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1	Virus removal by glacier-derived suspended fine sediment in the Arctic
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13	
14	Abstract
15	Viruses are a major source of mortality for phytoplankton and bacteria and are therefore seen
16	as drivers of food web dynamics and biogeochemical cycling in the marine pelagic
17	environment. Previous studies have shown that aquatic viruses adsorb to suspended sediment,
18	which theoretically decreases the mortality pressure on their microbial hosts. This process is
19	of particular ecological importance in the Arctic, where coastal systems contain large
20	amounts of suspended fine-sediment, supplied by melting and calving glaciers. The aim of
21	this study was to investigate the effects of glacier-derived fine sediment on marine Arctic
22	microbes during summer in Storfjorden, Svalbard (78°N, 20°E). We sampled for microbial
23	abundances over transects with increasing sediment concentration towards three different
24	glaciers, and examined the adsorption of the natural virus community to previously collected
25	glacier-derived sediment. Our data show declined abundances of phytoplankton (<20µm) and

26 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 27 vicinity of the glaciers. Linear regressions showed negative linear relationships of VBR with 28 29 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 30 virioplankton upon addition of glacier sediment. Sediment additions (of ecologically relevant 31 concentrations of 100, 200 and 500 mg L⁻¹ to natural seawater) caused viral losses varying 32 between 38 and 66% of the total virus community. Such high viral losses translate into lower 33 34 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 35 main flow of carbon and other elements in the process. Further study to the possible 36 37 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 38 increase with global warming. 39

40

Keywords: Arctic; Glacier sediment; Bacteria; Phytoplankton; Viruses; Global warming
Abbreviations: VBR: virus to bacteria ratio; VPR: virus to phytoplankton ratio

Melting and calving glaciers in the polar regions are responsible for high supplies of sediment 46 47 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 48 (Hill and Nadeau 1989). Especially the smallest size classes remain suspended in the water 49 50 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 51 52 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 53 54 consequences for trophic transfer efficiency and biogeochemical fluxes (Sommaruga 2015, 55 Fuhrman et al. 2015). The increased turbidity that results from suspended sediment may 56 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 57 interference or ingestion of sediment particles (Arendt et al. 2011, Salter et al. 2011, 58 Sommaruga 2015). 59

Another suggested effect of glacier sediment is the adsorption of viruses to these 60 particles (De Corte et al. 2011, Maat et al. 2019). Viruses are parasites that use the 61 62 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 63 unicellular microorganisms (Suttle 2005). They drive microbial community dynamics, kill a 64 substantial share of the microbial biomass on a daily basis (Evans et al. 2009, Mojica et al. 65 66 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 67 90% of the marine pelagic bacterial standing stock on a daily basis. Lytic viruses typically 68

69 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 70 zone, leading to increased bacterial respiration through a process called the viral shunt (Suttle 71 72 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 73 biogeochemical cycling (Brussaard et al. 2008, Breitbart 2012). As viral lysis is a density-74 75 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 76 77 mitigated by seasonal or long-term increases in sediment input. Viruses adsorb to sediment particles through electrostatic binding, van der Waals 78 binding or hydrophobic interactions and this binding is affected by variables such as pH, 79 80 sediment mineralogy and size of the viruses (Moore et al. 1981, Syngouna and 81 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 82 83 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 84 was experimentally demonstrated that different virus populations, including an Arctic 85 phycovirus, strongly adsorb to glacier-derived fine-sediment (up to 90%; Maat et al 2019). 86 Moreover, the production of progeny virus was strongly delayed in the presence of glacier 87 88 sediment. By adsorption to sediment particles, the viruses are thus at least temporarily not

the system when the sediment settles to the sea floor (Lawrence et al. 2002, Maat et al. 2019).

available for infecting new host cells, and the viruses may even be removed long-term from

91 If this holds true under natural conditions in Arctic coastal waters, the fine-sediment is

89

92 expected to strongly reduce viral mediated mortality of microorganisms and consequently

93 affect their population dynamics and the cycling of carbon and other key elements in the94 pelagic marine environment.

The melting and calving rate of glaciers, and subsequently the inflow of glacier-95 96 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, 97 which is also the period of highest biological productivity (Hop et al. 2002, Svendsen et al. 98 2002, Murphy et al. 2016). How long and to what distance sediment particles stay in the 99 upper water column depends on the sinking rate of the sediment, water mass transport and 100 101 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 102 103 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.

