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MARINE BIOLOGY

Distribution of Bacterioplankton with Active Metabolism in Waters of the St. Anna Trough, Kara Sea, in Autumn 2011

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Abstract—The distribution of bacterioplankton with active electron transport chains, as well as bacteria with intact cell membranes, was investigated for the first time in the region of St. Anna Trough in the Kara Sea. The average number of bacteria with active electron transport chains in the waters of the St. Anna Trough was 15.55×10^3 cells mL^{-1} (the limits of variation were $1.06–92.17 \times 10^3$ cells mL^{-1}). The average number of bacteria with intact membranes was 33.46×10^3 cells mL^{-1} (the limits of variation were 6.78 to 103.18×10^3 cells mL^{-1}). Almost all bacterioplankton microorganisms in the studied area were potentially viable, and the average share of bacteria with intact membranes was 92.1% of the total number of bacterioplankton (TNB) (the limits of variation were 76.2 to 98.4%). The share of bacteria with active metabolisms was 38.2% of the TNB (the limits of variation were 5.6–93.4%). The shares of the bacteria with active metabolisms were maximum in areas with the most stable environmental conditions (on the shelf and in deep water), whereas on the slope, where the gradients of water temperature and salinity were maximum, these values were lower.

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INTRODUCTION

It is known that bacterioplankton (BP) is an important element in carbon cycle. Its activity promotes mineralization of different organic compounds including anthropogenic. Numerous data on microorganisms possessing active electron transport chains in water microbial biocenoses have been obtained in recent years. It has been demonstrated that share of these bacteria in water microbiocenoses is impermanent and makes up 3–65%. This bacteria pool results in active heterotrophic processes in water environments [11, 13, 14]. The share of cells with intact membranes is another important indicator reflecting the state of heterotrophic BP, since the integrity of cell membranes is necessary to maintain the viability of any cells [11, 14].

The data on the number and distribution of bacteria with active an electron transport system as well as number of bacteria with intact membrane in Kara Sea, particularly in deep depressions, has not yet been obtained. Thus, the goal of the present work was to study the distribution of these microorganisms.

MATERIALS AND METHODS

The samples for determining microbiological parameters were collected during the cruise 59 of the R/V *Akademik Mstislav Keldysh* (September 24–29, 2011) on transects along the eastern (stations 33, 37, 39, 42) and western (stations 44, 45, 48) spurs of the St. Anna Trough (Fig. 1). The depths of the transects were 122 (station 33) to 526 (station 45) m. On the eastern transect, samples were collected on an adjacent shelf at a depth less than 150 m (station 33), in upper part of the slope of the eastern spur at a depth of over 300 m (station 37), the lower part of the slope of the eastern spur (station 39), and the abyssal part of the trough at a depth of over 400 m (station 42). On the western transects, the samples were collected in upper part of the slope at a depth less than 150 m (statin 44), on continental slope at a depth about 300 m (station 48), and abyssal part of the trough at a depth over 500 m (station 45) (Fig. 1).

The samples for microbiological analysis were collected on 5–7 horizons and their number depended on a depth at a station and pycnocline location. Rosette sampler equipped with bathometers and CTD probe was used for the samples collection. The samples of water were poured into sterile polystyrene tubes and processed on board ship.

The following microbiological parameters were determined in the samples: number of BP with active electron transport chain (CTC + BP), number of BP with intact cell membranes (IMB) and with damaged

