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WATER QUALITY AND PROTECTION: ENVIRONMENTAL ASPECTS

Assessing the Abundance, Biomass, and Production of Heterotrophic Bacteria in Upper Volga Reservoirs

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Abstract—Two reservoirs in the Upper Volga were studied to determine the abundance, biomass, and production of planktonic, epiphyte, and benthos bacterial communities and to assess their contribution to the formation of the total abundance and productivity of bacteria. The abundance and production of heterotrophic bacteria per 1 cm^3 of bottom sediments were $10–10^2$ times greater than those in epibioses of higher aquatic plants and $10^3–10^4$ times greater than those in water mass. In the mesoeutrophic Rybinsk Reservoir and eutrophic Ivan'kovo Reservoir, bacteriobenthos accounts for 90.4 and 98.8% of the total biomass and 95.8 and 99.5% of the total production of heterotrophic bacteria; bacterioplankton, for 9.55 and 1.19% of biomass and 4.12 and 0.45% of production; and bacterioepiphyton, for 0.05 and 0.03% of biomass and 0.03 and 0.02% of production. The obtained data demonstrate the important role of benthic bacterial communities in the Upper Volga reservoirs.

Keywords: bacterioplankton, bacterioepiphyton, bacteriobenthos, Upper Volga reservoirs
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INTRODUCTION

Heterotrophic bacteria are an important component of aquatic ecosystems, where they play the main role in organic matter destruction and the recycling of biogenic elements [8]. An appreciable portion (≥50%) of the total carbon flow in planktonic trophic networks pass through heterotrophic bacteria [15]. Clearly, to understand the regularities of functioning and to assess the self-cleaning capacity of freshwater ecosystems requires data on the abundance and functional activity of bacteria in all habitats of these ecosystems.

In the Volga reservoirs, as well as in the majority of other water bodies, the communities of heterotrophic bacteria are known much better [4] than the epibioses of higher aquatic plants [10] and bottom sediments (BS) [1, 6]. The structural and functional characteristics of planktonic, periphytonic, and benthic bacterial communities in the Volga reservoir have not been compared by up-to-date methods. The role of communities in the formation of the total abundance and production of heterotrophic bacteria in various habitats of reservoirs has not been assessed. Such studies have also been rare in other aquatic ecosystems [17].

The objective of this study is to determine the structural and functional characteristics of planktonic, epiphyton, and benthic bacterial communities and to assess the contribution of these communities to the formation of the total abundance and production of heterotrophic bacteria in the eutrophic Ivankovo and mesoeutrophic Rybinsk reservoirs.

MATERIALS AND METHODS

The Ivankovo Reservoir (water area of 327 km^2, water volume of 1.2 km^3, average depth of 3.4 m, and water exchange coefficient of 10.6 $year^{-1}$) and the Rybinsk Reservoir (water area of 4550 km^2, water volume of 25.4 km^3, average depth of 5.6 m, and water exchange coefficient of 1.9 $year^{-1}$) are located in the Upper Volga Region [11]. These morphometric characteristics correspond to the normal maximum operating level (NMOL), which is 124 m for the Ivankovo Reservoir and 102 for the Rybinsk Reservoir. According to the most recent estimates, the degree of overgrowth with higher aquatic plants of the Rybinsk and Ivankovo reservoirs is 4.1 and 29.2% of water area, respectively [7].

The bacterial communities of the reservoirs were studied in July and August 2005–2007 and 2012. The structural and functional parameters of bacterioplankton and bacteriobenthos (in the top 2-cm layer of BS) were measured at 20 stations of the Rybinsk Reservoir on July 17–18, 2012, and at 12 stations of the Ivankovo Reservoir on August 10–12, 2012 (Fig. 1). The bacterioepiphyton of the Ivankovo and Rybinsk reservoirs was studied in August 2005 and July–

Table 1. Bacterioplankton abundance (*N*), average cell volume (*V*), biomass (*B*), and production (*P*) in the Ivankovo and Rybinsk reservoirs

