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Article

Chlorophyll Content and Photosynthetic Activity of Phytoplankton in Reservoirs of the Volga River (Russia)

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Abstract: Using the fluorescent method in the modification of Krasnoyarsk State University, we study development (as chlorophyll content, ΣCHL) and photosynthetic activity of phytoplankton in seven large flat reservoir of the Volga River cascade (Russia) in August 2015–2017. In period of maximal warming of water, average ΣCHL varied in limits of 19.4–33.7 $\mu\text{g L}^{-1}$ in the Upper Volga, 8.5–27.8 $\mu\text{g L}^{-1}$ in the Middle Volga, and 5.2–11.3 $\mu\text{g L}^{-1}$ in the Lower Volga. Photosynthetic activity coefficient (PhAC) varied mostly in limits of 0.12–0.59 with average of 0.22–0.38 and only in 2017 decreased to minimal <0.10 and average <0.20. The average PhAC values shows the normal physiological state of the phytoplankton of the Upper Volga during all periods of observation, occasional decrease of PhAC in the Middle Volga, and low photosynthetic activity in the Lower Volga. A decrease in the average ΣChl and PhAC in 2017 was under cyclonic windy weather with a large amount of precipitation, low solar radiation, and large volume of flow. Trend towards a decrease in ΣCHL , like decrease in PhAC from the Upper Volga to the Lower Volga is explained by increasing in the flow rate and volume of runoff downstream the Volga River.

Keywords: phytoplankton; chlorophyll; algae phylum; coefficient of photosynthetic activity (PhAC); Volga River reservoirs

1. Introduction

The study of the autotrophic community of aquatic ecosystems is a crucial part of hydroecological research. Planktonic algae produce the main stock of autochthonous organic matter in large lakes and reservoirs. An energy base for organisms of higher trophic levels is creating and the water column is enriching with oxygen by photosynthesis [1–3]. A special place among the indicators of the abundance and functioning of phytoplankton is given to photosynthetic pigments which have been used extensively nowadays in production hydrobiology. The primary pigment of green plants – chlorophyll *a* (CHL) – provides important information about the development and state of algocoenoses and the state of water environment [1,4]. The unique optical properties of chlorophyll – the ability to absorb and emit light radiation in a narrow wavelength range [5] – are the basis for methods to define it.

Phytoplankton forms the foundation of the trophic pyramid in reservoirs of the Volga River – the largest river in Europe [6,7]. Research of the pigments in the Volga River was started in the middle of the XX century [8] and they have been supplemented with new data nowadays [9–11] which are summarized in [12]. Most of these studies were carried out with standard spectrophotometric method [13]. Recently, we have begun to use fluorescent diagnostics of phytoplankton and preliminary data of the fluorescence CHL determination showed good agreement with the results of spectrophotometry [14].

Measurement of CHL fluorescence directly in natural water makes it possible to quickly analyze a large series of samples and evaluate a number of phytoplankton characteristics without affecting its integrity. The coefficient of photosynthetic activity (PhAC) is a direct indicator of the algocoenoses state [15]. PhAC characterizes the effective quantum yield of photochemical energy conversion

[16,17]. These mechanisms are associated with the functioning of photosystem II (PS II) reflecting the absorption efficiency of solar energy by algae during photosynthesis [18]. The quantum yield of photosynthesis (i.e., PhAC) serves as a measure of photosynthetic activity under electron-saturated reaction centers [19,20]. PhAC varies depending on a wide range of factors, reflecting the physiological state of photosynthetic organisms [21]. Application of PhAC to the assessment of productivity and state of natural algae communities seems to be a promising aspect of hydrobiological research [22,23]. The first data on PhAC of the Volga phytoplankton were obtained by us for the reservoirs of the Upper Volga previously [24,25].

The main purpose of this work is to study the total content of chlorophyll *a* with the proportion of the main algae taxa, and assess the photosynthetic activity of phytoplankton with the relationship between PhAC and chlorophyll in the water of the Volga River reservoirs.

2. Materials and Methods

2.1. Site Description

The Volga River, at 3690 km, is the longest river in Europe [26,27]. The river network of the Volga looks like a branching tree in the north that evolves into a single trunk rooting as a delta in the Caspian Sea in the south. The Volga catchment area is located on the Russian Plain, covering various latitudinal and climatic zones from the southern taiga to semi-desert. The most of the Volga River from the town of Tver’ to Volgograd that is over 2500 km long, is affected by an uninterrupted cascade of eight large shallow reservoirs, considerably slowing the flow velocity of the river. The reservoirs differ in terms of morphometry, optical regime, chemistry, lateral inflow, water exchange, and trophic status. A schematic map of the reservoirs is shown in Figure 1 and their basic characteristics are given in Table 1.

Table 1. Basic abiotic characteristics of the Volga River reservoirs according to [26,27].

Parameters	Upper Volga		Middle Volga			Lower Volga	
	Iva nko vo	Ugl ich	Gor ky	Ch ebo ksa	Kui bys hev	Sar ato v	Vol gog rad
Total water input, km ³ per year	10.07	11.46	49.53	118.89	244.3	248.3	259.2
Surface area, km ²	327	249	1591	1080	6150	1831	3117
Length, km	120	143	430	321	484	348	546
Mean depth, m	3.4	5.0	6.1	4.2	8.9	7.3	10.1
Total storage, km ³	1.12	1.25	8.82	4.60	57.30	12.87	31.45
Water exchange, year ⁻¹	10.6	10.1	6.1	20.9	4.2	19.1	8.0
Transparency, m	0.8	0.8	1.2	1.2	1.5	2.2	2.0
Water color, Cr-Co degree	53	51	53	42	38	36	34
Conductivity, μSim cm ⁻¹	240	250	206	355	315	345	424
Total nitrogen, mg L ⁻¹	1.34	1.27	1.09	1.14	1.08	0.99	0.98
Total phosphorus, μg L ⁻¹	90	93	68	124	145	127	134

