phycology

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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 studied the development (as chlorophyll content, ∑CHL) and photosynthetic activity of phytoplankton in seven large flat reservoirs of the Volga River cascade (Russia) in August 2015–2017. In the period of the maximal warming of water, average ∑CHL varied in limits of 19.4–33.7 μg L^{-1} in the Upper Volga, 8.5–27.8 μg L^{-1} in the Middle Volga, and 5.2–11.3 μg L^{-1} in the Lower Volga. The photosynthetic activity coefficient (PhAC) varied mostly in limits of 0.12–0.59, with an 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 the phytoplankton of the Upper Volga during all periods of observation, with an occasional decrease in PhAC in the Middle Volga and low photosynthetic activity in the Lower Volga. A decrease in the average ∑Chl and PhAC in 2017 was under cyclonic windy weather with a large amount of precipitation, low solar radiation, and large volume of flow. A trend towards a decrease in ∑CHL, like a decrease in PhAC from the Upper Volga to the Lower Volga, is explained by an increase in the flow rate and volume of runoff downstream of the Volga River.

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

Citation: Mineeva, N.; Semadeni, I. Chlorophyll Content and Photosynthetic Activity of Phytoplankton in Reservoirs of the Volga River (Russia). *Phycology* **2023**, 3, 368–381. https://doi.org/10.3390/phycology3030024

Academic Editor: Sang Heon Lee

Received: 14 July 2023
Revised: 1 August 2023
Accepted: 7 August 2023
Published: 10 August 2023

1. Introduction

The study of the autotrophic community of aquatic ecosystems is a crucial part of hydroecological research. Planktonic algae are the main source of primary production in freshwater systems. In the process of photosynthesis, they produce the bulk of the stock of autochthonous organic matter in large lakes and reservoirs, which forms the energy base for organisms of higher trophic levels. The role of algae is significant in carbon balance and enrichment of the water column with dissolved oxygen. The energy and resource fluxes through the entire biosphere are greatly influenced by pelagic primary producers [1–4].

A special place among the indicators of the abundance and functioning of phytoplankton is given to photosynthetic pigments, which are 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 the water environment [1,5]. The unique optical properties of chlorophyll—the ability to absorb and emit light radiation in a narrow wavelength range [6]—are the foundation for methods to define it.

Phytoplankton form the basis of the trophic pyramid in the largest river in Europe, the Volga River, which has now been transformed into a cascade of reservoirs [7,8]. Research of the pigments in the Volga River was started in the middle of the XX century [9], and these studies have been supplemented with new data [10–12], which are summarized in [13]. Most of these studies were carried out with the standard spectrophotometric method [14]. Recently, we have begun to use fluorescent diagnostics of phytoplankton, and data of the fluorescence CHL determination showed good agreement with the results of standard spectrophotometry [15]. Measurement of CHL fluorescence directly in natural water makes it possible to quickly analyze a large series of samples and evaluate a range of phytoplankton characteristics without affecting its integrity. This is the advantage of fluorescent diagnostics over methods that require the isolation of samples. These include the flask method for determining primary production or preliminary deposition of algae on a filter as standard spectrophotometric determinations of pigments.

The coefficient of photosynthetic activity (PhAC) is a direct indicator of the algocenoses state [16]. PhAC characterizes the effective quantum yield of photochemical energy conversion [17,18]. These mechanisms are associated with the functioning of photosystem II (PS II), reflecting the absorption efficiency of solar energy by algae during photosynthesis [19]. The quantum yield of photosynthesis (i.e., PhAC) serves as a measure of photosynthetic activity under electron-saturated reaction centers [20,21]. PhAC varies depending on a wide range of factors, reflecting the physiological state of photosynthetic organisms [22]. The application of PhAC to the assessment of productivity and state of natural algae communities seems to be a promising aspect of hydrobiological research [23,24]. The first data on PhAC of the Volga phytoplankton were obtained by us for the reservoirs of the Upper Volga previously [25,26].

Recently, reservoirs have been created on many large rivers around the world [27]. With a significant interest in assessing the development and functioning of phytoplankton in rivers with hydraulic structures, most of the studies were carried out in their estuary zones [28–30] or on individual reservoirs [31,32] and less often for a cascade of reservoirs [33,34]. The peculiarity of the Volga lies in the fact that, with a significant length from north to south, the river crosses a range of natural zones, which makes it possible to trace the zonal and azonal features in the development of biota.

Our data were collected in the shortest possible time throughout the entire Volga cascade. The main purpose of this work was 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 in years with different hydroclimatic conditions.

2. Materials and Methods

2.1. Site Description

The Volga River, at 3690 km, is the longest river in Europe [35,36]. 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. In accordance with the geographical zonality, three sections are distinguished in the cascade: the 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). Climate of the Upper Volga basin and Middle Volga basin is moderate continental, while in the Low Volga basin, it is mostly continental. Mean annual air temperature varies from 2.8–3.4 °C in the north of the basin to 7.1–8.6 °C in the south. The warmest month is July, averaging from 16.7–19.2 °C to 21.5 °C and 25.1 °C. Annual precipitation is from 548 to 706 mm in the upper basin, 282 to 626 mm in the middle basin, and decreases to 175–340 mm in the south [36].

