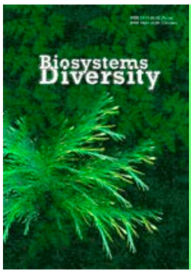

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Strusture, biomass and production of the biotic component of the ecosystem of an growing eutrophic reservoir

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Using our own data and data from the literature, we assessed the total biomass of the biotic component of the ecosystem of the Ivankovo Reservoir (Upper Volga, Russia), a eutrophic reservoir which is becoming overgrown with macrophytes. The biotic component of freshwater ecosystems is formed by communities of multicellular and unicellular organisms and viruses in the water layer (plankton) and bottom sediments (benthos) and also macrophytes and autotrophic and heterotrophic organisms growing on their surface (epiphyton). The biomass of the biotic component of the Ivankovo Reservoir equaled 39,853 tons C. Plankton, benthos and macrophytes with epiphyton equaled 3.6%, 41.6% and 54.8% of the total biomass respectively. We determined the contribution of higher aquatic plants, algae, cyanobacteria, heterotrophic bacteria, viruses, protozoans, multicellular invertebrates and fish to the formation of total biomass. The largest share was taken up by higher aquatic plants (54.5%). The second largest share was taken by heterotrophic bacteria (37.4%), most of which live in the bottom sediments. The high concentration of bacteria and invertebrates in the bottom sediments indicate significant provision of the organic substrates from the water column. The biomass of fish, the highest trophic link in the reservoir, equaled 15.0% of the biomass of their potential food substrates, invertebrate animals, and 0.7% of the total biomass of the biotic component. The greater part of the autochthonous organic compound in the reservoir is formed as a result of activity of phytoplankton, which provides 69.4% of total primary production of macrophytes, phytoepiphyton, phytoplankton and phytobenthos. The total primary production during the vegetation period was approximately forty times higher than the annual production of the fish. Currently, the share in the phytoplankton of large colonial cyanobacteria not consumed by zooplankton, the share of non-heterocystic species of cyanobacteria capable of heterotrophic feeding and the share of mixotrophic flagellates is increasing. Eutrophication of the reservoir is significantly stimulated by the development of macrophytes, and, presumably, the contribution of macrophytes to the total primary production of the reservoir will continue to increase.

Keywords: groups of hydrobionts; communities of hydrobionts; structure; products; reservoir

Introduction

The biotic component of freshwater ecosystems is formed by the communities of multicellular and unicellular organisms and viruses which live in the water column (plankton) and bottom sediments (benthos), and also macrophytes and autotrophic and heterotrophic organisms growing on their surface (epiphyton). Currently, in freshwater reservoirs, carbon of organic compounds synthesized by the primary producers (higher aquatic plants, algae, cyanobacteria, photosynthesizing and chemosynthetic bacteria), is delivered to higher trophic levels, and, finally, to the highest link – to fish via different routes: phytoplankton (phytobenthos, macrophytes) – invertebrates – fish (direct food chain); "dead" organic compound of autotrophic organisms (detritus of vegetative origin) – bacteria – invertebrates – fish (detritus of the food chain); dissolved organic matter released by autotrophic organisms during photosynthesis (autotrophic DOM) – bacteria – protozoa (microbial "loop") – multicellular invertebrates – fish (Sommaruga, 1995; Wetzel, 1995; Porter, 1996; Pomeroy et al., 2007). Also, heterotrophic bacteria involve a significant amount of allochthonous organic carbon into the trophic webs of aquatic ecosystems, especially such as rivers and reservoirs, and also areas affected by anthropogenic pollution.

Quantitative studies of flows of carbon and energy in trophic webs, and finally, determination of the pattern of structural-functional organisation of freshwater ecosystems, and also the assessment of their transformations which occur as a result of anthropogenic impact and climate change require factual data on the structure, biomass and products of biological communities of the water layer, bottom sediments and the entire biotic component (Stone et al., 1993; Kazantseva, 2003; MacKay et al., 2009; Sipkay et al., 2009). The literature includes a much larger amount of data on the significance of the total biomass of plankton and the contribution of algae and cyanobacteria, heterotrophic bacteria, protozoa and, multicellular zooplankton to its formation in lakes and reservoirs of different trophic status than on benthos and epiphyton communities (Christoffersen et al., 1990; Del Giorgio & Gasol, 1995; Fahnenstie et al., 1998; Straile, 1998; Hart & Stone, 2000; Degermendzhy, Gulati, 2002; Comerma et al., 2003; Kazantseva, 2003; Auer et al., 2004; Chróst et al., 2009; Kopylov et al., 2010, 2014). Significant structural components of many small freshwater bodies are higher aquatic autotrophic and heterotrophic organisms and plant growing on their surface (epiphyton) (Vadeboncoeur & Steinman, 2002; Cronin et al., 2006).

