RESEARCH ARTICLE

Relative importance of nanoflagellate grazing and viral lysis for the mortality of heterotrophic bacteria and *Synechococcus* spp. in a high-latitude fjord (Adventfjorden, Svalbard) during the summer

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Abstract

Viral lysis and grazing play crucial but distinct roles in microbial community dynamics and carbon cycling. Yet, their relative influence on the abundance of heterotrophic bacterial and picophytoplankton populations, especially in Arctic fjords, remains poorly understood. To address this knowledge gap, we conducted modified dilution experiments in Adventfjorden, Svalbard, to quantify microbial growth, grazing pressure and virus-induced mortality. Our results showed that the abundance of virus-like particles (VLP) ranged between 1.4 and 8.9 × 10^6 viruses ml^{-1}, with a negative correlation to salinity. This suggests that freshwater inputs, such as meltwater, could contribute to higher VLP abundance in these waters. The VLP-to-bacteria ratio varied between 9.8 and 700.9, with a large variation below a salinity of 28 PSU and an inverse correlation with salinity. Grazing, primarily by nanoflagellates, emerged as the dominant factor in reducing heterotrophic bacterial and *Synechococcus* spp. populations, accounting for 12–55% and 20–110% of their production losses, respectively. This study was conducted in summer, when meltwater discharges entered coastal waters in Svalbard fjords at an extremely high rate, providing an opportunity to study microbial processes under projected future warming conditions.

Keywords

Svalbard fjords; microbial mortality; carbon cycling; nitrogen cycling; microbial loop; polar microbial ecology

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Abbreviations

Exp.: experiment
FCM: flow cytometer
HNF: heterotrophic nanoflagellates
PNF: pigmented nanoflagellates
VBR: VLP-to-bacteria ratio
VLP: virus-like particles

To access the supplementary material, please visit the article landing page

Introduction

High-latitude fjords provide a vital contribution to the fishing industry (Meire et al. 2017). These systems exhibit steep spatial and temporal gradients significantly influenced by seasons (Marquardt et al. 2016). Global warming has caused many land glaciers to retreat, resulting in meltwater discharges and suspended sediment entering coastal marine environments (Zaborska et al. 2006). Increasing freshwater inputs and nutrient release from glaciers and rivers further promote ecosystem complexity (Kim et al. 2020).

In Svalbard, several fjords are fed by glaciers and are particularly vulnerable to global and local warming (Dahlke et al. 2020), as melting glaciers and declining sea ice substantially alter fjord conditions (Muckenhuber et al. 2016). This vulnerability is further amplified in spring and summer when warmer Atlantic waters mix with frigid Arctic waters, increasing sea-ice melt and freshening surface waters (Vernet et al. 2019). In addition, physicochemical properties of these fjords are affected by a diverse set of factors—hydrography, light availability, nutrient concentrations, salinity, turbidity, among others—all of which impact microbial communities (Wang et al. 2009; Iversen & Seuthe 2011; Jain et al. 2020; Parli et al. 2021; Hörstmann et al. 2024). A warming climate and diminished ice cover are predicted to alter phytoplankton communities in marine ecosystems. Previous studies indicate that nanoplankton and picoplankton dominance varies by season in high-latitude fjords (Azzaro et al. 2021; Parli et al. 2021). A recent study found that *Synechococcus* spp. is a critical component

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of carbon and nitrogen cycling in marine ecosystems and its importance increases in warmer Arctic waters (Parli et al. 2021). Such warming has been observed to increase the abundance of *Synechococcus* spp. (Flombaum et al. 2013) and other microorganisms with important roles in the marine food web (Vincent et al. 2009).

The extreme environmental variability in Svalbard fjords makes it an ideal place to study how environmental variables affect microbial communities (Wang et al. 2009; Iversen & Seuthe 2011). In recent years, several studies have described the diverse microbial communities in Kongsfjorden (Bhaskar et al. 2020; Azzaro et al. 2021; Von Friesen et al. 2023; Guo et al. 2024; Kim et al. 2024) and in other parts of the Svalbard archipelago (Owrid et al. 2000; Vaquer-Sunyer et al. 2013; Garcia-Lopez et al. 2019; Zhang et al. 2022). In Kongsfjorden, bacterial production has also been studied (Engel et al. 2013; Motegi et al. 2013; Piquet et al. 2016), but fewer studies have examined phytoplankton and microbial communities in other Svalbard fjords, including Adventfjorden (Kubiszyn et al. 2017; Müller et al. 2018; Marquardt et al. 2019). Little is known about heterotrophic bacteria and picophytoplankton growth and mortality in these fjords.

