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AQUATIC MICROBIOLOGY

Structure and Functioning of the Microbial Loop in a Boreal Reservoir

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Abstract—The abundance and biomass of the main components of the microbial plankton food web ("microbial loop")—heterotrophic bacteria, phototrophic picoplankton and nanoplankton, heterotrophic nanoflagellates, ciliates and viruses, production of phytoplankton and bacterioplankton, bacterivory of nanoflagellates, bacterial lysis by viruses, and the species composition of protists—have been determined in summer time in the Sheksna Reservoir (the Upper Volga basin). A total of 34 species of heterotrophic nanoflagellates from 15 taxa and 15 species of ciliates from 4 classes are identified. In different parts of the reservoir, the biomass of the microbial community varies from 26.2 to 64.3% (on average 45.5%) of the total plankton biomass. Heterotrophic bacteria are the main component of the microbial community, averaging 63.9% of the total microbial biomass. They are the second (after the phytoplankton) component of the plankton and contribute on average 28.6% to the plankton biomass. The high ratio of the production of heterotrophic bacteria to the production of phytoplankton indicates the important role of bacteria, which transfer carbon of allochthonous dissolved organic substances to a food web of the reservoir.

Keywords: microbial loop, bacterioplankton, viruses, phototrophic pico- and nanoplankton, heterotrophic nanoflagellates, ciliates, boreal reservoir

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INTRODUCTION

Procaryotic and eukaryotic microorganisms form microbial food webs (a microbial loop) that play an important role in the structural and functional organization of aquatic ecosystems [3, 14]. Heterotrophic bacteria consume a considerable part of soluble organic compounds generated by primary producers in a waterbody and received from catchment area and transform it to a suspended form available for other hydrobionts. Picoplankton and nanoplankton contribute greatly to the formation of biomass and productivity of freshwater phytoplankton. In turn, the main consumers of autotrophic and heterotrophic picoplankton, heterotrophic flagellates, are consumed by infusoria. Protists serve as food to metazoic plankton, and this provides the interaction between microbial loop and grazing linear trophic chain. Viruses greatly affect bacteria and other components of the microbial community [21].

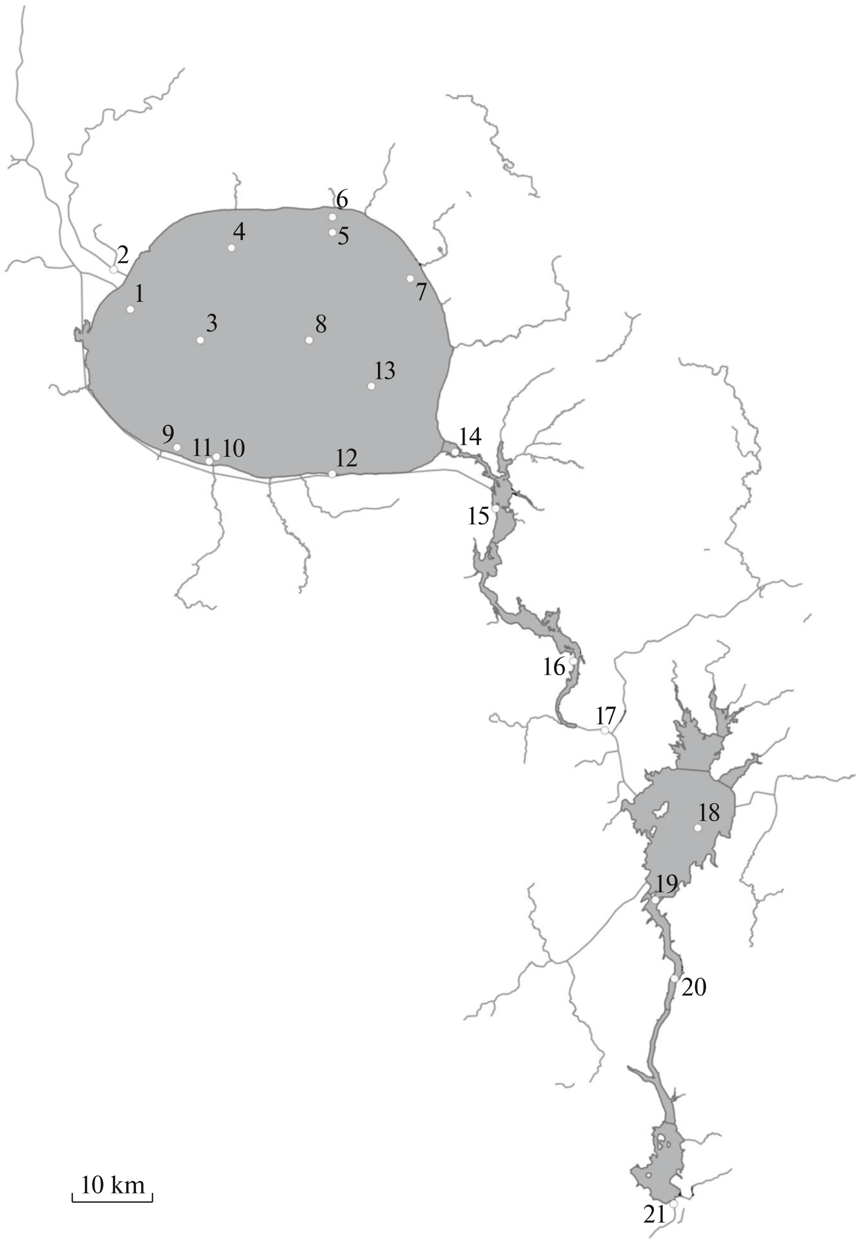
Episodic microbiological investigations were carried out in the Sheksna Reservoir starting in the first years after its impoundment. The data of these researches concerning the number and biomass of bacteria and abundance of physiological groups of microorganisms indicate the important role of microorganisms in the destruction processes and self-purification of this waterbody situated in the Boreal zone [9, 13]. However, the structure and functions of the microbial community in the Sheksna Reservoir are much less studied than in other Volga River reservoirs [2, 3].

