



Article

Spatial distribution and photosynthetic activity of phytoplankton in the Rybinsk Reservoir in the summer period of 2018–2020

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Abstract. The spatial distribution of chlorophyll *a* (Chl *a*) and photosynthetic activity coefficient (PAC) of phytoplankton in the Rybinsk Reservoir was studied using fluorescent analysis in July–August 2018–2020. Under various hydrometeorological conditions, the content of Chl *a* varied as 0.26–116 µg/L, averaging 16.7–21.2 µg/L. The spatial distribution of Chl *a* in 2019 was characterized by moderate patchiness, in 2018 and 2020, by highly pronounced randomness (coefficients of variation $C_v = 69, 91, \text{ and } 140\%$, respectively). The PAC varied from 0.01 to 0.58, averaging 0.30–0.42. PAC below 0.3 were noted in 8–47% of cases, reflecting the development of phytoplankton under stressful conditions. The spatial distribution of PAC was more uniform than that of Chl *a* ($C_v = 18\text{--}130\%$). PAC depended on Chl *a* content non-linearly ($R^2 = 0.50$).

Key words: chlorophyll, PAC, quantum yield, monitoring, fluorescence, Upper Volga River, algocoenosis state, pigments

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Научная статья

Пространственное распределение и фотосинтетическая активность фитопланктона Рыбинского водохранилища в летний период 2018–2020 гг.

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Аннотация. В июле–августе 2018–2020 гг. с использованием флуоресцентной диагностики исследовано пространственное распределение хлорофилла *a* (Хл *a*) и коэффициента фотосинтетической активности (КФА) фитопланктона Рыбинского водохранилища. При различных гидрометеорологических условиях содержание Хл *a* изменялось в диапазоне 0.26–116 мкг/л при средних значениях 16.7–21.2 мкг/л. Пространственное распределение Хл *a* в 2019 г. характеризовалось умеренной, в 2018, 2020 гг. – высокой неоднородностью при коэффициентах вариации $C_v = 69, 91$ и 140% соответственно. Величины КФА варьировали от 0.01 до 0.58 при средних значениях 0.30–0.42. В 8–47% случаев отмечены КФА ниже 0.3, отражающие развитие фитопланктона в стрессовых условиях. Пространственное распределение КФА более однородно, чем распределение Хл *a* ($C_v = 18–130\%$). Эмпирически выведена нелинейная зависимость КФА от содержания Хл *a* ($R^2 = 0.50$).

Ключевые слова: хлорофилл, КФА, квантовый выход, мониторинг, флуоресценция, Верхняя Волга, состояние альгоценоза, пигменты

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Introduction

The Rybinsk Reservoir is studied by hydrologists and ecologists for many years (Struktura..., 2018). Planktonic algae, which produce the bulk of organic matter and transform the incoming energy of solar radiation into the ordered energy of bonds of organic molecules during photosynthesis (Todoreenko, 2016), are sensitive to external factors (Elizarova, 1999; Suggett et al., 2010). Various indicators and methods are used to assess the state of algocenoses, including chlorophyll *a* concentration, primary production,

abundance and biomass of phytoplankton (Korneva, 2015; Metody... 1975; Mineeva, 2004, 2009, 2021; Sigareva, 2012). Nowadays, instrumental measurements for chlorophyll concentration (including fluorescence) are becoming widespread, the methods for measuring the photosynthetic activity and the efficiency of the quantum yield of photosystem II (PS II) getting much development (Gaevsky et al., 1993; Goltsev et al., 2014; Ivanova et al. et al., 2014; Matorin and Rubin, 2012; Popik, 2015).

The spatial heterogeneity of the environment is one of the important stabilizing factors in the functioning of any ecosystem. When studying large water areas, researchers are faced with heterogeneity in the phytoplankton distribution (Koreneva, 2017; Mineeva, 2004; Piirsoo et al., 2008). This peculiarity is associated with various hydrodynamic processes, vital activity of aquatic organisms, nutrient limitation, etc. (Ekologicheskie..., 1993; Mineeva, 2021; Tesfay, 2007). Large-scale phytoplankton heterogeneity provides a number of competitive advantages; it is characterized by large-scale both space and time (dozens of days and thousands of kilometers). This work continues the series of long-term extended studies on the development of phytoplankton in the Rybinsk Reservoir and its horizontal distribution (Struktura..., 2018).

The study aims to assess the spatial heterogeneity and photosynthetic activity of phytoplankton in the Rybinsk Reservoir during periods with different hydroclimatic conditions.

Materials and methods

The Rybinsk Reservoir (N 58°22'30" E 38°25'04") is located in the southern taiga subzone; it is large (4580 km²) and relatively shallow (average depth of 5.6 m) water body. About 20% of its total area is occupied by shallow waters with the depths of less than 2.0 m, about 25%, by the depths exceeding 8 m. The reservoir is divided into four sections (Rybinskoe..., 1972): Volga, Sheksna, and Mologa reaches, located along flooded riverbeds, and the Main Reach, which occupies the vast central part of the reservoir (Fig. 1).