Most of the Volga River from the town of Tver′ to Volgograd, which is over 2500 km long, is affected by an uninterrupted cascade of eight large shallow reservoirs, considerably slowing the flow velocity of the river. A schematic map of the reservoirs is shown in Figure 1, and their basic characteristics are given in Table 1. The reservoirs differ in terms of morphometry, optical regime, chemistry, lateral inflow, water exchange, and trophic status. With a change in conditions in the drainage basin, the total amount of ion conductivity increases, and the color intensity 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 that the development of algae is not limited [36].

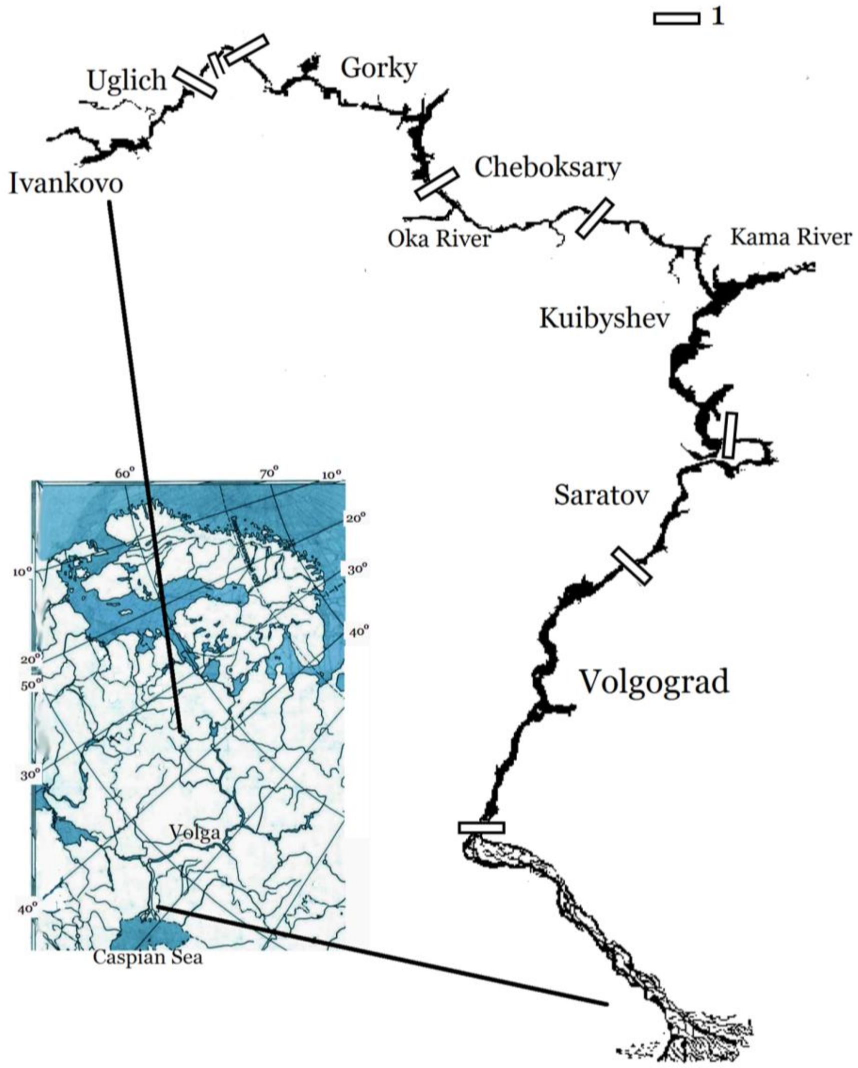

Figure 1. Schematic map of the Volga River reservoirs according to [13]; 1—boundary of reservoirs.

Table 1. Basic abiotic characteristics of the Volga River reservoirs according to [35,36].

Parameters	Upper Volga		Middle Volga			Lower Volga	
	Ivankovo	Uglich	Gorky	Cheboksary	Kuibyshev	Saratov	Volgograd
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

2.2. Sampling

Our data include the route surveys carried out at seven run-of-river Volga reservoirs in the midsummer. In 2015–2017, samples were taken at 50–60 stations of the Upper and Middle Volga, as well as at 6 stations of the Saratov reservoir in 2016 and at 19 stations of the Lower Volga in 2017. Surveying each reservoir lasted 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 the research vessel in natural water on a stationary fluorimeter PFL-3004 (Krasnoyarsk, Russia) [37,38]. Fluorescent diagnostics is highly expressive and can detect low (<1 μg L^{-1}) concentrations of chlorophyll directly in natural water. The standard error of fluorescence yield measuring does not exceed 2% [26].

The method is based on the specifics of light-harvesting pigment–protein complexes of the diatoms, green algae, and cyanoprokaryots (blue-green algae), which makes it possible to determine the total amount of ∑CHL 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 was measured devoid of algae. Total chlorophyll *a* amount (ΣCHL, μg L^{-1}) 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 [39].

