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PHYTOPLANKTON, PHYTOBENTHOS, AND PHYTOPERIPHYTON

Phytoplankton in the Littoral and Pelagial Zones of the Rybinsk Reservoir in Years with Different Temperature and Water-Level Regimes

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Abstract—The features of the floristic composition and dynamics of the biomass of phytoplankton in shallow and deep areas of the Volga reach in the Rybinsk Reservoir have been studied during years with different thermal and water-level regimes (2009–2011). The floristic diversity and biomass of phytoplankton increase with a decrease in depth. The increase in water temperature at low water level stimulates phytoplankton vegetation in the pelagial zone and a decrease in biomass in the littoral zone, while a high diversity of algocenoses is recorded irrespective of habitat. The contribution of filamentous algae and cyanoprokaryotes to the biomass increases in the shallow littoral part; in the open part of the reservoir, the biomass of mixotrophic flagellates decreases. Their abundance, as well as the abundance of zignematales, increases with decreasing depth.

Keywords: phytoplankton, floristic and cenotic diversity, biomass, temperature and water level, Rybinsk reservoir, shallow area

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INTRODUCTION

Littoral shallow areas are the nesting sites for birds, spawning and feeding grounds of juvenile fish, and effective biofilters of contaminants inflowing from the watershed [29]. Flows of matter and energy between aquatic and terrestrial biocenoses are regulated in the littoral zone. One particular ecotonic community of organisms which live under conditions of high variability of abiotic factors when in continuous contact with allochthonous organic and mineral matters and products of their primary transformation is formed in the littoral zone [8]. The water level is one of the key factors in the formation of waterbody productivity [19] affecting the abundance, taxonomic composition, and size characteristics of phytoplankton [4, 5, 10, 23, 25, 27, 28, 32, 36]. Temperature determines the course of all biological, hydrological, and hydrochemical processes and regulates oxygen consumption, life-span of aquatic organisms, phenology of communities, trophic relations, degree of water bloom caused by cyanoprokaryotes (blue-green algae and cyanobacteria), and the trophic status of waters [30, 31, 33]. Water level and temperature regimes of waterbodies are integral indicators of climate changes, causing the reorganization of biological communities, the study of which is necessary for predicting the consequences of transformations of aquatic systems under conditions of the modern dynamics of climate. Shallow parts of reservoirs can be polygons for the study of the response of hydrobiont communities to short-term variations in water temperature and level. The Rybinsk Reservoir is a large shallow water body which is the third stage in the cascade of the Volga reservoirs. The littoral shallow zone may occupy up to 41% of its area at the normal background level (NBL) [1]. Phytoplankton in the littoral zone of the reservoir had been studied sporadically from the 1950s until the 1990s [2, 6, 21, 22]. During that period shallow areas underwent considerable changes in respect to pattern and degree of overgrowth, as well as the composition of higher aquatic vegetation [14, 17]. Against the background of a long-term (1947–2008) temperature rise in the water surface, the duration of the period with water temperature ≥20°C increased in the pelagial part of the Rybinsk Reservoir [13].

The aim of this study is to characterize features of the phytoplankton formation in different littoral shallow water areas and in the deepwater part of the Rybinsk Reservoir in years with different temperature and level regimes.

MATERIALS AND METHODS

The samples were collected in the littoral part of the Volga reach in the Rybinsk Reservoir (Fig. 1, stations *2* and *3*) one to six times a month in May–Sep-

