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ZOOPLANKTON, ZOOBENTHOS, AND ZOOPERIPHYTON

Seasonal and Annual Variation of Virioplankton Abundance in Rivers Running through an Industrial City (City of Cherepovets, Upper Volga)

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Abstract—In April to October 2009–2011, the species composition and seasonal changes in abundance and biomass of heterotrophic nanoflagellates were studied in the Sheksna River and in the small Yagorba and Serovka rivers running through a large industrial center. A total of 48 species and forms of colorless flagellates were recorded in the rivers. The abundance and biomass of heterotrophic nanoflagellates (average for 3 years) were 5788 cells/mL and 251.5 mg/m^3, correspondingly, in the Yagorba River; 6164 cells/mL and 266.2 mg/m^3 in the Serovka River; and 4450 cells/mL and 193.5 mg/m^3, correspondingly, in the littoral zone of the Sheksna River. The maximal values (10.1–11.6 thousand cells/mL and 591–654 mg/m^3) were more frequently recorded in the second half of summer. A high positive correlation was observed between the biomass of single bacterial cells and heterotrophic nanoflagellates. In 2010, in all rivers with extremely high water temperatures, the abundance and biomass of heterotrophic nanoflagellates in summer was significantly higher than in other years.

Keywords: heterotrophic nanoflagellates, species composition, abundance, biomass, small rivers

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INTRODUCTION

Heterotrophic nanoflagellates (HNFs) are an important structural component in planktonic communities. They play a critical role in the functioning of the pelagic trophic webs of aquatic ecosystems [5]. In many fresh waterbodies, heterotrophic nanoflagellates are the main consumers of planktonic bacteria; sometimes they graze all daily production of bacterioplankton [5]. Bacteriotrophic nanoflagellates play a crucial role in the absorption and elimination of pathogenic microorganisms which enter natural aquatic environments with wastewaters [11]. The quantitative distribution of HNFs and their role in the functioning of planktonic communities in rivers, especially in small rivers, compared to lakes and reservoirs has been studied to a lesser degree [6, 7, 9, 13, 18]. Small rivers running through large industrial centers are the most polluted water objects in the Upper Volga region [12]. They include watercourses within the precincts of a large industrial center (Cherepovets). These rivers are subjected to the long-term impact of municipal and industrial wastewaters. The results of the previous studies indicated excessive amounts of different organic compounds entering the rivers and negative changes in the structure and functioning of planktonic and benthic communities [2, 3].

The aim of this study is to study the species composition, dynamics of abundance, and biomass of HNFs and determine the factors responsible for their development in rivers flowing within the boundaries of Cherepovets.

MATERIALS AND METHODS

This study was conducted in April to October 2009– 2011. Water samples were collected at three stations: in the small Serovka River, in the small Yagorba River (which receives water from the Serovka River), and at the station in the littoral of the large Sheksna River (which receives water from the Yagorba River). The depth at stations was 1 m. Water samples for a quantitative calculation of HNFs were fixed immediately after sampling in glutaraldehyde to a final concentration of 2% and kept in the dark at 4°C for <1 month.

The species composition of HNFs was determined in live water samples using phase-contrast microscopy. The abundance of heterotrophic nanoflagellates was estimated by epifluorescence microscopy using DAPI stain and black nuclear filters with a pore diameter of

0.2 μm (Nuclepore) [20]. The abundance and biomass of different groups of bacteria: solitary, aggregated (bacteria associated with suspended particles or in microcolonies), and filamentous were determined. The samples were examined under a ×1000 Olympus BX51 epifluorescence microscope (Japan) equipped with an image-analysis system.

The specific growth rate of bacteria (μ, h^{-1}) was determined in experiments using eukaryotic antibiotic (thiram) [19]. The final concentration of the antibiotic in water samples was 2 mg/L. The μ value for solitary and aggregated bacteria was calculated by changes in the cell abundance and for filamentous bacteria by changes in their biomass. The bacterial production was calculated as the product of μ and biomass.

Assuming that a heterotrophic nanoflagellate clarifies a water volume equal to 10^5 of its body volume at 20°C in 1 h [17], approximate grazing rates of natural populations of HNFs on solitary bacteria were calculated. We made temperature corrections $h(T)$ in our calculations [4]:

$$h(T) = Q_{10}^{0.10(T-20)},$$

where T is the current temperature and Q_{10} is the temperature coefficient (the van't Hoff factor), which represents the factor by which the rate of process increases for every 10°C rise in temperature. The Q_{10} coefficient was equal to 2.25 [1].

Spearman's rank correlation coefficient was used to determine the relationship between parameters at the significance level 0.05.