Parameter	Ivankovo Reservoir		Rybinsk Reservoir	
	minimum–maximum	average ± error	minimum–maximum	average ± error
N, 10^6 cell/cm^3	4.58–11.32	7.59 ± 0.45	5.10–12.81	7.62 ± 0.42
V, μm^3	0.045–0.163	0.087 ± 0.009	0.036–0.067	0.051 ± 0.002
B, mg/m^3	338–902	624 ± 46	243–578	381 ± 19
B, mg C/m^3	87.4–199.7	148.6 ± 7.8	70.0–165.1	105.6 ± 5.3
P, mg C/(m^3 day)	51.1–228.7	95.9 ± 1.3	24.2–110.4	70.6 ± 5.8

August 2005–2007, respectively. The objects of the study were epibioses of different macrophyte groups: aero-aquatic species (marsh sedge (Carex acuta)); emergent species (common bulrush (Scirpus lacustris), rooting bulrush (Scirpus radicans), reed sweet grass (Gliceria maxima), common reed grass (Phragmites australis), mace reed (Typha latifolia), horsetail riverine (Equisetum fluviatile)); emophyte with floating leaves (arrowhead sagittifolious (Sagittaria sagittifolia), white water lily (Nymphaea candida), water persicaria (Persicaria amphibia), yellow water lily (Nuphar lutea)); emophytes (meakin (Myriophyllum spicatum), clasping-leaved pondweed (Potamogeton perfoliatus), and crab's-claw (Stratiotes aloides)).

The abundance and sizes of heterotrophic bacteria were determined by epifluorescence microscopy with the use of fluorochrome DAPI and black nuclear filters with pore diameters of 0.17 μm [20]. When preparing microscopic preparations, the samples of bottom sediments and macrophyte fouling were diluted by distilled water pre-filtered through membrane filters with pore diameter of 0.2 μm; next, sodium pyrophosphate was added as a detergent, and ultrasound was applied [23]. The preparations were inspected under epifluorescence microscope Olympus BX51 (Japan) with magnification of 1000 and a system of image analysis. The biomass of bacteria was calculated as the product of the total number multiplied by the average volume of the bacterial cell. The concentration of organic carbon in the wet biomass of bacteria was calculated by the equation relating the volume and carbon content of a cell [19].

The production of heterotrophic bacterioplankton and bacteriobenthos was measured by the inclusion of ^{3}H-thymidine in the DNA of bacterial cells [14]. Bacterioepiphyton production in the Rybinsk Reservoir was determined by radiocarbon method by dark assimilation of CO_2 [9]. The average values of the specific growth rate obtained in the Rybinsk Reservoir were used to calculate bacreioepiphyton and bacteriobenthos production in the Ivankovo Reservoir. The primary phytoplankton production was determined by radiocarbon method in the photic water layer from the surface to the triple Secchi depth [9].

RESULTS OF STUDIES

The temperature of surface water layer in the Ivankovo Reservoir in the study period varies within the range 21.9–28.2°C (on the average, 23.7 ± 0.5°C), and that of bottom layer was 20.8–27.0°C (on the average, 22.3 ± 0.6°C). Secchi depth was 0.7–1.1 m (on the average 0.8 ± 0.04 m). Phytoplankton primary production per unit water volume varied from 218 to 1814 mg C/(m^3 day) (on the average, 923 ± 151 mg C/(m^3 day)), and that under unit surface area varied from 321 до 4191 mg C/(m^2 day) (on the average, 1689 ± 318 mg C/(m^2 day)).

In the Rybinsk Reservoir, water temperature on the surface varied within the range of 20.4–22.0°C (on the average, 21.1 ± 0.1°C), and that at the bed, within the range of 20.2–21.3°C (on the average, 20.8 ± 0.1°C). Secchi depth was 0.8–1.2 m (on the average, 0.9 ± 0.3 m). Phytoplankton primary production per unit water volume varied from 153 to 973 (on the average, 569 ± 53) mg C/(m^3 day), and that under unit surface area, from 289 to 1850 mg (on the average, 1080 ± 10) mg C/(m^2 day).

