Estuarine, Coastal and Shelf Science 217 (2019) 37–44

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Virioplankton of the Kara Sea and the Yenisei River estuary in early spring

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ARTICLE INFO

Keywords:
Virioplankton
Bacterioplankton
The Kara Sea
The Yenisei estuary
Early spring

ABSTRACT

Here we present our research results on the virioplankton of the shelf zone of the Kara Sea. This is the first study of viruses and bacteria done in the Kara Sea in early spring when viruses can play an important role in the abundance and production control of the bacterioplankton. All other studies cover July–September, that is, when the Kara Sea is completely ice-free and the community of viruses and bacteria is in an absolutely different stage of development. The samples were collected and processed on board of the vessel "Norilskiy Nickel" (project Aker ACS 650) between March 29 and April 8, 2016 on the regular cruise Murmansk – Dudinka. The abundance of bacteria (N_B) and viruses (N_V) located both underneath the ice and in the open waters of the Kara Sea and the Yenisei River estuary varied within a range of (0.075–0.429) $\times 10^6$ cells $\times$ ml^{-1} and (0.30–2.11) $\times 10^6$ viral particles $\times$ ml^{-1}, respectively, and the N_V/N_B ratio varied from 2.6 to 15.4. A positive correlation was found between N_B and N_V ($R = 0.70$, $p = 0.05$). Viruses with capsid diameter of 16–297 nm were registered in the water samples examined. The transmission electron microscopy data show that the fraction of the virus-infected bacterial cells is about 0.2–2.3% of total N_B. The mean viral-induced mortality of the bacteria calculated from all the sampling stations in the Kara Sea and the Yenisei River estuary was 7.8 $\pm$ 1.2% (with a range from 1.4 to 20.2%) of the daily bacterioplankton production. Our results show that viruses play an important role in the abundance and production of bacterioplankton control in early spring.

1. Introduction

Microbial communities (viruses, bacteria, protozoa), in which heterotrophic bacteria are the key component, play the important role of a link between the autochthonous and allochthonous dissolved organic matter stocks and the multicellular zooplankton in pelagic food webs (Wheeler et al., 1996; Middelboe et al., 2002). Viruses are most abundant in such microbial communities (Wommack and Colwell, 2000). In pelagic food webs the carbon content of bacteria can be either transferred to the upper trophic levels when consumed by protozoa and multicellular filter feeders or, alternatively, contribute to the dissolved organic matter stocks as a result of viral-induced cell lysis (Weinbauer, 2004; Kopylov and Kosolapov, 2011; Vaqué et al., 2017). The results of mathematical modelling (Murray and Jackson, 1992), experiments (Lenski, 1988) and empirical observations (Weinbauer and Suttle, 1999) all suggest that the rate of viral infection of bacterioplankton inhabiting oligotrophic waters is lower than those of eutrophic environments. In the former case bacterioplankton demonstrates a higher population density and a better physiological state.

In cold polar waters the bacteriophage-induced bacterial mortality varies considerably: from less than 1% up to 100% of the daily bacterial production (Guixa-Boixereu et al., 2002; Wells and Deming, 2006, Steward et al., 2007). The majority of research projects on virioplankton conducted in the Arctic region took place from late spring till early autumn and only a few studies were performed in early spring (Steward et al., 1996, 2007; Wells and Deming, 2006; Maranger et al., 2015; Venger et al., 2016).

Estuaries of major rivers play a leading role in controlling the impact of continental processes on marine ecosystems and the transformation of allochthonous material brought by river runoff (Lisitsyn,

Abbreviations: CA, coastal area; MA, marine area; PSS, practical salinity scale; *FVIC*, the frequency of visibly virus-infected bacterial cells; *FIC*, the frequency of virus-infected bacterial cells; *BS*, burst size; i.e., the number of matured viral particles in a given bacterial cell; *VMB*, viral-mediated mortality of bacteria; P_V, virioplankton production; T_V, viral turnover time

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https://doi.org/10.1016/j.ecss.2018.10.015
Received 18 April 2018; Received in revised form 15 October 2018; Accepted 22 October 2018
Available online 26 October 2018
0272-7714/ © 2018 Published by Elsevier Ltd.

1995). This is also very true for the Kara Sea to which about 1100 km^3 of fresh water annually flows through estuaries of the Ob and Yenisei rivers (Stein, 2000: Volkov et al., 2002). Earlier it was shown that in late summer and autumn the estuary zone, compared with the sea areas, is characterized by much higher values of biomass and phytoplankton production. However, in the early spring the opposite picture is observed: the coastal water in the western part of the Kara Sea were more productive than the water of the near-estuary water of the Ob and the Yenisei rivers. At the same time, neither the biogenic elements nor iron are limiting factors, while the development of phytoplankton is restrained by a lack of light under ice (Mosharov et al., 2018).

Studies of the spatial distribution of structural and functional characteristics of bacterio- and virioplankton in the Kara Sea in August–September revealed maximum values for these parameters in the estuaries of the rivers and in the coastal water (Kopylov et al., 2012, 2015). Similar studies were not carried out in early spring, so we could not judge the activity of plankton viruses in this period of the year and assess the effect of seasonal changes on the number of viruses, the degree of their infection with bacteria and the role of viral lysis in the mortality of bacterioplankton in these parts of the Kara Sea shelf.

The aim of this study is to determine the abundance and size distribution of virioplankton, frequency of visibly infected cells and the extent of viral-mediated mortality of heterotrophic bacteria in early spring, at the beginning of the seasonal ice melt, both underneath the ice and in open water. Therefore, we have focused on the evaluation of the top-down effect that viruses have on the abundance and production of bacterioplankton in the cold waters of the shelf zone of the Kara Sea in early spring.

