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Long-Term Dynamics of Chlorophyll in Plankton of Different Sites in a Large Plain Reservoir

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Abstract—On the basis of field observations in 2009–2019, the seasonal and long-term dynamics of chlorophyll at six standard stations of the Rybinsk Reservoir is considered. The fluorescence method is used to determine chlorophyll. The average chlorophyll content at stations varies from the minimum 3.5–10.8 to the maximum 16.9–40.5 µg/L in different years and from 12.0 at station 5 (Sredny Dvor) up to 21.6 µg/L at station 2 (Mologa) on average for the entire period. The seasonal dynamics of chlorophyll is characterized by spring; summer; and, in some years, autumn maxima. With the same type of seasonal dynamics, the change in chlorophyll at the stations is to varying degrees coupled in the years of observation and is most often correlated in neighboring areas. Significant differences in the amount of chlorophyll at the stations are observed during surveys carried out within one day and are determined by the complex hydrological structure of the reservoir; active dynamic processes; and, in the spring, by the thermal regime. The presence of stable large circulation zones smoothes out the spatial differences of chlorophyll, the average seasonal concentrations of which do not differ significantly at all six stations in years with an average water level, and at four stations of the Main Reach in extremely high-water years. A close correlation in long-term dynamics is revealed for the average chlorophyll concentrations for the growing season at six stations, as well as at each station and the reservoir as a whole. The results of the work confirm the reliability of the data obtained for assessing the ecological state of the Rybinsk Reservoir.

Keywords: chlorophyll, phytoplankton, standard stations, long-term observations, Rybinsk Reservoir

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INTRODUCTION

The role of phytoplankton in the functioning of freshwater ecosystems and the formation of their biological productivity is well known. The algae growth determines the nutritive base, the production potential of biotopes, and ecological state of water bodies (Vinberg, 1960; Kitaev, 2007). The study of spatial and temporal dynamics, as well as environmental factors that are directly associated with the community development, are the most important aspects of the study of phytoplankton (Padisák, 2004). Photosynthetic pigments, which are universal ecological and physiological characteristics of the development and photosynthetic activity of algae of a high informative value, are widely used in the study of the autotrophic link in the

aquatic food webs. The identification of pigments is a useful tool for the study of long-term trends in the phytoplankton development and assessment of the state of fresh, marine, and oceanic waters. Long-term series records were obtained for many water bodies around the world (Ruggiu et al., 1998; Kangur et al., 2002; Chen et al., 2003; Babanazarova and Lyashenko, 2007; Mendesab et al., 2011; Canfield et al., 2018; Lamont et al., 2019; Gao et al., 2020; etc.).

Studies on plant pigments in the water of the Rybinsk Reservoir have been carried out at the Institute for Biology of Inland Water, Russian Academy of Sciences, since the middle of the 20th century (*Fitoplankton* ..., 1999; *Ekologicheskies* ..., 2001; *Struktura* ..., 2018). Since 2009, the extensive data obtained by the standard spectrophotometric method (SCOR-UNESCO, 1966) have been supplemented with fluorescent diagnostics (Mineeva, 2016; Mineeva and Semadeni, 2020), which makes it possible to determine chlorophyll directly in natural water, evaluate some characteristics of phytoplankton without affecting its integrity, and timely analyze a large volume of material. All these years, the studies have been carried out at six

Abbreviations: Chl_{Bac}, chlorophyll *a* of diatoms; Chl_{Chl}, chlorophyll *a* of green algae; Chl_{Cyan}, chlorophyll *a* of cyanoprokaryotes; ΣChl *a*, total chlorophyll *a*; C_v, coefficient of variation; H_{mix}, depth of mixing; *n*, number of surveys; *p*, significance level; *r*, correlation coefficient; *r*_{0.05}, tabulated value of *r* at *p* < 0.05; R², coefficient of determination; *t*, Student's *t*-test; Z_S, Secchi disk transparency; Z_{Chl}, transparency calculated using chlorophyll content; Z_{eu}, euphotic zone depth.

standard stations, using the data obtained as a basis for the analysis of the state and successional changes in the reservoir ecosystem. In this regard, it is important to know to what extent the development of phytoplankton is interrelated between different parts of the water area and how it reflects the situation in the reservoir as a whole. The aim of this study is to make a comparative analysis of the seasonal and long-term dynamics of chlorophyll at standard stations in the Rybinsk Reservoir.