Bacterioplankton. The average values of bacterioplankton abundance in the two reservoirs were found to be similar, but the abundance and biomass of bacteria in the Ivankovo Reservoir were larger than those in the Rybinsk Reservoir by factors of 1.7 and 1.6, respectively (mg/m^3) (Table 1). The specific growth rate of planktonic bacteria in the Ivankovo Reservoir varied within the range of 0.334–2.030 (on the average, 0.679 ± 0.432) day^{-1}, and that in the Rybinsk Reservoir, within the range of 0.274–1.250 (on the average, 0.691 ± 0.290) day^{-1}. Bacterioplankton production in the Ivankovo Reservoir was 1.4 times greater than that in the Rybinsk Reservoir.

Bacterioepiphyton. The average abundance of bacterioepiphyton of emergent plants and emophytes in the Ivankovo Reservoir was 1.4–2.4 times greater than that in the Rybinsk Reservoir (Table 2). The average cell volume of epiphyton bacteria in the Ivankovo Reservoir was lower than that in the Rybinsk Reservoir. The result was that the biomasses of bacterioepiphyton of different plant groups in the Ivankovo Reservoir

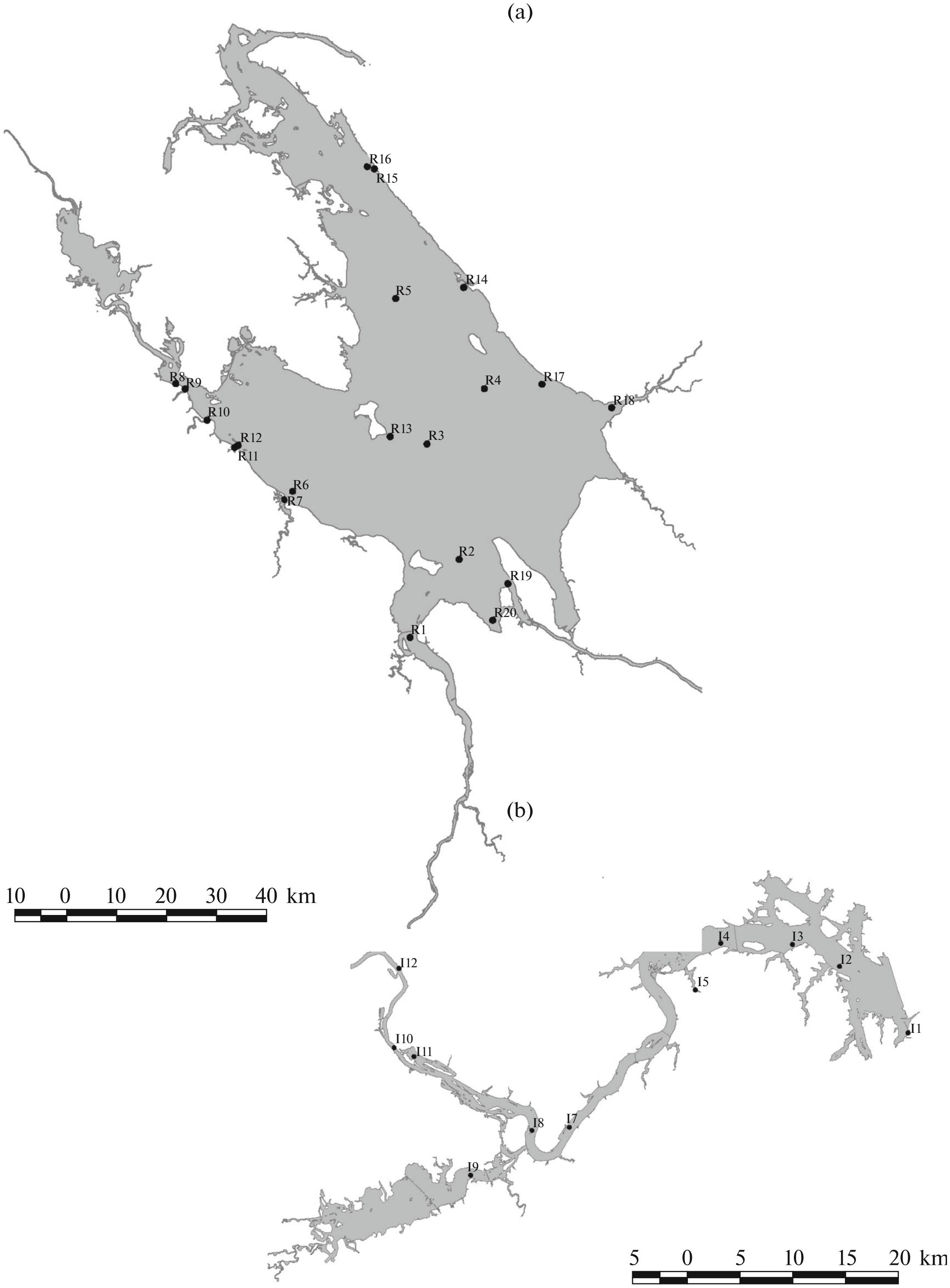

Fig. 1. Layout of sampling stations in (a) the Rybinsk and (b) the Ivankovo reservoir.

were greater than those in the Rybinsk Reservoir by factors of 1.2–1.8 (in μg/cm^2) or 1.1–2.0 (in μg C/cm^2). In both reservoirs, the values of the abundance and biomass of epiphyton bacteria decreased in the series of plant groups: aero-aquatic—emergent—emophytes