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STRUCTURE AND FUNCTIONING OF AQUATIC ECOSYSTEMS

Structure of the Biotic Component in the Rybinsk Reservoir Ecosystem: Importance of Heterotrophic Bacteria (Review)

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Abstract—The total biomass of the biotic component of the ecosystem has been determined and the contribution of the main ecological groups—autotrophic and heterotrophic organisms from different habitats—to its formation has been estimated in a large plain meso-eutrophic reservoir (Rybinsk Reservoir, Upper Volga). Particular attention is paid to the role of heterotrophic bacteria in the structure and functioning of the biota in the reservoir. The total biomass of the biotic component of the ecosystem is 71536 t C, which is 5.2% of the total organic carbon in the reservoir. Higher aquatic plants make the largest contribution to the formation of the biomass in the reservoir. Their biomass, including epiphyton, was 6.0 and 1.9 times larger than the biomass of plankton and benthos, respectively. Heterotrophic bacteria, most of which inhabit bottom sediments, rank second in respect to their contribution to the total biomass. The comparison of the total primary production of all phototrophic organisms and the carbon demand of heterotrophic bacteria indicates the importance of allochthonous organic matter in the functioning of the reservoir ecosystem.

Keywords: large plain reservoir, structure of biotic component, plankton, benthos, epiphyton, higher aquatic plants, bacteria

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INTRODUCTION

Knowledge of the structural and functional organization of aquatic ecosystems is impossible without studying the biological communities inhabiting all biotopes. Studies on the structure of the biotic component in fresh water bodies are not numerous [5, 31].

In recent decades, considerable changes have occurred in diversity, structure, productivity, and functioning of hydrobiont communities in the ecosystem of the Rybinsk Reservoir. [28]. This is, to a greater degree, due to the changes in the temperature regime of the reservoir. An assessment of the response of the thermal regime in the reservoir to local climate warming has demonstrated a stable tendency to an increase in average water temperature in the surface horizon in summer (by 0.9°C in July-August) and autumn (by 0.7°C in October) during the period of 1976–2010 when compared to the norm [4]. In the open water period, the average rate of its increase is 0.76°C/10 years and the maximum rate (in July) is 1°C/10 years. The duration of the ice-free period has increased by 20 days, mainly due to later freeze-up dates [4]. In the past decade, numerous data on the structural and functional characteristics of the communities of plankton, benthos, and higher aquatic plants have been obtained by researchers of the Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences. However, the structure of the biotic component of the ecosystem has still not been considered.

The aim of this study is to determine the total biomass of the biotic component (auto- and heterotrophic organisms, as well as viruses (TBV)) in the Rybinsk Reservoir ecosystem and to estimate the contribution of plankton, benthos, macrophytes with epiphyton and the main groups of autotrophic and heterotrophic organisms into its formation, and the proportion of TBV in the total amount of organic matter. In this study, special attention is paid to the role of heterotrophic bacteria in the structural and functional organization of the biotic component in the reservoir.

MATERIALS AND METHODS

The work is based on the results of hydrochemical (concentration of organic carbon) and hydrobiological (content of plant pigments in water and bottom sediments, phytoplankton and its production, bacterioplankton and its production, virioplankton, protists, zooplankton, and macrozoobenthos) studies conducted at six standard stations in the Rybinsk Reservoir in 2009 [15, 17, 21, 26, 27]. The degree of overgrowth of the reservoir, biomass, and production of macrophytes, as well as ichthyomass, were determined in the same year [20, 25]. In addition, data on the quantitative development of epiphyton, bacteriobenthos, viriobenthos, benthic protists, and meiobenthos obtained in previous years were used in the work [1, 2, 7, 11, 12, 18, 24]. The studies on epiphyton and meiobenthos were limited to the Volga Reach of the reservoir.

The carbon content in cells of heterotrophic bacteria (C, fg C/cell) was calculated using the allometric equation: $C = 120V^{0.72}$, where V is the cell volume, μm^3 [33]. The carbon content per one viral particle was taken as 0.055 fg C [36]. The phytoplankton biomass in carbon units was calculated based on the chlorophyll concentration *a* (Chl *a*): C = 25(Chl *a*) [34]. The carbon content was accepted to be 10% of the wet weight of phytoplankton [35, 37], 22% of heterotrophic nanoflagellates [30], 13% of infusoria [38], and 5% of metazooplankton [19, 32]. The accepted caloric value of meiobenthos and macrozoobenthos was equal to 1 and 0.8 cal/mg of wet weight, respectively. It was assumed that the caloric value of plankton fish and benthic fish was 1.5 cal/mg and 1.1 cal/mg of wet weight, respectively [6]. In order to bring to conformity different calculated values, the relationships 1 mg C = 3.333 mg O; 1 mg C = 10.1 cal were used.