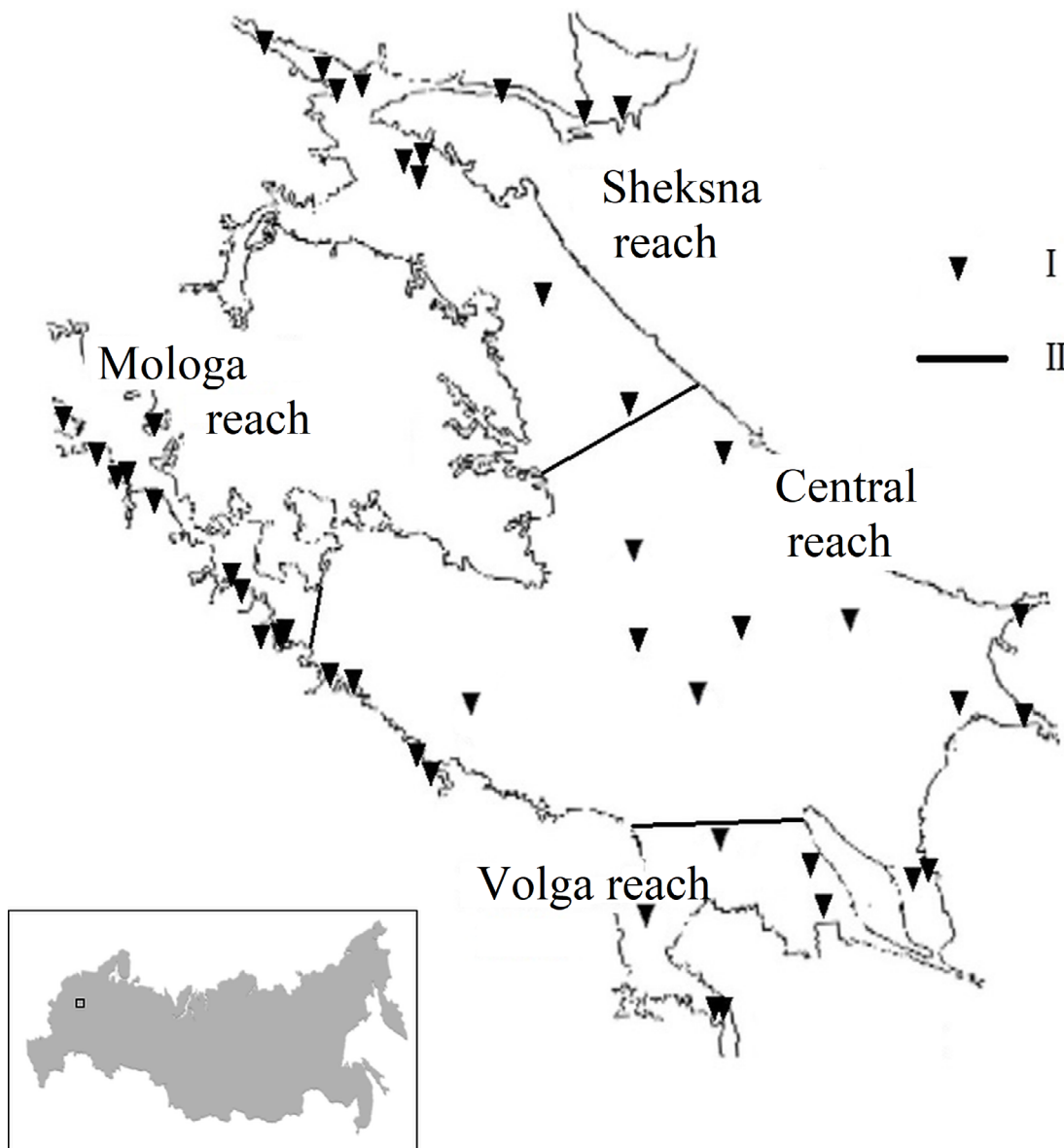


Fig. 1. Schematic map of the Rybinsk Reservoir with the location of sampling stations. I – stations, II – boundaries.

Table 1. Meteorological conditions in a week before sampling in 2018–2020.

Year	Average wind speed (gusts), m/s	Cloudiness, %	Precipitation, mm	Share of still days, %	Average air temperature, °C
2018	2.2 (5)	50	12	17.2	18.4
2019	1.7 (5)	40	29	35.9	12.5
2020	3.1 (9)	60	78	12.5	17.0

The material was collected at 30 deep-water (channel) and at 17 shallow-water (at the mouths of small rivers and coastal) stations (Fig. 1) in July–August 2018–2020 (the warmest period of the year). Samples were taken with an Elgmork bathometer in the euphotic zone (0–2 m).

The content of chlorophyll *a* (Chl *a*) was determined, equal to its total amount in the three main divisions of freshwater algae (cyanobacteria, diatoms, and green: Chl_{Cyan}, Chl_{Bac}, and Chl_{Chl}), and the coefficient of photosynthetic activity (PAC), or effective quantum yield of photosystem II. Both indicators were measured using the PFL-3004 fluorimeter according to the methodology developed at the Krasnoyarsk State University (Gaevsky et al., 2005). In order to determine Chl *a*, the fluorescence yield at wavelength ~680 nm was measured upon excitation of natural water by light with the wavelengths of 410, 490, and 540 nm before and after the addition of simazine (electron transport chain (ETC) inhibitor) to the sample. The Chl *a* concentration was calculated using the system of equations developed by V.M. Gol'd et al. (1986). In order to calculate PAC, the fluorescence yield of natural water was determined upon excitation with white light at an intensity of 150 W/m² before and after the addition of simazine to the sample cuvette, then PAC was calculated by the equation:

$$K\Phi A = F'_{\max} / F_{\max} - F_t$$

where F'_{\max} is the maximum fluorescence of the sample adapted to light after ETC inhibitor was added; F_t is the stationary fluorescence in the light (Gol'd et al., 1986).

