



# Structure of viroplankton and viral lysis of prokaryotes on the shelf of Siberian Arctic seas: impact of large river runoff

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## Abstract

A small amount of information about the composition and functioning of prokaryotes and viruses in the Kara, Laptev and East Siberian seas makes it impossible to provide a quantitative assessment of all parameters of the carbon cycle which is necessary to analyze and predict the impact of climate change on the entire Arctic biota. Of particular interest are the areas of the inner and outer shelf of the Arctic seas which are, on the one hand, a zone of mixing of river and sea waters of the Ob, Yenisei, Lena, Indigirka and Kolyma rivers with a large amount of the smallest detrital particles; on the other hand, it is a zone of highly saline marine areas, which determined the task of our study. The modern methods of studying the structural and functional characteristics of microorganisms are used in the work: epifluorescence microscopy and transmission electron microscopy; the growth rate and production of plankton heterotrophic prokaryotes were determined by dilution method in situ and the method involving application of antibiotics, modified for natural habitats. On the shelf of the Siberian Arctic seas, the abundance of free viruses, frequency of visibly infected prokaryotic cells and viral-mediated mortality of prokaryotes values varied within  $0.1\text{--}13.6 \times 10^6$  viruses  $\text{mL}^{-1}$ ,  $0.2\text{--}5.6\%$  abundance of prokaryotes,  $1.4\text{--}64.4\%$  production of heterotrophic prokaryotes, respectively. We suggest that the input of a large amount of the smallest organic particles on which a significant amount of viruses is absorbed into the coastal waters of the Siberian seas (including riverine–marine water mixing zone) leads to a decrease in viral infection and mortality of prokaryotes.

**Keywords** Heterotrophic prokaryotes · Picodetritus particles · Viruses · Viral lysis of prokaryotes · Siberian Arctic seas and rivers

## Abbreviations

RMMZ	Riverine and marine water mixing zone
MZ	Marine water zone
PPD	Particles of pico-sized detritus
$N_{\text{PPD}}$	Abundance of particles of pico-sized detritus
$N_{\text{PPDV}}$	Abundance of particles of pico-sized detritus with attached viruses
$N_{\text{PR}}$	Abundance of prokaryotes
$N_{\text{PRV}}$	Abundance of prokaryotes with attached viruses
$N_{\text{PRVIC}}$	Abundance of visibly infected prokaryotic cells
$V_{\text{PR}}$	Volume of prokaryotic cell
$B_{\text{PR}}$	Biomass of prokaryotes

$P_{\text{PR}}$	Production of heterotrophic prokaryotes
$N_{\text{VF}}$	Abundance of free viruses
$N_{\text{VPR}}$	Abundance of viruses attached to prokaryotic cells
$N_{\text{VPPD}}$	Abundance of viruses attached to particles of pico-sized detritus
$D_{\text{VF}}$	Capsid diameter of free viruses
$F_{\text{VIC}}$	Frequency of visibly infected prokaryotic cells
$N_{\text{PRVIC}}$	Abundance of infected prokaryotic cells
BS	Burst size
FIC	Frequency of infected prokaryotic cells
VMPR	Viral-mediated mortality of prokaryotes
VIM	Viral-induced mortality of prokaryotes
$P_{\text{V}}$	Viroplankton production
$T_{\text{V}}$	Viroplankton turnover time

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## Introduction

The current state and changes in the Arctic Basin, both climatic and anthropogenic, largely depend on the processes occurring on the shelf of the marginal Arctic seas, mainly in areas of the strong continental runoff impact on the marine environment and biota (Lisitzin 1995; Gordeev et al. 1996; McClelland et al. 2012). Huge volumes of fresh water (2300–2500 km<sup>3</sup> per year) containing large amounts of allochthonous nutrients and suspended and dissolved terrigenous material and pollutants (more than 150 million tons) enter the Arctic seas with Siberian river runoff (Flint et al. 2018). In the estuarine zone of the Ob and Yenisei rivers and in the zones adjacent to the Lena, Indigirka, and Kolyma estuaries, freshwater runoff interacts with marine water, forming unique high-gradient pelagic biotopes, where the matter entering with continental runoff is subjected to biogeochemical transformation (Flint et al. 2010).

In aquatic ecosystems, including the riverine and marine water mixing zone, heterotrophic prokaryotes play a key role in the decomposition and transformation of organic matter, both natural and anthropogenic, and are an important component of planktonic food webs through which the majority of the carbon flux passes (Cole et al. 1988; Wheeler et al. 1996). Protozoan grazing and viral lysis are the major cause of bacterioplankton mortality (Wommack and Colvell 2000; Anderson and Rivkin 2001; Weinbauer 2004; Vaque et al. 2008). When bacteria are consumed by protozoans, a significant amount of bacterial carbon enters higher levels of the food web. As a result of viral lysis, carbon of lysed cells does not pass to higher trophic levels but enters the environment (“viral shunt”) and is actively involved in metabolism of heterotrophic bacteria, i.e., captured in the microbial loop (Wommack and Colvell 2000; Middelboe et al. 2002).

Studies conducted in different Arctic regions have demonstrated that viruses are the most numerous component of the plankton community and play a significant role in the functioning of microbial communities in cold waters, as well as in temperate and tropical marine waters (Suttle 2007; Maranger et al. 2015; Sandaa et al. 2018). In the meantime, until recently, data on the ecological role of viruses in the Siberian Arctic seas were not available.

There are very few works focused on the study of planktonic microbial communities on the inner shelf of the Siberian Arctic seas that receive large river discharge, as well as factors that determine the structural and functional characteristics of heterotrophic microorganisms and viruses. Such studies are of interest, especially for predicting possible changes in the structural and functional organization of planktonic microbial communities due to an increase in the temperature of the surface waters of the Arctic seas and an increasing runoff of Siberian rivers (Gordeev 2000).

The aim of this work was to study the effects of runoff from large Siberian rivers on the structural and functional characteristics of virus communities on the inner and outer shelves of the Siberian Arctic seas. Based on the published (Kopylov et al. 2015, 2017, 2020, 2021a, b) and unpublished new data, this article is the first to briefly overview the features of the virioplankton structure, the level of viral infection, and virus-induced mortality of heterotrophic prokaryotes in the riverine and marine waters mixing zone versus those in the zones significantly less subjected to the effect of runoff from the Ob and Yenisei rivers in the Kara Sea; the Lena River in the Laptev Sea; and the Indigirka and Kolyma rivers in the East Siberian Sea.

## Materials and methods

### Study sites and sampling

The studies were conducted in the riverine–marine water mixing zone (RMMZ): in the Kara Sea, in the northern part of the Yenisei estuary in September 17–22, 2011 (Kopylov et al. 2015), and the northern part of the Ob estuary in September 3–7, 2013 (Kopylov et al. 2017); in the Laptev Sea, in the area adjacent to the Lena Delta in September 8–14, 2015 (Kopylov et al. 2020); in the East Siberian Sea, in areas adjacent to the Kolyma estuaries in September 8–9, 2017 (Kopylov et al. 2021a) and Indigirka in September 5–7, 2017 (Kopylov et al. 2021b), and in outer shelf high-salinity marine water zones (MZ) (Table 1, Fig. 1). Water samples were collected during cruises 59, 63, and 69 of the R/V *Akademik Mstislav Keldysh* and cruise 125 of the R/V *Professor Shtockman* with 5-L Niskin bottles on a Rosette 32 sampler equipped with a CTD (SBE-911, Sea Bird Equipment, USA).

