Long-term dynamics of photosynthetic pigments in plankton of a large plains reservoir

N. M. Mineeva

Papanin Institute for Biology of Inland Waters Russian Academy of Sciences, Borok, Russia

Mineeva, N. M. (2021). Long-term dynamics of photosynthetic pigments in plankton of a large plains reservoir. Biosyst. Divers., 2021, 29(1), 10–16. doi:10.15421/012102

Introduction

It is well known that global climatic changes that have a significant impact on the structure and dynamics of biological communities of aquatic ecosystems (Adrian et al., 2009; Bertani et al., 2016; Ökkan et al., 2016) continue to take place at the beginning of the 21st century (Vörösmarty, 2014). An increase in temperature is considered as a eutrophication factor that changes the availability of nutrients, promotes increase in the internal phosphorus load, as well as a more abundant and prolonged vegetation of cyanoprokaryotes (blue-green algae) (Jeppesen et al., 2005; Winder & Hunter, 2008). To analyze and predict changes occurring in biological communities under these conditions, long-term observations which are carried out in many water bodies of the world (Rugiu et al., 1998; Kangur et al., 2002; Chen et al., 2003; Bhanuzarova & Lyushenko, 2007; Canfield et al., 2018; Lamont et al., 2019; Gao et al., 2020) are required. Photosynthetic pigments, which are the universal ecological and physiological characteristics of the development and photosynthetic activity of algae, as well as the ecological state of water bodies, are widely used in the study of the autotrophic community in aquatic ecosystems. The main plant pigment, chlorophyll \( \alpha \) (CHL), is a physiological marker that effectively indicates changes in the external environment.

The study of plant pigments in the water of the Rybinsk Reservoir has been carried out in the IBIW RAS since the middle of the 20th century using the standard spectrophotometric method (SCOR-UNESCO, 1966). Long-term data have made it possible to study the seasonal and interannual dynamics of pigments, its relationship with regional and global environmental factors (Pautova & Rosenberg, 1999; Kopylov, 2001; Sygareva et al., 2016; Lazarava, 2018). In 2009, we began additionally use fluorescent method diagnostics, which allowed us to determine the chlorophyll content directly in natural water, obtain a number of phytoplankton characteristics without damaging its integrity, and quickly analyze a large data set (Mineeva, 2016; Mineeva & Semadeni, 2020). Differentiated determination of chlorophyll in cyanoprokaryotes, diatoms and green algae made it possible to obtain new data on the seasonal and interannual dynamics of large taxonomic groups of phytoplankton, their contribution to the total chlorophyll content and their relationship with environmental factors in the years with different hydroclimatic conditions. The objective of this work was a comparative analysis of these data, which continue and supplement a long-term series of observations.

Materials and methods

The data were collected at six standard stations in the Rybinsk Reservoir (Fig. 1) during the growing seasons of 2009–2019 with a frequency of 1–2 times a month.

Fig. 1. Location of observation stations in the Rybinsk Reservoir

The samples were taken with a 1 m Elgmork bathometer from the entire water column (0 m – bottom). During the study period, more than 500 observations were made at the reservoir stations and more than 940 sam-
The heating of the water column is related to the air temperature with coefficient of determination $R^2 = 0.74$. The water temperature in May – October 2016–2019 was close to the long-term average (13.6 °C), lower than the average for 2000–2012 (15.0 °C), but exceeded the average in 2009–2010. The maximum water temperature in summer was generally 20–24 °C, reaching abnormally high values (25–27 °C) in 2010 and 2018 (Table 2). The annual amount of precipitation generally corresponded to the climatic norm (436–887 mm, average 655 mm). The average amount of precipitations for May – October 2000–2019 was 395 mm, 72% and 80% of this amount fell in 2013 and 2014, 140% in 2012. According to the water content, 10 out of 11 years of observations referred to the high-water period with the inflow volume significantly exceeding the norm in 2017. Only in the extremely low-water year of 2014, did the inflow sharply decrease. In accordance with the inflow volume, the reservoir level was minimal in 2014 and exceeded the normal level of 101 m BS in 2009–2012, 2016, 2017. Judging by the dynamics of Wolf numbers, the observations covered an 11-year cycle of solar activity (Table 1). The transparency and colour of the water were characterized by values typical for the reservoir (Table 2). Over the 11-year observation period, there occurred a moderate linear increase in the mean annual air temperature ($R^2 = 0.21$), winter and annual NAO indices ($R^2 = 0.31$ and 0.25), but a decrease in the average seasonal and especially summer water temperature ($R^2 = 0.27$ and 0.56).