At the same time, no studies have been conducted which focus on the structure of the entire biotic component of a large freshwater body, including the main groups of hydrobionts: macrophytes, algae and cyanobacteria, viruses, heterotrophic bacteria, protozoa, multicellular invertebrates and fish.

The Ivankovo Reservoir was created in 1937 and is one of the oldest in the cascade of the Volga Reservoirs. The peculiarity of the reservoir is its shallowness: a water area less than 2 m in depth covers around 48% of the reservoir's area at normal head water level. Since the 1970s, according to the content of chlorophyll "a" in the water, this reservoir has been characterized as eutrophic, and the extent of its overgrowth by higher aquatic plants reached 17% of the water surface area in 1957 (Ekzertsev, 1958; Pyrina & Lyashenko, 2005). During the existence of the reservoir, multiple data have been collected on the structural-functional characteristics of the communities of autotrophic and heterotrophic organisms which live in the water layer and bottom sediments (Ekzertsev, 1978; Abakumov et al., 2000; Kopylov, 2001). However, the structure of the entire biotic component of the ecosystem of this water body has not since been analyzed.

This study constitutes the first attempt to assess the total biomass of the biotic component of the ecosystem of a eutrophic reservoir overgrown by macrophytes, Ivankovo Reservoir (Upper Volga), and to determine the contribution of macrophytes with epiphyton, plankton, benthos and the communities of various autotrophic and heterotrophic organisms to its formation, and also to determine the primary production of the organic matter in the water body and determine the role of macrophytes, phytoplankton, phytoepiphyton and phytobenthos in this process.

Materials and methods

In the study, we used the results of our research conducted in the Ivankovo Reservoir in July-August of 2005–2012, particularly: assessing the primary production of phytoplankton, concentration of chlorophyll "a" in the water, biomass of virio- and bacterioplankton, virio- and bacteriobenthos (in the upper 2 cm layer of the bottom sediments), bacterioepiphyton, plankton and benthos heterotrophic nanoflagellates, plankton ciliates, multicellular zooplankton and macrozoobenthos (Kopylov & Kosolapov, 2008; Kopylov et al., 2011, 2015; Rybakova & Kopylov, 2017). Also we used the literature data on biomass and production of phytobenthos, content of chlorophyll in the epiphyton and benthos, higher aquatic plants and meiobenthos (Ekzertsev, 1978; Devyatkin, 1983; Kopylov, 2001; Shcherbina, 2002). The surveys of plankton and benthos macroorganisms were conducted in the same areas of the Reservoir. Because there are no data on tempi of epiphyton photosynthesis, the number of viruses and heterotrophic nanoflagellates in epiphyton, concentration of benthos ciliates and Sarcodina in the Ivankovskoe Reservoir, we used the data on another reservoir in the Upper Volga – the Rybinskoe Reservoir (Myl'nikova, 1977; Kopylov et al., 2014).

The ichthyomass was assessed using the data on the Reservoir's mean biomass of pelagic and demersal fish in August 1982 and 1985: 4.6 ± 3.8 (range 0.4–16.1) and 1.7 ± 0.8 (0.2–3.8) t/km^2 respectively (Poddubnyy, 1988).

The biomass of phytoplankton, expressed in carbon units, was determined on the assumption that the concentration of chlorophyll "a" is: C = 25 × [chlorophyll] (Reynolds, 2006). We assumed that the content of carbon in the wet material of phytoplankton equals 10% (Rodhe, 1948; Strickland, 1960).