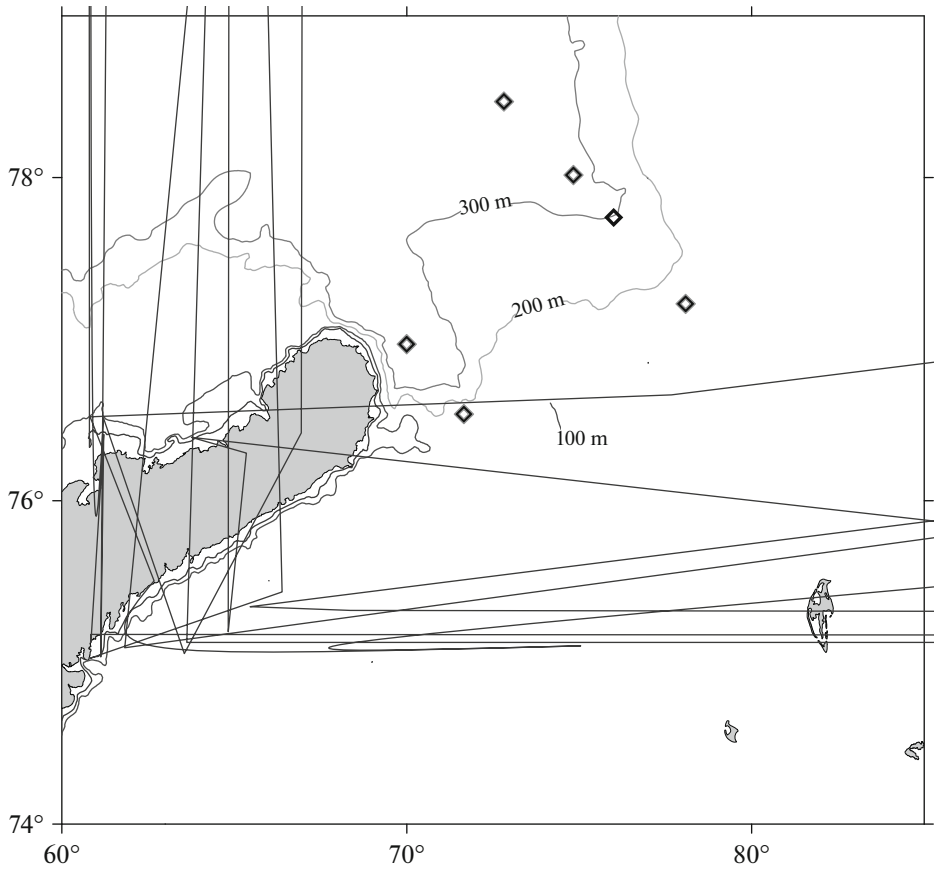

Fig. 1. Location of sampling sites on two transects in water area of St. Anna Trough, Kara Sea, in Autumn 2011.

Distribution of microbiological parameters on two transects in St. Anna Trough, Kara Sea, in Autumn 2011 (average ± confidence interval)

Station	Horizon, m	TNB, $\times 10^3$ cells ML^{-1}	IMBN, $\times 10^3$ cells mL^{-1}	Share of IMBN in TNB, %	CTC + BP, $\times 10^3$ cells mL^{-1}	Share of CTC + BP in TNB, %
Eastern transect						
33	2	73.31 ± 0.03	68.22 ± 0.03	93.0	55.94 ± 0.03	76.3
	9	65.05 ± 0.03	60.17 ± 0.03	92.5	27.97 ± 0.02	43.0
	15	104.88 ± 0.04	103.18 ± 0.04	98.4	92.17 ± 0.03	87.8
	30	59.96 ± 0.03	58.48 ± 0.03	97.5	43.86 ± 0.03	73.1
	60	37.93 ± 0.02	36.65 ± 0.02	96.7	32.42 ± 0.02	85.5
	122	23.31 ± 0.02	20.76 ± 0.02	89.1	7.95 ± 0.01	34.1
Average		60.74	57.91	94.5	43.38	66.65
37	7	76.28 ± 0.03	69.71 ± 0.03	91.4	15.26 ± 0.03	20.00
	12	40.68 ± 0.02	38.35 ± 0.02	94.3	14.62 ± 0.03	35.94
	30	36.23 ± 0.02	33.90 ± 0.02	93.6	6.67 ± 0.03	18.42
	40	19.70 ± 0.01	18.22 ± 0.01	92.5	7.31 ± 0.03	37.10
	75	23.52 ± 0.01	21.61 ± 0.01	91.9	3.50 ± 0.001	14.86
	200	28.39 ± 0.01	27.33 ± 0.01	96.3	1.91 ± 0.001	6.72
	311	28.39 ± 0.01	26.91 ± 0.01	94.8	12.71 ± 0.02	44.78
Average		36.17	33.72	98.5	8.85 ± 0.001	25.40
39	0	60.81 ± 0.03	56.15 ± 0.03	92.3	21.29 ± 0.02	35.02
	15	66.11 ± 0.03	63.77 ± 0.03	96.5	11.12 ± 0.01	16.83
	30	48.10 ± 0.02	46.40 ± 0.03	96.5	3.18 ± 0.001	6.61
	75	31.99 ± 0.02	30.93 ± 0.02	96.7	6.36 ± 0.001	19.87
	150	27.12 ± 0.02	25.43 ± 0.02	93.8	7.63 ± 0.001	28.13
	250	40.26 ± 0.02	35.38 ± 0.02	87.9	12.39 ± 0.01	30.79
	354	26.70 ± 0.02	20.55 ± 0.02	77.0	19.07 ± 0.01	71.43
Average		43.01	39.80	91.5	11.58	29.81
42	5	32.84 ± 0.03	30.51 ± 0.02	92.90	18.12 ± 0.01	55.16
	15	19.92 ± 0.01	17.37 ± 0.01	87.23	12.71 ± 0.01	63.83
	25	53.82 ± 0.03	50.85 ± 0.03	94.49	7.95 ± 0.001	14.76
	40	22.67 ± 0.02	21.82 ± 0.02	96.26	21.29 ± 0.01	93.93
	50	25.21 ± 0.02	23.73 ± 0.02	94.12	20.98 ± 0.01	83.19
	100	15.26 ± 0.01	13.98 ± 0.01	91.67	4.45 ± 0.001	29.17
	463	16.10 ± 0.01	13.77 ± 0.01	85.53	7.3 ± 0.001	45.39
Average		26.54	24.58	91.7	13.26	55.06
Western transect						
44	5	34.32 ± 0.02	31.36 ± 0.02	91.0	12.08 ± 0.01	35.19
	10	35.17 ± 0.02	31.99 ± 0.02	93.8	11.44 ± 0.01	32.53
	20	16.95 ± 0.01	15.89 ± 0.01	97.0	8.48 ± 0.01	50.00
	60	20.98 ± 0.02	20.34 ± 0.01	86.4	7.42 ± 0.01	35.35
	120	17.16 ± 0.01	14.83 ± 0.01	94.9	6.99 ± 0.01	40.74
	153	28.82 ± 0.01	27.33 ± 0.01	91.4	9.75 ± 0.001	33.82
Average		25.57	23.62	92.4	9.36	37.94

