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EXPERIMENTAL ARTICLES

Effect of Preliminary Filtration on the Functional Characteristics of Bacterioplankton from Lake Khanka

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Abstract—The dependence of the functional characteristics of bacterioplankton from the loess of Lake Khanka on the pore size of filtering materials was investigated. Soluble organic matter (SOM), bacteria, and bacterial consumers adsorbed on particles suspended in the lake water were found to filter differently depending on the pore size of the filtering material. Filters with pore size 4.5 μm (filters II) retained up to 20% of SOM and 20–30% of bacterial cells. Filters III with pore size 2.87 μm retained almost 50% of SOM and about 40% of bacteria. The double layer of gauze no. 72 (referred to as filter I) with pores size 40 μm was unable to completely retain bacterial consumers. In the case of filtrates I and II, the generation time of bacterioplankton decreased with its increasing average daily concentration. In the case of filtrate III, the generation time of bacterioplankton was minimum and did not depend on its concentration. Oxygen consumption rates per one bacterial cell and per unit biomass in filtrates increased with decreasing pore size of the filters through which they had passed. The bacterial biomass and oxygen consumption rate increased exponentially in filtrates III and logarithmically in filtrates I.

Key words: bacterioplankton, preliminary filtration, organic matter, functional characteristics.

One of the important characteristics of bacterioplankton is its generation time, which is defined as the time in which the number of bacteria in a water filtrate doubles. This parameter results from the rates of bacterial cell division and death and, hence, is an indicator of the metabolic activity of bacteria. The methodological aspects of the determination of the generation time are still the subject of debate. The proper determination of this parameter is complicated by the fact that the population of bacterial cells in both unfiltered water and water filtrates depends on the time of day or night [1–4]. Furthermore, extending the incubation time may lead to an overestimation of the generation time by more than two times.

This problem emerges because bacterioplankton occurs in a body of water in the form of individual cells, their aggregates, or microcolonies, and cells adsorbed on the surface of suspended mineral and organic particles [5, 6]. To determine the generation time of bacterioplankton properly, it is recommended that water samples are preliminarily filtered through 2- to 5-μm-pore-sized filters or a double layer of gauze no. 72–76 to remove zoo- and phytoplankton [2, 3, 7–10]. Filtration removes large detrital particles, part of the bacterioplankton, and most of the phyto- and zooplankton. This affects nutritional relations between zoo- and bacterioplankton, due to which the bacterial population in filtered water samples usually increases in an unpredictable mode [2]. The filtration also affects the composition of bacterioplankton and induces cyclic changes in its population and heterotrophic activity [11, 12]. All these factors make adequate evaluation of the generation time of bacterioplankton difficult.

The aim of the present work was to determine in what way the functional characteristics of bacterioplankton depend on the pore size of the filtering materials used for the preliminary removal of bacterial consumers from water samples.

MATERIALS AND METHODS

Experiments were performed with water samples from Lake Khanka, which is characterized by the presence of a great amount of suspended terrigenous particulate material (up to 154 mg/l) with the mean size of particles from 0.6 to 1.6 μm [13]. The lake water was sampled in the open lake (stations 9, 83, 84, and 133), coastal zone (st. 113 located at a distance of 500 m from the shore), in the river mouth (st. 68 and 74), and in the Komissarovka River (st. 72).

The total number of bacterial cells was determined by the direct microscopy of specimens stained with fluorescamine [14]. Alternatively, water samples were filtered through 0.17-μm-pore-sized filters stained with Sudan Black B, and the residue cells on the filters were enumerated microscopically. A total of 20 microscopic

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Table 1. Bacterioplankton population (million cells/ml) in the filtrates I, II, and III of water samples immediately after filtration (N_1) and 1 day afterwards (N_2) and the estimated values of its generation time (g)