The carbon content in the cells of heterotrophic bacteria (C, fg C/cell) was calculated using the following allometric equation: $C = 120 \times V^{0.72}$, where V – cell volume, µm^3 (Norland, 1993). The carbon concentration in 1 virus particle was considered to equal 0.055 fg C (Steward et al., 2007). We assumed that the content of carbon in wet biomass of heterotrophic nanoflagellates equaled 22% (Børsheim & Bratbak, 1987), ciliates – 13% (Turley et al., 1986), metazooplankton – 5% (Dumont et al., 1975). Food energy of meiobenthos was assumed to equal 1 cal/mg, macrozoobenthos – 0.8 cal/mg of raw mass. We assumed that the food energy of pelagic fish equaled 1.5 cal/mg, demersal fish – 1.1 cal/mg of raw mass (Kolpakov, 2016). In the calculations, we accepted that the content of the organic matter in wet biomass of macrophytes equals 14% (Papchenkov, 2013), and 1 g of organic matter of macrophytes is equivalent to 0.5 g of organic carbon (Zhukova, 2005).

For converting different units of calculation, we used the following ratios: 1 mg C = 3.333 mg O and mg C = 10.1 cal.

During the comparison of the data, we used mean values of the parameters and the standard errors of the average.

Results

Hydrological-hydrochemical characteristic of the ecosystem. The Ivankovo Reservoir is the first level of the Volga-Kama cascade of reservoirs. Normal head water level in the reservoir is 124 m, full capacity at normal head water level is 1120 M m^3, the surface area of the water body is 327 km^2, length – 134 km, average depth – 3.4 m. The Reservoir is distinctive for having a stable level of water throughout the summer-autumn period (Ekzertsev, 1978; Avakyan et al., 1987).

The Reservoir is rich in biogenic elements – the concentration of its main elements in the water (80–90 µg/l of the total phosphorus and 1.3–1.5 mg/l of total nitrogen on average for separate reaches, Kopylov (2001)) corresponds to the norm for eutrophic water bodies. The average surface water temperature (near the bottom) for the Reservoir in the second half of summer equaled 23.5 ± 0.4 ºC (21.9 ± 0.2 ºC) in 2005, and 23.8 ± 0.3 ºC (20.1 ± 0.4 ºC) in 2012. The mean transparency of the water as measured by Secchi disk in 2005 and 2012 was the same: 85 ± 4 and 85 ± 3 cm in 2005 and 2012 respectively. The content of oxygen dissolved in water in the surface and pre-bottom horizons in 2005 ranged within 5.9–9.7 and 0.02–7.20 mg/l respectively, and 6.4–8.9 and 0.4–5.5 mg/l respectively in 2012.

Plankton. The total biomass of the plankton community in the Reservoir equaled 1,448.8 t C. The main contribution to its formation was made by phytoplankton (Table 1). In relation to the contribution to the plankton biomass, the heterotrophic bacteria took second place. The proportion of the total biomass of the food objects (phytoplankton and bacterioplankton) to the biomass of their consumers (non-predatory zooplankton) equaled 6 : 1, and the proportion of the biomass of non-predatory to the predatory zooplankton equaled 3 : 1, the proportion of the total biomass of the zooplankton to the fish was 1 : 1. It is important to note that a significant share of the phytoplankton was represented by large colonial cyanobacteria, and due to the large sizes of their colonies they were not consumed by the zooplankton.

In the Ivankovo Reservoir, the heterotrophic bacterioplankton is represented by free-swimming single cells (on average, 79.36 ± 2.30% of the total biomass of bacterioplankton); bacteria attached to detritus particles of 5–100 µg (14.92 ± 1.53% of the bacterioplankton biomass) size; and bacterial filaments (3.00 ± 0.65%). Therefore, heterotrophic bacteria can serve as food objects both for a large number of protozoa species, and for thin and large multicellular filtrators. The number of detritus particles inhabited by the bacteria ((34.2 ± 7.0) × 10^3 particles/ml), equaled 50.7% of the total number of detritus particles of size less than 100 µg ((67.5 ± 15.5) × 10^3 particles/ml) (Kopylov & Kosolapov, 2008). According to our assessments, at average diameter of a detritus particle equaling 11 µg, only the mass of small detritus particles inhabited by the bacteria (2351 mg C/m^3) is 1.6 times larger than the total plankton biomass.