Microbial communities are regulated by mortality processes in terms of abundance, species composition and elemental cycling (Pomeroy et al. 2007; Suttle 2007). The relative contributions of nanoflagellates and VLP to carbon and energy flows can vary considerably between systems (Maranger et al. 2015). There is a crucial difference between these two types of mortality in aquatic food webs: grazers transfer nutrients and carbon to higher trophic levels (Ortmann et al. 2011; Tsai et al. 2016), while viral lysis recycles nutrients within the microbial loop (Shelford et al. 2012; Töpper et al. 2013). A study of the effects of sea-ice melting on heterotrophic bacterial carbon transport in the Arctic microbial trophic web (Boras et al. 2010) demonstrated that meltwater input increased phytoplankton growth, bacterial production and bacterial grazing pressure. Under typical conditions, prokaryotic abundance and viral activity are tightly coupled, but this relationship may be weakened by environmental disturbances. For example, runoff from adjacent land can disrupt this coupling in near-shore Arctic waters (Choi et al. 2003). Ultraviolet (UV) radiation and suspended particles have also been suggested to reduce the strength of the correlation between prokaryotic and VLP abundance (De Corte et al. 2011). A high suspended particle load likely lowers VLP infectivity since most VLP tend to sediment more rapidly if they attach to particles from upper waters (Simon et al. 2002). As summer temperatures rise, freshwater plumes released from melting glaciers decrease salinity and increase turbidity (Van de Poll et al. 2018).

In this study, we explored how summer conditions—elevated temperatures, continuous daylight, suspended sediment loads and meltwater—impacted the dynamics of heterotrophic bacteria, *Synechococcus* spp., nanoflagellates and VLP in a fjord in Svalbard. We also investigated the growth and mortality rates—due to viral lysis and nanoflagellate grazing—of heterotrophic bacteria and *Synechococcus* spp. under varying summer conditions. We hypothesized that the freshening and cooling associated with glacial meltwater would lower microbial abundance and activity, leading to shifts in growth and mortality patterns.

Material and methods

Sampling

The sampling sites were in Isfjorden, the largest fjord in Svalbard, Norway, which stretches approximately 107 km in length and up to 20 km in width. Adventfjorden (Fig. 1), a smaller branch of the Isfjorden system situated on the western coast of Spitsbergen, measures about 8.3 km in length and 3.4 km in width. The Advent and Longyear rivers discharge substantial amounts of sediment-laden water into Adventfjorden during the summer and autumn, that is, June–October (Dobrzyn et al. 2005).

Surface water samples were collected at a depth of approximately 0.5 m at a station close to the shore (Site C) and a station further out in the water, in the mouth of Adventfjorden (Site A), (78°15.6′N, 15°31.8′E), close to Longyearbyen. The sampling took place between 7 and 14 August 2024 (Fig. 1). In order to examine the microbial response to environmental factors at Site C, surface waters were sampled three to four times a day using a 20 L polycarbonate carboy. We collected water samples only once from Site A, from a boat, to measure heterotrophic bacteria and *Synechococcus* spp. growth and mortality. The seawater samples were collected in a clean bucket and transported in polycarbonate carboys to the laboratory. Temperature and salinity were measured immediately after collection using a HI98194 multiparameter waterproof meter (Hanna Instruments).

Modified dilution experiments

We estimated the growth rates of heterotrophic bacteria and *Synechococcus* spp., as well as the rates of nanoflagellate grazing and viral lysis, using a modified dilution experiment based on the methodology described by Evans et al. (2003). During the study period, three modified dilution experiments (C1, C2 and C3) were conducted at the near-shore—or "coastal"—station, Site C,

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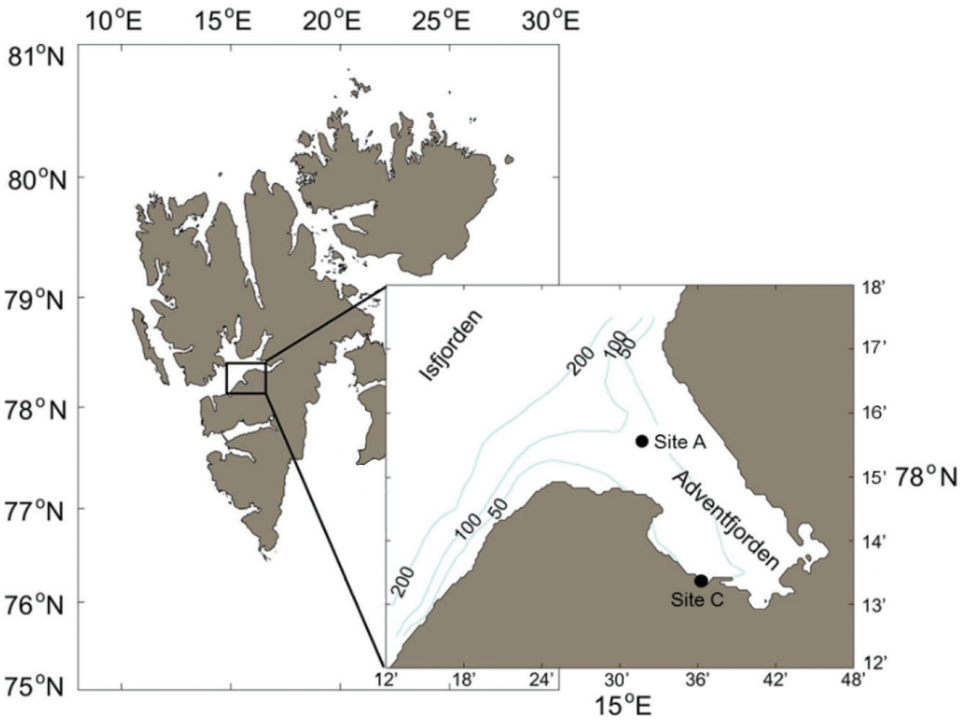