### Table 1

| Year | Air temperature, °C | Precipitation, mm | Inflow, m³/s | Level, m | Wolf numbers | NAO index |
|------|---------------------|-------------------|-------------|---------|-------------|-----------|
| 2009 | 13.4 ± 0.3          | 370 ± 22          | 18.47 ± 0.8 | 101.19 ± 0.3 | 5.34 ± 0.29 |          |
| 2010 | 14.9 ± 0.4          | 403 ± 23          | 12.47 ± 0.8 | 101.05 ± 0.3 | 5.90 ± 0.34 |          |
| 2011 | 14.4 ± 0.1          | 372 ± 22          | 11.92 ± 0.8 | 101.05 ± 0.3 | 6.12 ± 0.36 |          |
| 2012 | 13.7 ± 0.2          | 358 ± 19          | 14.09 ± 0.8 | 101.29 ± 0.4 | 5.38 ± 0.47 |          |
| 2013 | 14.4 ± 0.5          | 285 ± 13          | 13.80 ± 0.8 | 100.95 ± 0.4 | 6.54 ± 0.52 |          |
| 2014 | 13.7 ± 0.7          | 315 ± 20          | 4.54 ± 0.8  | 99.81 ± 0.4  | 1.42 ± 0.22 |          |
| 2015 | 13.4 ± 0.1          | 464 ± 23          | 14.26 ± 0.8 | 100.32 ± 0.7 | 6.42 ± 0.20 |          |
| 2016 | 14.1 ± 0.4          | 435 ± 22          | 14.59 ± 0.8 | 101.15 ± 0.8 | 4.67 ± 0.46 |          |
| 2017 | 12.1 ± 0.8          | 478 ± 23          | 23.00 ± 0.8 | 101.63 ± 0.8 | 2.70 ± 0.27 |          |
| 2018 | 13.4 ± 0.9          | 473 ± 23          | 16.77 ± 0.8 | 100.93 ± 1.0 | 2.97 ± 1.00 |          |
| 2019 | 13.1 ± 0.1          | 497 ± 23          | 15.16 ± 0.8 | 100.86 ± 1.0 | 2.72 ± 1.38 |          |

### Table 2

| Year | Temperature, °C | Transparency, m | Color, Cr Co degree |
|------|-----------------|-----------------|---------------------|
| 2009 | 6.4 ± 0.4       | 19.9 ± 0.4      | 46.0 ± 0.4          |
| 2010 | 2.7 ± 0.2       | 23.1 ± 0.8      | 16.1 ± 0.2          |
| 2011 | 7.1 ± 0.4       | 22.2 ± 0.8      | 18.2 ± 0.2          |
| 2012 | 9.4 ± 0.3       | 23.3 ± 0.8      | 16.7 ± 0.2          |
| 2013 | 6.6 ± 0.6       | 20.6 ± 0.6      | 17.5 ± 0.6          |
| 2014 | 7.2 ± 0.4       | 19.5 ± 0.6      | 17.1 ± 0.6          |
| 2015 | 11.8 ± 0.6      | 17.4 ± 0.6      | 15.5 ± 0.6          |
| 2016 | 1.1 ± 0.2       | 21.2 ± 0.6      | 13.9 ± 0.6          |
| 2017 | 4.4 ± 0.6       | 17.7 ± 0.6      | 13.0 ± 0.6          |
| 2018 | 3.5 ± 0.5       | 21.0 ± 0.5      | 13.4 ± 0.5          |
| 2019 | 5.8 ± 0.8       | 18.3 ± 0.8      | 14.0 ± 0.8          |

The seasonal dynamics of ΣCHL, that is dynamics of phytoplankton biomass, were characterized by two or three peaks with differences in the timing of the onset, the duration, and the ratio of values in different years (Fig. 3).

