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Virus removal by glacier-derived suspended fine sediment in the Arctic

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ABSTRACT

Viruses are a major source of mortality for phytoplankton and bacteria and are therefore seen as drivers of food web dynamics and biogeochemical cycling in the marine pelagic environment. Previous studies have shown that aquatic viruses adsorb to suspended sediment, which theoretically decreases the mortality pressure on their microbial hosts. This process is of particular ecological importance in the Arctic, where coastal systems contain large amounts of suspended fine-sediment, supplied by melting and calving glaciers. The aim of this study was to investigate the effects of glacier-derived fine sediment on marine Arctic microbes during summer in Storfjorden, Svalbard (78°N, 20°E). We sampled for microbial abundances over transects with increasing sediment concentration towards three different glaciers, and examined the adsorption of the natural virus community to previously collected glacier-derived sediment. Our data show declined abundances of phytoplankton (< 20 μm) and bacteria towards all 3 glaciers. Viral abundances, however, showed an even stronger decline with the virus to bacterium ratio (VBR) reducing from 10–16 in open water to 3–6 in the vicinity of the glaciers. Linear regressions showed negative linear relationships of VBR with turbidity and sediment. This negative relation between suspended sediment and Arctic marine virus abundances is further confirmed by very high adsorption rates of in situ Arctic marine virioplankton upon addition of glacier sediment. Sediment additions (of ecologically relevant concentrations of 100, 200 and 500 mg L^{-1} to natural seawater) caused viral losses varying between 38 and 66% of the total virus community. Such high viral losses translate into lower contact rates between host and virus, reducing host mortality. Sediment inflow through glaciers may thus affect marine pelagic food web dynamics via viruses, possibly altering the main flow of carbon and other elements in the process. Further study to the possible consequences for food web structure and biogeochemical cycling is essential, as Arctic glacier-derived sediment inflow does not only fluctuate seasonally but is also expected to increase with global warming.

1. Introduction

Melting and calving glaciers in the polar regions are responsible for high supplies of sediment into coastal waters (Hill and Nadeau, 1989; Svendsen et al., 2002). This sediment is produced by abrasion of the underlying bedrock and typically contain very small clay and silt particles (Hill and Nadeau, 1989). Especially the smallest size classes remain suspended in the water column for a very long time, giving a milky white color to the water also known as 'glacier milk' (Svendsen et al., 2002). These particles are suspended throughout the water column and overlap in size range with the microbial plankton, i.e. protists, bacteria and viruses (Sommaruga, 2015). Disturbances at the base of the marine pelagic food web can have large consequences for trophic transfer efficiency and biogeochemical fluxes (Sommaruga, 2015; Fuhrman et al., 2015). The increased turbidity that results from suspended sediment may reduce light availability and as such can limit phytoplankton primary production (Cloern, 1987), whereas zooplankton grazing on protists and bacteria may be reduced due to the interference or ingestion of sediment particles (Arendt et al., 2011; Salter et al., 2011; Sommaruga, 2015).

Another suggested effect of glacier sediment is the adsorption of viruses to these particles (De Corte et al., 2011; Maat et al., 2019). Viruses are parasites that use the metabolism of the host to propagate. In the pelagic marine environment viruses typically reach abundances of 10^{10} L^{-1} of which the majority infect the numerically dominant unicellular microorganisms (Suttle, 2005). They drive microbial

Abbreviations: VBR, virus to bacteria ratio; VPR, virus to phytoplankton ratio

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community dynamics, kill a substantial share of the microbial biomass on a daily basis (Evans et al., 2009; Mojica et al., 2016), and are involved in the prevention and termination of phytoplankton blooms (Brussaard, 2004b). Lara et al. (2013) demonstrated that in the Arctic, viruses can kill up to 90% of the marine pelagic bacterial standing stock on a daily basis. Lytic viruses typically liberate their progeny through lysis of the host cell, releasing the host's cell content in the process. In this way viruses change the composition of dissolved organic matter in the pelagic zone, leading to increased bacterial respiration through a process called the viral shunt (Suttle, 2007). Hence, processes that affect viral activity can have a large indirect impact on the functioning of the whole system in terms of population dynamics, food web composition and biogeochemical cycling (Brussaard et al., 2008; Breitbart, 2012). As viral lysis is a density-dependent process, i.e. lower virus abundances reduce the chance for infection and host mortality, these influences of viruses on the food web and biogeochemical cycling could be mitigated by seasonal or long-term increases in sediment input.