Fig. 1 Locations of sampling stations near the shore (Site C) and out near the mouth of the fjord (Site A) in Adventfjorden, Svalbard.

on 8, 12 and 13 August 2024, whereas the same experiment at Site A was performed only once, on 11 August 2024. Each process was carried out as described by Tsai et al. (2013). The natural sample (whole seawater) was passed through a 10 µm mesh, then filtered through a type PC 47 mm Nuclepore filter with a pore size of 0.2 µm (grazer-free seawater) and finally filtered by tangential flow through a 30 kDa filter (grazer+viral-free seawater). To evaluate the grazing mortality, the whole seawater was then diluted with grazer-free seawater in a four-point dilution series: 25, 50, 75 and 100% whole seawater. An additional similar dilution series was prepared by diluting the whole seawater with the grazer+viral-free seawater, to modify both grazing and viral mortalities.

Triplicate 50 ml polycarbonate tubes of each dilution experiment were incubated under natural light in a water bath set at the sampling temperature of the seawater. Samples were collected from each tube at the beginning (T_0) and the end of 24-hr incubation (T_{24}) to assess heterotrophic bacterial and *Synechococcus* spp. abundances. The apparent growth rate (k) of heterotrophic bacteria and *Synechococcus* spp. was calculated for each set (grazer-free and grazer+viral-free seawater) at the start and the end of the experiment using the equation ln (N_{24}/N_0)/t (Landry & Hassett 1982). The N_{24} and N_0 values represent the final and initial abundances of heterotrophic bacteria and *Synechococcus* spp., respectively, while t represents the 24-hr experiment duration.

In accordance with the method reported by Evans et al. (2003), we estimated nanoflagellate grazing rates (mg) and mortality rates due to nanoflagellate grazing combined with viral lysis (mg+mv) by linear regression on the plot of k versus fractions of seawater filtered through a 10 µm mesh (Fig. 2a). The apparent growth rate of heterotrophic bacteria and *Synechococcus* spp., k (30 kDa), was determined using grazer+viral-free seawater as diluent in the 30 kDa dilution series. This relationship is expressed in Eqn. 1:

$$k(30\ \text{kDa}) = \ln\ (N_{24}/N_0)/t = \mu - (mv + mg) \times D, \qquad (1)$$

where D represents the fraction of 10 µm filtered seawater.

The instantaneous growth rates of heterotrophic bacteria and *Synechococcus* spp. (hereafter simply called "growth" and denoted by the character μ) were determined as the y-intercept value of the regression line obtained with the grazer+viral-free series (Fig. 2a). The combined grazing and viral-induced mortality (mv+mg) coefficient was derived from the slope of the same dilution series (Fig. 2a).

As illustrated in Fig. 2a, there were two dilution series prepared using whole seawater (D = 1): a grazer+viral-free seawater dilution series, used to measure the impact of both viral lysis and nanoflagellate grazing (mv+mg) on mortality; and a grazer-free seawater series,

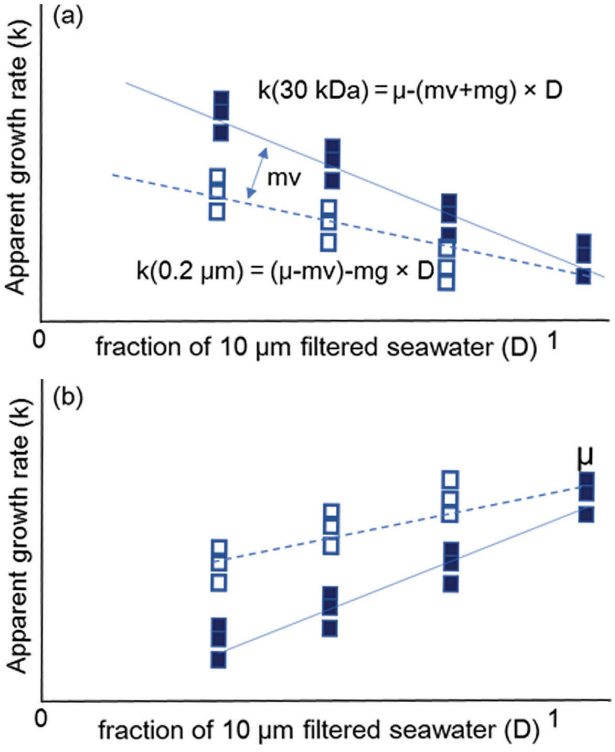

Fig. 2 Dilution plots of apparent growth rate (*k*) versus seawater fraction (*D*). (a) Slopes from the 0.2 µm and 30 kDa series estimate grazing (*mg*) and total mortality (*mg*+*mv*), respectively. (b) The y-intercept indicates the instantaneous growth rate (*µ*).

