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EXPERIMENTAL ARTICLES

# Size Structure and Morphological Composition of the Pechora Sea Winter Bacterioplankton and Conditions of Its Formation

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**Abstract**—Analysis of conditions of formation of microplanktonic microbial communities (MC) was carried out for the Pechora Sea using the data of winter 2002–2005. The patterns of distribution of different MC groups in different water types are discussed. Regular variations of the indices of abundance in a gradient of physicochemical variables were revealed. The estimated average bacterial numbers for under-ice conditions were $234 \times 10^3$ cells/mL, with the average cell volume of 0.58 μm$^3$ and total cell area ~550 mm$^2$/L. The estimated total microbial biomass in the 0–25 m water horizon of the Pechora Sea is $187 \times 10^9$ g wet biomass.

*Keywords*: ice cover, water masses, bacterioplankton numbers, microbial communities, size structure, nanobacteria, bacilli, vibrios

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The distribution, conditions of development, and characteristics of the main morphological groups of bacterioplankton are discussed based on the results of microbiological survey of the Pechora Sea during winter seasons of 2002–2005. Assessment of diversity and size structure of microbial communities (MC) makes it possible to estimate both the productivity of marine ecosystems and their general stability [1–3]. For microorganisms, an increment in cell area ($S$) per unit volume ($V$) determines variations in their assimilatory capacity [3, 4] and an increase of their metabolic activity within marine microplankton [5–8]. These variations may be revealed by comparative analysis of MC characteristics in different seasons, e.g., by the area/volume ratio ($S/V$) [9–11]. Throughout the year, three groups (psychrophiles, psychrotrophs, and mesophiles) dominate cyclically in the communities of subarctic Russian seas [1, 5, 11, 13]. This determines the capacity of MC to carry out their specialized functions in the ecosystems all year round, independent of the development of other planktonic groups [6, 7, 11]. The exogenous successions developing even during winter due to the abiotic factors affecting planktonic biocenoses result in variations in the size structure, which regulates the activity of the groups with different specialization (microalgae, bacteria, etc.) [3, 6–10]. The published data on the microbiological parameters in ice-covered subarctic seas are insufficient to provide for the reliability of most conclusions [10–15]. Analysis of the conditions of the winter activity of bacterioplankton and quantitative assessment of the effect of various factors on its development are therefore in demand [6, 8, 10, 11, 16].

Very few unclassified publications exist on the ice-covered period for the Pechora Sea [17, 18]. Such publications are especially scarce for the parameters analyzed in the present work, including the indices of microflora development [6, 8, 19].

The goal of the present work was to analyze the conditions and patterns of development of bacterioplankton communities in the Pechora Sea in mid-winter (in the first half of February) using the data of several sequential years.

## MATERIALS AND METHODS

Microbiological investigation was carried out at the Pechora Sea and at the adjoining areas of the Barents, White, and Kara seas remote from the coastal zone and fast ice. A set of physicochemical and microbiological parameters was determined for the 0–100 m layer of ice fields of different concentration. The present works deals with the data collected from February 1 to 15 in 2002, 2003, and 2005. Location of the sampling stations is shown on Fig. 1.

Microbiological observation of this period covered up to 60% of the Pechora Sea area (Fig. 1). At 31 stations, over 60 samples were collected for determination of the physicochemical and biological parameters [6]. Water samples from clearings and ice field faults from depths to 5 m were collected in motion, while those from up to 100 m were collected at stations using 2- and 6-L plastic bathometers [7, 8].

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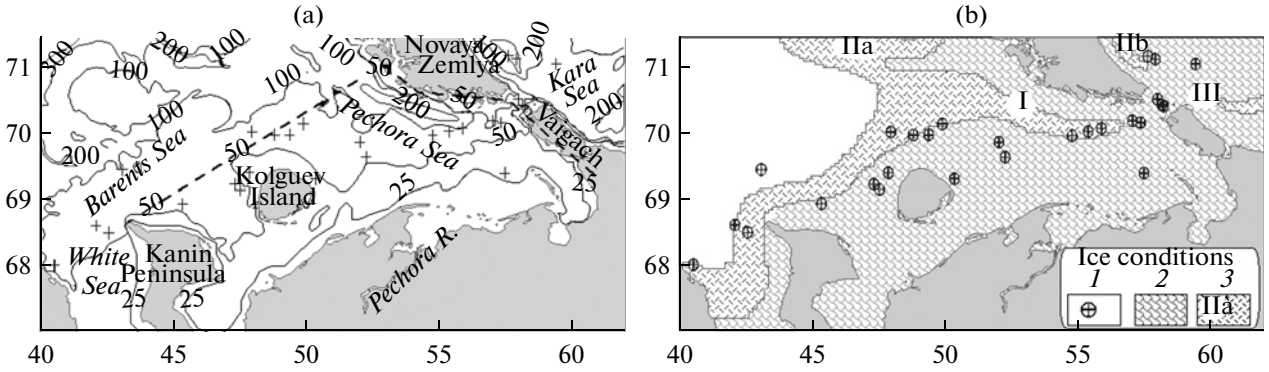


**Fig. 1.** Characterization of the investigated Pechora Sea area and location of sampling stations in February 1–15: location of microbiological stations (2002–2005), isobathic curves for 25, 50, 100, 200, and 300 m are indicated by isolines, geographical borders of the sea [17, 18] are indicated by a broken line (a); and averaged ice conditions for February 1–15, with numbers and shading indicating: stations (*1*), close ice ≥8b (*2*), rarefaction of ice fields and stationary clearings (*3*).

**Parameters of the physicochemical complex.** Salinity (*S, ‰*) was determined by conductivity, temperature ($T_w$, °C) was measured with reversing thermometers, and pH and Eh were measured using an I-135 potentiometer [20]. The forms of biogenic elements were analyzed in the filtrates through nuclear filters with the pores of $d_{eff}$ = 0.45 μm (Dubna, Russia) in Nucleopor mounts [4, 7–9]. Nitrite nitrogen ($NO_2$, μg N/L) was determined according to Griess–Illosvay, nitrates ($NO_3$, μg N/L) were reduced to nitrites [20]. In dissolved organic matter (DOM), nitrogen ($N_{DOM}$) and phosphorus ($P_{DOM}$) were determined in the filtrates by "wet incineration" according to Wolderram (on a water bath in acidic–alkaline medium at 120°C and ~1.5 atm) [7–9]. Total content of biologically available organic matter (OM) for compounds of various biochemical stability (in carbon units $C_{org}$, mg C/L) was determined from experimental BOD curves obtained for $T_w$ = 20–22°C. Splitting of kinetic BOD curves into the easily oxidized ($C_{ex}$) and persistent ($C_{av}$) fractions was carried out using the two-stage oxidation model, by the formalized graphic analytic method [7, 8].