The primary production of phytoplankton and heterotrophic bacteria was determined by the ^{14}C method [23]. It was assumed that the coefficient of utilization of assimilated food for growth K_2 was taken equal to 0.3 in heterotrophic bacteria in the Rybinsk Reservoir [22].

RESULTS AND DISCUSSION

Hydrological and hydrochemical characteristics of the ecosystem. In 2009, the water level in the Rybinsk Reservoir was 101.87–101.73 m BS (Baltic System) from May until the middle of July and was close the normal operating level. In the second half of the vegetation period, the water level gradually decreased from 101.54 m at the end of July to 100.41 m at the end of September. The average level for May–October was 101.21 ± 0.08 m; at such a water level, the water volume was 18.4 km^3 and the surface area was 4115 km^2. The total water inflow into the reservoir reached 45.06 km^3 (surface runoff, 42.48 km^3, precipitation, 2.58 km^3); the total water discharge was 44.24 km^3 (discharge from the dam, 42.47 km^3, evaporation, 1.77 km^3) [16]. According to the data obtained at the meteorological station of the city of Kostroma [28], the total solar radiation falling on the surface of the Rybinsk Reservoir was 2602 MJ/m^2 in May–October 2009. From May to October at six standard stations in the pelagial part of the reservoir, water transparency varied from 1.0 to 2.2 m; water temperature ranged from 6.4 to 22.8°C in the surface layer and from 6.1–21.6°C near the bottom. In June, the total content of organic carbon (C_{org}) in water averaged within 13.9–16.0 mg/L (on average 14.7 mg/L), suspended organic matter (C_{SOM}) was 1.1–2.2 mg/L (on average 1.5 mg/L), and dissolved organic carbon (C_{DOM}) was 12.4–13.8 mg/L (on average 13.1 mg/L) [27].

It follows that the concentration of dissolved organic matter (DOM) was an order of magnitude higher than that of suspended organic matter (SOM). The calculations based on these data demonstrated that water in the reservoir contained 270 112 t C_{org}, 241 776 t C_{DOM}, and 28 336 t C_{SOM}.

The comparatively small depth of the Rybinsk Reservoir, its large surface area, and its complex bottom relief are the causes for the extremely diverse conditions of bottom-sediment formation. In different types of bottom sediments, values of the volume weight (dry) (V_d) of the sample varied within 0.2–2.2 g/cm^3, the content of organic matter ranged from 0.2 to 89.5% V_d or 3.4 to 268.0 mg/cm^3, and the content of C_{org} was 0.1 to 38.5% V_d or 1.7 to 115.5 (on average 39.6 ± 1.0) mg/cm^3 [28]. The minimum concentrations of C_{org} were recorded in pebbles and sand; the maximum concentrations were found in peaty silt, deposits of macrophytes, and swampy soils. According to estimates made by V.V. Zakonnov [3], the content of C_{org} in bottom sediments is 8 176 000 t when their average thickness in the reservoir is 14.8 cm. Hence, it may be approximately estimated that the upper (0–2 cm) layer contains 1 104 865 t of C_{org}.

Plankton. Viruses and heterotrophic bacteria are the most numerous components of plankton in the reservoir (Table 1). The total plankton biomass average for the vegetation period amounted to 6808 t C. Phytoplankton made the largest contribution to its formation. Its biomass exceeded the total biomass of the main consumers of algae, protists, and metazoan peaceful zooplankton 1.8 times. Biomasses of planktonic protozoa and metazoa were comparable.

During the vegetation period of 2009, the content of C_{SOM} averaged 28 336 t in the entire water volume of the reservoir; the plankton biomass constituted 24% of its amount. The weight of dead C_{SOM} (detritus) was 21 528 t and was an order of magnitude higher than the biomass of its main consumer, peaceful zooplankton (Table 1). As was reported earlier [5], detritus plays an important role in the feeding of freshwater zooplankton. According to our data, in the Rybinsk Reservoir, up to 70% of detritus particles from 5 to 100 μm are inhabited by bacteria, so zooplankton consumes considerable amounts of bacteria together with detritus.