The goal of the present paper is to study the structural and functional characteristics of the main components of microbial food web in the Sheksna Reservoir during the summer period.

MATERIALS AND METHODS

The Sheksna Reservoir was impounded on the Sheksna River in 1963. It is situated in the sub-zone of middle taiga between 59°30′ N and 60°50′ N and represents part of the Volga–Baltic waterway. At a normal maximum operating level (113 m), the reservoir length is 262 km, maximal width (in the region of Lake Beloye) is 33 km, surface area is 1665 km^2, catchment area is 19 445 km^2, mean depth is 3.9 m, and coefficient of conditional water turnover is 0.96 $year^{-1}$ [13].

Three main parts are defined in the waterbody: the Kovzha Belozerskaya River (Kovzhinskii), Lake Beloye (Belozerskii), and the riverine—sunken channel and floodplain of the Sheksna River (Sheksninskii). During the study period of August 8–13,



Schematic map of locations of sampling stations in the Sheksna Reservoir: (1–21) numbers of stations.

2007, the sampling was performed at all three parts: Kovzhinskii (sampling stations 1–2), Belozerskii (3–13), and Sheksninskii (14–21) (figure). Since the Kovzhinskii part has a small surface area and water mass volume, it was considered as part of the lacustrine area of the reservoir. Integrated samples were collected by mixing the water taken using a Plexiglas bathometer with a 1-m increment from water surface to bottom. These samples were immediately preserved with glutaraldehyde to a final concentration of 2% and were stored for less than 1 month in dark at 4°C.

Temperature, electric conductivity, and concentration of dissolved oxygen were measured using a portable YSI Model 85 (YSI, Inc., United States) multiparametric probe. The values of water pH were analyzed with portable 100 ISFET (Beckman Instruments, Inc., United States) pH meter. Water color (WC) was determined applying the method of comparison with artificial standards and was expressed in degrees by the chromium-cobalt color scale. The concentration of dissolved organic matter (DOM) was measured by the method of high-temperature catalytic burning and subsequent analysis using a LiquiTOC II (Elementar, Germany) automatic carbon analyzer [22].

Viruses, bacteria, heterotrophic flagellates, picoplankton, nanophytoplankton, and infusoria were

Table 1. Depth (H), transparency (Z), color (WC), temperature (T), and electric conductivity (EC) of water, concentration of dissolved oxygen (O_2) and dissolved organic matter (DOM) in the Sheksna Reservoir during the period of August 8–13, 2007

