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WP1, D1.7, D11 Role of viruses in controlling microbial mortality at the surface of glaciers

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Lead Author:	Annika Morische (AU)
Author(s):	
Contributors:	
Reviewed by:	Alexandre Anesio
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Estimation of the role of viruses in controlling microbial mortality at the surface of glaicers

1. The Role of Viruses in Supraglacial Habitats and their Influence on Carbon Cycling

Viruses play an integral role in marine and freshwater ecosystems, where they are among the most abundant and dynamic community members (Bratbak et al., 1990; Maranger & Bird, 1995; Maranger et al., 1994). Aquatic systems are dominated by bacteria, the main hosts of viruses, as viral replication is density dependent (Fuhrman, 1999). Within these systems, viruses can exert strong top-down control on microbial populations and influence biogeochemical cycling through the lysis of host cells. Viral lysis may be especially important in oligotrophic ecosystems, where released nutrients can be rapidly used by non-infected microorganisms (Noble & Fuhrman, 1999; Wilhelm & Suttle, 1999). Glacial surfaces and associated aquatic habitats, once considered inhospitable to active biological processes, are now known to sustain high microbial abundances (Anesio et al., 2009). Measurements from Arctic cryoconite holes indicate that viral abundances can reach 10^7 particles ml^{-1}, with virus-to-bacterium ratios suggesting that viral infection substantially control bacteria mortality in surface habitats (Anesio et al., 2009; Bellas et al., 2013).

Microbial host density and diversity in turn influence viral dynamics, with viral abundance generally increasing alongside host availability (Anesio et al., 2007). High viral production rates often exceed bacterial production, accounting for the loss of nearly all newly produced bacterial cells (Bellas et al., 2013). Studies in ultra-oligotrophic freshwater environments of Antarctica and the Arctic highlight the persistence of viral communities, as a large proportion of bacteria are visibly infected by phages despite low bacterial densities (Säwström et al., 2007). These findings indicate that in glacial systems, virioplankton can be sustained over time where host-density might be low and slow growing (Säwström et al., 2007). Moreover, the influence of viruses in these environments extends beyond immediate ecological effects. By employing diverse and sometimes unusual life strategies, viruses may shape the genetic structure of microbial communities and maintain long-term host associations (Bellas et al., 2015).

Transplantation experiments have shown that viruses from cryoconite holes can infect bacterial communities from proglacial lakes, demonstrating broad host ranges and the capacity for cross-ecosystem interactions (Anesio et al., 2007). Viral marker gene analyses have revealed a wide diversity of viruses in these habitats, including bacteriophages, cyanophages, nucleocytoplasmic large DNA viruses, and virophages, with hosts ranging from Cyanobacteria and Alphaproteobacteria to eukaryotic algae and amoebae (Bellas et al., 2015; Perini et al., 2024). Genome analyses uncovered multiple novel viral groups, including phage-plasmids with partition genes and toxin-antitoxin modules, as well as a phage carrying a CRISPR/Cas system capable of conferring immunity to its bacterial host against other phages. The glacier surface is therefore a reservoir of highly novel and endemic viral lineages, many of which cannot be taxonomically assigned and likely represent unique evolutionary adaptations to extreme conditions (Bellas et al., 2015). This viral diversity likely has implications for downstream environments, as shifts in viral community composition can alter microbial community structure and function beyond the glacier margin (Bellas et al., 2015; Liu et al., 2023).

Viral-mediated release of organic substrates is potentially a major pathway for dissolved organic matter (DOM) export from glacier surfaces. Under the “kill the winner” dynamic, higher microbial growth rates can trigger increased viral lysis, releasing labile DOM that is rapidly available to heterotrophic microbes downstream (Liu et al., 2023; Rassner et al., 2016). The transformation of refractory DOM into more labile forms through viral activity can alter the composition of DOM exported from glaciers, with potential consequences for downstream biogeochemical cycling and ecosystem functioning (Bellas et al., 2013; Ma et al., 2018; Zhao et al., 2019). As glaciers retreat due to climate warming, the potential of viruses in regulating microbial dynamics, facilitating carbon and nutrient fluxes, and shaping downstream ecosystems will become increasingly relevant.

2. Release of Dissolved Organic Matter During Viral Lysis

The lysis of microbial cells by viruses is likely an essential pathway for the release of DOM in aquatic ecosystems. In glacial environments, viral production can match or exceed bacterial production, contributing substantially to the DOM pool through the release of cellular contents. This process transfers particulate organic carbon (POC) contained within microbial biomass into the dissolved phase, where it becomes readily available for uptake by heterotrophic microorganisms (Anesio et al., 2009; Wilhelm & Suttle, 1999).