Table. (Contd.)

Station	Horizon, m	TNB, $\times 10^3$ cells ML^{-1}	IMBN, $\times 10^3$ cells mL^{-1}	Share of IMBN in TNB, %	CTC + BP, $\times 10^3$ cells mL^{-1}	Share of CTC + BP in TNB, %
45	0	41.95 ± 0.02	38.77 ± 0.02	92.4	20.55 ± 0.02	48.99
	10	54.45 ± 0.03	51.49 ± 0.03	94.6	26.70 ± 0.02	49.03
	20	45.98 ± 0.02	41.53 ± 0.02	90.3	29.24 ± 0.02	63.59
	55	59.96 ± 0.03	57.63 ± 0.03	96.1	31.57 ± 0.02	52.65
	100	21.61 ± 0.01	18.22 ± 0.01	84.3	6.14 ± 0.01	28.43
	526	13.98 ± 0.01	12.71 ± 0.01	90.9	2.97 ± 0.001	21.21
Average		39.66	36.73	91.4	19.53	43.98
48	0	44.07 ± 0.03	41.74 ± 0.03	94.7	2.97 ± 0.001	6.73
	20	16.95 ± 0.02	16.10 ± 0.02	95.0	1.27 ± 0.001	7.50
	40	11.44 ± 0.02	10.38 ± 0.02	90.7	1.48 ± 0.001	12.96
	60	13.35 ± 0.02	11.23 ± 0.02	84.1	1.91 ± 0.001	14.29
	110	8.90 ± 0.01	6.78 ± 0.001	76.2	1.70 ± 0.001	19.05
	170	13.56 ± 0.02	12.71 ± 0.02	93.8	3.60 ± 0.001	26.56
	240	19.07 ± 0.02	17.59 ± 0.02	92.2	1.06 ± 0.001	5.56
Average		18.19	16.65	89.5	2.00	13.24

TNB—total the number of BP, $\times 10^3$ cells mL^{-1}; IMBN—number of BP with intact cell membranes, $\times 10^3$ cells mL^{-1}; CTC + BPN—number of BP with active electron transport chains, $\times 10^3$ cells mL^{-1}.

26.54×10^3 cells mL^{-1} (the limits of variation were 15.26 to 53.82×10^3 cells mL^{-1}) (table and Fig. 2).