used to measure the effect of nanoflagellate grazing (*mg*). In this regression, the difference between the two slopes represents the mortality rate due to viral lysis of heterotrophic bacteria and *Synechococcus* spp. (*mv*). Observation of positive correlations between the dilution factor and *k* in both dilution series indicates that the assumptions of the dilution method were not met in Fig. 2b, and neither nanoflagellate grazing nor viral lysis had any significant impact on heterotrophic bacterial and *Synechococcus* spp. abundance.

When heterotrophic bacterial abundance was diluted with the whole seawater, the lytic pressure (*mv*) remained constant because most VLP remained in the grazer-free fraction, while the grazing pressure (*mg*) decreased. The apparent growth rate of heterotrophic bacteria and *Synechococcus* spp., *k* (0.2 µm), was calculated using grazer-free seawater as a diluent in the grazer-free seawater dilution series. This relationship can be expressed in Eqn. 2:

$$k(0.2\ \mu\text{m}) = \ln (N_{24}/N_0)/t = (\mu - mv) - mg \times D \qquad (2)$$

The nanoflagellate grazing (*mg*) coefficient was estimated on the basis of the slopes of the dilution series in grazer-free seawater. Viral-induced mortality of heterotrophic bacteria and *Synechococcus* spp. is indicated by the difference between the slopes of the two regression analyses (Fig. 2a). Therefore, the relationship can be expressed in Eqn. 3:

$$mv = (mv + mg) - mg \qquad (3)$$

In a study done by Tsai et al. (2018), a different pattern was observed. As shown in Fig. 2b, a, positive relationships between the fraction of whole seawater and *k* meant that the pattern failed to meet the assumptions of the dilution method. Previous studies reported that the growth of heterotrophic bacteria and *Synechococcus* spp. was lower in incubations diluted with grazer+viral-free seawater compared to incubations diluted with grazer-free seawater, which contains viruses (Suttle 2000; Tsai et al. 2018), suggesting possible nutrient limitation. The equation $mv = (mv+mg) - mg$ does not allow the estimation of grazing pressure (*mg*) or total mortality (*mg*+*mv*) in this situation, because they are unreliable estimates with negative values.

In this study, we also measured the instantaneous growth rates (*µ*) of heterotrophic bacteria and *Synechococcus* spp. in 100% fraction of whole seawater (Tsai et al. 2018; Fig. 2b).

Flow cytometric analyses

To quantify the amount of nanoflagellates, *Synechococcus* spp., heterotrophic bacteria and VLP in seawater, 2 ml seawater samples were collected from each treatment, preserved in 0.5% paraformaldehyde (final concentration), then frozen in liquid nitrogen and—within two days—transported to the laboratory, where they were stored at –20 °C. A CytoFLEX S FCM (Beckman Coulter), equipped with a 488 nm air-cooled argon-ion laser, standard 525 nm filter and SYBR signal trigger, was used to analyse the samples. To minimize interference from high particle density, VLP were diluted 1:10 in TE buffer (pH 8.0, EM grade) before staining. Diluted samples were stained with SYBR Green I (1:50 000 dilution of the commercial stock) for 10 min at 80 °C, in the dark. The samples were then cooled to 25 °C in an ice bath and analysed using an FCM and the method delineated by Brussaard (2004). A blank control of TE buffer stained with SYBR Green I was used to detect and eliminate buffer noise. Heterotrophic bacteria in the samples were stained with SYBR Green I (1:10 000 dilution of the commercial stock) for 15 min in the dark and then processed by FCM according to Hammes & Egli (2010). Picophytoplankton was analysed according to Calvo-Díaz & Morán (2006) based on chlorophyll fluorescence (> 650 nm) and phycoerythrin fluorescence (578 nm) as well as light scatter signals.

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PNF were identified based on pigment autofluorescence and forward-angle light scatter. HNF were stained with SYBR Green I and identified using green and red fluorescence along with relative side scatter cytograms, as described by Christaki et al. (2011). By utilizing 2 µm beads, the forward scatter threshold could be defined between picophytoplankton (size < 2 µm) and nanophytoplankton (2–20 µm). In the FCM process, only fluorescent particles were counted, as measurements were triggered by autofluorescence. A modified HNF protocol was created for FCM analysis on the basis of the method of Rose et al. (2004), from the one originally developed for bacterial counting in marine environments. By reducing the fluorescence detector voltage for side scatter and green fluorescence, HNF were distinguished from other cells based on their high fluorescence and high forward scatter.