MATERIALS AND METHODS

The material was collected at six stations in the Volga and Main reaches in the Rybinsk Reservoir once or twice a month during the vegetation seasons of 2009–2019. Samples were collected with 1-m Elgmork water sampler at 0–2 m, 2–6 m, and 6 m–bottom horizons. In the paper, the average chlorophyll content for these layers was used, which was determined using the fluorescence method (Gol'd et al., 1986). This method makes it possible to estimate the total amount of pigment (ΣChl) by its content in the main representatives of freshwater phytoplankton, cyanoprokaryotes (Chl_{Cyan}), diatoms (Chl_{Bac}), and green algae (Chl_{Chl}). Chlorophyll fluorescence was measured on a stationary PFL-3004 fluorimeter (Krasnoyarsk State University). The procedure of analysis was described earlier; the results of the fluorescent determination of chlorophyll coincide well with the results of the standard spectrophotometric method (Mineeva, 2016).

Water transparency, temperature, and color were measured at all stations. To assess the contribution of phytoplankton to the total amount of suspended matter, the ratio of transparency measured with the Secchi disk (Z_s) to that calculated based on the chlorophyll content was used (Z_{Chl}) ($Z_{\text{Chl}} = 5.7\Sigma\text{Chl}^{-0.44}$ (Bul'on, 1985)). To characterize the light-dependent status of algae, the depth of the euphotic zone (Z_{eu}) was calculated that was 2.6 times higher than Z_c (Mineeva, 2009), as well as the ratio of Z_{eu} to the mixing layer H_{mix} , for which the depth of the stations was taken under the homothermic conditions.

Statistical data analysis, including calculations of the mean values, their errors, correlation, regression analysis and analysis of variance, and plotting the graphs, was made using standard PC software packages. The Spearman rank correlation coefficient was used to assess the strength of the relationship between the variables.

The Rybinsk Reservoir, the third stage of the Volga cascade, is a large relatively shallow reservoir with a slow water exchange rate (the average coefficient of conditional water exchange is 1.9 yr^{-1}) located in the subzone of the southern taiga ($58^{\circ}00' - 59^{\circ}05' \text{ N}$, $37^{\circ}28' - 39^{\circ}00' \text{ E}$). With a mirror area of 4500 km^2 and an average depth of 5.6 m, their ratio (~ 800) indicates

a high degree of openness of the reservoir (Kitaev, 2007). The water area of the reservoir is subdivided into four heterogeneous areas (reaches) occupied by water masses with specific hydrophysical and hydrochemical characteristics. Three reaches are located along flooded channels of the main tributaries, Volga, Mologa, and Sheksna rivers. River waters are gradually transformed into the water mass of the reservoir proper, which occupies a lakelike central part, the Main reach constituting $\sim 70\%$ of the total area (Rybinskoe ..., 1972).

The years of observations in the multiyear time series were generally characterized as warm, but they differed significantly in weather conditions (Struktura ..., 2018). Water temperature in May to October was close to the average long-term temperature (13.6°C), and in 2009–2015 it exceeded the average values. The maximum summer water temperature was mostly $20 - 24^{\circ}\text{C}$, reaching abnormally high values of $25 - 27^{\circ}\text{C}$ in 2010 and 2018. According to the water level, 10 out of 11 years of observations were high-water years, with the inflow volume greatly exceeding the norm in 2017 and, in the extremely low-water year of 2014, the inflow drastically decreased.

The level of the reservoir exceeded the normal headwater level of 101 m BS in 2009–2012, 2016, and 2017 and was extremely low in 2014 (<http://www.rushydro.ru/hydrology/informer/?date>).

RESULTS

Standard stations cover the main part of the water area in the Rybinsk Reservoir (Fig. 1) and reflect the transition of river waters into the water mass of the reservoir. Deeper stations are located on the flooded riverbeds of the Volga (stations 1, 2), Sheksna (station 5), and Mologa (station 6) rivers, while stations 3 and 4 are in the central part of the Main Reach with a depth close to the average for the reservoir. During the study period, the average hydrological and hydrochemical parameters at the stations are characterized by similar values (Table 1). Against the general background, station 1, which receives the waters of the Ivankovo and Uglich reservoirs and preserves the conditions of flowing water, is characterized by higher temperature, transparency, mineralization, and content of biogenic substances. The minimum transparency was recorded at station 6, which is reached by the most colored and least mineralized waters of the Mologa River, and the maximum concentration of total nitrogen was recorded at station 5 due to the probable effect of the Cherepovets Industrial Complex. The average depth of the euphotic layer is $\sim 3 \text{ m}$ and is 4.1–4.9 times lower than the depth of the mixing layer and 2.1–2.7 times lower than that at channel stations in the floodplain. The Z_s/Z_{Chl} ratio, which is significantly lower than one, indicates the low contribution of algae to the total content of suspended particulate matter (Table 1). The coefficients of variation of the above parameters are $\leq 35\%$.