Viruses adsorb to sediment particles through electrostatic binding, van der Waals binding or hydrophobic interactions and this binding is affected by variables such as pH, sediment mineralogy and size of the viruses (Moore et al., 1981, Syngouna and Chrysikopoulos 2010, Katz et al., 2018). Most studies on this topic are however in an experimental setting, whereas the number of in situ studies is limited (Hewson and Fuhrman, 2003; Drewes et al., 2016). Hence, only little is known on the ecological relevance of virus to sediment adsorption, especially for the rapidly warming polar waters. Only very recently, it was experimentally demonstrated that different virus populations, including an Arctic phycovirus, strongly adsorb to glacier-derived fine-sediment (up to 90%; Maat et al., 2019). Moreover, the production of progeny virus was strongly delayed in the presence of glacier sediment. By adsorption to sediment particles, the viruses are thus at least temporarily not available for infecting new host cells, and the viruses may even be removed long-term from the system when the sediment settles to the sea floor (Lawrence et al., 2002; Maat et al., 2019). If this holds true under natural conditions in Arctic coastal waters, the fine-sediment is expected to strongly reduce viral mediated mortality of microorganisms and consequently affect their population dynamics and the cycling of carbon and other key elements in the pelagic marine environment.

The melting and calving rate of glaciers, and subsequently the inflow of glacier-derived sediment into the water column, is largely driven by temperature (Luckman et al., 2015; Paterson, 2016). Sediment concentrations are generally higher in the summer season, which is also the period of highest biological productivity (Hop et al., 2002; Svendsen et al., 2002; Murphy et al., 2016). How long and to what distance sediment particles stay in the upper water column depends on the sinking rate of the sediment, water mass transport and water column mixing (Hill and Nadeau, 1989). Although complex, it can be anticipated that with global warming, the sediment inflow and concentrations in the water column will be higher, further increasing the ecological relevance of sediment-virus interaction.

The aim of this study was to investigate the effects of glacier-derived sediment on natural Arctic virus communities in Storfjorden, Svalbard in 2 ways: *i*) by analysis of the in situ virus to host ratio over a transect with increasing distance to 3 glaciers, and *ii*) by virus adsorption assays, i.e. addition of previously collected glacier-derived sediment to 0.2 μm filtered seawater and subsequent analysis of free virus abundances.

2. Materials & methods

2.1. Sampling

The research (conducted within the SEES Scientific Expedition Edgeøya Svalbard, August 2015) focused on 3 transects over increasing distance from glaciers in Storfjorden, Svalbard (Fig. 1): Dunérbukta (78.188889°N, 18.801944°E), Freemansundet (78.269167°N, 21.792778°E) and Russebukta (77.595°N, 21.045833°E), respectively