PAC is a dimensionless value that ranges 0–0.83, where 0.83 is the maximum value obtained for a healthy culture (Gol'tsev et al., 2014). When assessing photosynthetic activity based on PAC, the following ranges are used (Kurochkina, 2019): 0–0.3 refers to low photosynthetic activity (at which inhibition of solar energy absorption processes and damage to the integrity of photosystems can be observed); 0.3–0.5, to normal photosynthetic activity; > 0.5, to high photosynthetic activity (observed under optimal conditions, when algae develop (grow) actively).

The STATISTICA 10 (Statsoft, Russia), PAST 4.03 (Oyvind Hammer, Norway), and Excel 2016 (Microsoft, USA) software packages were used for statistical

data processing. Meteorological data (air temperature, wind speed, and direction) were downloaded from the online archives of weather forecast website www.rp5.ru for the station Cherepovets¹. Water characteristics of the reservoir (level, inflow, flow) were obtained from the RusHydro website² and from published data (Struktura..., 2018).

Results and discussion

Growing seasons of 2018–2020 were characterized by different hydrometeorological conditions (Table 1). In each growing season, the westerly, southerly, and northerly winds prevailed, their total average share reached up to 61–65%. Calm conditions were noted in 6–8% of cases. The easterly and northeasterly winds were least of all recorded. In 2020, the larger share of southerly winds (up to 10%) and smaller, of westerly ones, was observed compared to the other years under consideration. The average wind speed was 2.7 m/s in each study year.

The growing season of 2018 was characterized by the highest average air temperature (12 °C). In the week prior to sampling date, northerly and northeasterly winds prevailed (> 52%) with the share of calm hours amounting to 17% (Fig. 2). The year of 2019 was the coldest year (average air temperature of the growing season was 10.6 °C), windless year (average wind speed 2.3 m/s, calm days were 20% of total), and low-water year. A week before the material was collected, southwesterly winds prevailed (27% of cases) with a high share of calm weather. In 2020, the growing season was characterized by higher wind speed (2.9 m/s) and heavy precipitation. The hydrometeorological situation in late July–early August was unfavorable for phytoplankton vegetation. There was a change in seasonal weather conditions with a change in the prevailing winds from the westerly ones to the northerly ones. Wind speeds reached 9 m/s; precipitation was observed daily for two weeks.

According to previously obtained data (Semadeni and Mineeva, 2019), the bulk of phytoplankton in the daytime is concentrated in the photic layer (> 80% of the recorded maximum Chl *a* and PAC values),

¹ https://rp5.ru/Archive_weather_in_Cherepovets (accessed: 10.09.21)

² <http://www.rushydro.ru/hydrology/informer/> (accessed: 12.09.21)

which for the Rybinsk Reservoir is 0–2 m. At low wind speed, elevated Chl *a* concentration is confined to the southern part of the reservoir and shallow water areas. At steadily directed winds (exceeding 2 m/s), the photic layer may be subjected to intense wind action, changing the photosynthetic activity of phytoplankton (Mosharov and Sergeeva, 2018). In the reservoir, a horizontal displacement of algae in the direction of the dominant winds was noted (Mineeva, 2004).

During the study period, Chl *a* concentration corresponded to values typical of high summer (Struktura..., 2018). In the summer of 2018, the content of Chl *a* varied within 4.5–80 µg/L. As calm weather and low wind (2.5 m/s) predominated, the spatial distribution of Chl *a* was non-uniform ($C_v = 91\%$). The highest concentration of Chl *a* was noted in the central and southern parts of the reservoir (Fig. 3). This pattern of pigment distribution in the reservoir is typical for the summer period of maximum water heating (Mineeva, 2021). High Chl *a* (> 60 µg/L) was recorded in the southern part of the Main Reach in the zone of the local ecotone, where various water masses were confluent and mixing. High values of Chl *a* (> 40 µg/L) were also noted in the upper Sheksna Reach near the city of Cherepovets and in the Sheksna River. The pigment concentration was significantly lower in the other parts of the reservoir, with minimal values registered in the Mologa Reach (< 5 µg/L).

The biomass ratio of the main taxonomic groups of phytoplankton is similar to the data published earlier (Korneva, 2015; Struktura..., 2018;): Chl_{Cyan} and Chl_{Bac} contribute the most to total Chl *a*. At the Volga Reach, the contribution of Chl_{Cyan} reaches 78%, while that of Chl_{Bac} is the lowest. At the Main and Mologa reaches, the contribution of Chl_{Cyan} and Chl_{Bac} is close to the average, 63–67% and 24–31%, respectively (Table 2). At the Sheksna Reach, more than a half of Chl *a* is represented by Chl_{Bac} (57%), only a third (32%), by Chl_{Cyan}. The contribution of Chl_{Chl} is low, varying from 5% at the Volga Reach up to 10% at the Sheksna Reach. Generally, average relative content of Chl_{Cyan} and Chl_{Bac} is 62 and 31%, respectively, in the Rybinsk Reservoir.