The spring peak with average ΣCHL concentrations of 13–32 μg/L was recorded at the water temperatures of 6–9 °C to 11–15 °C in May – early June 2011, 2012, 2016, 2018, 2019; summer peak (27–45 μg/L) – during the period of maximum warming up in July – September 2010–2014, 2016, 2018; the most noticeable autumn peak (30 μg/L) in October 2014 at the temperature of 7.5 °C. Two seasonal peaks at a lower ΣCHL content were observed in 2009 and 2017. The maximum summer and spring values are comparable in 2009, 2011, 2012, 2016 and 2017; the summer peak dominated the seasonal dynamics in 2010, 2013, 2018, while in 2019 it was less than the spring one. The spring and summer maxima are separated by an early summer phytoplankton depression, during which the ΣCHL content decreased against the background of the seasonal change in communities.
The analysis of 11-year data revealed five periods in the seasonal cycle of $\Sigma$CHL. Each period is characterized by uniform temperature conditions and transparency. The average values of temperature and transparency for each period are equal to their medians. The $\Sigma$CHL variability is minimal in early summer with the seasonal change of communities but is significantly higher during the spring and summer phytoplankton maxima; the arithmetic averages in all cases exceed the medians by 25–30%. The development of phytoplankton in spring and early summer is accompanied by a decrease in the content of mineral nitrogen, while changes in mineral phosphorus and total forms of biogenic elements during the entire growing season are small (Table 3).

**Table 3**

| Parameter | Spring | Early summer | Mid summer | Late summer | Autumn |
|-----------|--------|--------------|------------|-------------|--------|
| $n$       | 54     | 92           | 218        | 86          | 89     |
| $\Sigma$CHL, $\mu g/L$ | 15.9 ± 1.9 | 8.9 ± 0.6 | 20.4 ± 1.0 | 21.2 ± 1.6 | 6.3 ± 0.5 |
| Temperature, °C | 89 ± 0.5 | 15.7 ± 0.3 | 20.4 ± 0.2 | 15.0 ± 0.2 | 7.2 ± 0.3 |
| Transparency, m | 1.20 ± 0.03 | 1.11 ± 0.03 | 1.13 ± 0.02 | 1.06 ± 0.04 | 1.12 ± 0.04 |
| $N_{max}$ mg/L* | 0.45 | 0.31 | 0.19 | 0.14 | 0.14 |
| $P_{max}$ mg/L* | 21 | 18 | 21 | 26 | 65 |
| TN, mg/L* | 0.99 | 1.02 | 0.91 | 1.02 | 0.93 |
| TP, $\mu g/L$ | 48 | 48 | 64 | 67 | 140 |

* – data obtained in 2001–2012 (Lazareva, 2018).

The fluorescence method makes it possible to estimate chlorophyll content of the three main divisions of algae (Table 4). In most cases concentration of $\Sigma$CHL was determined by the amount of CHL$_{Cyan}$ in 2010, 2016, 2017, 2019 the dominant influence belonged to CHL$_{Bac}$, in 2017–2019 the role of CHL$_{Chl}$ was noticeable as well, and in 2011 $\Sigma$CHL equally depended on all three components (Table 5).