2. Material and methods

2.1. Study area and sampling design

Water samples were collected from March 29 to April 8, 2016 on board the vessel “Norilskiy Nickel” (Aker ACS 650 project) at 18 stations along the vessel's course from the Kara Strait to the Yenisei River estuary and back to the Kara Strait. Stations were located in the Yenisei River estuary, in the coastal area (CA) and in the marine area (MA) (Fig. 1). Temperature was measured using the SBE-39 probe and LCD-thermometer (HANNA Checktemp-1). Salinity (in Practical Salinity Scale) was measured using a Kelilong PHT-028 salinity meter (China). Surface water samples for biological variables and dissolved organic carbon (DOC) were collected with a sterile 10-L bucket container from the side of the ship by hand. DOC concentration was measured by high-temperature combustion with a Shimadzu TOC-VCPH/CPN analyzer equipped with an SSM 5000A attachment. The precision and accuracy of our measurements were determined by comparison to external laboratory standards, namely solutions of potassium hydrogen phthalate and sodium hydrogen carbonate diluted to different concentrations and

Table 1
Values of temperature (T), salinity (S) and dissolved organic carbon (DOC) content in the water samples.

Station, number	T, °C	S, pss	DOC, mg/l	State of the sea surface
Yenisei River estuary				
14	−0.1	1.82	4.4	ice
8	−0.1	6.77	4.6	ice
Coastal area				
16	−1.2	24.28	4.2	ice
18	−0.5	28.57	−*	ice
7	−1.2	30.42	3.9	ice
19	−1.2	31.26	4.6	ice
20	−1.1	31.67	3.0	ice
4	−1.3	31.06	5.1	ice
21	−1.3	−*	3.9	ice
Marine area				
22	−1.3	35.34	2.8	open water
3	−1.5	28.10	4.0	ice
23	−0.9	35.43	2.8	open water
24	−1.3	34.84	2.7	ice
2	−1.1	33.46	4.0	ice
25	−1.3	33.70	−*	open water
26	−1.4	−*	1.9	open water
1	−1.1	33.70	3.8	ice
27	−1.3	34.54	2.0	open water

Note: * — no data available.

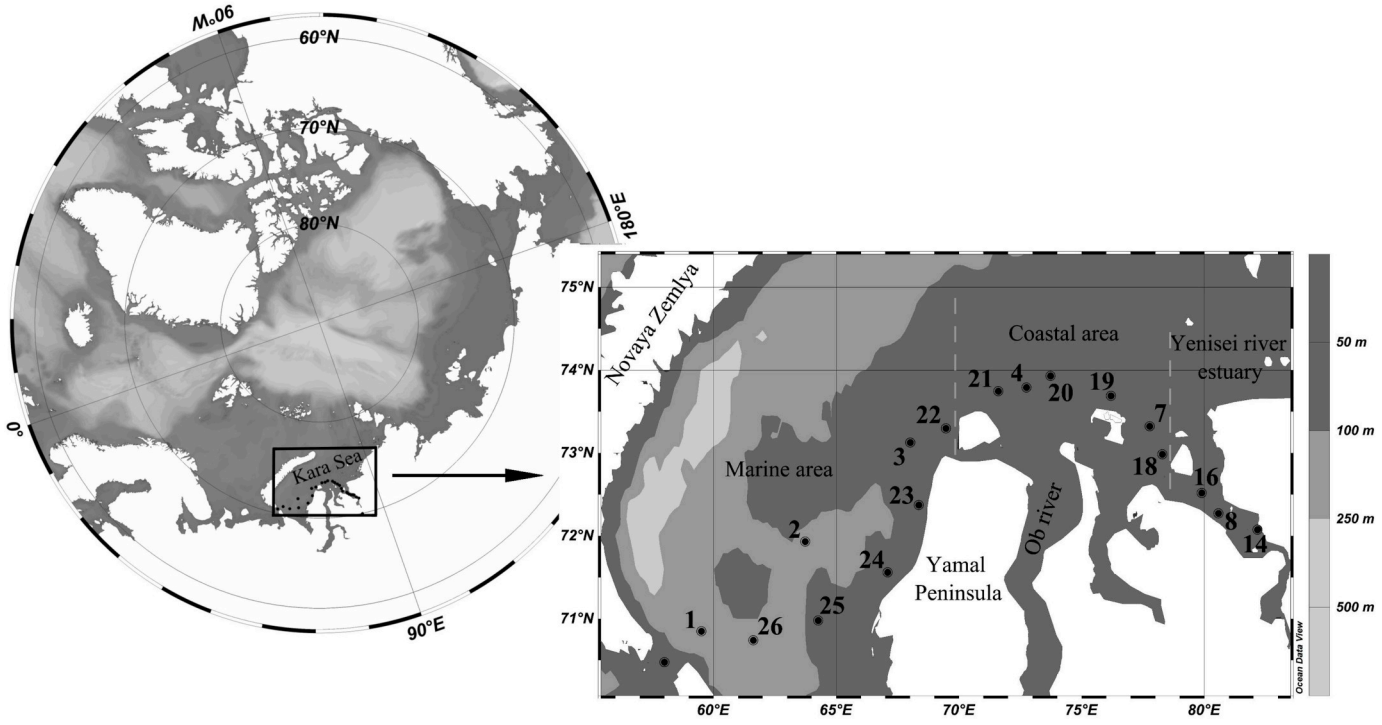

Fig. 1. The scheme of the locations of the sampling stations (The data was collected from March to April 2016 from the vessel “Norilskiy Nickel”).

amounting to ± 5% and 1%, respectively (Belyaev et al., 2010).

The water surface was covered with ice almost everywhere that was 30–50 cm thick. In such places samples were taken in free water spaces formed of an icebreaker. However, open water were also present in the area studied. During the study season the ice-free areas were located in the Kara Strait and further to the east up to the western coast of the Yamal Peninsula (Table 1).

2.2. Laboratory analyses

For the dissolved organic carbon, the range of the measurable concentrations was from 0.05 to 25000 mg of C × l^{-1} in a sample of 100 µl.