**Characteristics of the total bacterioplankton.** The sample for total bacterioplankton (0.5 mL) was filtered under vacuum (~0.1–0.2 atm) through Sudan black-stained nuclear filters with $d_{eff}$ = 0.09 μm (Dubna, Russia) in a calibrated mounting [7, 8]. The filtering area was 1 cm in diameter. The sample was fixed with ethanol vapors and treated as described in [21]. As a fluorochrome, 0.02% fluorescamine (4-phenylspiro-[furan-2(3*H*),1-phthalan]-3,3'-dione) in borate buffer was used. In an alkaline environment, the stain reacts specifically with the primary amines of bacterial cell envelopes, resulting in bright fluorescence under near-UV excitation [21]. Cell shape and number, as well as cell size (by an ocular micrometer) were determined according to Razumov [22]. Fluorescent microscopy and field count at magnifications of ×900–1500 (oil immersion) were carried out using MLD-1U1.1 and Biolam D2U1.1 microscopes equipped with a modified OI-30 UKhL 2.2 attachment (LOMO, Russia) [7, 21, 22].

Total parameters of bacterioplankton abundance in terms of cell number, biomass, volume, and area of fluorescamine-stained surface $\Sigma(N, B, V, S)_i$ were calculated according to [2]. The Σ sign applies only to the integral MC parameters, e.g., $\Sigma N_b$ is the total bacterioplankton number ($10^3$ cells/mL). To calculate cell volumes $V_i$ (μm$^3$) and areas $S_i$ (mm$^2$/L), their shapes were approximated as simple geometrical objects (sphere, cylinder, prism, ellipsoid, or wedge). More complex shapes were treated as combinations of simple shapes [2].

Separation of bacterial cells into fractions for the fluorescamine-stained preparations on nuclear filters was carried out according to the general recommendations described in [1, 2, 4, 22, 23]. Cell shape (rotary body), length ($L$), and the ratio between $L$ and characteristic diameter $d$ were the criteria used to determine up to ten major morphological groups of bacteria. To obtain reliable results, the number of analyzed cells in different groups was differentiated according to the "rule of 1000": in each size fraction or morphological group, the product of the number of cells and the number of fields examined should be at least 1000 [2]. In case of lower products, the cells of this group were counted to reach the required value (independent on the other fractions) or examined at least 1–2% of the total filter area [6–8]. According to our data, this procedure results in medium relative error of the general indices of bacterial abundance $\Sigma(N, B, V, S)_i$ was ±30% [6].

**Isolation of groups and size fractions.** Spherical (coccoid) were identified as microorganisms of spherical or almost spherical shape at $L/d_{max} \le 1.2$ [22, 23]. Two size fractions of the cocci were considered: small and large ones, designated as $(N, B, V, S)_{kk1}$ and

$(N, B, V, S)_{kk2}$, respectively. The small cocci subgroup consisted of the cells with $d_{av} \le 0.5$ μm (volume $V \le 0.04$ μm$^3$), which are considered nanobacteria, an ultraplankton fraction [13, 24]. Oval cells with $3.5 \ge L/d_{max} \ge 1.2$, forming the group of ellipsoidal cells or coccobacilli, of close-to-ellipsoidal shape, were designated as $(N, B, V, S)_{ell}$. Elongated cylindrical cells, or rods, comprised microbial groups of diverse ecological specialization [1, 4, 22, 23]. For practical reasons, rod-shaped cells were subdivided into groups according to the following criteria: shape (straight, tapered, bend, or curved), $L/d$ value ≥ 8 (thin and other ones), and length $L$ (short or long). Using these criteria, up to five groups of rods were determined [7]. The groups of relatively short and thin cells $(N, B, V, S)_{Cit}$ and large rods $(N, B, V, S)_{pl2}$ were the most prominent ones. The "branching" forms of indefinite length formed a separate group designated $(N, B, V, S)_{wtv}$. Curved and tapered rod-shaped forms were termed vibrios. This group included thin cells of vibrios ($L/d_{max} \ge 8$), as well as *Mycrocyclus* and some myxobacteria, sharing the curved, slightly tapered shape $(N, B, V, S)_{vbr}$ [7, 23]. Coiled forms were designated as marine spirilla [22, 23]. Prosthecate bacteria with characteristic projections (group 13 in the Bergey's manual) and bacteroids with indefinite cell shape, as well as the cells without well-formed envelopes, were combined into one group, designated $(N, B, V, S)_{prs}$ [23].

This scheme of differentiation between the groups of most commonly occurring shapes of bacterial cells makes it possible to assess their total abundance, as well as the individual cenotic groups characteristic of marine bacterioplankton of freezing seas in winter [1, 2, 4, 22].

## RESULTS

**Ice conditions, water types, and conditions for bacterial development.** Investigation of the Pechora Sea was carried out from board of the *Arktika* and *Rossiya* nuclear-powered icebreakers (Murmansk Steamship Co., Russia). Microbiological stations were located in the drift ice zone, at a distance from fast ice, which at the time of sampling occupied the coastal area of 1–2 to 15 km [14, 17]. The ice conditions in this area in the first half of February are shown on Fig. 1b. Materials of visual observations along the icebreaker route, supplemented with satellite imaging data (maps of satellite monitoring according to NOAA, http://www.natice.noaa.gov) were used to characterize the conditions for February 1–15. Stationary clearings beyond the fast ice zone, which are a part of the Northern Sea Route, are marked on Fig. 1b with Roman numerals: Pechorskaya, I; West and East Novozemel'skaya, IIa and IIb, respectively; and Amderminskaya, III [12, 17, 18].

The major water masses (WM) of the Pechora Sea in midwinter were determined from the mixing triangles (marked with ovals on Fig. 2a) using the $T_w$, $S$ parameters.

The following WM types were determined in the central Pechora Sea and adjacent waters WM. Waters with $S$ exceeding 34.4‰ and $T_w$ from −1.8 to +0.5°C were represented by the Barents Sea waters (BarWM) of the winter modification [12, 17, 18]. Formation of desalinated waters with $S \le 33.4$‰ and $T_w$ close to the freezing point was affected by the flows from the White Sea (WhFL) and the Pechora Gulf (PechFL) [12, 17, 18]. Transformed Barents Sea WM (BarWMtr), with $33.4 < S < 34.4$‰ and $T_w$ from 0.5 to −2.3°C, formed a separate group. These WM varieties should be considered as pelagic biotopes of the winter Pechora Sea plankton [6, 8, 19].