109 2. Materials &	Methods
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111 *2.1. Sampling*

- 112 The research (conducted within the SEES Scientific Expedition Edgeøya Svalbard, August
- 113 2015) focused on 3 transects over increasing distance from glaciers in Storfjorden, Svalbard
- 114 (Fig. 1): Dunérbukta (78.188889°N, 18.801944°E), Freemansundet (78.269167°N,

115 21.792778°E) and Russebukta (77.595°N, 21.045833°E), respectively influenced by the tide-

- 116 water glaciers Ulvebreen and Freemanbreen and the land-terminating glacier Kvalpyntfonna.
- 117 Small motorized inflatable boats were used for sampling of physicochemical and biological
- variables. Surface water (0.5 m depth) was gently pumped into a 5L PP vacuum bottle
- 119 (Nalgene[®], NY, USA) with a manual vacuum pump. Water was brought onboard the wet lab
- 120 of M/V Ortelius, where samples were further processed.
- 121

122 2.2. Variables sampled

- 123 Temperature, salinity, chlorophyll *a* fluorescence (Chl-a) and turbidity were measured with a
- 124 Seabird electronics CTD package (SeaBird 19+) equipped with an in-line fluorometer
- 125 (WS3S, WETLabs), turbidity sensor measuring at 700 nm (ECO NTU, WETLabs), and a

spherical sensor (SPQA, LICOR) for Photosynthetically Active Radiation (PAR).

127 Water for dissolved inorganic nutrient (nitrate and phosphate) analysis was filtered

- through a 0.2µm Acrodisc Supor syringe filter (Pall, NY, USA) into a clean screw cap pony
- 129 vials (Perkin Elmer, MA, USA) and stored at -20°C until analysis in the home lab using a
- 130 TRAACS autoanalyzer 800+ according to Hansen and Koroleff (1999).
- 131 Sediment was collected by filtering 3L of seawater over a 47mm GF/F (Whatmann,
- 132 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 12h (corrected for filter

weight). Some of the sediment filters were lost during transport and therefore no data are 134 available (marked with 'n.d.' in Table 1). Samples for flow cytometric enumeration of 135 phytoplankton (3.5 mL) were fixed with 0.5% final concentration of 18% v/v formaldehyde 136 (Sigma-Aldrich, St. Louis, MO, USA) buffered with 10% w/v hexamine. Samples for 137 bacteria and viruses (1 mL) were fixed with 0.5% final concentration glutaraldehyde (25% 138 EM-grade, Sigma-Aldrich, St. Louis, MO, USA). Both types of samples were fixed at 4°C 139 140 for 30 min, after which they were flash frozen in liquid nitrogen. Phytoplankton were enumerated according to Marie et al. (1999) and bacteria and viruses according to Brussaard 141 142 et al. (2004) 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 <20 143 µm diameter. Bacteria and viruses were diluted in TE-buffer (pH 8.2; Mojica et al. 2014), 144 145 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 146 express 5 (De Novo Software, Glendale 275 CA, USA). Flow cytometer virus populations 147 were divided into 3 groups according to Brussaard et al. (2004), whereby V1 and V2 were 148 regarded to be comprised largely of bacteriophages, while V3 (also) contained putative 149 phytoplankton viruses. Final calculated abundances (per mL) were used to calculate the ratio 150 of viruses to their potential microbial hosts, i.e. the virus to bacteria ratio (VBR) and virus to 151 phytoplankton ratio (VPR). Microbial abundances and VBR were plotted against the distance 152 153 to the glacier. The distance was calculated in the mapping program toposvalbard (https://toposvalbard.npolar.no/; © Norwegian Polar Institute, Tromsø, Norway; last accessed 154 on June 12, 2019) updated in 2012, 2011 and 2010 for Dunérbukta, Freemansundet and 155 156 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. 157

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159 *2.3. Virus adsorption assays*

The adsorption of viruses to the sediment was tested by adding previously collected glacier 160 sediment (collected and cleaned as described in Maat et al. 2019) to natural seawater from 3 161 different stations in Storfjorden. The number of un-adsorbed viruses was then followed over 162 time, whereby the sediment with adsorbed viruses was removed by centrifugation at each 163 time-point. Samples for the adsorption assays were taken and further processed on the 22nd, 164 24th and 25th of August from Dunérbukta (8.74 km from coast), Freemansundet (2.53 km 165 from coast), and Russebukta (6.50 km from coast; Fig. 1). On these localities, the water 166 167 showed lowest turbidity (optically relatively clear) and was thus minimally influenced by glacier sediment. Onboard, 0.5L of water was filtered through a GF/F glass fiber filter 168 (Whatmann, Maidstone, UK), after which the water was divided into 12 mL glass tubes (10 169 170 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 171 concentration sediment. The tubes were subsampled for virus abundance before sediment 172 addition and then at T0h, T2h and T24h, with T0 being sampled within 10 min after sediment 173 addition. Before sampling, the tubes were gently mixed. The subsamples (1 mL) were 174 immediately centrifuged in 2 mL Eppendorf tubes (Hamburg, Germany) for 5 min at $3500 \times$ 175 g to spin down the sediment with potentially attached viruses. The virus abundances in the 176 supernatant, i.e. the viruses that are not attached to the sediment, were then sampled and fixed 177 178 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 179 preferred method. This was however not feasible on the moving ship and therefore the 180 181 centrifugation method (e.g. Hewson and Fuhrman 2003) was chosen as best alternative method. 182

183

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

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

186

187 where Ct is the virus abundance of the control (without sediment) at time point t and St the 188 virus abundance of the sediment treatment at time point t.