Biomass of heterotrophic bacteria is the main food source for most species of protists and an additional food for many species of peaceful zooplankton. In the reservoir it was slightly lower than the biomass of phytoplankton (Table 1), which indicates the important role of bacteria in the feeding of not only heterotrophic nanoflagellates and infusoria, but zooplankton as well.

The paths of the carbon flux transport in the planktonic food web in the Rybinsk Reservoir are the classi-

Table 1. Average for the vegetation-period abundance (*N*) and biomass (*B*) of the main components of the plankton community and their contribution (%) to the total biomass of plankton (TBP) in the Rybinsk Reservoir

Component	*N*, ind./m^3	*B*			
		mg/m^3	mg C/m^3	t C/waterbody	% TBP
FP	(108 ± 14) × 10^9	1220 ± 320	147	2705	39.73
BAC	(5.2 ± 0.2) × 10^{12}	575 ± 19	126	2318	34.05
VIR	(30.6 ± 2.0) × 10^{12}	7.0 ± 0.4	2	37	0.54
HNF	(2.2 ± 0.2) × 10^9	111 ± 11	24	442	6.49
INF	(8.6 ± 0.3) × 10^5	203 ± 12	26	478	7.02
PZP	(113 ± 19) × 10^3	550 ± 70	30	552	8.11
PrZP	(12 ± 3) × 10^3	330 ± 45	15	276	4.05
ZP	(125 ± 12) × 10^3	880 ± 110	45	828	12.16

Hereinafter: FP, total of pico-, nano-, and microphytoplankton; BAC, heterotrophic bacteria; VIR, viruses; HNF, heterotrophic nanoflagellates; INF, infusoria; PZP, peaceful zooplankton; PrZP, predatory zooplankton; and ZP, total metazooplankton.

Table 2. Average abundance (*N*) and biomass (*B*) of the main components of epiphyton and their contribution (%) to the total biomass of epiphyton (TBE) in the Rybinsk Reservoir for the vegetation period

Component	*N*, ind./m^2	*B*			
		mg/m^2	mg C/m^2	t C/waterbody	% TBE
PhE	(4.3 ± 0.1) × 10^9	2040 ± 75	204	153.78	86.71
BAC	(11.1 ± 2.4) × 10^{11}	138 ± 7	30	23.0	12.97
VIR	(5.2 ± 1.4) × 10^{11}	0.2 ± 0.05	0.03	0.02	0.01
HNF	(1.4 ± 0.3) × 10^8	3.0 ± 0.7	0.7	0.55	0.31

PhE, phytoepiphyton.

cal grazing food chain (phytoplankton–zooplankton–fish), detritus chain (detritus–zooplankton–fish), and microbial loop (DOM–bacteria–protists–viruses–DOM or zooplankton) [9]. The ratio of the content of C_{org} in phytoplankton, bacterioplankton, and detritus is 1.2 : 1.0 : 9.3. The ratio of the total amount of C_{org} in food (phytoplankton + bacteria + detritus) and first-order consumers (peaceful zooplankton + heterotrophic nanoflagellates + infusoria) was 18 : 1, and the ratio of the biomass of first-order consumers and second-order consumers (predatory zooplankton) was 5.3 : 1. It should be taken into account that predator–prey relationships are possible among peaceful zooplankton; in particular, large Daphnia and calanoid copepods can filter protists and young (nauplii) copepods.

Macrophytes and epiphyton. In 2009, the area of macrophyte overgrowths in the Rybinsk Reservoir was 186 km^2; the summer biomass of macrophytes was 905160 t of wet weight, 123040 t of organic matter, or 61520 t of carbon [20]. The maximum biomass of higher aquatic plants was recorded in summer; according to our estimates, its average value reached 41010 t of carbon during the vegetation season of 2009. Macrophyte production during the vegetation period amounted to 1700100 t of wet weight, 256100 t of dry weight, 231100 t of organic matter, or 115550 t of carbon [20].

In the Rybinsk Reservoir, the surface area of higher aquatic plants was 861.66 km^2, including 4.66 of semiaquatic plants, 348.65 of semisubmerged plants, 488.65 of submerged plants, and 19.69 km^2 of hydrophytes with floating leaves [20, and Papchenkov oral communication]. If we accept that 30% of the surface area of semiaquatic and 70% of the surface area of semisubmerged plants are in the water column, the surface area of submerged macrophytes was 753.8 km^2.