From each station a 7 ml sample was fixed with a formaldehyde neutral solution (1%, final concentration), filtered onto a nucleopore black filter (0.2 µm pore size) and stained with DAPI at a 1 µg × ml^{-1} (final concentration) for bacterial enumeration (Porter and Feig, 1980). Observation and counts were made under an epifluorescent microscope (Leica DM 5000 B) at a magnification of × 1000. The bacterial wet biomass was estimated based on the individual cell volume using ImageScope Colour image analysis software. The bacterial biomass carbon was estimated based on bacterial cell volume, using the formula:

$$fgC \times cell^{-1} = 133.754 \times V^{0.438},$$

where fgC × $cell^{-1}$ – carbon content (in femtograms) per a bacterial cell, V – cell volume (μm^3) (Romanova and Sazhin, 2010).

Bacterial production and the rate of consumption of bacterioplankton by the species of the upper trophic levels were estimated by using a method involving the application of antibiotics (Sherr et al., 1986), modified for natural habitats (Weisse, 1989). Immediately after water samples were collected, they were poured into 100-ml sterile transparent polystyrene bottles; antibiotics were added to some of them. The bottles were placed into a heat chamber located on the upper deck and were exposed for 8–12 h in the dark. The period of exposure was chosen based on our experimental data on antibiotic activity dynamics in arctic water. The grazing of nano- and microflagellates on bacteria was estimated using samples with antibiotics (benzylpenicillin, 1 mg × l^{-1}; vancomycin, 200 mg × l^{-1}), which stopped bacterial growth but had no influence on the grazers. Samples without antibiotics were exposed as control group. All the sample preparations were performed on deck at an air temperature close to the temperature of the surface water layer. For more detail on the method application please see Sazhin et al. (2010). Each experiment (bacterial production and the rate of consumption) was replicated twice (Kirchman, 1993).

The bacterial consumption rate d based on the experimental data was made taking into account the 1 h time lag in the effect of the antibiotics:

$$d = (\ln(N_{t\ ant}/N_0) - r)/(t\text{-}1),$$

where N_0 is the initial bacterioplankton abundance, $N_{t\ ant}$ – the final bacterial abundance in the experiment of the application antibiotics, r – the bacterial growth rate in control group, d – the bacterial growth rate in the experiment (assumed to reflect the population mortality rate due to consumption of bacteria and other causes), t – the duration of the experiment.

Daily production was calculated as:

$$P_b = (B_0 + B_{t\ contr}) \times 24 \times (r\text{-}d)/2,$$

where B_0 – is the initial bacterial biomass, $B_{t\ contr}$ – the final bacterial biomass in the experiment without the application of antibiotics, r – the bacterial growth rate in the control group of bacterioplankton, d – the bacterial growth rate in experiment (Zaika, 1983). The P/B coefficients are the ratio of bacterioplankton production to the mean values for the initial and final bacterial biomass in the control samples. All of the calculations were performed independently for the two replicates for each sampling station. The calculation of the bacterial production was done according to the average values of the number and biomass of bacterioplankton.

Viral particles, just as the bacterial cells, were counted under an epifluorescent microscope using a SYBR Green I fluorochrome and Whatman Anodisc aluminium oxide membrane filters with a pore size of 0.02 µm (Noble and Fuhrman, 1998). One ml of filtered water was fixed with neutral formaldehyde solution (1%final concentration). Filters were analysed under an Olympus BX51 (Olympus, Japan) epifluorescent microscope using Olympus Image Analysis Software. For each water sample, three filters were analysed, counting a minimum of 400 viruses to assess viral biomass, for each viral particle, we used a carbon content of 0.055 fgC × $virus^{-1}$ (Steward et al., 2007).

The frequency of visibly infected cells (*FVIC*, estimated as a fraction of the total number of bacterial cells), the mean number of the fully matured phages in bacteria (i.e. Burst Size (*BS*), particles × $cell^{-1}$) and the capsid size of the viruses were estimated using transmission electron microscopy. The 50 ml samples were centrifuged at 100 000 g (35 000 rpm) for 2 h using 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 prepared in that way 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 analysed under a JEM 1011 electron microscope (Jeol, Japan) at × 50000–150000 magnification. No less than 800 bacterial cells were analysed for each grid.

To calculate the fraction of the infected heterotrophic bacterial cells to the total bacteria cell number (i.e. *FIC*), we used the following equation (Binder, 1999):

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

The viral-mediated mortality of the bacteria (*VMB*), i.e. the fraction that the virus-induced mortality is of the total bacterial mortality or production, was estimated as (Binder, 1999):

$$VMB = (FIC + 0.6 \times FIC^2)/(1 – 1.2 \times FIC)$$

The absolute values of both the *FVIC* and the *FIC* were used. According to this approach the bacterial production is assumed to be equal to the total mortality of the bacterioplankton. The number of bacteria that die following the viral-induced lysis (i.e. the viral-induced mortality of the bacteria, *VIM*, cells × ml^{-1} × day^{-1} or mgC × m^{-3} × day^{-1}) was estimated as:

$$VIM = VMB \times P_B,$$

where P_B – is the production of bacterioplankton (cells × 10^3 × ml^{-1} × day^{-1} or mgC × m^{-3} × day^{-1}). The production of virioplankton (P_V, particles × ml^{-1} × day^{-1}) was estimated according to the following equation:

$$P_V = BS \times VIM,$$

where the *VIM* is measured in cells × ml^{-1} × day^{-1}. Viral turnover time (T_V) was calculated by dividing of abundance virioplankton by the value of production. The amount of easily assimilated organic matter (in mgC × m^{-3} × day^{-1}) that is released into the aquatic environment following virus-induced bacterioplankton lysis was calculated as the difference between the *VIM* and P_V. The resulting values were apparently overestimated because the calculations did not take into account the energetic losses due to viral capsid protein synthesis as well as those associated with the viral nucleic acid replication processes. This kind of data is still not available and has not been published elsewhere yet.