**Table 4**

| Year | $\Sigma$CHL, $\mu g/L$ | CHL$_{Cyan}$, $\mu g/L$ | CHL$_{Bac}$, $\mu g/L$ | CHL$_{Chl}$, $\mu g/L$ |
|------|------------------------|------------------------|------------------------|------------------------|
| 2009 | 7.9 ± 0.5 (21/3.5) | 5.4 ± 0.4 (49/3.5) | 63.3 ± 1.9 (70/15.0) | 26.0 ± 1.9 (106/19.0) |
| 2010 | 11.3 ± 1.2 (17/10.7) | 5.1 ± 0.6 (58/17.2) | 46.2 ± 2.9 (112/14.3) | 6.0 ± 1.0 (185/21.0) |
| 2011 | 24.1 ± 2.0 (12/10.7) | 16.1 ± 1.4 (112/14.3) | 60.2 ± 2.4 (112/14.3) | 7.5 ± 1.0 (169/21.0) |
| 2012 | 8.9 ± 0.6 (21/3.5) | 11.7 ± 0.6 (80/10.7) | 61.3 ± 1.6 (59/17.2) | 6.5 ± 0.4 (80/10.7) |
| 2013 | 27.6 ± 1.7 (21/3.5) | 21.7 ± 1.6 (59/17.2) | 70.0 ± 1.8 (79/22.0) | 5.5 ± 0.4 (90/15.7) |
| 2014 | 20.9 ± 2.2 (21/3.5) | 13.4 ± 2.2 (59/17.2) | 59.6 ± 2.9 (104/14.2) | 7.2 ± 0.9 (124/3.4) |
| 2015 | 14.8 ± 1.0 (21/3.5) | 8.3 ± 0.6 (52/14.7) | 30.0 ± 3.3 (89/8.5) | 6.2 ± 0.6 (38/4.5) |
| 2016 | 13.0 ± 1.3 (21/3.5) | 6.0 ± 0.7 (130/13.3) | 58.2 ± 2.2 (118/4.3) | 6.6 ± 1.0 (160/2.9) |
| 2017 | 7.8 ± 0.6 (21/3.5) | 3.1 ± 0.2 (88/6.3) | 44.6 ± 2.2 (98/2.3) | 4.4 ± 0.5 (139/2.4) |
| 2018 | 13.6 ± 1.6 (21/3.5) | 10.9 ± 1.6 (134/7.9) | 70.4 ± 2.4 (158/6.6) | 4.4 ± 0.4 (174/1.0) |
| 2019 | 11.9 ± 1.0 (21/3.5) | 5.7 ± 0.5 (92/9.0) | 50.2 ± 2.2 (110/3.8) | 5.0 ± 0.8 (170/2.0) |

* – data obtained in 2001–2012 (Lazareva, 2018).

The amount of CHL$_{Cyan}$ and CHL$_{Bac}$ did not correlate. With a wide range of values, the minimum chlorophyll content of each algal division did not exceed 1 $\mu g/L$. The predominant values of CHL$_{Bac}$ and CHL$_{Cyan}$...
are limited to 10 µg/L (Fig. 2). In different years, the highest concentration of CHLChl reached 18.4–92 µg/L, CHLChl 25.1–130 µg/L, CHLBac 1–4 µg/L and 16 µg/L in 2011. A noticeable amount of CHLChl was present in the reservoir throughout the growing season, with the highest occurring during the summer phytoplankton maximum. The seasonal dynamics of CHLChl was characterized by a spring peak in all the years, and by the second autumn peak in 2014. In 2010, 2011, 2013, 2015, 2017, high concentrations of CHLBac were also noted in summer. At low CHLChl concentrations, its seasonal dynamics are not pronounced (Fig. 3). CHLBac and CHLCyan made the main contribution to ƩCHL, their ratio varied in different years. The values averaged over the growing season show that CHLBac, CHLCyan more often prevailed in the ƩCHL pool, particularly in 2013 and 2018. The difference between the shares of CHLChl and CHLBac was not large in 2010 and 2015–2017, the percentage of CHLChl increased in 2017–2019 (Table 4).

Table 5
| Year | n | CHLChl | CHLBac | CHLCyan |
|------|---|--------|--------|---------|
| 2019 | 69| 0.68   | 0.11   | 0.21    |
| 2020 | 69| 0.66   | 0.12   | 0.22    |

The average ƩCHL content varied from the minimum <10 µg/L in 2009 and 2017 to the maximum 18.4–27.6 in 2011–2014 and was characterized by intermediate values in other years. The minimum and maximum CHLCyan values also were noted in these years. The more stable variability of ƩCHL within the trophic categories ranges from insignificant in mesotrophic and eutrophic waters to moderate in oligotrophic waters; CHLBac variability is moderate, CHLChl variability is higher, and CHLCyan variability is maximal (Table 7).