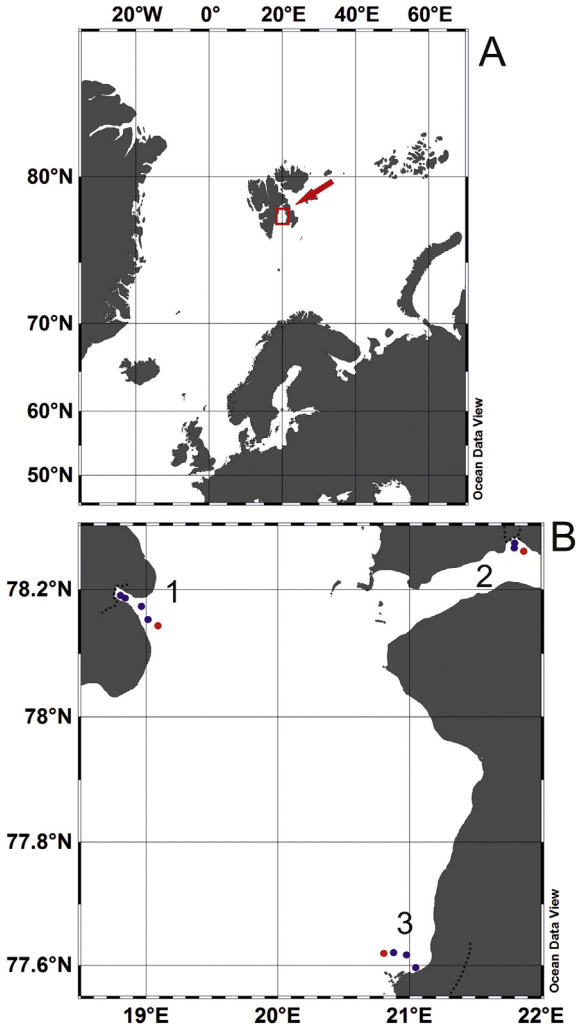

Fig. 1. Map showing the location of Svalbard in Northern hemisphere (A) and the sampled glacier sites in Storfjorden, Svalbard (B), being Dunérbukta (1), Freemansundet (2) and Russebukta (3). Sampling stations are depicted as blue and red dots of which the red ones were additionally sampled for the adsorption assays. The coastlines of the original map in panel B have been adjusted in Corel Draw to correct for glacier retreat. The black dashed lines represent the approximate glacier fronts in 2015. The maps with stations were made in Ocean Data View (Schlitzer, 2018). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

influenced by the tide-water glaciers Ulvebreen and Freemanbreen and the land-terminating glacier Kvalpyntfonna. Small motorized inflatable boats were used for sampling of physicochemical and biological variables. Surface water (0.5 m depth) was gently pumped into a 5 L PP vacuum bottle (Nalgene®, NY, USA) with a manual vacuum pump. Water was brought onboard the wet lab of M/V Ortelius, where samples were further processed.

2.2. Variables sampled

Temperature, salinity, chlorophyll *a* fluorescence (Chl-a) and turbidity were measured with a Seabird electronics CTD package (SeaBird 19+) equipped with an in-line fluorometer (WS3S, WETLabs), turbidity sensor measuring at 700 nm (ECO NTU, WETLabs), and a spherical sensor (SPQA, LICOR) for Photosynthetically Active Radiation (PAR).

Water for dissolved inorganic nutrient (nitrate and phosphate) analysis was filtered through a 0.2 μm Acrodisc Supor syringe filter (Pall, NY, USA) into a clean screw cap pony vials (Perkin Elmer, MA, USA) and stored at −20 °C until analysis in the home lab using a

Table 1
Water temperature (°C), salinity, turbidity (NTU), sediment concentration (mg L^{-1}) and concentrations (μM) of dissolved nitrate (NO_3^-) and phosphate (PO_4^{3-}) of the different sampling stations at different distances (km) from the 3 different glaciers sites. n.d. is not determined. *distance to shore for Russebukta.

	Distance*	Temperature	Salinity	Turbidity	Sediment	NO_3	PO_4
Dunérbukta 2015-08-22	0.37	2.2	29.5	7.8	37.0	0.52	0.11
	2.3	2.2	30.9	3.2	15.4	0.83	0.13
	4.5	2.3	31.2	2.2	11.3	0.25	0.07
	6.7	2.3	31.5	1.6	12.2	0.43	0.10
	8.7	2.5	31.8	1.2	12.6	0.64	0.13
Freemansundet 2015-08-24	0.46	−0.7	29.2	9.5	42.0	2.19	0.10
	1.1	0.9	31.3	8.3	23.9	0.57	0.15
	2.5	1.1	31.6	3.1	*n.d.*	0.37	0.16
Russebukta 2015-08-25	0.19	2.1	26.1	5.1	*n.d.*	1.64	0.06
	3.1	1.4	29.3	5.4	*n.d.*	0.28	0.06
	5.0	0.9	31.2	1.2	*n.d.*	0.06	0.06
	6.5	0.9	31.4	1.0	*n.d.*	0.26	0.07

TRAACS autoanalyzer 800+ according to Hansen and Koroleff (1999).