Station no., date	N_1 (I)	N_2 (I)	g (I)	N_1 (II)	N_2 (II)	g (II)	N_1 (III)	N_2 (III)	g (III)
113, Aug. 26	1.80	2.44	54.7	1.39	1.70	82.6	0.68	2.16	14.4
83, Aug. 31	1.80	2.17	89.0	1.39	2.26	34.2	1.43	2.44	31.1
84, Aug.31	1.92	3.11	34.5	1.70	2.82	32.9	2.03	2.92	45.8
9, Sept. 2	1.86	2.40	65.3	1.50	3.25	21.5	1.57	2.93	26.7
133, Sept. 2	1.15	2.60	20.4	1.26	2.93	19.7	0.84	2.65	14.5
83, Sept. 4	–	–	–	2.00	5.03	18.0	1.82	4.25	19.6
84, Sept. 4	1.64	5.09	14.7	1.69	5.96	13.2	1.24	4.05	14.0
68, Sept. 2	2.41	3.34	51.0	1.98	3.32	32.2	1.81	4.04	20.7
74, Aug. 26	2.26	3.93	30.1	1.10	2.25	23.2	–	–	–
72, Aug. 28	1.32	5.99	11.0	1.75	6.16	13.2	1.14	4.40	12.3
72, Sept. 4	2.03	5.05	18.2	1.49	3.78	17.9	1.39	3.61	17.4
Average	1.82	3.61	38.9 ± 7.3	1.57	3.59	28.1 ± 5.4	1.40	3.35	21.7 ± 3.0

fields were examined for each water sample using an ML-2B light microscope at a magnification of 1000×. The generation time g expressed in h and bacterial production P were determined by direct bacterial count, using two sets of water samples in one of which bacterial consumers were removed by filtration. The filtration was performed using three types of filters: polyester filters with pore sizes of 2.87 μm (filters III) and 4.5 μm (filters II) and a double layer of gauze no. 72 with a pore size of about 40 μm (referred to as filter I) [15, 16]. The filtrates obtained were used to estimate the content of soluble organic matter (SOM) in water samples [13, 17] and to evaluate the fraction of SOM adsorbed on the surface of particles suspended in lake water.

RESULTS AND DISCUSSION

The amount of terrigenic suspended material in the Lake Khanka water varies from 24 to 50×10^9 particles/l [1], exceeding the total concentration of bacteria in the water ($(0.34–6) \times 10^9$ cells/l) by one–two orders. The high density of suspended particulate material and, hence, the small distances between particles (30 to 40 μm) results in that bacterial cells tend to attach to the particles and that filters with different pore sizes retain different amounts of attached bacteria (Table 1).

The fraction of bacterial cells retained by filters I, II, and III averaged 20, 32, and 40%, respectively (Table 1). The difference between the data for filters I and III was statistically significant ($t = 2.19$, while the critical value for t was 2.09). In 70% of the cases, the number of bacteria in filtered samples decreased with the decreasing filter pore size.

The adsorption of SOM on suspended particulate material also led to the dependence of its concentration in filtrates on the filter pore size: the SOM concentration was the lower the smaller filter pores were (Table 2). The amount of SOM in the river water filtrates was less than in the lake water filtrates, presumably because the mean size of particles in the river water was greater than that in the lake water. Filters with 2.87-μm pore sizes retained almost half of the soluble organic matter; therefore, filtration through such filters must considerably interfere with the estimation of bacterioplankton production.

The average amount of soluble organic matter (calculated per one cell) in the lake water before and after filtration through 4.5-μm filters was, respectively, 1.23 and 1.35×10^{-9} mg/cell in 1995 and 0.89 and 1.20×10^{-9} mg/cell in 1997 (i.e., was almost the same in these years). On the other hand, the mean number of bacterial cells before and after such filtration was, respectively, 1.78 and 1.08 million cells/ml in 1995 and 5.02 and 3.43 million cells/ml in 1997. Statistical analysis of these data showed that there is a direct correlation between the amount of soluble organic matter and the bacterioplankton population with a correlation coefficient of 0.68 (unfiltered water samples) and 0.92 (filtered water samples).

The measurements of the generation time of bacterioplankton in filtrates I, II, and III gave comparable results in 42% of the cases (filtrates I and II of the lake water samples taken at st. 72, 84, and 133 and filtrates II and III of the lake water samples taken at st. 9' and 83). At the same time, data for all three filtrates of the lake

water samples taken at st. 113 and 68 significantly differed. The observed differences were statistically insignificant (t = 1.04 and t = 1.88, while the critical values for t were 2.09 and 2.10, respectively). Similar data were obtained for the water samples taken at st. 72 (the Komissarovka River) and at st. 68 and 74 (river mouths). The largest variations in the generation time estimations were observed for filtrates II and III of the lake water samples taken in the open lake and in the coastal zone. In general, the generation time was found to be independent (in a statistical sense) of the pore size of the filters commonly used for the removal of bacterial consumers from water samples. At the same time, the filtrates III passed through 2.87-μm-pore-sized filters exhibited a decreased generation time, presumably due to a lesser bacterial population and better nutritional conditions.