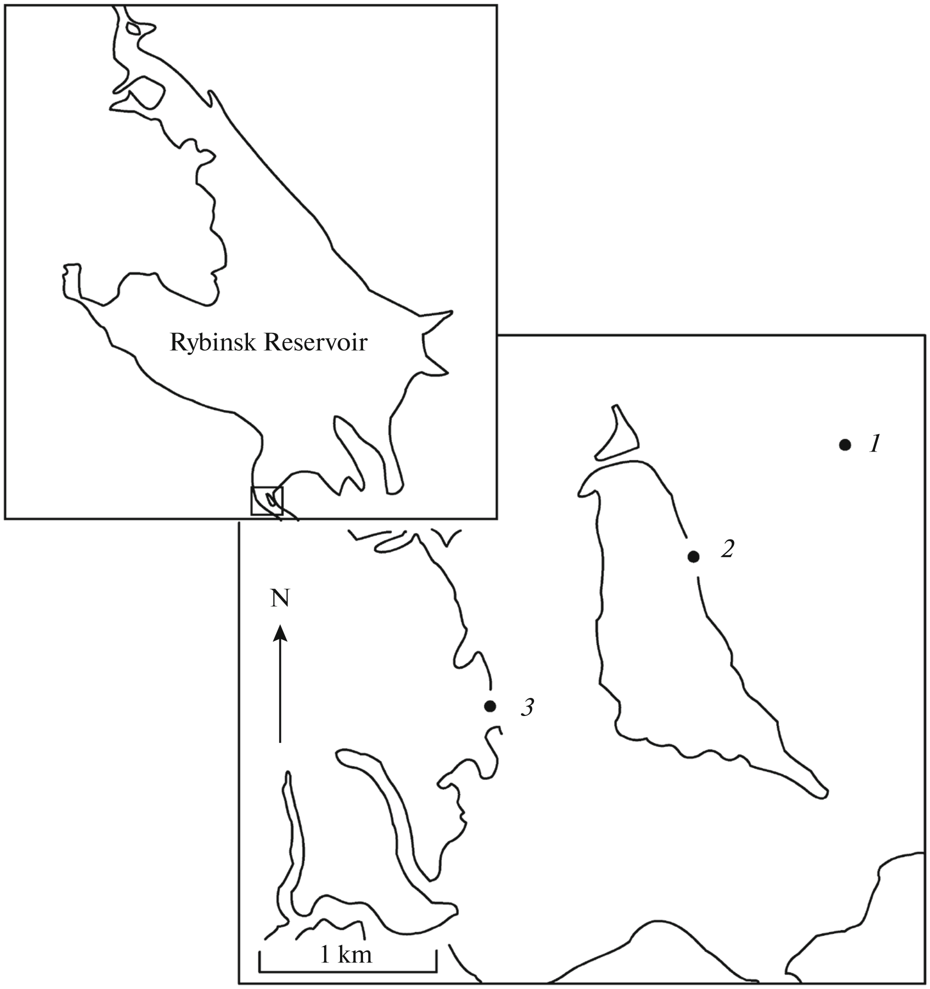

Fig. 1. Scheme of location of sampling stations in the littoral and deepwater parts of the Volga reach in the Rybinsk Reservoir: (*1*) deepwater station, (*2*) open shallow part, and (*3*) protected shallow part.

tember 2009, April–September 2010, and May–July 2011. The studies were conducted in protected (2009–2011) and open (2009–2010) shallow areas with depths of 0.4–0.8 m. For a comparative analysis, we used samples collected at a deepwater (10–12 m) station opposite the former village of Koprino (Fig. 1, station *1*). Samples were collected from the entire water column: samples were taken with a weighted bucket at shallow water stations and with an Elgmork sampler at the deepwater station. Phytoplankton was concentrated by direct successive filtration through membrane filters with 5 and 1.2 μm pore sizes and fixed in Lugol's solution with the addition of formaldehyde and glacial acetic acid. Algae were counted and identified in an Uchinskaya-2 counting chamber with a volume of 0.01 mL. The phytoplankton biomass was determined by cell-volume measurements (a volume counting technique); the species which constituted ≥10% of the total abundance and biomass were considered dominant [12, 15].

The cenotic diversity of algocenoses was estimated using the Shannon index [18]; the floristic similarity of phytoplankton in the surveyed sites was estimated by the Sørensen index [16]. Based on the complete list of algae, a hierarchical cluster analysis was performed using Euclidean distance as a dissimilarity measure. Grouping of habitats according to the presence or absence of the species was made by Ward's method.