Table 6
| Parameter | Regression equation | R² |
|-----------|---------------------|----|
| ƩCHL     | y = 8.80 + 17.55x - 2.96x² + 0.14x³ | 0.74 |
| CHLCyan  | y = 7.91 + 12.97x - 2.20x² + 0.10x³ | 0.55 |
| CHLBac   | y = -0.27 + 3.96x - 0.64x² + 0.03x³ | 0.59 |
| CHLChl   | y = -0.450 + 0.113x + 0.041x³ | 0.60 |

Table 7
| Parameter | Oligotrophic | Mesotrophic | Moderately eutrophic | Eutrophic | Polytrophic | Hyper-trophic |
|-----------|--------------|-------------|----------------------|-----------|-------------|--------------|
| ƩCHL µg/L| 6.1 ± 0.1    | 12.3 ± 0.1  | 21.0 ± 0.2           | 37.9 ± 0.5| 70.6 ± 5.8  |
| CHLChl  µg/L| 0.9 ± 0.1 | 3.3 ± 0.1   | 7.7 ± 0.2            | 12.3 ± 0.3| 25.6 ± 1.0  | 49.7 ± 3.6    |

Assessment of the influence of environmental factors on the seasonal dynamics of phytoplankton reveals a moderate positive relationship between ƩCHL and water temperature in 2009, 2010, 2014, 2015, 2018 (R² = 0.56–0.67), a moderate negative relationship with transparency in 2010–2015, and with water colour in 2015 (R² = 0.50–0.51); ƩCHL does not depend on the depth of the station. The community plasticity index calculated from the correlation coefficients varies from 0.09 in 2017 to 0.42 in 2015, averaging 0.22 ± 0.03 over the entire study period. The example of 2010 shows that accounting for hydrochemical factors does not affect the assessment of the state of the community: the plasticity index is 0.26 for the general data for all years, 0.22 for the hydrochemical block, and 0.24 on average (Fig. 4).

The development of phytoplankton in the Rybinsk Reservoir is characterized by significant seasonal and interannual variations, and the ƩCHL content varies within a wide range. The main part of ƩCHL is accounted for by cyanoprokaryotes and diatoms, which corresponds to the taxonomic composition of algenoses (Korneva, 2015). A significant

BioSyst. Divers., 2021, 29(1)
amount of $\text{CHL}_{\text{Cyan}}$ is present during most of the growing season due to an increase in the period of development of cyanoprokaryotes under climate warming (Jeppesen et al., 2005). The low content of $\text{CHL}_{\text{Chl}}$ is consistent with the low amount of $\text{CHL}$, determined by spectrophotometric (Mineeva, 2004) and chromatographic (Breton et al., 2000) methods. The increase in the contribution of $\text{CHL}_{\text{Cyan}}$ to $\Sigma \text{CHL}$ in recent years is a sign of an increase in the abundance of green algae, which contain $\text{CHL}$. The seasonal development of plankton is an annually repeating process influenced by external factors and internal interactions (Reynolds, 2006). The seasonal variation of chlorophyll in the Rybinsk Reservoir corresponds to the classical model (Sommer et al., 2012) and is characterized by two or three peaks. The timing of their onset, duration, and ratio of values vary in different years. A short spring maximum of $\Sigma \text{CHL}$ with a predominance of $\text{CHL}_{\text{Cyan}}$ was recorded in early May – early June in 2011, 2012, 2016, and 2019. Apparently, in other years, it ended before the start of observations due to the earlier opening of the reservoir (Lazarova, 2018), which was a trigger of vegetation in spring forms (Reynolds, 2006). The summer peak, formed by cyanoprokaryotes and diatoms (Korneva, 2015), was insignificant in 2009 and 2017, when the state of the ecosystem was characterized as mesotrophic. The first year, which was not distinguished against the general background by either the temperature regime or the water content conditions, ended the cycle of the decline in the phytoplankton productivity in the reservoir (Lazarova, 2018). Chlorgen content in the Rybinsk Reservoir, as well as in other reservoirs of the Volga River (Kopylov et al., 2012), was not too large in 2010. However, the conditions of the abnormally hot summer in 2010 were the driving force for the subsequent growth of trophic state and the formation of a prolonged summer phytoplankton maximum with high concentrations of $\Sigma \text{CHL}$ and $\text{CHL}_{\text{Cyan}}$ in 2011–2016. Later, in 2017, lower temperatures combined with extreme inflow volumes, limited the mass vegetation of cyanoprokaryotes and the development of the summer maximum.