The average TNB value detected at stations of the western transect was lower than that detected at stations on the eastern transect, 29.16×10^3 cells mL^{-1} (the limits of variation were $8.90–64.62 \times 10^3$ cells mL^{-1}). The highest TNB values in waters of the western area were detected at station 45, and the average value was 39.66×10^3 cells mL^{-1} (the limits of variation were 13.98 to 59.96×10^3 cells mL^{-1}).

Analysis of the vertical TNB distribution revealed that on both transects, its values were maximum in the surface layer (0–10 m). The average TNB in the surface layer was 60.81×10^3 cells mL^{-1} (the limits of variation were 32.84 to 76.29×10^3 cells mL^{-1}). The TNB value decreased with increasing depth and was minimum on the depths exceeding 250 m (table).

Number of bacterial cells with intact membranes. Because cell membrane integrity is necessary for cells viability, we considered the number of BP with intact membranes (IMBN) as the pool of viable BP.

The highest IMBN value was 38.30×10^3 cells mL^{-1} (the limits of variation were $13.77–103.18 \times 10^3$ cells mL^{-1}), was detected in the water column of the eastern transect. In the waters of the western transect, the average IMBN value was almost two times lower, 26.93×10^3 cells mL^{-1} (the limits of variation were $6.78–59.96 \times 10^3$ cells mL^{-1}). The spatial distribution of IMBN values was as follows: on the eastern transect, the maximum average IMBN value was detected at station 33, whereas the minimum value was detected at station 42. On the western transect, the maximum average IMBN value was detected in the waters of abyssal station 45, whereas the minimum values were detected in the waters of station 48 (Fig. 2).

The vertical distribution of potentially viable BP was characterized by a higher number in the upper layer of the water column (0–15 m) on both the eastern and western transects. The average IMBN value in this layer was 56.38×10^3 cells mL^{-1} (the limits of variation were $17.37–103.18 \times 10^3$ cells mL^{-1}). The number of BP cells with intact membranes decreased with increasing depth and was the minimum at depths of 251–463 m. The average IMBN value in this layer was 20.41×10^3 cells mL^{-1} (the limits of variation were $13.77–26.91 \times 10^3$ cells mL^{-1}). In the deepest horizon (526 m) at station 45, the IMBN value was 12.71×10^3 cells mL^{-1} (table).

To compare the relative number of potentially viable cells in TNB in different habitats, the IMBN percentage in TNB was calculated. It was shown that almost all BP in the water column of the St. Anna Trough was viable. The average share of IMBN in the microbial biocenosis was 92.07%, and the limits of variation were relatively low (76.19–98.38%) (table).

Number of BP with active electron transport chains. The high activity of electron transport chains of bacterial cells determined using tetrazolium salts is applied

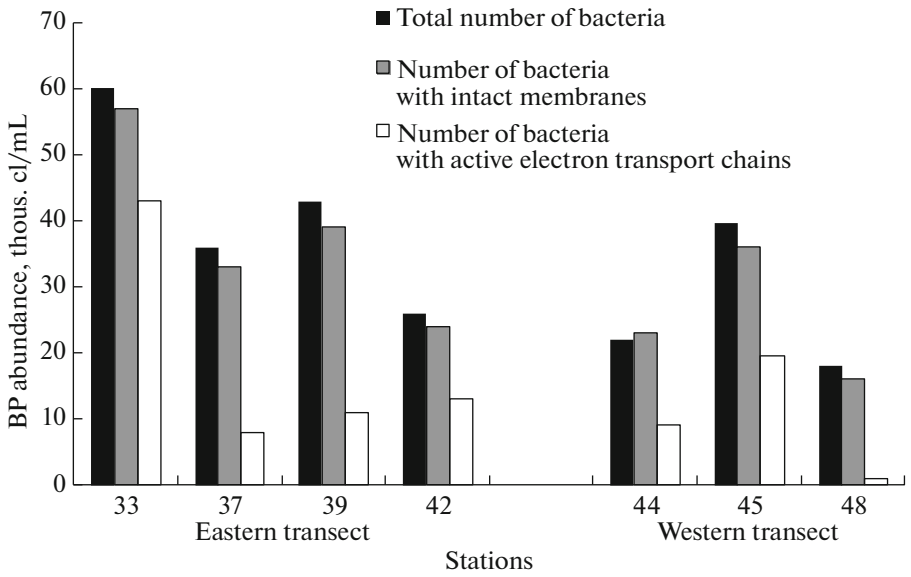

Fig. 2. Distribution of average TNB, IMBN, and CTC + BPN in water column on two transects in St. Anna Trough, Kara Sea, in Autumn 2011.

to estimate the number of metabolically active cells [17, 23, 24].