Sediment was collected by filtering 3 L of seawater over a 47 mm GF/F (Whatmann, Maidstone, UK). Samples were stored at −20 °C. After return to the NIOZ, dry weights of the sediment load were determined by ashing the filters at 400 °C for 12 h (corrected for filter weight). Some of the sediment filters were lost during transport and therefore no data are available (marked with 'n.d.' in Table 1). Samples for flow cytometric enumeration of phytoplankton (3.5 mL) were fixed with 0.5% final concentration of 18% *v*/v formaldehyde (Sigma-Aldrich, St. Louis, MO, USA) buffered with 10% *w/v* hexamine. Samples for bacteria and viruses (1 mL) were fixed with 0.5% final concentration glutaraldehyde (25% EM-grade, Sigma-Aldrich, St. Louis, MO, USA). Both types of samples were fixed at 4 °C for 30 min, after which they were flash frozen in liquid nitrogen. Phytoplankton were enumerated according to Marie et al. (2001) and bacteria and viruses according to Brussaard (2004a,b) using a benchtop BD FACSCalibur flow cytometer. Good quality counting, i.e. cells are smaller than the laser width, restricted phytoplankton enumeration to cells with < 20 μm diameter. Bacteria and viruses were diluted in TE-buffer (pH 8.2; Mojica et al., 2014), stained with SYBRGreen I (Life Technologies Ltd., Paisley, UK) and measured with the trigger on green fluorescence. All flow cytometry data were analyzed with the program FCS express 5 (De Novo Software, Glendale 275 CA, USA). Flow cytometer virus populations were divided into 3 groups according to Brussaard (2004a,b), whereby V1 and V2 were regarded to be comprised largely of bacteriophages, while V3 (also) contained putative phytoplankton viruses. Final calculated abundances (per mL) were used to calculate the ratio of viruses to their potential microbial hosts, i.e. the virus to bacteria ratio (VBR) and virus to phytoplankton ratio (VPR). Microbial abundances and VBR were plotted against the distance to the glacier. The distance was calculated in the mapping program toposvalbard (https://toposvalbard.npolar.no/; © Norwegian Polar Institute, Tromsø, Norway; last accessed on June 12, 2019) updated in 2012, 2011 and 2010 for Dunérbukta, Freemansundet and Russebukta, respectively. As the glacier that influences Russebukta is a land-terminating glacier, the distance was taken to the coastline where the glacier water enters the fjord.

2.3. Virus adsorption assays

The adsorption of viruses to the sediment was tested by adding previously collected glacier sediment (collected and cleaned as described in Maat et al., 2019) to natural seawater from 3 different stations in Storfjorden. The number of un-adsorbed viruses was then followed over time, whereby the sediment with adsorbed viruses was removed by centrifugation at each time-point. Samples for the adsorption assays were taken and further processed on the 22nd, 24th and 25th of August from Dunérbukta (8.74 km from coast), Freemansundet (2.53 km from coast), and Russebukta (6.50 km from coast; Fig. 1). On these localities, the water showed lowest turbidity (optically relatively clear) and was thus minimally influenced by glacier sediment. Onboard, 0.5 L of water was filtered through a GF/F glass fiber filter (Whatmann, Maidstone, UK), after which the water was divided into 12 mL glass tubes (10 mL for each tube). For each of the 3 experiments, 3 tubes served as control tubes without sediment, whereas other triplicate tubes received either 100, 200 or 500 mg L^{-1} final concentration sediment. The tubes were subsampled for virus abundance before sediment addition and then at T0 h, T2 h and T24 h, with T0 being sampled within 10 min after sediment addition. Before sampling, the tubes were gently mixed. The subsamples (1 mL) were immediately centrifuged in 2 mL Eppendorf tubes (Hamburg, Germany) for 5 min at 3500 × *g* to spin down the sediment with potentially attached viruses. The virus abundances in the supernatant, i.e. the viruses that are not attached to the sediment, were then sampled and fixed as described in paragraph 2.2. Maat et al. (2019) described that centrifugation can lead to some non-specific sediment loss and that a 'settling-removal' approach is therefore a preferred method. This was however not feasible on the moving ship and therefore the centrifugation method (e.g. Hewson and Fuhrman, 2003) was chosen as best alternative method.