Statistical analysis

In this study, we used an analysis of variance to test the significance of the regression lines. When both grazer-free and grazer+viral-free seawater treatments gave similar results with marginal differences in the y-intercept, we used an *F*-test to determine if there were significant differences in the slope of regression lines when compared with each other. Data analysis was performed with Statistical Package for the Social Sciences (SPSS) 21. A p value of < 0.05 was considered significant.

Results

In situ environmental conditions and microbial community patterns

At the coastal site, the temperature of the surface water varied between 8.3 to 13.8 °C, with an average of 10.6 °C (Fig. 3a). Warmer surface water (18.0 °C) was observed at Site A (Fig. 3a). Salinity ranged between 0.7 and 33.9 PSU and significant differences in salinity were found from day to day (Fig. 3b).

In this study, *Synechococcus* spp. were most abundant on 14 August at 22:00, when there were 25.6×10^3 cells ml^{-1}, and were lowest on 12 August at 06:00, with 0.5×10^3 cells ml^{-1} (Fig. 3c). As for heterotrophic bacteria, a minimum of 0.1×10^5 cells ml^{-1} was observed on 8 August

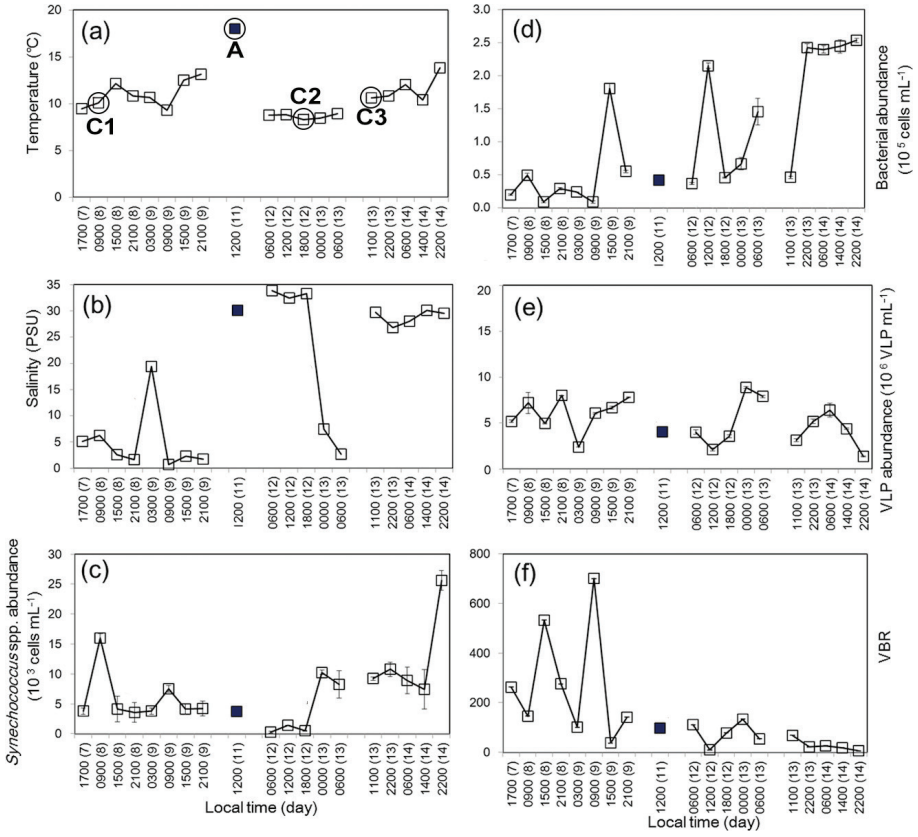

Fig. 3 Temporal variations of (a) temperature, (b) salinity, (c) abundance of *Synechococcus* spp., (d) bacterial abundance, (e) VLP abundance and (f) VBR during the study period. The data from four modified dilution experiments (C1, C2, C3 and A) are shown in (a).

and a maximum of 2.5×10^5 cells ml^{-1} was detected at the end of the sampling period on 14 August (Fig. 3d). The abundance of VLP ranged between 1.4 and 8.9×10^6 VLP ml^{-1}, with the lowest numbers at the end of sampling period on 14 August (Fig. 3e). The VBR varied between 9.8 (12 August) and 700.9 (9 August) and showed the higher values on 8 and 9 August (Fig. 3f). For the VBR values, there was a large variation (37.1–700.8) below 28 PSU of salinity and an inverse correlation with salinity (Fig. 4). Virus-like particles, however, had relatively higher average values of $6.40 \pm 3.16 \times 10^6$ VLP ml^{-1} below 28 PSU (*t*-test, $p < 0.05$).