with floating leaves—fully submerged. In the Rybinsk Reservoir, the specific growth rate varied within the range of 0.490–0.890 (on the average, 0.678 ± 0.088) day^{-1} for the bacterioepiphyton of aero-aquatic plants; 0.490–1.750 (on the average,

Table 2. Abundance (*N*), average cell volume (*V*), biomass (*B*), and production (*P*) of bacterioepiphyton (here and in Table 4, AA is aero-aquatic, EM is emergent, EFL is emergent with floating leaves, FS is fully submerged plant; given above the line is the variation range of a parameter, below the line is the average value ± error of the mean)

Plants	*N*, 10^6 cell/cm^2	*V*, μm^3	*B*, mg/m^2	*B*, mg C/m^2	*P*, μg C/(cm^2 day)
Ivankovo Reservoir					
EM	36–513 203 ± 23	0.066–0.257 0.124 ± 0.007	3.3–60.5 22.9 ± 2.5	0.8–13.2 5.0 ± 0.5	0.77–12.68 4.78 ± 0.52
EFL	27–454 137 ± 53	0.065–0.259 0.122 ± 0.021	2.5–44.0 17.0 ± 4.9	0.6–10.1 3.2 ± 1.1	0.51–8.66 2.63 ± 1.11
FS	22–155 64 ± 17	0.092–0.149 0.115 ± 0.008	2.8–15.5 7.0 ± 1.6	0.7–3.5 1.6 ± 0.4	0.63–3.13 1.39 ± 0.33
Rybinsk Reservoir					
AA	134–282 175 ± 36	0.082–0.148 0.123 ± 0.015	16.8–23.1 20.0 ± 1.3	3.7–6.6 4.4 ± 0.4	2.11–4.12 2.99 ± 0.51
EM	2–232 142 ± 24	0.082–0.273 0.139 ± 0.018	0.5–24.0 16.4 ± 2.2	0.1–5.6 3.6 ± 0.5	0.05–9.44 3.52 ± 0.74
EFL	8–176 94 ± 18	0.074–0.402 0.165 ± 0.029	3.3–45.0 13.5 ± 4.0	0.5–7.8 2.9 ± 0.7	0.15–4.77 2.14 ± 0.40
FS	2–51 26 ± 6	0.111–0.403 0.200 ± 0.044	0.8–6.8 4.0 ± 0.8	0.1–1.2 0.8 ± 0.2	0.05–2.50 0.85 ± 0.33