The Spearman's rank correlation coefficient with a significance level of 0.05 was used to test for the strength of the relationship between the two variables. Standard error values were calculated as a measure of dispersion of the mean values in the dataset.

Table 2
Abundance (N_B, 10^6 cells × ml^{-1}), biomass (B_B, mgC × m^{-3}) and daily production (P_B) of bacterioplankton, the fraction of bacteria with viral particles attached to them of the total abundance of bacterioplankton (N_{BV}/N_B, %), the number of bacteria that died due to the viral-mediated lysis of bacteria (*VIM*, 10^3 cells × ml^{-1} × day^{-1}).

Station, number	N_B	B_B	P_B		N_{BV}/N_B, %	*VIM*
			10^6 cells × ml^{-1}	mgC × m^{-3}		
Yenisei River estuary						
14	0.25 ± 0.025	4.66 ± 0.45	0.78	14.57	14.42	74.1
8	0.35 ± 0.083	4.15 ± 0.98	0.10	1.04	17.50	3.7
Coastal area						
16	0.34 ± 0.049	6.57 ± 0.96	0.21	4.13	20.23	38.0
18	0.18 ± 0.029	2.14 ± 0.34	0.07	0.88	24.30	6.7
7	0.15 ± 0.018	2.34 ± 0.28	0.27	2.26	20.63	25.6
19	0.27 ± 0.041	3.70 ± 0.57	0.22	1.72	7.60	4.8
20	0.19 ± 0.022	2.65 ± 0.31	0.34	4.88	20.30	3.4
4	0.21 ± 0.037	2.49 ± 0.44	0.51	6.15	17.33	48.4
21	0.20 ± 0.051	2.73 ± 0.69	0.24	3.00	13.20	5.3
Marine area						
22	0.09 ± 0.005	2.61 ± 0.15	0.14	2.64	22.90	5.2
3	0.08 ± 0.005	1.41 ± 0.16	0.19	3.42	24.75	38.4
23	0.08 ± 0.003	2.98 ± 0.13	0.12	4.02	20.25	9.4
24	0.11 ± 0.007	4.61 ± 0.27	0.40	14.34	18.80	14.8
2	0.07 ± 0.006	1.51 ± 0.13	0.04	0.92	23.53	2.1
25	0.12 ± 0.021	2.42 ± 0.45	< 0.01	< 0.1	16.30	-*
26	0.13 ± 0.008	4.39 ± 0.25	0.17	3.88	13.80	20.6
1	0.10 ± 0.017	1.27 ± 0.22	0.23	2.93	21.79	17.9
27	0.31 ± 0.056	4.29 ± 0.78	0.29	3.99	14.18	22.6

Note: * — the values were not calculated, since the bacterioplankton production at this station approached 0.

3. Results

The mean value of temperature of the surface water layer in the Yenisei River estuary (+0.1°C) was higher than that measured for the waters in the adjacent zone to the estuary – the coastal area (CA), as well as the marine area (MA) of the Kara Sea shelf (the mean values for the CA and MA were −1.1 ± 0.1 °C and −1.2 ± 0.1°C, respectively). On the contrary, the salinity values were higher for both of these areas (the mean values for the CA and MA were 29.54 ± 1.14 and 33.64 ± 0.84, respectively), compared to those measured in the estuarine water (4.30). The concentration of dissolved organic carbon in the water samples collected decreased from the stations located more eastward to those located in the western section of the transect. The calculated mean values were: 4.5 mg × l^{-1} for the Yenisei River estuary, 4.1 ± 0.3 for CA and 3.0 ± 0.3 mg × l^{-1} for MA (Table 1).

The abundance (N_B) and biomass (B_B) of bacterioplankton from the surface water layer at the sampling stations studied varied considerably (Table 2). The minimum and maximum values for the N_B and B_B measurements differed 5.7 and 6.4 times, respectively. The maximum values were registered in the samples from the mixing zone of the fresh Yenisei River waters with the marine water of the Kara Sea, as well as from the Kara Strait. The mean values of N_B и B_B for the areas studied were: 0.30 × 10^6 cells × ml^{-1} and 4.41 mgC × m^{-3} for the Yenisei estuary, 0.22 ± 0.02 × 10^6 cells × ml^{-1} and 3.23 ± 0.59 mgC × m^{-3} for the CA, 0.12 ± 24 × 10^6 cells × ml^{-1} and 2.82 ± 0.44 mgC × m^{-3} for the MA. The average volume of bacterial cells from the CA (0.039 ± 0.005 μm^3) was higher than that of the bacterioplankton cells from the Yenisei River (0.027 μm^3).

The number of bacteria that had viral particles attached to them (N_{BV}) varied between 16 × 10^3 and 68 × 10^3 cells × ml^{-1}, with a mean value of 31 ± 4 × 10^3 cells × ml^{-1}. The fraction that N_{BV} is of the total bacterioplankton abundance (N_{BV}/N_B) varied between 7.6% and 24.8%, with a mean value of 18.4 ± 1.1% (Table 2). The mean N_{BV}/N_B values for the samples taken in the CA and the MA showed only a slight difference: 17.6 ± 2.1% and 19.6 ± 1.4%, respectively.