We found that HNF and PNF exhibited similar abundance patterns, ranging from 0.2 to 24×10^2 cells ml^{-1} and 0.4 to 26.1×10^2 cells ml^{-1}, respectively (Supplementary Fig. S1).

Modified dilution experiments

Salinity levels at Site C were noticeably decreased in experiment (Exp.) C1 because of local melting or runoff on the day of 8 August (Table 1). Site A, influenced by Atlantic Water, was warmer compared with Site C (18.0 °C). During Exp. C2 and C3 at Site C, higher salinity was recorded when the tide was high, whereas the lower salinity in C1 coincided with a non-high tide (Table 1). A greater abundance of *Synechococcus* spp. and VLP was observed in Exp. C1, whereas HNF and PNF were more abundant in Exp. C2, C3 and A (Table 1).

A least-squares regression analysis was conducted to determine whether an increase in *k* was directly proportional to the dilution factor (Supplementary Fig. S2). In the grazer+viral-free seawater dilution series, the regression lines indicated bacterial growth rates ranging from 0.97 to 1.57 d^{-1} (Table 2). Positive relationships between the fraction of whole seawater and *k* were observed in Exp. C2 for heterotrophic bacteria, indicating that the dilution method did not fully meet its assumptions and *k* in 100% fraction of whole seawater was used to calculate conservative heterotrophic bacterial growth rates (μ = 1.41 d^{-1}; Supplementary Fig. S2b). Significant grazing mortality of bacteria was observed in Exp. C2, C3 and A (0.18–0.87 d^{-1}; Supplementary Fig. 2b–d), but not in Exp. C1 (Table 2), in which viral lysis was notable (0.28 d^{-1}), while grazing mortality of bacteria was not significant (Supplementary Fig. S2a).

The y-intercepts of the grazer+viral-free seawater dilution series, representing μ without grazing or lytic pressure, was 1.63 (C1), 2.49 (C3) and 3.19 d^{-1} (A) for *Synechococcus* spp. (Supplementary Fig. S2e, g, h). Moreover, a significant positive linear relationship between *k* and fraction of whole seawater in both dilution series was detected in the Exp. C2 analyses for *Synechococcus* spp. (Supplementary Fig. S2f). In this study, we estimated the average growth rate of *Synechococcus* spp. in Exp. C2 from 100% fraction of whole seawater,

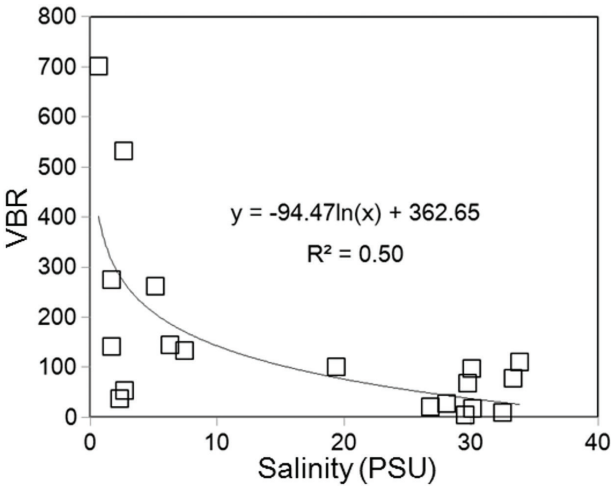

Fig. 4 VBR found at different salinities. The line shows the fitted exponential curve.

Table 1 Temperature, salinity and abundance (± standard deviation) of microbial community components at the beginning of each experiment.

	Experiment			
	C1	C2	C3	A
Temperature (°C)	10.1	8.3	10.6	18.0
Salinity (PSU)	6.3	33.3	29.7	30.1
Synechococcus spp. (10^3 cells ml^{-1})	16.0±2.1	0.5±0.2	3.6±0.9	3.8±0.8
Bacteria (10^5 cells ml^{-1})	0.5±0.2	0.5±0.1	0.5±0.2	0.4±0.3
Viruses (10^6 cells ml^{-1})	7.2±2.4	3.6±0.7	3.2±1.1	4.1±1.2
HNF (10^2 cells ml^{-1})	1.8±0.6	5.9±0.8	7.5±1.8	4.1±0.6
PNF (10^2 cells ml^{-1})	1.1±0.4	2.9±0.7	2.0±0.9	2.1±0.5

Table 2 Heterotrophic bacterial and *Synechococcus* spp. growth (μ) and mortality rates due to viral infection (*mv*) and nanoflagellate grazing (*mg*) obtained from the modified dilution experiments.

	Experiment			
	C1	C2	C3	A
Heterotrophic bacteria				
μ (d^{-1})	0.97	1.41 [a]	1.55	1.57
mg (d^{-1})	nd	0.18	0.81	0.87
mv (d^{-1})	0.28	nd [b]	nd [b]	nd [b]
Synechococcus spp.				
μ (d^{-1})	1.63	4.12 [a]	49	3.19
mg (d^{-1})	1.79	nd [b]	54	0.63
mv (d^{-1})	nd [b]	nd [b]	nd [b]	nd [b]

[a] Growth rate was estimated from 100% fraction of whole seawater.
[b] Non-detectable value.