RESULTS

High concentrations of planktonic bacteria were recorded in the rivers under study. In April to October 2009–2011, the total abundance of bacterioplankton (N_B) ranged within (5.9–33.8) × 10^6 cells/mL (on average 18.8 × 10^6 cells/mL for three years) in the Serovka River, (6.7–51.6) × 10^6 cells/mL (on average 18.7 × 10^6 cells/mL) in the Yagorba River, and (4.7–36.5) × 10^6 cells/mL (on average 15.8 × 10^6 cells/mL) in the Shekna River.

Solitary cells prevailed in the total abundance of bacterioplankton in all rivers. During a 3-year period of studies, solitary cells averaged 86.4–87.9% of N_B; the portion of aggregated bacterial cells and filamentous bacteria was 12.0–13.2% and 0.1–0.4% of N_B, respectively.

The total biomass of bacterioplankton (B_B) was significantly greater in small rivers than in the Sheksna River due to the larger size of bacterial cells (Table 1). The biomass of solitary bacteria (B_{sol}) provided the main portion of the total biomass of bacterioplankton and was 62.9 ± 11.1% on average for 3 years in the Serovka River, 76.2 ± 5.5% in the Yagorba River, and 80.6 ± 3.4% in the Sheksna River. The biomass of filamentous bacteria was significantly higher in the small rivers than in the Sheksna River, and the biomass of aggregated bacterial cells in the Serovka River exceeded their biomass in the Yagorba and Sheksna rivers. The portion of filamentous bacteria averaged 21 ± 8.4, 12.0 ± 4.4, and 5.3 ± 0.4%; that of aggregated bacteria was 16.1 ± 3.2, 11.8 ± 5.4, and 14.1 ± 3.9%, respectively in B_B for 3 years.

The ratio of biomass of different groups of bacteria and their contribution to the total biomass varied during the period under study. Solitary bacteria were more often the main component of B_B. However, the portion of filamentous bacteria in B_B was 91.1% (August 28, 2010) and the portion of aggregated bacteria reached 33.2% (September 15, 2009) in the Serovka River and 43.3 (June 16, 2011) and 59.0% (July 15, 2009), respectively, in the Yagorba River. The maximal contribution of aggregated and filamentous bacteria to the formation of B_B was 50.1% (August 7, 2009) and 19.3% (October 14, 2009), respectively. Thus, planktonic bacterial communities in small urban rivers differ from their communities in the Sheksna River in higher values of filamentous biomass and their contribution to the total biomass of bacterioplankton. A total of 48 species and forms of HNFs belonging to 12 orders were detected in the rivers under study (Table 2). The maximal number of HNF species was recorded in the Sheksna River (34) and the minimal number of species was recorded in the Serovka River (26). Twenty-eight species were found in the Yagorba River. The diversity of colorless flagellates was formed by the representatives of the orders Craspedida (Choanaflagellates), Kinetoplastida, and Chrysomonadida. However, some differences were observed in the distribution of HNFs in the rivers. A total of 14 species (29% of the total species composition) were recorded in all rivers. Some species and forms of flagellates were found only in one river. Six species were recorded in the Serovka River and six species in the Yagorba River; seven species were recorded in the Sheksna River. Most flagellate species belong to bacteriodetritophages. Five predatory species (*Phyllomitus apiculatus*, *Allantion tachyploon*, *Colponema loxodes*, *Kathablepharis ovalis*, and *Kathablepharis* sp.) and three omnivorous species (*Paraphysomonas imperforate*, *P. vestita*, and *Goniomonas truncate*) were identified [22].

From April to October the abundance and biomass of HNFs at the river stations varied significantly (Figs. 1, 2; Table 3). The maximal and minimal values of abundance (N_F) and biomass (B_F) differed 2.1–5.4 and 5.2–13.8 times in the Serovka River; 2.2–6.8 and 2.5–7.0 times in the Yagorba River; and 3.7–5.8 and 3.2–11.5 times, respectively, in the Sheksna River. The average cell volume of colorless flagellates varied from 19 to 113 μm^3. The seasonal dynamics of HNF concentrations differed between small rivers and the Sheksna River and in one river in different years. In the Serovka and Yagorba rivers, relatively high concentrations of HNF in the first half of April were followed by

Table 1. Total biomass of bacterioplankton (ΣB) and biomass of solitary bacteria (B_{sol}), aggregated bacteria (B_{ag}), and filamentous bacteria (B_f) in rivers, mg/m^3