Ten water samples were taken from horizons of 0, 5, 6, 8, 10, 16, 20, 25 m at 3 stations in the RMMZ in the Kara Sea in the northern part of the Yenisei estuary (depths станций 20–28 m). Twelve samples of water were taken from horizons of 0, 5, 6, 8, 12, 15, 16, 18, 20 m at 3 stations in the RMMZ in the Kara Sea in the northern part of the Ob estuary (depths of stations of 16–23 m). Eight water samples were taken from horizons of 0, 8, 10, 20 m at 3 stations in the RMMZ in the Laptev Sea, in the area adjacent to the Lena Delta (depths of stations of 10–23 m). Ten water samples were taken from horizons of 0, 6, 8, 10, 11, 17, 20 m at 2 stations in the RMMZ adjacent to the mouth of the Indigirka River (depths of stations of 13–21 m). Eleven water samples were taken from horizons of 0, 5, 8, 13, 16, 17, 20 m at 2 stations in the RMMZ adjacent to the mouth of the Kolyma River (depths of stations of 17–22 m). Five water samples were taken from horizons of 0, 9, 30, 60, 115 m on the outer shelf in the Kara Sea, at a station in MZ

**Table 1** Coordinates, depth, salinity, and water temperature in RMMZ and MZ on the shelf of Siberian Arctic seas

Zone (number of data)	Coordinates	Depth of stations, m	Temperature (°C) <sup>a</sup>	Salinity <sup>a</sup>
Kolyma River → East Siberian Sea				
RMMZ (11)	(70°26'N 163°04'E)–(71°22'N 164°20'E)	17–22	2.3–6.7 (5.4 ± 2.1)	17.0–26.7 (19.7 ± 4.7)
MZ (9)	(74°23'N 168°11'E)–(73°20'N 166°48'E)	47	– 1.7 to 0.5 (– 1.0 ± 1.0)	29.4–31.8 (30.7 ± 1.2)
Indigirka River → East Siberian Sea				
RMMZ (10)	(71°28'N 152°53'E)–(72°19'N 154°32'E)	13–21	0.2–6.2 (3.8 ± 2.5)	15.0–30.1 (21.6 ± 5.8)
MZ (12)	(74°52'N 160°10'E)–(76°09'N 163°03'E)	45–59	– 1.6 to 0.5 (– 1.0 ± 0.9)	30.1–33.2 (31.2 ± 1.1)
Lena River → Laptev Sea				
RMMZ (8)	(71°99'N 130°30'E)–(72°40'N 130°30'E)	10–23	– 0.6–7.1 (4.3 ± 3.5)	3.0–31.5 (17.9 ± 31.5)
MZ (11)	(76°77'N 125°82'E)–(77°39'N 130°30'E)	71–90	– 1.6 to 3.0 (– 0.4 ± 1.7)	27.0–34.2 (32.6 ± 2.8)
Yenisei River → Kara Sea				
RMMZ (10)	(71°50'N 82°52'E)–(73°48'N 79°59'E)	20–28	– 0.5 to 9.6 (4.7 ± 4.0)	0.1–31.7 (16.7 ± 14.2)
MZ (5)	(77°12'N 78°07'E)	120	– 1.1 to 4.8 (1.6 ± 2.6)	27.3–34.4 (32.6 ± 2.9)
Ob River → Kara Sea				
RMMZ (12)	(71°44'N 72°47'E)–(72°44'N 73°27'E)	16–23	– 0.6 to 8.1 (5.6 ± 3.2)	1.0–29.6 (11.1 ± 10.0)
MZ (8)	(73°44'N 72°57'E)–73°21'N 73°00'E)	30–37	– 1.5 to 6.8 (0.3 ± 3.4)	11.1–32.7 (27.9 ± 8.7)

<sup>a</sup>Minimum and maximum values (mean ± standard deviation)

located to the north of the Yenisei estuary (station depth of 120 m). Eight water samples were taken from horizons of 0, 8, 15, 20, 23, 27, 35 m in the Kara Sea at 3 MZ stations located to the north of the Ob estuary (depths of 30–37 m). Eleven water samples were taken from horizons of 0, 8, 20, 26, 45, 60, 70, 83 m in the Laptev Sea at 3 stations in the MZ (depths of stations of 71–90 m). Twelve water samples were taken from horizons of 0, 15, 17, 20, 25, 27, 33, 42, 47, 54 m in the East Siberian Sea, at 3 stations in the MZ located north of the mouth of the Indigirka River (depths of stations of 45–59 m). Nine water samples were taken from horizons of 0, 15, 20, 26, 20, 33, 35, 47 m at 2 stations in the MZ located north of the mouth river Kolyma in the East Siberian Sea (depth of stations of 47 m).

Temperature and salinity data were obtained by the SBE-911 via temperature and conductivity sensors. Water subsamples (150 mL) for microscopic studies were fixed with 25% glutaraldehyde (final concentration 1%) immediately after sampling.

### Prokaryote abundances and sizes

The abundance and size of heterotrophic prokaryotes were estimated by epifluorescence microscopy. From 2 to 7 mL of fixed water subsample was poured onto a black Nuclepore filter (pore size 0.2 µm) and stained with DAPI (4',6-diamidino-2-phenylindole) at a final concentration of 1 µg mL<sup>-1</sup> (Porter and Feig 1980). Counts were done under an Olympus BX51 epifluorescent microscope (Olympus, Japan) using Cell F Image Analysis Software at 1000× magnification. On each filter, at least 400 prokaryotes were counted and the

dimensions of at least 100 cells were measured. The carbon content in prokaryotic cells ( $C$ , fgC cell<sup>-1</sup>) was calculated using the allometric equation  $C = 120 \times V^{0.72}$ , where  $V$  is the mean volume of prokaryotic cells, µm<sup>3</sup> (Norland 1993).

### Growth and production of heterotrophic prokaryotes

The growth rate and production of plankton heterotrophic prokaryotes were determined by dilution method according to changes in their abundance in isolated water samples which were exposed to in situ temperature in a temperature-controlled chamber for 36–40 h. Samples of the sea water were diluted 1:10 with water filtered through a 0.2 µm pore size membrane filter to remove phagotrophic organisms (Ducklow and Hill 1985; Tremaine and Mills 1987). Sample volume to carry out the dilution method was 100 mL.

All experiments were conducted in three replicates. The prokaryotic specific growth rate ( $\mu$ , h<sup>-1</sup>) was calculated according to the formula:  $\mu = (\ln N_t - \ln N_0)/t$ , where  $N_0$  and  $N_t$  are initial and final abundances of prokaryotes,  $t$  is the incubation time, h. The production of prokaryotic plankton ( $P_{PR}$ , mg C m<sup>-3</sup> day<sup>-1</sup>) was calculated as the product of the prokaryotic specific growth rate and biomass in undiluted sea water.

The heterotrophic prokaryote production in the Kara Sea was estimated by a method involving application of antibiotics (Sherr et al. 1986), modified for natural habitats (Weisse 1989; Sazhin et al. 2010). In contrast to the original method, the water pre-filtration to remove the mesozooplankton was not applied, taking into account its low



viral abundance, between 0.2 and 1.0 mL of water was poured onto the Anodisc filters. For each water sample, two filters were analyzed; counts yielded a minimum of 600 viruses. The carbon content in the viral particles was taken as  $0.055 \text{ fg C virus}^{-1}$  (Steward et al. 2007).

Concurrently, viruses were counted and their sizes were determined using transmission electron microscopy (Bettarel et al. 2000). Viruses were identified on the basis of morphology (round or hexagonal capsid structures, tailed and nontailed), size and staining characteristics. In addition, we measured the capsid size of viruses, determined the proportion of prokaryotic cells with attached viruses of the total prokaryotic abundance, the proportion of smallest detrital particles with attached viruses of the total abundance of smallest detrital particles, the abundance of viruses attached to one prokaryotic cell and to one detrital particle.

### Viral activities

Transmission electron microscopy was used to estimate the frequency of visibly infected cells (*FVIC*, estimated as the share (%) of total prokaryotic abundance), the mean number of fully matured phages in prokaryotes [i.e., burst size (*BS*), viruses cell<sup>-1</sup>]. Samples (50 mL) were centrifuged at  $100,000 \times g$  for 2 h on an OPTIMA L-90k ultracentrifuge (Beckman Coulter, USA) on Pioloform/carbon-coated 400-mesh nickel grids to obtain a bacteria and phage concentrate. Two grids were thus prepared for each water sample. The grids were then positively stained at room temperature with 1% aqueous solutions of uranyl acetate and lead citrate. The grids were further analyzed under a JEM 1011 electron microscope (Jeol, Japan) at  $50,000 \times$ – $150,000 \times$  magnification. No less than 800 prokaryotic cells were analyzed per grid.

To calculate the fraction of infected cells to the total heterotrophic prokaryotic abundance (i.e., *FIC*, %), the following equation was used (Binder 1999):

$$FIC = 7.1 \times FVIC - 22.5 \times FVIC^2.$$

The viral-mediated mortality of prokaryotes (*VMPR*) (expressed as a percentage of the production of heterotrophic prokaryotes,  $P_{PR}$ ) was estimated as (Binder 1999):

$$VMPR = (FIC + 0.6 \times FIC^2) / (1 - 1.2 \times FIC).$$

The absolute values of both *FVIC* and *FIC* were used.