RESULTS

The years of studies differed considerably in hydrometeorological conditions. In 2009, the period with water temperature ≥20°C was short and lasted from the end of July to the beginning of August. In 2010, water temperature reached the maximum values (21–28°C) in mid-July to mid-August; in 2011, water temperature 20–24°C was recorded from the beginning of July to the end of August. The seasonal patterns of the water level were of the same type, with the maximum in June and a gradual decrease (by ~40 cm) by autumn

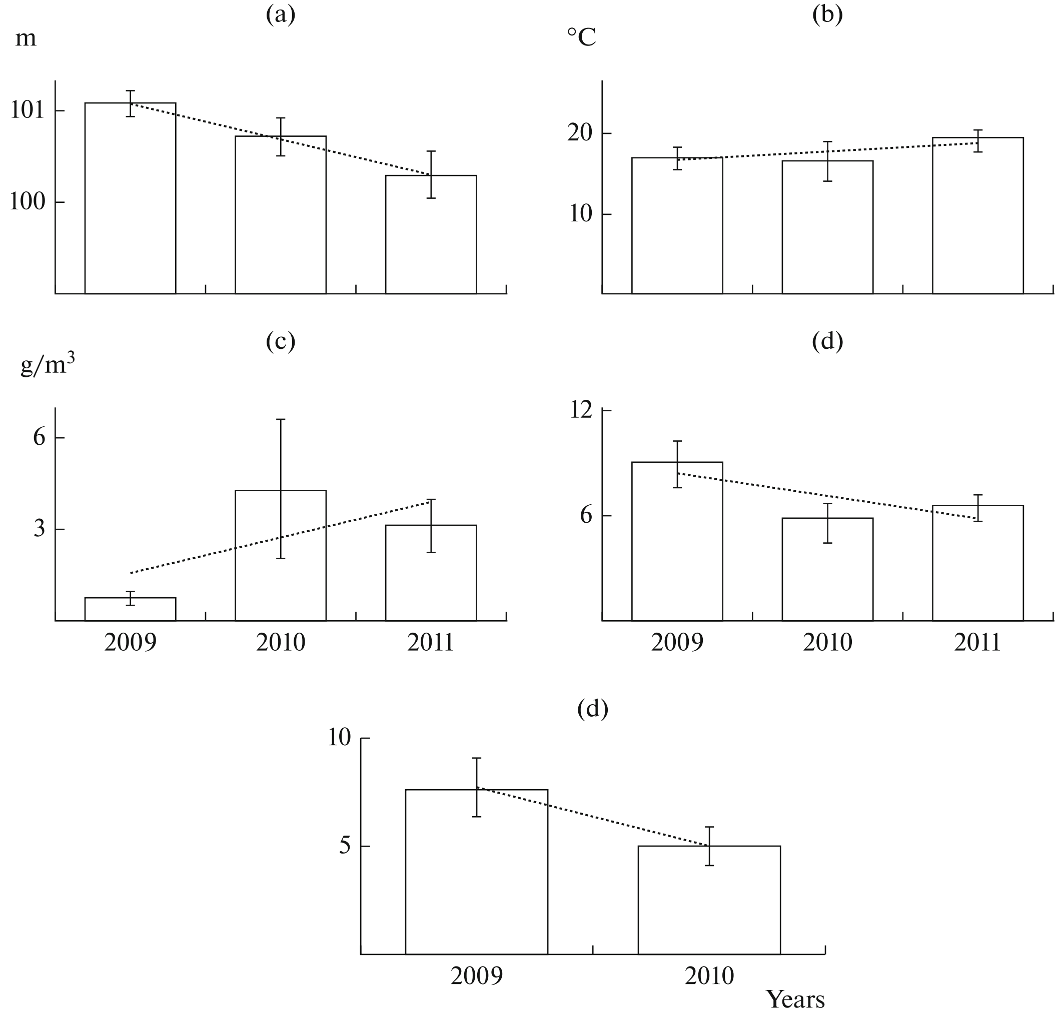

Fig. 2. Water level (a), temperature (b) and biomass of phytoplankton in a deepwater part of the reservoir (c), and protected (d) and open (e) shallow parts in years of studies (average values with standard error; dotted line is the line of the trend).