189

190 *2.4. Statistics*

191 All statistical analyses were done with the program SigmaplotTM 14 (Systatsoftware Inc,

192 Chicago II, USA). For the adsorption experiments, significant differences between virus

abundances of the sediment treatments and the controls without sediment were tested with

194 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

196 test the potential effects of environmental variables on VBR were done with VBR as

197 dependent variable (we excluded VPR from statistical analysis due to its more hypothetical

198 nature, using putative algal virus population V3).

202 *3.1. Transects*

203 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 204 and sediment load were highest. There were differences between the glaciers: Russebukta 205 displayed the lowest salinity in the proximity of the glacier (26.1 vs 29.2 and 29.5 for 206 Dunérbukta and Freemansundet, respectively) but relatively also the lowest turbidity (5.1 vs 207 208 7.8 and 9.5 for Dunérbukta and Freemansundet, respectively). Turbidity, which generally increased towards the glaciers, was correlated to suspended sediment (linear regression, 209 210 $r^2=0.84$, p=0;004, n=7; Table 1). Temperature did not show a general trend with glacier 211 distance but showed the lowest values close to Freemansundet (Table 1). Nutrient 212 concentrations were highly variable and not correlated to glacier distance (Table 1). Overall, there was also no clear correlation between nutrients and Chl-a (Table 1 & 2). 213 The relatively low Chl-a (Dunérbukta and Russebukta) and phytoplankton 214 abundances (Freemansundet and Russebukta) near the glacier, despite relatively high nutrient 215 concentrations (Table 2), suggest that the higher glacier sediment load negatively affected 216 phytoplankton growth. Maat et al. (2019) recorded reduced growth in phytoplankton cultures 217 due to the presence of glacier-derived sediment. In that study, lower growth rates were not 218 219 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) 220 and mechanical disturbance may have affected phytoplankton abundances and Chl-a biomass 221 222 (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 223 224 coastal marine phytoplankton are typically very resilient over the salinity range described

225 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, 226 Sommaruga 2015, Arendt et al. 2016). Bacterial abundances displayed similar spatial 227 228 dynamics as phytoplankton with more than 30% lower abundances towards all 3 glaciers. Although direct processes such as adsorption of cells to sediment or varying grazing rates (as 229 described for phytoplankton) cannot be excluded, it seems most likely that the lowered 230 231 biomass of the photoautotrophs lead to reduced dissolved organic carbon (DOC) availability for bacterial growth (Azam et al. 1983). 232

233 The viral abundances declined even stronger towards the glaciers than the abundances of phytoplankton and bacteria, with reductions of more than 70% for all 3 glaciers. 234 Consequently, VBR values strongly declined by up to 80% towards the glaciers (Fig. 3), 235 236 whereby the actual ratios were largely comparable between the 3 study sites. VBR correlated 237 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 238 adsorption to suspended sediment particles. Theoretically, salinity can lead to virus decay or 239 affect infectivity processes, but such effects have not been reported for the relatively small 240 salinity changes that we encountered (Mojica and Brussaard, 2014). Moreover, De Corte et 241 al. (2011) found a decreasing VBR in Kongsfjorden, Svalbard, towards the summer season, 242 and hypothesized this may in part be due to glacier-derived sediment input (not quantified). 243 244 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 245 a role. Compared to bacterial viruses (phage), phytoplankton viruses are typically larger and 246 247 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 248 2000, Syngouna and Chrysikopoulos 2010). The virus to phytoplankton ratio (VPR, see 249

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).

256

257 *3.2. Virus adsorption experiments*

All 3 glacier sites showed rapid (within 10 min) adsorption of viruses to a sediment load of $\geq 200 \text{ mg L}^{-1}$, 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 24h, 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 265 continued adsorption after the 2h post sediment addition time point. Since the interaction 266 between viruses and particles is a density dependent process (Murray and Jackson 1992), it 267 could likely be related to the 2 - 3 times lower virus starting abundances compared to the 268 other stations (0.7±0.1 vs. 1.5±0.2 and $1.9\pm0.2 \times 10^7$ ml⁻¹ for Dunérbukta, Freemansundet 269 and Russebukta, respectively). Moreover, this reduced adsorption may be the result of the 270 specific natural virioplankton community as different marine viruses have been found to 271 272 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 273 adsorption between the different virus groups V1, V2 and V3 (Supplementary Table S2). 274