Based on this information and the data on abundance and biomass of the epiphyton components of different macrophyte species, the total biomass of epiphyton in the reservoir was calculated, which constituted 177350 t C_{org}, or 0.4% of the biomass of higher aquatic plants. Photosynthesizing organisms were the main component (87%) of the biomass of epithyton on macrophytes (Table 2).

Benthos. The distribution of benthic organisms in the Rybinsk Reservoir depends on the structure of the soil complex. In 2009, the average content of vegetative pigments in bottom sediments of the reservoir, calculated with account for areas of different types of sediments, was 10.8 ± 2.7 mg/(m^2 · mm of wet soil)

Table 3. Average abundance (*N*) and biomass (*B*) of the main components of benthos and their contribution (%) to the total biomass of benthos (TBB) in the reservoir for the vegetation period

Component	*N*, ind./m^2	*B*			
		mg/m^2	mg C/m^2	t C/waterbody	% TBB
PhB	–	2.2*	55	226	1.0
BAC	$(17.0 \pm 2.8) \times 10^{13}$	$(1.8 \pm 0.4) \times 10^4$	4020	16542	77.1
VIR	$(11.8 \pm 1.2) \times 10^{13}$	51.4 ± 5.2	6	25	0.1
HNF	$(2.4 \pm 0.1) \times 10^9$	107 ± 9	24	99	0.5
INF	$(6.0 \pm 2.2) \times 10^4$	61 ± 24	8	33	0.2
MeZB	$(230 \pm 60) \times 10^3$	3100	310	1276	5.9
MacroZB	$(1.1 \pm 0.6) \times 10^3$	9900	792	3259	15.2

PhB, phytobenthos; MeioZB, meiozoobenthos; MacroZB, macrozoobenthos.
* Concentration of chlorophyll *a*, mg/(m^2 mm).

[26]. A considerable part of chlorophyll *a* in bottom sediments is the products of its degradation, pheopigments (80% of the total concentration); the content of the active form of the pigment amounted to 2.2 mg/(m^2 ·mm) (Table 3).

Heterotrophic bacteria were the most numerous component of the benthic community in the reservoir; their average abundance exceeded the abundance of viruses. The total benthic biomass reached 21460 t C_{org}, which constituted 1.9% of the amount of organic carbon in the upper (0–2 cm) layer of sediments. Bacteria made the main contribution (77%) to the benthic biomass formation (Table 3). The biomass of metazoic zoobenthos was an order of magnitude higher than the biomass of benthic protists.

Biological component of the ecosystem. More than 1170 species of plankton algae and cyanobacteria [10], >400 species of higher aquatic plants, 70 species of heterotrophic flagellates and 150 species of infusoria [13, 29], >420 species of plankton, and 310 benthic metazoic invertebrates [1, 14, 21], as well as 54 fish species [25], live in the Rybinsk Reservoir. The reservoir is inhabited by 10.5×10^{65} extracellular viral particles, 7.9×10^{65} heterotrophic bacteria, 2.0×10^{39} algae and cyanobacteria (without phytobenthos), 5.0×10^{55} heterotrophic flagellates, 1.6×10^{30} infusoria, 145×10^{13} specimens of multicellular invertebrates, and $>130 \times 10^9$ specimens of fish. Planktonic viruses with a capsid diameter of 20 nm (4×10^{-6} μg) had the minimum size (and wet weight) among hydrobionts; catfish with a length of ~1.7 m (~39 kg) had the maximum size [25].

The total biomass of auto- and heterotrophic organisms, as well as viruses living in the ecosystem of the Rybinsk Reservoir, constituted 71536 t C_{org}, which was 5.2% of the total (in water and the upper layer of sediments) organic matter (1374977 t C). The ratio of living to dead C_{org} was 1 : 18. Higher aquatic plants made the greatest contribution to the formation of the total biomass of biota and the total biomass of autotrophic organisms (Table 4; Figs 1a, 1b). Metazoan invertebrates prevailed in the total biomass of eukaryotic heterotrophic organisms (Fig. 1c). In 2009, fish stocks (higher trophic level) were estimated as 16000± 2000 t of wet weight [25], which amounted to 2.9% of the total biomass of all organisms and was 3 times lower than the biomass of invertebrate animals (Table 4).