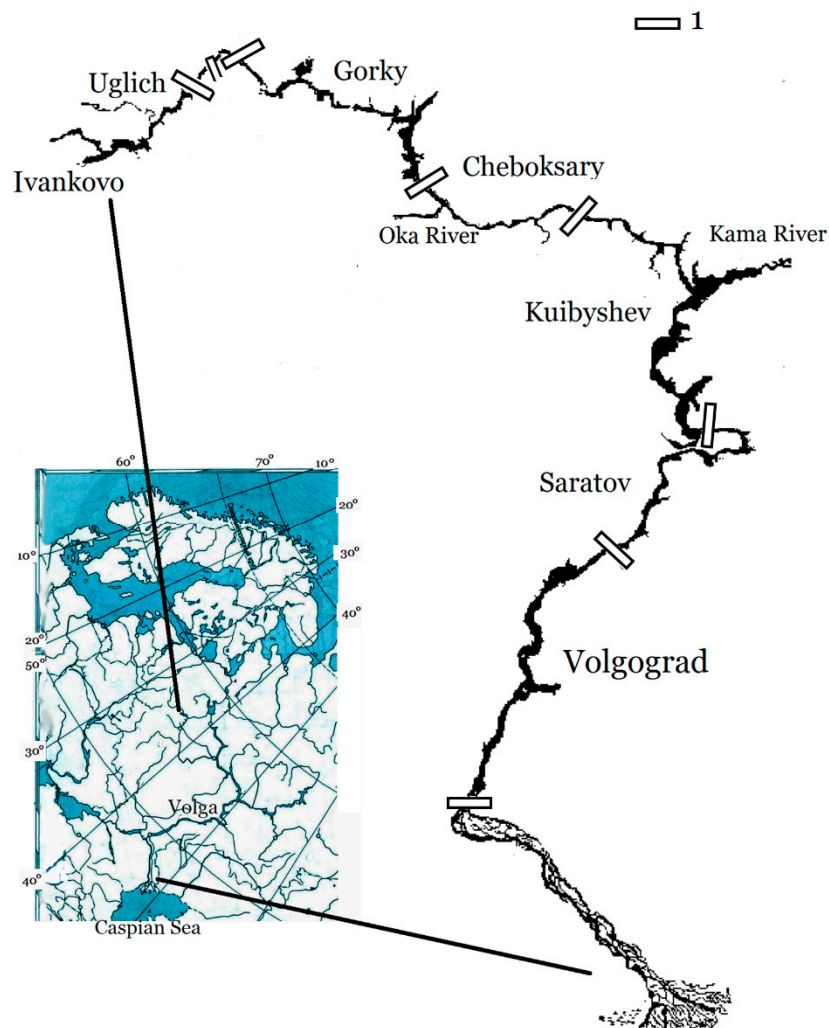


Figure 1. Schematic map of the Volga River reservoirs according to [12]. 1 – boundary of reservoirs.

With a change of conditions in the drainage basin, the total amount of ions – conductivity – increases and the color of the water decreases from the Upper Volga to the Lower Volga. Water transparency increases with the depth in lower reservoirs. The content of nitrogen and phosphorus compounds in the entire cascade is high enough to not limit the development of algae [27]. In accordance with the geographical zonality, three sections are distinguished in the cascade that are Upper Volga (56°51'N, 35°55' E – 57°29' N, 38°17' E), Middle Volga (58°03' N, 38°50' E – 53°31' N, 49°25' E), and Lower Volga (53°28' N, 49°42' E – 46°23' N, 48°02' E).

2.2. Sampling

Our data includes the route surveys carried out at seven run-of-river Volga reservoirs in the mid summer. In 2015–2017, samples were taken at 50–60 stations of the Upper and Middle Volga, also at 6 stations of the Saratov reservoir in 2016, and at 19 stations of the Lower Volga in 2017. Surveying each reservoir took 2–3 days. We used integral samples obtained by mixing equal volumes of water taken from each meter of the water column from surface to bottom with a 1 m Elgmork bathometer.

2.3. Chlorophyll

Fluorescence of chlorophyll was measured on board of the research vessel in natural water on a stationary fluorimeter PFL-3004 (Krasnoyarsk University) [28,29]. Modification of the method is based on the specifics of light-harvesting pigment-protein complexes of the diatoms, green algae, and cyanoprokaryots (blue-green algae) that makes it possible to determine the total amount of ΣCHL by its content in these main taxa of freshwater phytoplankton. The fluorescence intensity was measured in the red region of the spectrum (~ 680 nm) when excited by light with wavelengths of 410 ± 10 , 490 ± 10 , and 540 ± 10 nm. The measurement was repeated after the addition of ETC inhibitor simazine (at a concentration of 10^{-5} M) to the cuvette, thereby increasing the fluorescence yield to a maximum level. To introduce a correction for the presence of colored organic matter, at the same wavelengths, fluorescence of water filtered through a membrane filter with a pore diameter of ~ 0.5 μm , i.e., was measured devoid of algae. Total chlorophyll *a* amount (ΣCHL) was calculated as the sum of its concentration in diatoms, cyanoprokaryotes, and green algae (respectively, Bacillariophyta, CHL_{Bac} ; Cyanoprokaryota, CHL_{Cyan} ; Chlorophyta, CHL_{Chl}). Equations for calculating CHL_{Bac} , CHL_{Cyan} , and CHL_{Chl} are given in [30].

2.4. Photosynthetic Activity of Algae

The photosynthetic activity of algae was determined using the coefficient of photosynthetic activity (PhAC), which is assessed using the variable fluorescence index. The fluorescence yield of natural water was measured in the red region of the spectrum (680 nm) upon excitation with white light in the range of 400–620 nm at an intensity of 150 W m^{-2} before and after adding the ETC inhibitor simazine to the sample cuvette. PhAC was calculated using the formula (1) from [31].

$$\text{PhAC} = \frac{(F'_{\text{max}} - F_t)}{(F'_{\text{max}})} \quad (1)$$

F'_{max} , maximum fluorescence of light-adapted algae after the addition of an inhibitor;

F_t , steady-state fluorescence upon adaptation to a given light intensity.