The production of bacterioplankton (P_B) varied considerably between the studied areas and reached maximum values in the Yenisei River estuary and near the western coast of the Yamal Peninsula (Table 2). The mean P_B values in CA (0.27 ± 0.14 × 10^3 cells × ml^{-1} × day^{-1} and 3.29 ± 1.86 mgC × m^{-3} × day^{-1}) did not differ significantly from those in the MA samples (0.18 ± 0.12 × 10^3 cells × ml^{-1} × day^{-1} and 2.42 ± 1.76 mgC × m^{-3} × day^{-1}). An exception from the mean P_B values in the MA is the data for station 24 off the western coast of the Yamal Peninsula (Table 2). In the meantime, the *P/B*-coefficient values varied from 0.11 to 0.76 per day in the CA and from 0.18 to 0.64 per day in the MA, with mean values of 0.34 ± 0.23 per day and 0.38 ± 0.24 per day, respectively. The only exception was registered at sampling station number 25 located in the MA, where the values of both bacterial production and the *P/B*-coefficient were close to zero.

The number of free viruses (N_V) also varied considerably: the minimum and maximum N_V values differed by 7 times, having the following mean values: 1.6 × 10^6 viruses × ml^{-1} in the Yenisei River estuary, 1.6 ± 0.2 × 10^6 viruses × ml^{-1} in the CA and 0.7 ± 0.1 × 10^6 viruses × ml^{-1} in the MA (Table 3). The mean values of N_V/N_B were 5.6, 7.5 ± 0.8, 6.4 ± 1.3 for the three areas studied, respectively. A positive correlation was found between N_V and N_B ($R = 0.70$, $p = 0.05$).

The capsid size of the free viral particles from the Kara Sea and the Yenisei River estuary varied from 16 to 297 nm (Table 3). The mean capsid diameter values were: 78 nm for the water samples taken from the Yenisei River estuary, 85 ± 5 nm for those from the CA and 74 ± 3 nm for those from the MA. The fraction that the viral particles with a capsid size of 18–40, 40–60, 60–100, 100–150, 150–200 and more than 200 nm were of the total virioplankton abundance was 10.1 ± 2.2, 29.5 ± 2.0, 40.8 ± 2.8, 15.3 ± 1.7, 2.6 ± 0.9 and 1.7 ± 0.4%, respectively, for the 16 sampled marine stations, and 8.6, 24.7, 50.2, 10.8, 4.8 и 0.9% for the two estuarine sampling stations.

In the studied water samples bacterial cells were most frequently infected by phages with a capsid size less than 150 nm. Viruses of this size category accounted for 84.3–100% (95.5 ± 0.8%) of the total virioplankton abundance. The average capsid size of the phages attached to the bacterial cells (62 ± 4 nm) was 6.3 times smaller than the average size of the bacterial cells (392 ± 11 nm; as calculated from the data on the average volume of bacterial cells).

As is known, the frequency of contacts between viral particles and bacterial cells depends on their respective abundance, the physico-

Table 3
Abundance of free viruses (N_V)*, the capsid size of the free viruses (D_V)*, the abundance of viruses attached to bacterial cells (N_{VB}), the capsid size of the attached viruses (D_{VB})*.

Station, number	N_V, 10^6 particles × ml^{-1}	D_V, nm	N_V/N_B	N_{VB}, 10^3 particles × ml^{-1}	D_{VB}, nm
Yenisei River estuary					
14	1.79 ± 0.05	31 – 176 / 75 ± 3	7.0	48	73 – 92 / 83 ± 6
8	1.47 ± 0.04	26 – 201 / 81 ± 4	4.1	89	25 – 112 / 51 ± 6
Coastal area					
16	2.11 ± 0.10	30 – 182 / 82 ± 3	6.3	110	29 – 61 / 38 ± 3
18	1.76 ± 0.05	32 – 196 / 85 ± 5	9.8	58	25 – 97 / 53 ± 6
7	1.39 ± 0.02	29 – 185 / 69 ± 3	9.3	36	30 – 88 / 52 ± 6
19	1.82 ± 0.03	51 – 207 / 93 ±	6.8	27	38 – 118 / 67 ± 14
20	1.14 ± 0.09	30 – 226 / 77 ± 4	6.0	50	88 – 92 / 89 ± 2
4	2.09 ± 0.12	31 – 207 / 77 ± 3	10.0	50	28 – 89 / 53 ± 8
21	0.90 ± 0.03	37 – 220 / 113 ± 7	4.4	31	63 – 94 / 79 ± 6
Marine area					
22	0.82 ± 0.01	24 – 261 / 69 ± 4	9.6	31	22 – 123 / 54 ± 11
3	1.19 ± 0.03	30 – 216 / 76 ± 4	15.4	34	41 – 110 / 75 ± 8
23	0.47 ± 0.01	29 – 216 / 76 ± 4	6.1	22	27 – 103 / 49 ± 10
24	0.30 ± 0.02	16 – 230 / 86 ± 4	2.6	27	28 – 119 / 63 ± 10
2	0.50 ± 0.02	35 – 262 / 81 ± 4	6.9	21	23 – 108 / 45 ± 7
25	0.52 ± 0.03	16 – 246 / 77 ± 4	4.2	27	20 – 138 / 48 ± 10
26	0.77 ± 0.02	25 – 297 / 71 ± 5	5.8	26	30 – 96 / 53 ± 6
1	0.39 ± 0.01	23 – 129 / 55 ± 2	3.9	31	92 – 105 / 98 ± 5
27	1.06 ± 0.04	36 – 149 / 76 ± 3	3.4	62	52 – 75 / 63 ± 5

Note: *minimum and maximum values, the mean value ± standard deviation is given in the denominator of the fraction.

chemical parameters of the water, as well as on the size of a given bacterial cell and a given viral capsid (Murray and Jackson, 1992). Apparently, the relatively larger size of rods (2 × 0.5 μm), vibrios (1.6 × 0.7 μm) and spirochetes (6 × 1.3 μm) compared to the cocci cell (mean size: 0.4 μm; range: 0.2–0.7 μm), contributes to a higher frequency of contact between these morphological types of bacteria and phages and, as a consequence, to the higher probability of viral infection of these bacteria.