The autumn peak occurred during a favourable combination of light conditions and supply of the cells with mineral nutrients (Sommer et al., 2012). During the study period, autumn peak was observed in 2014 only, and earlier it was observed in the years with predominance of sunny weather, which ensures the penetration of a sufficient amount of light energy into the water column (Mineeva, 2004). In spring and autumn, with mixing of the water column, which contributes to the maintenance of cells in the suspended state and provides the uptake of nutrients (Yang et al., 2016), diatom peaks are observed in many water bodies of the temperate zone (Reynolds, 2006; Sommer et al., 2012). Despite the interannual peculiarities of seasonal dynamics and a wide range of values, five stages were distinguished in the seasonal cycle of $\Sigma \text{CHL}$ in the reservoir. Each stage was characterized by homogeneous temperature and transparency, indicating the adaptability of communities to the specific conditions of a certain season. The $\Sigma \text{CHL}$ content within each stage was variable, the average concentrations were higher than their medians, which confirms the complex unaccounted for or uncontrolled external impact on the biota. In large, shallow water bodies that are a dynamic environment, the course of the seasonal succession of phytoplankton is subject to frequent disturbing external effects (Honti et al., 2007, Sommer et al., 2012; Yang et al., 2016). Nonlinear dynamics of average chlorophyll concentrations demonstrate the community’s response to changing external conditions and confirms the conclusion about the cyclical nature of these changes. The maximum development of algae is observed in dry years with calm weather, increased insolation and water temperature, and the minimum is observed under opposite conditions.
(Pyrina, 2000; Mineeva 2004; Pyrina et al., 2006). Depending on the characteristics of the water body, the most important factors in the development of phytoplankton can be physical, chemical, or biotic (Chen et al., 2003; Reynolds, 2006; Yang et al., 2016). During the years of the study, we observed a negative correlation of the mean seasonal concentrations of ƩCHL, CHL_{Cyan} and CHL_{Bac} with the water content parameters (i.e., inflow volume, reservoir level, precipitation amount) limiting the development of phytoplankton. Similar relationships were found for the long-term dynamics of phytoplankton biomass (Komeva, 2015). The average values of ƩCHL and CHL_{Cyan} moderately depend on the water temperature, while this effect was not significant for CHL_{Bac}.

In the presence of weather anomalies, close attention is paid to the temperature factor in the study of aquatic biota (Jeppe <1992>. Temperature does not limit the growth of diatoms, but affects the development of cyanoprokaryotes (Chen et al., 2003), for which the lower temperature limit is 12–16 °C, and the optimal one is 20 °C and higher (Tryfon & Moustaka-Gouni, 1997; Tan, 1991). The broad temperature range (5–20 °C), favourable for the diatoms of the Rybinsk Reservoir, corresponds to the vegetation of thermophilic forms in summer, cold-loving ones in spring and autumn; for cyanoprokaryotes it is limited to 20–25 °C (Mineeva, 2016). In the summer of 2010, at the water temperatures >25 °C, which is not typical of temperate latitudes, CHL_{Bac} but not CHL_{Cyan} formed the ƩCHL pool, although in southern water bodies the abundant development of cyanoprokaryotes was observed at 30 °C and above (Chu et al., 2007).