The highest average content of Chl *a* (28 µg/L) has been recorded at the Volga and Sheksna reaches; at the Main Reach, it did not exceed 18 µg/L. Such values are typical for eutrophic waters. At the Mologa Reach, the content of Chl *a* (10.1 µg/L) is close to that observed in mesotrophic waters (Table 2). In the entire reservoir, the average value (21.2 µg/L) is the highest over three years of observations. This is due to weak mixing of the water column and the ascending of the blue-green algae into the surface water layer.

In 2019, Chl *a* distribution over the water area of the Rybinsk Reservoir was moderately heterogeneous ($C_v = 69\%$). The range of values was shifted leftwards compared to 2018 (2.2–68.0 µg/L). Active

vegetation of phytoplankton was noted in the northern part of Main Reach and at the Sheksna Reach, as well as in the southeastern part of the reservoir. Maximum Chl *a* (35–68 µg/L) were registered at the Main Reach. Chl *a* concentration did not exceed 24 µg/L at three other reaches. Minimum values (< 5 µg/L) were noted at the Mologa Reach and in the eastern part of the Main Reach (Fig. 3).

The chlorophyll ratio of the main divisions of algae differed from the values obtained in 2018. Chl_{Cyan} predominated (50–56%), but the share of Chl_{Bac} decreased down to 35% at the Main and Sheksna reaches, while the share of Chl_{Bac} increased up to 44–51% at the Volga and Mologa reaches compared to the previous year. The relative content of Chl_{Chl} at the Main and Volga reaches was the highest for the study period (15–22%). The average relative content of Chl_{Cyan} and Chl_{Bac} in the reservoir was 47 and 40%, respectively.

The average concentration of Chl *a* at the Volga, Main, and Sheksna reaches were 18.4, 19.2, and 20.3 µg/L, respectively; this corresponded to eutrophic waters. At the Mologa Reach, the value of this indicator was almost two times lower (11 µg/L), i.e., moderately eutrophic waters (Table 2). In 2019, the average Chl *a* concentration in the entire reservoir was lower than in 2018 (17.6 µg/L). In the coastal zone of the Sheksna Reach, Chl *a* concentration was 36% higher than at deep-water stations; in the Mologa Reach near the shore, it decreased by 15%. No significant differences were found in the other two reaches.

The year of 2020 is characterized by the widest range of values (from 0.26 to 116 µg/L) and the most heterogeneous spatial distribution of Chl *a* ($C_v = 140\%$). The maximum concentration of Chl *a* were noted in the southern part of the Volga Reach and at the Sheksna Reach (116 and 91 µg/L, respectively). High values were also registered in the western part of the Mologa Reach (66 µg/L). There were no large accumulations of algae in the open areas: the lowest Chl *a* (< 5 µg/L) was recorded in the center of the reservoir (Fig. 3).

In total Chl *a*, Chl_{Bac} dominated at the Mologa and Sheksna reaches (81% and 50%), while Chl_{Cyan} dominated at the Main and Volga reaches (53% and 59%). The contribution of Chl_{Chl} was low (5–10%). The average relative content of Chl_{Cyan} and Chl_{Bac}, in contrast to the two previous years, was characterized by an increase in the share of the latter up to 48%.

Average concentration of Chl *a* at the Volga, Sheksna, and Mologa reaches (25, 15.6, 18.3 µg/L) correspond to the eutrophic waters, while the Main Reach (12.4 µg/L) is moderately eutrophic (Table 2). Lower water temperature, constant wind activity with heavy precipitation led to a decrease in photosynthetic activity due to the competitive advantage of small-sized algae with lower productivity (Winder and Summer, 2012). This is expressed in a decrease in the

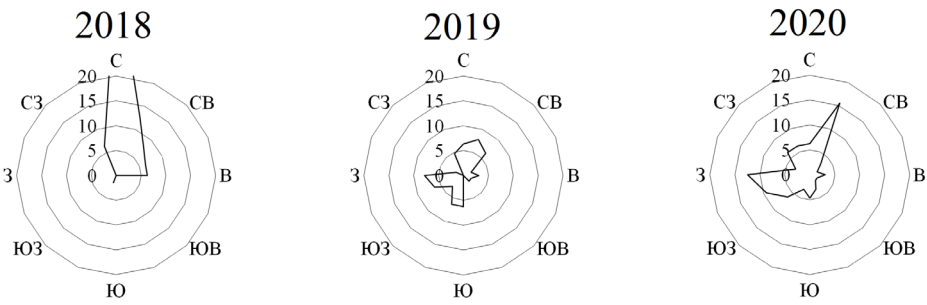


Fig. 2. Wind rose: winds prevailing a week before sampling in 2018–2020.