Fig. 1. Schematic map of the Rybinsk Reservoir and sampling stations. Figures denote station numbers (Koprino, Mologa, Navolok, Izmailovo, Sredny Dvor, and Breitovo, 1–6, respectively); lines are boundary of reaches.

The ΣChl content at all stations varies from <1 to $50\text{--}130\text{ }\mu\text{g/L}$; the average values for some years vary from the minimum of $3.5\text{--}10.8$ to the maximum of $6.9\text{--}40.5\text{ }\mu\text{g/L}$ and the average values for the entire study period vary from 12.0 to $21.6\text{ }\mu\text{g/L}$, respectively (Table 2).

The lowest ΣChl concentrations were recorded at station 5 and the highest ones at station 2. A significant variation of ΣChl was found at each station at the coefficients of variation $C_v \sim 100\%$ in the Volga Reach and $74\text{--}90\%$ in the Main Reach. Judging by the frequency of occurrence, concentrations of $\Sigma\text{Chl} < 10\text{ }\mu\text{g/L}$ typical for mesotrophic waters prevail at stations 1, 3, and 5, and at stations 2, 4, and 6, concentrations of $10\text{--}30\text{ }\mu\text{g/L}$ typical for eutrophic conditions prevail. Values of $>30\text{ }\mu\text{g/L}$ constituted a small proportion of the integral sample ($7\text{--}12\%$) in the Main Reach and a more noticeable proportion (23%) in the Volga Reach at station 2 (Fig. 2). In some periods of studies, the ΣChl content varied to a different degree over the reservoir area. More frequently (in 62% cases according to the data of 91 sampling events), the maximum and minimum values differed by $2\text{--}5$ times, more seldom (29%) by $6\text{--}10$ times, and more significantly in 9% of cases.

The chlorophyll content of the main divisions of algae is also characterized by a wide range of values (Table 2). The coefficients of variation for Chl_{Cyan} , Chl_{Bac} , and Chl_{Chl} , with a few exceptions, are $>100\%$. The average amount of Chl_{Cyan} for the stations varies from 8.5 to $12.2\text{ }\mu\text{g/L}$ and that of Chl_{Bac} from 2.9 to $8.8\text{ }\mu\text{g/L}$; similar low values are found for Chl_{Chl} . The

Fig. 2. Frequency of occurrence of chlorophyll (ΣChl) at standard stations in the Rybinsk Reservoir in 2009–2019 (% of the total number of observations n). $\square <10$, $\blacksquare 10\text{--}30$, and $\blacksquare >30\text{ }\mu\text{g/L}$. At stations 1 and 2, $n = 276$; at stations 3, 5, and 6, $n = 269$; at station 4, $n = 176$.

maximum values of the above parameters were obtained at station 2. The content of Chl_{Cyan} and Chl_{Bac} determines the total chlorophyll amount, averaging $55.6\text{--}74.4\%$ and $24.2\text{--}41.8\%$ of its total stock (Table 2). This contribution varies annually and seasonally. Chl_{Bac} may constitute a considerable ($>90\%$) proportion of the ΣChl in spring and late autumn and Chl_{Cyan} in summer months and early autumn; their seasonal dynamics is not correlated (Mineeva and Semadeni, 2020).

At a significant range of ΣChl concentrations, their distribution in the seasonal cycle during the years of study is asymmetric at all stations. This is demonstrated by standard error bars on the plot box, as well as the medians which differ from the arithmetic mean by $1.3\text{--}1.5$ times (Fig. 3, Table 2). The outliers beyond the lower 25% quartile are in most cases small and are most noticeable only in 2013 at stations 1–4 and 6 and, in 2014, at station 2. The outliers beyond the upper 75% quartile are much more significant, especially at stations 1, 3, 4, and 6 in 2011; at stations 1–3, 5, and 6 in 2013; and at stations 1 and 3–6 in 2018.