The dependence of the generation time on the average daily concentration of bacteria (N_{av}) is shown in Fig. 1. It is evident that, for filtrates I and II, these parameters are related inversely (the correlation coefficients r(I) = –0.68 and r(II) = –0.61, respectively). The dependence was stronger for filtrates that were passed through gauze. By contrast, the generation time of bacteria in filtrates III passed through 2.87-μm filters was maximum and independent of the average daily bacterial concentration (the correlation coefficient r(III) = 0.02). At an average daily concentration of bacteria of 3–4 million cells/ml, the generation times became almost the same (10–20 h) for all filtrates. The high values of the generation time (50–80 h) observed for filtrates I passed through gauze at the low average daily bacterial concentration may be due to the presence of bacterial consumers in these filtrates, since the size of the protistoplankton present in Lake Khanka (< 30 μm) is less than that of the gauze pore size (about 40 μm).

As was shown by Drabkova [7] for the lakes of middle and southern taiga, the generation time of bacteria determined by direct count [8] considerably increased during the periods when the bacterial population was maximum. For instance, during the periods of unfrozen water, the coefficient of correlation between these parameters for Lakes Terenkul', Argayash, and Dlinnoe Snidzinyas was 0.7–0.9. In Lake Atkul', the slow rate of cell division was accompanied by a poor bacterial population (r = 0.47). In the case of Lake Bolshoe Shantropai, the relationship between bacterial population and its generation time was inverse (r = –0.56).

Analysis of the correlation between the generation time and the initial and average numbers of bacteria in the Kiev Reservoir showed that it is positive and insignificant in the first case (r = 0.17–0.34), while is negative and weak in the second case (r = –0.12 to –0.45) [2]. The positive correlation between the generation time and the average number of bacteria was observed for Lake Baikal for the period when the water was unfrozen. During the period the water was frozen, the correlation between these parameters was negative [9].

Table 2. Effect of the filter pore size on the relative content of soluble organic matter (SOM) in the water sample filtrates

Year	Water sampling location	Percent of SOM*	
		4.5-μm filter	2.87-μm filter
1995	Lake	83	62
	River	78	47
1997	Lake	99	59
	River mouth	82	50
	River	87	49

* SOM content in unfiltered water is taken to be 100%.

A positive correlation between the generation time and the average number of bacteria was also observed for the Angara reservoirs [3]. A negative correlation between these parameters was observed for the Yenisey River water filtered through 4.5-μm filters (r = –0.91, –0.42, and –0.24 as calculated from the data obtained in, respectively, 1994, 1997, and both of these years).

When calculated from the 1992 data, the Lake Khanka water filtered through 2.87-μm filters exhibited a positive weak correlation between the generation time and the initial and average daily concentrations of bacterial cells (r = 0.39 and 0.14, respectively). When the water was filtered through 4.5-μm filters, the positive correlation between these parameters became stronger: r = 0.87 and 0.65, respectively, as calculated from the 1995 data, and r = 0.68 and 0.37, as calculated from the 1997 data. At the same time, when calculated from the 1996 data, the correlation under discussion turned out to be negative and weak (r = –0.03 for the water samples filtered through 4.5-μm filters). At last, when calculated from the total data of all these years, the coefficient of correlation between the generation time and the

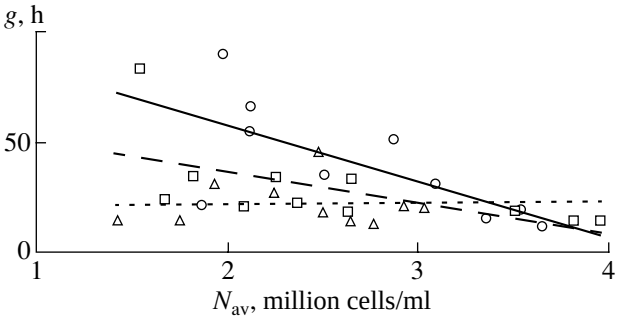

Fig. 1. Dependence of the generation time of bacterioplankton on its average daily concentration in the water filtrates passed through filters with different pores: (○, solid line) 40-μm-pore-size double gauze layer; (□, broken line) 4.5-μm-pore-size filter; and (△, dotted line) 2.87-μm-pore-size filter.