The distribution of these WM in the 0–2 m water layer according to analysis of the $T_w$, $S$ indices is shown on Fig. 2b. The estimated areas of BarWM and BarWMtr occurrence in the Pechora Sea surface layer in winter are ~25 and ~35%, respectively. The WhFL affects the southern part of the sea, west of 53° E, while the PechFL expands to the east [12, 17, 18]. Water mixtures affected by WhFL are estimated as 25%, while the PechFL, as ~15% of the sea area (Figs. 1, 2).

Analysis of the $T_w$, $S$ indices in 2002–2005 indicated stability of the distribution of the winter WM forms shown on Fig. 2b. Weight average values ($X_{av}$) could be therefore calculated, using the data on the area ($s_i$) occupied by a given WM: $X_{av} = (\Sigma x_i s_i)/\Sigma s_i$, where $x_i$ is the average value for WM and $\Sigma s_i$ is the investigated area. Results of averaging of the physicochemical parameters characterizing the conditions of bacterial development in the winter WM and $X_{av}$ in the Pechora Sea area are summarized in Table 1.

Weighted average values of $X_{av}$ (considering $s_i$ of a given WM, see above) are listed in the bottom line of Table 1. To compare the characteristics of the flow currents, the data for the northeastern part of the White Sea for the same period (WhWM) are presented [19]. The WhWM are not used here and further on for $X_{av}$ calculation for the Pechora Sea area.

Analysis of Table 1 revealed that rating of the physicochemical parameters according to their level in a WM, with some variations, formed stable sequences, WM rows [6, 8, 19]. For convenience, here and further on the results of $X_{av}$ comparison from Table 1 are presented in the form {parameter $x_i$} → {row of WM rated according to $x_i$ values}:

$$\{T_w\text{-}S, \text{ Eh, } NO_3, O_2 \text{ and } C_{av}\} \rightarrow \{\text{BarWM} > \text{BarWMtr} > \text{PechFL} > \text{WhFL}\}, \quad \text{(A)}$$

$$\{NO_2, \text{ pH, } SiO_2 \text{ and } P_{DOM}\} \rightarrow \{\text{BarWM} < \text{BarWMtr} < \text{PechFL} < \text{WhFL}\}, \quad \text{(B)}$$

According to the procedure of $x_i$ rating, two types of distribution in WM are characteristic for the physicochemical variables: A, descending (max → min)

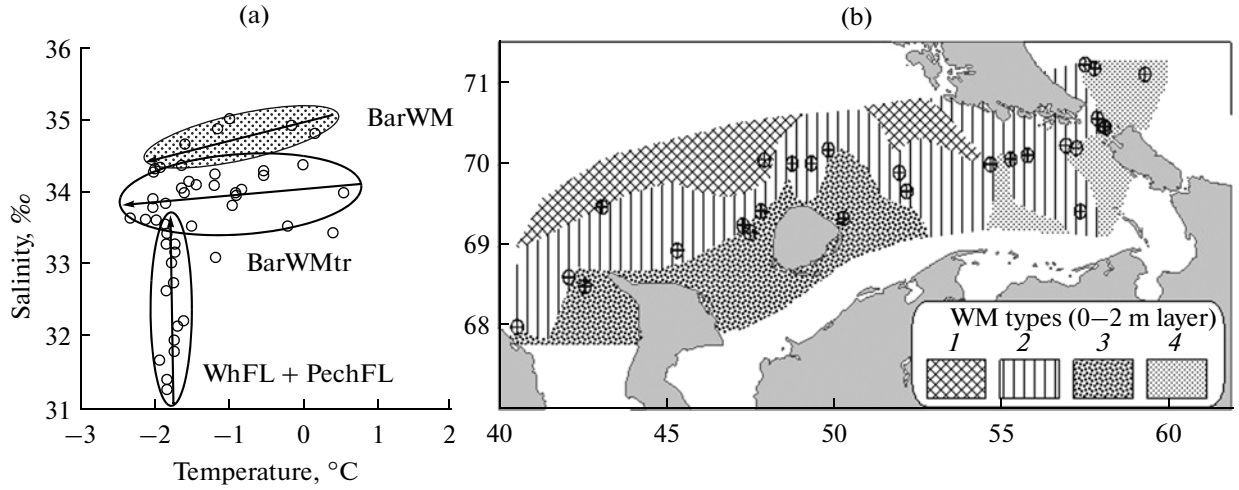


**Fig. 2.** Analysis of *T, S* diagrams for Pechora Sea water in midwinter 2002–2005 (see text): WM varieties, with areas of the $T_w$, *S* parameters for WM indicated by ovals and direction of their transformation shown by arrows (a) and distribution of the winter WM in the 0–2 m layer, with shading indicating: BarWM (*1*), BarWMtr (*2*), WhFL (*3*), and PechFL (*4*) (abbreviations according to [12, 18]).

and B, ascending (min → max) rows. Considering the general direction of water transfer from NWW to SEE, formation of such structures in $x_i$ arrays depends on the presence of stable spatial gradients along WM (grad $X_i$). Their formation is associated with pairwise interactions of adjoining WM: BarWM ↔ BarWMtr ↔ (WhFL ↔ PechFL) and river flow. As a result, the characteristics change gradually in the direction of water transfer, as ±grad $X_i$ [6, 8, 19]. The regulation occurs in accordance with the position of the regions of WM advection, direction of their transfer, and the character of WM interlaying in the water column. This distribution of physicochemical $x_i$ along both types of WM (AB) indicates existence of certain relationships, which may develop only in the case of a stable of the active layer in the Pechora Sea (Fig. 2b).

The regions of distribution of WM and directions of transformation of their properties (Figs. 1, 2; Table 1) indicate that quasistationary circulation of marine (BarWM) and desalinated (WhFL and PechFL) waters is reproduced each early February in the Pechora Sea. Its stability is determined by the pressure of BarWM, which are varieties of North Atlantic waters (see. Figs. 1, 2) arriving to this area with the Kanin and Kolguevo–Pechora currents [12, 17, 18]. Transformation of WM characteristics occurs under close ice due to the action of meteorological factors and the interaction with desalinated WhFL and PechFL waters.