Table 1
Mean reservoir values (±mean error) of the number (N) and biomass (B) of the main groups of plankton organisms and their shares (%) in the total biomass of the Ivankovo Reservoir

Component	N, ind./m^3	B			
		mg/m^3	mg C/m^3	t C/water body	% of plankton biomass
Phytoplankton	–*	24 ± 6**	600	672.0	46.4
Bacteria	(11.9 ± 1.9) × 10^{12}	1255 ± 75	285	319.2	22.1
Viruses	(55.2 ± 9.9) × 10^{12}	–	3	3.4	0.2
Flagellates	(3.1 ± 0.3) × 10^9	154 ± 17	34	38.1	2.6
Ciliates	(12.7 ± 0.5) × 10^5	215 ± 14	28	31.4	2.2
Non-predatory zooplankton	(180 ± 88) × 10^3	1921 ± 815	96	107.5	7.4
Predatory zooplankton	(48 ± 20) × 10^3	962 ± 395	48	53.8	3.7
Pelagic fish	–	1343	199	223.4	15.4

Note: * – here and in the Tables 2–4, dashes indicate absence of data; ** – chlorophyll content.

Macrophytes and epiphyton. Currently, the extent of overgrowth of the Ivankovo Reservoir water area with higher aquatic plants equals

29.2% of the water surface area, and their biomass weighs 310 thousand t, which corresponds to 43.4 thousand t of the organic matter or 21.7 thousand t C (Papchenkov, pers comm).

In 2005, the area occupied by higher aquatic plant cover equaled 19,830 ha (198.3 km^2), and the area occupied by hygrohelophytes (air-aquatic plants) was 66.8 ha, helophyte (emergent plants) cover – 6,817.8 ha, hygrophytes (submerged plants with floating leaves) – 984.6 ha and fully submerged plants occupied 11,960.8 ra (Papchenkov, pers comm). If we assume that the water layer contains 30% of air-aquatic plants and 70% of surface of the emergent plants, then the area of the surface of the macrophytes under the water equals 17,737.9 ha (177.4 km^2).

Using these data, and also the results of assessing the number and biomass of the epiphyton components, we calculated the total biomass of the Reservoir's epiphyton, which equaled 124.67 t C, which corresponded to only 0.6% of the biomass of the higher aquatic plants. The main component of the macrophytes' overgrowth was algae and cyanobacteria (Table 2).

Table 2
The Reservoir's mean values (± mean error) of the number (N) and biomass (B) of the main components of epyphyton and their share (%) in the total epiphyton biomass of the Reservoir

Component	N, ind./m^2	B			
		mg/m^2	mg C/m^2	t C/water body	% epiphyton biomass
Phytoepiphyton	–	26.3 ± 3.9*	658	116.73	93.63
Bacteria	(18.2 ± 2.6) × 10^{11}	202 ± 27	44	7.81	6.26
Viruses	(5.2 ± 1.4) × 10^{11}	0.2 ± 0.05	0.03	0.01	0.01
Flagellates	(1.4 ± 0.3) × 10^8	3.0 ± 0.7	0.7	0.12	0.10
Total	–	–	–	124.67	100.00

Note: * – chlorophyll content.

Benthos. The biomass of phytobenthos in the Ivankovo Reservoir was assessed using the results of its assessment in the Ivankovo reach (Ekzertsev, 1978). In the second half of the summer, in the shallow area of the upper layer of the bottom sediments (less than 2 m depth), the phytobenthos biomass ranged within 4.8–6.1 (5.5 ± 0.3) g/m^2, and in deeper areas (2–5 m deep) – within 1.6–19.2 (8.8 ± 2.3) g/m^2. It should be mentioned that the phytobentos, apart from the typical "benthos" species constantly living in the bottom, contained algae and cyanobacteria, which live in the water column. According to our assessments, the Reservoir's mean biomass of phytobenthos, for both the shallow-water and deep areas, equaled 7.8 g/m^2 (Table 3).

The total biomass of benthos in the Reservoir equaled 16,580 t C. The main contribution to its formation was made by heterotrophic bacteria, the second greatest contribution by non-predatory invertebrates (Table 3). The proportion of the total biomass of phyto- and bacteriobenthos to the biomass of non-predatory zooplankton was 10 : 1. High concentrations of vegetative pigments (chlorophyll and products of its degradation – phaeopigments) in the upper 2–5 cm layer of the bottom sediments of the Reservoir (Sigareva, 2012) indicate a significant content of "dead" organic matter of vegetative origin, which is, most likely, an important food substrate for benthos organisms. The proportion of the biomass of non-predatory to the predatory zooplankton equaled 6 : 1, and the total biomass of zoobenthos to fish was 27 : 1.