Parameter	2009	2010	2011	Average for 3 years
		Serovka R.		
T, °C	1.0–24.0 / 12.1 ± 2.7	2.0–26.0 / 15.1 ± 2.7	2.0–21.0 / 12.3 ± 2.1	13.2 ± 1.0
ΣB	959–12805 / 3323 ± 1227	1393–26993 / 7370 ± 2362	1784–13798 / 3978 ± 1263	4890 ± 1254
B_{sol}	832–10500 / 2664 ± 1023	970–6660 / 3105 ± 691	1030–6630 / 2642 ± 548	2803 ±151
B_{ag}	83–2229 / 452 ± 228	24–12237 / 1660 ± 1097	16–1571 / 488 ± 153	867 ± 397
B_f	1–877 / 207 ± 90	21–24582 / 2605 ± 2203	72–5597 / 848 ± 597	1220 ± 717
		Yagorba R.		
T, °C	1.0–24.0 / 11.7 ± 5.5	6.0–27.0 / 15.6 ± 2.5	2.0–22.0 / 12.5 ± 2.2	13.3 ± 1.2
ΣB	1091–4088 / 2622 ± 354	1282–21962 / 4398 ± 1798	1441–6641 / 3361 ± 576	3460 ± 515
B_{sol}	922–3255 / 1829 ± 261	1100–20085 / 3837 ± 1706	1125–3658 / 2411 ± 327	2692 ± 596
B_{ag}	43–2412 / 592 ± 243	14–1172 / 235 ± 101	45–683 / 248 ± 72	358 ± 117
B_f	5–477 / 201 ± 61	37–995 / 326 ± 105	36–2877 / 702 ± 318	410 ± 150
		Sheksna R.		
T, °C	1.0–22.0 / 11.2 ± 2.4	4.0–26.0 / 15.7 ± 2.4	2.0–0.0 / 11.6 ± 2.1	12.8 ± 1.4
ΣB	667–3779 / 1938 ± 386	336–6497 / 2889 ± 547	981–3079 / 1915 ± 275	2247 ± 321
B_{sol}	583–3282 / 1431 ± 281	336–6159 / 2461 ± 513	799–2905 / 1584 ± 247	1825 ± 321
B_{ag}	22–1862 / 421 ± 191	0–953 / 257 ± 88	74–616 / 225 ± 63	301 ± 61
B_f	4–373 / 86 ± 44	0–1016 / 171 ± 91	14–231 / 106 ± 25	121 ± 26

Here and in Tables 3 and 5: minimal and maximal values are above the line; the average value ± error of mean is under the line.

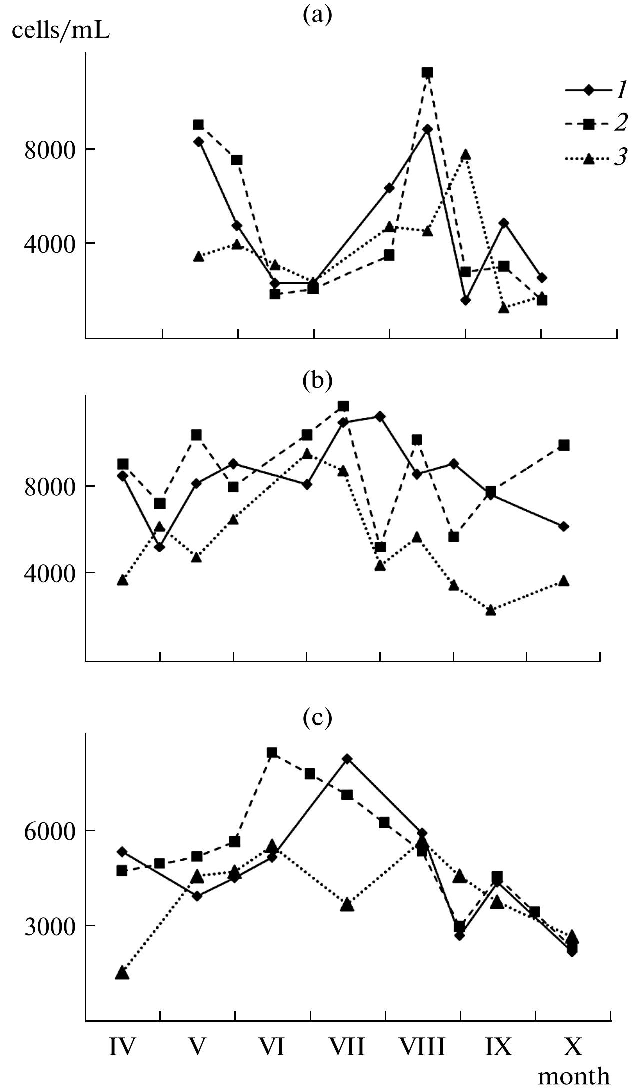

Fig. 1. Seasonal changes in abundance (cells/mL) of heterotrophic nanoflagellates in (*1*) Serovka, (*2*) Yagorba, and (*3*) Sheksna rivers in (a) 2009, (b) 2010, and (c) 2011.