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 a 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 Formula (1) from [40].

$$PhAC = (F'_{max} - F_t)/(F'_{max}) \tag{1}$$

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 [41]. 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 shows the approach of fluorescence to its biological maximum, which is actually not observed in situ [42–44].

2.5. Statistics

Standard software packages for a personal computer Statistic10 (StatSoft Inc., Tulsa, OK, 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 (X ± SE). To determine the relationships between chlorophyll content and PhAC, we used Pearson correlation coefficient, significant at $p < 0.05$. Analysis of variance (ANOVA) was used to compare the average chlorophyll concentration and PhAC in the Upper, Middle, and Lower Volga.

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 °C in 2015 and 21.9–24.7 °C in 2016. The start of the growing season in 2017 was cold and rainy [45]; however, the summer heating reached normal temperatures of 21.0–23.0 °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 of summer, the summer maximum of phytoplankton is formed. The content of ∑CHL 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 μg L^{-1}, in the Uglich reservoir from 10–17 to 30–46 μg L^{-1}, in the Gorky reservoir from 8 to 44 μg L^{-1} in 2015 and 2016, and from 1 up to 13 μg L^{-1} in 2017. In the Cheboksary reservoir, the highest concentrations (16–52 μg L^{-1}) were obtained in 2015, and these were lower (3–38 μg L^{-1}) in 2016 and 2017. In the Kuibyshev reservoir, as in the Gorky reservoir, higher values (from 2–8 to 39–50 μg L^{-1}) were obtained in 2015 and 2016, with lower values (1–15 μg L^{-1}) in 2017. In the Lower Volga, ∑CHL concentrations were lower and varied in a narrow range, from 2–5 to 10–20 μg 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}, CHL_{Chlor}) and in total (∑CHL) 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}		CHL_{Chlor}		∑CHL
		μg L^{-1}	%	μg L^{-1}	%	μg L^{-1}	%	μg L^{-1}
Ivankovo	2015	3.0–42.0 13.5 ± 3.6	26–86 64 ± 6	0.8–11.7 4.7 ± 1.0	8–58 29 ± 5	0.3–3.9 1.1 ± 0.3	2–18 7 ± 1	4.3–49.0 19.4 ± 4.0
	2016	4.8–49.1 19.7 ± 5.4	37–87 62 ± 4	1.7–12.6 6.7 ± 1.8	12–61 32 ± 4.2	0.5–3.0 1.2 ± 0.3	1–11 5 ± 1	8.4–56.2 33.7 ± 11.1
	2017	1.3–29.1 6.8 ± 2.1	11–58 31 ± 4	1.2–31.8 14.8 ± 3.2	36–85 62 ± 4	0.2–3.7 1.5 ± 0.3	3–18 7 ± 1	3.2–45.7 23.1 ± 4.9
Uglich	2015	2.2–28.5 16.6 ± 3.0	20–84 62 ± 6	3.2–14.2 8.0 ± 1.2	12–74 35 ± 6	0.3–1.7 0.8 ± 0.1	2–7 3 ± 1	17.1–35.2 25.3 ± 3.6
	2016	10.9–27.1 18.2 ± 1.5	40–85 68 ± 4	3.9–26.1 8.6 ± 2.2	14–57 29 ± 4.0	0.3–1.6 0.8 ± 0.2	1–5 3 ± 1	16.7–45.9 27.6 ± 2.8
	2017	2.3–16.3 7.9 ± 1.5	23–52 40 ± 3	7.1–13.9 10.2 ± 0.9	44–73 55 ± 3	0.4–1.4 0.9 ± 0.1	2–7 5 ± 1	10.4–31.3 19.0 ± 2.0
Gorky	2015	7.2–27.8 19.9 ± 1.6	46–91 71 ± 4	2.6–14.0 7.6 ± 1.0	9–53 28 ± 4	0.0–2.1 0.3 ± 0.2	0.1–6 1 ± 0.4	15.6–36.1 27.8 ± 1.5
	2016	6.4–36.6 17.7 ± 2.3	76–98 90 ± 2	0.3–6.4 1.8 ± 0.5	2.2–22 9 ± 2	0.0–1.1 0.1 ± 0.1	0.1–2 1 ± 0.3	8.5–44.1 19.6 ± 2.7
	2017	0.7–12.2 6.1 ± 1.0	55–98 79 ± 3	0.2–1.6 1.1 ± 0.1	1–35 18 ± 3	0.0–0.5 0.2 ± 0.0	1–9 3 ± 1	1.2–13.1 7.4 ± 1.0
Cheboksary	2015	0.5–26.1 17.8 ± 2.6	2–89 60 ± 10	1.6–33.0 18.3 ± 6.8	10–97 40 ± 10	0.0–0.4 0.2 ± 0.0	0.1–1 0.5 ± 0.1	16.2–52.1 36.3 ± 6.9
	2016	3.8–18.7 11.0 ± 1.9	14–97 66 ± 6	0.5–31.4 3.6 ± 1.2	3–82 30 ± 6	0.0–1.3 0.6 ± 0.1	0.1–7 4 ± 1	5.2–38.1 15.1 ± 2.2
	2017	0.4–17.4 5.0 ± 1.9	1–98 61 ± 11	0.4–27.5 4.7 ± 3.4	2–86 32 ± 9	0.0–3.9 0.8 ± 0.5	1–12 7 ± 2	3.5–31.8 10.5 ± 3.6
Kuibyshev	2015	1.6–22.8 10.6 ± 2.0	59–93 78 ± 3	0.6–13.6 2.7 ± 0.9	7–35 21 ± 3	0.0–2.5 0.3 ± 0.2	0.1–6 1 ± 0.5	2.2–38.9 13.6 ± 2.8
	2016	6.7–47.2 17.6 ± 2.0	44–95 79 ± 2.9	0.6–11.9 3.5 ± 0.6	5–46 17 ± 2	0.1–3.0 0.8 ± 0.2	0.2–12 4 ± 1	7.9–49.9 21.9 ± 2.0
	2017	0.7–13.3 6.2 ± 1.0	37–98 72 ± 5	0.1–6.5 1.9 ± 0.6	1–62 22 ± 5	0.1–0.8 0.4 ± 0.1	1–15 6 ± 1	1.3–15.0 8.5 ± 1.1
Saratov	2015	4.0–18.4 9.5 ± 1.3	74–88 82 ± 1	1.0–2.6 1.7 ± 0.2	10–26 17 ± 1	0.0–0.3 0.1 ± 0.0	0.5–2 1 ± 0.1	5.1–20.8 11.3 ± 1.4
	2017	1.5–10.1 4.6 ± 1.7	78–96 83 ± 5	0.3–0.8 0.5 ± 0.1	2–25 14 ± 4	0.1–0.2 0.1 ± 0.0	1–6 3 ± 1	2.0–10.7 5.2 ± 1.5
Volgograd	2017	0.6–14.2 6.6 ± 1.2	28–93 78 ± 6	0.1–2.2 1.1 ± 0.2	2–63 18 ± 6	0.2–0.4 0.3 ± 0.1	1–9 4 ± 1	2.1–15.8 8.0 ± 1.1