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which is about 4.12 d^{-1} (Table 2). Furthermore, in Exp. C1, C3 and A, nanoflagellate grazing was the primary mortality factor, with grazing rates ranging from 0.63 to 2.54 d^{-1} (Table 2).

Discussion

Our findings reveal significant temporal variations in heterotrophic bacteria, *Synechococcus* spp. and viral populations, shedding light on the carbon flux within the microbial food web of Adventfjorden, Svalbard. In the Arctic Ocean, grazing mortality rates ranged from as low as 1% (Steward et al. 2007) to as high as 28% of bacterial production (Middelboe et al. 2002). Also, grazing in the Arctic Ocean in summer ranged from "non-detected" to 96% bacterial production day^{-1} (Anderson & Rivkin 2001). In this study, in the coastal waters of this Arctic fjord in summer, most heterotrophic bacterial and *Synechococcus* spp. production was removed by nanoflagellates, thereby transferring it to higher trophic levels.

Microbial assemblages

In previous studies, *Synechococcus* spp. has survived at temperatures as low as 4 °C (Paulsen et al. 2016). Cold-adapted picophytoplankton is present in both the Arctic (Zhang et al. 2015) and Antarctic oceans (Doolittle et al. 2008), but they are mostly absent from polar ocean environments (Pedrós-Alió et al. 2015). Increasing temperatures are expected to result in a relatively greater abundance of small phytoplankton in marine ecosystems (Tremblay et al. 2012). In Svalbard, warming over the last few decades has been observed (Dahlke et al. 2020), and polar waters may be warming and increasing *Synechococcus* spp. abundance (Flombaum et al. 2013). Moreover, we found that *Synechococcus* spp. abundance differed dramatically over time, ranging from 0.5 to 25.6 × 10^3 cells ml^{-1} (Fig. 3c), which is similar to that reported by Paulsen et al. (2016). Additional environmental factors such as light availability, nutrient level, temperature and salinity affect *Synechococcus* spp. variation (Scanlan et al. 2009; Paulsen et al. 2016; Parli et al. 2021). In this study, we found that the peak value of *Synechococcus* spp. (16.0 × 10^3 cells ml^{-1}; Fig. 3c) was associated with freshwater plumes discharged from glacier melting (salinity < 10 PSU) and had a high growth rate of 1.63 d^{-1} in our incubation experiment (Table 2). Consistent with our results, Nelson et al. (2014) reported that *Synechococcus* spp. might adapt to low-salt, cold waters. Their frequent occurrence in Arctic lakes and rivers further suggests that freshwater runoff may also contribute to the spread of *Synechococcus* spp. into the Arctic Ocean (Vincent et al. 2000). In contrast, Paulsen et al. (2016) found that *Synechococcus* spp. abundance decreases exponentially with decreasing temperature, but remains highest in ice-associated waters influenced by Atlantic inflow (salinity > 34.9 PSU). Because of this association, *Synechococcus* spp. are often considered indicators of saline Atlantic Water entering the Arctic, as indicated by its decreasing abundance with decreasing salinity (Paulsen et al. 2016). In this study, the higher *Synechococcus* spp. abundance observed on 14 August (> 16.0 × 10^3 cells ml^{-1}; Fig. 3c) coincided with high salinity (29.6 PSU), suggesting that Atlantic inflow and advective transport may also have contributed to the presence of *Synechococcus* populations in the fjord.

The VLP abundances recorded in this study are within the range reported by Middelboe et al. (2002) and Boras et al. (2010) for the Arctic Ocean. However, some studies have reported higher levels of VLP (up to 2.0 × 10^7 VLP ml^{-1}) in the southern Beaufort Sea and Amundsen Gulf (Payet & Suttle 2008). Our research shows that glacier meltwater altered microbial processes substantially. It is interesting to note that the VLP abundance was significantly higher in waters more strongly affected by meltwater, such as the low-salinity water of our near-shore site. Our analysis found no significant correlation between VLP abundance and heterotrophic bacterial abundance ($p > 0.05$). Also, we found no high viral lysis rates on heterotrophic bacteria or *Synechococcus* species (Table 2). It is likely that the high number of VLP observed was not caused by bacteriophages, as suggested by Boras et al. (2010), who proposed that VLP inflow caused by meltwaters may have explained large VLP abundance. As reported by other studies, sea ice can be an important source of VLP, containing up to 1.19 ×10^8 VLP ml^{-1} melted sample (Gowing et al. 2004; Deming & Eric Collins 2017). In this situation, much higher VBR (up to 100–700) in the coastal water with lower salinity (< 28 PSU) was observed in our study. The high ratio of VLP-to-bacteria in the ice indicated that bacteria were rare in the ice, while VLP were abundant (Deming & Eric Collins 2017).