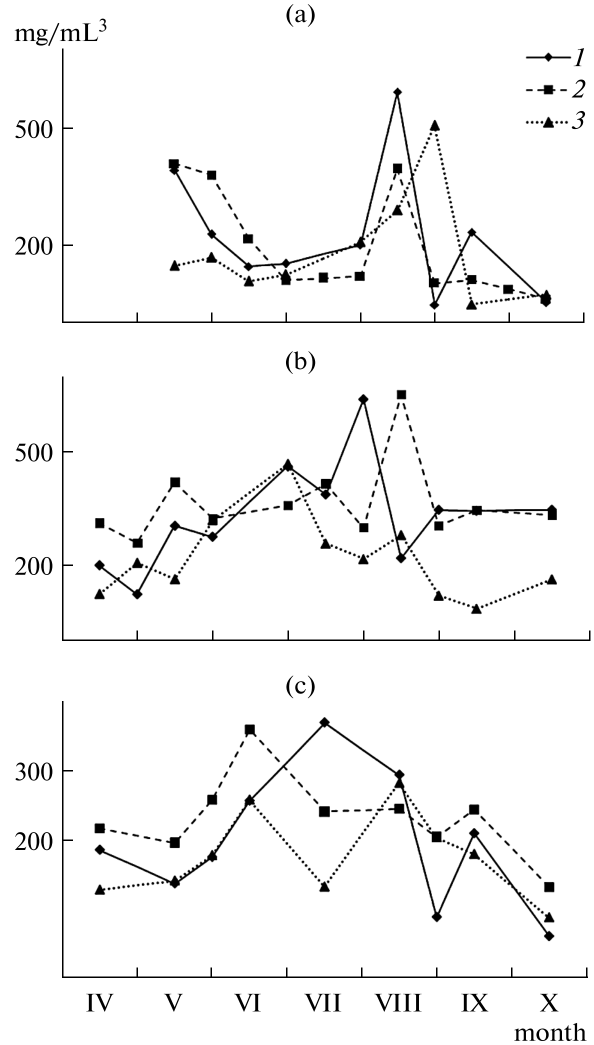

Fig. 2. Seasonal changes in biomass (mg/m^3) of heterotrophic nanoflagellates in (*1*) Serovka, (*2*) Yagorba, and (*3*) Sheksna rivers in (a) 2009, (b) 2010, and (c) 2011.

their decrease in the first half of May and an increase in the second half of May and the beginning of July. In summer the maximal values of N_F and B_F were observed in August 2009, at the end of July–August 2010, and in June (Yagorba River) and July (Serovka River). In autumn the abundance of HNF increased greatly in the Serovka River in 2009 and 2011 and in the Yagorba River in 2010 and 2011. In the Sheksna River, HNF concentrations gradually increased from spring to summer. The maximal values of N_F and B_F were recorded at the beginning of September 2009, at the beginning of July 2010, and in June and August 2011. In autumn the abundance of HNFs did not increase significantly.

In all rivers, the values of the N_B/N_F, B_F/B_B, and B_F/B_{sol} ratios varied within a wide range, but on average during a 3-year period they did not differ significantly (Table 3). High values of the B_F/B_{sol} ratio (37–38%) indicated a critical role of GNF in controlling the biomass of solitary bacteria during these years. A moderate positive correlation was found between the abundance (biomass) of HNFs and water temperature. The coefficient of correlation (R) was 0.37 and 0.40 in the Serovka River; 0.32 and 0.44 in the Yagorba River; and 0.49 and 0.35, respectively, in the Sheksna River. A higher positive correlation was found between the total abundance of bacterioplankton and the abundance of HNF: $R = 0.63$ in the Serovka River, 0.65 in the Yagorba River, and 0.74 in the Sheksna River. At the same time, a high positive correlation was found only between biomass of HNFs and solitary bacteria and less correlation was found between the biomass of