The average ∑CHL concentrations in reservoirs varied from 11.3 ± 1.4 to 27.8 ± 1.5 in 2015, from 19.6 ± 2.7 to 33.7 ± 11.1 in 2016, and from 9.1 ± 2.5 to 30.5 ± 3.9 in 2017 (Figure 2).

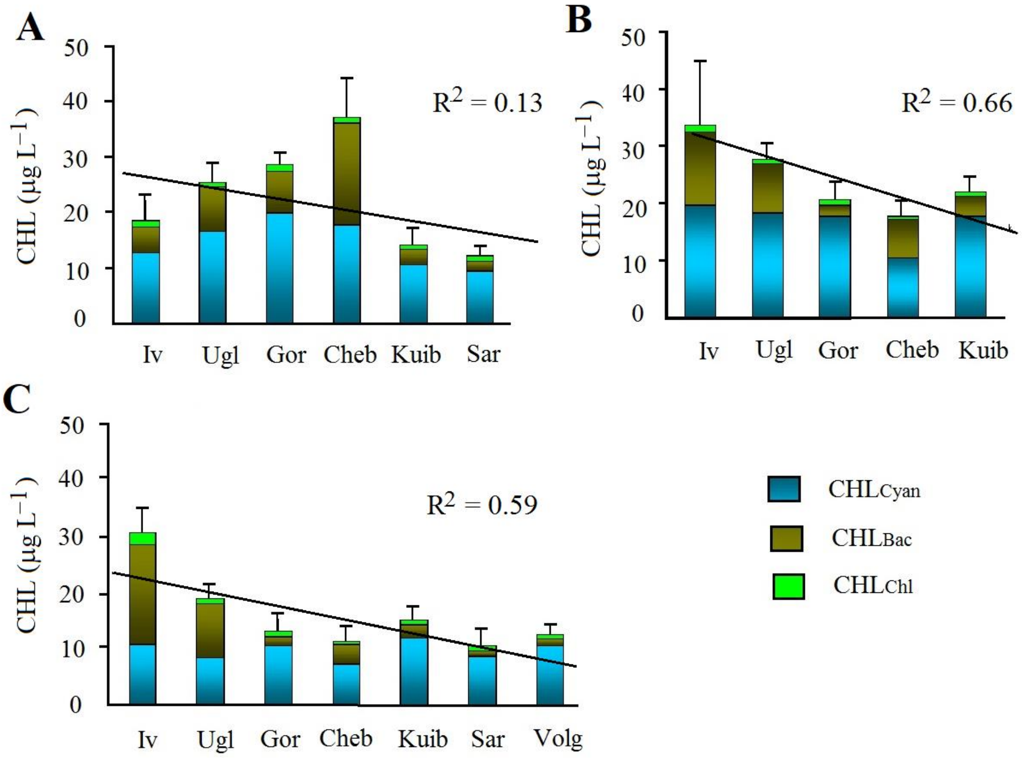

Figure 2. Average chlorophyll content in basic phytoplankton taxa (CHL_{Cyan}, CHL_{Bac}, CHL_{Chlor}) and in total (∑CHL) equal to their sum in the Volga River reservoirs in years of study (2015–2017, (**A**–**C**), respectively). Error bar and trend dotted line are given for ∑CHL; R^2—coefficient of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

Average ∑CHL tended 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 ∑CHL in the Cheboksary reservoir (Figure 2).