The seasonal dynamics of chlorophyll is characterized by alternating rises and falls. The spring maximum of ΣChl with average concentrations of $24\text{--}34\text{ }\mu\text{g/L}$ for the entire period of studies at stations 1–4 and $13\text{--}14\text{ }\mu\text{g/L}$ at stations 5 and 6 is formed in May at a water temperature from 15.3°C at station 1 to 6.8°C at station 5 (Fig. 4). It was recorded simultaneously at all six stations only in 2012; at two stations in the Volga Reach and at station 6 also in 2013, 2015, 2016, and 2018; and at two or three stations in the central part in 2016, 2017, and 2019. In some cases, low ($3\text{--}5\text{ }\mu\text{g/L}$) concentrations of ΣChl were also recorded in the spring. They were observed at all stations in 2010, at central stations in 2015; in the southern and western parts in 2017; and at the northernmost station 5 in 2013, 2015, and 2018. Water temperature during these periods was mostly $5.5\text{--}10.1^\circ\text{C}$; in 2010, it was $\sim 3^\circ\text{C}$ in the central part of the reservoir. In early summer, in June, the ΣChl content at a temperature of $16\text{--}17^\circ\text{C}$ decreased to $9\text{--}11\text{ }\mu\text{g/L}$ at stations 1, 2, and 6 and to $7\text{--}8\text{ }\mu\text{g/L}$ at other stations.

Table 1. Characteristics of standard stations in the Rybinsk Reservoir

Parameter	Koprino (1)	Mologa (2)	Navolok (3)	Izmailovo (4)	Sredny Dvor (5)	Breitovo (6)
Coordinates	58°04.23' N 38°17.56' E	58°12.47' N 38°27.34' E	58°22.38' N 38°23.22' E	58°27.44' N 38°28.47' E	58°30.31' N 38°21.01' E	58°19.20' N 37°56.58' E
Depth, m	11.6 ± 0.1	12.9 ± 0.1	7.5 ± 0.1	5.9 ± 0.1	13.1 ± 0.2	12.2 ± 0.1
Temperature, °C	16.1 ± 0.5	15.4 ± 0.6	15.1 ± 0.6	15.2 ± 0.6	15.2 ± 0.6	16.0 ± 0.6
Z _S , m	1.19 ± 0.04	1.15 ± 0.04	1.12 ± 0.03	1.13 ± 0.03	1.13 ± 0.03	1.02 ± 0.03
Color, Cr-Co degree	55 ± 2	55 ± 2	57 ± 2	55 ± 1	55 ± 1	68 ± 3
Z _{eu} , m	3.0 ± 1.0	3.0 ± 1.8	2.9 ± 1.6	2.9 ± 1.3	2.9 ± 1.3	2.6 ± 1.3
H _{mix} /Z _{eu} , rel. units	4.1 ± 0.1	4.7 ± 0.1	2.7 ± 0.1	2.1 ± 0.1	4.8 ± 0.2	4.9 ± 0.1
Z _S /Z _{chl} , rel. units	0.54 ± 0.24	0.66 ± 0.28	0.57 ± 0.19	0.61 ± 0.19	0.54 ± 0.22	0.54 ± 0.23
Total nitrogen, mg/L*	0.95	0.98	0.76	0.79	1.08	0.83
Total phosphorus, µg/L *	95	62	50	54	60	60
Mineralization, Mg-eqv/L**	4.88	4.54	4.48	4.50	4.47	4.29

Average values for the study period and their standard errors are given. Station number is given in brackets.

* Average for 2008–2013.

** 2004–2013, respectively, according to (*Struktura ...*, 2018).

Table 2. Chlorophyll content at standard stations in the Rybinsk Reservoir in 2009–2019

Station number	ΣChl	Chl _{Cyan}		Chl _{Bac}		Chl _{Chl}	
	µg/L	µg/L	%	µg/L	%	µg/L	%
1	15.3 ± 1.7 (104)	8.5 ± 1.3 (151)	55.6	6.4 ± 0.9 (137)	41.8	0.4 ± 0.1 (148)	2.6
2	21.6 ± 2.1 (95)	12.2 ± 1.4 (112)	56.5	8.8 ± 1.3 (142)	40.7	0.6 ± 0.2 (284)	2.8
3	14.6 ± 1.4 (89)	10.1 ± 1.3 (117)	69.2	4.1 ± 0.7 (165)	28.1	0.4 ± 0.1 (181)	2.7
4	15.5 ± 1.2 (75)	11.2 ± 1.1 (94)	72.2	3.9 ± 0.6 (141)	25.2	0.4 ± 0.1 (146)	2.6
5	12.0 ± 0.9 (74)	8.9 ± 0.9 (98)	74.2	2.9 ± 0.3 (100)	24.2	0.3 ± 0.0 (128)	2.6
6	15.3 ± 1.3 (80)	9.7 ± 1.2 (113)	63.4	5.3 ± 0.5 (83)	34.6	0.4 ± 0.1 (136)	2.5

Average values and their standard error are given. The coefficient of variation (%) is in brackets. See Table 1 for station numbers.