Table 2. Species composition of heterotrophic flagellates in rivers

Species	Rivers		
	Serovka	Yagorba	Sheksna
Choanoflagellida Kent, 1880			
Monosiga ovata Kent, 1880	+	–	+
M. sp.	–	–	+
Codonosiga botrytis Kent, 1880	+	+	+
C. sp.	–	–	+
Salpingoeca minuta Kent, 1880	–	–	+
S. napiformis Kent, 1880	–	+	–
S. pixidium Kent, 1880	–	+	–
Lagenoeca ruttneri Bourrelly, 1952	–	+	–
Bicosoecida Clark, 1868			
Bicosoeca exilis Penard, 1921	–	+	+
B. lacustris (Clark) Skuja, 1948	–	+	+
B. petiolata (Stein) Bourrelly, 1951	–	–	+
Bicosoeca sp.	–	+	–
Kinetoplastida Honigberg, 1963			
Bodo designis Skuja, 1948	+	+	+
B. minimus Klebs, 1893	+	+	+
B. saltans Ehrenberg, 1832	+	–	+
B. saliens Larsen et Patterson, 1990	+	–	–
B. ovatus (Duj.) Stein, 1878	+	–	+
B. rostratus (Kent) Klebs, 1893	–	–	+
Parabodo nitrophilus Skuja, 1948	+	–	–
Rhynchomonas nasuta (Stokes) Klebs, 1893	+	+	+
Phyllomitus apiculatus Skuja, 1948	+	+	+
Euglenida Bütschli, 1884			
Entosiphon sulcatum Stein, 1878	+	–	–
Petalomonas pusilla Skuja, 1948	+	+	+
P. minuta Hollande, 1942	+	–	–
P. steini Klebs, 1893	–	–	+
Chrysomonadida Engler, 1898			
Anthophysa vegetans (O.F. M.) Stein, 1878	–	+	+
Siphomonas fritschii Pringcheim, 1946	+	+	–
Spumella major Skuja, 1956	+	–	+
S. vivipara (Ehrenb.) Pascher, 1912	+	+	+
S. cylindrica Skuja, 1956	+	+	+
S. sp. 1	+	+	+
S. sp. 2	–	+	+
S. sp. 3	–	+	+
Paraphysomonas imperforata Lucas, 1967	+	+	+
P. vestita (Stokes) De Saedeleer, 1929	+	+	+
P. sp.	–	+	–

Table 2. (Contd.)

Species	Rivers		
	Serovka	Yagorba	Sheksna
Cryptomonadida Senn, 1900			
Goniomonas truncata (Fresenius) Stein, 1887	+	+	+
Ciliophryida Febvre-Chevalier, 1985			
Actinomonas mirabilis Kent, 1880	+	–	–
Cercomonadida Poche, 1913, emend. Vickerman, 1983, emend. Mylnikov, 1986			
Allantion tachyploon Sandon, 1924	+	–	–
Cercomonas longicauda Dujardin, 1841		–	+
Heteromita minima (Hollande, 1942) Mylnikov et Karpov, 2004	+	–	+
H. reniformis (Zhukov, 1978) Mylnikov et Karpov, 2004	+	+	+
Protaspis simplex Vørs, 1992	–	+	+
Thaumatomonadida Shirkina, 1987			
Thaumatomonas seravini Mylnikov and Karpov, 1993	–	–	+
Ancyromonadida Cavalier-Smith, 1997			
Ancyromonas sigmoides Kent, 1880	+	+	+
Colponemida Cavalier-Smith, 1993			
Colponema loxodes Stein, 1878	–	+	–
Kathablepharida Cavalier-Smith, 1993			
Kathablepharis ovalis Skuja, 1948	–	+	–
K. sp.	–	–	+
Total	26	28	34

(+) Absence of species; (–) presence of species.

HNF and aggregated bacteria (Table 4). No correlation was found between the biomass of HNF and filamentous bacteria.

Values of abundance and biomass of HNF averaged for a 3-year period were 1.3 times higher in small rivers than at the littoral station in the Sheksna River (Table 3). Values of N_B/N_F, B_F/B_B, and B_F/B_{sol} ratios did not differ significantly. The biomass of HNF averaged for 3 years was <10% of the biomass of solitary bacterial cells (B_{sol}), which were their main food objects. The B_F/B_B ratio was 1.6 times lower than the B_F/B_{sol} ratio in the Serovka River and 1.3 lower than in other rivers (Table 3).

In summer 2010, when water temperature in the surface layer reached 26–27°C, values of the total abundance and biomass of HNF at all stations were 1.7–1.8 and 1.5–1.8 times higher in small rivers and 1.3–1.2 times higher, respectively, in the Sheksna River than in 2009 and 2011 (Table 3).

DISCUSSION

The maximal values of the abundance of plankton HNF ((8.2–11.1) × 10^3 cells/mL) in the small urban Serovka and Yagorba rivers were within the range of maximal values (N_F ((7.5–38.0) × 10^3 cells/mL) recorded in the Dunabe River and some rivers of North America and were higher the maximal values ((2.5–6.0) × 10^3 cells/mL) in small rivers flowing in the rural area of the region [9, 10]. The analysis of the dynamics of abundance and biomass of HNF from April to October in the rivers under study demonstrated that changes in these parameters depended to a greater degree on the parameters of bacterioplankton than on variations in water temperature. In spring and autumn, the abundance of HNF reached 8–10 thousand cells/mL at water temperature 4–11°C in small rivers. Apparently, the main reason for the high abundance of HNFs (under favorable trophic conditions) was the absence of grazing by large infusoria, cladocerans, and rotifers on these protozoans. Thus, in the Rybinsk Reservoir, grazing of heterotrophic nanoflagellates by nonpredatory metazoan zooplankton in summer was on average 7–9 times higher than in spring and autumn [8]. Apparently, the pattern of the seasonal dynamics of HNFs in rivers greatly depends on the intensity of their grazing by consumers.