Impacts of viral lysis and grazing on bacteria and picophytoplankton

Detecting positive slopes—such as the positive slopes resulting from the linear regressions in the grazer+viral-free seawater dilution series (Supplementary Fig. S2b, f)—in dilution experiments is problematic (Tijdens et al. 2008). One hypothesis suggests that the observed *k* in the experimental treatments can be attributed to variations in grazing and viral lysis, as well as the dilution of predators, while the intrinsic growth rate of the prey remains constant (Landry & Hassett 1982). With increasing potential predation, the *k* of the prey increases,

contradicting a key assumption of the experiment (Tijdens et al. 2008). The y-intercept, which usually represents the intrinsic growth rate of organisms, must be interpreted differently as well. It would be better to estimate μ from undiluted incubations rather than y-intercept, which would represent growth rate in the absence of grazers and VLP. For this reason, we estimated the average growth rate of *Synechococcus* spp. from 100% fraction of whole seawater, which is about 4.12 d^{-1} (Table 2).

We found that *Synechococcus* spp. growth rates were clearly lower in treatments where viral abundance was reduced in Exp. C2 (Supplementary Fig. S2f), suggesting that active viruses stimulated *Synechococcus* spp. growth. This limitation could result in underestimating grazing and/or lysis, as observed once in our experiment. Moreover, several studies have demonstrated that diluted water can contain substances that limit phytoplankton growth, further contributing to reduced k (Middelboe & Lyck 2002; Weinbauer et al. 2011). In Exp. C2, the grazer+viral-free seawater dilution treatment with higher salinity (33.3 PSU) showed significantly lower growth rates of *Synechococcus* spp., indicating that the presence of active VLP may have stimulated *Synechococcus* spp. growth (Table 1; Supplementary Fig. S2f). Moreover, Weinbauer et al. (2011) reported that viral lysis of heterotrophic bacteria could have released nutrients that stimulated the growth of *Synechococcus* spp.

Heterotrophic nanoflagellates play a major role in controlling heterotrophic bacterial abundance in polar systems throughout most of the year (Anderson & Rivkin 2001; Boras et al. 2010; Lara et al. 2013). These observations agree with our results, which show that nanoflagellate grazing is important for controlling heterotrophic bacterial and picophytoplankton communities (Table 2). Moreover, several researchers have observed that grazing rates in cold Antarctic waters increase with rising temperatures (Vaqué et al. 2009). It is therefore important to study long-term changes in picoplankton community structure and nanoflagellate grazing ability as a result of the effects of environmental factors. Further, these data will help us understand the changes in the entire marine ecosystem in Arctic fjords. In contrast to grazing, VLP readily caused heterotrophic bacterial mortality in one of four experiments using the dilution approach (Table 2). The contribution of VLP to heterotrophic bacterial mortality in Arctic waters has been estimated at varying levels depending on the location. In Arctic waters, viral infections shunt heterotrophic bacterial carbon and nutrients into the dissolved organic matter pool at rates equal to or higher than the flux caused by protistan grazing (Steward et al. 1996; Wells & Deming 2006). It has been demonstrated that viral lysis is responsible for removing varying levels of heterotrophic bacterial production, from 1% (Steward et al. 2007) to 100% (Wells & Deming 2006). A dilution technique was used to determine that viral lysis accounted for 60–100% of mortality in Arctic coastal waters that were enriched with settling particles (Wells & Deming 2006). In the present study, a significant amount of viral lysis of heterotrophic bacteria (about 29% of the heterotrophic bacterial production) was observed in one of four incubation experiments conducted in low-salinity water with a high VBR. It is likely that this is due to the high VLP abundance in Exp. C1 (Table 1). The greater contribution of VLP than grazers to heterotrophic bacterial mortality in our study aligns with the low abundance of nanoflagellates (Table 2). This implies that the organic matter derived from heterotrophic bacteria is cycled within the bacterial pool rather than being directly transferred to higher trophic levels. In addition, the study was conducted during a time in the summer when meltwaters entered the fjord at a very high rate, providing an opportunity to explore microbial processes under the warmer conditions that are likely to prevail in the future.

Conclusion

In our summer study of a Svalbard fjord, most heterotrophic bacterial and *Synechococcus* spp. production was removed by nanoflagellates, thereby transferring it to higher trophic levels. We did not find high viral lysis rates on heterotrophic bacteria or *Synechococcus* spp. in our incubation experiments. It is likely that the high number of VLP was potentially influenced by glacial melt. This study highlights how summer meltwater conditions, marked by suspended sediments and salinity variations, affect the balance between viral lysis and grazing, with significant implications for carbon cycling and microbial food web structures in a warming Arctic. Understanding these dynamics is crucial as climate change continues to alter meltwater flows and freshwater inputs, impacting microbial community function and Arctic ecosystem health.

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Disclosure statement

The authors declare no conflict of interest.

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