The rate of viral-induced mortality of prokaryotes (*VIM*, cell mL<sup>-1</sup> day<sup>-1</sup> or mgC m<sup>-3</sup> day<sup>-1</sup>) was calculated by the equation  $VIM = VMPR \times P_{PR}$ . The production of virioplankton ( $P_V$ , viruses mL<sup>-1</sup> day<sup>-1</sup>) was calculated by the equation  $P_V = BS \times VIM$ , where *VIM* is cells mL<sup>-1</sup> day<sup>-1</sup>. The viral turnover time ( $T_V$ ) was estimated as the viral abundance divided by viral production. The amount of labile organic

matter released from lysed prokaryotic cells into the water was calculated as the difference between *VIM* and  $P_V$ . The values obtained are overstated, since the calculations did not take into account energy consumption by viruses for capsid protein synthesis and nucleic acid replication. Such data are still unknown and unavailable in the literature.

### Statistical analyses

Correlations between the parameters were analyzed using the Pearson's correlation coefficient calculated by Past 4.03 software (Hammer et al. 2001) and regarding the prerequisites for the data analyzed. The differences between the biological parameters in the described zones were detected using an independent sample *t* test for equality of the means.

## Results

### Environmental parameters

Freshwater of Siberian Rivers with a lower density than seawater spread in the upper layer of coastal sea water with a thickness of 6–15 m. The salinity in the upper layer of the water column increased with distance from the river mouth due to horizontal and vertical mixing of riverine and sea water. In our research, the average salinity for the water column in RMMZ was 7–15 times lower than that in MZ; water temperature, conversely, was 3–6 times higher (Table 1) (Flint et al. 2018).

In areas of the inner shelf of Arctic seas adjacent to mouths of large Siberian rivers, coastal marine water, along with desalination, is enriched with dissolved and suspended organic matter, in particular, with the smallest organic particles from 0.25 to 3.0 μm stained with DAPI, which are pico-sized detritus (PPD) (Mostajir et al. 1995; Wells and Deming 2003). The maximum concentration (up to  $35 \times 10^5$  particles mL<sup>-1</sup>) of such PPD was detected in RMMZ of the East Siberian Sea near the Kolyma estuary (Table 2). In MZ, the average abundances of the PPD ( $N_{PPD}$ ) were three to nine times lower than in RMMZ. The proportion of PPD with attached viruses in  $N_{PPD}$  was on average  $21.9 \pm 8.7\%$  (range: 10.7–31.7%) for RMMZ and  $25.5 \pm 4.7\%$  (range: 21.3–31.0%) for MZ. The maximum number of viruses attached to one detrital particle was 15.

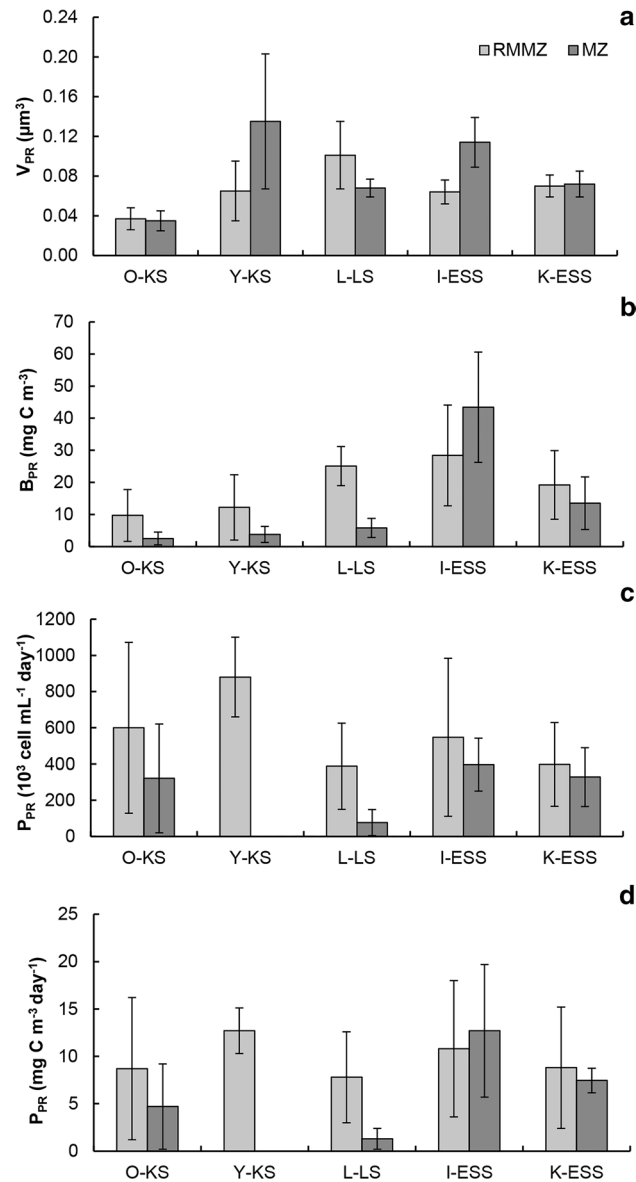
### Abundance and production of prokaryotes

In our studies, the abundance of prokaryotes in the Kara and Laptev seas ( $N_{PR}$ ) was significantly higher in RMMZ than in MZ: by 2.5–6.0 times. The same tendency was observed in the East Siberian Sea where these values differed by 1.3–1.4 (Table 2). On the shelf of Siberian Arctic

**Table 2** Abundance of particles of pico-sized detritus ( $N_{PPD}$ ), abundance of prokaryotes ( $N_{PR}$ ), abundance of free viruses ( $N_{VFR}$ ), total abundance of viroplankton ( $N_{VPT}$ ) in RMMZ and MZ

Zone	$N_{PPD}$ , $10^5$ particles $mL^{-1}$			$N_{PR}$ , $10^5$ cells $mL^{-1}$			$N_{VFR}$ , $10^5$ viruses $mL^{-1}$			$N_{VPT}$ , $10^5$ viruses $mL^{-1}$		
	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max
Kolyma River—East Siberian Sea												
RMMZ	8.8 $\pm$ 10.8	2.9–34.9	11.2 $\pm$ 5.4	5.3–21.0	67.2 $\pm$ 35.5	32.0–130.9	6 $\pm$ 3	3–10	73.8 $\pm$ 33.9	36.0–135.0		
MZ	3.5 $\pm$ 4.1	1.7–11.4	7.74 $\pm$ 4.24	3.4–13.3	81.0 $\pm$ 36.6	43.0–136.3	11 $\pm$ 12	5–39	84.7 $\pm$ 36.0	46.6–138.2		
Indigirka River—East Siberian Sea												
RMMZ	8.2 $\pm$ 3.7	3.3–12.8	19.1 $\pm$ 11.0	4.7–34.1	41.4 $\pm$ 13.1	23.0–51.5	3 $\pm$ 1	2–5	51.1 $\pm$ 1.3	31.3–66.4		
MZ	1.2 $\pm$ 1.2	0.4–4.6	14.2 $\pm$ 5.6	17.5–26.2	56.9 $\pm$ 22.7	30.2–102.9	4 $\pm$ 3	2–7	62.0 $\pm$ 21.3	37.9–106.1		
Lena River—Laptev Sea												
RMMZ	4.1 $\pm$ 2.6	1.0–8.0	17.3 $\pm$ 9.8	7.7–30.9	24.4 $\pm$ 12.6	10.0–43.9	2 $\pm$ 1	1–3	31.1 $\pm$ 13.7	12.8–50.4		
MZ	0.6 $\pm$ 0.5	0.2–2.0	3.5 $\pm$ 1.7	1.5–6.4	7.7 $\pm$ 10.2	1.2–36.8	4 $\pm$ 2	2–12	8.5 $\pm$ 10.7	1.6–39.0		
Yenisei River—Kara Sea												
RMMZ	2.9 $\pm$ 0.7	2.0–3.7	8.7 $\pm$ 9.0	0.7–22.2	23.6 $\pm$ 23.4	2.5–54.8	3 $\pm$ 2	2–6	30.2 $\pm$ 25.4	4.0–67.5		
MZ	0.4 $\pm$ 0.2	0.2–0.6	1.5 $\pm$ 0.1	1.4–1.6	4.8 $\pm$ 1.0	3.6–5.7	7 $\pm$ 2	5–8	5.4 $\pm$ 0.9	4.2–6.2		
Ob River—Kara Sea												
RMMZ	2.1 $\pm$ 1.2	1.0–4.0	6.0 $\pm$ 4.1	0.5–12.5	11.1 $\pm$ 8.2	2.1–27.5	3 $\pm$ 3	2–10	14.8 $\pm$ 9.9	2.7–31.1		
MZ	0.7 $\pm$ 0.6	0.2–2.3	2.4 $\pm$ 2.5	0.3–7.3	9.3 $\pm$ 8.6	2.5–29.2	7 $\pm$ 6	2–22	10.6 $\pm$ 6.5	3.9–18.0		