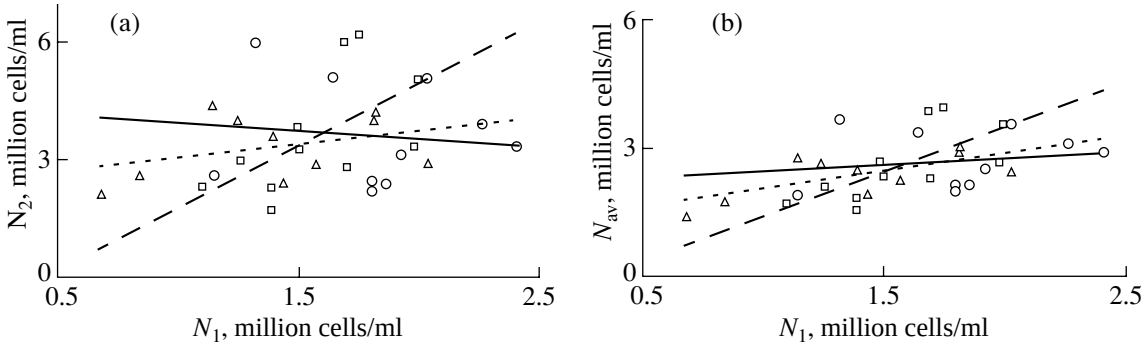

Fig. 2. Concentration of bacterioplankton in the water filtrates (a) after 1-day incubation (N_2) and (b) its average daily value (N_{av}) versus its initial concentration (N_1). For designations, see Fig. 1.

initial and average concentrations of bacterial cells was 0.31 and 0.59, respectively.

The evaluation of the bacterial population in filtrates immediately after filtration and after a 1-day incubation showed that the number of bacteria in the filtrate I passed through gauze tended to decrease in the course of incubation (r(I) = –0.12) (Fig. 2a). This might be due to the consumption of bacteria by protozoans, since 50% of these present in the Lake Khanka water are less than 30 μm in size and, hence, can pass through 40-μm gauze pores. Moreover, larger protozoans, due to their flexibility, may also pass through the gauze pores. It should be noted that about two thirds of infusorians in Lake Khanka are probably bacterial consumers [18].

The number of bacteria in filtrates II passed through 4.5-μm filters increased in the course of a 1-day incubation (r = 0.60) (Fig. 2a). The same tendency (r = 0.36) was observed for filtrates III passed through 2.87-μm filters; in this case, however, the increase in the number of bacterial cells was not so pronounced as in the case of filtrates II, and their initial number was greater (Fig. 2a).

Figure 2b shows the relationship between the initial and average daily concentrations of bacteria for all three types of filtrates. It is evident that, in all cases, the average daily bacterial concentration increased with an increasing initial concentration. In the case of the lake water filtration through 4.5- and 2.87-μm filters, the average daily bacterial concentration increased more (r(II) = 0.70 and r(III) = 0.69, respectively) than in the case of its filtration through gauze (r = 0.17).

The calculation of the biomass production per one bacterial cell (P/N), per the unit biomass increase ($P/\delta B$), and per unit biomass (P/B) showed that the values of bacterial production in all three types of filtrates were almost the same (Table 3).

According to certain data in the literature [19–21], particles suspended in water predominantly bind easily oxidizable components of SOM. As a result, filtration through 2.87-μm filters removes easily oxidizable

Table 3. Average functional characteristics of lacustrine bacterioplankton obtained with the preliminary filtration of water samples through filters with different pore sizes

Bacterioplankton characteristic	Filtration through		
	double gauze layer	4.5 μm	2.87 μm
R/N, ng C/(l day cell)	0.08 ± 0.01*	0.17 ± 0.05	0.34 ± 0.07
R/B, day^{-1}	1.94 ± 0.34*	1.86 ± 0.32*	7.45 ± 1.62
$R/\delta B$, day^{-1}	3.59 ± 0.82	3.60 ± 0.75	5.53 ± 1.14
P/N, ng C/(l day cell)	0.022 ± 0.005	0.027 ± 0.003	0.030 ± 0.005
P/B, day^{-1}	0.54 ± 0.12	0.61 ± 0.08	0.70 ± 0.14
$P/\delta B$, day^{-1}	0.91 ± 0.04	0.85 ± 0.12	0.88 ± 0.12
Sample number	11	11	15

* Data that significantly differ (P = 0.01) from those for the water filtrate passed through 2.87-μm filter.