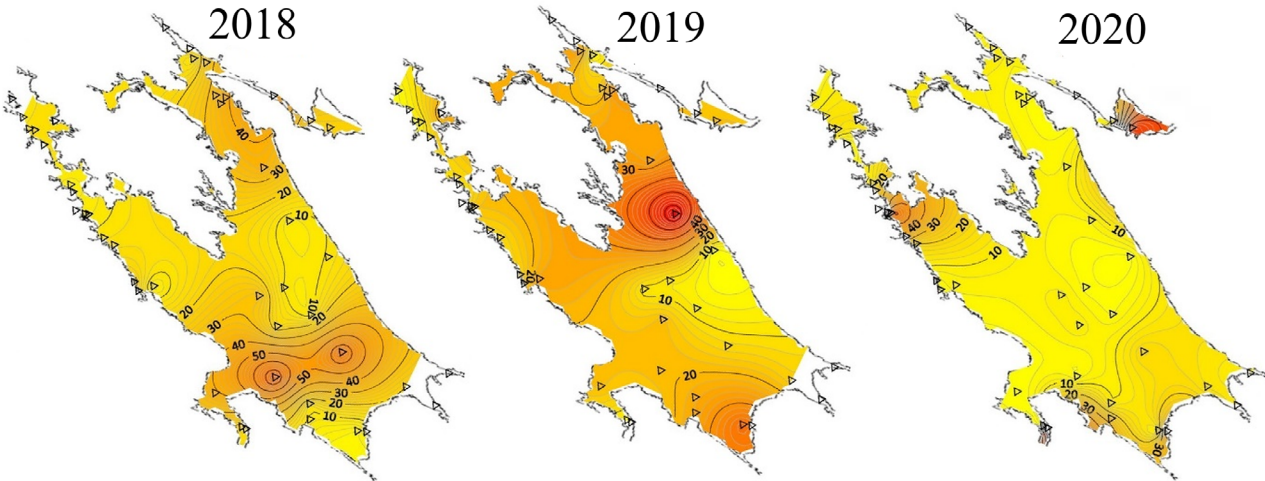


Fig. 3. Spatial distribution of Chl a (µg/L) in the Rybinsk Reservoir in the summer period of 2018–2020.

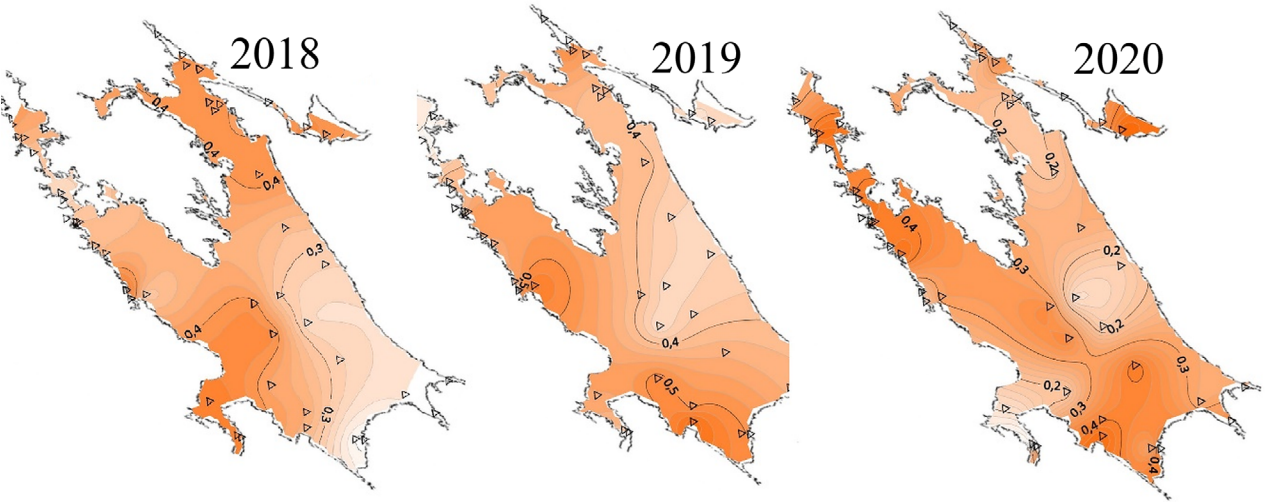


Fig. 4. Spatial distribution of PAC in the Rybinsk Reservoir in the summer period of 2018–2020.

Table 2. Average content of chlorophyll a and share of chlorophyll of main algae taxa. Chl_{Cyan} – chlorophyll of cyanobacteria; Chl_{Bac} – chlorophyll of diatoms; Chl_{Chl} – chlorophyll of green algae.

Year	Reach	Chl a, $\mu\text{g/L}$	Chl_{Cyan} , %	Chl_{Bac} , %	Chl_{Chl} , %
2018	Volga	28.5 ± 12.2	78	17	5
	Main	18.9 ± 5.1	67	24	9
	Mologa	27.9 ± 7.1	63	31	6
	Sheksna	10.1 ± 1.4	33	57	10
	Total for Rybinsk Reservoir	21.2 ± 3.51	62	30	8
2019	Volga	18.4 ± 3.2	34	44	22
	Main	19.2 ± 4.5	50	35	15
	Mologa	20.2 ± 3.4	42	51	7
	Sheksna	11.1 ± 2.6	56	35	9
	Total for Rybinsk Reservoir	17.6 ± 2.03	47	40	13
2020	Volga	25.2 ± 9.9	59	34	7
	Main	12.4 ± 2.4	53	37	10
	Mologa	15.6 ± 0.9	15	81	4
	Sheksna	18.3 ± 7.2	40	50	10
	Total for Rybinsk Reservoir	16.7 ± 3.4	43	48	9

average Chl a concentration down to $16.7 \mu\text{g/L}$, the lowest for the entire study area over the entire study period. Under such conditions, the vegetation of algae in the semi-closed parts of the reservoir is more intense (Pyrina et al., 1976). A significant difference in the content of Chl a has been registered at deep-water and shallow-water coastal stations of each reach: in shallow waters, the values were 2–4 times higher than in the open part of the reservoir.