seas, the average cell volume of prokaryotes was between 0.035 and 0.135  $\mu\text{m}^3$ . In the Kara and Laptev seas the biomass of prokaryotes in RMMZ was significantly higher than in MZ ( $t$  19 = 2.13,  $p$  = 0.007;  $t$  12 = 2.2,  $p$  = 0.003;  $t$  15 = 2.36,  $p$  = 0.001 for Ob, Yenisei and Lena rivers respectively) (Fig. 2). The opposite situation was observed in the western part of the East Siberian Sea, where in the area of the inner shelf receiving Indigirka



**Fig. 2** Means ( $\pm$  standard deviation) of cell volumes of prokaryotes,  $V_{PR}$ ,  $\mu\text{m}^3$  (a); biomass of prokaryotes,  $B_{PR}$ ,  $\text{mgC m}^{-3}$  (b); production of prokaryotes,  $P_{PR}$ ,  $10^5 \text{ cell mL}^{-1} \text{ day}^{-1}$  (c) and production of prokaryotes,  $P_{PR}$ ,  $\text{mgC m}^{-3} \text{ day}^{-1}$  (d) in RMMZ and MZ in the areas where Siberian rivers flow into the Arctic seas (O-KS Ob River-Kara Sea, Y-KS Yenisei River-Kara Sea, L-LS Lena River-Laptev Sea, I-ESS Indigirka River-East Siberian Sea, K-ESS Kolyma River-East Siberian Sea)

River runoff, the biomass of prokaryotes in RMMZ was 1.5 times lower than in MZ ( $t$  13 = 2.16,  $p$  = 0.009) due to the higher average volume of prokaryotic cells in outer shelf waters and the small difference between the abundance of prokaryotes in waters of the inner and outer shelf (Fig. 2). The difference in prokaryotic production ( $P_{PR}$ ) between RMMZ and MZ was statistically significant ( $t$  19 = 2.12,  $p$  = 0.05;  $t$  16 = 2.45,  $p$  = 0.019 for Ob and Lena rivers, respectively) only in the Kara and Laptev seas (Fig. 2).

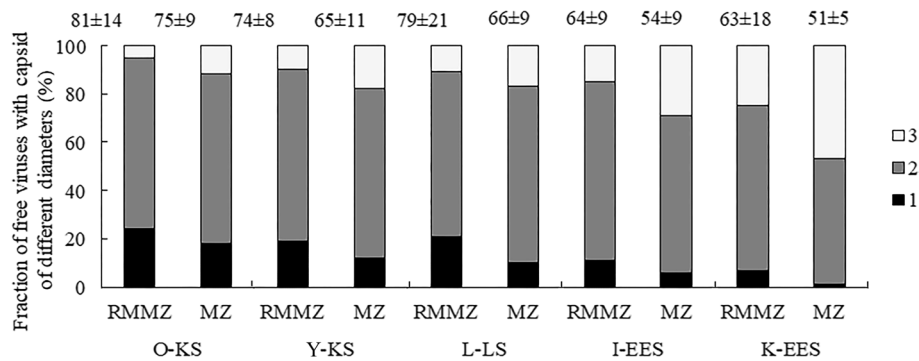
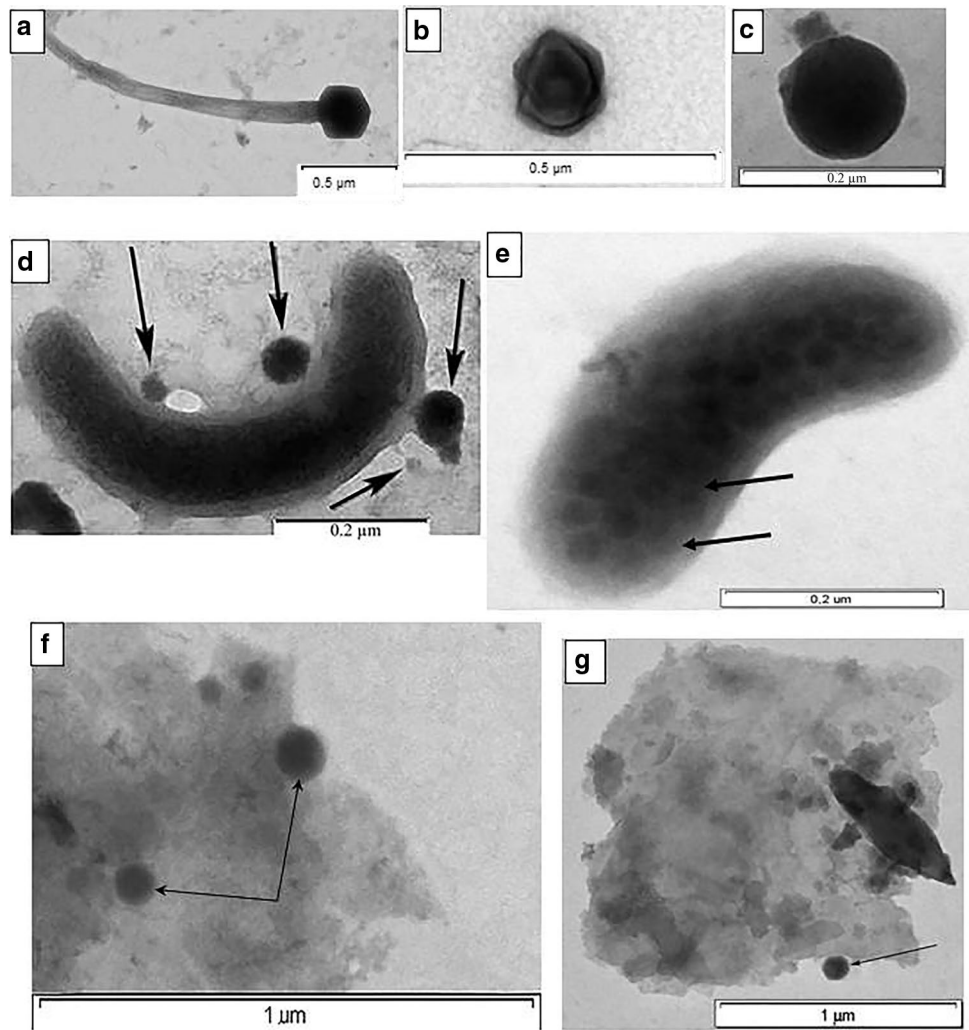
The  $N_{PR}/N_{PPD}$  ratio in RMMZ in the Kara and Laptev seas (3.0–4.2) was markedly higher than in the East Siberian Sea (1.3–2.3). The ratio was 1.2–10.2 times higher in MZ versus RMMZ. The proportion of prokaryotes with attached viruses in  $N_{PR}$  was on average  $17.1 \pm 2.9\%$  (range: 10.0–31.0%) for the surveyed RMMZ and  $16.5 \pm 3.9\%$  (range: 8.8–38.9%) for MZ. In all samples studied, 1 to 7 viruses were most often attached to the surface of one prokaryotic cell; in rare cases, up to 30 viruses were attached.

