74 | 0.064 ± 0.021 | 64.2 ± 12.21 | 2.10–6.01 | 0.188–0.539 | 20.3 | 342–978 |
| GrIS    | 67°5′34.70″N 50°1′8.90″W |      | 5.4  | 02/08/10 | 23.2 ± 1.42 | 19.6 ± 1.34 | 1.2 |                          |                              |                              |                  |                |             |
| GrIS    | 67°6′15.40″N 49°48′26.60″W |      | 11   | 02/08/10 | 24.5 ± 1.66 | 18.2 ± 2.87 | 1.3 |                          |                              |                              |                  |                |             |
| GrIS    | 67°6′56.70″N 49°24′5.20″W |      | 27   | 02/08/10 | 20.4 ± 3.93 | 9.71 ± 1.42 | 2.1 |                          |                              |                              |                  |                |             |
| GrIS    | 67°7′36.40″N 49°0′36.00″W |      | 42   | 02/08/10 | 14.4 ± 0.66 | 7.65 ± 0.67 | 1.9 |                          |                              |                              |                  |                |             |

Mean 14.8 ± 7.3 8.62 ± 6.78 2.1 7.06 ± 1.80 0.091 ± 0.043 57.8 ± 12.9 1.89–5.41 0.137–0.393 29.4 598–1710

a Calculations are expressed as a range assuming 10.68–30.53 fg C bacterial cell⁻¹ calculated from mean cell biovolume of 0.102 μm³ assuming a range of carbon conversion factors from 105V to 2181V where V = μm³ (Posch et al 2001).

b Calculation assumes a burst size of 2.4 from the TEM measurements and that all infections are lytic.
sediment dilutions as above to a final concentration of 1 \( \mu g \) ml\(^{-1} \). Treatments were incubated for 24 h before a 100 \( \mu l \) subsample was removed, fixed and made into a slide, as described above. Triplicate incubations in which mitomycin C was not added, served as controls. The percentage of lysogenic bacteria was calculated according to Weinbauer and Suttle (1996).

2.5. Bacterial production

Bacterial carbon production (BCP) was measured alongside VP in each cryoconite hole \((n = 8)\) by \(^3\)H-leucine incorporation, modified from the method of Smith and Azam (1992) (see supplementary information 1, available at stacks.iop.org/ERL/8/045021/mmedia). Briefly nine 1.5 ml subsamples from each cryoconite hole were removed and transferred to sterile 1.7 ml microcentrifuge tubes. Incorporation was started by addition of \(^3\)H-leucine (100 nM final conc.). Three of the tubes were incubated as killed controls by the immediate addition of 100 \( \mu l \) glutaraldehyde. The tubes (six live, three killed) were incubated at \( in \text{ } situ \) temperature for 3 h and incorporation was stopped by addition of 100 \( \mu l \) glutaraldehyde (2% final conc.). BCP was converted to new bacterial cell production (NCP) by dividing BCP by the conversion factors calculated from the biovolume (10.68–30.53 fg C cell\(^{-1} \)) to produce a range of values.

2.6. Viral dynamics calculations

Viral turnover (VT) was calculated by dividing VP rates by initial viral abundances. The virus mediated mortality (VMM) of bacterial cells (cells lysed g\(^{-1} \) h\(^{-1} \)) was calculated by dividing VP values by the viral burst size \((B_z)\). VMM was further divided by the NCP rate (cells g\(^{-1} \) h\(^{-1} \)), calculated from \(^3\)H-leucine incorporation, to give a range of value for the virus induced bacterial mortality (VIBM) in each incubation expressed as a percentage of bacterial production.

2.7. Statistics

All data were tested for normality prior to statistical analysis using a Kolmogorov–Smirnov test conducted in SPSS (16.0) or SigmaPlot (12.0).

3. Results

3.1. Virus and bacterial abundances

Virus abundances in independent cryoconite holes in both Greenland and Svalbard ranged from 5.62 \times 10^8 to 24.5 \times 10^8 VLP g\(^{-1} \) dry weight sediment (ML and GrIS 11 km respectively), with a mean across all sites of 14.8 \pm 7.3 \times 10^8 VLP g\(^{-1} \) (table 1). Bacterial abundances ranged from 2.68 \times 10^8 to 19.6 \times 10^8 cells g\(^{-1} \) (RG2 and GrIS 5.4 km respectively), with mean abundances of 8.62 \pm 6.8 \times 10^8 cells g\(^{-1} \). We can report that the coefficient of variation of VLP and BDC within cryoconite holes was generally less than 0.3, which was similar to the variation between cryoconite holes from the same site.