(Fig. 2a). The part of the protected shallow area was 60% covered with higher aquatic vegetation, with the dominance of common reed, lakeshore bulrush, water smartweed, and pondweeds.

Phytoplankton in the protected shallow zone had the highest taxonomic richness (316 taxa below the rank of genus). In the open littoral part and a deepwater part, 198 and 170 taxa were recorded, respectively. In 2010–2011, during the period of high temperatures and lower water level, algocenoses were enriched, mainly with green algae (Table 1).

In 2009, 2010, and 2011, the Shannon indexes of algocenoses in the protected shallow part varied within 3.34–4.78, 3.29–5.00, and 2.28–4.74 bit/(mg L), respectively. The minimum values of the index were recorded in the pelagial part of the reservoir (1.61–4.02, 1.72–3.74, and 2.03–3.37 bit/(mg L); in the open littoral zone they were 3.16–4.60 bit/(mg L) in 2009, and 2.02–4.21 bit/(mg L) in 2010.

The highest floristic similarity of algoflora was observed in the protected and open shallow areas in 2010–2011 (the Sørensen index 0.68–0.79); the maximum differences were found between the protected shallow zone and the deepwater part (0.34–0.57). Clustering of the floristic composition has shown a separate cluster of the deepwater part of the reservoir. A distinct recurrence of the sequence of this habitat is observed in the dendrogram (Fig. 3) in years. Shallow parts constituted the second cluster in which two groups are distinguished: the first group is formed by protected and open shallow parts during the period of increased water temperature (2010–2011); the second group includes shallow parts of the previous 2009 (Fig. 3).

The phytoplankton biomass varied from 2.20 to 15.1 g/m^3 in the protected shallow zone in 2009 and from 2.49 to 13.9 g/m^3 in 2010 (Fig. 2d). Diatoms (25 and 32% of the total biomass, respectively), cryptophytes (26 and 16%), euglenids (18 and 25%), dinoflagellates (10 and 12%), and green algae (12 and 10%)

Table 1. Number of taxa below the rank of genus in divisions of plankton algae in different parts of the Volga reach in the Rybinsk Reservoir during the years of surveys

Division of algae	Shallow part					Deepwater part		
	protected			open				
	2009	2010	2011	2009	2010	2009	2010	2011
Cyanoprokaryota	14	18	16	15	15	8	9	11
Chrysophyta	13	12	9	12	12	5	3	5
Bacillariophyta	24	24	24	25	25	19	23	29
Xanthophyta	8	8	10	6	6	0	1	1
Cryptophyta	8	6	5	6	6	4	4	5
Dinophyta	1	5	4	1	1	3	4	4
Chlorophyta	85	93	120	67	67	32	61	62
Euglenophyta	32	34	27	13	13	1	7	3
Total	185	200	215	145	145	72	112	120

made a considerable contribution to the biomass in 2009 and 2010. In 2011, the biomass varied within the same ranges as in two previous years (from 2.42 to 11.6 g/m^3). The contribution of diatoms (37%) was high; the proportion of green algae (37%) increased significantly; and the share of cryptophytes (9%), dinoflagellates (3%), and euglenids (8%) decreased.

The average total biomass of phytoplankton for the vegetation period was lower in the open shallow part than in the protected shallow part (Fig. 2e). The biomass was mainly formed by diatoms (54–64%); they were accompanied by cryptophytes (9–13%), dinoflagellates (8–10%), and green algae (11%). The minimum average biomass was recorded in the open part of the reservoir (Fig. 2c), where diatoms (72–88%) dominated during all years of survey. In 2010–2011 compared to 2009, the biomass of blue-green algae increased in the pelagial part (to 22% in 2011); the proportion of cryptomonads, on the contrary, decreased from 14 to 2%.