### Structure and abundance of viroplankton

Viroplankton included free viruses ( $N_{VF}$ ), viruses attached to prokaryotic cells ( $N_{VPR}$ ), and viruses attached to particles of pico-sized detritus ( $N_{VPPD}$ ) (Fig. 3). The abundance of free viruses ( $N_{VF}$ ) in the East Siberian Sea tended to be lower in RMMZ than in MZ, whereas in the Kara and Laptev seas, on the contrary,  $N_{VF}$  was significantly higher in RMMZ than in MZ ( $t$  20 = 2.1,  $p$  = 0.085;  $t$  12 = 2.26,  $p$  = 0.032;  $t$  15 = 2.36,  $p$  = 0.005 for Ob, Yenisei and Lena rivers respectively) (Table 2). The  $N_{VF}/N_{PR}$  ratio in shelf waters of the Siberian Arctic seas varied between 1.5 and 39.1, and was on average higher in MZ (4–11) than in RMMZ (2–6). The capsid diameter of free viruses ( $D_V$ ) ranged between 16 and 389 nm and was on average higher in RMMZ than in MZ. The proportion of viruses with  $D_V$  less than 40 nm was higher in MZ, while the proportion of large viruses with  $D_V$  larger than 100 nm was higher in RMMZ (Fig. 4).

The abundance of viruses attached to prokaryotic cells ( $N_{VPR}$ ) and their proportion in the total amount of viroplankton ( $N_{VT}$ ) in RMMZ (on average  $1.9\text{--}4.8 \times 10^5$  viruses  $\text{mL}^{-1}$  and 4–14%, respectively) tended to be slightly higher than in MZ (on average  $0.3\text{--}4.4 \times 10^5$  viruses  $\text{mL}^{-1}$  and 3–10%, respectively). At the same time, the abundance of viruses attached to PPD ( $N_{VPPD}$ , on average  $(1.7\text{--}4.9) \times 10^5$  viruses  $\text{mL}^{-1}$ ) ( $t$  19 = 2.13,  $p$  = 0.001;  $t$  12 = 2.18,  $p$  < 0.0001;  $t$  16 = 2.45,  $p$  = 0.009;  $t$  18 = 2.36,  $p$  = 0.002 for Ob, Yenisei, Lena and Indigirka rivers respectively) and their proportion in  $N_{VT}$  in RMMZ (12–15%) ( $t$  14 = 2.26,  $p$  = 0.014;  $t$  12 = 2.2,  $p$  = 0.007;  $t$  16 = 2.31,  $p$  = 0.092;  $t$  10 = 2.23,  $p$  = 0.044 for Ob, Yenisei, Lena and Indigirka rivers respectively) were significantly higher than those in MZ (on average  $0.2\text{--}1.6 \times 10^5$  viruses  $\text{mL}^{-1}$  and 2–5%, respectively) in

**Fig. 3** Electron micrographs of viruses in shelf waters of the Siberian Arctic seas: **a–c** free virus particle; **d** prokaryotes with viruses on surface—black arrows indicate viruses on cell surface; **e** virus-infected prokaryotes—black arrows indicate viruses inside cell; **f, g** viruses attached to detrital particle, black arrows indicate viruses attached to detrital particle



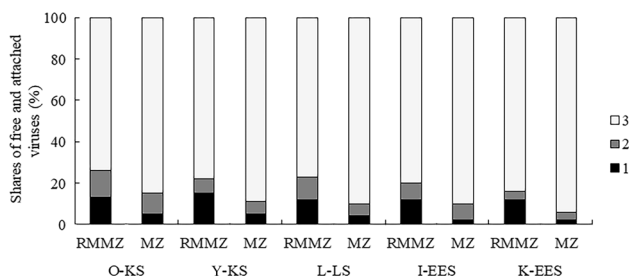
**Fig. 4** Fraction (%) of free viruses with capsid diameters < 40 nm (1), 40–100 nm (2) and > 100 (3) in RMMZ and MZ in the areas where the Siberian rivers flow into the Arctic seas (*O-KS* Ob River-Kara Sea, *Y-KS* Yenisei River-Kara Sea, *L-LS* Lena River-Laptev Sea,

*I-EES* Indigirka River-East Siberian Sea, *K-EES* Kolyma River-East Siberian Sea). Numerals indicate the average diameter of capsids of free viruses (mean ± SD, nm)

the Laptev and Kara Seas and had the same tendency in the East Siberian Sea.

The  $N_{VPPD}/N_{VT}$  ratio reached 35–39% in the East Siberian Sea and 21–25% in the other two seas. As a result, the virioplankton structure in RMMZ differed from that in MZ by a





**Fig. 5** Shares (%) of free viruses (3); viruses attached to the cells of prokaryotes (2) and viruses attached to the particles of pico-sized detritus (1) in the total abundance of viroplankton in RMMZ and MZ in the areas where Siberian rivers flow into the Arctic seas (*O-KS* Ob River-Kara Sea, *Y-KS* Yenisei River-Kara Sea, *L-LS* Lena River-Laptev Sea, *I-EES* Indigirka River-East Siberian Sea, *K-EES* Kolyma River-East Siberian Sea)

higher proportion of viruses attached to PPD and a lower proportion of free viruses (Fig. 5).

### Viral infection and virus-mediated mortality of prokaryotes

The frequency of visibly infected cells ( $FVIC$ ) and the viral-mediated mortality of prokaryotes ( $VMPR$ ) in shelf waters of the Siberian Arctic seas varied widely ( $0.2\text{--}5.6\%$   $N_{PR}$  to  $1.4\text{--}64.4\%$   $P_{PR}$ , respectively (Table 3). The maximum  $FVIC$  and  $VMPR$  values, with the exception of the Indigirka River, an East Siberian Sea section, were found in the RMMZ. The average values of  $FVIC$  and  $VMPR$  in the RMMZ of all three seas did not differ significantly, while in the MZ of the East Siberian Sea they were 1.6–2.3 times higher than in the MZ of the Kara and Laptev seas.

A moderate negative correlation between  $N_{VPPD}$  and  $FVIC$  ( $r = -0.45$ ,  $p = 0.04$ ,  $n = 21$ ) and a moderate positive correlation between  $P_{PR}$  and  $FVIC$  ( $r = 0.51$ ,  $p = 0.03$ ,  $n = 21$ ) were found in RMMZ of the East Siberian Sea.

Rod-shaped prokaryotes predominated in  $N_{PR}$  in all RMMZ, whereas on the outer shelf of seas, rod-shaped prokaryotes dominated in three MZ, and vibrio-shaped prokaryotes, in two MZ (Fig. 6). The proportion of coccus-shaped prokaryotes and vibrio-shaped prokaryotes in the total abundance of infected prokaryotes tended to be higher in MZ than in RMMZ. At the same time, infected filamentous prokaryotes were either not detected in MZ or their proportion in  $N_{PRVIC}$  was significantly lower than that in RMMZ.

The average number of viruses inside prokaryotic cells (BS) on the shelf of the Siberian Arctic seas varied within 5.7–17.4 viruses per cell, reaching maximum values in the RMMZ of the Kara Sea (Table 3). With the exception of the Yenisei River—the Kara Sea region, the differences in BS between RMMZ and MZ were not significant.

The minimum and maximum ratio of  $N_{PRVIC}$  to the abundance of prokaryotes with attached viruses ( $N_{PRV}$ ) differed by an order of magnitude: from 5 to 56 cells with attached viruses per one cell with visible intracellular viruses. The average  $N_{PRVIC}/N_{PRV}$  ratios in the East Siberian Sea were close, whereas they differed by 1.6–2.0 times in the Kara Sea. In the entire data set,  $N_{PRVIC}$  and  $N_{PRV}$  were positively correlated ( $r = 0.92$ ,  $p < 0.005$ ,  $n = 83$ ).

As a result, viruses lysed on average for RMMZ and MZ: in waters of the East Siberian Sea  $(0.3\text{--}0.5) \times 10^5$  and  $(0.3\text{--}0.4) \times 10^5$  cells  $\text{mL}^{-1} \text{day}^{-1}$ , respectively; in waters of the Laptev Sea,  $0.3 \times 10^5$  and  $0.03 \times 10^5$  cells  $\text{mL}^{-1} \text{day}^{-1}$ , respectively; and in waters of the Kara Sea  $(1.0\text{--}1.4) \times 10^5$  and  $0.3 \times 10^5$  cells  $\text{mL}^{-1} \text{day}^{-1}$ , respectively.

### Viral production

The lytic viral production ( $P_V$ ) in RMMZ in the Kara Sea was essentially higher than in RMMZ in the Laptev and East Siberian seas (Table 3). At the same time, if the average  $P_V$  values in the East Siberian Sea were similar in RMMZ and MZ or differed only by 1.6 times, in other seas they differed by 6.8–7.1 times. The average  $T_V$  values in the Kara Sea area subjected to the effect of the Ob River runoff were markedly higher than in other studied areas of the Siberian Arctic seas. The minimum  $T_V$  values were recorded in the East Siberian Sea (Table 4).