PhAC values <0.10 correspond to the presence of cells with a non-functional photosynthetic apparatus [32]. Values of 0.10 – 0.30 characterize the low photosynthetic activity of phytoplankton and/or its growth under stress conditions; values of 0.30 – 0.50 correspond to the normal photosynthetic activity of phytoplankton in natural water bodies; values >0.50 indicate a high photosynthetic activity of algae under favorable hydrological and weather conditions. PhAC ~ 0.70 show the approach of fluorescence to its biological maximum, which is actually not observed *in situ* [33–35].

2.5. Statistics

Standard software packages for a personal computer Statistic10 (StstSoft Inc., USA) were used for statistical data processing, i.e., for calculating averages, their errors, correlation, regression, and dispersion analysis. The data are given as mean value with standard error ($\bar{X} \pm \text{SE}$). To determine the relationships between chlorophyll content and PhAC we used Pearson correlation coefficient significant at $P < 0.05$.

3. Results

The data obtained in August are confined to the period of maximum warming of the water column. The average water temperature in the reservoirs was 18.0 – 20.9 $^{\circ}\text{C}$ in 2015, and 21.9 – 24.7 $^{\circ}\text{C}$ in 2016. The start of the growing season in 2017 was cold and rainy [36], however, the summer heating reached normal temperature of 21.0 – 23.0 $^{\circ}\text{C}$. Water transparency increased from north to south, varied within the limits typical for reservoirs, and averaged 0.8 – 1.1 , 1.0 – 1.3 , and 1.8 – 2.2 m in the Upper, Middle, and Lower Volga.

Usually in the middle summer the summer maximum of phytoplankton is formed. The content of ΣCHL during the years of research was characterized by a wide range of values (Table 2). In the Ivankovo reservoir, it varied from the minimum 3 – 8 to the maximum 49 – 56 $\mu\text{g L}^{-1}$, in the Uglich

reservoir from 10–17 to 30–46 $\mu\text{g L}^{-1}$, in the Gorky reservoir from 8 to 44 $\mu\text{g L}^{-1}$ in 2015 and 2016 and from 1 up to 13 $\mu\text{g L}^{-1}$ in 2017. In the Cheboksary reservoir, the highest concentrations (16–52 $\mu\text{g L}^{-1}$) were obtained in 2015, lower (3–38 $\mu\text{g L}^{-1}$) in 2016 and 2017. In the Kuibyshev reservoir, as in the Gorky reservoir, higher values (from 2–8 to 39–50 $\mu\text{g L}^{-1}$) were obtained in 2015 and 2016, and lower values (1–15 $\mu\text{g L}^{-1}$) in 2017. In the Lower Volga, ΣCHL concentrations were lower and varied in a narrow range from 2–5 to 10–20 $\mu\text{g L}^{-1}$. The minimum and maximum concentrations in each survey differed by a factor of 10–20 in the Ivankovo and Kuibyshev reservoirs and by a factor of 2–10 in all the others.

Table 2. Chlorophyll content in basic phytoplankton taxa (CHL_{Cyan} , CHL_{Bac} , $\text{CHL}_{\text{Chlor}}$) and in total (ΣCHL) in the Volga River reservoirs in years of study (above the line limits, below the line mean values with standard error).