The relative virus losses at each time point were respectively calculated as:

$$Relative\ loss = \frac{Ct - St}{Ct} \times 100\%$$

where *Ct* is the virus abundance of the control (without sediment) at time point *t* and *St* the virus abundance of the sediment treatment at time point *t*.

2.4. Statistics

All statistical analyses were done with the program Sigmaplot™ 14 (Systatsoftware Inc., Chicago Il, USA). For the adsorption experiments, significant differences between virus abundances of the sediment treatments and the controls without sediment were tested with one-way ANOVAs and subsequently and Holm-Šídák pairwise comparisons. Significant differences ($p = 0.05$) are depicted in Supplemental Table 1 and Fig. 3. Linear regressions to test the potential effects of environmental variables on VBR were done with VBR as dependent variable (we excluded VPR from statistical analysis due to its more hypothetical nature, using putative algal virus population V3).

3. Results & discussion

3.1. Transects

Glacier influence on the water column was revealed by changes in salinity and turbidity along the transect (Table 1). Salinity was, as expected, lower close to the glaciers, whereas turbidity and sediment load were highest. There were differences between the glaciers: Russebukta

Table 2
Chlorophyll a (mg L^{-1}) and abundances of phytoplankton (< 20 µm; $\times 10^3$ mL^{-1}), bacteria ($\times 10^6$ mL^{-1}), viruses ($\times 10^7$ mL^{-1}), and the virus to bacteria ratio (VBR) and virus to phytoplankton ratio (VPR) over different distances (km) from the 3 different glaciers sites.

	Distance	Chl-a	Algae	Bacteria	Viruses	VBR	VPR
Dunérbukta	0.37	0.08	8.2	0.8	0.3	3	13
	2.3	0.73	3.9	1.0	0.9	10	127
	4.5	0.25	10.8	1.4	2.2	16	88
	6.7	0.41	6.0	1.1	1.4	13	120
	8.7	0.37	5.5	1.0	1.0	10	87
Freemansundet	0.46	0.15	2.0	0.8	0.4	5	26
	1.1	0.39	3.1	1.4	1.3	9	183
	2.5	0.43	3.5	1.4	1.4	10	139
Russebukta	0.19	0.46	2.1	1.0	0.6	6	102
	3.1	0.30	3.4	1.2	1.2	10	119
	5.0	0.25	3.9	1.4	1.8	13	161
	6.5	0.41	5.3	1.4	1.7	12	140

displayed the lowest salinity in the proximity of the glacier (26.1 vs 29.2 and 29.5 for Dunérbukta and Freemansundet, respectively) but relatively also the lowest turbidity (5.1 vs 7.8 and 9.5 for Dunérbukta and Freemansundet, respectively). Turbidity, which generally increased towards the glaciers, was correlated to suspended sediment (linear regression, $r^2 = 0.84$, $p = 0.004$, $n = 7$; Table 1). Temperature did not show a general trend with glacier distance but showed the lowest values close to Freemansundet (Table 1). Nutrient concentrations were highly variable and not correlated to glacier distance (Table 1). Overall, there was also no clear correlation between nutrients and Chl-a (Tables 1 & 2).