## Discussion

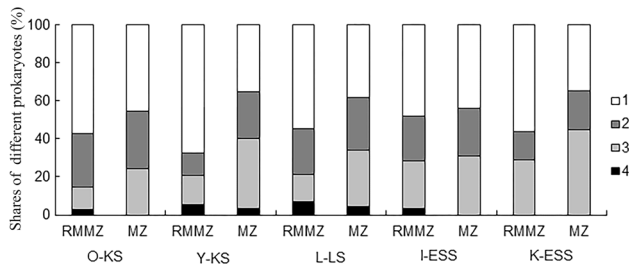
### Characteristics of particle-rich waters

Rivers flowing into Siberian Arctic seas are characterized by a high concentration of terrigenous suspended matter. Indigirka and Kolyma are the most turbid rivers among all the major rivers of the Russian Arctic. The average concentration of suspended matter in the river runoff in the East Siberian Sea is  $134 \text{ g m}^{-3}$ , which is 3–7 times higher than for rivers that flow into all other seas of the Russian Arctic (Gordeev et al. 1996).

The maximum concentrations of particles found in the RMMZ in the Siberian Arctic seas ( $3.8\text{--}34.9 \times 10^5 \text{ mL}^{-1}$ ) were higher than the concentrations of particles found nearshore in the vicinity of the mouths of Canadian Arctic rivers. On the Beaufort Shelf, the concentration of particles in the surface waters ( $\leq 6 \text{ m}$ ) was maximum near the Mackenzie River Delta ( $1.7 \times 10^5 \text{ mL}^{-1}$ ), which then declined to the observed minimum of  $2.75 \times 10^3 \text{ mL}^{-1}$  off the shelf (Wells et al. 2006). In Franklin Bay, surface particle concentrations at the station near the mouth of the Holton River ( $3.0 \times 10^4 \text{ mL}^{-1}$ ) were an order of magnitude higher than

**Table 3** Frequency of visibly infected cells of prokaryotes (FVIC, %  $N_B$ ), frequency of infected cells of prokaryotes (FIC, %  $N_B$ ), viral-mediated mortality of prokaryotes (VMPR, %  $P_{PR}$ ), number of mature phages inside infected cells (BS, viruses/cell), and ratio of the abundance of infected cells to the abundance of cells with attached viruses ( $N_{PRVIC}/N_{PRV}$ , %) in RMMZ and MZ

Region	FVIC		FIC		VMPR		BS		$N_{PRVIC}/N_{PRV}$	
	Mean ± SD	Min–max	Mean ± SD	Min–max	Mean ± SD	Min–max	Mean ± SD	Min–max	Mean ± SD	Min–max
Kolyma River—East Siberian Sea										
RMMZ	1.1 ± 0.4	0.5–1.6	7.5 ± 3.3	3.5–10.8	8.6 ± 3.9	3.7–13.2	8.2 ± 8.7	4–47	5.9 ± 2.7	2.5–8.7
MZ	1.1 ± 0.2	1.0–1.3	7.6 ± 1.2	6.9–8.8	8.7 ± 1.5	7.8–10.4	8.7 ± 6.0	4–23	5.9 ± 0.8	5.3–6.9
Indigirka River—East Siberian Sea										
RMMZ	1.1 ± 0.4	0.6–1.7	7.6 ± 2.9	4.2–11.4	8.8 ± 3.6	4.5–13.9	5.7 ± 3.0	4–15	6.4 ± 1.9	3.9–9.0
MZ	1.2 ± 0.5	0.6–2.5	8.1 ± 3.2	4.2–16.3	9.5 ± 4.6	4.5–22.3	7.8 ± 2.8	4–18	7.8 ± 3.3	5.2–15.7
Lena Lena—Laptev Sea										
RMMZ	1.0 ± 0.6	0.3–1.7	7.0 ± 4.3	2.1–11.4	7.9 ± 5.0	2.2–13.9	6.7 ± 6.0	3–25	5.8 ± 2.8	2.0–9.4
MZ	0.7 ± 0.2	0.3–1.2	4.6 ± 1.6	2.1–8.2	5.0 ± 2.0	2.2–9.5	7.8 ± 11.8	3–61	5.5 ± 2.3	2.2–10.0
Yenisei River—Kara Sea										
RMMZ	0.9 ± 0.5	0.2–1.9	6.2 ± 3.5	1.4–12.7	7.2 ± 4.5	1.4–16.1	17.4 ± 14.7	4–75	7.2 ± 4.9	3.7–19.2
MZ	0.5 ± 0.3	0.2–1.0	3.6 ± 2.1	1.4–6.9	3.9 ± 2.4	1.4–7.8	9.3 ± 6.6	5–47	3.5 ± 1.7	1.8–4.5
Ob River—Kara Sea										
RMMZ	1.3 ± 1.5	0.3–5.6	8.8 ± 9.0	2.1–32.7	12.4 ± 18.2	2.2–64.4	14.2 ± 9.9	4–131	5.8 ± 4.5	1.9–17.9
MZ	0.7 ± 0.5	0.3–1.7	4.9 ± 3.0	2.1–11.4	5.4 ± 3.9	2.2–13.9	12.3 ± 11.4	4–101	3.7 ± 1.8	1.8–8.2



**Fig. 6** Shares (%) of rod-shaped prokaryotes (1), coccus-shaped prokaryotes (2), vibrio-shaped prokaryotes (3), filamentous prokaryotes (4) in the total number of infected prokaryotes in RMMZ and MZ in the areas where Siberian rivers flow into the Arctic seas (O-KS Ob River-Kara Sea, Y-KS Yenisei River-Kara Sea, L-LS Lena River-Laptev Sea, I-ESS Indigirka River-East Siberian Sea, K-ESS Kolyma River-East Siberian Sea)

**Table 4** Production of viruses ( $P_V$ ,  $10^3$  viruses  $\text{mL}^{-1} \text{day}^{-1}$ ) and turnover time of virioplankton abundance ( $T_V$ , day) in RMMZ and MZ

Zones	$P_V$ , $10^5$ viruses $\text{mL}^{-1} \text{day}^{-1}$		$T_V$ , day	
	Mean $\pm$ SD	Min–max	Mean $\pm$ SD	Min–max
Kolyma River—East Siberian Sea				
RMMZ	2.4 $\pm$ 3.0	0.3–8.4	76 $\pm$ 80	5–205
MZ	1.8 $\pm$ 0.4	1.3–2.2	41 $\pm$ 16	30–52
Indigirka River—East Siberian Sea				
RMMZ	3.1 $\pm$ 3.2	0.6–8.6	20 $\pm$ 13	6–41
MZ	3.2 $\pm$ 2.0	1.1–7.7	23 $\pm$ 17	8–62
Lena River—Laptev Sea				
RMMZ	1.6 $\pm$ 1.3	0.7–3.5	23.2 $\pm$ 15.3	7–48
MZ	0.2 $\pm$ 0.2	0.1–0.6	37.1 $\pm$ 19.1	11–80
Yenisei River—Kara Sea				
RMMZ	32.0 $\pm$ 53.9	0.1–120.3	32.2 $\pm$ 32.1	0.4–80
MZ	nd	nd	nd	nd
River Ob—Kara Sea				
RMMZ	18.8 $\pm$ 48.8	0.4–172.5	6.0 $\pm$ 6.8	0.2–20.2
MZ	2.6 $\pm$ 3.4	0.4–8.7	6.1 $\pm$ 5.2	1.0–15.3

nd no data

in surface waters of other marine stations ( $8.9 \times 10^3 \text{ mL}^{-1}$ ) (Wells et al. 2006).

### Factors affecting virus dynamics and prokaryote-virus interactions

Analysis of data on the distribution of temperature, salinity, abundance of microorganisms and viruses in the Siberian Arctic seas (Kopylov et al. 2015, 2017, 2020, 2021a, b) showed that on the shelf of the Kara Sea and the Laptev Sea, between water temperature ( $T$ ,  $^{\circ}\text{C}$ ) and  $N_{PR}$  and between  $T$  and  $P_{PR}$  strong positive correlations existed (respectively,  $r = 0.69$ ,  $p < 0.005$ ,  $n = 77$  and  $r = 0.8$ ,  $p < 0.005$ ,  $n = 52$ ).