275 The majority of the viruses adsorbed within the first 2h post sediment addition despite the virus abundances still remaining relatively high (Fig. 3). As the tubes were resuspended 276 before sampling and the viruses were thus exposed to the sediment regularly, it seems that the 277 278 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 279 sediment (Hewson and Fuhrman 2003, Maat et al. 2019). In our experiments, a maximum 280 binding capacity was already reached with 3×10^4 viruses per mg sediment. However, 281 besides sediment weight, also particle size distribution and total surface area of the sediment 282 283 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 284 not the result of the type of sediment or the method used. Instead, it may be due to virus 285 286 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 287 from waters as clear as possible, there were still low concentrations of sediment present (i.e. 288 12.6 mg L⁻¹ for Dunérbukta and similar turbidity of 1-3 NTU for the other 2 sites). The 289 environment may thus have selected for viruses that are not so easily adsorbed to sediment. 290 291 Local differences between de 3 sites may be due to variation in sediment composition and concentration or organic matter load (Carlson et al. 1968, Syngouna and Chrysikopoulos 292 293 2010, Maat et al. 2019). Alternatively, dissolved organic matter in our filtered seawater 294 samples may potentially have occupied binding sites for viruses, reducing the maximum adsorption capacity of the sediment (Carlson et al. 1968, Stotzky et al. 1981, Maat et al. 295 2019). The 2 tide-water glacier influenced sites, i.e. Dunérbukta and Freemansundet, 296 297 displayed different virus adsorption dynamics whereas Russebukta showed adsorption, which was comparable to Dunérbukta despite being influenced by a land-terminated glacier. 298

Our study shows that in Arctic coastal waters virus abundances strongly decreased closer to 301 the glaciers. Considering the increasing sediment load (turbidity, despite lowered microbial 302 biomass) towards the glacier, the viruses are most likely (temporarily) removed from the 303 upper water column by the sediment particles. This is further strengthened by the observed 304 virus removal upon sediment addition to the filtered natural seawater. Although adsorption 305 306 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 307 308 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 309 spring and summer season when glacier melt is highest (Svendsen et al. 2002, Luckman et al. 310 311 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. 312 Hypothetically, such lowered impact of viruses would stimulate trophic transfer efficiency 313 and carbon export (Suttle 2007, Brussaard et al. 2008). We observed, however, that the 314 abundances of phytoplankton and bacteria also decreased towards the glacier, although to a 315 lesser extent. To our knowledge glacier influence on marine microorganisms is an 316 understudied topic. Our study indicates that it should be considered in future studies, to allow 317 for a better mechanistic understanding on the impact that (global warming-induced) glacier 318 319 melt has on Arctic marine food webs.

320

321

322 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.

324	D.S.M and R.J.W.V. performed the analyses. D.S.M wrote the original draft. All authors
325	contributed to writing, review and editing and approved the final article.

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339 References

- 341 Arendt, K.E., Dutz, J., Jónasdóttir, S.H., Jung-Madsen, S., Mortensen, J., Møller, E.F.,
- Nielsen, T.G., 2011. Effects of suspended sediment on copepods feeding in a glacial
- influenced sub-Arctic fjord. J. Plankton Res. 33, 1526-1537.
- 344 https://doi.org/10.1093/plankt/fbr054.
- 345
- 346 Arendt, K.E., Agersted, M.D., Sejr, M.K., & Juul-Pedersen, T., 2016. Glacial meltwater
- 347 influences on plankton community structure and the importance of top-down control (of
- primary production) in a NE Greenland fjord. Estuar. Coast Shelf. Sci. 183, 123-135.
- 349 <u>https://doi.org/10.1016/j.ecss.2016.08.026</u>.
- 350
- Azam, F., Fenchel, T., Field, J.G., Grey, J.S., Meyer-Reil, L.A., Thingstad, F., 1983. The
- ecological role of water-column microbes. Mar. Ecol. Prog. Ser, 10, 257-263.
- 353 https://doi.org/10.3354/meps010257
- 354
- Brand, L.E., 1984. The salinity tolerance of forty-six marine phytoplankton isolates. Estuar.
- 356 Coast Shelf. Sci. 18, 543-556. https://doi.org/10.1016/0272-7714(84)90089-1.
- 357
- Breitbart, M., 2012. Marine viruses: truth or dare. Ann. Rev. Mar. Sci. 4, 425-448.
- 359 https://doi.org/10.1146/annurev-marine-120709-142805.
- 360
- Brown, C.M., Lawrence, J.E., Campbell, D.A., 2006. Are phytoplankton population density
- 362 maxima predictable through analysis of host and viral genomic DNA content? J. Mar. Biol.
- 363 Assoc. U.K. 86, 491-498. https://doi.org/10.1017/S0025315406013397.