In 2010 (a year with anomalously high summer temperature of water), values of bacterioplankton and its main consumers of heterotrophic nanoflagellates were higher than in years with a temperature regime

Table 3. Abundance (N_F, cells/mL) and biomass (B_F, mg/m^3) of planktonic heterotrophic nanoflagellates in the rivers

Parameter	2009	2010	2011	Average for 3 years
		Serovka R.		
N_F	1648–8826 / 4677 ± 894	5181–11094 / 8018 ± 778	2155–8198 / 4670 ± 596	5788 ± 1115
N_B/N_F	1706–6842 / 3194 ± 532	1039–4044 / 2708 ± 276	2523–5920 / 4262 ± 321	3388 ± 459
B_F	42.8–591.3 / 223.8 ± 57.6	124.3–643.4 / 3338 ± 42	60.3–368.9 / 196.8 ± 32.7	251.5 ± 41.9
$B_F/\Sigma B$, %	1.6–23.4 / 6.7 ± 2.3	0.8–25.0 / 4.5 ± 2.1	2.1–11.4 / 5.1 ± 1.0	5.4 ± 0.6
B_F/B_{sol}, %	3.8–26.5 / 8.4 ± 2.6	4.8–37.2 / 10.8 ± 3.2	2.7–12.6 / 7.6 ± 1.1	8.9 ± 1.0
		Yagorba R.		
N_F	1648–11217 / 4761 ± 1182	5181–11583 / 8581 ± 686	2298–8368 / 5150 ± 670	6164 ± 1214
N_B/N_F	1238–5564 / 2802 ± 512	1743–4458 / 2695 ± 238	2809–4764 / 3824 ± 233	3107 ± 360
B_F	57.7–406.3 / 208.3 ± 47.9	260.3–654.2 / 366.0 ± 32.5	131.0–358.7 / 224.3 ± 21.2	266.2 ± 50.2
$B_F/\Sigma B$, %	2.6–19.1 / 7.9 ± 1.8	3.0–32.8 / 8.4 ± 2.3	3.9–13.5 / 6.7 ± 1.0	7.7 ± 0.5
B_F/B_{sol}, %	5.8–24.2 / 11.3 ± 2.2	3.2–38.3 / 9.4 ± 2.8	7.0–17.4 / 9.3 ± 1.2	10.0 ± 0.6
		Sheksna R.		
N_F	1335–7772 / 3996 ± 642	2326–9420 / 5313 ± 667	1512–5641 / 4040 ± 443	4450 ± 432
N_B/N_F	1373–5189 / 3033 ± 640	1275–6243 / 3652 ± 442	3042–6925 / 3949 ± 388	3545 ± 270
B_F	44.0–505.2 / 182.3 ± 47.0	86.1–471.0 / 220.1 ± 33.0	86.8–282.0 / 178.0 ± 21.0	193.5 ± 13.4
$B_F/\Sigma B$, %	5.5–13.4 / 9.4 ± 1.0	3.2–37.4 / 7.6 ± 2.9	6.8–12.9 / 9.2 ± 0.7	8.7 ± 0.6
B_F/B_{sol}, %	7.3–17.8 / 12.7 ± 1.3	3.3–37.4 / 8.9 ± 2.8	8.6–15.9 / 11.1 ± 0.9	10.9 ± 1.1

Table 4. Coefficients of correlation between biomass of heterotrophic nanoflagellates and biomass of different groups of bacterioplankton in the rivers

Parameter	Rivers		
	Serovka	Yagorba	Sheksna
B_{sol}	0.66	0.62	0.74
B_{ag}	0.34	Nc	0.27
B_f	Nc	Nc	Nc

Nc means correlation is not found.

close to norm. The increase in water temperature to the highest values for the region caused an increase in the biomass of HNFs in strongly polluted small rivers and in the Sheksna River. Water temperature in the rivers was on average 15.2–16.8°C over the period from July to the beginning of September 2009 and 2011 and 23.6–23.8°C in 2010. The biomass of HNFs was on average 1.7 times higher in the Serovka River, 1.8–2.3 times higher in the Yagorba River, and only 1.1–1.3 times higher in the Sheksna River than in the previous years. Apparently, a significant increase in water temperature in natural water objects leads to a sharp increase in the activity and biomass of microhet-

Table 5. Total production of bacterioplankton ($P_{\Sigma B}$), production of solitary bacteria (P_{sol}), aggregated bacteria (P_{ag}), and filamentous bacteria (P_f) and the rate of grazing by heterotrophic nanoflagellates (C) on solitary bacteria in the rivers, mg/m^3 day)