No. of samplings station	H, m	Z, cm	WC, degr	pH	DOM, mg C/L	EC, µS/cm		T, °C		O_2, mg/L	
						Surf.	Bot.	Surf.	Bot.	Surf.	Bot.
	Belozerskii reach										
1	4.7	120	63	7.81	9.15	142	153	21.2	20.2	9.31	8.09
2	2	180	64	8.02	9.19	156	163	22.5	22.4	8.90	8.08
3	5.5	115	43	7.38	7.37	132	144	20.7	20.3	9.19	9.03
4	5.2	110	50	8.30	7.69	131	130	20.5	20.2	10.62	9.73
5	5	110	52	8.04	8.19	129	137	21.2	19.8	10.59	7.85
6	1.3	100	65	8.22	9.27	127	–	21.4	–	9.99	–
7	4	120	60	8.20	8.86	125	133	22.0	19.6	10.89	7.80
8	5.5	120	56	8.11	8.54	125	125	20.3	20.3	8.91	8.54
9	5	110	56	8.41	8.52	135	134	20.7	20.5	9.90	9.70
10	5	120	54	8.50	8.39	133	133	20.6	20.4	9.00	8.82
11	1.3	100	59	8.06	8.81	195	–	21.1	–	7.79	–
12	4.5	115	60	8.40	9.14	128	127	21.2	20.8	9.18	9.05
13	4.5	105	62	8.31	9.06	120	120	20.6	20.6	8.98	8.64
	Sheksninskii reach										
14	4	50	61	8.39	8.97	127	127	20.7	20.6	8.73	8.66
15	5.5	70	74	8.32	10.10	131	131	21.4	21.4	8.56	8.36
16	9	70	68	8.41	9.57	191	190	22.1	21.6	8.00	7.52
17	5	80	65	8.44	9.32	193	193	22.2	21.4	8.27	7.88
18	4.5	120	76	8.17	10.26	165	165	21.1	21.0	8.05	7.90
19	7	120	76	7.93	10.24	166	165	21.3	21.1	7.60	6.76
20	7	140	73	8.30	10.03	162	162	21.8	21.5	8.73	8.19
21	9	140	64	8.51	9.22	157	173	22.7	20.0	9.90	6.73

Surf., surface water layer; Bot., near-bottom water layer.

studied using light and epyfluorescent microscopy. The production of phytoplankton was determined by the radiocarbon technique, the production of heterotrophic bacterioplankton was determined by the method of dissolving, and the consumption of bacteria by protists was determined by the method of fluorescent-labeled bacteria. The abovementioned methods and techniques for determining the viral lysis of bacteria, as well as values of the coefficients for the conversion of wet biomass of microorganisms to carbon, are given in papers [2–4].

Species composition of heterotrophic ciliates and infusoria was studied using light and phase-contrast microscopy of nonpreserved samples of ambient water. Detected protists were diagnosed based on morphological features [1, 8, 17, 23].

The variability of studied parameters was assessed by the variation coefficient (C_v). To find correlation dependences between studied parameters, the nonparametric Spearman coefficient of rank correlation was applied.

RESULTS

During the study period in the Sheksna Reservoir, depths (H) at the sampling stations varied from 1.3 m to 9 m (Table 1). Water transparency (Z) changed from 50 cm to 180 cm; on average this value was higher (111 cm) and less variable (C_v = 6.7%) in Lake Beloye compared to the riverine part (99 cm, C_v = 35.7%). The water in the part of the Sheksna River from the riverhead to Siz'menskii reach was less transparent. The water pH values were weakly alkaline: 7.4–8.5 (on average 8.2). Water color was within the limits of 43–76°, values typical for Upper Volga reservoirs in summer time; this value was higher at the riverine part compared to the lacustrine area: on average 70 and 56°, respectively. The concentration of dissolved organic matter varied within the 7.4–10.3 mg C/L (C_v = 8.5%) range and 8.5 and 9.7 mg C/L on average for the lacustrine and riverine parts, respectively. Water electric conductivity fluctuated from 120 to 195 µS/cm (C_v = 16.7%) and on average was higher in the riverine part (163 µS/cm) compared to the lacus-

Table 2. Production of phytoplankton (P_{PHY}) and bacterioplankton (P_{BAC}) and consumption of bacteria by heterotrophic nanoflagellates and their lysis by viruses

No. of sampling station	P_{PHY}		P_{BAC}		Consumption		Lysis	
	mg C/(m^3 day)	mg C/(m^2 day)	mg C/(m^3 day)	mg C/(m^2 day)	10^6 cells/(mL day)	P_{BAC}, %	10^6 cells/(mL day)	P_{BAC}, %
	Belozerskii reach							
1	370	932	135	635	–	–	–	–
2	333	1259	148	296	1.13	14.38	0.29	3.69
3	266	642	170	935	1.42	10.06	1.21	8.57
4	726	1677	233	1165	1.20	12.22	1.03	10.49
5	287	663	245	1225	2.76	22.01	1.08	8.61
6	228	479	132	172	2.83	32.95	0.97	11.29
7	215	542	149	596	1.49	15.39	0.36	3.72
8	232	585	89	490	2.51	55.29	0.68	14.98
9	471	1088	102	510	2.69	42.36	0.95	14.96
10	172	433	97	485	1.88	32.98	0.35	6.14
11	288	605	83	108	1.04	19.73	0.45	8.54
12	167	403	73	329	1.54	31.95	0.18	3.73
13	256	564	119	536	1.20	16.51	0.39	5.36
	Sheksnisnkii reach							
14	689	723	88	352	1.31	20.34	0.55	8.54
15	744	1094	109	600	1.17	23.35	0.27	5.39
16	425	625	102	918	2.46	34.45	0.61	8.54
17	489	822	107	535	1.85	22.02	1.26	15.00
18	163	411	70	315	2.58	50.79	1.13	22.24
19	208	524	127	889	1.07	14.54	2.15	29.21
20	248	729	150	1050	1.38	9.12	–	–
21	388	1141	97	873	1.08	13.88	2.65	34.06