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

Parameter	Source of Variation	SS	df	MS	F	P	Fcr
∑CHL	Between groups Within groups	7962 38,526	2 262	3981 147	27.1	0.00	3.03
CHL_{Cyan}	Between groups Within groups	454 26,134	2 262	227 99	2.28	0.10	3.03
CHL_{Bac}	Between groups	3408	2	1704	43.5	0.00	3.02
PhAC	Within groups Between groups	10,262 0.251	262 2	39.2 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 phyla also varied widely. The minimum amount of CHL_{Cyan} was <1–5 µg L^{-1}, and the maximum values in 2015 and 2016 reached 49 µg L^{-1} in the Ivankovo reservoir, 28 µg L^{-1} in the Uglich, 36 µg L^{-1} in the Gorky, and 47 µg L^{-1} in the Kuibyshev reservoir. In 2017, CHL_{Cyan} in these reservoirs was lower, and the maximum values did not exceed 12–29 µg L^{-1}. In the Cheboksary, Saratov, and Volgograd reservoirs, the maximum values were less than 10–26 µg 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. The value decreased to 4.6 ± 1.7–9.5 ± 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 ∑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.

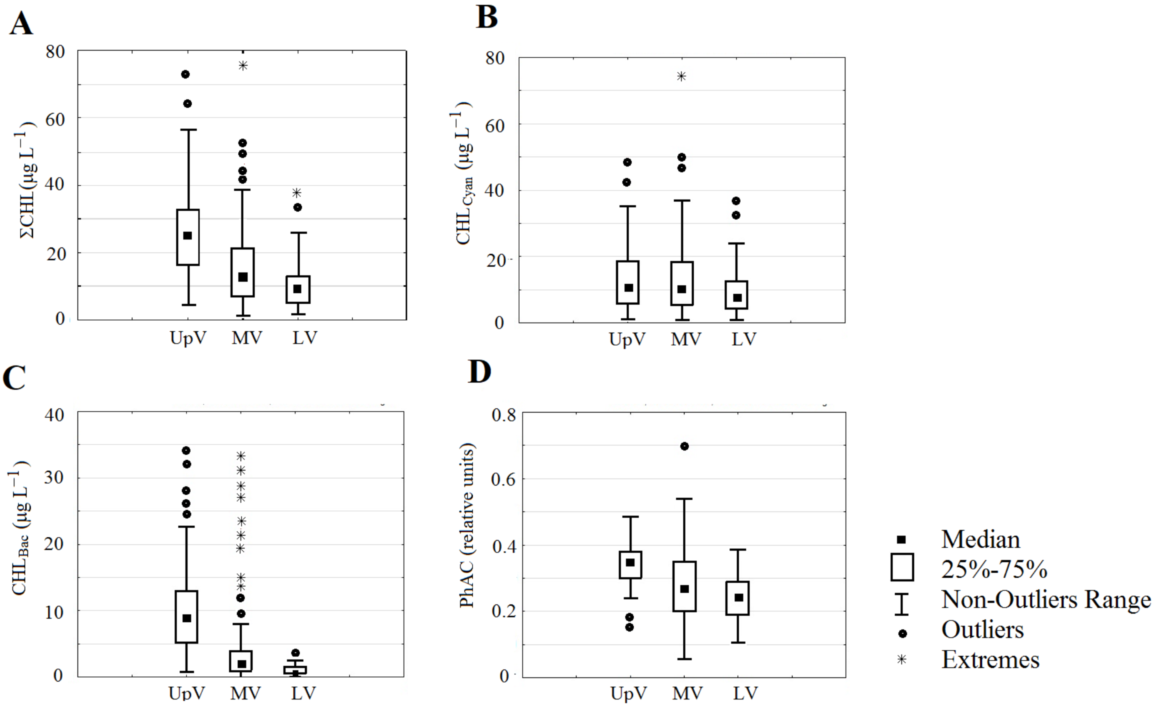

Figure 3. Box plots of chlorophyll concentrations in total (∑CHL (**A**), CHL_{Cyan} (**B**), CHL_{Bac} (**C**), and PhAC (**D**) in the Upper, Middle, and Lower Volga (UpV, MV, LV, respectively)). Data are averaged over three years of study.