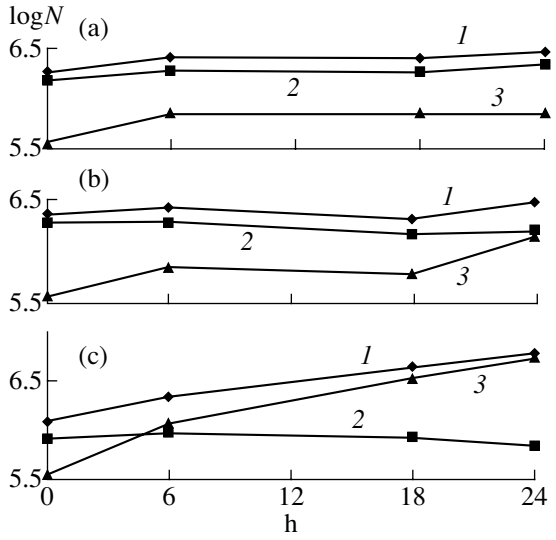

Fig. 3. Growth of bacterioplankton in (a) unfiltered water samples and those filtered through (b) 40-μm double gauze layer and (c) 2.87-μm filters: (*1*) total number of cells; (*2*) cocci; and (*3*) rod-shaped bacteria.

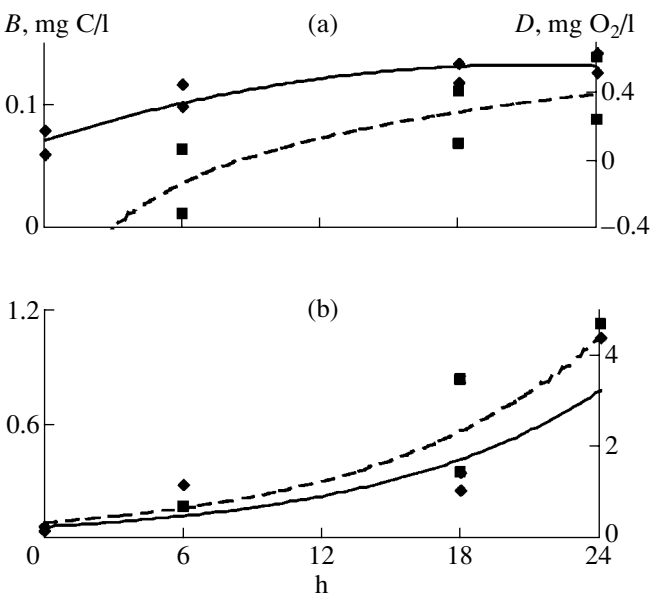

Fig. 4. Dynamics of the bacterioplankton biomass (◆) and oxygen consumption rate (■) in the water filtrates passed through (a) 40-μm double gauze layer and (b) 2.87-μm filters in the course of 1-day incubation (water samples were taken at st. 113).

organic matter, while more recalcitrant compounds remain in the water sample filtrates. This leads to an increase in the amount of oxygen necessary for the production of a certain amount of the bacterial biomass. When calculated per one bacterial cell, the consumption of oxygen (R/N) in filtrates increased with the decreasing filter pore size. In this case, the values of oxygen consumption per unit biomass (R/B) and per the unit biomass increase ($R/\delta B$) were almost the same for filtrates I and II, which were passed through 40- and 4.5-μm filters, but were significantly higher for filtrate III, which was passed through a 2.87-μm filter (we must recall that the last filtrate exhibited the lowest generation time of bacterioplankton). The energy yield coefficient K_2 was calculated by three methods. In the first method, K_2 was defined as the amount of degraded organic matter allowing for the lake trophism [7, 15]. The calculated values of K_2 for filtrates I, II, and III were 0.39, 0.44, and 0.40, respectively. In the second method, K_2 were calculated allowing for the rate of oxygen consumption in particular filtrates. In this case, oxygen consumption turned out to be minimum in filtrate I and maximum in filtrate III, while, conversely, the coefficient K_2 was minimum for filtrate III and maximum for filtrate I. Namely, K_2 was equal to 0.30, 0.23, and 0.13 for filtrates I, II, and III, respectively. This type of situation is typical of polluted bodies of water [22]. In the third method, K_2 were calculated allowing for the bacterial biomass accumulated in filtrates [23]. In this case, the energy coefficients K_2 for filtrates I, II, and III comprised 0.34, 0.37, and 0.24, respectively. It is evident that these values of K_2 are medium when compared with the K_2 values calculated by the first and second methods and, presumably, are the most likely. In the filtrates II and III (filtration through 4.5- and 2.87-μm filters, respectively) of water samples taken at st. 9′, 83, 84, 113, 133, and 68, the number of cocci and rod-shaped bacteria after 1 day of incubation increased, on average, by 2.3 times. However, in filtrate I, passed through gauze, the bacterial population did not increase at all.