Parameters	Rivers		
	Serovka	Yagorba	Sheksna
$P_{\Sigma B}$	333–4836 / 1719 ± 504	259–6319 / 2089 ± 702	131–2533 / 945 ± 248
P_{sol}	268–2789 / 1202 ± 311	223–3240 / 1257 ± 380	96–2377 / 765 ± 232
P_{ag}	6–415 / 127 ± 45	9–302 / 110 ± 30	17–315 / 104 ± 38
P_f	37–2512 / 390 ± 268	12–2941 / 722 ± 374	7–286 / 76 ± 29
C_F	81–2730 / 889 ± 345	95–2589 / 1024 ± 315	50–1797 / 492 ± 185
C_F/P_{sol}, %	21.1–129.5 / 74.0 ± 12.1	42.6–114.4 / 81.5 ± 17.5	35.2–95.0 / 64.3 ± 6.7
$C_F/P_{\Sigma B}$, %	14.4–87.5 / 51.7 ± 8.2	35.8–72.7 / 49.0 ± 4.1	26.0–70.8 / 52.1 ± 5.7

erotrophic organisms to a greater degree in waterbodies and watercourses with high amounts of dissolved organic matter, i.e., in polluted aquatic systems.

Planktonic heterotrophic nanoflagellates actively graze on solitary bacteria [16, 21], consuming from 10 to 168% of the daily production of bacterioplankton in mesotrophic and eutrophic lakes [5]. We found a high positive correlation between the biomass of solitary bacteria and HNFs. Because the size of detritus particles colonized by bacteria (a diameter of particles from 7 to 75 μm) was equal to or significantly higher than the size of HNF cells, heterotrophic nanoflagellates can consume only bacteria attached to the surface of detritus particles. A weak positive correlation between the biomass of aggregated bacterioplankton and biomass of HNF testifies to the minor role of detritus microflora in feeding of planktonic HNF. Large filamentous bacteria (length of filaments from 7 to 150 μm) inhabiting the rivers under study cannot be feeding objects of small HNF.

Calculations of grazing rates of natural HNF populations on solitary bacteria in the studied rivers in April to October 2011 have demonstrated that HNFs are the main consumers of solitary bacteria. However, their role in grazing the total bacterioplankton production was not as pronounced (Table 5). In the second half of summer, grazing by heterotrophic nanoflagellates on solitary bacteria in small rivers exceeded 100% (Table 5). At the same time, during the periods under study, the production of filamentous bacteria reached its maximal values (49–60% of the total bacterioplankton production). Apparently, as a result of the decrease in the abundance of solitary cells of bacteria, filamentous bacteria gained a competitive advantage in using nutrients. Thus, during these periods heterotrophic nanoflagellates had a significant impact on changes in the size structure of the bacterial community.

CONCLUSIONS

A high abundance of heterotrophic nanoflagellates was recorded in the small rivers and in the littoral zone of the Sheksna River running through a large industrial center (Cherepovets). A total of 48 species and forms of colorless flagellates were detected in the rivers. The maximal values of abundance and biomass of HNFs were more often recorded in the second half of summer. In April to October, the average HNF biomass made up 8.9–10.9% of the biomass of solitary bacteria and 5.4–8.7% of the total bacterioplankton biomass. A high positive correlation was found between the total abundance of bacterioplankton and the abundance of HNFs, as well as between the biomass of solitary bacteria and the biomass of HNFs. Heterotrophic nanoflagellates are the main consumers of bacterioplankton in the rivers under study. During the vegetation period, they graze on average from 64.3 to 81.5% of the daily production of solitary bacteria and from 49.0 to 52.1% of the total daily production of bacterioplankton.

REFERENCES

1. Vinberg, G.G., Temperature coefficient of van't Hoff and Arrhenius equation in biology, *Zh. Obshch. Biol.*, 1983, vol. 44, no. 1, pp. 3–42.

2. *Vliyanie stokov Cherepovetskogo promyshlennogo uzla na ekologicheskoe sostoyanie Rybinskogo vodokhranilishcha* (Influence of Wastewaters of the Cherepovets Industrial Unit on the Ecological State of the Rybinsk Reservoir), Rybinsk: Inst. Biol. Vnutr. Vod AN SSSR, 1990.

3. Dzyuban, A.N. and Krylova, I.N., Assessment of the state of bacterioplankton and bacteriobenthos of the Rybinsk Reservoir near Cherepovets (Vologda oblast), *Biol. Vnutr. Vod*, 2000, no. 4, pp. 68–78.

4. Ivleva, I.V., *Temperatura sredy i skorost' energeticheskogo obmena u vodnykh zhivotnykh* (Ambient Temperature and the Energy Metabolism Rate in Aquatic Animals), Kiev: Nauk. Dumka, 1981.

5. Kopylov, A.I. and Kosolapov, D.B., *Mikrobnaya "petlya" v planktonnykh soobshchestvakh morskikh i presnovodnykh ekosistem* (Microbial "Loop" in the Plankton Communities of Marine and Freshwater Ecosystems), Izhevsk: KnigoGrad, 2011.