In fresh water bodies, higher plants and phytoplankton, along with abiotic factors, have a considerable effect on changes in the surface area; water volume; and, finally, the period of existence of the reservoir. The development of higher aquatic plants results in the accumulation of deposits of dead parts of macrophytes. Their excess causes the formation of mats, which merge into the bottom and form land areas, thus alienating part of the water area. The sedimentation of dead phytoplankton results in organic matter accumulating in bottom sediments.

In 2009, the phytoplankton biomass in the Rybinsk Reservoir was an order of magnitude lower than the biomass of macrophytes (Table 4), but the production of phytoplankton was three times greater than the production of macrophytes during the vegetation period. As was reported earlier [5, 8, 9], colonial cyanobacteria reach a high abundance both in the reservoir and in eutrophic lakes. The large sizes of colonies make them inaccessible for most representatives of zooplankton, which graze <50% of the primary production of phytoplankton during the vegetation period [8, 9]. A considerable amount of suspended organic matter apparently remains in the water column and supplements the stock of plankton detritus or settles to the bottom of the reservoir. Average long-term rates of sediment accumulation are 2.3 mm per year with account for the entire area of the reservoir at the normal operating level, including the area of bottom erosion [3].

The role of macrophytes in carbon fluxes in the food web in the Rybinsk Reservoir is still unclear. The area occupied by macrophytes increases in the reser-

Table 4. Biomass of photo- and heterotrophic organisms and viruses and their contribution (%) to the total biomass of live organisms in the reservoir

Component	t C	% OBBC
Phototrophs:	44095	61.64
Algae + cyanobacteria	3085	4.31
Macrophytes	41010	57.33
Heterotrophs:	27441	38.36
Fish	2080	2.91
Invertebrates	6416	8.97
Bacteria	18883	26.40
Viruses	62	0.08

OBBC, total biomass of the biotic component.

voir, whose regime of filling is unstable from year to year, and the dynamics of overgrowths is of pulsating character, which indicates a general tendency toward a constant reduction of the water area [20].

According to the data of V.G. Papchenkov [20] in 2009, the degree of overgrowths in the Rybinsk Reservoir (water level 101.2 m BS) was 3.5 times higher and the biomass and production of macrophytes was 3 times higher when compared to 2003. From 2005 until 2010, the chlorophyll content in water and the primary production of phytoplankton on average for a photic zone increased 1.8 and 1.6 times, respectively [28]. A steady trend for climate warming in the region and, as a result, an increase in water temperature upon the existing hydrological regime will lead to an increase in the proportion of macrophytes in the total biomass of the biotic component in the ecosystem of the reservoir and a higher excess of the biomass of macrophytes over the biomass of plankton in the subsequent years.

Heterotrophic bacteria. Structural and functional characteristics of the communities of heterotrophic bacteria differed in various habitats of the reservoir. For the vegetation period, the average abundance of bacteria in 1 cm^3 of water and the epiphyton of higher aquatic plants and bottom sediments constituted $(5.2 \pm 0.2) \times 10^6$, $(11.1 \pm 2.3) \times 10^8$, and $(8.5 \pm 1.4) \times 10^9$ cells; biomass was $(126 \pm 4.4) \times 10^{-3}$, 30 ± 6, and 201 ± 49 μg C, and production was $(39 \pm 3) \times 10^{-3}$, 27 ± 5 and 51 ± 2 μg C/day, respectively. Heterotrophic bacteria, most of which inhabit bottom sediments, rank second after macrophytes in respect to their contribution to the total biomass (Table 4, Fig. 1d).

Bacteria play a crucial role in organic-matter mineralization and prevent its accumulation in aquatic ecosystems. In the Rybinsk Reservoir, the ratio of the biomass of phototrophic organisms (primary producers) to the biomass of bacteria (destructors) was 2.3. During the vegetation period, bacteria use the following substrates: earlier accumulated DOM and SOM stocks; excretions of DOM by living macrophytes, algae, and cyanobacteria; organic matter (OM) unassimilated by consumers during feeding; OM of dead hydrobionts; and allochthonous OM inflowing from the catchment area.

The primary organic matter produced by photosynthesizing organisms in water bodies is the basis of functioning of the entire food web, including the microbial community. The comparison of the primary production with the production of heterotrophic bacteria for a vegetation period may characterize the ratio of production/destruction processes in aquatic ecosystems.