In July–August, during the period of water temperature rise to 20°C and above, the summer phytoplankton maximum is formed with average ΣChl concentrations of 35–40 µg/L for all years at stations 1, 2, and 6 and 26–30 µg/L at stations 3–5. The summer maximum mostly prevails in the seasonal cycle, but it is inferior to the spring maximum in some years (more often in 2016–2019), and in 2009, 2017, and 2019 the summer peak was not observed (Fig. 4). In late summer and early autumn, when the temperature of water mass begins to fall, the pigment content first decreases slightly, and at a water temperature below 10°C it reaches the minimum values of 2–7 µg/L. However, in late autumn, high values may be observed: in October 2014, 23 and 41 µg/L in the Volga Reach at water temperature of 7–10°C; in October 2018, 10–15 µg/L at the same temperature at stations 2, 3, and 5 and, in November, at 3.6°C at station 4.

In general, the similar seasonal dynamics of phytoplankton is observed at all stations, which is characterized by the change in the rise and fall of ΣChl. However, these phenomena are not synchronous and changes in ΣChl at the stations during the growing season are correlated, to a varying degree, during the study years. The maximum number of reliable correlations (8–10 out of 15 possible for each year) was found in 2010, 2012, and 2018; the minimum (3 and 1) was in 2009 and 2017; intermediate (5–7) was in the remaining years; and the largest number of high correlation coefficients >0.7 (9 out of 10) was in 2018. Most frequently (in 5–7 cases out of 11 years of studies), the seasonal pattern of chlorophyll is correlated in adjacent (neighboring) sections of the reservoir, as is evidenced by reliable correlation coefficients obtained for station 2 and stations 3 and 6; for station 3 and stations 4, 5, and 6 (Table 3).

Fig. 3. Box plots of chlorophyll concentrations at stations 1–6 (a–f, respectively) in 2009–2019. (1) Boundaries of 25% and 75% quartiles, (2) median, (3) max, and (4) min.

In the absence of a stable seasonal dynamics of chlorophyll in different parts of the reservoir, the results of the cluster analysis show a sufficiently close correlation of the quantitative phytoplankton development between stations in the years of studies (Fig. 5). A common cluster is most often formed by the stations in the Main Reach (in 2010–2012, 2017, 2019, all stations; in 2013–2015, stations 3–5) located in the central part of the reservoir and only in 2010 in two stations of the Volga Reach. It is common when one station stands apart, mainly station 1, as well as stations 2, 4, and 6; station 2 is often adjacent to the stations in the central part of the reservoir; in 2013 and 2015, station 6 is combined with the Volga stations.

Despite the specificity of seasonal dynamics and quantitative development of phytoplankton in different parts of the reservoir, the results of the analysis of variance demonstrate the absence of significant differences in the ΣChl content at the stations for all study years (Table 4). Differences were found only in 2009 and 2017 at contrast ΣChl concentrations at the stations of the Volga Reach, but they become insignificant when these stations are excluded from calculations. The comparison of the average ΣChl concentrations at the stations during the growing season shows the presence of a close correlation between them in the long-term dynamics. Only in three cases are the correlation coefficients <0.70 (Table 5). The ΣChl concentrations at station 1 explains 76% of the

variation of the average parameter for the reservoir; at stations 2 and 6 it is 85 and 88%; and, at stations 3–5 it is 53–59%.

DISCUSSION

Depending on the features of the water body, the determining factors of development of aquatic organisms can be physical, chemical, or biotic (Chen et al., 2003; Reynolds, 2006; Yang et al., 2016). The phytoplankton in the Rybinsk Reservoir does not experience a shortage of biogenic substances (Mineeva et al., 2021), the seasonal changes of which occur within natural fluctuations and indicate the stabilization of their regime in the last 40 years (Stepanova et al., 2013). Standard stations are located in parts which are heterogeneous in morphometry. With the similarity of the average long-term hydro-optical parameters (Table 1), the transparency, color, and depth of the euphotic zone change significantly during the growing season (Mineeva, 2009) and, in fact, the phytoplankton lives at the stations under different hydro-optical conditions. Namely, the light regime has a significant effect on the development and productivity of algae and becomes a limiting factor when algae are sufficiently provided with biogenic nutrition and/or when water transparency is low (Kalff, 2002; Nasci-

Fig. 4. Seasonal dynamics of chlorophyll at standard stations in the Rybinsk Reservoir in 2009–2019; (a) stations 1 and 2, (b) stations 3 and 4, and (c) stations 5 and 6.

mento Moura et al., 2012; Burson et al., 2018). The light regime, characterized by transparency (Dovgii, 1977), is one of the main factors affecting the long-term dynamics of the phytoplankton in the Rybinsk Reservoir (Mineeva, 2021).