The content of ƩCHL, CHL_{Cyan}, and CHL_{Bac} is negatively related to the water transparency and colour, the characteristics of hydrooptical conditions, which are fundamentally important for the development and photosynthetic activity of phytoplankton (Chen et al., 2003; Reynolds, 2006). At the same time, chlorophyll itself belongs to the optically active components of the aquatic environment and affects the formation of underwater light field, deteriorating its characteristics with excessive development of algae (Mineeva, 2004).

With the complex impact of environmental conditions on the aquatic ecosystem and the difficulties in identifying the main factors, the publications of recent years analyze the relationship of ecosystem indicators with markers of global processes, the NAO index and Wolf numbers (Ottersen et al., 2001; George et al., 2004; Pyrina et al., 2006; Makimov et al., 2009; Lazareva et al., 2013; Mineeva, 2019). Their influence on the productivity of phytoplankton is considered either as indirect or as integral (cumulative). Correlation analysis is considered the main method for studying this impact on ecological processes (Ottersen et al., 2001).

Comparison of averaged parameters for the growing season revealed positive dependence of ƩCHL, CHL_{Cyan}, and CHL_{Bac} on Wolf numbers, which was previously noted for the long-term dynamics of phytoplankton productivity in different water bodies (Pyrina, 2000; Yevstafiev & Bondarenko, 2002; Pyrina et al., 2006; Trifonova et al., 2008). A moderate positive correlation, as well as for the pigment characteristics in the Ivankovo and Uglichen reservoirs (Mineeva, 2019), was obtained between ƩCHL, CHL_{Cyan}, and the annual NAO. The NAO index, Wolf numbers, temperature, and underwater light conditions, as well as the volume of inflow and water level are among the priority factors regulating the long-term dynamics of phytoplankton in the Rybinsk Reservoir.

Conclusion

In the years with contrasting hydroclimatic conditions and water content (2009–2019), the chlorophyll concentrations in the plankton of the Rybinsk Reservoir varied within a broad range with significant variability of the mean seasonal values, which indicates the low stability of the community. In accordance with the average ƩCHL values, the trophic status of the reservoir was assessed as mesotrophic in 2009 and 2017, eutrophic in 2011–2014, and moderately eutrophic in other years. With an increase in the trophic concentrations of CHL_{Cyan}, CHL_{Bac} and the relative content of CHL_{Bac} increased, while the proportion of CHL_{Cyan} in the ƩCHL fund decreased. In the seasonal cycle of phytoplankton, there were five periods with stable temperature conditions and transparency, but significant variability of ƩCHL. The effect of environmental factors on the development of phytoplankton varied in different years. A moderate positive relationship with water temperature and a moderate negative relationship with transparency were seen for the seasonal dynamics of ƩCHL. The dependence of ƩCHL on the influence of external factors may be studied in more detail in the long-term aspect. The NAO indices, Wolf numbers, temperature and underwater light conditions, as well as the inflow volume and water level are among the priority factors regulating the long-term dynamics of phytoplankton in the reservoir.

The work was carried out in the framework of the state task of the Ministry of Education and Science of Russia AAAA-A18-11802660006-1. The author is sincerely grateful to T. P. Zakina for sampling in the field.

References

Adrian, R., O'Reilly, C. M., Zaguroge, H., Baines, S. B., Hessen, D. O., Keller, W., Livingston, D. M., Sommaruga, R., Strahle, D., Van Donk, E., Weyhenmeyer, G. A., & Winder, M. (2009). Lakes as sentinels of climate change. Limnology and Oceanography, 54, 2283–2297.

Almon, A. F. (1999). Variabel'nost' produktsionnykh khlaristik viehodnych eko- sistem [Variability of the production characteristics of aquatic ecosystems]. Bio- logiya Vnutrennikh Vod, 1–3, 70–75 (in Russian).

Almon, A. F. (2001). Elementy teori funktsinoinovaniya viodhodnych eko- sistem [Elements of the theory of functioning of aquatic ecosystems]. Naaka, Saint Petersburg (in Russian).

Babunazarova, O. V., & Lyashenko, O. A. (2007). Ingling-term longing changes in the physical-chemical environment of the shallow, enriched Lake Nero from statis- tical and functional analyses of its phytoplankton. Journal of Plankton Research, 29(7), 747–756.