Biotic component of the ecosystem. The total biomass of all auto- and heterotrophic organisms, and also viruses which inhabit the Ivankovo Reservoir equaled 39853 t C. Above-the-bottom biomass (macrophytes with epiphyton and plankton) was 1.4 times higher than the biomass in the bottom sediments. At the same time, the total biomass of the plankton (1,449 t C) was significantly lower than the biomass of macrophytes with epiphyton (21,825 t C), and the biomass of benthos (16,580 t C). The main contribution to the formation of the total biomass of autotrophic organisms and to the formation of the total biomass of the biotic component was made by the higher water plants (Table 4). In the total biomass of animals, multicellular invertebrates predominated. At the same time, their biomass in the bottom deposits was ten times higher than in the water layer.

Table 3
The Reservoir's mean values (± mean error) of the number (N) and biomass (B) of the main components of the benthos and their share (%) in the total biomass of benthos in the Reservoir

Component	N, ind/m^2	B			
		mg/m^2	mg C/m^2	t C/water body	% of benthos biomass
Phytobenthos	–	7800	780	255	1.54
Bacteria	(89.6 ± 11.2) × 10^{13}	26.4 × 10^4	44632	14595	88.02
Viruses	(62.3 ± 1.2) × 10^{13}	51.4 ± 5.2	31	10	0.06
Flagellates	(12.8 ± 0.5) × 10^9	578 ± 56	125	41	0.25
Ciliates	(12.5 ± 3.5) × 10^4	69 ± 13	9	3	0.02
Sarcodina	2.2 × 10^4	17	2	1	0.01
Meiobenthos	(224 ± 70) × 10^3	6700 ± 1900	663	217	1.31
Macrozoobenthos	(2.0 ± 0.6) × 10^3	45306 ± 32400	3588	1173	7.07
Predatory macrozoobenthos	(0.4 ± 0.2) × 10^3	8630 ± 4300	684	224	1.35
Demersal fish	–	1700	185	61	0.37

Table 4
Biomass of autotrophic and heterotrophic organisms and viruses and their shares (%) in the total biomass of the biotic component of the Reservoir's ecosystem

Component	t C	% of the total biomass
Autotrophic organisms, including.:	22 744	57.07
Algae + cyanobacteria	1 044	2.62
Macrophytes	21 700	54.45
Heterotrophic organisms, including.:	17 096	42.90
Protozoa	115	0.29
Multicellular invertebrates	1 775	4.46
Fish	284	0.71
Bacteria	14 922	37.44
Viruses	13	0.03
The total biomass of the biotic component	39 853	100.00

In share of the total biomass, the heterotrophic bacteria, most of which live in the bottom sediments, took second place after the macrophytes (Table 4). Finally, we determined that in the Reservoir the proportion of the biomass of autotrophic organisms (primary producers), invertebrates (consumers of the 1 and 2 orders), fish (the highest trophic level) and heterotrophic bacteria is 80 : 7 : 1 : 53.

Primary production of the organic matter. The primary production of the macrophytes during the vegetative season in 1979 equaled 68 thousand t of organic matter or 34 thousand t C (Pyrina & Lyashenko, 2005). The annual production was assumed to be the total biomass of the above-ground parts of the plants in the flowering period, and the adjustment for their autumn increment was not made, and the loss during the leaf fall was not considered. The production of the higher aquatic plants during the vegetative season of 2005 was assessed as 43.6 thousand t of organic matter or 21.8 thousand t C (Papchenkov, pers comm). In our assessments, we used the production of macrophytes, obtained in 2005.

The production of epiphyton during the vegetative season in the Ivankovo Reservoir, assessed using the season's mean value of tempi of epiphyton photosynthesis among different species of macrophytes in the Rybinskoe Reservoir, equaled 8.3 ± 2.7 µg C / (cm^2 × day) (Kopylov et al., 2014), assessed as 2.7 thousand t C.