**Integral characteristics of bacterioplankton abundance.** The described characteristics of WM circulation make it possible to pool the data for sequential years into a single array and to determine its uniform

**Table 1.** Averaged physicochemical parameters ($x_i$) for the Pechora Sea winter WM in February 1–15 2002–2005

| Parameters WM type | Row, *n* | $T_w$ | *S* | $pH_{25}$ | $NO_2$ | $NO_3$ | $N_{DOM}$ | $P_{DOM}$ | $C_{ex}$ | $C_{av}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | | °C | ‰ | dimensionless unit | μg N/L | | | μg P/L | mg C/L | |
| BarWM | 8 | –0.85 | 34.84 | 7.91 | 0.8 | 113 | 781 | 9.2 | 2.18 | 1.18 |
| BarWMtr | 25 | –1.45 | 33.98 | 7.92 | 1.5 | 88.2 | 308 | 14.9 | 2.27 | 1.07 |
| PechFL | 6 | –1.63 | 32.60 | 8.01 | 1.8 | 97.7 | 471 | 15.6 | 2.36 | 0.70 |
| WhFL | 14 | –1.51 | 32.76 | 8.02 | 2.1 | 68.4 | 537 | 14.6 | 2.03 | 1.05 |
| WhWM* | 9 | –1.07 | 27.43 | 7.95 | 2.0 | 60.1 | 381 | 21.1 | 2.51 | 1.72 |
| **$X_{av}$** | | **–1.34** | **33.68** | **7.95** | **1.5** | **90.8** | **508** | **13.5** | **2.20** | **1.04** |

*n* designates the length of a row, $T_w$ is water temperature, °C; *S* is salinity, ‰; $pH_{25}$ is pH adjusted for 25°C; $NO_2$ is nitrite concentration, μg N/L; $NO_3$ is nitrate concentration, μg N/L; $N_{DOM}$ is nitrogen-containing DOM, μg N/L; $P_{DOM}$ is phosphorus-containing DOM, μg P/L; $C_{ex}$ is the content of unstable OM, mg C/L; $C_{av}$ is the content of biochemically stable OM, mg C/L;

* Data for WhWM were not used for $X_{av}$ calculation.

**Table 2.** Parameters of total abundance of Pechora Sea bacteria in midwinter

| Parameters WM type | Row, $n$ | $\Sigma N_b$ | $\Sigma B_b$ | | $\Sigma S_b$ | $V_{av}$ | $S/V_b$ | $N/B_b$ |
|---|---|---|---|---|---|---|---|---|
| | | $\times 10^3$ cells/mL | μg/L | μg C/L | $mm^2$/L | $\mu m^3$ | $10^6$ $m^{-1}$ | $10^9$ cells/mg |
| BarWM | 7 | 288 | 547 | 43.4 | 1130 | 1.39 | 3.66 | 0.78 |
| BarWMtr | 31 | 199 | 180 | 18.4 | 492 | 0.70 | 4.72 | 1.50 |
| PechFL | 8 | 256 | 161 | 14.6 | 528 | 0.35 | 5.61 | 2.13 |
| WhFL | 14 | 215 | 182 | 20.7 | 500 | 0.74 | 4.43 | 1.13 |
| WhWM* | 9 | 222 | 180 | 16.0 | 544 | 0.49 | 4.85 | 1.35 |
| $X_{av}$ | 60 | **234** | **269** | **24.7** | **659** | **0.83** | **4.52** | **1.32** |

$n$ designates the length of a row, $\Sigma N_b$ is total number of bacteria, $\times 10^3$ cells/mL; $\Sigma B_b$ is total biomass (wet weight), μg/L; $\Sigma B_b$ is the same in carbon units, μg C/L; $\Sigma S_b$ total cell area, $mm^2$/L; $V_{av}$ is average cell volume, $\mu m^3$; $S/V_b$ is specific area (dispersion) for communities, $10^6$ $m^{-1}$; $N/B_b$ is the "number–wet biomass" index, $10^9$ cells/mg (other designations as in Table 1).

parts based on the relevant WM. The possible cases are characterization of conditions of bacterioplankton development and calculation of the relevant parameters for the individual kinds of winter WM [6, 8, 19]. The averaged results on the total bacterial abundance are presented in Table 2, which preserves the structure of Table 1).

To calculate MC biomass in carbon units [2, 22], $C_{org}$ was calculated from cell volume using the modified Stratmann's equation ($C_{org} = 120\ V^{0.72}$), where $V_i$ is the volume of the cells of a given morphological group ($\mu m^3$), since in the case of bacteria this procedure is the most reliable one [6, 8].

The parameters of integral abundance $\Sigma(N, B, V, S)_b$ for bacteria listed in Table 2 according to WM, results in the rows of (AB) kind, for example:

$$\{\Sigma S_b \text{ and } V_{av}\} \rightarrow \{\text{BarWM} > \text{BarWMtr} > \text{PechFL} > \text{WhFL}\}, \quad \text{(A)}$$

$$\{S/V_b\} \rightarrow \{\text{BarWM} < \text{BarWMtr} < \text{PechFL} < \text{WhFL}\}. \quad \text{(B)}$$

Thus, in the rows for sequential years, pairwise interactions between different winter WM form stable relationships between the parameters of the microbiological and physicochemical complexes. Distribution of WM parameters over the Pechora Sea area determines the development of inhabiting bacterioplankton and the changes in the course of water movement under close ice (see Figs. 1, 2 and Tables 1, 2). Emergence of the ±grad $X_i$-type structures in the array of parameters characterizing bacterioplankton abundance is also based on the rapid renewal of WM of the Barents Sea origin (see above). The distribution of the total numbers ($\Sigma N_b \times 10^3$ cells/mL) is presented on Fig. 3a, while that of the average cell volume ($V_{av}$, $\mu m^3$) in the 0–2 m surface layer is shown on Fig. 3b.

The total MC number estimated by graphical analysis of Fig. 3 was $\Sigma N_b \approx 230 \times 10^3$ cells/mL, with the average cell volume $V_{av} \approx 0.58\ \mu m^3$ [6, 8]. The distribution of $V_{av}$ and $\Sigma N_b$ characterizes the changes in bacterial abundance in the winter bacterioplankton communities and corresponds to the state space formed by WM biotopes forming the parameters of the ecological niches for MC and its component groups [1]. This relation between the overall parameters of abundance and environmental conditions is evidently realized at the level of $N_i$ and $B_i$ for individual groups and fractions.

**Structure of the dominant groups.** Midwinter bacterioplankton communities of the Pechora Sea WM consisted of numerous morphological types, according to their ecological specialization [1, 22, 23]. Microbial forms widespread in other biotopes and under other conditions were revealed in significant numbers. For analysis, the dominant (cocci, coccobacilli, and large rods) and subdominant morphological groups (small rods, curved, vibrios, etc.) were determined for MC. Table 3 presents the data on $N_i$ and $B_i$ for the dominant bacterial forms [6], specifying the conclusions reached by analysis of environmental conditions (the structure of Tables 1 and 2 is preserved).