The number of viral particles registered on the surface of a single bacterial cell varied between 1 and 8 particles per a cell. The abundance of viruses that were attached to bacterial cells (N_{VB}) varied between 21 × 10^3 particles × ml^{-1} and 110 × 10^3 particles × ml^{-1}. The mean values registered for the studied areas were: 68 × 10^3 viruses × ml^{-1} in the Yenisei River estuary, 52 ± 11 × 10^3 viruses × ml^{-1} in the CA and 30 ± 4 × 10^3 viruses × ml^{-1} in the MA. The N_{VB}/N_V ratio varied from 1.5 to 9.2% with the following mean values for the three areas: 4.4% for the Yenisei River estuary, 3.2 ± 0.4% for the CA and 5.2 ± 0.7% for the MA.

The capsid size of the viral particles attached to bacterial cells varied from 20 to 138 nm in the Kara Sea and the Yenisei River estuary and had the following mean values for the studied areas: 67 nm in the estuary, 62 ± 7 nm in the CA and 61 ± 6 nm in the MA (Table 3).

The frequency of visibly infected cells (*FVIC*), i.e. the fraction of bacterial cells containing visible mature viral particles in the total bacterioplankton abundance varied from 0.2 to 2.3% of N_B. The mean values for the areas studied were 0.8% N_B for the Yenisei River estuary, 0.9 ± 0.3% N_B for the CA and 1.0 ± 0.2% N_B for the MA (Table 4).

Based on the *FVIC* estimation results, we found that the fraction of virus-infected bacteria to the total abundance of bacterioplankton (*FIC*)

Table 4
The frequency of visibly infected bacterial cells (*FVIC*, % N_B), the frequency of infected cells (*FIC*, % N_B), the viral-mediated mortality of the bacteria (*VMB*, % P_B), the number of viral particles present in a bacterial cell, i.e. the mean burst size (*BS*, particles per cell, the production of virioplankton (P_V, 10^3 viruses × ml^{-1} × day^{-1}), the turnover time of the virioplankton (T_V, day).

Station, number	*FVIC*	*FIC*	*VMB*	*BS*	P_V	T_V
Yenisei River estuary						
14	1.2	8.2	9.5	5.0 ± 0.3	370.5	4.8
8	0.5	3.5	3.7	6.0 ± 0.9	22.2	67.5
Coastal area						
16	2.1	13.9	18.1	5.0 ± 0.7	190.0	11.0
18	1.2	8.2	9.5	10.0 ± 3.2	67.0	26.8
7	1.2	8.2	9.5	5.0 ± 0.9	128.0	10.9
19	0.3	2.1	2.2	12.0 ± 0.7	57.6	31.2
20	0.2	1.4	1.4	6.0 ± 0.2	20.4	53.9
4	1.2	8.2	9.5	6.0 ± 1.1	290.4	7.2
21	0.3	2.1	2.2	11.0 ± 1.2	58.3	15.4
Marine area						
22	0.5	3.5	3.7	5.0 ± 0.7	26.0	30.7
3	2.3	15.1	20.2	6.0 ± 0.9	230.4	5.2
23	1.0	6.9	7.8	7.0 ± 3.2	65.8	7.6
24	0.5	3.5	3.7	13.0 ± 6.3	192.4	1.6
2	0.7	4.9	5.3	4.0 ± 0.2	8.4	59.5
25	1.0	6.9	7.8	5.0 ± 0.5	-*	-*
26	1.5	10.1	12.1	7.0 ± 1.7	144.2	5.5
1	1.0	6.9	7.8	13.0 ± 8.0	180.7	2.2
27	1.0	6.9	7.8	7.0 ± 3.0	158.2	6.3

Note: * — the values were not calculated, since the bacterioplankton production at this station approached 0.

varied from 1.4 to 15.1% N_B with an average value of 5.8% N_B for the Yenisei River estuary, 6.3 ± 0.4% N_B for the CA and 7.2 ± 1.2% N_B for the MA (Tab. 4).

The *FVIC* was not affected by the N_B distribution. However, a weak positive correlation was found between the *FVIC* and the N_{BV}/N_B ratio ($R = 0.35$, $p = 0.05$), as well as a moderate positive correlation between the *FVIC* and the N_V/N_B ratio ($R = 0.50$, $p = 0.05$). A strong positive correlation was found between the abundance of virus-infected bacterioplankton (cells × ml^{-1}) and the number of viral particles attached to bacterial cells (viruses × ml^{-1}) ($R = 0.90$, $p = 0.05$).

The viral-mediated mortality of bacteria (*VMB*) varied between 1.4% and 20.2% of P_B, reaching maximum values in the south-eastern part of the sea. The mean *VMB* values for the area studied were: 6.6% of P_B for the Yenisei River estuary, 7.5 ± 2.3% of P_B for the CA and 8.5 ± 1.7% of P_B for the MA. The average number of bacteria that died due to the viral-induced cell lysis was 38.9 × 10^3 cells × ml^{-1} × day^{-1} in the Yenisei River estuary, 18.9 ± 7.0 × 10^3 cells × ml^{-1} × day^{-1} in the CA and 16.4 ± 4.0 × 10^3 cells × ml^{-1} × day^{-1} in the MA (Table 2).

The number of phages in a single virus-infected bacterial cell, i.e. the burst size (*BS*), varied from 4 to 37 bacteriophages per cell. In the areas studied the maximum and the mean *BS* values for the collected samples were: 6 and 5 phages per cell in the Yenisei River estuary. The maximum *BS* in the CA was 24 (station number 18) and the mean *BS* was 8 ± 1 phages per cell. The maximum *BS* in the MA was 37 (station number 1) and the mean *BS* was 7 ± 1 phages per cell (Tab. 4).

For all of the areas studied the main contribution to the abundance of total bacterioplankton was made by cocci and ellipsoids (60–75% of the abundance of total bacterioplankton). Rods and vibrios, as well as filaments and spirochetes were also present, though in lower numbers (18–32% and 6–8% of the abundance of total bacterioplankton, respectively) (Fig. 2).