Reservoir	Year,	CHL_{Cyan}		CHL_{Bac}		$\text{CHL}_{\text{Chlor}}$		ΣCHL
		$\mu\text{g L}^{-1}$	%	$\mu\text{g L}^{-1}$	%	$\mu\text{g L}^{-1}$	%	$\mu\text{g L}^{-1}$
Ivankovo	2015	<u>3.0–42.0</u>	<u>26–86</u>	<u>0.8–11.7</u>	<u>8–58</u>	<u>0.3–3.9</u>	<u>2–18</u>	<u>4.3–49.0</u>
		13.5 \pm 3.6	64 \pm 6	4.7 \pm 1.0	29 \pm 5	1.1 \pm 0.3	7 \pm 1	19.4 \pm 4.0
	2016	<u>4.8–49.1</u>	<u>37–87</u>	<u>1.7–12.6</u>	<u>12–61</u>	<u>0.5–3.0</u>	<u>1–11</u>	<u>8.4–56.2</u>
		19.7 \pm 5.4	62 \pm 4	6.7 \pm 1.8	32 \pm 4.2	1.2 \pm 0.3	5 \pm 1	33.7 \pm 11.1
	2017	<u>1.3–29.1</u>	<u>11–58</u>	<u>1.2–31.8</u>	<u>36–85</u>	<u>0.2–3.7</u>	<u>3–18</u>	<u>3.2–45.7</u>
		6.8 \pm 2.1	31 \pm 4	14.8 \pm 3.2	62 \pm 4	1.5 \pm 0.3	7 \pm 1	23.1 \pm 4.9
Uglich	2015	<u>2.2–28.5</u>	<u>20–84</u>	<u>3.2–14.2</u>	<u>12–74</u>	<u>0.3–1.7</u>	<u>2–7</u>	<u>17.1–35.2</u>
		16.6 \pm 3.0	62 \pm 6	8.0 \pm 1.2	35 \pm 6	0.8 \pm 0.1	3 \pm 1	25.3 \pm 3.6
	2016	<u>10.9–27.1</u>	<u>40–85</u>	<u>3.9–26.1</u>	<u>14–57</u>	<u>0.3–1.6</u>	<u>1–5</u>	<u>16.7–45.9</u>
		18.2 \pm 1.5	68 \pm 4	8.6 \pm 2.2	29 \pm 4.0	0.8 \pm 0.2	3 \pm 1	27.6 \pm 2.8
	2017	<u>2.3–16.3</u>	<u>23–52</u>	<u>7.1–13.9</u>	<u>44–73</u>	<u>0.4–1.4</u>	<u>2–7</u>	<u>10.4–31.3</u>
		7.9 \pm 1.5	40 \pm 3	10.2 \pm 0.9	55 \pm 3	0.9 \pm 0.1	5 \pm 1	19.0 \pm 2.0
Gorky	2015	<u>7.2–27.8</u>	<u>46–91</u>	<u>2.6–14.0</u>	<u>9–53</u>	<u>0.0–2.1</u>	<u>0.1–6</u>	<u>15.6–36.1</u>
		19.9 \pm 1.6	71 \pm 4	7.6 \pm 1.0	28 \pm 4	0.3 \pm 0.2	1 \pm 0.4	27.8 \pm 1.5
	2016	<u>6.4–36.6</u>	<u>76–98</u>	<u>0.3–6.4</u>	<u>2.2–22</u>	<u>0.0–1.1</u>	<u>0.1–2</u>	<u>8.5–44.1</u>
		17.7 \pm 2.3	90 \pm 2	1.8 \pm 0.5	9 \pm 2	0.1 \pm 0.1	1 \pm 0.3	19.6 \pm 2.7
	2017	<u>0.7–12.2</u>	<u>55–98</u>	<u>0.2–1.6</u>	<u>1–35</u>	<u>0.0–0.5</u>	<u>1–9</u>	<u>1.2–13.1</u>
		6.1 \pm 1.0	79 \pm 3	1.1 \pm 0.1	18 \pm 3	0.2 \pm 0.0	3 \pm 1	7.4 \pm 1.0
Cheboksary	2015	<u>0.5–26.1</u>	<u>2–89</u>	<u>1.6–33.0</u>	<u>10–97</u>	<u>0.0–0.4</u>	<u>0.1–1</u>	<u>16.2–52.1</u>
		17.8 \pm 2.6	60 \pm 10	18.3 \pm 6.8	40 \pm 10	0.2 \pm 0.0	0.5 \pm 0.1	36.3 \pm 6.9
	2016	<u>3.8–18.7</u>	<u>14–97</u>	<u>0.5–31.4</u>	<u>3–82</u>	<u>0.0–1.3</u>	<u>0.1–7</u>	<u>5.2–38.1</u>
		11.0 \pm 1.9	66 \pm 6	3.6 \pm 1.2	30 \pm 6	0.6 \pm 0.1	4 \pm 1	15.1 \pm 2.2
	2017	<u>0.4–17.4</u>	<u>1–98</u>	<u>0.4–27.5</u>	<u>2–86</u>	<u>0.0–3.9</u>	<u>1–12</u>	<u>3.5–31.8</u>
		5.0 \pm 1.9	61 \pm 11	4.7 \pm 3.4	32 \pm 9	0.8 \pm 0.5	7 \pm 2	10.5 \pm 3.6
Kuibyshev	2015	<u>1.6–22.8</u>	<u>59–93</u>	<u>0.6–13.6</u>	<u>7–35</u>	<u>0.0–2.5</u>	<u>0.1–6</u>	<u>2.2–38.9</u>
		10.6 \pm 2.0	78 \pm 3	2.7 \pm 0.9	21 \pm 3	0.3 \pm 0.2	1 \pm 0.5	13.6 \pm 2.8
	2016	<u>6.7–47.2</u>	<u>44–95</u>	<u>0.6–11.9</u>	<u>5–46</u>	<u>0.1–3.0</u>	<u>0.2–12</u>	<u>7.9–49.9</u>
		17.6 \pm 2.0	79 \pm 2.9	3.5 \pm 0.6	17 \pm 2	0.8 \pm 0.2	4 \pm 1	21.9 \pm 2.0
	2017	<u>0.7–13.3</u>	<u>37–98</u>	<u>0.1–6.5</u>	<u>1–62</u>	<u>0.1–0.8</u>	<u>1–15</u>	<u>1.3–15.0</u>
		6.2 \pm 1.0	72 \pm 5	1.9 \pm 0.6	22 \pm 5	0.4 \pm 0.1	6 \pm 1	8.5 \pm 1.1
Saratov	2015	<u>4.0–18.4</u>	<u>74–88</u>	<u>1.0–2.6</u>	<u>10–26</u>	<u>0.0–0.3</u>	<u>0.5–2</u>	<u>5.1–20.8</u>
		9.5 \pm 1.3	82 \pm 1	1.7 \pm 0.2	17 \pm 1	0.1 \pm 0.0	1 \pm 0.1	11.3 \pm 1.4
	2017	<u>1.5–10.1</u>	<u>78–96</u>	<u>0.3–0.8</u>	<u>2–25</u>	<u>0.1–0.2</u>	<u>1–6</u>	<u>2.0–10.7</u>
Volgograd	2017	<u>4.6–1.7</u>	<u>83 \pm 5</u>	<u>0.5 \pm 0.1</u>	<u>14 \pm 4</u>	<u>0.1 \pm 0.0</u>	<u>3 \pm 1</u>	<u>5.2 \pm 1.5</u>
		<u>0.6–14.2</u>	<u>28–93</u>	<u>0.1–2.2</u>	<u>2–63</u>	<u>0.2–0.4</u>	<u>1–9</u>	<u>2.1–15.8</u>
		6.6 \pm 1.2	78 \pm 6	1.1 \pm 0.2	18 \pm 6	0.3 \pm 0.1	4 \pm 1	8.0 \pm 1.1

Average ΣCHL concentrations in reservoirs varied from 11.3 \pm 1.4 to 27.8 \pm 1.5 in 2015, from 19.6 \pm 2.7 to 33.7 \pm 11.1 in 2016, and from 9.1 \pm 2.5 to 30.5 \pm 3.9 in 2017 (Figure 2).