The relatively low Chl-a (Dunérbukta and Russebukta) and phytoplankton abundances (Freemansundet and Russebukta) near the glacier, despite relatively high nutrient concentrations (Table 2), suggest that the higher glacier sediment load negatively affected phytoplankton growth. Maat et al. (2019) recorded reduced growth in phytoplankton cultures due to the presence of glacier-derived sediment. In that study, lower growth rates were not caused by reduced light intensity (turbidity), but possibly by mechanical disturbance of the sediment particles. At the 3 glaciers studied here, a combination of turbidity (light limitation) and mechanical disturbance may have affected phytoplankton abundances and Chl-a biomass (Cloern, 1987). Phytoplankton cells may have also been removed through adsorption themselves (Yu et al., 2017). The lower salinity could have played a role as well, although coastal marine phytoplankton are typically very resilient over the salinity range described here (Brand, 1984). Alternatively, zooplankton grazing on phytoplankton varied over the transect, but to date limited, inconclusive data are available on this topic (Arendt et al., 2011; Sommaruga, 2015; Arendt et al., 2016). Bacterial abundances displayed similar spatial dynamics as phytoplankton with > 30% lower abundances towards all 3 glaciers. Although direct processes such as adsorption of cells to sediment or varying grazing rates (as described for phytoplankton) cannot be excluded, it seems most likely that the lowered biomass of the photoautotrophs lead to reduced dissolved organic carbon (DOC) availability for bacterial growth (Azam et al., 1983).

The viral abundances declined even stronger towards the glaciers than the abundances of phytoplankton and bacteria, with reductions of > 70% for all 3 glaciers. Consequently, VBR values strongly declined by up to 80% towards the glaciers (Fig. 2), whereby the actual ratios were largely comparable between the 3 study sites. VBR correlated negatively with salinity, turbidity and sediment load (Table 3). We believe it is most likely that this decrease in VBR with increasing proximity to the glaciers is the result of virus adsorption to suspended sediment particles. Theoretically, salinity can lead to virus decay or affect infectivity processes, but such effects have not been reported for the relatively small salinity changes that we encountered (Mojica and Brussaard, 2014). Moreover, De Corte et al. (2011) found a decreasing

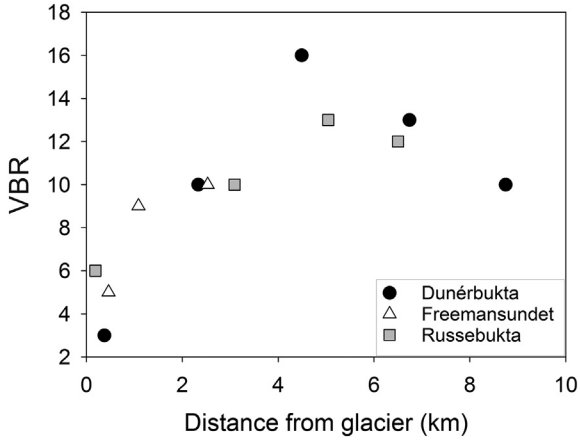

Fig. 2. Scatterplots of virus to bacteria ratio (VBR) against distance from the glaciers for Dunérbukta (black circles), Freemansundet (white triangles) and Russebukta (grey squares).

Table 3
Linear regressions with function, sample size (N), r^2, and *p*-value of salinity, turbidity and sediment concentration as independent variable and virus to microbial host as dependent variable.

	function	N	r^2	p
Salinity	$y = -33.5 + (1.42\ x)$	12	0.41	0.025
Turbidity	$y = 13.6 - (0.94\ x)$	12	0.61	0.003
Sediment	$y = 16.2 - (0.31\ x)$	7	0.79	0.008

VBR in Kongsfjorden, Svalbard, towards the summer season, and hypothesized this may in part be due to glacier-derived sediment input (not quantified). Drewes et al. (2016) found higher VBRs in an alpine lake that was not influenced by glaciers, as compared to similar but highly turbid glacier-fed lakes. In both cases, salinity did not play a role. Compared to bacterial viruses (phage), phytoplankton viruses are typically larger and of different morphology (Suttle, 2007), which may affect the mechanisms and strength of adsorption to the sediment particles (Kapuscinski and Mitchell, 1980; Chattopadhyay and Puls, 2000; Syngouna and Chrysikopoulos, 2010). The virus to phytoplankton ratio (VPR, see Material and Methods) decreased by approximately 80% towards Dunérbukta and Freemansundet and by almost 30% for Russebukta and is thus comparable to VBR (Table 2). The generally 10 times higher virus to host ratio for the putative phytoplankton versus bacterial viruses is similar to the typical virus to host ratios found in literature and is a consequence of their typically larger viral burst size (Weinbauer, 2004; Brown et al., 2006; Short, 2012).