trine one (133 μS/cm). No marked stratification of water column was observed. The temperature (T) of the surface water layer reached 20.3–22.7°C, exceeding the temperature of the near-bottom layer by less than 2.7°C. In the surface layer, the concentration of dissolved oxygen fluctuated from 7.6 to 10.9 mg/L (86–124% of saturation); near the bottom, it fluctuated from 6.7 to 9.7 mg/L (74–108%). Noticeable stratification of the water column was noted only in the deepwater near-dam reach of the reservoir (sampling station 21), where temperature and oxygen content in the surface water layer were higher by 2.7°C and 3.2 mg/L, respectively, while electric conductivity was 16 μS/cm lower than near the bottom.

The values of phytoplankton primary production, both per unit of water volume (P_{PHY}) and per unit of surface area (ΣP_{PHY}), varied considerably over the reservoir area: mean 351 mg C/(m^3 day) (C_v = 56.1%) and 759 mg C/(m^2 day) (C_v = 43.3%) (Table 2). On average, the phytoplankton production was lower in Lake Beloye than at the Sheksninskii part: 301 and 419 mg C/(m^3 day) versus 698 and 759 mg C/(m^2 day), respectively.

The number and biomass of bacterioplankton on average for the reservoir were 7.81 × 10^6 cells/mL (C_v = 21.8%) and 142 mg C/m^3 (C_v = 21.7%), respectively (Table 3). A high number of bacteria (>10^7 cells/mL) was registered in the lacustrine (sampling station 3) and riverine (sampling stations 14 and 16) parts of the reservoir. Minimal values of number and biomass were revealed in the Siz'menskoye reach (sampling station 18). These parameters were almost indistinguishable in a comparison of the lacustrine (mean 7.75 × 10^6 cells/mL and 143 mg C/m^3, respectively) and riverine parts (7.91 × 10^6 cells/mL and 140 mg C/m^3, respectively).

Specific growth rate in bacteria fluctuated from 0.0165 to 0.0590 h^{-1} (mean 0.0373 h^{-1}, C_v = 30.2%). The production of bacterioplankton was high, averaging 125 ± 47 mg C/(m^3 day) or 620 ± 320 mg C/(m^2 · day) (Table 2). Mean production of bacteria per unit of water volume in Lake Beloye was higher than at the Sheksninskii part: 136 and 106 mg C/(m^3 day), respectively; on the other hand, under 1 m^2 was lower: 600 and 691 mg C/(m^2 day), respectively.

Moderate positive correlation (r = 0.381) between production of heterotrophic bacteria and phytoplankton primary production as calculated under 1 m^2 was revealed.

Table 3. Number (N) and biomass (B) of heterotrophic bacterioplankton, picophytoplankton, virioplankton, heterotrophic nanoflagellates, nanophytoplankton and infusoria, and number of species (S) of heterotrophic nanoflagellates and infusoria