The average number of metabolically active bacteria (CTC + BP) in the water columns of both transects was 15.55 × 10^3 cells mL^{-1} (the limits of variation were 1.06–92.17 × 10^3 cells mL^{-1}). The highest CTC + BP value was detected in the water column of the eastern transect. In this case, the average CTC + BP value was 18.37 (the limits of variation were 1.91–92.17 × 10^3 cells mL^{-1}). The maximum number of active bacteria was detected in waters of shelf station 33. The average value at this station was 43.38 × 10^3 cells mL^{-1} (the limits of variation were 7.95–92.17 × 10^3 cells mL^{-1}). The minimum CTC + BP values were detected at station 42, 13.26 × 10^3 cells mL^{-1} (the limits of variation were 4.45–21.29 × 10^3 cells mL^{-1}) (table and Fig. 2).

The average CTC + BP value in the waters of the western transect was about two times lower than that on the eastern transect, 9.86 × 10^3 cells mL^{-1} (the limits of variation were 1.06–31.57 × 10^3 cells mL^{-1}). The highest number of physiologically active BP was revealed in the waters of deepest station 45. The average CTC + BP value at this station was 19.53 × 10^3 cells mL^{-1} (the limits of variation were 2.97–31.57 × 10^3 cells mL^{-1}). The minimum value was 2.0 × 10^3 cells mL^{-1} (the limits of variation were 1.06–3.60 × 10^3 cells mL^{-1}), detected in the waters of station 48 situated above the shelf break (table and Fig. 2).

Analysis of the vertical CTC + BP distribution in the water columns of both transects revealed that the value of this parameter was the highest in the surface layer (at a depth of 0–15 m) of the water columns (the average values on the eastern and western transects were 29.91 and 20.16 × 10^3 cells mL^{-1}, respectively). The average number of metabolically active BP at most stations decreased with increasing depth and reached the minimum at depths of 100–200 m. Only at two stations (37 and 39) at a depth exceeding 300 m were the CTC + BP values higher than those in the upper layers of the water column, 12.71 and 19.07 × 10^3 cells mL^{-1}, respectively. At the greatest depth (526 m at station 45), the CTC + BP values were low (2.97× 10^3 cells mL^{-1}) (table).

The average share of CTC + BP in TNB in the water columns for both transects was 38.17% (the limits of variation were 34.1–87.8%). The lowest share of CTC + BP was detected at station 37 situated above the shelf break, 25.4% (the limits of variation were 6.72–44.78%) (table and Fig. 3).

The average share of CTC + BP in TNB for stations of the western transect was detected in the waters of deepest station 45, 43.98% (the limits of variation were 21.21–63.59%). The minimum average value was detected at station 48 situated above the shelf break, 13.24% (the limits of variation were 5.56–26.56%) (table and Fig. 3).

Analysis of the vertical distribution of the share of CTC + BP in TNB revealed significant differences between the waters of three areas (above the shelf break, in the deep-water area, and on the continental shelf). In water areas above the shelf break with a strong gradient of the hydrological parameters (stations 37, 39, 48), the maximum values of the share of CTC + BP in TNB were associated with horizons below 170 m.

In the deep-water area and on the shelf, where the hydrological conditions were more stable, the maxi-