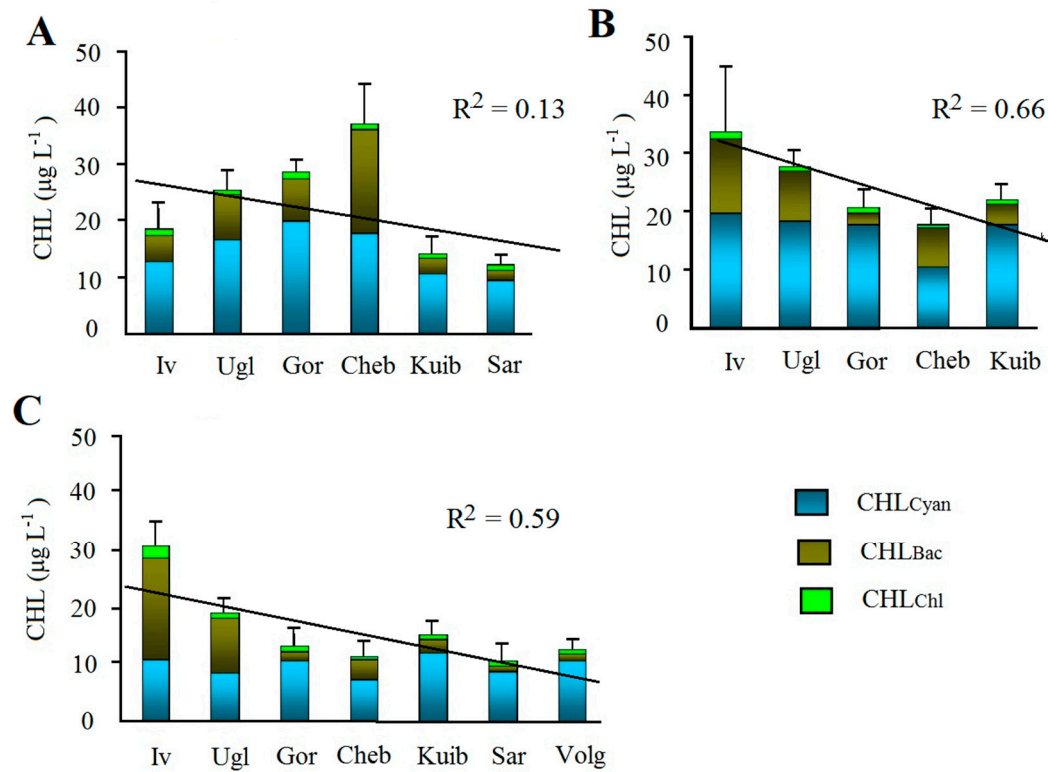


Figure 2. Average chlorophyll content in basic phytoplankton taxa (CHL_{Cyan} , CHL_{Bac} , $\text{CHL}_{\text{Chlor}}$) and in total (ΣCHL) equal to their sum in the Volga River reservoirs in years of study (2015–2017, A–C, respectively). Error bar and trend dotted line are given for ΣCHL ; R^2 – coefficient of determination. Reservoirs: Iv – Ivankovo, Ugl – Uglich, Gor – Gorky, Chev – Cheboksary, Kuib – Kuibyshev, Sar – Saratov, Volg – Volgograd.

Average ΣCHL tends to decrease downstream from the reservoirs of the Upper Volga to the reservoirs of the Lower Volga. This is most clearly shown by the data averaged over the years of observation (Figure 3A) and confirmed by the results of ANOVA (Table 3). However, this decrease was significant in 2016 and 2017 ($R^2 = 0.83$ and 0.59) but was disturbed in 2015 due to the high concentration of ΣCHL in the Cheboksary reservoir (Figure 2).

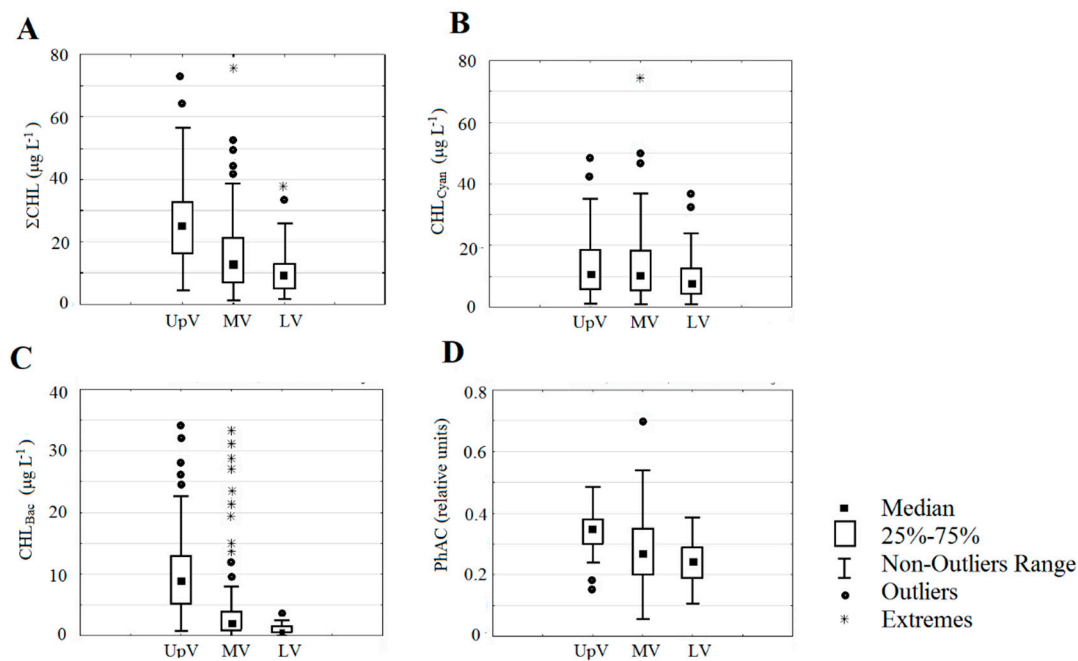


Figure 3. Box plots of chlorophyll concentrations in total (Σ CHL, A), CHL_{Cyan} (B), CHL_{Bac} (C), and PhAC (D) in the Upper, Middle, and Lower Volga (UpV, MV, LV, respectively). Data are averaged over three years of study.