According to Tables 2 and 3, wet $B_i$ of the dominant groups was 14, 22, and 33% (31.5, 63, and 80 μg/L) of $\Sigma B_b$ for cocci, ellipsoids (coccobacilli), and large rods, respectively. Over 55% of $\Sigma B_b$ was represented by large rods and coccobacilli. The relative and absolute numbers $N_i$ of these groups and fractions were 71% of $\Sigma N_b$ ($165 \times 10^3$ cells/mL) for cocci, 3% ($11 \times 10^3$ cells/mL) for coccobacilli, and 12% ($27.5 \times 10^3$ cells/mL) for large rods. Up to 90% of the total number of cocci was represented by nanobacteria with the average $N_{kk1} = 135 \times 10^3$ cells/mL. Rating of $N_i$ and $B_i$ for the dominant groups by WM reproduced, with some variations, the (AB) rows. For example, $B_i$ of bacteria with the largest cells ($B_{kb}$, $B_{pl2}$) was characterized by formation of descending rows max → min of the (A) type:

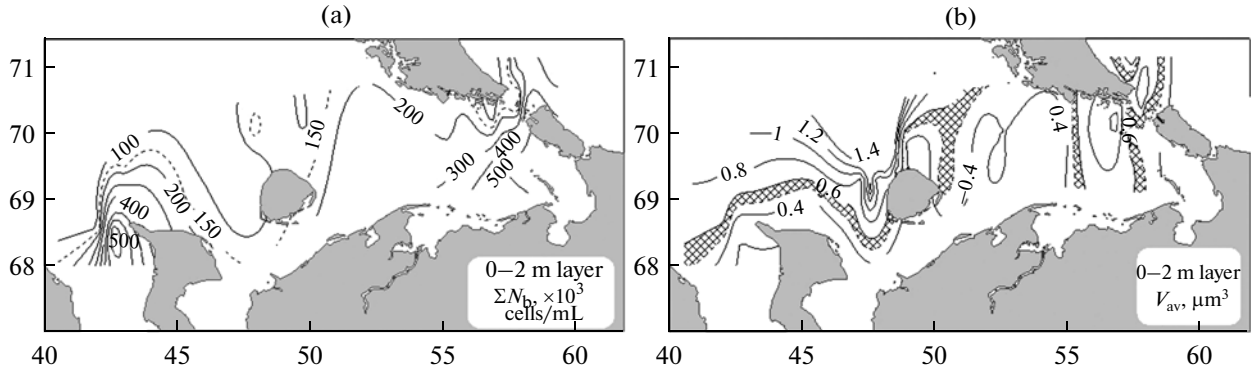


**Fig. 3.** Distribution of integral parameters of Pechora Sea bacterioplankton abundance in the 0–2 m layer: total bacterial numbers ($\Sigma N_b$, $\times 10^3$ cells/mL), major isolines every 100, minor (broken lines), every $50 \times 10^3$ cells/mL (a) and average cell volumes ($V_{av}$, μm³), major isolines 0.2 μm³, average weighted $V_{av}$ are marked by shading (b).

$$\{B_{pl2} \text{ or } B_{kb}\} \rightarrow \{\text{BarWM} > \text{BarWMtr} > \text{PechFL} > \text{WhFL}\}. \quad \text{(A)}$$

This result confirms stability of the described correlation between the biotope properties and the parameters of the microbiological complex associated with ±grad $X_i$. The same relationships should therefore be true for the $N_i$ and $B_i$ of the dominant morphological groups. The distribution of biomass of large rods $B_{pl2}$ (μg/L) and of the number of nanobacteria $N_{kk1}$ ($\times 10^3$ cells/mL) are presented on Figs. 4a and 4b, respectively.

According to Fig. 2, the distribution of large rods and nanobacteria in winter, WM correlated with variations in the characteristics of the biotopes. The $B_{pl2}$ and $N_{kk1}$ values were therefore regularly distributed over the Pechora Sea area in the direction of WM transfer to NEE under close ice fields and corresponded to the parameters of the group niches for these morphological groups of bacteria. For bacterial nanocells, $N_{kk1}$ under the Pechora Sea ice fields was approximately half of that for the Barents Sea (both in summer and in winter) [5, 9–12].

**Structure of the subdominant groups.** Table 4 lists the $N_i$ and $B_i$ values for some subdominant morphological groups, specifying the composition and formation of the diversity for Pechora Sea bacterioplankton communities in winter.

Figures 5a and 5b show the N distribution for small rods with $L/d_{av} \geq 8$ ($N_{Cit}$, $\times 10^3$ cells/mL) and of vibrios (curved and tapered forms) ($N_{vbr}$, $\times 10^3$ cells/mL), respectively.

Similar to other parameters of bacterioplankton abundance, $N_{Cit}$ and $N_{vbr}$ were distributed along the

**Table 3.** Averaged for WM $N_i$ and $B_i$ of the dominant groups of the Pechora Sea bacterioplankton in midwinter

| Parameters WM type | Spheroids, $(L/d_{max}) \leq 1.2$ | | | Large rods, $3.5 < (L/d_{av}) \leq 8$ | | | Ellipsoids, $1.2 < (L/d_{max}) \leq 3$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | $N_{kk1}$ | $N_{kk2}$ | $\%\Sigma N_b$ | $N_{pl2}$ | $B_{pl2}$ | $\%\Sigma B_b$ | $N_{kb}$ | $B_{kb}$ | $\%\Sigma B_b$ |
| | $\times 10^3$ cells/mL | | % | μg/L | | % | μg/L | | % |
| BarWM | 146 | 32.4 | 66.4 | 37.9 | 144 | 30.1 | 24.8 | 144 | 31.2 |
| BarWMtr | 115 | 19.5 | 70.2 | 34.2 | 71.5 | 38.7 | 8.1 | 46.7 | 21.4 |
| PechFL | 161 | 42.6 | 80.8 | 23.8 | 37.0 | 30.8 | 4.3 | 21.2 | 18.2 |
| WhFL | 139 | 21.4 | 69.9 | 19.4 | 52.0 | 30.1 | 4.8 | 30.0 | 18.3 |
| WhWM* | 124 | 20.4 | 67.3 | 41.6 | 99.1 | 43.8 | 9.3 | 24.7 | 16.4 |
| $X_{av}$ | **135.4** | **26.7** | **70.7** | **29.9** | **79.5** | **33.2** | **10.9** | **63.0** | **22.6** |