The maximum of CHL_{Bac} in individual reservoirs was mainly from 11.7 to 31.8 μg L^{-1} and was less (0.8–6.4 μg 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 μg L^{-1} were obtained in the Ivankovo reservoir in 2016 and 2017, in the Uglich reservoir in all years, and in the Cheboksary reservoir in 2016. In all other cases, the average concentrations of CHL_{Bac} were below 5 μg L^{-1} (Figure 2). The share of it in ΣCHL was basically 14–35%. It decreased to 9% in the Gorky reservoir in 2016 and increased to 40–60% in the Ivankovo and Uglich reservoirs in 2017, and in the Cheboksary reservoir in 2015. Like ∑CHL, average CHL_{Bac} significantly declined downstream from the reservoirs of the Upper Volga to the reservoirs of the Lower Volga (Figure 3C, Table 3). For CHL_{Bac}, as for ∑CHL, there was a decrease in the lower reservoirs compared to the upper ones that was 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 μg L^{-1}, with the average being 1.1–1.5 μg L^{-1} in the Ivankovo reservoir and usually <1 μg L^{-1} in all the others (Table 2, Figure 2). The contribution of CHL_{Chl} to ΣCHL varied very little, both within the cascade as well as during the observation periods, with the average being 0.5–6.8%. We do not consider the spatial and temporal dynamics of CHl_{Chl} because of its low content.

The photosynthetic activity coefficient (PhAC) changed to a lesser extent than ∑CHL. 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 was 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 the 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 the 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 ± 0.02–0.28 ± 0.03) PhAC values were 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 ± SE	Min–Max	X ± SE	Min–Max	X ± SE
Ivankovo	0.17–0.38	0.35 ± 0.01	0.37–0.59	0.38 ± 0.03	0.27–0.43	0.35 ± 0.02
Uglich	0.27–0.4	0.31 ± 0.02	0.18–0.57	0.31 ± 0.03	0.27–0.44	0.36 ± 0.02
Gorky	0.24–0.70	0.38 ± 0.03	0.14–0.44	0.26 ± 0.02	0.09–0.26	0.16 ± 0.01
Cheboksary	0.18–0.52	0.35 ± 0.03	0.18–0.44	0.33 ± 0.02	0.08–0.4	0.22 ± 0.04
Kuibyshev	0.12–0.39	0.26 ± 0.02	0.2–0.39	0.29 ± 0.02	0.06–0.36	0.24 ± 0.03
Saratov	0.19–0.38	0.28 ± 0.03	–	–	0.10–0.25	0.17 ± 0.02
Volgograd	–	–	–	–	0.12–0.38	0.25 ± 0.02

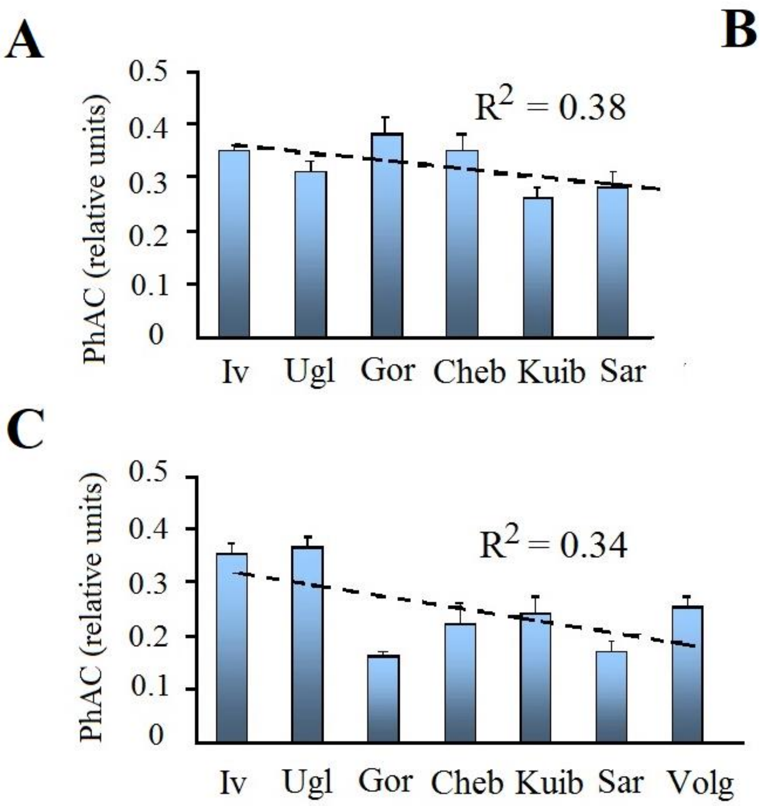

Figure 4. Coefficient of photosynthetic activity (PhAC) of phytoplankton in the Volga River reservoirs in years of study (2015–2017, (**A**–**C**), respectively). Mean values with standard error; dotted line—trend line; R^2—coefficient of determination. Reservoirs: Iv—Ivankovo, Ugl—Uglich, Gor—Gorky,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

PhAC is closely related to ∑CHL content (Figure 5). This dependence is non-linear and is best approximated by a polynomial equation. It shows the classical decrease in the photosynthetic activity of algae with an increase in population density along with demonstrating growth slowdown of PhAC and its decrease at high pigment concentrations that are above 40 μg L^{-1}. Therefore, it is not surprising that there was a decrease in PhAC from the upper reservoirs to the lower ones (Figure 4). In each year, this decrease was less significant than the decrease in ∑CHL (R^2 = 0.30–0.37). 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).