Rods and vibrios accounted for the largest fraction of the virus-infected bacteria (56–82% of the total virus-infected bacterioplankton abundances), with lower numbers observed for cocci, ellipsoids, filaments and spirochetes (10–41% and 3–8%). That is, the phages infected bacterial cells of different morphology at a different rate. At the same time, the fraction of the virus-infected rods, vibrios, filaments and

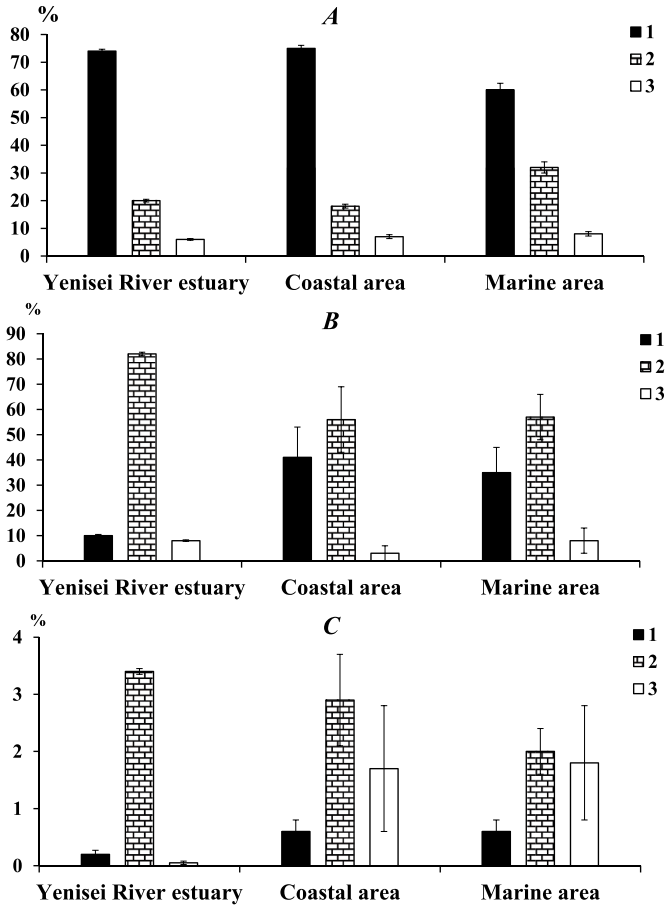

Fig. 2. Percentage (%) of bacterial cells of various morphology to the total bacterioplankton abundance (*A*); % of infected bacterial cells of various morphology to the total number of infected bacterial cells (*B*), % of infected bacterial cells of various morphology to the number of bacterial cells of a given type (*C*). 1- cocci and ellipsoids, 2 - rods and vibrios, 3 - filaments and spirochetes.

spirochetes in the total abundance values for bacteria of respective morphology in the Kara Sea (2.0–2.9% and 1.7–1.8%, respectively) was lower than that in the Yenisei River estuary (3.4% and 2.0%, respectively). However, the frequency of occurrence of virus infection in cocci and ellipsoids in the marine areas (0.6%) was considerably higher than in the Yenisei River estuary (0.2%). (Fig. 2).

The P_V and T_V values calculated for the samples taken in the Yenisei River estuary and at the marine stations varied considerably (Tab. 4). The mean P_V and T_V values were: $116 \pm 36 \times 10^3$ particles $\times$ ml^{-1} $\times$ day^{-1} and 22 ± 6 days in the CA and $126 \pm 29 \times 10^3$ viruses $\times$ ml^{-1} $\times$ day^{-1} and 15 ± 7 days in the MA.

4. Discussion

In late March and early April 2016 the water temperature under the sea ice and in the open water in the shelf zone of the Kara Sea and in the Yenisei River estuary was slightly higher than the temperature commonly registered for the water layer located beneath the sea ice (from -1.8 to -1.5°C) in the open areas of the Kara Sea during the winter (Dumanskaya, 2014). The study period in the areas of the Kara Sea sampled coincided with the "blooming" of diatoms located on the bottom surface of the sea ice. This assumption is based on both the appearance of the lower surface of the ice that was brown in colour and the remains of the characteristic colonies of ice algae (mainly *Nitzschia frigida*) in the samples of the surface water. An intense phytoplankton bloom with a prevalence of diatoms located only at the northern point of the Yamal peninsula under the 40–50 cm thick sea ice, as well as in the open marine waters near the Kara Strait. Moreover *Phaeocystis pouchetii* was starting to grow, then although it had not reached the peak yet at that time (Sazhin et al., 2017). In those conditions the frequency of virus-infected cells and the viral-mediated mortality of the bacteria were both relatively high. The mean values of the *FVIC* and *VMB* (1.0 ± 0.2% and 8.0 ± 1.3%, respectively) in the surface waters of the sea in early spring were lower than those calculated for the samples taken from the coastal water (water temperature: 0.4–6.0°C, *FVIC*: 1.6 ± 0.3%, *VMB*: 13.9 ± 3.2%). However the *FVIC* and *VMB* values for the marine samples were higher compared to those calculated for the samples taken from the surface layer of the open marine water in late summer (water temperature: 2.9–5.3°C, *FVIC*: 0.6 ± 0.1%, *VMB*: 4.5 ± 0.9%) (Kopylov et al., 2012, 2015).

Using the data on the average size of the free viral particles and assuming the carbon content factors for viruses and bacteria, we calculated the virioplankton biomass (the viral tail fibers were not taken into account). The mean content viruses carbon were 0.31 ± 0.06 mgC $\times$ m^{-3} (range 0.04–0.79 mgC $\times$ m^{-3}), that was equivalent to 6.4 ± 1.2% (range 1.4–13.8%) of bacterioplankton biomass. Thus, in early spring, as well as in summer and in autumn, the planktonic viruses, being the most abundant component of plankton, make a considerable contribution to the total biomass of the pelagic microbial community of the Kara Sea (Kopylov et al., 2012, 2015).