Table 3. Results of comparison of the average chlorophyll and PhAC in the Upper, Middle, and Lower Volga using oneway ANOVA.

Parameter	Source of variation	SS	df	MS	F	P	Fcr
Σ CHL	Between groups	7962	2	3981	27.1	0.00	3.03
	Within groups	38526	262	147			
CHL_{Cyan}	Between groups	454	2	227	2.28	0.10	3.03
	Within groups	26134	262	99			
CHL_{Bac}	Between groups	3408	2	1704	43.5	0.00	3.02
	Within groups	10262	262	39.2			
PhAC	Between groups	0.251	2	0.125	15.1	0.00	3.04
	Within groups	1.588	191	0.008			

SS, sum of squared deviations; df, number of degrees of freedom; MS, mean square; F, F-test; Fcr, F critical; P, significance level.

The content of chlorophyll for each of the three algae phylum also varied widely. The minimum amount of CHL_{Cyan} was $<1\text{--}5\text{ }\mu\text{g L}^{-1}$, and the maximum values in 2015 and 2016 reached $49\text{ }\mu\text{g L}^{-1}$ in the Ivankovo reservoir, $28\text{ }\mu\text{g L}^{-1}$ in the Uglich, $36\text{ }\mu\text{g L}^{-1}$ in the Gorky, and $47\text{ }\mu\text{g L}^{-1}$ in the Kuibyshev reservoir. In 2017, CHL_{Cyan} in these reservoirs was lower, and the maximum values did not exceed $12\text{--}29\text{ }\mu\text{g L}^{-1}$. In the Cheboksary, Saratov, and Volgograd reservoirs, the maximum values were less than $10\text{--}26\text{ }\mu\text{g L}^{-1}$ in all years. Average concentrations of CHL_{Cyan} in 2015 and 2016 varied from 13.5 ± 3.6 to 19.9 ± 1.6 in the Upper and Middle Volga. It decreased to $4.6 \pm 1.7\text{--}9.5 \pm 1.3$ in the Lower Volga, as well as in 2017 in the Upper and Middle Volga (Figure 2). The contribution of CHL_{Cyan} to the total Σ CHL ranged from 60 to 90% on average, and only in 2017 in the Upper Volga it decreased to 30–40%. The highest percentage of CHL_{Cyan} over 80% was recorded in Gorky (2016) and in Saratov reservoirs. The change in CHL_{Cyan} in the cascade of reservoirs is not clear (Figure 3B, Table 3) and only a downward trend can be seen in its amount in the lower reservoirs.

The maximum of CHL_{Bac} in individual reservoirs was mainly from 11.7 to $31.8\text{ }\mu\text{g L}^{-1}$ and was less ($0.8\text{--}6.4\text{ }\mu\text{g L}^{-1}$) in the Gorky reservoir (2016, 2017) as well as in the Lower Volga. Average

concentrations of CHL_{Bac} in limits of 7.6–18.3 $\mu\text{g L}^{-1}$ were obtained in Ivankovo reservoir in 2016 and 2017, in Uglich reservoir in all years, and in Cheboksary reservoir in 2016. In all other cases, the average concentrations of CHL_{Bac} were below 5 $\mu\text{g L}^{-1}$ (Figure 2). The share of it in ΣCHL basically was 14–35%. It decreased to 9% in Gorky reservoir in 2016 and increased to 40–60% in Ivankovo and Uglich reservoirs in 2017, in Cheboksary reservoir in 2015. Like ΣCHL average CHL_{Bac} is significantly declining downstream from the reservoirs of the Upper Volga to the reservoirs of the Lower Volga (Figure 3C, Table 3). For CHL_{Bac} , as for ΣCHL , there is a decrease in the lower reservoirs compared to the upper ones that is confirmed by the results of dispersion analysis. At the same time, no significant decrease in CHL_{Cyan} was detected (Table 3).

Maximal CHL_{Chl} did not exceed 1–4 $\mu\text{g L}^{-1}$, with average being 1.1–1.5 $\mu\text{g L}^{-1}$ in Ivankovo reservoir and usually <1 $\mu\text{g L}^{-1}$ in all other (Table 2, Figure 2). The contribution of CHL_{Chl} into ΣCHL varied very little both within the cascade as well as during the observation periods, with average being 0.5–6.8%. We do not consider the spatial and temporal dynamics of CHL_{Chl} because of its low content.

Photosynthetic activity coefficient (PhAC) changed to a lesser extent than ΣCHL . The maximum and minimum values of PhAC in each reservoir differed by 1.5–3 times, and only in the Cheboksary and Kuibyshev reservoirs in 2017 the difference between them increased up to 5–6 times. In reservoirs of the Upper Volga, in different years PhAC varied from the minimum 0.17 to the maximum of 0.38–0.59 in Ivankovo and 0.40–0.57 in the Uglich reservoir, and in both the average values were similar in all years. In the reservoirs of the Middle Volga, the PhAC range was wider, from a minimum <0.10 to a maximum of 0.43 in Gorky, 0.52 in Cheboksary, and 0.39 in Kuibyshev reservoirs. In 2017, there was a significant decrease in the average PhAC in the Gorky and Cheboksary reservoirs. In the Lower Volga, both the marginal (0.10–0.38) and average ($0.17 \pm 0.02 - 0.28 \pm 0.03$) PhAC values are lower than in other reservoirs. For the Saratov reservoir, a decrease in PhAC was noted in 2017 (Table 4, Figure 4).

Table 4. Coefficient of photosynthetic activity (PhAC) of phytoplankton in the Volga River reservoirs in 2015-2017.