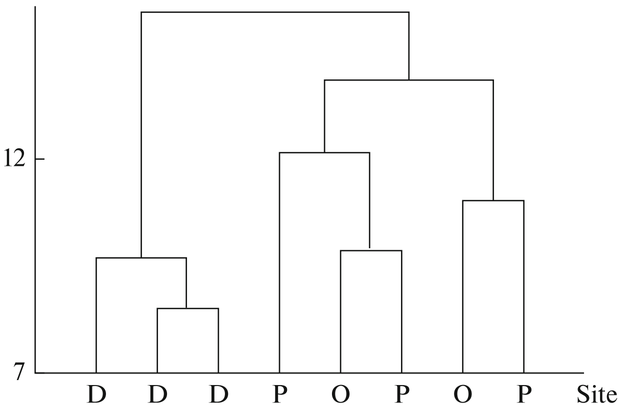

Fig. 3. Dendrogram of the floristic similarity of phytoplankton in shallow parts and deepwater part of the reservoir in the years of studies: (D) deepwater part of the reservoir, (P) protected shallow part, and (O) open shallow part. The Euclidian distance is along the ordinate axis.

The seasonal pattern of the phytoplankton biomass in the protected shallow area had four peaks in 2009 (Fig. 4). The late spring (May) peak (11.4 g/m^3) was caused by diatoms *Stephanodiscus hantzschii* Grun.; in July (15.1 g/m^3), in addition to diatoms, it was associated with cryptophytes *Cryptomonas curvata* Ehr. and *C. ovata* Ehr., dinoflagellates, and euglenids. The maximum in August (13.1 g/m^3) was caused by a complex of green algae, euglenids, and diatoms; the autumn (September) peak (12.9 g/m^3) was mainly caused by cryptomonads and euglenids. The phytoplankton biomass was lower in 2010 when compared to the previous year. The seasonal dynamics was characterized by one peak at the end of June (13.9 g/m^3) with the dominance of diatoms (*Aulacoseira granulata* (Ehr.) Sim., *Melosira varians* Ag.) and euglenids (*Euglena* sp.). In 2011, diatoms (*Aulacoseira granulata*) and green streptophyte algae adapted to highly colored acidic waters (such as *Desmidium swartzii* Ag., *Mougeotia* sp., *Spirogyra* sp., *Zygnema* sp.) prevailed in the biomass.

In 2009, in the open shallow part, three peaks of the biomass were recorded: in May (7.99 g/m^3) and July (17.2 g/m^3) with the dominance of diatoms *Stephanodiscus hantzschii, Ulnaria ulna* (Nitzsch) P. Compère, and *Navicula* sp., and in August (12.5 g/m^3) they were formed by cyanoprokaryotes *Microcystis aeruginosa* Kütz. The seasonal dynamics of phytoplankton in 2010 was also characterized by three peaks. The maximum values were recorded at the beginning of May (8.34 g/m^3) due to diatoms and at the beginning (8.67 g/m^3) and at the end (9.10 g/m^3) of June due to diatoms and dinoflagellates *Peridiniopsis kevei* Grigorszky et Vasas and