3.2. Virus adsorption experiments

All 3 glacier sites showed rapid (within 10 min) adsorption of viruses to a sediment load of ≥200 mg L^{-1}, resulting in 25–50% loss (Fig. 3). At lower sediment concentrations, i.e. 100 mg L^{-1}, Russebukta showed still a relatively large initial virus decrease of 40% whereas at Freemansundet there was no significant initial decrease at all. Two hours post sediment addition, losses had also increased for Freemansundet (38% for 100 mg L^{-1}). After 24 h, Dunérbukta site still showed increased adsorption, up to 62%. Final total losses were between 38 and 66% of the total natural virus community.

It is difficult to assess why the virus community, in particular of Dunérbukta showed continued adsorption after the 2 h post sediment addition time point. Since the interaction between viruses and particles is a density dependent process (Murray and Jackson, 1992), it could likely be related to the 2–3 times lower virus starting abundances compared to the other stations (0.7 ± 0.1 vs. 1.5 ± 0.2 and

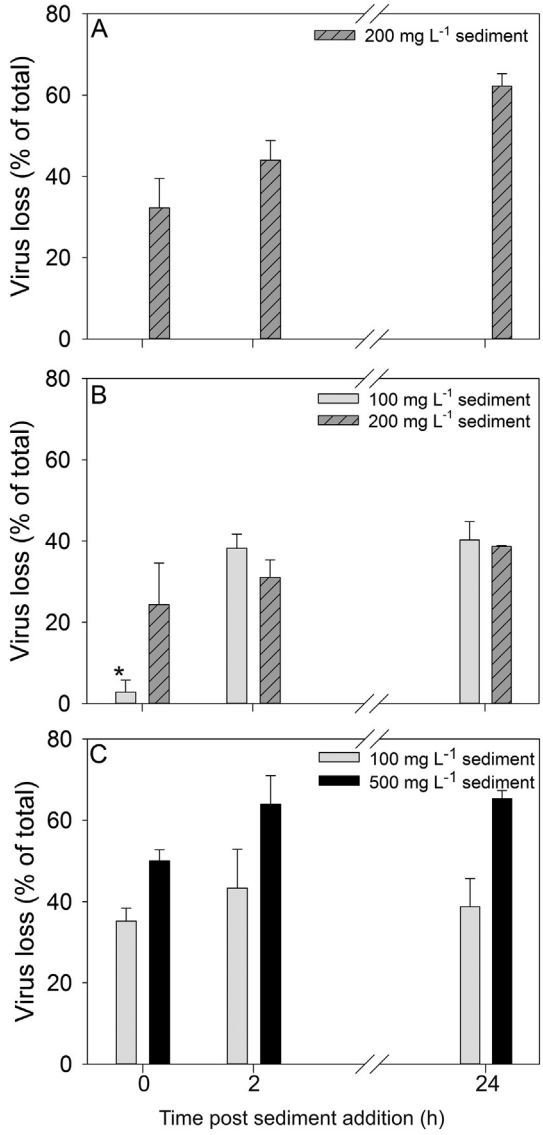

Fig. 3. Relative losses of total viruses (compared to controls without sediment) during the adsorption experiments (mean % ± S.D.) for Dunérbukta (200 mg L^{-1} sediment; A), Freemansundet (100 & 200 mg L^{-1} sediment) and Russebukta (100 & 500 mg L^{-1} sediment). Samples were taken 0-10 min, 2 h and 24 h post sediment addition. The 100, 200 and 500 mg L^{-1} sediment concentrations are respectively depicted as light grey, dark grey and black bars. Non-significant loss compared to the control is depicted with an asterisk.