VLP and bacterial abundances were positively and significantly related across all sample sites (regression equation \( y = 0.988x + 6.121 \times 10^8, n = 12, R^2 = 0.76, P < 0.001 \)) with a virus to bacteria ratio (VBR) between 1.2 and 4.4 (mean 2.1 \pm 1). Over the 42 km transect of the ablation zone of the Greenland ice sheet. Distances are from the nearest deglaciated point.

![Figure 2. Virus like particle abundance (solid circles) and bacterial abundances (open circles) in cryoconite holes over a transect of the ablation zone of the Greenland ice sheet.](image-url)

For the purposes of comparing abundance variability, samples from Greenland were divided into outlet glacial locations and the ice sheet itself. Stibal et al (2012b) previously demonstrated that the marginal sites of the GrIS (<3.6 km from the margin) are physically and chemically different from the ice sheet interior because of their slope and proximity to deglaciated areas. Hence all cryoconite holes \((n = 5)\) from sites RG1 and 2 (Greenland) (~1 km from the ice sheet margin) were considered part of the Russell Glacier (figure 1). Abundance data from 5.4 to 42 km on the transect across the GrIS \((n = 12)\) were considered together as representative of the main ablation zone of the ice sheet and are subsequently referred to as GrIS sites. Cryoconite holes from ML and AB represented Svalbard cryoconite holes \((n = 3)\). Using the above criteria, there were significant differences in VLP abundances between sites (ANOVA \( P = 0.001 \)). GrIS VLP abundances (sites 5.4–42 km) were approximately 2–4 times greater than the glacial sites in Svalbard and Greenland (post hoc Scheffé,
**Figure 3.** Transmission electron microscopy images of bacteria extracted from cryoconite hole sediment showing the minimum and maximum observed burst size of 2 and 4 viruses per cell. Cells were considered infected when two or more virus particles were visible. Scale bar represents 1000 nm.

\[ P < 0.01 \]. However, no significant differences were detected in VLP abundance between Svalbard and Greenland glacial sites (post hoc Scheffé, \( P > 0.05 \)). Mean bacterial abundances were approximately 4 times greater on the main GrIS (Sites 5.4–42 km) than the Svalbard or Greenland glacial sites (ANOVA \( P < 0.001 \) followed by post hoc Scheffé, \( P < 0.05 \)), but again no significant differences were found between Svalbard and Greenland glacial bacterial counts (post hoc Scheffé, \( P < 0.05 \)).

### 3.2. Burst size

Visible virus infection in bacterial cells was clearly resolved using TEM (figure 3) by visualizing over 140 bacteria. Bacterial cells exhibited very low numbers of visible virus particles with a range of between 2 and 4 viruses per cell (mean 2.4 ± 0.5). No cells appeared replete with viruses. All viruses infecting bacteria were round or hexagonal in shape and were approximately 30–90 nm across. The frequency of visibly infected cells (FVIC) was calculated as 21 ± 6%.

### 3.3. Virus and bacterial production

Rates of virus production (VP) in independent cryoconite holes ranged from 4.41 × 10^7 VLP g\(^{-1}\) h\(^{-1}\) (RG2) to 8.98 × 10^7 VLP g\(^{-1}\) h\(^{-1}\) (ML) with a mean of 7.06 ± 1.8 × 10^7 VLP g\(^{-1}\) h\(^{-1}\) across all sites (table 1). No increase in VLP abundances was detected in the killed controls and lysogeny was also not detected in any of the mitomycin C incubations during the VP experiments. Viral turnover (VT) was calculated to range from 0.04 h\(^{-1}\) (RG2) to 0.16 h\(^{-1}\) (ML). Mean bacterial biovolume from cryoconite hole sediment was calculated to be 0.102 \( \mu \)m\(^3\), thus the mean bacterial carbon content (CC) for cryoconite heterotrophic bacteria was calculated to range from 10.68 to 30.53 fg C cell\(^{-1}\). Bacterial carbon production (BCP) in cryoconite holes ranged from 35.4 to 73.3 ng C g\(^{-1}\) h\(^{-1}\) (ML and RG2 respectively), (mean 57.8 ± 12.9 ng C g\(^{-1}\) h\(^{-1}\)). Using the CC conversion values BCP was equivalent to a mean new cell production (NCP) rate of 1.89–5.41 × 10^6 cells g\(^{-1}\) h\(^{-1}\). Mean bacterial turnover, expressed as the ratio of NCP to bacterial abundance, ranged from 0.137 to 0.393 d\(^{-1}\). VP was significantly related to bacterial abundance and could be predicted by the regression equation \( y = 0.298x - 3.325 \times 10^7 \) (\( n = 8, R = 0.943, P < 0.005 \)). There was no significant correlation between bacterial production and virus production (\( n = 8, R = 0.56, P > 0.05 \)), nor any correlation between bacterial production and bacterial abundance (\( n = 8, R = 0.46, P > 0.05 \)). By using the burst size derived from TEM measurements, viruses were calculated to account for the mean abatement of 598%–1710% of the heterotrophic bacterial production across all sites (table 1).