The effective quantum yield of fluorescence is one of the parameters assessing the state of the photosynthetic apparatus of phytoplankton (Goltsev and Kaladzhii, 2016; Hartig et al., 1998; Mosharov and Sergeeva, 2018). The photosynthetic activity coefficient (PAC) characterizes the proportion of light quanta used in photosynthetic reactions of PS II (Maxwell and Johnson, 2000), and reflects the efficiency of solar energy absorption.

In 2018, PAC values in the Rybinsk Reservoir varied from 0.19 to 0.51 ($C_v = 22\%$). The pattern of PAC distribution (Fig. 4) was similar to that of Chl a (Fig. 3). PAC values above 0.40 were noted in the northern part of the water area in the Sheksna Reach ($\text{PAC}_{\text{av}} = 0.41$) and in the Sheksna River, as well as at the Volga Reach ($\text{PAC}_{\text{av}} = 0.38$). Low PAC (< 0.30) were observed singly at the Mologa Reach and in the eastern part of the reservoir. The predominance of certain division of algae did not affect the overall photosynthetic activity. Thus, at the Mologa, Main, and

Volga reaches, Chl_{Cyan} dominated in total Chl a, at the Sheksna Reach, this was Chl_{Bac} with approximately equal PAC values. At seven stations, $\text{PAC} < 0.3$ were noted, which indicated the inhibition of photosynthetic processes (Rubin, 2005). PAC exceeding 0.50 was noted only at one station (Table 3). We argue that the mass development of phytoplankton organisms leads to intercompetition for light and nutrients, which is expressed by a decrease in the efficiency of solar energy absorption at chlorophyll concentrations of more than $40 \mu\text{g/L}$. The average PAC at the Main and Mologa reaches (0.33) is close to the critical low value; at the Sheksna and Volga reaches, they are higher (0.41 and 0.39, respectively) and correspond to the normal functioning of phytoplankton community (Table 4). The average PAC for the entire reservoir was 0.36.

In 2019, a range of PAC was close to that observed in 2018 (0.26–0.58), with low variability ($C_v = 18\%$). The spatial distribution of PAC also differed little comparing to 2018 (Fig. 4), but did not coincide with the distribution of Chl a (Fig. 3). High values of PAC (> 0.50) were noted in different areas of the Volga, Main, and Sheksna reaches, while the minimum values (< 0.30) were recorded in the Mologa Reach. The maximum average PAC (0.49) was registered at the Volga Reach, where the Chl_{Bac} share reached 72% in the total Chl a, accompanied by high share of Chl_{Chl} (25%). Similar data were obtained by other researchers (Darchambeau et al. al., 2014; Ratan, 2017). The

Table 3. Frequency of occurrence of PAC value range in the Rybinsk Reservoir in 2018–2020.

Year	PAC		
	< 0.3	0.3–0.5	0.5–0.7
2018	23%	71%	3%
2019	8%	76%	16%
2020	47%	53%	0%
Total	26%	67%	6%

Table 4. PAC values (mean \pm error of mean) at the reaches of the Rybinsk Reservoir.

Reach	Year		
	2018	2019	2020
Volga	0.39 \pm 0.03	0.49 \pm 0.03	0.23 \pm 0.06
Main	0.33 \pm 0.06	0.42 \pm 0.02	0.30 \pm 0.03
Mologa	0.33 \pm 0.07	0.36 \pm 0.02	0.41 \pm 0.02
Sheksna	0.41 \pm 0.06	0.43 \pm 0.02	0.27 \pm 0.04

highest average PAC (0.46) was also noted here. At the Main, Sheksna, and Mologa reaches, lower mean values were obtained (0.42, 0.43, and 0.36, respectively). The first two were characterized by the Chl_{Cyan} to Chl_{Bac} ratio typical for the summer period (~60% to ~30%, respectively); at the Mologa Reach, more than half of the total Chl *a* was represented by Chl_{Bac} . The photosynthetic activity of algae from deep-water and shallow-water stations differed insignificantly in most cases. At the Mologa Reach, the average PAC at the riverbed stations was 11% higher than in the coastal zone. In 8% of cases, PAC was below 0.30, in 16%, exceeded 0.5. Compared to 2018, phytoplankton vegetated under more favorable conditions in 2019. The average PAC was 0.41 for the entire reservoir.