$N_{kk1}$ is the number of small cocci (nanobacteria with $d_{av} < 0.5$ μm [24]), $\times 10^3$ cells/mL; $N_{kk2}$ is the number of large cocci ($d_{av} \geq 0.5$ μm), $\times 10^3$ cells/mL; $N_{kk}$ is the ratio of all cocci, % of $\Sigma N_b$; $N_{pl2}$ is the number of large rods ($L/d_{av} \geq 8$), $\times 10^3$ cells/mL; $B_{pl2}$ is dry biomass of large rods, μg/L; $\%B_{pl2}$ is the share of dry rod biomass, % of $\Sigma B_b$; $N_{kb}$ is the number of ellipsoidal forms ($1.2 \leq (L/d_{max}) \leq 3$), $\times 10^3$ cells/mL; $B_{kb}$ is wet biomass of ellipsoids, μg/L; $\%B_{kb}$ is relative $B$ of the ellipsoids, % of $\Sigma B_b$. Other designations are as in Tables 1, 2.

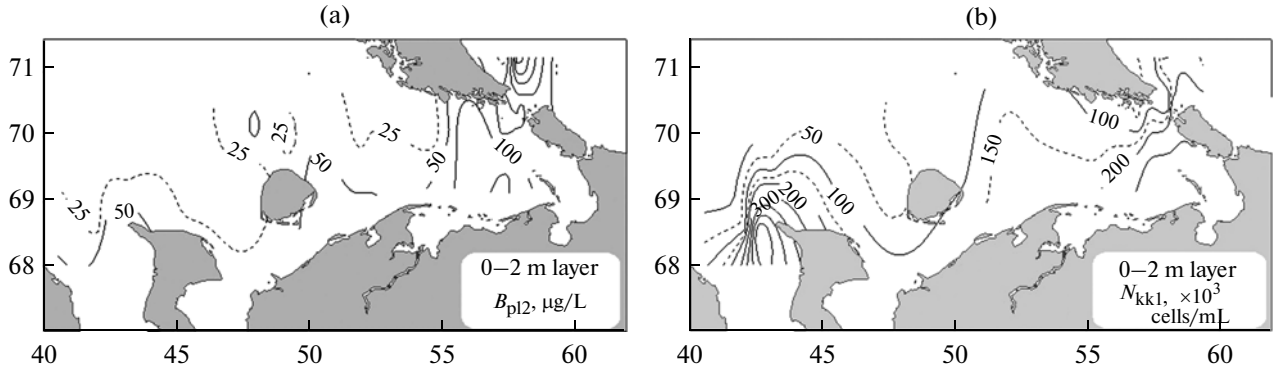


**Fig. 4.** Distribution of the parameters for the dominant Pechora Sea bacterioplankton in the 0–2 m layer in winter: biomass of large rods ($B_{pl2}$, μg/L), major isolines every 50, minor (broken lines), every 25 μg/L (a) and number of nanobacteria (cocci, $d_{av} \le 0.5$ μm), $N_{kk1}$, ×10³ cells/mL, major isolines every 100, minor ones, every 50 × 10³ cells/mL.

WM area according to the parameters of their group niches, i.e., they were arranged in the direction of transfer to NEE.

Table 5 lists cell volumes ($V_i$, μm³) of the major bacterial groups and fractions of Pechora Sea WM in winter.

The data of Table 5 were used to calculate the biomass of the individual morphological groups in carbon units (Table 2). While the average value for the Pechora Sea area $V_{av} = 0.58$ μm³ (see Fig. 3b), their values for bacterial communities of different WM types could differ fourfold, from 0.35 to 1.39 μm³). The group $V_i$ values for winter seasons show the tendency for higher variability of the average cell volumes and higher calculation error for the morphological groups and for MC as a whole with increasing $V_i$. Thus, small cells of the dominant and subdominant bacterial groups had the most stable parameters for $V_i$ in all WM types.

## DISCUSSION

**WM distribution and group niches in grad $X_i$.** The following row illustrates the sequence of division of the nucleus of North Atlantic currents, which penetrate the Pechora Sea in one of the branches: ... → BarWM ↔ BarWMtr ↔ WhFL ↔ PechFL → ... river flow. Their interaction with the environment results in formation of ±grad $X_i$, which determine the characteristics of the group niches of the winter bacterioplankton microflora [1, 11, 13]. In the course of analysis of bacterial diversity and growth conditions, these relationships make it possible to group experimental data or to subdivide them into homogeneous arrays. For bacterial groups forming over 60% of $\Sigma B_b$ ($B_{pl2}$, $B_{kb}$, and $B_{wtv}$, see Tables 3–5), the information derived from these WM rows oriented due to stable transfer (types A and B) may be summarized as follows:

Maximal development of bacteria in winter plankton occurs in saline and relatively warm BarWM at the initial stage of their transformation under close ice, with their properties regularly changing in ±grad $X_i$ in the direction of water transfer [6, 8].

The winter biotopes of Pechora Sea MC are affected by strongly transformed WM of North Atlantic origin.

This results in stable orientation of the Pechora Sea winter WM in the direction of transfer and in stable ±grad $X_i$ of most of the parameters involved in econiche formation for the major morphological groups of bacterioplankton.

Under ice cover, the parameters of development of different bacterial groups are distributed according to variations in the WM properties characteristic for a given climatic zone and are rapidly transformed by the action of meteorological factors and desalinated waters [7, 8, 17, 18].

Due to the same reasons, homogenous distribution of the mineral forms of biogenic elements, as well as of carbon-, phosphorus-, and nitrogen-containing DOM, was not characteristic for the Pechora Sea and adjoining waters. Among the typical features of DOM in winter was close association of their content with WM distribution in a given area. Moreover, a stable association between DOM content and development of the groups of winter microplankton with different specialization was revealed [6, 8, 9, 15, 19]. This pattern was observed for both photo(litho)autotrophs and for heterotrophs, as was confirmed by other works [10–15]. The presence of bacteria within the winter microplankton maintained the complex structure of the OM pool and of other growth substrates. In the under-ice conditions, this is the factor responsible for activity of the other specialized groups of microplankton [6, 8, 19].