Negative correlations were observed between salinity ( $S$ ) and  $N_{PR}$  ( $r = -0.74$ ,  $p < 0.005$ ,  $n = 77$ ) and between  $S$  and  $P_{PR}$  ( $r = -0.84$ ,  $p < 0.005$ ,  $n = 52$ ). At the same time, on the shelf of the East Siberian Sea, no relationship between the  $N_{PR}$ ,  $P_{PR}$  and  $T^{\circ}\text{C}$ . Only a negative correlation was detected between water salinity and  $P_{PR}$ :  $r = -0.5$ ,  $p < 0.001$ ,  $n = 37$ .

According to the results of other microbiological studies in the coastal waters of the Siberian Arctic seas, the maximum abundance and biomass of planktonic prokaryotes were recorded, as a rule, in the zones near deltas and estuaries of the rivers, and the prokaryotic abundance and biomass decreased beyond the effect of river runoff significantly (Sorokin and Sorokin 1996; Meon and Amon 2004; Mosharova et al. 2016; Bezzubova et al. 2020).

The results of  $N_{VF}$  and  $N_{VF}/N_{PR}$  determination in the Siberian Arctic seas are within the range of values recorded in the central Arctic and other Arctic seas, namely  $(0.1–64.1) \times 10^6$  viruses  $\text{mL}^{-1}$  and  $0.8–70.0$  respectively (Steward et al. 1996, 2007; Howard-Jones et al. 2002; Hodges et al. 2005; Clasen et al. 2008; Venger et al. 2016). The FVIC and VMPR in shelf waters of the Siberian Arctic seas were in the range of values of these parameters recorded in the central Arctic and other Arctic seas:  $0–5.2\%$  and  $< 1.0–57.9\%$   $P_{PR}$  respectively (Steward et al. 1996, 2007; Howard-Jones et al. 2002; Hodges et al. 2005; Clasen et al. 2008; Venger et al. 2016).

On the shelf of the Kara and Laptev seas, positive correlations were observed between  $N_{PR}$  and  $N_{VF}$ , as well as between  $N_{PR}$  and  $N_{PRVIC}$ , between  $P_{PR}$  and  $N_{PRVIC}$ , between  $T$  and  $N_{PRVIC}$ :  $r = 0.74$ ,  $p < 0.005$ ,  $n = 77$ ;  $r = 0.7$ ,  $p < 0.005$ ,  $n = 77$ ;  $r = 0.58$ ,  $p < 0.005$ ,  $n = 52$  and  $r = 0.67$ ,  $p < 0.005$ ,  $n = 77$  respectively. The  $N_{VF}$  and  $N_{PRVIC}$  were negatively correlated with  $S$ :  $r = -0.73$ ,  $p < 0.005$ ,  $n = 77$  and  $r = -0.72$ ,  $p < 0.005$ ,  $n = 77$ , respectively. At the same time, no correlations were found between  $N_{PR}$  and  $N_{VF}$  and between  $T$  and  $N_{PRVIC}$  on the shelf of the East Siberian Sea, but positive correlations were found between  $N_{PR}$  and  $N_{PRVIC}$  ( $r = 0.74$ ,  $p < 0.005$ ,  $n = 41$ ), as well as between  $P_{PR}$  and  $N_{PRVIC}$  ( $r = 0.59$ ,  $p < 0.005$ ,  $n = 41$ ).

Whereas in the Kara and Laptev seas the average FVIC and VMPR were higher by 1.4–1.9 times in RMMZ than in MZ, the values of the parameters were similar in these zones of the East Siberian Sea (Table 3).

The close values of viral infection of prokaryotes in waters with positive (in RMMZ) and negative (in MZ) temperatures in the East Siberian Sea are apparently explained by a relatively small difference between the values of abundance and production of prokaryotes affecting the degree of their infection in RMMZ and MZ compared to other Siberian Arctic Seas.

Based on the experimentally obtained values of the specific growth rate of heterotrophic prokaryotes ( $\mu$ ) in RMMZ (range =  $0.241–0.398 \text{ day}^{-1}$ , mean =  $0.308 \text{ day}^{-1}$ ;  $T = 0.2–6.7 \text{ }^{\circ}\text{C}$ ) and in MZ (range =  $0.211–0.344 \text{ day}^{-1}$ ,

mean =  $0.278 \text{ day}^{-1}$ ,  $T = -0.5$  to  $-1.7 \text{ }^\circ\text{C}$ ), the community of planktonic prokaryotes in the outer shelf of the East Siberian Sea is adapted to negative water temperature conditions. As a result, in the East Siberian Sea, the average prokaryote production in RMMZ and MZ differed only by 1.2 times, whereas in the Laptev and Kara Seas prokaryote production in RMMZ was higher than in MZ by 2–6 times.

As shown previously, planktonic bacteria in the North Water Polynya can grow and reproduce viruses at subzero temperatures at rates comparable to bacteria in temperate systems, if the rate of organic carbon supply is sufficiently high and even though their temperature growth optima are always much higher than in situ temperatures (Middelboe et al. 2002). During the study period, the organic carbon supply of planktonic prokaryotes inhabiting inner and outer shelf of the East Siberian Sea differed slightly. The concentrations of dissolved organic carbon (DOC) in the East Siberian Sea in September 2017 at stations adjacent to the Indigirka River estuary and on the outer shelf were comparable: 2.0–15.6 and 0.2–24.3 mg C L<sup>-1</sup>, respectively; at stations adjacent to the Kolyma River estuary and on the outer shelf, 2.0–13.9 and 2.0–10.6 mg C L<sup>-1</sup>, respectively. The DOC concentrations were determined at the same stations and in the same samples, where heterotrophic prokaryotes and viruses were examined. The maximum values were recorded in the near-bottom layers. The DOC distribution in the offshore area has no or an extremely weak correlation with river runoff (Flint et al. 2018). Furthermore, at the end of the growing season, mortality of planktonic organisms was observed in the shelf waters of the East Siberian Sea. The vertical flux of organic carbon of dead organisms (larvacean houses and carcasses of copepods) and fecal pellets, determined on the shelf in the western part of the East Siberian Sea using sediment traps, was 54–55 mg C m<sup>-2</sup> day<sup>-1</sup> in the plume zone of the Indigirka River and 32–45 mg C m<sup>-2</sup> day<sup>-1</sup> in the marine area of the shelf (Drits et al. 2019).

At the same time, a high content of the smallest detrital particles in the water mixing zones can decrease the level of infection and mortality of prokaryotes. Contacts between viruses and the smallest suspended organic particles are more frequent at a higher  $N_{\text{ppd}}$  in the East Siberian Sea compared to other Siberian Arctic seas; as a result, a significant amount of free viruses is adsorbed to PPD, which reduces the possibility of viral infection of new prokaryotic cells (Murray and Jackson 1992). Accordingly, the frequency of contacts between viruses and prokaryotes decreases in these waters, which apparently decreases the level of viral infection and virus-induced mortality of prokaryotes. This phenomenon was described earlier (Murray and Jackson 1992). The low abundance of viruses during the transitional period from spring to summer is explained by the adsorption of viruses to inorganic suspended particles entering the coastal waters of Arctic seas with runoff from adjacent areas and to

organic (detrital) particles formed in large quantities after phytoplankton bloom (Schoemann et al. 2005). As a result of glacier melting in the Arctic, a large amount of small inorganic and organic particles, to which a significant amount of viruses are adsorbed, enter the coastal waters, which leads to a decrease in viral infection and mortality of algae and prokaryotes (Maat et al. 2019a). The researchers have suggested that during further global warming, viral losses will increase due to adsorption to suspended particles entering the marine environment from melting Arctic glaciers (De Corte et al. 2011; Maat et al. 2019b).