In 2020, under unstable hydrometeorological conditions, the PAC range was the widest (0.02–0.47), and the spatial distribution was characterized by the highest heterogeneity observed for all the considered years ($C_v = 143\%$). High PAC (> 0.40) were noted locally at all reaches of the reservoir (Fig. 5). The minimum values (< 0.30) were registered in the open areas of the Main and Volga reaches. In these zones, Chl_{Cyan} dominated in the total Chl *a* (53–58%). A higher concentration of Chl_{Bac} was recorded in the semi-closed part of the reservoir. The average PAC (0.23, 0.27, and 0.30) reflected the development of phytoplankton under stress conditions at the Volga, Sheksna, and Main reaches, respectively. At the semi-closed Mologa Reach, $\text{PAC}_{\text{av}} = 0.41$. The maximum PAC was noted in the shallow semi-closed areas of the reservoir and in the river mouths. The PAC was

higher in the coastal zone comparing to the channel stations: at the Volga Reach, by 36%, at the Mologa Reach, by 6%. PAC < 0.3 was noted in 47% of cases, PAC exceeding 0.5 was not registered. The average PAC_{av} for the entire reservoir was 0.30, the lowest for the entire study period.

The content of Chl *a* is considered to be a universal ecological and physiological characteristic of the photosynthetic activity of algae; this indicator reflects the amount of synthesized biomass under the prevailing environmental conditions and the physiological state of organisms. In pristine, anthropogenically undisturbed ecosystems, the relationship between the quantum yield and Chl *a* is most often positive (Mosharov and Sergeeva, 2018; Popik, 2015). In the Rybinsk Reservoir in 2018, the relationship between PAC and Chl *a* is moderate ($r = 0.55$), the relationship with the relative amount of Chl_{Bac} and Chl_{Chl} is closer ($r = 0.66$ and 0.76 , respectively). In 2019, a significant relationship is observed only with the share of Chl_{Chl} ($r = 0.59$). In 2020, the closest correlation of PAC with Chl *a* is obtained ($r = 0.78$), less pronounced with the shares of Chl_{Bac} and Chl_{Chl} ($r = 0.61$ and 0.66 , respectively). For the entire period of studies (2018–2020), the relationship between PAC and Chl *a* is characterized by moderate tightness ($r = 0.64$). If one excludes the Chl *a* values exceeding 40 $\mu\text{g/L}$ from the dataset, which are characteristic of eutrophic and hypereutrophic water bodies, the correlation coefficient increases ($r = 0.73$).

In general, Chl *a* is related to PAC non-linearly. When ranking PAC values by chlorophyll content, an approximation equation with a high coefficient