$1.9 \pm 0.2 \times 10^7$ mL^{-1} for Dunérbukta, Freemansundet and Russebukta, respectively). Moreover, this reduced adsorption may be the result of the specific natural virioplankton community as different marine viruses have been found to show different adsorption rates for the same type of sediment and comparable physiochemical conditions (Maat et al., 2019). This is also implied by the differences in adsorption between the different virus groups V1, V2 and V3 (Supplementary Table S1).

The majority of the viruses adsorbed within the first 2 h post sediment addition despite the virus abundances still remaining relatively high (Fig. 3). As the tubes were resuspended before sampling and the viruses were thus exposed to the sediment regularly, it seems that the binding capacity of the sediment reached a maximum. There are only limited data published on this, showing a respective maximum binding capacity of 0.17 and 1.1×10^8 viruses per mg sediment (Hewson and Fuhrman, 2003; Maat et al., 2019). In our experiments, a maximum binding capacity was already reached with 3×10^4 viruses per mg sediment. However, besides sediment weight, also particle size distribution and total surface area of the sediment are important. We used exactly the same batch of sediment as Maat et al. (2019) and the same centrifugation assay as used by Hewson and Fuhrman (2003), so the difference is probably not the result of the type of sediment or the method used. Instead, it may be due to virus features that affect the adsorption capacity, such as total virus concentration and the morphology and isoelectric point of the viruses. Besides, even though we sampled viruses from waters as clear as possible, there were still low concentrations of sediment present (i.e. 12.6 mg L^{-1} for Dunérbukta and similar turbidity of 1–3 NTU for the other 2 sites). The environment may thus have selected for viruses that are not so easily adsorbed to sediment. Local differences between de 3 sites may be due to variation in sediment composition and concentration or organic matter load (Carlson Jr et al., 1968; Syngouna and Chrysikopoulos, 2010; Maat et al., 2019). Alternatively, dissolved organic matter in our filtered seawater samples may potentially have occupied binding sites for viruses, reducing the maximum adsorption capacity of the sediment (Carlson Jr et al., 1968; Stotzky et al., 1981; Maat et al., 2019). The 2 tide-water glacier influenced sites, i.e. Dunérbukta and Freemansundet, displayed different virus adsorption dynamics whereas Russebukta showed adsorption, which was comparable to Dunérbukta despite being influenced by a land-terminated glacier.

3.3. Conclusions

Our study shows that in Arctic coastal waters virus abundances strongly decreased closer to the glaciers. Considering the increasing sediment load (turbidity, despite lowered microbial biomass) towards the glacier, the viruses are most likely (temporarily) removed from the upper water column by the sediment particles. This is further strengthened by the observed virus removal upon sediment addition to the filtered natural seawater. Although adsorption was in absolute terms lower than in the few previous studies, we show that an additional influx of relevant concentrations of glacier sediment still led to a removal of 40 to 60% of the present viruses. The glacier-derived sediment acts thus as an important loss factor for viruses in these Arctic coastal waters. Glacier-derived sediment concentrations are highest during the spring and summer season when glacier melt is highest (Svendsen et al., 2002; Luckman et al., 2015; Murphy et al., 2016). During these productive seasons, d virus removal by glacier sediment may thus lead to reduced mortality rates for phytoplankton and bacteria. Hypothetically, such lowered impact of viruses would stimulate trophic transfer efficiency and carbon export (Suttle, 2007; Brussaard et al., 2008). We observed, however, that the abundances of phytoplankton and bacteria also decreased towards the glacier, although to a lesser extent. To our knowledge glacier influence on marine microorganisms is an understudied topic. Our study indicates that it should be considered in future studies, to allow for a better mechanistic understanding on the impact that (global warming-induced) glacier melt has on Arctic marine food webs.

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Disclosure

No conflict of interest. C.P.D.B. and D.S.M. conceptualized and designed the study. All authors contributed to field sampling. D.S.M. performed the onboard experiments. D.S.M and R.J.W.V. performed the analyses. D.S.M wrote the original draft. All authors contributed to writing, review and editing and approved the final article.

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