- 365 Brussaard, C.P.D., 2004a. Optimization of procedures for counting viruses by flow
- 366 cytometry. Appl. Environ. Microbiol. 70, 1506–1513.
- 367 https://doi.org/10.1128/AEM.70.3.1506-1513.2004.
- 368
- 369 Brussaard, C.P.D., 2004b. Viral Control of Phytoplankton Populations—a Review. J. Eukar.
- 370 Microbiol. 51, 125-138. https://doi.org/10.1111/j.1550-7408.2004.tb00537.x.
- 371
- 372 Brussaard, C.P.D., Wilhelm, S.W., Thingstad, F., Weinbauer, M.G., Bratbak, G., Heldal, M.,
- 373 Kimmance, S.A., Middelboe, M., Nagasaki, K., Paul, J.H. and Schroeder, D.C., 2008.
- Global-scale processes with a nanoscale drive: the role of marine viruses. ISME J. 2, 575.
- 375 https://doi.org/10.1038/ismej.2008.31
- 376
- 377 Carlson Jr, G.F., Woodard, F.E., Wentworth, D.F., Sproul, O.J., 1968. Virus inactivation on
- 378 clay particles in natural waters. J. Water Pollut. Control Fed. R89-R106, available online:
- https://www.jstor.org/stable/25036033 (last accessed June 11, 2019).

380

- Chattopadhyay, S., Puls, R.W., 2000. Forces dictating colloidal interactions between viruses
 and soil. Chemosphere. 41, 1279-1286. https://doi.org/10.1016/S0045-6535(99)00519-6.
- 384 Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity in
- estuaries. Cont. shelf res. 7, 1367-1381. https://doi.org/10.1016/0278-4343(87)90042-2.

387	De Corte, D., Sintes, E., Yokokawa, T., Herndl, G.J., 2011. Changes in viral and bacterial
388	communities during the ice-melting season in the coastal Arctic (Kongsfjorden, Ny-Ålesund).
389	Environ. Microbiol. 13, 1827-1841. https://doi.org/10.1111/j.1462-2920.2011.02497.x.
390	
391	Drewes, F., Peter, H., Sommaruga, R., 2016. Are viruses important in the plankton of highly
392	turbid glacier-fed lakes? Sci. Rep. 6, 24608. https://doi.org/10.1038/srep24608.
393	
394	Evans, C., Pearce, I., & Brussaard, C. P., 2009. Viral-mediated lysis of microbes and carbon
395	release in the sub-Antarctic and Polar Frontal zones of the Australian Southern Ocean.
396	Environ. Microbiol. 11, 2924-2934. https://doi/10.1111/j.1462-2920.2009.02050.x.
397	
398	Fuhrman, J.A., Cram, J.A., Needham, D.M., 2015. Marine microbial community dynamics
399	and their ecological interpretation. Nature Reviews Microbiology, 13, 133.
400	https://doi.org/10.1038/nrmicro3417
401	
402	Hansen, H.P., Koroleff, F., 1999. Determination of nutrients, in: Grasshoff, K. Kremling, K.,
403	Ehrhart, M. (Eds.), Methods of seawater analysis. Third ed. Wiley VCH, Weinheim. pp. 159-
404	228.

- 405
- Hewson, I., Fuhrman, J.A., 2003. Viriobenthos production and virioplankton sorptive
- 407 scavenging by suspended sediment particles in coastal and pelagic waters. Microb. Ecol. 46,

408 337-347. https://doi.org/10.1007/s00248-002-1041-0.

410	Hill, P.R., Nadeau, O.C, 1989. Storm-dominated sedimentation on the inner shelf of the
411	Canadian Beaufort Sea. J. Sediment. Res. 59, 455-468. https://doi.org/10.1306/212F8FC1-
412	2B24-11D7-8648000102C1865D.
413	
414	Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K.,
415	Mehlum, F., Gulliksen, B., Wlodarska-Kowalczuk, M. and Lydersen, C., 2002. The marine
416	ecosystem of Kongsfjorden, Svalbard. Pol. Res., 21, 167-208. https://doi.org/10.1111/j.1751-
417	8369.2002.tb00073.x
418	
419	Kapuscinski, R.B., Mitchell, R., 1980. Processes controlling virus inactivation in coastal
420	waters. Water Res. 14, 363-371. https://doi.org/10.1016/0043-1354(80)90084-6.
421	
422	Katz, A., Peña, S., Alimova, A., Gottlieb, P., Xu, M., Block, K.A., 2018. Heteroaggregation
423	of an enveloped bacteriophage with colloidal sediment and effect on virus viability. Sci. Total
424	Environ. 637, 104-111. https://doi.org/10.1016/j.scitotenv.2018.04.425.
425	
426	Lawrence, J.E., Chan, A.M., Suttle, C.A., 2002. Viruses causing lysis of the toxic bloom-
427	forming alga
428	Heterosigma akashiwo (Raphidophyceae) are widespread in coastal sediment of British
429	Columbia, Canada. Limnol. Oceanogr. 47, 545–550.
430	https://doi.org/10.4319/lo.2002.47.2.0545.
431	
432	Lara, E., Arrieta, J.M., Garcia-Zarandona, I., Boras, J.A., Duarte, C.M., Agustí, S.,
433	Wassmann, P.F. and Vaqué, D., 2013. Experimental evaluation of the warming effect on

434 viral, bacterial and protistan communities in two contrasting Arctic systems. Aquat. Microb.