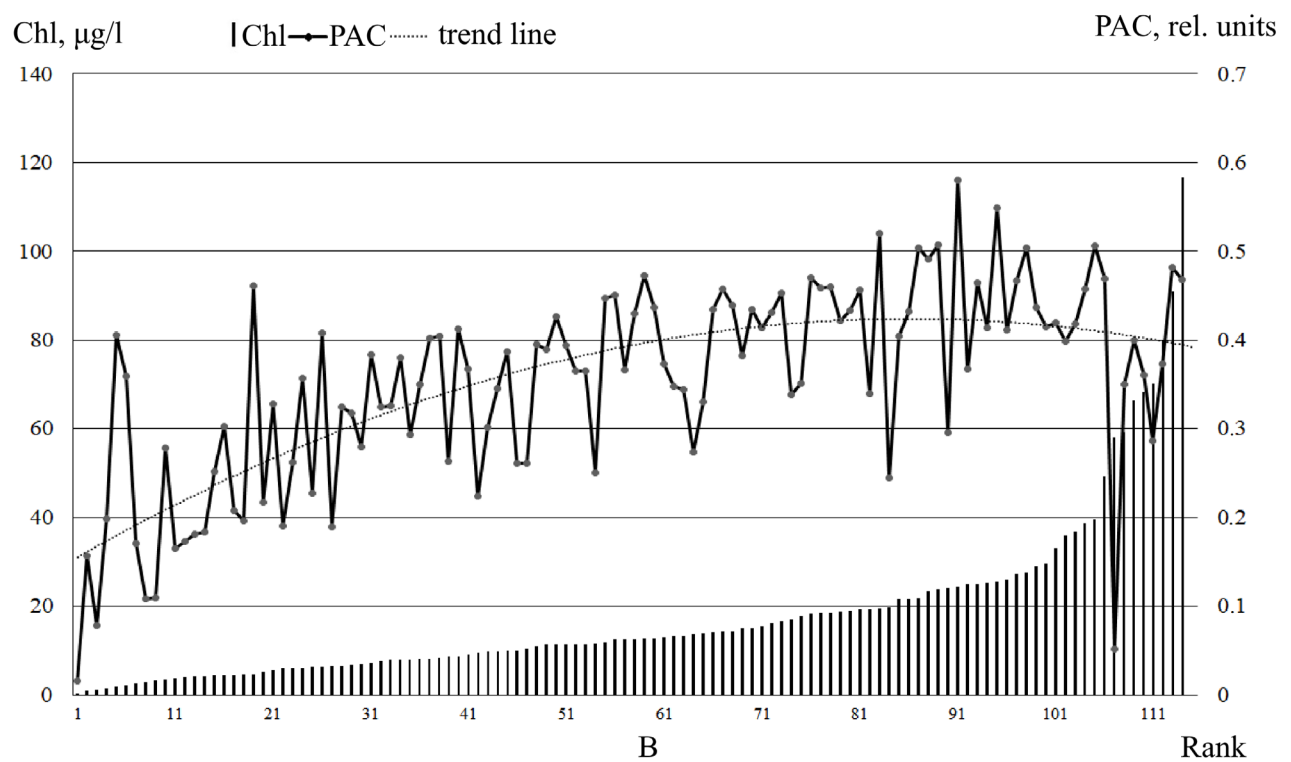
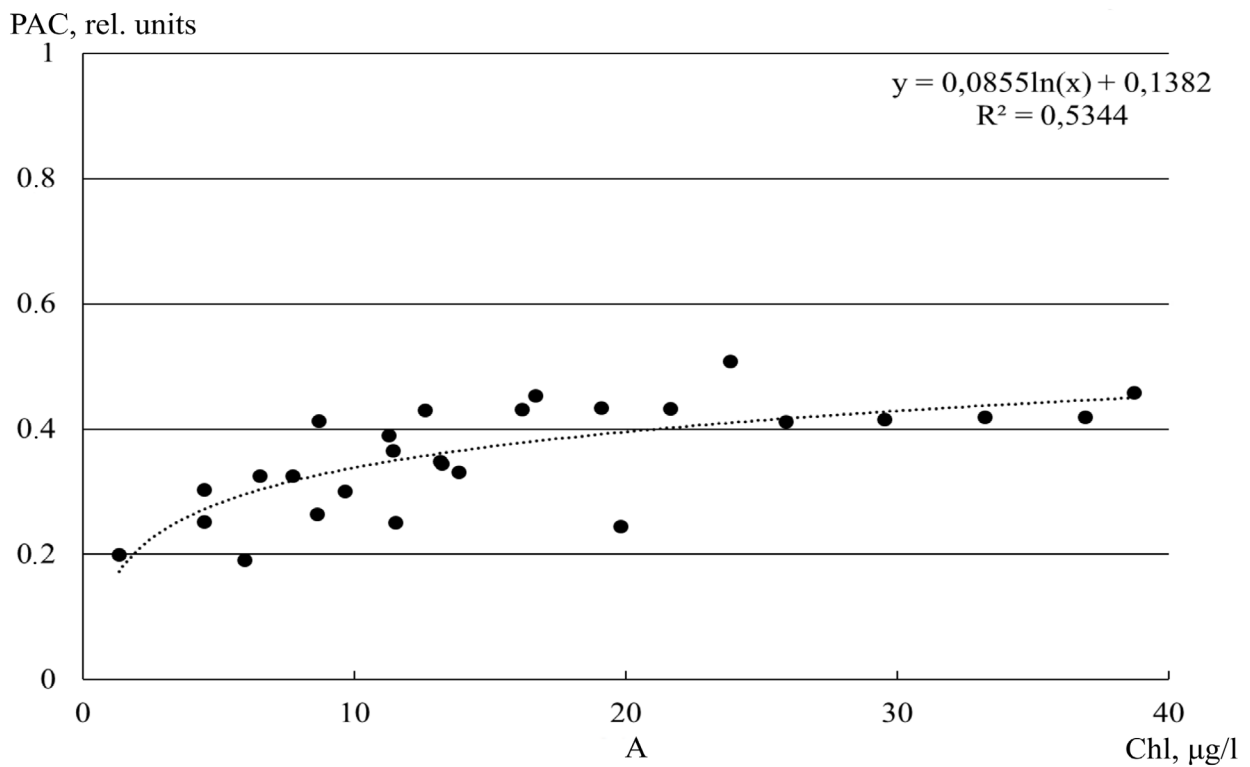


Fig 5. Dependence of PAC on Chl a content in 2018 (A) and in 2018–2020 (B).

of determination has been obtained both for certain years (Fig. 5A) and for the entire dataset (Fig. 5B):

$$K\Phi A = -0.00005 \times X_{\text{Chl}}^2 + X_{\text{Chl}} + 0.148 \\ (n = 114, R^2 = 0.50).$$

For the entire data series, the relationship is non-linear; a logarithmic increase of PAC up to 0.5 occurs along an increase of Chl *a* concentration up to 40 µg/L. The maximum activity of the photosynthetic apparatus (PAC = 0.58) is observed at Chl *a* concentration of 20 to 40 µg/L. As Chl *a* content increases further, PAC decreases (Fig. 5). In 2018, the relationship between PAC and Chl *a* at > 40 µg/L has a shape of logarithmic curve except two stations.

Conclusions

The spatial distribution of chlorophyll in the Rybinsk Reservoir in summer is characterized by a high degree of heterogeneity, when coefficients of variation range from 69% at prevailing calm weather and low wind speed up to 140% at strong winds and heavy precipitation. Chlorophyll concentration is generally higher in coastal areas and in semi-closed shallow water areas than at deep (open) riverbed stations.

PAC, determined for the phytoplankton of the Rybinsk Reservoir for the first time, ranges 0.3–0.5 in most of cases (66%), which indicates a normal physiological state of algae. PAC less than 0.3 makes up a significant share at unstable hydrometeorological conditions.

The spatial distribution of PAC and Chl *a* do not coincide with each other. High PAC is observed throughout the entire water area of the reservoir, depending on the conditions of a certain year; high PAC is registered most often in the southern and northern parts of the reservoir. In 2018 and 2019, a horizontal displacement of algae along the wind direction has been noted, which did not affect PAC. The relationship between PAC and Chl is not linear. The maximum activity of the photosynthetic apparatus is observed in the range of chlorophyll concentrations from 20 to 40 µg/L. At Chl *a* above 40 µg/L, PAC decreases.

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