Table 3. The abundance (*N*), average cell volume (*V*), biomass (*B*), and production (*P*) of bacteriobenthos

Parameter	Ivankovo Reservoir		Rybinsk Reservoir	
	minimum–maximum	average ± error	minimum–maximum	average ± error
N, 10^9 cell/cm^3	19.6–93.5	44.9 ± 5.7	3.71–14.98	7.73 ± 0.71
V, μm^3	0.109–0.665	0.334 ± 0.038	0.120–0.278	0.205 ± 0.012
B, mg/cm^3	7.3–19.7	13.2 ± 0.9	0.47–2.53	1.51 ± 0.14
B, mg C/cm^3	1.19–3.07	2.20 ± 0.14	0.10–0.46	0.28 ± 0.02
P, mg C/(cm^3 day)	1.95–5.04	3.61 ± 0.23	0.19–1.06	0.46 ± 0.05

0.961 ± 0.126) day^{-1}, for emergent plants; 0.298–1.960 (on the average, 0.857 ± 0.126) day^{-1} for emophytes with floating leaves; and 0.159–2.020 (on the average, 0.894 ± 0.259) day^{-1} for fully submerged plants. As the result, the production of heterotrophic bacteria in the epibioses of different groups of higher aquatic plants in the Ivankovo Reservoir was 1.2–1.6 times greater than that in the Rybinsk Reservoir.

Bacteriobenthos. The abundance, average cell volume, and the biomass of bacteriobenthos in the Ivankovo Reservoir were higher than those in the Rybinsk Reservoir by factors of 5.8, 1.6, and 8.7 (mg/cm^3) (7.8 (mgC/cm^3)), respectively (Table 3). The specific growth rate of bacteriobenthos in the Rybinsk Reservoir varied within the range of 0.528–4.224 (on the average, 1.642 ± 0.216) day^{-1}. Bacteriobenthos production in the Ivankovo Reservoir was also far greater than that in the Rybinsk Reservoir.

DISCUSSION OF RESULTS

The structural-functional characteristics of bacterioplankton (except for its abundance) in the eutrophic Ivankovo Reservoir were higher than those in the mesoeutrophic Rybinsk Reservoir. The values of bacterioplankton abundance, biomass, and production, obtained for these water bodies, show them to be eutrophic [5].

The abundance of heterotrophic bacteria in the epiphytone of macrophytes in different water bodies varies within the range of 10^5–10^7 cell/cm^2 [13, 16]. The values of this parameter in the Upper Volga reservoirs lie in the upper part of this range.

The abundance of bacteriobenthos in most aquatic ecosystems varies within the range of 10^8–10^{10} cell/cm^3 [21, 22]. Note that the abundance of benthic bacteria in the Rybinsk Reservoir in 2012 was close to the data obtained in the previous years [6]. The high abundance of bacteria found in the BS of the Ivankovo Reservoir is typical of eutrophic and hypertrophic lakes [24].

The average values of the abundance (and biomass) of heterotrophic bacteria in the water mass, epiphyton (the thickness of epibioses was taken equal to 1 mm) and BS (the top 2-cm layer), calculated per 1 cm^3 for the Ivankovo Reservoir, were $(7.59 \pm 0.45) \times 10^6$ cell/cm^3 (0.148 ± 0.008 μg C/cm^3), $(1.35 \pm 0.30) \times 10^9$ cell/cm^3 (32.7 ± 9.8 μg C/cm^3), and $(44.9 \pm 5.7) \times 10^9$ cell/cm^3 (2.20 ± 0.14 mg C/cm^3), respectively; the respective values for the Rybinsk Reservoir were $(7.62 \pm 0.42) \times 10^6$ cell/cm^3 (0.106 ± 0.005 μg C/cm^3), $(1.09 \pm 0.32) \times 10^9$ cell/cm^3 (29.3 ± 7.7 μg C/cm^3), and $(7.73 \pm 0.71) \times 10^9$ cell/cm^3 (0.28 ± 0.02 mg C/cm^3).