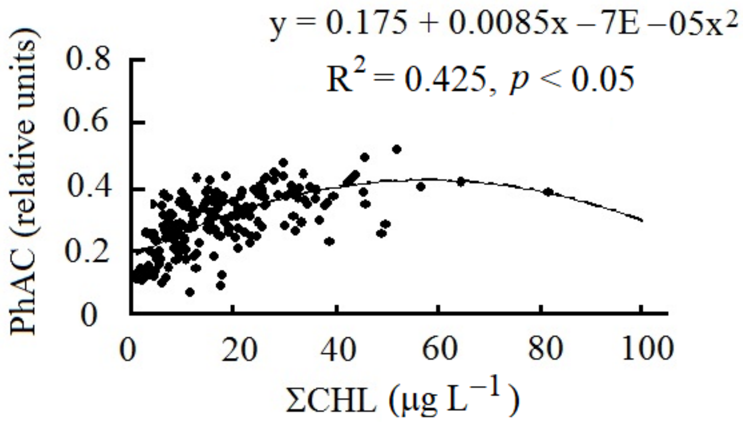

Figure 5. Dependence of PhAC on chlorophyll content in the Volga River reservoirs.

The relationship of PhAC with ∑CHL, 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 trophy. 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 states estimated via average ∑CHL.

Trophic State	∑CHL, μg 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

There are a number of large rivers in the world that have been turned into chains of reservoirs. However, data on spatial trends in the distribution and production potential of phytoplankton in the cascade as a whole are scarce (see, for example, [33,34,46]), so the results of our work are of considerable interest.

The study of summer phytoplankton is important because negative trends caused by eutrophication or climate changes become apparent in water ecosystems 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 [10].

Volga 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 [35,36]. 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 (Table 2). An increased amount of chlorophyll is usually observed in shallow water areas, in the mouth sections of tributaries, and in dam extensions [10]. Differences in weather conditions influenced the quantitative development of phytoplankton and changes in ∑CHL in the years of study. During these three years, 2017 stands out, when a decrease in the average content of ∑CHL was noted. 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 [45].

Fluorescent analysis makes it possible to estimate the chlorophyll content of the three algal phyla typical for freshwater phytoplankton. With differences in the specific content of chlorophyll in the large taxonomic groups of algae [47], these data do not quantify the biomass of the phyla but are of interest for a comparative analysis of their development. The amount and ratio of CHL_{Cyan} and CHL_{Bac} correspond to the composition of summer phytoplankton, which is characterized by the dominance of cyanoprokaryotes or cyanoprokaryotes and diatoms [48]. A decrease in the average content of CHL_{Cyan} in all water bodies, like a decrease in ∑CHL, was noted in 2017. Weather conditions in the Volga region and especially in the Upper Volga were unfavorable for the development of cyanoprokaryotes, which usually make up the majority of phytoplankton in summer [48]. As for CHL_{Bac}, it decreased in the Middle and Lower Volga but became higher in comparison to previous years in the Upper Volga since diatoms are well adapted to existence in conditions of an actively mixed water column [49].

The photosynthetic activity coefficient (PhAC) changed less than ∑CHL, and it looked like a more stable parameter as well as photosynthesis measured via the oxygen flask method [8]. The same PhAC range was obtained for phytoplankton of the Yangtze River [30], Lake Shira [50], and earlier in reservoirs of the Upper Volga, including Rybinsk reservoir, which also had a low PhAC variation [25,26]. Like photosynthesis, PhAC is closely correlated with chlorophyll and shows changes in waters of different trophic states. However, as can be seen from Figure 5, PhAC decreases under a high content of chlorophyll. Therefore, one should expect an inhibition of photosynthetic activity during climatic changes, expressed in increasing temperature of water bodies, changing availability of nutrients, increasing internal phosphorus load, and the development of cyanoprokaryotes [51–53]. Previously, we showed a decrease in the photosynthetic activity of phytoplankton with the growth of CHL_{Cyan}. At high CHL_{Cyan} concentrations, PhAC does not exceed 0.28, while with an increase in CHL_{Bac} to a maximum, the average PhAC value reaches 0.44 [26].

The average PhAC values correspond to the normal physiological state of the phytoplankton of the Upper Volga during all periods of observation. In the Middle Volga, the situation is different. Phytoplankton of the Gorky reservoir were characterized by normal photosynthetic activity in 2015 and the 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 decreased, which was probably due to an increase in the volume of water runoff. 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 under adverse conditions [32].