6. Kopylov, A.I. and Kosolapov, D.B., The structure of the microbial plankton community of the lower Ob Riveer (near Salekhard), *Sib. Ekol. Zh.*, 2011, no. 1, pp. 3–11.

7. Kopylov, A.I., Kosolapov, D.B., Romanenko, A.V., et al., Heterotrophic microorganisms in the planktonic food webs of riverine ecosystems, *Usp. Sovrem. Biol.*, 2006, vol. 126, no. 3, pp. 273–284.

8. Kopylov, A.I., Lazareva, V.I., Pyrina, I.L., et al., Microbial "loop" in the planktonic food web of a large plain reservoir, *Usp. Sovrem. Biol.*, 2010, vol. 130, no. 6, pp. 544–556.

9. Kosolapova, N.G., Quantitative distribution and taxonomic structure of the community of heterotrophic flagellates in the main biotopes of a small lowland river, *Gidrobiol. Zh.*, 2007, vol. 43, no. 3, pp. 57–67.

10. Tikhonenkov, D.V., Community structure and quantitative abundance of planktonic heterotrophic flagellates (Protista) in the Il'da River (Yaroslavl oblast), in *Ekosistemy malykh rek: bioraznoobrazie, ekologiya, okhrana* (Ecosystems of Small Rivers: Biodiversity, Ecology, and Conservation), Yaroslavl: Printkhaus, 2008, pp. 292–294.

11. Trunova, I.O., *Biologicheskie faktory samoochishcheniya vodoemov i stochnykh vod* (Biological Factors of Self-Purification of Water Bodies and Wastewaters), Leningrad: Nauka, 1979.

12. *Ekologicheskie problemy Verkhnei Volgi* (Environmental Problems of the Upper Volga), Yaroslavl: Yaroslav. Gos.-Tekhn. Univ., 2001.

13. Basu, B.K. and Pick, F.R., Factors related to heterotrophic bacterial and flagellate abundance in temperate rivers, *Aquat. Microb. Ecol.*, 1997, vol. 12, pp. 123–129.

14. Carlough, L.A. and Meyer, J.L., Protozoans on two south-eastern blackwater rivers and their importance to trophic transfer, *Limnol., Oceanogr.*, 1989, vol. 34, pp. 163–177.

15. Caron, D.A., Technique for enumeration of heterotrophic and phototrophic nanoplankton using epifluorescence microscopy, and comparison with other procedures, *Appl. Environ. Microbiol.*, 1983, vol. 46, no. 2, pp. 491–498.

16. Cleven, E.-J. and Weisse, T., Seasonal succession and taxon-specific bacterial grazing rates of heterotrophic nanoflagellates in Lake Constance, *Aquat. Microb. Ecol.*, 2001, vol. 23, pp. 147–161.

17. Fenchel, T., Ecology of heterotrophic microflagellates. II. Bioenergetics and growth, *Mar. Ecol.: Proc. Ser.*, 1982, vol. 8, pp. 225–231.

18. Kiss, A.K., Acs, E., Kiss, K.T., and Torok, J.K., Structure and seasonal dynamics of the protozoan community (heterotrophic flagellates, ciliates, amoeboid protozoa) in the plankton of a large river (River Danube, Hungary), *Eur. J. Protistol.*, 2009, vol. 45, no. 2, pp. 121–138.

19. Newell, S.Y., Sherr, B.F., Sherr, E.B., and Fallon, R.D., Bacterial response to presence of eukaryote inhibitors in water from a coastal marine environment, *Mar. Environ. Res.*, 1983, vol. 10, pp. 147–157.

20. Porter, K.G. and Feig, Y.S., The use of DAPI for identifying and counting of aquatic microflora, *Limnol., Oceanogr.*, 1980, vol. 25, no. 5, pp. 943–948.

21. Sanders, R.W., Porter, K.G., Bennett, S.J., and DeBiase, A.E., Seasonal patterns of bacterivory by flagellates, ciliates, rotifers and cladocerans in a freshwater planktonic community, *Limnol., Oceanogr.*, 1989, vol. 34, pp. 673–687.

22. Tikhonenkov, D.V., Mazei, Y.A., and Mylnikov, A.P., Species diversity of heterotrophic flagellates in white sea littoral sites, *Eur. J. Protistol.*, 2006, vol. 42, pp. 191–200.

23. Vörös, L., V.-Balogh, K., Herodek, S., and Kiss, K.T., Underwater light conditions, phytoplankton photosynthesis and bacterioplankton production in the Hungarian section of the River Danube, *Arch. Hydrobiol. Suppl. Large Rivers*, 2000, vol. 11, pp. 511–532.

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