435 Ecol. 70, 17-32. https://doi.org/10.3354/ame01636.

436

- 437 Luckman, A., Benn, D.I., Cottier, F., Bevan, S., Nilsen, F., Inall, M., 2015. Calving rates at
- tidewater glaciers vary strongly with ocean temperature. Nat. Commun. 6, 8566.
- 439 https://doi.org/10.1038/ncomms9566.

440

- 441 Maat, D.S., Prins, M.A., Brussaard, C.P.D., 2019. Sediment from Arctic tide-water glaciers
- remove coastal marine viruses and delay host infection. Viruses. 11, 123.
- 443 https://doi.org/10.3390/v11020123.

444

- 445 Marie, D., Partensky, F., Vaulot, D., Brussaard, C.P.D., 2001. Enumeration of Phytoplankton,
- 446 Bacteria, and Viruses in Marine Samples. In: Current Protocols in Cytometry. John Wiley &

447 Sons, NJ, USA, 2001, Vol. 10, pp. 11.11.1-11.11.15.

- 448
- 449 Mojica, K.D.A., Brussaard, C.P.D., 2014. Factors affecting virus dynamics and microbial
- 450 host-virus interactions in marine environments. FEMS Microbiol. Ecol. 89, 495–515.
- 451 https://doi.org/10.1111/1574-6941.12343.
- 452
- 453 Mojica, K.D., Evans, C., Brussaard, C.P., 2014. Flow cytometric enumeration of marine viral
- 454 populations at low abundances. Aquat. Microbiol. Ecol. 71, 203-209.
- 455 https://doi.org/10.3354/ame01672.

- 457 Mojica, K.D.A., Huisman, J., Wilhelm, S.W., Brussaard, C.P.D., 2016. Latitudinal variation
- 458 in virus-induced mortality of phytoplankton across the North Atlantic Ocean. ISME J. 10,

459 500–513. https://doi.org/10.1038/ismej.2015.130.

- 460
- 461 Moore, R.S., Taylor, D.H., Sturman, L.S., Reddy, M.M., Fuhs, G.W., 1981. Poliovirus
- 462 adsorption by 34 minerals and soils. Appl. Environ. Microbiol. 42, 963-975.

463 https://aem.asm.org/content/42/6/963 (last accessed on June 11, 2019).

- 465 Murphy, E.J., Cavanagh, R.D., Drinkwater, K.F., Grant, S.M., Heymans, J.J., Hofmann, E.E.,
- 466 Hunt, G.L., Johnston, N. M., 2016. Understanding the structure and functioning of polar
- 467 pelagic ecosystems to predict the impacts of change. Proc. R. Soc. B. 283, 1646.
- 468 https://doi.org/10.1098/rspb.2016.1646.
- 469
- 470 Murray, A.G., Jackson, G.A., 1992. Viral dynamics: a model of the effects of size, shape,
- 471 motion and abundance of single-celled planktonic organisms and other particles. Mar. Ecol.
- 472 Prog. Ser. 89, 103-116. https://doi.org/10.3354/meps089103.
- 473
- 474 Paterson, W.S.B., 2016. The physics of glaciers. Third ed. Elsevier, Amsterdam. pp. 26 78.
 475
- 476 Salter, I., Böttjer, D., Christaki, U. 2011. The effect of inorganic particle concentration on
- 477 bacteria–virus–nanoflagellate dynamics. Environ. Microbiol. 13, 2768–2777. https://doi.org/
- 478 10.1111/j.1462-2920.2011.02547.x.
- 479
- 480 Schlitzer, R., Ocean Data View, https://odv.awi.de, 2018.
- 481

482 Short, S.M., 2012. The ecology of viruses that infect eukaryotic algae. Environ. Microbiol.

483 14, 2253-2271. https://doi.org/10.1111/j.1462-2920.2012.02706.x.

484

- 485 Sommaruga, R., 2015. When glaciers and ice sheets melt: consequences for planktonic
 486 organisms. J. Plankton Res. 37, 509-518. https://doi.org/10.1093/plankt/fbv027.
- 487
- Stotzky, G., Schiffenbauer, M., Lipson, S.M., Yu, B.H., 1981. Surface interactions between
 viruses and clay minerals and microbes: mechanisms and implications. Viruses and wastewater
 treatment. 1981, 199-204, doi: 10.1016/B978-0-08-026401-1.50032-4.
- 491
- 492 Suttle, C.A., 2005. Viruses in the sea. Nature. 437, 356–61. https://doi/10.1038/nature04160.
 493
- 494 Suttle, C.A., 2007. Marine viruses—major players in the global ecosystem. Nat. Rev.
 495 Microbiol. 5, 801. https://doi.org/ 10.1038/nrmicro1750.
- 496
- 497 Svendsen, H., Beszczynska-Møller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland,
- 498 S., Børre Ørbæk, J., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., 2002. The
- 499 physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard.