### 4. Discussion

This study provides evidence that viruses are highly abundant and active components of cryoconite hole ecosystems, with the potential to significantly impact upon bacterial mortality and the cycling of organic carbon. Virus dynamics in cryoconite holes appear to proceed at rates comparable to other sedimentary ecosystems, despite the extreme conditions they inhabit. Virus abundances and production are similar to median values reported from both freshwater and marine global sediments (table 2; Danovaro et al 2008a, 2008b). The high rates of viral production measured in cryoconite holes results in a rapid mean viral turnover of 0.091 h\(^{-1}\), which is also paralleled in marine sediments (mean 0.071 h\(^{-1}\); Danovaro et al 2008b). These high rates of virus production may be key to maintaining viral numbers in supraglacial ecosystems in response to the continual destruction of viruses in by such factors such as UV-B radiation (Suttle and Feng 1992), extracellular enzymatic degradation and adsorption to sediment particles (Noble and Fuhrman 1997). Assuming lytic interactions, virus production must come at the detriment of a large number of host organisms. Whilst both cyanobacteria and algae are also subjected to viral infection, heterotrophic bacteria are usually the main hosts for viruses in the environment because of their numerical dominance. Cyanobacteria made up 0.5%–18.3% (mean 10.5%) of the total cell counts over a similar transect of the GrIS (Stibal et al 2012b), and <0.8 ± 1.4% of the microbial community by abundance on four Svalbard glaciers (Stibal et al 2006). Hence, the most abundantly available hosts for viruses in cryoconite holes are heterotrophic bacteria. This is reinforced with TEM data which revealed that 21 ± 6% of the heterotrophic bacterial community displayed visible virus infection, meaning on average ~18% of the total virions in cryoconite sediments were intracellular at any one time. As visible infection only occurs in the latter stage of infection, the real infection rates are likely to be much greater. Concurrently, viral and bacterial abundances over all activity sites and across our Greenland transect were positively correlated, and virus production was strongly correlated with bacterial abundance, suggesting heterotrophic bacteria are the main virion production factories in cryoconite hole ecosystems. Our transect data further revealed that the greatest virus and bacterial abundances are found further into the ablation zone of the Greenland ice sheet at 5–11 km. This implies that our viral and bacterial activity measurements likely do not represent values across the ablation zone, which may
be significantly higher. Especially when considering virus production was correlated with bacterial abundance.

Assuming all viruses produced are from lytic infection of heterotrophic bacteria, viruses were calculated to be responsible for the mean abatement of 598–1710% of all heterotrophic bacteria, viruses were calculated to be significantly higher. Especially when considering virus production was correlated with bacterial abundance.

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DOM is recycled to the heterotrophic community, the overall efficiency of carbon uptake is reduced (Motegi et al. 2009). Thus the likely dominance of the viral shunt in cryoconite holes may help to explain the high rates of respiration relative to bacterial production previously found in these habitats (Anesio et al. 2010).

Given the potentially limiting nature of DOC on glacial surfaces, the continued viral mediated release of organic carbon may promote growth in the non-infected microbial community. However, supraglacial ecosystems may be subjected to significant flow of glacial meltwater, which could export DOC to downstream ecosystems. Over the Greenland ice sheet, debris bound organic carbon is significantly less at the marginal sites (sites < 5.4 km from the ice margin) and is negatively correlated with slope (Stibal et al. 2012b). Recent evidence also suggests dissolved organic matter (DOM) in glacial run off is composed of highly labile carbon and is a significant contributor to bacterial productivity in downstream marine ecosystems (Hood et al. 2009). Further to this, Hood et al. (2009) found that this glacial DOM is microbial in origin. Therefore, the virally induced release of organic carbon from cryoconite bound bacteria could enhance its export from supraglacial environments and stimulate microbial communities in hydrologically connected ecosystems.

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