The ratio of the mixing zone (in the conditions of homothermy, the depth of the station) to the euphotic zone indicates a different light status of algae (the availability of light energy for them). For all observations without exception, this ratio is significantly greater than one, and the situation in which the algaecolony would be constantly in the illuminated layer ($H_{\text{mix}}/Z_{\text{eu}} = 1$) (Bormans et al., 2005) was not found at any station. The water transparency in the Rybinsk Reservoir is mostly determined by the total amount of suspended particulate matter, in which the proportion of the algal component is low (the Z_s/Z_{chl} ratio < 1) (Mineeva, 2009). The input of the suspended matter occurs when the bottom sediments are resuspended under effect of the wind action, to which the open water area of a large shallow water body is often exposed. The agitation of bottom sediments changes

not only the underwater light conditions, but also the concentration of nutrients (Öterler et al., 2015), providing their additional supply to the water column. Therefore, weather conditions (wind action) can be one of the factors affecting the phytoplankton development and, consequently, variations in the trophic status of the reservoir.

The Rybinsk Reservoir is a water body with a complex hydrological structure and water masses of various geneses with specific physical and chemical parameters. The presence of wind and runoff currents, as well as circulation zones, is a specific feature of the hydrodynamics of the reservoir. Morphometric and morphological characteristics of the reservoir, the interaction of water masses, and hydrological processes affect the spatial distribution of organisms (Bakastov and Litvinov, 1971; Rybinskoe ..., 1972; Litvinov and Rivier, 1991; *Ekologicheskies* ..., 1993). The complex hydrological structure determines the macroscale heterogeneity of the horizontal distribution of phytoplankton, which is associated with the formation of fields with different productivities and trophic state (*Ekologicheskies* ..., 1993; *Struktura* ..., 2018). As a result, significant differences are found in the amount of chlorophyll at the stations during 1-day surveys. A similar difference for the sites far from each other at a distance comparable with the location of standard stations in the Rybinsk Reservoir was found in a number of lakes and reservoir (Antenucci et al., 2005; Bormans et al., 2005; Rakočević, 2012; Yang et al., 2020). The spatial heterogeneity indicates a difference in the factors controlling the phytoplankton growth and the course of its seasonal succession in different areas, which is typical for shallow water bodies with a large water area (Wetzel, 2001). Local weather conditions (solar radiation inflow and wind speed and direction) within a large water area may differ even under a similar synoptic situation in the region, and patchiness of phytoplankton distribution may be a result of spatial variations of biological processes (growth, grazing, controlled buoyancy, vertical migrations) or advective transport (Wiedner et al., 2002; Reynolds, 2006).

The distribution of plankton in the Rybinsk Reservoir is regulated by the presence of large circulation zones and smaller multidirectional cycles (Butorin et al., 1982; *Ekologicheskies* ..., 1993). According to observations and calculations, the movement of zooplankton aggregations in the reservoir in the direction of integral transport can reach 7–9 km per month, taking into account the two-layer flow, and can be an order of magnitude greater without taking into account the latter (Bakastov and Litvinov, 1971). The diameter of zooplankton aggregations is estimated to be 10–12 km, which is comparable to the size of the nuclei of the main circulation zones. The highest het-

erogeneity in the distribution of plankton is observed during prolonged calm weather (Litvinov and Rivier, 1991). Circulation flows arising under the wind action and bottom relief can carry out algae aggregations to the open part which were brought into shallow waters by the wind-driven effect (*Ekologicheskies ...*, 1993); this is often observed during the mass vegetation of cyanoprokaryotes. Of six standard stations, 4 and 6 are located closer to the shore, where the summer rise of chlorophyll can be associated with a wind surge. Based on the scheme of integrated water circulation (Butorin et al., 1982), it can be suggested that station 3 is located in the zone of interaction of three large circulation formations and station 5 is in the center of an anticyclonic vortex in the northern part of the Main Reach. Apparently, the circulation processes smooth the spatial heterogeneity of phytoplankton, and the content of chlorophyll in adjacent areas of the reservoir is often correlated. In years with an average water level, large circulation zones are quite stable during the growing season, but can be disturbed in years with extreme water levels (Butorin et al., 1982). The presence of these zones probably reduced and made insignificant the differences in the average seasonal concentrations of chlorophyll at the stations during 9 of the 11 years of studies. The significant differences were found in 2009 and 2017, the first year of which was characterized by a high water level against the general background and, the second, by an extreme water level with an inflow volume of 18.47 and 23.0 km³ in May–October, respectively (Mineeva, 2021). During these years, the seasonal dynamics of chlorophyll is weakly correlated at the stations.