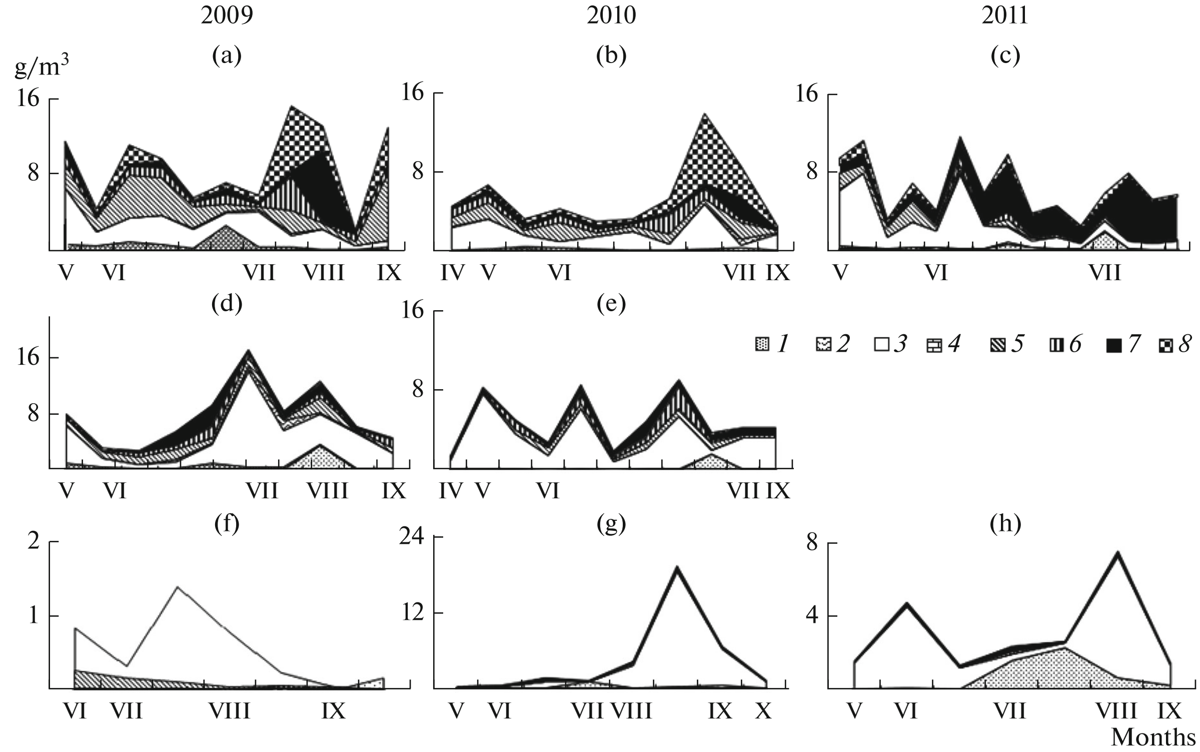

Fig. 4. Seasonal dynamics of the phytoplankton biomass in protected (a–c) and open (d, e) shallow parts and the deepwater part (f–h) in different years: (*1*) Cyanoprokaryota, (*2*) Chrysophyta, (*3*) Bacillariophyta, (*4*) Xanthophyta, (*5*) Cryptophyta, (*6*) Dinophyta, (*7*) Chlorophyta, and (*8*) Euglenophyta. Months are presented along the abscissa axis.

Peridiniopsis sp. The mass development of cyanoprokaryotes was observed at the beginning of August 2009 (*Microcystis aeruginosa*) and at the end of July 2010 (*Anabaena* sp. and *Aphanizomenon flos-aquae* (L.) Ralfs).

The seasonal dynamics in the deepwater part of the reservoir was determined mainly by diatoms (*Cyclotella meneghiniana* Kütz., *Stephanodiscus hantzschii, Aulacoseira ambigua,* and *A. granulata* (Fig. 4f–4h). These species usually form spring, summer, and autumn maxima of phytoplankton [12]. In 2009 and 2010, the spring peak of diatoms was weakly expressed; in 2011 it was prolonged. The summer peak in 2010 and 2011 was formed, mainly, by diatoms; in 2009 the peak was formed by diatoms accompanied by cyanoprokaryotes. The mass development of *Anabaena* sp. and *Aphanizomenon flos-aquae* (2010), *Microcystis aeruginosa*, *M. wesenbergii* (Kom.) Kom., and *Aphanizomenon flos-aquae* (2011) was recorded in July.

DISCUSSION

A comparative analysis of phytoplankton in different habitats of the Rybinsk Reservoir has demonstrated that the taxonomic diversity of algae was higher in the shallow part than in the deepwater part upon the maximum diversity of euglenids and green algae. The highest species richness was observed in the protected shallow zone overgrown with higher aquatic vegetation. It is suggested that macrophytes have advantages in the consumption of nutrients, thus suppressing the development of phytoplankton [20], but such a pattern is not always manifested. The studies conducted in overgrown and open parts in lakes of Argentine demonstrated the presence of a greater number of algae in areas with vegetation [26].

Over the period from 2009 to 2011, the floristic richness of phytoplankton increased both in shallow parts and the deepwater part of the reservoir under an increase in temperature and drop in water level. Similar results were obtained in the course of long-term studies on phytoplankton in the Volga River: the floristic richness of algae increased in the dry phase, which indicated its indirect relationship with the parameters of the water regime in reservoirs [12].