According to our data, the Reservoir's mean integral primary production of phytoplankton in August of 2005 equaled 1157 ± 353 mg C / (m^2 × day) or 35.8 g C / (m^2 × month). If we assume that the Ivankovo Reservoir, similarly to the Rybinskoe, has the primary production of phytoplankton in August equaling around 20% of the total 6-month (May to October)primary production of phytoplankton, then the primary production of the plankton over the vegetative season equaled 179 g C/m^2, and 58.5 thousand t C in the entire Reservoir.

On average, the tempi of phytobenthos photosynthesis in the shallow water area of the Reservoir in May–August equaled 195 ± 135 (ranging 0–860) mg O_2 / (m^2 × day) or 65 ± 45 mg C / (m^2 × day). If we presume that the area of potential benthos photosynthesis (about 1 m depth) is comparable to the area of macrophyte overgrowth (29.2%), then, considering the temperature adjustments in September–October, the primary production of phytobenthos over the vegetative period equaled 1.3 thousand t C.

As a result, the total primary production of the organic matter in the Reservoir equaled 84.3 thousand t C in the season. At the same time, the share of macrophytes, phytoepiphyton, phytoplankton and phytobenthos equaled 25.9%, 3.2%, 69.4% and 1.5% of the total biomass respectively, i.e. the main primary producers of the organic matter in the Reservoir were the plankton algae and cyanobacteria. At the same time, in the Reservoir, we observed a tendency towards gradual increase in the share of macrophytes in the total primary production.

Discussion

Currently, the Ivankovo Reservoir continues to become gradually overgrown by higher aquatic plants which make the greatest contribution to the formation of the total biomass of the ecosystem's biotic component. We observed a tendency towards an increasing contribution of macrophytes to the total primary production, which in 1973 equaled 22% of the total production of macrophytes and phytoplankton (Pyrina & Lyashenko, 2005), and 27% in 2005.

In freshwater ecosystems, part of the primary organic matter which is synthesized by the autotrophic organisms, does not become involved in the trophic web, and is deposited in the bottom. As the higher aquatic plants in the Reservoir develop, the dead parts of the macrophytes settle and accumulate. Their excess leads to the formation of floating mats of macrophytes, which after growing into the bottom, form land structures, separating a part of the water body (Papchenkov, 2013). The role of macrophytes in the carbon flows in the trophic web of the Ivankovo Reservoir remains undetermined. However, the observed processes of swamp-formation in the shallow-water areas, formation of floating mats (with total area of 50 km^2) and colonisation of the floating mats by willows, the roots of which closely connect the mats to the bottom and shore, indicate that a significant part of the primary production of macrophytes is not consumed by hydrobionts.

In the Volga reservoirs, we observed an increase in the share of cyanobacteria in the total biomass of phytoplankton. A significant component of the Ivankovo Reservoir's phytoplankton was large colonial cyanobacteria (Korneva, 2015). Their ability to form large viscous colonies and synthesize toxins protects them from being eaten by zooplankton. In water bodies with a significant level of colonial cyanobacteria' development, plankton invertebrates usually consume not less than the half of primary production of phytoplankton (Stone et al., 1993; Kazantseva, 2003; Kopylov et al., 2010). Cyanobacteria and algae, which have lost their vitality and not been consumed, settle in the bottom from the water column, where they serve as a source of food for benthos heterotrophic organisms and participate in the formation of bottom sediments.

The high content of vegetative pigments in the upper layer of bottom sediments of the Ivankovo Reservoir, 1.6–1.8 times higher than in the other Upper Volga Reservoirs (Sigareva, 2012), indicates a signifycant sedimentation of the organic matter of plankton autotrophic organisms from the water column, which serves as a substrate for benthos organisms. The benthos biomass was assessed as ten times higher than the biomass of plankton. The main share in it was taken by heterotrophic bacteria, then multicellular invertebrates, the biomass of which in the bottom sediments was ten times higher than in the water column.

As demonstrated above, in the process of consumption of large colonial cyanobacteria (*Microcystis aeruginosa*) by fish (*Carassius*), the cyanobacteria maintained their photosynthesizing activity during their passage through the fish intestine, and moreover their passage through the intestine stimulated their growth. This direct stimulating effect of plankton-consuming fish on large colonial cyanobacteria can be a mechanism of intensifying and prolonging the "bloom" of the water caused by the cyanobacteria (Kolmakov et al., 2001).