Reservoir	2015		2016		2017	
	Min–max	X \pm SE	Min–max	X \pm SE	Min–max	X \pm SE
Ivankovo	0.17–0.38	0.35 \pm 0.01	0.37–0.59	0.38 \pm 0.03	0.27–0.43	0.35 \pm 0.02
Uglich	0.27–0.4	0.31 \pm 0.02	0.18–0.57	0.31 \pm 0.03	0.27–0.44	0.36 \pm 0.02
Gorky	0.24–0.70	0.38 \pm 0.03	0.14–0.44	0.26 \pm 0.02	0.09–0.26	0.16 \pm 0.01
Cheboksary	0.18–0.52	0.35 \pm 0.03	0.18–0.44	0.33 \pm 0.02	0.08–0.4	0.22 \pm 0.04
Kuibyshev	0.12–0.39	0.26 \pm 0.02	0.2–0.39	0.29 \pm 0.02	0.06–0.36	0.24 \pm 0.03
Saratov	0.19–0.38	0.28 \pm 0.03	–	–	0.10–0.25	0.17 \pm 0.02
Volgograd	–	–	–	–	0.12–0.38	0.25 \pm 0.02

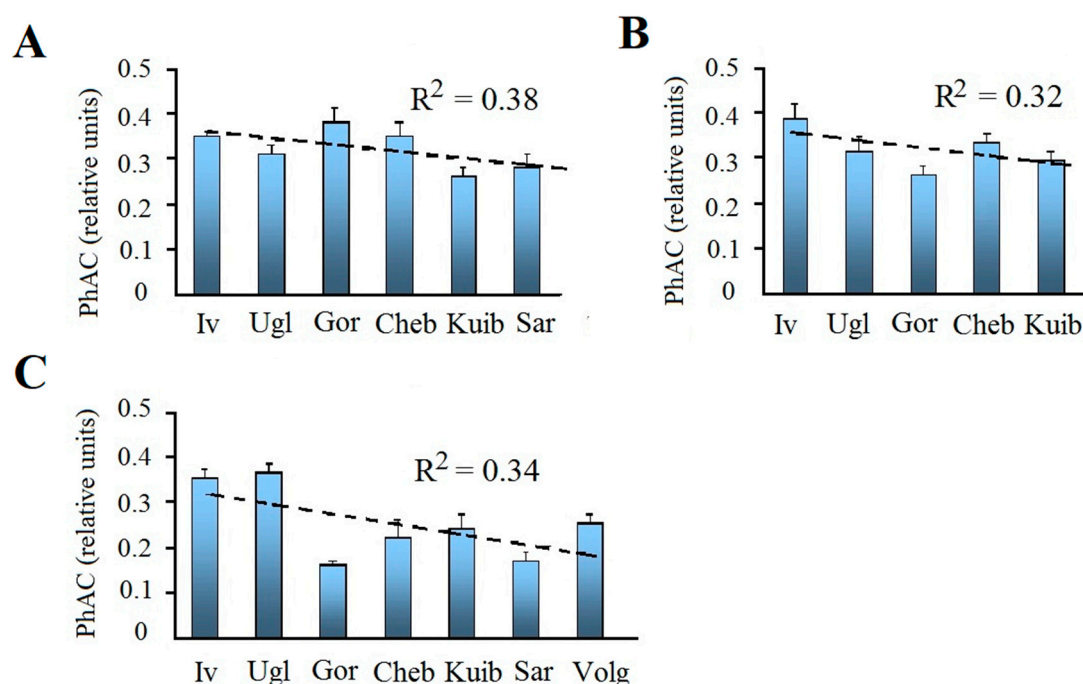


Figure 4. Coefficient of photosynthetic activity (PhAC) of phytoplankton in the Volga River reservoirs in years of study (2015–2017, A–C, respectively). Mean values with standard error; dotted line – trend line; R^2 – coefficient of determination. Reservoirs: Iv – Ivankovo, Ugl – Uglich, Gor – Gorky, Chev – Cheboksary, Kuib – Kuibyshev, Sar – Saratov, Volg – Volgograd.

PhAC is closely related to ΣCHL content (Figure 5). This relationship is described by a polynomial function and demonstrates slowdown in the growth of PhAC and its decrease at high pigment concentrations that are above $40 \mu\text{g L}^{-1}$. Therefore, it is not surprising that there is a decreasing in PhAC from the upper reservoirs to the lower ones (Figure 4). In each year, this decrease is less significant than the decrease in ΣCHL ($R^2 = 0.30\text{--}0.37$). However, according to the data averaged over three years, it can be traced very clearly and is confirmed by the results of ANOVA (Figure 3D, Table 3).

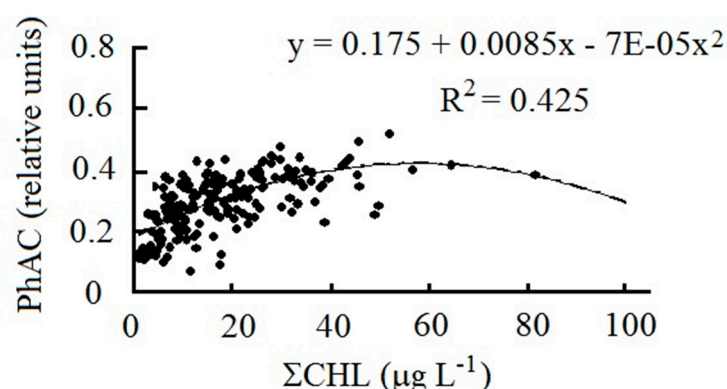


Figure 5. Dependence of PhAC on chlorophyll content in the Volga River reservoirs.

The relationship of PhAC with ΣCHL , which is an indicator of the trophic state of water bodies, makes it possible to assess the photosynthetic activity of phytoplankton in waters of different trophicity. Average PhAC values increase threefold at the transition from low productive oligotrophic waters to

highly productive hypertrophic ones (Table 5). The state of phytoplankton was characterized by low photosynthetic activity in oligotrophic waters and by normal activity in all others.

Table 5. Change in PhAC in waters of different trophic state estimated by ΣCHL .