During the period of our studies, as before [9], there was a tendency for chlorophyll and PhAC to decrease from the Upper Volga to the Lower Volga. A similar trend has been traced for the phytoplankton biomass and species richness [48]. This is explained by an increase in the flow and volume of runoff downstream of the Volga, as well as by a significant decrease in the number and volume of lateral tributaries [36]. The water regime limits the development of phytoplankton, as evidenced by the negative relationship of the average CHL concentrations for reservoirs in 2015–2020 with the total volume of inflow for May–October [12]. The limitation of phytoplankton development by high water content was also observed in other rivers. Thus, in the Thames River, the abundance of algae decreases in years with high water discharge, and changes in physical parameters have a great effect on the development of phytoplankton [54]; high concentrations of chlorophyll in the lower reaches of the Mississippi River were recorded during periods of low runoff [55].

The Volga River basin is located in different geographical zones, which determines the specifics of climatic conditions and the catchment area of reservoirs. In the Upper Volga, the drainage basin is located in the forest zone with excessive moisture and a relatively low amount of salts. In the Middle Volga, whose basin extends to the forest-steppe zone, conditions change dramatically. The Middle Volga receives the waters of the two largest tributaries, the Oka and Kama, which change the hydrochemical background. This is due to an increase in mineralization, since the Oka basin is characterized by the occurrence of carbonate rocks and the presence of karst, and the Kama runoff is formed in the mountainous Urals. The Lower Volga region belongs to an arid region, where the volume of lateral tributaries is sharply reduced, and the forest-steppe and steppe zones are replaced by semi-desert [36]. The ecosystems of the Lower Volga reservoirs, which close the cascade, are most dependent on the changing flow of the Volga River [56].

With a large length of the cascade from north to south and a pronounced geographical zonality, each reservoir of the Volga River is a unique water body with specific relationships between biota and environmental factors. A combination of abiotic parameters (i.e., total nitrogen, total phosphorus, water temperature, transparency, color, electrical conductivity) affects the development of phytoplankton in reservoirs in different ways. Judging by coefficients of determination, the set of these factors determines the moderate variation in $\sum$CHL in the Ivankovo and Uglich reservoirs in the Upper Volga as well as the Volgograd reservoir in the Lower Volga (R^2 = 0.48–0.59) but significantly controls the development of phytoplankton in the Gorky, Cheboksary, and Kuibyshev reservoirs in the Middle Volga (R^2 = 0.71–0.75), and has little effect on phytoplankton in the Saratov reservoir (R^2 = 0.21) [57–59]. It can be assumed that the development of phytoplankton in the Volga reservoirs is differently regulated by habitat conditions in the reservoir–catchment system. To the greatest extent, the dependence of phytoplankton development on the abiotic regime in the reservoir is observed when conditions change in the catchment area, like in the Middle Volga, and to a lesser extent in the Saratov reservoir, which is characterized by high water exchange and whose configuration resembles a slowly flowing river [36].

5. Conclusions

This study on the productivity and development of phytoplankton in the Volga River cascade in the summer period showed a wide range of chlorophyll concentrations with uneven large-scale distribution and significant differences between the maximum and minimum $\sum$CHL in reservoirs with a complex hydrodynamic regime. Average $\sum$CHL varied in limits of 19.4–33.7 μg L^{-1} in the Upper Volga, 8.5–27.8 μg L^{-1} in the Middle Volga, and 5.2–11.3 μg L^{-1} in the Lower Volga. The chlorophyll content of basic algal phyla corresponds to the composition of summer phytoplankton with the dominance of cyanoprokaryotes or cyanoprokaryotes and diatoms. CHL_{Cyan} accounted for 31–68% of the $\sum$CHL 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.

The photosynthetic activity coefficient (PhAC) changed less than $\sum$CHL and varied mostly in limits of 0.12–0.59, with an 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 in PhAC in the Middle Volga, and low photosynthetic activity in the Lower Volga. PhAC is closely correlated with $\sum$CHL and changes in waters of different trophic states. In the interannual dynamics, a decrease in the average $\sum$Chl and CHL_{Cyan} in all water bodies and a decrease in PhAC in the Middle and Lower Volga were noted in 2017 under cyclonic windy weather, with a large amount of precipitation, low solar radiation, and a large volume of flow. There is a previously identified trend towards a decrease in $\sum$CHL, like a decrease in PhAC from the Upper Volga to the Lower Volga, which is explained by an increase in the flow rate and volume of runoff downstream the Volga River.

Author Contributions: N.M.: conceptualization; leading and coordinating the drafting of the manuscript; supervision of research; data analysis; data curation and visualization; manuscript writing, reviewing, and editing. I.S.: field sampling; data analysis; manuscript writing; statistical data analyses; drafting of the manuscript with a focus on interpretation of the results; figure plotting. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Papanin Institute for Biology of Inland Waters Russian Academy of Sciences (IBIW, Borok) through the state task "Diversity, structure and functioning of algae and plant communities in continental waters" (121051100099-5).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available upon request to the corresponding author.

Acknowledgments: We thank Olga Makarova and Vera Solovyeva for sampling support and also the crew of the Academician Topchiev science ship for logistical support and ship operation.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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