The specific growth rate of planktonic, epiphyte, and benthic bacteria in the study period was, on the average, 0.657, 0.848, and 1.642 day^{-1}, respectively. A possible cause of the slower increase in the abundance of planktonic bacteria is the lower proportion of active bacteria in the community. Thus, the abundance of active cells in the mesotrophic Örken Lake (Sweden) was 4, 37, and 46% of the abundance of bacterioplankton, bacterioepiphyton, and bacteriobenthos, respectively [18]. The specific growth rate of bacteriobenthos in the Upper Volga reservoirs varied within the range of this characteristic in freshwater BS, and exceeded the average values for lacustrine (0.8 day^{-1}) and riverine (1.3 day^{-1}) soils [21]. This may be due to the fact that the study was carried out in the middle and late summer at the highest warming of soils. The heterotrophic bacterial production in the water mass, epibioses of higher aquatic plants, and BS in the Ivankovo Reservoir was, on the average, 0.096 ± 0.013, 29.3 ± 9.9 μg C/(cm^3 day), and 3.61 ± 0.23 mg C/(cm^3 day), respectively; the respective characteristics in the Rybinsk Reservoir were 0.071 ± 0.025, 23.8 ± 5.8 μg C/(cm^3 day), and 0.46 ± 0.05 mg C/(cm^3 day). Thus, the structural–functional parameters of bacteriobenthos in the examined water bodies were far in excess of those of bacterioepiphyton and bacterioplankton.

According to data in [7], the area of water surface in the Ivankovo Reservoir covered by higher aquatic plants in 2005 was 19830 ha (198 km^2), of which hygrohelophytes (aero-aquatic plants) accounted for 66.8; helophytes (emergent plants), for 6818; hydrophytes (emophytes) with floating leaves, for 985; and fully submerged hydrophytes, for 11961 ha. In the Rybinsk Reservoir, the surface area covered by higher aquatic plants in 2009 was 86166 ha (862 km^2) with hygrohelophytes occupying 466 ha; helophytes, 34865 ha; hydrophytes with floating leaves, 1969 ha; and submerged hydrophytes, 48865 ha. These data were used to calculate the abundance, biomass, and production of epiphyte bacteria in the epibioses of different groups of higher aquatic plants in the Ivankovo and Rybinsk reservoirs. It was found that the main contribution to the total biomass and production of bacterioepiphyton in both reservoirs is due to the bacteria that develop in the epibioses of emergent plants, emophytes, and, to a lesser extent, emophytes with floating leaves (Table 4).

Table 4. Abundance (N, 10^{17} cell), biomass (B, 10^{11} μg C), and production (P, 10^{11} μg C /day) of heterotrophic bacteria in overgrowths of different groups of higher aquatic plants

Plants	Ivankovo Reservoir			Rybinsk Reservoir		
	N	*B*	*P*	*N*	*B*	*P*
AA	5.9	0.2	0.1	40.8	1.0	0.7
EM	1112.2	27.3	26.2	3972.9	100.8	98.8
EFL	135.9	3.2	2.6	185.1	5.7	4.2
FS	765.5	19.1	16.6	1271.0	39.1	41.5

The morphometric characteristics of reservoirs and the data of this study were used to evaluate the abundance and production of all heterotrophic bacteria in the reservoirs (Table 5). In both the eutrophic Ivankovo and the mesoeutrophic Rybinsk reservoirs, the major portion of bacteria was in BS. These bacteria contribute most to the total heterotrophic bacterial production in the reservoirs. The total abundance, biomass, and production of bacteriobenthos were greater than those of bacterioplankton by factors of 4–35, 9–83, and 23–221, respectively. The total abundance, biomass, and production of bacterioplankton were 0.3–2.4, 0.6–2.3, and 0.8–3.7% of those for bacterioplankton.