In many aquatic ecosystems, a significant part of bacterio- and phytoplankton is lysed by viruses, leading to the carbon from their cells not being released to the higher levels of the trophic webs. Despite viruses being the minimum part of the plankton biomass, they are important for the functioning of the plankton community of the Ivankovo Reservoir: the death rate among the heterotrophic bacteria and picocyanobacteria as a result of virus lysis reached 35% and 30% of their daily production respectively (Kopylov et al., 2011). Perhaps, the cyanophage-viruses in the Ivankovo Reservoir, similarly to the other reservoirs (Honjo et al., 2006; Tijdens et al., 2008), control the number and the production of large colonial cyanobacteria which cause the "bloom" of the water.

Because the mass of even small (to 100 µm) detritus particles in the Ivankovo Reservoir, which are inhabited by the bacteria, is 1.6 times higher than the total biomass of the plankton community, we can presume that the detritus is significant for the feeding of zooplankton and planktonophage fish, which is also typical for other freshwater reservoirs (Kazantseva, 2003), and a large amount of bacteria is consumed with detritus.

The biomass of fish in the Reservoir equaled 15% of the biomass of their potential food objects – invertebrates – and 0.7% of the total biomass of the biotic component. According to Poddubnyy et al. (1984), the fish productivity of the Ivankovo Reservoir is around 20 kg/ha (projected fish productivity – 45.9 kg/ha), which, according to our assessments, is equivalent to 8.4 t C. The proportion of the primary production of the organic matter of all photosynthesizing organisms in the vegetative period to the annual fish production is 10,036 : 1. It is clear that not all of new formed organic matter enters the trophic webs of the Reservoir.

Conclusion

During the relatively short period of its existence, the Ivankovo Reservoir has developed as a eutrophic water body with the highest level of overgrowth by higher aquatic plants among the Volga Reservoirs. The total biomass of the organisms and viruses in the Resevoir equaled 39,853 t C. Favourable conditions allow the macrophytes to synthesize 54.5% of the biomass of all the living organisms over the vegetative season. At the same time, the main producer of the primary organic matter in the Reservoir was phytoplankton which produced 69.4% of the total primary production. Eutrophication of the water body is to a large extent determined by the intensive development of macrophytes, increase in their biomass and production. It is likely that the share of the macrophytes in the total primary production of the Reservoir will continue to increase. The production of the fish community was forty times lower than the primary production of organic matter by autotrophic organisms.

The total biomass of heterotrophic organisms and viruses was 1.3 times lower than the total biomass of autotrophic organisms. Heterotrophic bacteria are the main component of the total biomass of heterotrophic organisms and in second place after the macrophytes by their contribution to the total biomass of the biotic component. The biomass of all the benthos heterotrophic organisms was 27 times greater than that of plankton, 45 times greater than that of bacteria, and 7 times greater than that of invertebrates. The high concentration of bacteria and invertebrates in the bottom sediments of the Reservoir indicate significant provision of organic substrates from the water layer.

The increase in the biomass of phytoplankton in the Reservoir is to a large extent the result of intense development of cyanobacteria, including the species which form large colonies. Therefore, the amount of organic matter of vegetative origin, which settles down to the bottom from the water column, will further increase, hastening the tempi of its accumulation in the bottom sediments. Now already, in some areas of the Reservoir in late summer, due to the consumption of oxygen by the benthos microorganisms, its concentration in the prebottom water layer decreases to 0.02–0.40 mg/l, which negatively influences the demersal multicellular animals.

Over the last few years, the conditions of high concentration of dissolved organic matter and low water transparency in the Reservoir have led to the increase in the content of nonheterocystic species of cyanobacteria capable of heterotrophic feeding and mixotrophic flagellates in the phytoplankton. Certainly, the organisms which combine the abilities of photosynthesis and heterotrophy are becoming a significant component of the plankton trophic web of the Reservoir.

The further eutrophication and increase in the total biomass of biotic component in the ecosystem of the Ivankovo Reservoir, despite the high intensity of the process of biotic natural purification, will be followed by decrease in the water quality. It is important to take this into account, because the Reservoir is an important source of water supply of the city of Moscow.

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