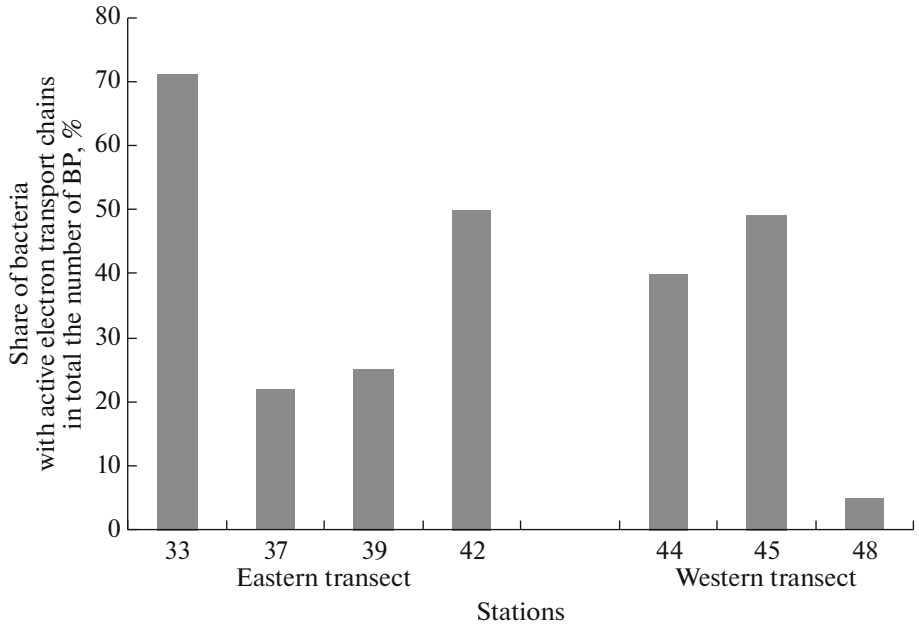

Fig. 3. Distribution of average shares of BP with active electron transport chains in water column on two transects in St. Anna Trough, Kara Sea, in Autumn 2011.

mum values of shares of active BP in TNB were detected at depths of 20–50 m (table).

DISCUSSION

Thus, during the period of our microbiological studies in the water area of the St. Anna Trough in the Kara Sea, we revealed that, despite low TNB values, the majority of the bacterial community mainly consisted of potentially viable cells. The average IMBN value in TNB in all samples was 92.07% (the limits of variation were 76.19–98.38%). Nevertheless, the average share of metabolically active BP (CTC + BP) in TNB was significantly lower, 38.17% (the limits of variation were very high, 5.55–93.9%). The distribution of viable and metabolically active BP in water column was unequal both in the horizontal and vertical directions.

Overall, in waters of the eastern transect, the maximum values of the microbiological parameters were found on the shelf (station 33) and decreased along the transect from the shelf slope (station 33) to deep-water areas of the trough (station 42). On the western transect, the maximum values of these parameters were detected at the deepest station 45 (Fig. 2).

In the present study, we used LIVE/DEAD dyes for microbiological studies in the Kara Sea for the first time. These dyes make it possible to count both the TNB and IMBN. Complete processing of samples was performed on board ship, whereas TNB in most cases was determined after the end of expedition in fixed samples using acridine orange or DAPI [4, 8, 19].

It is described in the literature that TNB obtained using LIVE/DEAD dyes is usually lower than that obtained using traditional fluorochromes. According to some works, TNB obtained using LIVE/DEAD dyes was only 60% of that obtained using DAPI [24]. The results obtained in the present study were slightly lower than TNB values obtained by Romanova and Sajin using DAPI, although comparable [8]. According to the data [8], the TNB values in the upper mixed layer of water above the slope of the St. Anna Trough were $(92 \pm 33) \times 10^3$ cells mL^{-1}. According to our results, the average number of BP in the upper layer of the water column (0–20 m) above the same slope was $(72 \pm 23) \times 10^3$ cells mL^{-1}. Furthermore, our results were comparable to those obtained using DAPI in the same area of the Kara Sea in August 2001 [19]. However, our results were considerably lower than those obtained in the same area using acridine orange [2]. Differences between the data obtained in different works may be due to application of different dyes as well as the interannual, seasonal, and spatial variability of the microbiological parameters in seawater [2]. It can be assumed that differences between the values of the number of BP obtained using different dyes can be explained by the peculiarities of how acridine orange (AO) and two other dyes (propidium iodide and SYTO-9) from the LIVE/DEAD kit interact with different cell structures. It is known that AO specifically binds to cell DNA and RNA, which results in a clear contrast with the background. Meanwhile, this dye cannot distinguish bacteria and the smallest particles of clay, detritus, and colloids, which can be stained nonspecifically or possess autofluorescence [7, 12, 22]. Furthermore, it was shown that AO can bind to viral particles [9]. This

results in overestimation of the number of BP, since not only bacteria but also large viral particles can be counted. At the same time, two fluorochromes applied in LIVE/DEAD kits can bind directly to bacterial cell membranes. One of them, SYTO 9, is retained only in cells with intact membranes, which makes it possible to avoid counting dead cells, abiotic suspensions, and viral particles. The possibility of applying LIVE/DEAD fluorochrome to determine TNB was demonstrated earlier with different studies performed in different regions including marine areas [21, 25].