Bartuni, I., Piraiccio, R., & Rossetti, G. (2016). Extreme climatic event triggers a lake regime shift that propagates across multiple trophic levels. Ecosystems, 19(1), 16–31.

Bilbuklative, E. S., Bilbuklative, E. M., Bulgakow, N. G., Ensh, Y. V., Konyukhov, I. V., Kopylov, A. L., Komeva, L. G., Lazareva, V. I., Levich, A. P., Litvinov, A. S., Maskorenkova, T. T., Mitropolskaya, I. V., Osipov, V. A., Oyukova, N. G., Poddubny, S. A., Pyrina, I. L., Risik, D. V., Sokolova, E. A., Sapanova, I. E., & Tseanovich, O. L. (2011). Dannyye sovmestnykh izmennyy biologii- cheskikh i fiziko-khloridikh khlaristik viehodnych eko- sistem Rybinskogo vod- kharinistichha [Data from joint measurements of biological and physicochemical characteristics of the ecosystem of the Rybinsk Reservoir]. Muka Press, Moscow (in Russian).

Brenet, E., Brunet, C., Sautour, B., & Broylini, J.-M. (2000). Annual variations of phytoplankton biomass in the Eastern English Channel: Comparison by pigment signatures and microscopic counts. Journal of Plankton Research, 22(8), 1423–1440.

Canfield, D. E., Bachmann, R. W., & Hoyer, M. V. (2018). Long-term chlorophyll trends in Florida lakes. Journal Aquat. Plant Manage, 56, 47–56.

Chen, Y., Qin, B., Teubner, K., & Dokulil, M. T. (2003). Long-term dynamics of phytoplankton assemblages: Microcystis domination in Lake Taihu, a large shallow lake in China. Journal of Plankton Research, 25(1), 445–453.

Chu, Z., Jin, X., Iwami, N., & Inamori, Y. (2007). The effect of temperature on growth characteristics and compositions of Microcystis aeruginosa and Oscilla- toria maleogeti in a shallow, eutrophic lake simulator system. Hydrobiologia, 581, 217–223.

Gao, N., Ma, Y., Zhao, M., Zhang, L., Zhan, H., Cai, S., & He, Q. (2020). Quantile analysis of long-term trends of near-surface chlorophyll-a in the Pearl River plan- water. Marine, 12(6), 1602.

Georg, D. G., Mabelly, S. C., & Hewitt, D. P. (2004). The influence of the North Atlantic Oscillation on the physical, chemical and biological characteristics of four lakes in the English Lake District. Freshwater Biology, 49, 760–774.

Gol'd, V. M., Gayevskiy, N. A., Shatov, I. Y., Popelnik, V. A., & Rybtsov, S. A. (1986). Opyt ispol'zovaniya fluorestsentsii dlya differentsial'noy otsenki soderz- xeniya khlorofila u planktonnykh vodokhranilishcha [Experience of using fluorescence for differential assessment of chlorophyll a content in planktonic algae]. Gidrobiologicheskoe Zhurnal, 22(3), 80–85 (in Russian).

Honti, M., Istvanovics, V., & Osztoics, A. (2007). Stability and change of phyto- plankton communities in a highly dynamic environment – the case of large, shallow Lake Balaton (Hungary). Hydrobiologia, 581, 225–240.

Jeppe, P., Sonnegaard, M., Jensen, J. P., Hovems, K. E., Arneville, O., Carvalho, L., Cowney, M. F., Denek, R., Dokule, M. T., Foy, B., Gerdes, D., Hamp- ton, S., Hilt, S., Kangur, K., Hier, J., Lammens, E. H. H. R., Lauridsen, T. L., Manka, M., Miracle, M. A. R., Moss, B., Noges, P., Persson, G., Phillips, G., Portielje, R., Romo, S., Scheltes, C. L., Strule, D., Taiti, I., Wille, E., & Wind- er, M. (2005). Lake responses to reduced nutrient loading – an analysis of con- temporal long-term data from 35 case studies. Freshwater Biology, 50(9), 1747–1771.