Assuming that the utilization coefficient of the assimilated substrates for bacterial growth is 0.3 [8], we can calculate that, in the study period, all heterotrophic bacteria in the Ivankovo Reservoir consumed 7907×10^{10} mg C/day. Their expenditure for energy exchange was 5535×10^{10} mg C/day, of which 99.5% were due to benthic bacteria. In the Ivankovo Reservoir, heterotrophic bacteria consumed 14558×10^{10} mg C/day. At the same time, the expenditure for energy exchange was 10191×10^{10} mg C/day, of which 95.9% were due to benthic bacteria.

The results obtained by the authors are in agreement with data on other aquatic ecosystems. Thus, in the Spree River (Germany), where 40% of the bed was occupied by macrophytes, the biomass and production of heterotrophic bacteria in the surface layer of bottom sediments were 6 and 17 times those in the water, respectively. The benthic bacteria were larger and more active than the planktonic ones. Bacterioepiphyton production was 14–67% of that of bacterioplankton. The total production of heterotrophic bacteria was higher than the primary production. This lowland river can be regarded as a heterotrophic sys-

Table 5. Abundance (N, 10^{20} cell), biomass (B, 10^{10} mg C), and daily production (P, 10^{10} mg C) of heterotrophic bacteria in water mass, overgrowths of higher aquatic plants, and BS of the reservoirs (given in parentheses is the share, % of the total value)

Parameter	Water mass	Overgrowths	BS	Total
Ivankovo Reservoir				
N	84.4 (2.79)	2.0 (0.07)	2933.2 (97.14)	3019.6
B	17.4 (1.19)	0.5 (0.03)	1438.8 (98.78)	1456.7
P	10.7 (0.45)	0.5 (0.02)	2360.9 (99.53)	2372.1
Rybinsk Reservoir				
N	1942.8 (21.63)	5.5 (0.06)	7034.3 (78.31)	8982.6
B	269.1 (9.55)	1.5 (0.05)	2548.0 (90.40)	2818.6
P	179.9 (4.12)	1.5 (0.03)	4186.0 (95.85)	4367.4

tem with the predominance of benthic processes [17]. The communities of benthic organisms contribute most to the metabolism of ecosystems in subarctic lakes in the northern Sweden. The share of phyto- and bacteriobenthos in the total production of these lakes was 86 ± 4%, in which heterotrophic bacteria accounted for 19% of total production in BS and 51% of production in water mass [12].

According to data in [2], the destruction in water in the reservoirs of the Volga–Kama chain and the Don is greater than the destruction in BS, their ratio increasing from north to south. Such geographic regularity is explained in [2] by the fact that, in northern water bodies, a considerable portion of organic substances has not enough time to decay in water and settles onto the bed, where they are actively decomposed by benthic bacteria, protists, and invertebrates. In southern reservoirs, especially eutrophic, the major portion of organic substances produced by photosynthesizing organisms and entering from the watershed decomposes in well heated water mass and few readily oxidizable organic compounds enter soils. Silt processes govern 30–35% of total destruction in water and BS in northern reservoirs, ~20% of that in the Middle Volga, and 10–12% of that in southern reservoirs. In addition, the contribution of benthic processes to the total destruction increases along the gradient of trophicity of aquatic ecosystem from oligotrophic to hypertrophic. The role of benthic processes is largest in dystrophic lakes. However, in later studies [3], the rate of destruction in BS was underestimated by 30–60% because of drawbacks of the utilized methods. In addition, it should be taken into account that, although bacteria play the principal role in organic matter destruction in water and soils, other aquatic organisms also contribute to these processes.

CONCLUSIONS

The abundance of heterotrophic bacteria in the eutrophic Ivankovo Reservoir is greater than that in the mesoeutrophic Rybinsk Reservoir. In these shallow-water systems, bacteriobenthos contributes most to the formation of the total abundance, biomass, and production of heterotrophic bacteria. Bacterioplankton and bacterioepiphyton play a far lesser role. The major portion of the biomass and production of bacterioepiphyton is formed by the bacteria that develop on the surface of emergent aquatic plants. The obtained data demonstrate the huge metabolic potential of benthic bacteria and their leading role in organic matter mineralization in Upper Volga reservoirs.

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