The total production of heterotrophic bacteria in the littoral part of the Rybinsk Reservoir overgrown with higher aquatic plants is formed by that of bacterioplankton (3.7%), bacterioepiphyton (7.4%), and bacteriobenthos (88.9%) and the total primary production is composed of the production of phytoplankton (14.3%), phytoepiphyton (3.8%), macrophytes (72.7%), and phytobenthos (9.2%). The bacterial production was 3.9 times lower than the primary production, and the demands of bacteria for substrates were 1.2 times lower (Table 5). It follows that OM synthesized by autotrophic organisms completely satisfied the demands of heterotrophic bacteria in the littoral shallow zone.

However, it is evident that at the end of the vegetation period a considerable amount of macrophyte biomass remains unassimilated and enters the food web of the reservoir as dead OM during the following vegetation period. The total heterotrophic bacterial production in the pelagic zone of the reservoir was formed by bacterioplankton (14%) and bacteriobenthos (86%) and exceeded the primary production of phytoplankton 1.7 times. The total ration of bacteria was 5.7 times higher than the production of algae and cyanobacteria. In the entire reservoir during the vegetation period (152 days from the middle of May to the middle of October), the demand for substrates by bacteria exceeded the total primary production of photosynthesizing organisms 4.4 times.

The data indicate that in 2009 heterotrophic bacteria, along with allochtonous OM, which was formed during the vegetation period and accumulated in the previous years, utilized a considerable amount of allochtonous

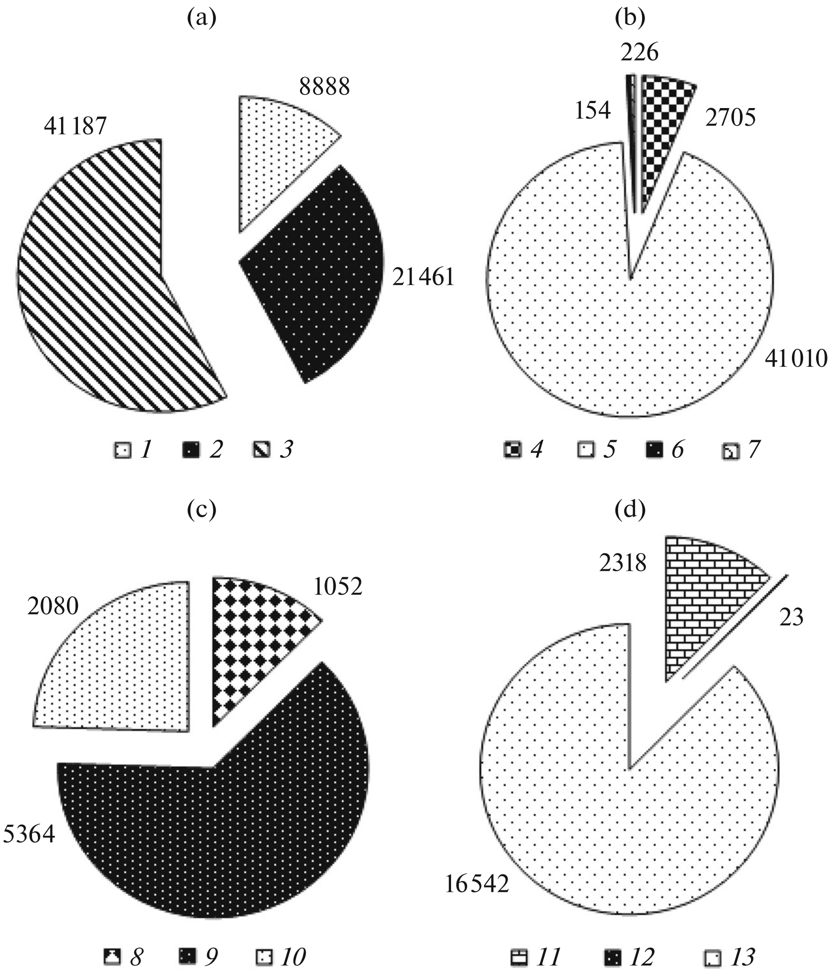

Fig. 1. Biomass (t C) of the biotic component of the ecosystem in the Rybinsk Reservoir: (a) total biomass of plankton and fish (*1*), benthos (*2*), and macrophytes and epiphyton (*3*); (b) total biomass of photosynthesizing organisms (phytoplankton (*4*), macrophytes (*5*), phytoepiphyton (*6*), and phytobenthos (*7*)); (c) biomass of eukaryotic heterotrophic organisms (protists (*8*), metazoic invertebrates (*9*), and fish (*10*)); and (d) biomass of heterotrophic bacteria in plankton (*11*), epiphyton (*12*), and benthos (*13*).