No. of sampling station	Bacteriop lankton		Picophytoplankton		Virioplankton		Nanoflagellates			Nanophytoplankton		Infusoria		
	N, 10^6 cells/mL	B, mg C/m^3	N, 10^3 cells/mL	B, mg C/m^3	N, 10^6 cells/mL	B, mg C/m^3	N, 10^6 cells/mL	B, mg C/m^3	S	N, cells/mL	B, mg C/m^3	N, ind./L	B, mg C/m^3	S
	Belozerskii reach													
1	5.27	128	132.9	32.9	16.9	1.69	–	–	8	–	–	1950	7.9	5
2	6.80	128	260.4	64.4	17.7	1.77	1068	14.3	3	534	7.1	1550	13.3	5
3	10.01	129	140.0	32.3	12.7	1.27	854	9	4	1068	15.4	2100	10.1	4
4	7.92	188	74.1	17.1	19.2	1.92	1068	6.7	3	641	9.1	2700	17.2	5
5	8.34	173	129.9	30.0	12.4	1.24	1495	23.4	5	961	23.3	2850	11.7	5
6	10.83	169	218.9	50.6	17.6	1.76	1709	19.2	12	854	20.3	1650	8.3	6
7	7.78	143	137.6	31.8	19.2	1.92	1068	12.8	3	1495	38	2400	12.7	7
8	6.61	137	135.9	31.4	16.6	1.66	1068	34.7	4	641	13.4	1150	9.9	5
9	7.85	126	136.1	31.4	18.8	1.88	1495	31.4	8	534	6.1	3050	15.8	6
10	6.58	112	123.8	28.6	16.0	1.60	1282	8.7	13	641	9.8	1900	9.7	7
11	6.54	124	232.8	53.8	28.9	2.89	1175	9.6	13	748	20.5	2750	16.5	6
12	8.87	184	149.3	34.5	25.1	2.51	214	2.8	11	854	19.3	4150	38.7	5
13	7.39	121	225.3	52.0	30.5	3.05	1282	11.9	1	748	14.3	1250	6.8	5
	Sheksninskii reach													
14	10.18	185	95.9	22.1	30.3	3.03	748	6.8	10	641	30.3	1600	8.8	3
15	7.36	160	140.3	32.4	28.7	2.87	748	6.3	13	641	11.4	1600	10.2	6
16	10.27	151	97.9	22.6	39.3	3.93	1282	16.4	6	320	6.1	1400	14.6	6
17	9.13	176	123.7	28.6	33.1	3.31	961	12.4	6	534	9.7	1900	17.4	5
18	4.94	70	222.8	51.5	42.1	4.21	1602	38.4	5	1495	19.9	1500	20.6	3
19	7.36	127	121.9	28.2	53.3	5.33	1175	13.5	13	961	14	700	3.9	3
20	8.90	150	102.2	23.6	–	–	897	14.1	10	128	1.6	1050	15.2	6
21	5.17	97	80.2	18.5	55.7	5.57	2243	18.7	10	534	8.4	1050	22.6	7

The number of planktic viral particles (N_{VIR}) varied from 12.4 × 10^6 particles/mL in Lake Beloye (sampling station 5) to 55.7 × 10^6 particles/mL near the dam (sampling station 21), averaging 26.7 × 10^6 particles/mL (C_v = 47.6%) (Table 3). The number of virioplankton was higher than of bacterioplankton (N_{VIR}/N_{BAC}) by factors of 1.9–11.0 (mean 4.3). The values of N_{VIR} and N_{VIR}/N_{BAC} at the Sheksninskii reach (mean 40.3 × 10^6 particles/mL and 6.31, respectively) were almost twofold higher than in Lake Beloye (19.7 × 10^6 particles/mL and 3.31, respectively). Weak negative correlations between number of virioplankton and number, size, and biomass of bacterioplankton were revealed; with bacterial production the correlation was moderately negative (r = –0.319). The weak interrelations between bacteria and viruses may be explained by the fact that the virioplankton includes the viruses infecting not only bacteria, but other hydrobionts as well. As for the abiotic parameters, the number of virioplankton significantly negatively correlated with the concentration of dissolved oxygen (r = –0.559, $p < 0.05$) and positively with the content of dissolved organic matter (r = 0.718), color (r = 0.728), and water electric conductivity (r = 0.475).

For the whole reservoir, the number of picophytoplankton averaged 147 × 10^3 cells/m (C_v = 36.2%); biomass was 34.2 mg C/m^3 (C_v = 37.3%) (Table 3). Maximal number and biomass were registered in Lake Beloye opposite the Kema River mouth (sampling station 2). At the Bellozerskii part these parameters (mean 155 × 10^3 cells/m and 35.8 mg C/m^3) were higher than at the Sheksninskii part (mean 123 × 10^3 cells/mL and 28.4 mg C/m^3).

The contribution of photosynthesizing organisms to total picoplankton biomass averaged 19.9%, reaching the maximum in the Siz'menskii reach (sampling station 18), where the number and biomass of heterotrophic bacteria were minimal. A weak negative correlation between structural–functional parameters of phototrophic and heterotrophic components of picoplankton was observed.

The number of nanophytoplankton varied from 128 to 1495 cells/mL (mean 749 cells/mL, C_v = 44.8%); biomass varied from 1.6 to 38.0 mg C/m^3 (mean 14.9 mg C/m^3, C_v = 59.3%) (Table 3). Maximal values of these parameters were registered at the eastern part of Lake Beloye (sampling station 7). In addition, a high number of nanophytoplankton was noted at the Siz'menskii reach (sampling station 18), but at this site its biomass was approximately twofold lower (19.9 mg C/m^3) than at sampling station 7. The minimal number of phototrophic nanoplankton was registered at the Sheksninskii part (sampling station 20). The number and biomass of nanophytoplankton were on average 1.3–1.4 times higher at the lacustrine part than at the riverine sites. Moderate positive correlations between quantitative parameters of picoplankton and nanophytoplankton were revealed. The biomass of picophytoplankton was higher than of nanophytoplankton over most of the reservoir area.