The average seasonal concentrations of chlorophyll over a 11-year period differed by 2.6–4.7 times at stations 2–6 and by 8 times at station 1. This part of the Volga Reach, from the point of view of hydrology, is considered a large bay where either the accumulation or dispersion of algae occurs, depending on the wind direction (Podubnyi et al., 1990). When the distribution of phytoplankton is uneven in the water area of the reservoir, station 2 (*Struktura ...*, 2018), which is located at the boundary of the Volga and Main reaches and is an ecotone zone, is traditionally characterized by the maximum abundance (biomass, amount of ΣChl and chlorophyll of the main divisions of algae). It is known that, in the zones of transformation and mixing of water masses in freshwater and marine ecosystems, an intensification of physicochemical and biological processes and an increase in the biomass, abundance, and species diversity of aquatic organisms occur (*Ekologicheskies ...*, 1993; Krylov et al., 2010; Sakharova, 2017; Cadier et al., 2017). The lowest concentrations of chlorophyll were recorded at station 5, located to the north of the other stations.

Table 3. Years of studies during which reliable coefficients of correlation between chlorophyll content were obtained at stations in the Rybinsk Reservoir

Stations	Years of study
1–2	2010, 2013, 2016, 2018
1–3	2010, 2011, 2016, 2018
1–4	2010
1–5	2018
1–6	2012, 2013, 2015, 2018
2–3	2010, 2012, 2014, 2015, 2016, 2018, 2019
2–4	2010, 2012, 2015, 2019
2–5	2010, 2012, 2014, 2018
2–6	2009, 2012, 2013, 2014, 2018
3–4	2010, 2011, 2012, 2013, 2015, 2019
3–5	2010, 2011, 2012, 2013, 2014, 2015, 2018, 2019
3–6	2009, 2010, 2011, 2012, 2014, 2017, 2018
4–5	2011, 2013, 2015
4–6	2016
5–6	2009, 2011, 2014, 2015, 2016, 2018, 2019

$r = 0.5–0.7$, bold, $r > 0.7$, $r_{0.05} = 0.5$.

Table 4. Results of a comparison of the average chlorophyll concentrations for the growing season at standard stations in the Rybinsk Reservoir during the study years using one-way analysis of variance (ANOVA)

Year	Stations	SS	df	F	p
2009	1–6	1090	53	3.53	0.008
	3–6	472	35	0.97	0.420
2010	1–6	6694	46	0.27	0.928
2011	1–6	24068	53	1.48	0.213
2012	1–6	4820	53	1.95	0.103
2013	1–6	20092	59	1.87	0.116
2014	1–6	8154	33	1.55	0.206
2015	1–6	988	21	1.29	0.316
2016	1–6	9928	53	0.59	0.706
2017	1–6	2167	53	2.51	0.049
	3–6	471	35	1.86	0.156
2018	1–6	8504	53	0.08	0.996
2019	1–6	5383	53	0.33	0.891

SS, sum of squared deviations; df, number of degrees of freedom; F, F-test; F critical > 2.41; and p, significance level.

The seasonal development of plankton is an annually recurring process that is affected by external factors and internal interactions (Reynolds, 2006). In

Fig. 5. Dendrogram of similarity of standard stations in the Rybinsk Reservoir in terms of chlorophyll content in 2009–2019. The Euclidean distance is on the ordinate axis and the station numbers are on the abscissa axis.

large shallow reservoirs, which are an active dynamic environment, the course of seasonal succession of phytoplankton is subject to a frequent disturbing external effect (Honti et al., 2007; Sommer et al., 2012; Yang et al., 2016), which includes wind mixing (Bormans et al., 2005; Nascimento Moura et al., 2012), and also the operation of hydraulic structures in reservoirs. The seasonal dynamics of chlorophyll in the Rybinsk Reservoir corresponds to the classical model (Sommer et al., 2012) and is characterized by two or

three peaks. However, the timing of their occurrence and duration and concentrations of chlorophyll at stations change not only in years with different weather conditions, but they are not always synchronous in the same year (Mineeva, 2016; Mineeva and Semadeni, 2020). The probable reasons for this are discussed above. The development of the spring community is also associated with the thermal regime, which is confirmed by the difference in the timing of the onset of chlorophyll maxima at the stations and the water tem-

Table 5. Correlation coefficient between the average concentrations of chlorophyll during the growing season at standard stations

Station	Koprino	Mologa	Navolok	Izmailovo	Sredny Dvor	Breitovo
Koprino	1.00	—	—	—	—	—
Mologa	0.92	1.00	—	—	—	—
Navolok	0.75	0.73	1.00	—	—	—
Izmailovo	0.55	0.71	0.77	1.00	—	—
Sredny Dvor	0.69	0.76	0.59	0.77	1.00	—
Breitovo	0.80	0.85	0.72	0.75	0.95	1.00

$n = 11$; $r_{0.05} = 0.52$.

perature at which these maxima are formed and which is higher in the Volga Reach than in the Main Reach (Mineeva, 2004).