500 Polar Res. 21, 133-166. https://doi.org/10.3402/polar.v21i1.6479.

- 501
- 502 Syngouna, V.I., Chrysikopoulos, C.V., 2004. Interaction between viruses and clays in static
- and dynamic batch systems. Environ. Sci. Technol. 44, 4539-4544.
- 504 https://doi.org/10.1021/es100107a.
- 505

- 506 Weinbauer, M.G., 2004. Ecology of prokaryotic viruses. FEMS Microbial. Rev. 28, 127-181.
- 507 https://doi.org/ 10.1016/j.femsre.2003.08.001.
- 508
- 509 Yu, Z., Song, X., Cao, X., & Liu, Y., 2017. Mitigation of harmful algal blooms using
- 510 modified clays: Theory, mechanisms, and applications. Harmful algae. 69, 48-64.
- 511 https://doi.org/10.1016/j.hal.2017.09.004.

1 Tables & Figures

- *Table 1: Water temperature* (°*C*), *salinity, turbidity (NTU), sediment concentration (mg* L^{-1})
- 4 and concentrations (μM) of dissolved nitrate (NO_3^-) and phosphate (PO_4^{3-}) of the different
- 5 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
	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
Dunérbukta 2015-08-22	4.5	2.3	31.2	2.2	11.3	0.25	0.07
2013 00 22	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	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
2015-08-24	2.5	1.1	31.6	3.1	n.d.	0.37	0.16
	0.19	2.1	26.1	5.1	n.d.	1.64	0.06
Russebukta	3.1	1.4	29.3	5.4	n.d.	0.28	0.06
2015-08-25	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

10 Table 2: Chlorophyll a (mg L-1) and abundances of phytoplankton (<20µm; ×103 mL-1),

bacteria (×106 mL-1), viruses (×107 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
	0.37	0.08	8.2	0.8	0.3	3	13
Dunérbukta	2.3	0.73	3.9	1.0	0.9	10	127
Dunerbukta	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
Encompanyandat	0.46	0.15	2.0	0.8	0.4	5	26
Freemansundet	1.1	0.39	3.1	1.4	1.3	9	183
	2.5	0.43	3.5	1.4	1.4	10	139
	0.19	0.46	2.1	1.0	0.6	6	102
Russebukta	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

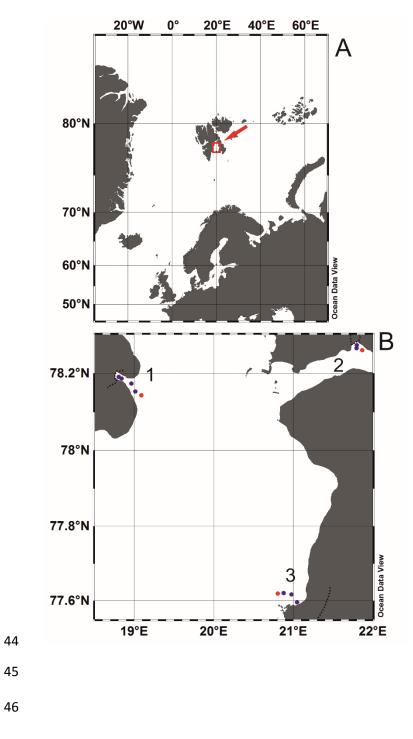
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- *Table 3: Linear regressions with function, sample size (N), r^2, and p-value of salinity,*
- 17 turbidity and sediment concentration as independent variable and virus to microbial host as
- *dependent variable.*