In total, 34 species of 15 large taxa of heterotrophic nanoflagellates were identified in the reservoir water column. The highest species diversity was a characteristic of orders Kinetoplastida (seven species) and Chrysomonadida (six species). The following species occurred most often: *Bodo designis* Skuja, 1948 (found in 90.5% samples), *Paraphysomonas imperforata* Lucas, 1967 (85.7%), *Spumella* sp. 1 (57.1%), *Codosiga botritis* Kent, 1880 (52.4%), and *Salpingoeca minor* Dangeard, 1910 (47.6%). The highest number of nanoflagellate species (13) was registered at sampling stations 10 and 11, situated at the southwestern part of Lake Beloye and at the sampling stations 15 and 19 at the Sheksninskii part (Table 3). Only one species of flagellates was found in Lake Beloye opposite the River Sheksna headwater (sampling station 13).

The majority of heterotrophic flagellates found are bacteriotrophes. There were identified five species of predatory flagellates feeding on other flagellates: *Phyllomitus apiculatus* Skuja, 1948, *Colpodella angusta* (Dujardin, 1841) Simpson et Patterson, 1996, *Kathablepharis ovalis* Skuja, 1948, *Aulocomonas hyalina* Skuja, 1956, and *Colponema loxodex* Stein, 1878.

Heterotrophic nanoflagellates are distributed over the reservoir area unevenly: maximal and minimal values of their number and biomass differed by factors of 10.5 and 13.7, respectively (Table 3). Maximal values of these parameters were noted at the center of Lake Beloye (sampling station 8) and Siz'menskii reach (sampling station 18); minimal values were at the southern part of the lake, opposite Belozersk (sampling station 12). The number and biomass of flagellates averaged 1172 ± 423 cells/mL and 38.4 ± 15.6 mg C/m^3, respectively.

In summer time, the species composition of infusoria in the reservoir was uniform. Only 15 species belonging to four classes were identified: Spirotrichea (6 species), Litostomatea (4), Prostomatea (4), and Oligohymenophorea (1). Three to seven species of infusoria were found in the samples (Table 3). The highest number of species was found in Lake Beloye (sampling stations 7 and 10) and near the dam (sampling station 21); the lowest number was found at the Sheksna River headwater (sampling station 14) and at Siz'menskii reach (sampling stations 18 and 19). The most widespread were the representatives of class Spirotrichea: *Tintinnidium fluviatile*, *Codonella cratera*, *Strombidium viride*, *St. pelagica*, and *Strobilidium velox*.

The number of infusoria varied from 700 to 4150 ind./L (mean 1917 ind./L, C_v = 43.0%); the biomass varied from 3.9 to 38.7 mg C/m^3 (mean 13.9 mg C/m^3, C_v = 53.0%) (Table 3). Maximal values of these parameters were registered in the lake near Belozersk (sampling station 12); minimal values were at

Siz'menskii reach near the Kovzha River inflow (sampling station 19). The number of infusoria in Lake Beloye was on average higher by a factor of 1.7 than at the Sheksninskii part, but the biomass values at both of these parts were approximately similar to each other: 14.3 and 14.2 mg C/m^3, respectively.

The ratio of the number of bacterioplankton to the number of heterotrophic nanoflagellates is a parameter characterizing the interrelations of these two groups of microorganisms. The value of this parameter varied from 2305 to 41449 (mean 8830 ± 8148). The maximal value was noted at the southern part of Lake Beloye near Belozersk (sampling station 12), where the number of nanoflagellates was minimal; at the lacustrine part the value was higher than at the riverine part: on average 9790 and 7817, respectively.

In the reservoir, heterotrophic nanoflagellates consumed bacteria at a rate of $(1.04–2.83) \times 10^6$ (mean 1.75×10^6) cells/(mL day), i.e., 9.1–55.3% (mean 24.7%) of daily production of heterotrophic bacterioplankton (Table 2). During the study period over the whole reservoir area, the rate of consumption of bacteria by flagellates was lower than their production. The strongest effect of protists upon bacterioplankton was registered in the center of Lake Beloye (sampling station 8) and at Siz'menskii reach (sampling station 18), where they consumed more than a half of bacterial production.

The viruses–bacteriophages lysed per day was $(0.18–2.65) \times 10^6$ (mean 0.87 ± 0.15) cells/mL, or 3.7–34.1% (mean 11.7 ± 8.5%) of the daily production of heterotrophic bacterioplankton (Table 2). The number of bacteria dying out because of viral lysis differed considerably at various parts of the reservoir (C_v = 74.3%). The share of bacterial production lysed by viruses was about twofold higher at the Sheksninskii part than at the Belozerskii part: 17.6 and 8.8%, respectively.