In the absence of synchronous dynamics of phytoplankton in different parts of the reservoir, local low (often high) concentrations of chlorophyll determine their asymmetric distribution in the seasonal cycle. Outliers beyond the upper 75% quartile in the box plot (Fig. 3) are caused by the seasonal phytoplankton maxima and high concentrations of Chl_{Cyan} in the summer–autumn period and Chl_{Bac} in spring and late autumn. The most pronounced seasonal peaks of Chl_{Cyan} and Chl_{Bac} were observed in the reservoir in 2011, 2013, and 2018 (Mineeva, 2021), that is, in years with a large range of ΣChl . At low concentrations of one of these components, the spread of ΣChl decreases.

The average concentrations of ΣChl at stations mostly corresponded to the category of mesotrophic waters in 2009 and 2017; moderately eutrophic in 2010 and 2019; eutrophic in 2011–2014 and 2018; and, at station 2, to the category of hypertrophic waters in 2011 and 2013. In 2015 and 2016, the trophic status of the sites changed from mesotrophic to eutrophic. Interannual variations of chlorophyll depending on the hydroclimatic conditions were found in water bodies of different regions. In highly eutrophic water bodies, they do not go beyond their trophic category (Babanazarova and Lyashenko, 2007; Rusanov et al., 2020); in moderately eutrophic, including the Rybinsk Reservoir, values typical for different trophic categories are observed in different years (Kangur et al., 2002; Mineeva, 2016; Mineeva and Semadeni, 2020).

The assessment of the external influence on the development of phytoplankton in the reservoir is complicated by the presence of factors that are difficult to take into account or uncontrolled, as is indirectly evidenced by a significant difference between the average concentrations of chlorophyll during the growing sea-

son and their medians. In fact, the development of biological communities in artificial water bodies is subject to the effect not only of local weather conditions and climate, but also of the operating mode of hydraulic structures. The maximum development of phytoplankton is observed in low-water years with calm weather and high insolation and water temperature; the minimum development is found under opposite conditions (Pyrina, 2000; Pyrina et al., 2006). In some years (2009, 2010, 2014, 2015, and 2018), a moderate positive relationship between the seasonal dynamics of ΣChl and the water temperature was found. For the average concentrations of ΣChl during the growing season, there is a positive dependence on temperature and the Wolf number, the indicator of solar activity, and the water volume (a large amount of precipitation and volume of inflow and a high water level) is a factor limiting the development of phytoplankton (Mineeva, 2021). Since the years of studies differed in weather conditions and water level, it is likely that various factors that determined the specifics of the development and seasonal dynamics of phytoplankton in particular areas of the reservoir also became the leading ones. As a result, the stations are grouped differently on the dendrograms in the years of studies (Fig. 5). Nevertheless, the absence of a significant difference in the content of ΣChl at the stations, as well as a close correlation of the average values for the growing season in the long-term dynamics, confirm the reliability of the data obtained for assessing the ecological state of the Rybinsk Reservoir.

CONCLUSIONS

The chlorophyll content at the standard stations in the Rybinsk reservoir is characterized by a wide range and significant variability of values. The seasonal dynamics of chlorophyll at all stations is marked by two or three peaks, the timing of which, duration, and

concentration of the pigment change not only in years with different weather conditions, but are not always synchronous during the same year. Significant differences in the amount of chlorophyll at the stations can be observed in the surveys performed within a day and are due to the complex hydrological structure of the reservoir; active dynamic processes; and, in the spring period, to the thermal regime as well. The presence of stable large circulation zones smoothes out the spatial differences of chlorophyll, the average seasonal concentrations of which do not differ significantly at all six stations in years with an average water level, and at four stations of the Main Reach in extremely high-water years. The absence of a significant difference in the average seasonal content of ΣChl at the stations during the study years, as well as a close correlation of the average values for the growing season in the long-term aspect, confirm the reliability of the data obtained for assessing the ecological state of the Rybinsk Reservoir.

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COMPLIANCE WITH ETHICAL STANDARDS

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