The evaluation of bacterioplankton in unfiltered water samples and their filtrates 6, 18, and 24 h after filtration (Fig. 3) showed that the bacterial population in the filtrates increased largely due to the growth of rod-shaped bacteria. The growth curves of bacterioplankton in unfiltered water samples and in their filtrates, which were passed through gauze, were almost the same. In unfiltered water samples, the bacterial population grew primarily due to the growth of cocci and, to a lesser degree, of rod-shaped bacteria. Presumably, the latter bacteria were consumed by zooplankton at a higher rate than cocci. After 1 day of incubation, the numbers of cocci and rod-shaped bacteria in filtrates I were almost the same. In filtrates III, the number of rods increased more rapidly and was greater than the number of cocci.

Measurements of bacterial biomass and respiration at 6-h intervals showed that the dynamics of these parameters in unfiltered water samples and filtrate I (filtration through gauze) were almost the same and comprised 0.11 mg C/l and 0.07 mg O_2/(l day) after 6 h of incubation and 0.12 mg C/l and 0.43 mg O_2/(l day) after 1 day of incubation (Fig. 4). In filtrate III, the bacterial biomass and oxygen consumption rate considerably

increased during the course of incubation, amounting to 0.28 mg C/l and 0.67 mg O_2/(l day) after 6 h of incubation and 1.05 mg C/l and 4.66 mg O_2/(l day) after 1 day of incubation. The time dependence of the biomass and bacterial respiration in filtrate I was approximated by a logarithmic curve (Fig. 4a), presumably due to the consumption of bacteria by protozoans. In the case of filtrate III (filtration through 2.87-μm filters), the increase in the bacterial biomass and respiration was exponential (Fig. 4b).

Thus, the investigation of the effect of the pore size of filters used for the preliminary filtration of water samples from the loess Lake Khanka showed that filtration through a double layer of gauze no. 72 with a pore size of 40 μm was unable to remove small protistoplankton less than 30 μm in size, which led to overestimated values of the generation time of bacteria. In this case, the time dependences of the bacterial biomass and respiration were logarithmic. Filters with 4.5-μm pores retained up to 20% of the SOM and 20–30% of the bacteria. Filters III with 2.87-μm pores retained almost 50% of the SOM and about 40% of the bacteria. In all cases, the generation time of bacteria tended to decrease, whereas bacterial production tended to increase when calculated both per one cell and per unit biomass. Filtration through 2.87-μm filters considerably reduced the concentration of bacteria in water samples and specifically influenced the content and composition of the SOM, so that the generation time of bacteria shortened, the rate of oxygen consumption per one cell increased, the energy coefficient K_2 decreased, the dependence of the average daily population of bacterioplankton on the generation time became weaker, and the morphological characteristics of bacterioplankton changed. The incubation of the filtrates that had passed through 2.87-μm filters led to an exponential rise in bacterial biomass and oxygen consumption. The foregoing suggests that the relevant parameters obtained using 2.87-μm filters for the preliminary filtration of water samples do not adequately reflect the processes occurring in Lake Khanka.

The filtration of the Lake Khanka water through filters with pore sizes 5–10 μm seems to be more appropriate for obtaining adequate functional characteristics of lacustrine bacterioplankton. In our opinion, this inference must be true not only for Lake Khanka, but also for other bodies of water which are characterized by the presence of small bacterioplankton consumers and of appreciable amounts of detritus and mineral suspended particles binding soluble organic matter and planktonic microorganisms.

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