In oligotrophic polar waters, viral-mediated DOM release has been shown to support substantial microbial respiration, effectively forming a rapid recycling loop that links primary production, viral infection, and heterotrophic consumption (Middelboe et al., 1996; Säwström et al., 2007). Importantly, the composition of DOM resulting from viral lysis differs from that produced through grazing or natural senescence (Ma et al., 2018). In marine systems, viral lysis has been associated with the release of oxygen-rich, labile DOM, including intracellular peptides and nucleotides that supply bioavailable nitrogen and phosphorus, which are quickly recycled within the microbial food web (Heinrichs et al., 2022; Ma et al., 2018; Middelboe et al., 1996). Furthermore, studies of mountain and polar DNA viruses suggest that viral-host interactions can transform refractory DOM into more labile forms by altering host metabolism and through the lysis process (Liu et al., 2023). Thus, viral activity influences not only microbial community structure and metabolism but also plays a critical role in shaping carbon cycling and the composition of organic matter across ecosystems, from oceans to glacial habitats.

Given the high irradiance and rapid turnover of meltwater in glacial systems, the immediate bioavailability of DOM produced via viral lysis may disproportionately sustain microbial loop processes, especially during peak melt periods.

3. Estimated DOC Contribution from Viral Infection in Surface Ice Habiats

Viruses are integral components of glacial microbial ecosystems, shaping community structure through infection and lysis (Anesio et al., 2007; Bellas et al., 2015; Bellas et al., 2013; Liu et al., 2023). By releasing cellular carbon and nutrients back into the environment, they may play a key role in carbon cycling and the redistribution of organic matter in surface ice habitats (Bellas et al., 2013; Rassner et al., 2016). In Arctic cryoconite holes, bacterial abundances averages around 10^5 cells mL^{-1}, while ice has been reported to host between $2*10^3$ and $2*10^6$ bacterial cells(Stibal et al., 2015). Viral abundance is usally much higher and ranging around 10^7 cells in cryconite holes and 10^6 in ice cores. Säwström et al. 2007 reporeted an average of 26,1 %s visibly infected cells by bacteriophages.

(1) $$C_{release}[\mu gC \times ml^{-1}] = 0.261 \times bacterial\ abundance\ [cell \times ml^{-1}] \times (26 \times 10^{-9})[\mu gC \times cell^{-1}]$$

Assuming an average bacterial cell carbon content of 26 fg C $cell^{-1}$ (Troussellier et al., 1997), potential carbon released ($C_{release}$; Eq. 1) during a single lytic event could range around 0.7 µg C L^{-1}. This represents an instantaneous release at any given time, assuming the bacterial population is sustained and the proportion of infected cells remains constant. Applying the same estimations for infected cells and bacterial carbon content to bacterial and viral abundace estimiates from ice samples viral lysis of bacteria could libarate 0.013 to 13 µg C L^{-1}. The potential carbon release estimates presented here are conservative, as they only consider visibly infected bacteria and assume that all infected cells undergo lysis with complete conversion of cellular carbon to dissolved form. This approach does not account for the contribution of other microbial groups such as autotrophic algae, despite evidence from studies on glacial giant viral diversity indicating a broad range of potential hosts (Perini et al. 2024).

Viral processes likely represent an essential pathway for organic carbon release and recycling within supraglacial habitats. Viral burst sizes in glacial have been reported to be the lowest viral burst sizes recorded in the literature (mean = 2.4)(Bellas et al., 2013). Moreover, in cryoconite holes, mean heterotrophic bacterial carbon production has been estimated at 57.8 ± 12.9 ng C g^{-1} h^{-1} (Range = 35.4- 73.3 ng C g^{-1} h^{-1}) (Bellas et al., 2013), with values likely higher when autotrophic taxa such as cyanobacteria are considered. As, viruses have the potential to account for the loss of all bacterial production in cryoconites or more and given the prevalence of virus in glacial habitats, they are likely to represent a major controlling factor in microbial carbon release.

(2) $$\frac{0.6\ mg \times L^{-1}}{(57.8 \times 10^{-6}\ )mg \times g^{-1} \times h^{-1}} = t_{target}$$

Assuming a hypothetical cryoconite hole with a volume of 1L and 10 g of dry weight, and excluding degradation and transformation processes, viral lysis could release an amount of carbon in approximately 1038 hours or 43 days (t_{target}; Eq. 2) equivalent to the average reported DOC content of a cryoconite hole, i.e., 50 µM (0.6 mg L^{-1}) as reported by Holland et al. (2019). Given the high turnover potential implied by this calculation, viral-mediated carbon release may constitute a substantial and rapid source of labile DOC in supraglacial environment.

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