Trophic state	ΣCHL , $\mu\text{g L}^{-1}$	PhAC, relative units
Oligotrophic	<3	0.12 ± 0.01
Mesotrophic	3–10	0.20 ± 0.01
Moderate eutrophic	10–15	0.27 ± 0.01
Eutrophic	15–30	0.32 ± 0.01
Hypertrophic	>30	0.38 ± 0.01

4. Discussion

The study of the summer phytoplankton is of considerable interest, because negative trends caused by eutrophication or climate changes become apparent in water ecosystem of the reservoir during this season. The data obtained in August are confined to the maximum warming of the water column and correspond to the summer maximum of phytoplankton, which is indicative for assessing the state of water bodies. Concentrations of chlorophyll (ΣCHL) in each reservoir were typical for this particular period of phytoplankton seasonal succession [9].

Each reservoir of the Volga River is a unique water body with specific conditions that control the development of biota. Reservoirs are characterized by a complex hydrodynamic regime, which is formed under the influence of factors including morphometry, flow velocity, intensive mixing, a developed network of tributaries, and the presence of heterogeneous water masses [27]. These features determine the uneven large-scale distribution of phytoplankton and, as a result, the significant difference between the maximum and minimum chlorophyll concentrations in each reservoir. An increased amount of chlorophyll is usually observed in shallow water areas, in the mouth sections of tributaries, in dam extensions [9]. Photosynthetic activity coefficient (PhAC) was changing less than ΣCHL and it looks like a more stable parameter as well as photosynthesis measured by the oxygen flask method [7]. The same PhAC range was obtained for phytoplankton of Lake Shira [37] and reservoirs of the Upper Volga including Rybinsk reservoir, which also had a low PhAC variation [24,25]. Like photosynthesis, PhAC is closely correlated with chlorophyll and shows changes in waters of different trophic state.

Fluorescent analysis makes it possible to estimate the chlorophyll content of the three algal phylums typical for freshwater phytoplankton. With differences in the specific content of chlorophyll in the large taxonomic groups of algae [38], these data do not quantify the biomass of the phylums, but are of interest for a comparative analysis of their development. The amount and ratio of CHL_{Cyan} and CHL_{Bac} corresponds to the composition of summer phytoplankton, which is characterized by the dominance of cyanoprokaryotes or cyanoprokaryotes and diatoms [39].

The average PhAC values correspond to the normal physiological state of the phytoplankton of the Upper Volga during all periods of observation. On the Middle Volga, the situation is different. Phytoplankton of the Gorky reservoir is characterized by normal photosynthetic activity in 2015, Cheboksary reservoir in 2015 and 2016. In other cases, PhAC reflects the low photosynthetic activity of algae. In the Kuibyshev and two reservoirs of the Lower Volga, photosynthetic activity is decreasing that is probably due to an increase in the volume of water runoff.

In the interannual dynamics of chlorophyll and photosynthetic activity, 2017 stands out when a decrease in the average content of ΣChl and CHL_{Cyan} in all water bodies and a decrease in average PhAC in the Middle and Lower Volga, was noted. A cyclonic windy weather prevailed for most of the season in 2017 with a large amount of precipitation, low solar radiation, and large volume of flow [36]. Weather conditions in the Volga region and especially in the Upper Volga were unfavorable for the development of phytoplankton and, in particular, cyanoprokaryotes, which usually make up the majority of phytoplankton in summer [39]. As for CHL_{Bac} , it decreased in the Middle and Lower Volga, but became higher in comparison with previous years in the Upper Volga since diatoms are well adapted to existence in conditions of an actively mixed water column [40]. With a general

decrease in PhAC in the Middle and Lower Volga in 2017, values <0.10 were obtained in each reservoir, which may indicate the presence of cells with a damaged photosynthetic apparatus [32].

During the period of our studies, as before [9], there is a tendency for chlorophyll and PhAC to decrease from the Upper Volga to the Lower Volga. A similar distribution has been traced for the phytoplankton biomass [39]. This is explained by increasing in the flow rate and volume of runoff downstream the Volga River, and these factors limit the development of phytoplankton. Ecosystems of the lower reservoirs that close the cascade are considered the least stable due to high dependence on the changing flow of the Volga River [41].

5. Conclusion

Study of productivity and development of phytoplankton in the Volga River cascade in summer period showed a wide range of chlorophyll concentration with uneven large-scale distribution and significant difference between the maximum and minimum ΣCHL in reservoirs with complex hydrodynamic regime. Average ΣCHL varied in limits of $19.4\text{--}33.7 \mu\text{g L}^{-1}$ in the Upper Volga, $8.5\text{--}27.8 \mu\text{g L}^{-1}$ in the Middle Volga, and $5.2\text{--}11.3 \mu\text{g L}^{-1}$ in the Lower Volga. Chlorophyll content of basic algal phylums corresponds to the composition of summer phytoplankton with the dominance of cyanoprokaryotes or cyanoprokaryotes and diatoms. CHL_{Cyan} accounted for 31–68% of the ΣCHL in the Upper Volga and 60–90% in the Middle and Lower Volga. The share of CHL_{Bac} was 29–62% and 9–40%, the share of CHL_{Chl} was 5–7% and 1–4% respectively.

Photosynthetic activity coefficient (PhAC) was changing less than ΣCHL and varied mostly in limits of 0.12–0.59 with average of 0.22–0.38 and only in 2017 decreased to minimal <0.10 and average <0.20 . The average PhAC values show the normal physiological state of phytoplankton in the Upper Volga during all periods of observation, occasional decrease of PhAC in the Middle Volga, and low photosynthetic activity in the Lower Volga. PhAC is closely correlated with ΣCHL and changes in waters of different trophic state. In the interannual dynamics, a decrease in the average ΣChl and CHL_{Cyan} in all water bodies and decrease in PhAC in the Middle and Lower Volga was noted in 2017 under cyclonic windy weather with a large amount of precipitation, low solar radiation, and large volume of flow. Currently, there is a previously identified trend towards a decrease in ΣCHL , like decrease in PhAC from the Upper Volga to the Lower Volga that is explained by increasing in the flow rate and volume of runoff downstream the Volga River.

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