Total biomass of planktic microorganisms varied from 170 to 282 (mean 221 mg C/m^3) (C_v = 14.4%). It reached maximal value in Lake Beloye near Belozersk (sampling station 12) and on average was slightly higher in the lake than at the Sheksninskii part: 231 and 214 mg C/m^3, respectively. Heterotrophic bacteria were the main component of the microbial community, comprising 34.2–78.3% (mean 63.9%) of the biomass of the latter. Phototrophic picoplankton was the second in importance, with the contribution to the formation of total microbial biomass ranging 7.1–28.1% (mean 15.6%). Phototrophic nanoplankton, heterotrophic nanoflagellates, and infusoria contributed 6.53, 7.14, and 6.28% to the total plankton biomass, respectively. The contribution of viruses was minimal: 1.25%.

DISCUSSION

Relatively high values of number, biomass, specific growth rate, and production of heterotrophic bacterioplankton in the Sheksna Reservoir indicate intensive production–destruction processes. The use of the value of efficiency of bacterioplankton growth in the neighboring Rybinsk Reservoir [6] made it possible to calculate that daily demand of the Sheksna Reservoir bacterioplankton for substrates varied from 233 to 817 (mean 417 ± 155) mg $C/(m^3$ day). That is, at the processes of production and respiration, bacteria consumed per day was 2.3–10.1% (mean 4.7 ± 2.12%) of the dissolved organic matter.

The number of bacterioplankton was higher than the number of heterotrophic nanoflagellates on average by a factor of 8830, indicating favorable trophic conditions for these protists, for which bacteria serve as a main food. A weak negative correlation between numbers of bacterioplankton and nanoflagellates was revealed; the correlation between their biomasses was moderate. Between the number of bacterioplankton and sizes and biomass of nanoflagellates, the correlation was significant: $r = -0.457$ and $r = -0.484$, respectively, at $p < 0.05$. The negative correlation between quantitative parameters of bacteria and flagellates means the presence of control of bacteria by these protists. In addition to bacteria, nanoflagellates may use other sources of food, such as phototrophic picoplankton and dissolved organic substrates. However, between the latter parameters and quantitative characteristics of flagellates, mainly only weak positive correlations were revealed.

It was shown earlier [2] that, in the Upper Volga reservoirs, picoplankton reaches the maximal quantitative development in the second half of summer, when it becomes a substantial component of phytoplankton. During the study period in the Sheksna Reservoir, we registered high values of number and biomass of phototrophic picoplankton; between these parameters and plankton primary production, weak negative correlations ($r = -0.364$ and -0.348, respectively) were revealed. These findings support the earlier revealed trend on the important role of organisms with sizes from to 2 μm in the oligotrophic waters and the increase in this role in the gradient of trophy [16]. It should be taken into the account that, as opposed to the number of heterotrophic bacteria, the number of picophytoplankton is subject to considerable seasonal variations and in various seasons the difference may be as high as three orders. During certain periods, the picophytoplankton comprises a considerable part of the ration for such protists as heterotrophic and mixotrophic flagellates and infusoria.

In the Sheksna Reservoir, the mortality of heterotrophic bacterioplankton due to consumption by heterotrophic flagellates and lysis by viruses comprised 18.1–73.0% (mean 37.3%) of its daily production. Presumably, cladocerans, rotifers, infusoria, mixotrophic flagellates, etc., consumed the rest of bacterial production. At the largest part (90%) of the studied reservoir, consumption of bacteria by flagellates exceeded the virus-induced mortality of bacteria. It was shown that, in the various types of aquatic ecosystems, in various seasons, heterotrophic nanoflagellates and viruses jointly utilize from 22 to 129% of daily production and, like in the Sheksna Reservoir, the mortality of bacteria due to consumption by flagellates usually surpasses their lysis by viruses [4, 15, 18, 20, 24].

In the Sheksna Reservoir, viruses lyse on average 15.5 ± 6.3% of the daily production of picocyanobacteria [5]. During the process of consumption of bacteria by flagellates and their lysis by phages, the remineralization of nutrients, first, of phosphorus, takes place. The latter usually limits the development of freshwater phytoplankton. By that means, protists and viruses accelerate the cycling of nutrients and stimulate photosynthesis of plankton [19, 21]. In the Sheksna Reservoir, the nutrients and illumination are the main factors limiting the photosynthesis rate during the period of maximal development of phytoplankton [13].