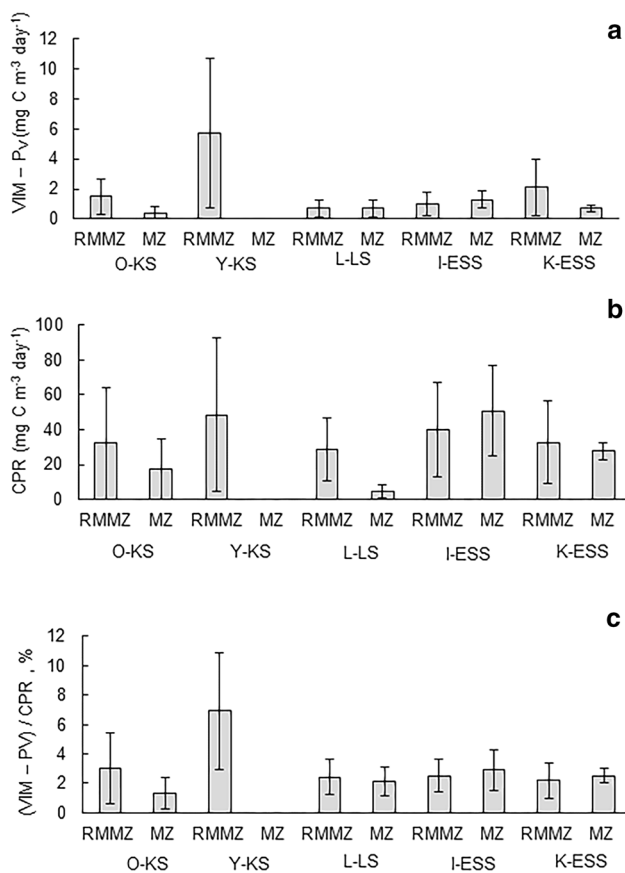
Warming of the Arctic causes increased river runoff, coastal erosion, and thawing of permafrost. Together, this leads to increasing washout of terrestrial dissolved and particulate organic matter into coastal Arctic ecosystems. This organic matter can be expected to affect both the carbon and nutrient flux through the microbial food web and composition of the microbial community (Müller et al. 2018). Permafrost degradation recorded in recent decades is causing an increase in Siberian river runoff into Arctic regions (Lisina et al. 2020). An increase in inflow to the Arctic seas of freshwater from Siberian rivers with an even higher content of suspended organic matter is probably leading to an increase in adsorption of viruses to suspended particles and a decrease in the role of viruses in the mortality of heterotrophic prokaryotes.

### Comparison of viral production in the Siberian Arctic Seas and in other Arctic regions

The  $P_V$  measured in the water column of the Siberian Arctic seas were either comparable with production rates previously reported for Arctic waters ( $1.1 \times 10^5$  to  $13.2 \times 10^5$  viruses mL<sup>-1</sup> day<sup>-1</sup> in the North Water Polynya by Middelboe et al. (2002);  $7.2 \times 10^5$  to  $122.4 \times 10^5$  viruses mL<sup>-1</sup> day<sup>-1</sup> in the North Sea by Winter et al. (2004);  $0.7 \times 10^5$  to  $18.5 \times 10^5$  viruses mL<sup>-1</sup> day<sup>-1</sup> in Franklin Bay by Wells and Deming (2003);  $0.2 \times 10^5$  to  $140 \times 10^5$  viruses mL<sup>-1</sup> day<sup>-1</sup> in the Chukchi Sea by Steward et al. (1996) and  $0.3 \times 10^5$  to  $77 \times 10^5$  viruses mL<sup>-1</sup> day<sup>-1</sup> on Canadian Arctic Shelf (CAS) by Payet and Suttle (2013) or lower ( $14.4$  to  $84 \times 10^5$  viruses mL<sup>-1</sup> day<sup>-1</sup>) at a depth of 1.5–3.0 m during the ice melting season in the Kongsfjorden by De Corte et al. (2011). The  $T_V$  values on the shelf of the Siberian Arctic seas were comparable to those obtained in CAS (stations in the Mackenzie–Amundsen Gulf System, Franklin Bay): range: 0.01–0.52 day<sup>-1</sup> (Payet and Suttle 2013).

### Viral lysis of prokaryotes as source of organic carbon for noninfected prokaryotic populations

Viral lysis causes the death of a host cell but also releases additional nutrients to the microbial food web. The release



**Fig. 7** The mean ( $\pm$  standard deviation) quantity of organic matter released by viral lysis of prokaryotes,  $VIM - P_V$ ,  $\text{mgCm}^{-3} \times \text{day}^{-1}$  (a); daily organic carbon requirements of prokaryotic plankton, CPR,  $\text{mgCm}^{-3} \times \text{day}^{-1}$  (b);  $(VIM - P_V)/CPR$  ratio, % (c) in RMMZ and MZ in areas where Siberian rivers flow into Arctic seas (O-KS Ob River-Kara Sea, Y-KS Yenisei River-Kara Sea, L-LS Lena River-Laptsev Sea, I-ESS Indigirka River-East Siberian Sea, K-ESS Kolyma River-East Siberian Sea)

of major nutrients (C, N and P) by viral lysis can relieve nutrient limitation and encourage the growth of noninfected bacterial populations (Noble and Fuhrman 1999; Wilhelm and Suttle 1999). In the Siberian Arctic Seas, the amount of organic carbon entering the aquatic environment as a result of viral lysis of prokaryotes ( $VIM - P_V$ ) ranged between 0.1 and  $47.2 \text{ mg C m}^{-3} \text{ day}^{-1}$  (on average  $0.7\text{--}6.9 \text{ mg C m}^{-3} \text{ day}^{-1}$ ) in RMMZ and between 0.04 and  $2.4 \text{ mg C m}^{-3} \text{ day}^{-1}$  (on average  $0.1\text{--}1.3 \text{ mg C m}^{-3} \text{ day}^{-1}$ ) in MZ (Fig. 7). As a result, the  $(VIM - P_V)/P_{PR}$  ratio varied between 2.2 and 64.4% (on average 7.0–25.6%) in RMMZ and between 1.1 and 22.2% (on average 4.8–10.7%) in MZ. Assuming that an average prokaryotic growth efficiency is 27% (Meon and Amon 2004), we calculated the daily organic carbon requirements of prokaryotic plankton (CPR) (Fig. 6). As a result, the  $(VIM - P_V)/CPR$  ratio varied between 0.6 and 17.4% (on average 1.9–6.9%) in RMMZ and between 0.3 and 6.0% (on average 1.3–2.9%) in MZ (Fig. 7).

The release of dissolved organic matter by viral lysis can lead to an increase in the prokaryotic production (by  $\sim 30\%$ ) (Fuhrman and Suttle 1993). Fischer and Velimirov (2002) showed that on average  $15.2 \mu\text{g C L}^{-1} \text{ day}^{-1}$  could potentially be released from viral lysis of bacterial cells, which corresponded to 46% of bacterial production in the water column. Thus, in general, the labile organic matter released by viral lysis of prokaryotes was a small source of carbon for noninfected heterotrophic prokaryotes on the shelf of Siberian Arctic Seas at the end of the growing season. However, in some RMMZs in the Kara Sea, the viral lysates were an important nutrient source for the noninfected prokaryotes.

## Conclusions

The structure of virioplankton in the area of the inner shelf in zones affected by river runoff differs from that in the area of the outer shelf by a higher proportion of viruses attached to the smallest detrital particles and a higher proportion of viruses with a capsid diameter greater than 100 nm. At the same time, adsorption of large amounts of viruses to detrital particles translates into lower contact rates between host and viruses, reducing mortality of heterotrophic prokaryotes. In the Kara and Laptev Seas, the mortality of prokaryotes due to viral lysis in the autumn period was on average significantly higher in the inner shelf area in RMMZ (in conditions of higher water temperature and higher abundance and production of prokaryotes) than in the outer shelf area in zones with higher water salinity. Among the areas studied in the shelf of the Siberian Arctic Seas, the highest values of virus-induced mortality of prokaryotes were recorded in the Ob River—Kara Sea mixing zone. In the East Siberian Sea, where the difference in the abundance and production of prokaryotes in the studied zones of the inner and outer shelf was less significant than in other seas and the content of the smallest detrital particles in RMMZ was maximum, the average values of virus-induced mortality of prokaryotes did not differ.

In general, according to our data, in autumn, planktonic viruses play a minor role in controlling the abundance and production of heterotrophic prokaryotes in shelf waters of the Siberian Arctic seas, but in some water layers, both on the inner and outer shelf, the role of viruses in the mortality of prokaryotes is significant.

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## Declarations

**Conflict of interest** The authors declare lack of any potential competing interests.

**Ethical Approval** Not applicable.

**Consent to participate** All authors have agreed to participate in the study.

**Consent for publication** Publication has been approved by all coauthors and the organization where the work was performed (Shirshov Institute of Oceanology RAS and Papanin Institute for Biology of Inland Waters RAS). Approval from the responsible authorities is not required. All authors have approved the manuscript for submission to “Polar Biology”.

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