Thus, our data, along with the results of [8, 19], confirmed that the LIVE/DEAD set of fluorochromes applied in the present study is applicable for determining TNB as well as for the counting of potentially viable microorganisms in Arctic marine areas.

Analysis of the distribution of BP with active electron transport chains revealed that the highest absolute and relative values of this parameter were detected at stations in areas with minimum vertical temperature and salinity gradients (at stations 33 and 44 on the shelf of the Kara Sea) as well as in in deep depressions (stations 42 and 45) (Fig. 3). In the waters of stations above the shelf break (i.e., in areas with the largest temperature and salinity gradients—stations 37, 39, and 48), the CTC + BP values, as well as its share in the TNB, were considerably lower than at stations in more stable conditions.

The vertical distribution of active BP in water columns at stations with larger temperature and salinity (stations 37, 39, 48) gradients showed a peculiarity. The values were maximum in the bottom layers. Meanwhile, the CTC + BP values in more stable conditions (for minimum vertical temperature and salinity gradients), on the shelf (stations 33 and 44), and in abyssal areas (stations 42 and 45) were maximum at depths of 20–30 m, which were supersaturated with oxygen in autumn 2011 [3].

Analysis of the dependence of the microbiological parameters on the chlorophyll *a* content in water [5], which is an indicator of phytoplankton biomass, revealed no significant correlation between these parameters in the studied water areas. In the Yenisei estuary, on the transect from river waters to the Kara Sea shelf adjacent to the mouth of the Yenisei River, a significant correlation ($r = 0.7$, $p < 0.001$) between these parameters was detected in our previous study [6]. Other researchers demonstrated a similar significant correlation in waters of shelf areas of the Mediterranean and Baltic seas [15, 24]. Furthermore, in lake environments, strict correlations between these parameters usually occur [15, 18]. It can be assumed that in highly productive ecosystems (shelves, estuaries, and lakes), the abundance of BP depends on the phytoplankton biomass. Since the chlorophyll *a* content is an indicator of phytoplankton abundance and its excretions represent an important labile substrate for heterotrophic BP, it is not surprising that phytoplankton under conditions of high abundance significantly affects the number and activity of BP. Meanwhile, in oligotrophic deep-water environments, where phytoplankton abundance is relatively low, BP must consume other sources of organic compounds not directly associated with phytoplankton [10]. Under these conditions, BP does not respond or responds weakly to fluctuations in chlorophyll *a* content in water, which was reflected by the absence of a significant correlation between these parameters.

Our assumption was confirmed by significant positive correlations ($r = 0.7$, $p < 0.05$) between microbiological parameters and the content of suspended organic carbon (SOC), which was demonstrated in [1]. Interestingly, a high share of metabolically active BP was detected not only at shelf station 44 but also at abyssal station 45 (Fig. 3). It was shown that the SOC content at stations 44 and 45 was high at most horizons. In oligotrophic areas, a high SOC directly affects the abundance of BP, including the number of metabolically active cells. It should be noted that no effect of the dissolved organic carbon (DOC) content in water on the number of viable BP was revealed [1]. River runoff is the main source of DOC in the Kara Sea [1]. Probably, the high resistance to microbial oxidation may be caused by predominantly terrigenous DOC (i.e., a high content of the humic fraction [16]). Therefore, BP activity weakly correlates with the DOC concentration.

CONCLUSIONS

Thus, studies performed in September 2011 in the St. Anna Trough demonstrated that, despite the fact that BP in this region was mainly represented by potentially viable microorganisms, the share of active cells in BP was relatively low. These results suggested that not all bacteria detected in the waters of the St. Anna Trough possessed active electron transport chains under existing environmental conditions. Probably, in some of these bacteria, electron transport chains did not function due to the absence of required amounts of available nutrient substrates. In contrast to the earlier studied Yenisei estuary [6], in the St. Anna Trough, no correlation between microbiological parameters and chlorophyll *a* content was revealed, which can be due to oligotrophic conditions in the waters of the trough.

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