In other parts of the Arctic region the values of the N_V and N_V/N_B ratio for samples taken from the surface water during the ice melting period were: $(1.7–2.8) \times 10^6$ viruses $\times$ ml^{-1} and 4.6–6.4 near Norway (De Corte et al., 2011), $(0.37–0.76) \times 10^6$ viruses $\times$ ml^{-1}; 1.3–1.7 near Greenland (Boras et al., 2010) and $(1.4–5.6) \times 10^6$ viruses $\times$ ml^{-1}; and 2.4–12.0 for the samples taken from the North Water polynya at a water temperature below 0 °C (Middelboe et al., 2002). The values of the NV and NV/NB ratio we obtained is very close to the data of Middelboe et al. (2002), the values of the NV is lower than the data of De Corte et al. (2011) and is more than the data of Boras et al. (2010). NV/NB ratio we obtained is more on average than the data received before (Boras et al., 2010; De Corte et al., 2011).

For the various biotopes in the Arctic Ocean the level of viral-mediated mortality of bacteria usually varies from 1% P_B (Steward et al., 2007) to 50.6% P_B (Boras et al., 2010). In the surface waters during the ice melting period the *VMB* varied between 2.2 and 23.6% P_B, with a mean value of 7.6 ± 7.1% P_B (Boras et al., 2010). Meanwhile, for the samples from the North Water polynya, at a water temperature of less than 0 °C, the *VMB* values varied from 6% to 28% P_B (Middelboe et al., 2002).

These results are consistent with our data on the viral-mediated mortality of bacterioplankton for the samples taken from the waters below the sea ice in the Kara Sea in early spring (mean value: 8.1 ± 1.9% P_B; range: 1.4–20.2% P_B).

Our data show that while the values of the mean abundance of bacterioplankton and virioplankton measured for the CA and the MA of the Kara Sea in early spring differed 1.8–2.3 times, there was no considerable difference for the two areas in the measured values of the N_V/N_B, N_{BV}/N_B, *FVIC* and P_V. What is more, in both areas the *FVIC* values reached the relatively high level of 2.1–2.3% N_B.

As is known, the frequency of contacts between viral particles and bacterial cells depends on their respective abundance, the physico-chemical parameters of the water, as well as on the size of a given bacterial cell and a given viral capsid (Murray, Jackson, 1992). Apparently, the relatively larger size of rods (2×0.5 μm), vibrios (1.6×0.7 μm) and spirochetes (6×1.3 μm) compared to the cocci cell (mean size: 0.4 μm; range: 0.2–0.7 μm), contributes to a higher frequency of contact between these morphological types of bacteria and phages and, as a consequence, to the higher probability of viral infection of these bacteria.

As the result of virus-induced cell lysis, about 40–1360 μgC $\times$ m^{-3} $\times$ day^{-1} of the lysed bacterial cells' organic matter (*VIM* –

P_V) was released into the water daily. It was only from 1.9 to 4.6 × 10^6 μgC × m^{-3} (0.0009–0.031% with overage value 0.010 ± 0.002%) of the dissolved organic matter content in the surface water layer of the visited sampling stations. At the same time, at those stations where photosynthesis was registered beneath the sea ice, the ($VIM - P_V$) values varied from 4 to 154% (mean value 62 ± 24%) of the primary production values for phytoplankton located under sea ice during the daylight period, while at the sampling stations located in the areas that were free from ice the values were 0.4–20.7% (mean value 11 ± 4%) of the primary production (Mosharov et al., 2018).

Taking the average ratio of bacterial production to bacterial ratio in the Kara Sea to be equal to 0.27 (Meon and Amon, 2004), we estimated the daily organic matter (C_B) requirements of the bacterioplankton in the studied areas. The C_B values for the bacterioplankton in the Yenisei River estuary varied from 3.8 to 54.0 (mean value: 28.9) mgC × m^{-3}, while at the stations located in the shelf zone of the Kara Sea the values varied from 3.3 to 52.7 (mean value:14.6 ± 3.0) mgC × m^{-3}. The amount of organic matter that was released into the water following viral-induced bacterial cell lysis and that could then again be assimilated by living bacteria varied from 1.0 to 2.5% of C_B in the Yenisei River estuary and from 0.4 to 5.4 (mean value: 2.1 ± 0.4) % of the C_B for the rest of the areas studied. Thus, this nutrient source was relatively unimportant for the heterotrophic bacterioplankton of the Kara Sea during the study period.

5. Conclusion

Viruses played a key role in controlling the abundance and production of bacterioplankton in the surface water layer (right below the sea ice and in the areas free from ice) in the Yenisei River estuary and in the shelf zone of the Kara Sea. The maximum values of the viral-mediated mortality of bacteria (*VMB*) registered below the sea ice at water temperature below 0 °C, were close to the maximum *VMB* values registered in the Kara Sea at a water temperatures above 0 °C. The fact that in the plankton samples a considerable number of bacteria had viral particles attached to them shows that the viruses were active during the study period. A strong positive correlation was shown between the number of virus-infected bacterial cells and the number of phages attached to the bacterial cells. Comparison of the average values of the structural and functional characteristics of the virioplankton from the coastal area and the marine area of the Kara Sea shelf showed that though during the study period the abundance of planktonic viruses was higher in the coastal area, the frequency of viral infection of bacterial cells was similar for the two areas.

Declarations of interest

None.

Acknowledgements

This study was supported by a RFBR grant (project No. 18-05-00326) and a RSF grant (research results of hydrochemical characteristics, project No. 14-50-00095). The authors are deeply grateful Nikolay Belyaev for DOC data and to Lynne Hulett for correcting the English translation. The authors are also grateful to the reviewers for their thorough work with the manuscript.

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