The published data on the chlorophyll content and zooplankton biomass in the Sheksna Reservoir [7] enables us to calculate the total biomass of planktonic community and assess the contribution of various groups of hydrobionts to its formation. The plankton biomass in Lake Beloye averaged 537 mg C/m^3; at the Sheksna part it was 479 mg C/m^3. The differences were inconsiderable. No substantial differences in the structures of planktonic communities between lacustrine and riverine parts were revealed. Microorganisms contributed to 26.2–64.3% (mean 45.5%) of the total biomass of plankton in the reservoir. Their share surpassed half of the biomass of the planktic community at one-third of the studied areas. Phytoplankton made the greatest contribution to the formation of the total biomass of planktic community: 39.2% on average. The contribution of heterotrophic bacterioplankton averaged 28.6%, but at some sites (sampling stations 11, 12, and 16) the biomass of bacterioplankton and its share in the total plankton biomass were higher than that of phytoplankton. Heterotrophic flagellates and infusoria made rather small and approximately equal to each other contributions to the formation of the biomass of planktic community: mean 3.3% and 2.9%, respectively. At the majority of reservoir sites, the biomass of protists was lower than the biomass of multicellular zooplankton. Only in the water of two sites (sampling station 2 near the Kema River inflow and sampling station 18 in the Siz'menskii reach) was an opposite phenomenon observed. On average, protists and zooplankton contributed to 6.3 and 5.2% of the total biomass of the planktic community, respectively.

In general, the structure of summer planktic community in the Sheksna Reservoir was similar to that in other Volga reservoirs situated to the south. In most of these reservoirs, the phytoplankton makes the main contribution to the formation of total biomass of plankton. Heterotrophic bacteria with biomass usually surpassing the biomass of zooplankton are the second component of plankton in terms of contribution [2].

The values of primary production of plankton revealed in the Sheksna Reservoir correspond to the waters of mesotrophic and eutrophic types [11]. The ratio of integral values of production of heterotrophic bacterioplankton to phytoplankton primary production was high, at some sites being >1 (Table 2). For the whole reservoir, this ratio averaged 0.88, being lower in Lake Beloye (0.83) than at the Sheksninskii part (0.98). This indicates that, for bacteria in the Sheksna Reservoir, like in other Volga reservoirs [12], substrates (first the allochthonous ones) other than phytoplankton photosynthesis are important. It was observed that phytoplankton primary production exceeded the production of heterotrophic bacteria at the shallow sites occupying a considerable part of the Sheksna Reservoir. On the contrary, at the deepwater sites the bacterial production was higher. A positive correlation ($r = 0.587$) between the depth of the reservoir and the ratio of integral values of production of bacterioplankton and phytoplankton was revealed.

According to N.M. Mineeva [10, 11], the destruction of organic matter under 1 m^2 of the Sheksna Reservoir surface, occurring during vegetation period mainly due to the activity of heterotrophic bacteria, exceeds plankton primary production by 1.3–2.3 times. The prevailing of destruction over the production, i.e., the negative direction of the balance of organic matter, is a characteristic of the whole cascade of Volga reservoirs.

Over the reservoir area, the ratio of biomass of heterotrophic (bacteria, protists, and zooplankton) to biomass of autotrophic (phytoplankton) organisms ((H/A) varied from 0.63 to 2.72 (mean 1.38). The biomass of heterotrophs was higher than of biomass autotrophs at the majority of sites: at 8 out of 13 sampling stations at the lacustrine part and at 7 out of 8 in the riverine part. A trend to decrease in H/A values with increase in plankton primary production ($r = -0.435$, $p < 0.05$) was revealed; i.e., at the less productive sites of the reservoir, the contribution of heterotrophic organisms to the formation of plankton biomass was higher.

The data presented here demonstrate that the Sheksna Reservoir is a heterotrophic system in the functioning of which bacteria utilizing allochthonous substrates along with autochthonous ones and transferring the carbon of these substrates to higher levels play an important role. Thus, the bacterioplankton particularly serves as a base of the reservoir food webs running functions similar to the functions of phytoplankton.

CONCLUSIONS

Phytoplanton makes the main contribution to the formation of the biomass of summer plankton in the Sheksna Reservoir. Heterotrophic bacteria are the second component in terms of importance. At most reservoir sites, the biomass of multicellular plankton was higher than the biomass of heterotrophic flagellates and infusoria. The production of heterotrophic bacterioplankton as calculated under 1 m^2 of the reservoir surface was only slightly lower than the phytoplankton primary production. This indicates that the Sheksna Reservoir is a heterotrophic system in the functioning of which heterotrophic bacteria involving the carbon of allochthonous organic matter to the food web play an important role. Heterotrophic flagellates and viruses utilized on average 37.3% of bacterial production. The consumption of bacteria by flagellates exceeded the virus-induced mortality of the former. The results presented here indicate the important role of microorganisms in the structural–functional organization, production–destruction processes, and self-purification of the Sheksna Reservoir.

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