The average vegetative biomass of phytoplankton in the parts studied is comparable with the values obtained in the previous years [2, 6, 21, 22]. According to the criteria of trophy [9] in respect to this parameter, shallow parts in the Volga reach are eutrophic waters and the open part is mesotrophic. The highest biomass is typical for the protected shallow part; it decreases with depth. With the increase in temperature and decrease in water level in 2010–2011, the average biomass decreased >1.5 times in the littoral part and, on the contrary, it decreased considerably (3–4 times) in the pelagial part (Fig. 2).

The seasonal courses of the phytoplankton biomass were similar in the open shallow part and deepwater part. The number of maxima and minima of biomass increases in the protected area, which is usually observed with a decrease in depth and increase in variability of aquatic environmental conditions [6, 12].

The structure of phytoplankton varied considerably with decreasing depth and increasing isolation from the open part. The biomass of diatoms and cyanoprokaryotes decreased in the open littoral part, but the biomass of mixotrophic flagellates (cryptophytes, dynoflagellates, euglenids, and chrysophytes) and green algae (Conjugatophyceae), the main part of which was constituted by filamentous Zygnematales, increased. A considerable increase in the biomass of summer forms of diatoms *Aulacoseira ambigua* and *A. granulata* typical of eutrophic well-heated waterbodies [34] and the increase in the proportion of cyanoprokaryotes were observed in the deepwater part of the reservoir.

The degree of the dominance of species which are able to mixotrophic feeding and green filamentous algae increases with the increase in the trophic status, organic contamination [3, 35], and in highly colored acidic waters [11, 24, 37]. The rise in temperature and drop in water level in 2009–2011 promoted more active vegetation not only of filamentous Conjugatophyceae, but macrophytes as well, in the protected shallow part. This, apparently, created unfavorable light conditions for phytoplankton development and negatively affected the values of the total biomass. At the same time, the proportion of mixotrophic flagellates well-adapted to light limitation and capable of phagotrophy as an additional way of feeding and obtaining energy increased. As strengthening of the position of mixotrophs and filamentous algae against the background of depression of the total phytoplankton biomass is observed under conditions of water dystrofication [24], the structural changes in the littoral algocenoses and decrease in their total biomass may be due to the processes of overgrowing with higher aquatic vegetation and waterlogging.

In the 1950s, diatoms played a major role in the formation of phytoplankton biomass in the shallow zones [4, 21]; in the 1970s–1990s, the abundance and diversity of flagellate forms increased [2, 7, 22]. Similar structural changes occurred in the pelagial part of the reservoir; the differences were in scales and rates of the processes [12].

Values of the Shannon index which characterize the diversity of algocenoses were comparable with values obtained in the 1990s [22]. Since that period, the parameters of the cenotic diversity of phytoplankton increased in the shallow zone. High variability of the aquatic environment in the littoral zone (wind mixing, fluctuation of the water level, and quicker warming and cooling of water) results in a constant appearance of new ecological niches that explains the contribution of a larger number of algae to the total biomass. On the contrary, in the pelagial part, the indexes of diversity decreased in the long term [12].

CONCLUSIONS

A comparative study of phytoplankton in different shallow parts and in a deepwater part of the Volga reach in the Rybinsk Reservoir has demonstrated that the floristic diversity was formed, mainly, by green algae and euglenids in the protected shallow part and green algae and diatoms in the open shallow and deepwater parts. The flora composition in habitats depended to a greater extent on depth and water temperature. The total floristic richness, cenotic diversity, and total biomass of phytoplankton, especially of flagellates (euglenids, dynoflagellates, cryptophytes, and chrysophytes) and green algae increased and the abundance of diatoms and cyanoprokariotes decreased with the decreasing depth of the biotope. In 2009–2011, with the rise of temperature and drop in the water level, the negative trend of the total biomass was observed in the shallow parts; for all that, the biomass of green algae and cyanoprokaryotes increased in the protected shallow zone. The biomass of different groups of phytoflagellates decreased in the open shallow zone and in the deepwater part of the reservoir; in the pelagial part, phytoplankton was enriched with green algae species and the biomass of cyanoprokaryotes increased.

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