**Integral bacterial abundance.** The estimated total number of bacteria in winter was $\Sigma N_b = 234 \times 10^3$ cells/mL (range from 200 to 290 × 10³ cells/mL), total cell area was $\Sigma S_b = 550$ mm²/L (500–1130 mm²/L), at the average MC dispersion $S/V_b =$

**Table 4.** Averaged for WM $N_i$ and $B_i$ of the subdominant groups of the Pechora Sea bacterioplankton in midwinter

| Parameters WM type | Rods ($L/d_{av}$) ≥ 8 | | | | | | Branching forms | | |
|---|---|---|---|---|---|---|---|---|---|
| | small rods | | | vibrios | | | | | |
| | $N_{Cit}$ | $B_{Cit}$ | $\%N_{Cit}$ | $N_{vbr}$ | $B_{vbr}$ | $\%N_{vbr}$ | $N_{wtv}$ | $B_{wtv}$ | $\%B_{wtv}$ |
| BarWM | 26.0 | 5.4 | 8.8 | 6.8 | 5.5 | 2.8 | 13.1 | 61.0 | 6.6 |
| BarWMtr | 13.8 | 2.3 | 7.3 | 5.0 | 2.0 | 2.2 | 0.4 | 5.5 | 2.3 |
| PechFL | 12.1 | 3.2 | 5.8 | 5.8 | 3.1 | 2.5 | 0.6 | 19.1 | 13.5 |
| WhFL | 20.3 | 5.9 | 9.1 | 6.9 | 5.7 | 4.6 | 0.6 | 5.9 | 3.6 |
| WhWM* | 16.7 | 3.0 | 8.6 | 7.4 | 5.9 | 3.1 | 0.6 | 3.2 | 1.5 |
| $X_{av}$ | **18.2** | **4.1** | **7.9** | **6.0** | **4.0** | **3.0** | **3.7** | **21.5** | **5.4** |

$(N, B)_{Cit}$ are $N_i$ and $B_i$ for small rods, $\times 10^3$ cells/mL (μg/L); $\%N_{Cit}$ is relative $N$ for small rods, % of $\Sigma N_b$; $(N, B)_{vbr}$ are absolute $N_i$ and $B_i$ for vibrios, $\times 10^3$ cells/mL (μg/L); $\%N_{vbr}$ is relative $N$ for vibrios, % of $\Sigma N_b$; $(N, B)_{wtv}$ are absolute $N_i$ and $B_i$ for branching microbial forms, $\times 10^3$ cells/mL (μg/L); $\%B_{wtv}$ is relative $B$ of branching forms, % of $\Sigma B_b$.

$4.5 \times 10^6$ m$^{-1}$. The peak-to-peak value for $\Sigma N_b$ and $V_{av}$ determined for the winter period in the ice-free area of the Barents Sea was in agreement with our results for ice-covered Pechora Sea [5, 9–15]. The estimated cell volume for under-ice conditions and $T_w$ close to the freezing point was 0.58 μm$^3$. This was more than twice higher than $V_{av}$ of bacteria from the ice-free part of the Barents Sea, confirming the conclusions of [5, 11]. The estimated total $\Sigma B_b$ for Pechora Sea MC in the 0–25 m layer with the volume of 698.4 km$^3$ was $187 \times 10^9$ g wet biomass [6].

**Composition and structure of the winter bacteriocenoses.** Microbial communities of the Pechora Sea winter plankton develop under conditions usually considered extreme: at $T_w$ close to the freezing point and under solid ice preventing the mixing of the water column. Under these conditions, however, relatively high abundance of various groups and their stable structure within MC were preserved. Comparative analysis of the data presented in Tables 3–5 and their distribution in different groups shown on Figs. 4, 5 demonstrate that a given ecological factor (see Table 1) had a specific effect on every form of bacteria. At the same time, the holistic order of formation of the composition was preserved. This finding supports the diversity and structure of heterotrophic microflora within winter microplankton [7, 9–12, 15, 16].

The relative contribution of the dominant bacterial morphological groups (see Table 3) confirmed the data obtained during winter seasons in the open part of the Barents Sea [9–15, 24]. Development of subdominant groups (Table 4) in midwinter was responsible for up to 14% of $\Sigma N_b$ and about 30% of $\Sigma B_b$ (see Tables 2, 4). For the group of small rods, the average $B_{Cit}$ = 4.0 μg/L, with the range from 0 to 32.4 μg/L, with

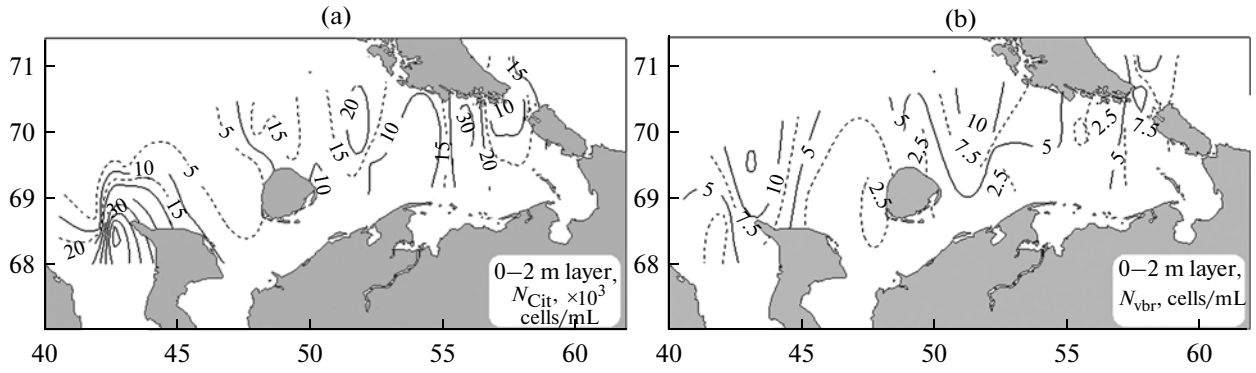


**Fig. 5.** Parameters for abundance of subdominant morphological groups of Pechora Sea bacteria in the 0–2 m layer in winter: distribution of small rods ($N_{Cit}$, $\times 10^3$ cells/mL), major isolines every 10, minor ones (broken lines), every $5 \times 10^3$ cells/mL (a); and distribution of vibrios ($N_{vbr}$, $\times 10^3$ cells/mL), major isolines every 5, minor ones, every $2.5 \times 10^3$ cells/mL (b).