	function	Ν	\mathbf{r}^2	р
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

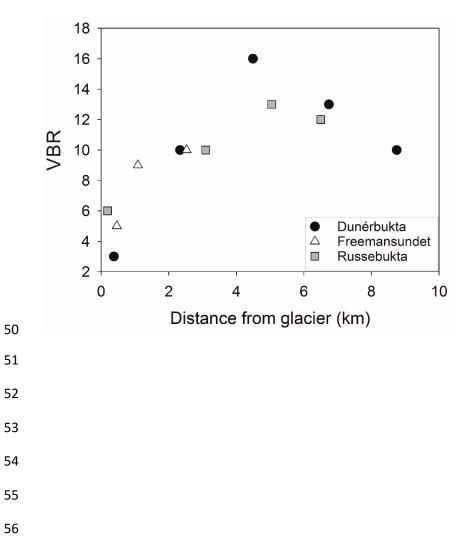
25	Figure 1: Map showing the location of Svalbard in Northern hemisphere (A) and the sampled
26	glacier sites in Storfjorden, Svalbard (B), being Dunérbukta (1), Freemansundet (2) and
27	Russebukta (3). Sampling stations are depicted as blue and red dots of which the red ones
28	were additionally sampled for the adsorption assays. The coastlines of the original map in
29	panel B have been adjusted in Corel Draw to correct for glacier retreat. The black dashed
30	lines represent the approximate glacier fronts in 2015. The maps with stations were made in
31	Ocean Data View (Schlitzer 2018).
32	
33	Figure 2: Scatterplots of virus to bacteria ratio (VBR) against distance from the glaciers for
34	Dunérbukta (black circles), Freemansundet (white triangles) and Russebukta (grey squares).
35	
36	Figure 3: Relative losses of total viruses (compared to controls without sediment) during the
37	adsorption experiments (mean % \pm S.D.) for Dunérbukta (200 mg L ⁻¹ sediment; A),
38	Freemansundet (100 & 200 mg L ⁻¹ sediment) and Russebukta (100 & 500 mg L ⁻¹ sediment).
39	Samples were taken 0-10min, 2h and 24h post sediment addition. the 100, 200 and 500 mg L ⁻
40	¹ sediment concentrations are respectively depicted as light grey, dark grey and black bars.
41	Non-significant loss compared to the control is depicted with an asterisk.
42	

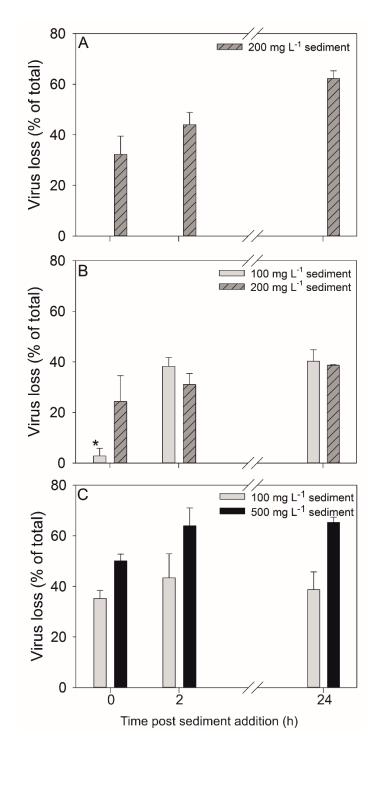
43 Figure 1



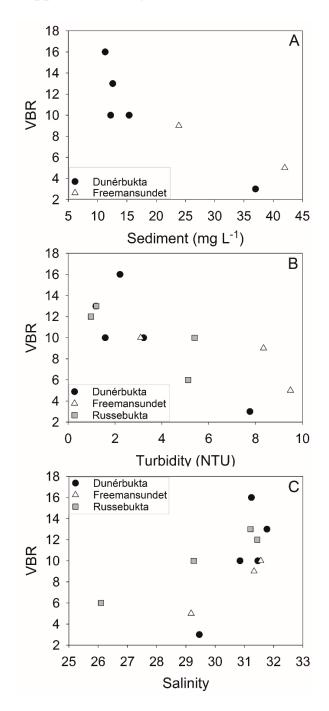
48 Figure 2







- 63 Supplemental Table 1: Relative losses of mean percentage V1, V2 and V3 (\pm s.d.) for the
- 64 different glaciers and sediment concentrations (mg L^{-1}) at three sampling time points, i.e. 0, 2
- 65 and 24 h after sediment addition. All values are based on a significant difference with the
 - Loss **V2** Sediment Time V1 **V3** 0 32 ± 7 31 ±8 $45 \pm \! 6$ Dunérbukta 200 2 $44 \pm \! 5$ 45 ±7 48 ± 2 24 $37 \pm \!\! 14$ 53 ± 9 66 ± 2 0 $5\pm 4^{*}$ $16 \pm 8*$ $15 \pm 9*$ 100 2 31 ±8 $35 \pm 12^*$ 43 ±3 $34 \pm 13*$ 24 43 ± 5 $27 \pm 10*$ Freemansundet 0 27 ± 12 $23 \pm 6*$ $12 \pm 10*$ 200 2 35 ± 2 34 ±3 $27 \pm 4*$ 40 ± 1 $31 \pm 4*$ $21 \pm 10*$ 24 0 39 ±3 22 ±6 22 ± 7 100 2 46 ± 9 38 ± 12 28 ± 10 24 50 ± 6 44 ±6 $39 \pm \! 6$ Russebukta 0 51 ±3 48 ± 2 41 ± 1 500 2 64 ± 7 66 ± 7 53 ±8 24 72 ± 1 69 ±3 63 ± 1
- 66 *control, expect for the ones depicted with an asterisk (*).*



Supplemental Figure S1: Scatter plots of virus to bacterium ratio (VBR) versus sediment
concentration (A), turbidity (B) and salinity (C) for Dunérbukta (black circles),

72 Freemansundet (white triangles) and Russebukta (grey squares). Sediment samples for

73 Russebukta were lost.