OM. It should be noted that the annual inflow of river waters in 2009 (42.5 km^2) greatly exceeded its average long-term value (32.8 km^3) [16] and, as a result, the input of allochtonous OM was higher than its average long-term value. Thus, our calculations indicate that allochtonous organic matter involved in the food web by heterotrophic bacteria is of great importance for the functioning of the biotic component in the reservoir.

From June to October, the average monthly consumption of organic carbon by planktonic bacteria (C_B) varied from 43 to 241 (on average 130 ± 29) mg C/(m^3 · day), which constituted 0.3–1.7% (on average 0.9 ± 0.2%) of the average monthly total (C_{SOM} + C_{DOM}) content of dead organic carbon (C_{org}) in the water column, 13.9–16.0 (on average 14.68 ± 0.36) g C/m^3. The max-

Table 5. Primary production of photosynthesizng organisms (P_{Ph}), production (P_B), and demands of heterotrophic bacteria for organic carbon (C_B) in the Rybinsk Reservoir

Parameter	Littoral zone	Pelagic zone	Entire reservoir, t C/season
	mg C/(m^2 day)		
P_{Ph}	5716	685	569690
P_B	1468	1181	746806
C_B	4893	3937	2489353

The area of the littoral zone is 186 km^2 and the average depth is ~1.1 m; the area of the pelagic zone is 3929 km^2 and the average depth is 6.4 m.

imum C_B/C_{org} ratio was recorded in July; the minimum ratio was recorded in October.

The concentration of easily assimilable labile OM (C_{lab}) ranged from 260 to 672 mg C/m^3 (on average 420 ± 78 mg C/m^3) [27]. The ratio of average monthly values of C_B to the content of the easily assimilable OM fraction (C_B/C_{lab}) varied from 10% in October to 63% in July and averaged 34.1 ± 9.5%. In summer, a weakly negative correlation was found between these parameters ($r = -0.24$, $p < 0.05$).

The amount of C_{org} consumed daily by bacterioplankton and bacterioepiphyton averaged 2400 t for the vegetation period. The amount of C_{org} spent by bacteria on energy metabolism, i.e., destroyed to mineral elements, constituted 1680 t/day. The total content of dead organic matter in water (on average for the vegetation period 263304 t C) decreased by 0.64% per day.

In the upper layer of bottom sediments, heterotrophic bacteria consumed 13603 t C/day on average for the vegetation period and their expenditures on energy metabolism amounted to 9522 t C/day. It constituted 0.87% of the average dead OM in bottom sediments for the vegetation period, which was estimated as 1086664 t C. Thus, in the ecosystem of the Rybinsk Reservoir, on average for the vegetation period, 11202 t C/day of dead OM was subjected to bacterial destruction. Its average vegetative content in the reservoir was 1349968 t C; during the vegetation period it decreased on average by 0.83% per day. The amount of organic matter destructed by heterotrophic bacteria in bottom sediments was 5.7 times higher than in the water column; the ratio of energy expenditures of bacteria on the exchange (R_B) to the total content of organic carbon (R_B/C_{org}) differed 1.3 times in these habitats.

CONCLUSIONS

The total biomass of the biotic component of the ecosystem in the Rybinsk Reservoir constitutes 71536 t C, or 5.2% of the total organic carbon in the reservoir. The ratio of living to dead C_{org} is 1 : 18. Higher aquatic plants dominate in the total biomass of the biota, which, to a greater degree, determines the distribution of the biomass of hydrobiont communities in different habitats. The biomass of macrophytes with epithyton is 6.0 and 1.9 times higher, respectively, than the biomass of plankton and benthos, and the total biomass of hydrobionts in the water column and epithyton is 2.3 times higher than that in bottom sediments. The data demonstrate the necessity of further studies on the role of macrophytes in the functioning of the food web of the reservoir. Heterotrophic bacteria, the largest part of which is in bottom sediments, are second to macrophytes in respect to their contribution to the total biomass formation. The comparison of the total primary production of all phototrophic organisms and the carbon demand of heterotrophic bacteria indicates the important role of allochthonous organic matter in the functioning of the reservoir ecosystem.

Bacteria decompose on average 0.83% of the total amount of dead organic matter to mineral elements during the vegetation period in the reservoir.

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