**Table 5.** Average volumes of cells ($V_i$, μm$^3$) of different groups of bacteria in the Pechora Sea to the middle phase of winter (February)

| Parameters Water type | $V_{kk1}$ | $V_{kk2}$ | $V_{kk}$ | $V_{kb}$ | $V_{Cit}$ | $V_{vbr}$ | $V_{pl2}$ | $V_{wtv}$ | $V_{av}$ |
|---|---|---|---|---|---|---|---|---|---|
| BarWM | 0.012 | 0.47 | 0.096 | 3.80 | 0.118 | 0.52 | 5.07 | 8.06 | 1.39 |
| BarWMtr | 0.012 | 0.58 | 0.086 | 3.50 | 0.115 | 0.64 | 2.09 | 4.10 | 0.70 |
| PechFL | 0.014 | 0.40 | 0.078 | 2.71 | 0.159 | 0.36 | 1.46 | 14.1 | 0.35 |
| WhFL | 0.020 | 0.64 | 0.095 | 4.51 | 0.154 | 0.57 | 3.07 | 2.61 | 0.74 |
| WhWM* | 0.013 | 0.61 | 0.101 | 2.83 | 0.134 | 0.44 | 1.76 | 2.69 | 0.49 |
| $X_{av}$ | **0.014** | **0.54** | **0.089** | **3.71** | **0.132** | **0.55** | **2.98** | **6.22** | **0.83** |

$V_{kkl}$ is cell volume for small cocci (nanobacteria, $d_{av} \le 0.5$ μm), μm$^3$; $V_{kk2}$ is cell volume for large cocci, μm$^3$; $V_{kk}$ is weighted average $V$ for all cocci, μm$^3$; $V_{kb}$ is the weighted average for coccobacilli, μm$^3$; $V_{Cit}$ small rods (*Cytophaga*), μm$^3$; $V_{vbr}$ for vibrios (curved cells), μm$^3$; $V_{pl2}$ for large rods, μm$^3$; $V_{wtv}$ branching forms, μm$^3$; $V_{av}$ is weighted average cell volume in MC, μm$^3$.

$N_{Cit} = 18.2 \times 10^3$ cells/mL (0–$79.6 \times 10^3$ cells/mL). The contribution of this group to the MC by biomass and by numbers was 2.2% of $\Sigma B_b$ (0–10.1%) and 8.0% (0–24.5%) of $\Sigma N_{bak}$, respectively. For vibrios, the average $B_{vbr} = 3.5$ μg/L (0–15.5 μg/L), at $N_{vbr} = 6.0 \times 10^3$ cells/mL (0–$39.2 \times 10^3$ cells/mL). The relative contribution to MC was $B_{vbr} = 2.4\%$ (0–21.1%) of $\Sigma B_b$ and $N_{vbr} = 3.0\%$ (0–21.0%) of $\Sigma N_b$. The absolute and relative $N_i$ and $B_i$ of these groups were close to those found in winter in the Barents [13] and Kara seas [7], as well as in the winter–autumn periods in the central and southwestern Barents Sea [10–12]. Taking into account the lysing activity of small rods (e.g., *Citophaga* sp.), and predatory activity of vibrios [13, 22–24], $N_i$ and $B_i$ of these groups may be considered an index of "bacteriocidal" activity of seawater [7, 8, 24]. According to our data, a high level of bacteriocidal activity was maintained in all WM types during winter (see Table 4, Figs. 3–5).

**Size structure.** According to Tables 2, 5 and Fig. 3b, the estimated $V_{av}$ of the cells determined by different methods was from 0.58 to 0.83 μm$^3$, with variations in different types of WM from 0.35 to 1.39 μm$^3$. The $V_{av}$ MC value below the ice was two times or more higher than $V_{av}$ for the non-freezing part of the Barents Sea [9–14]. Since the average $\Sigma N_b$ values for bacteria from the open and ice-covered sea were almost the same, an increase in $V_{av}$ was associated with an increase in the average $V_i$ of different groups, including small fractions (see Tables 3–5). This result confirms the conclusion of other works on the increase in $V_{av}$ of bacteria in winter and is analogous to the biogeographical Bergmann–Hesse rule of stating a statistical increase in the mass of warm-blooded animals in the south–north direction [5, 11].

It should be noted that $S/V$ values are among the most stable characteristics of MC and are on average $4.5 \times 10^6$ m$^{-1}$, varying from 3.7 m$^{-1}$ for BarWM to 5.6 m$^{-1}$ for PechFL. Thus, in spite of decreased assimilative capacity due to increasing $V_{av}$ in winter, the size structure of bacterial communities was generally preserved under winter conditions (Tables 3–5). In our opinion, analysis of the size structure of under-ice communities revealed that the group cell areas $S_i$ (mm$^2$/L) and their specific areas $S/V$ ($10^6$ m$^{-1}$) were important parameters. To some extent, they may characterize the functional activity of the groups of MC under various conditions, including the winter period (Tables 2, 5). Consideration of these parameters, e.g., during assessment of the effects of the oil-and-gas complex on marine ecosystems, will make it possible to determine their stability during the crucial periods [3, 6–8, 19].

Development of bacterioplankton in the winter Pechora Sea occurs under conditions which are usually considered extreme. According to our data, in general the peak-to-peak values for $\Sigma N_b$ and $V_{av}$ were in agreement with the results of microbiological investigation of marine biotopes under other conditions. All MC maintained relatively high abundance of the major morphological groups and the stable size structure, thus providing for their stable functioning under these conditions. No groups of microorganisms were removed from the communities, while no forms developed which were specific for the winter season. The winter WM preserved the high level of bacteriocidic activity. Analysis of conditions in the Pechora Sea WM demonstrated that most microorganisms in the com-

munities functioned optimally throughout the year, including the prolonged period of existence under ice, characteristic of subarctic seas. In all cases development of bacterioplankton was balanced with the other microplankton components [6, 8]. Stability of the processes of OM transformation was therefore maintained under winter conditions, as well as the possibility for activity of the groups with different specialization.

An important conclusion is that application of obsolete calculation schemes, especially those not considering the morphological composition communities, to determine the parameters of bacterial development will result in the values not reflecting the real microbial density in natural waters [2, 22]. To calculate the parameters of bacterioplankton abundance, morphology and size of the cells in the analyzed samples should be taken into account. Otherwise, the $B_i$ or $V_i$ distribution will simply repeat the $N_i$ distribution. We found that ~70% of $\Sigma N_{kk}$, i.e., of the measured and enumerated cells of the coccoid group, belonged to nanobacteria with volumes below 0.04 μm$^3$ (see Tables 3 and 5). The share of nanobacteria in the community did not fall below 55% of $\Sigma N_b$, even in winter (see Table 3), as was confirmed by other works [5, 10–13, 24]. Microplanktonic ultraforms freely pass through 0.2 μm pores [24]. Accurate determination of $N$ for bacterioplankton and other MC abundance parameters in the Russian Arctic seas during all seasons requires the application of the surface (nuclear) ultrafilters with effective pore diameter not exceeding 0.1 μm. The $d_{eff}$ 0.2–0.45 μm is presently recommended.

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