Limnological Conditions and Photosynthetic Pigments in Clearwater Lakes of the Volga-Vyatka Karst Province

M Yu Gorbunov
Samara Federal Research Scientific Center RAS, Institute of Ecology of Volga River Basin RAS, Togliatti, Russia

E-mail: myugor1960@gmail.com

Abstract. The features of summer stratification and vertical distribution of photosynthetic pigments (chlorophylls and bacteriochlorophylls) in five karst lakes in the Middle Volga region (Republics of Tatarstan and Mari-El) are studied. The water of the investigated lakes has low color and sulfate concentration and low-to-medium total dissolved salts content. Anoxic conditions develop in the hypolimnion in all lakes after the establishment of summer thermal stratification. Reduced iron and sulfur compounds are found in the anaerobic zones of most lakes. In these lakes, deep maxima of chlorophyll and bacteriochlorophylls are formed, indicating the presence of biomass maxima of microbial plankton, consisting of both oxygenic and anoxygenic phototrophs. The presented data demonstrate also a wide variety of features of both chemical stratification and vertical distribution of phototrophic organisms in the studied lakes, which are probably associated with differences in the limnological characteristics of lakes, their water composition, and the history of their existence.

1. Introduction

Forest Middle Volga region is a zone of classical karst [1]; most lakes at the watersheds, and even some floodplain and channel lakes on its territory are of karst origin. However, both because of the peculiarities of both the genesis [2] and the catchment area of the lakes, the ecosystems of the karst lakes in the region are very diverse. Judging by the monograph [3], which covers about 70 karst lakes in the Republics of Mari El and Tatarstan, the morphometric characteristics of the lakes and the physicochemical parameters of their ecosystems vary over a very wide range. The greatest interest of researchers was attracted by deep lake with highly mineralized water with high sulfate content [4, 5]; but they are rare exceptions, as the water of most karst lakes in the region has moderate and low salinity and low sulfate concentrations, usually <0.1 mM [3, 6]. At the same time, the color of water can vary over a very wide range, depending on the composition of the soil and vegetation of the catchment area. So, the lakes of the waterlogged Mari Polesye are characterized by the highest color and extremely low mineralization, and the lakes of the Vyatka Uval and the Kazan Kama region, with the exception of a few waterbodies of the bog landscape, and "blue" lakes [5], have medium mineralization and, according to our data, a moderate water color.

The high relative depth of young karst lakes leads the vertical stratification of the water column into a well-warmed surface layer (epilimnion), and the underlying cold-water layers (hypolimnion) [7]. Stratification prevents the penetration of oxygen into the hypolimnion, and low illumination prevents its formation due to oxygenic photosynthesis. Therefore, after stratification establishment in
lakes, hypolimnetic oxygen deficiency develops [8], which in eutrophic lakes or in conditions of high organic load from the catchment area quickly reaches the stage of exhaustion, at least in the bottom part of the hypolimnion [9]. In the absence of oxygen, organic matter sedimenting from the trophogenic layer into anoxic water mass is oxidized in anaerobic processes, leading to the accumulation of certain products of anaerobic respiration or fermentation in the anaerobic water mass.

The environmental conditions in the anaerobic zone of lakes are greatly influenced by the water chemistry. If sulfate concentration is high, sulfides, which are toxic to the vast majority of eukaryotic organisms and many prokaryotes, accumulate in the anoxic layers (euxinic type of anoxia). When sulfates are low or absent, the primary product of anaerobic respiration is reduced metal compounds, primarily iron (ferruginous type of anoxia), and since Fe(III) oxide compounds are insoluble in the near-neutral environment, Fe(II) reoxidation in the redoxcline induces the functioning of the "ferrous wheel" [10], which keeps iron in the anoxic zone.

In both cases, populations of planktonic organisms, primarily anoxygenic phototrophic bacteria (APB), develop in the redox zone between the aerobic and anaerobic water masses. They often form very narrow and dense zones of development ("microbial plates"), in which, along with APB, various pro- and eucaryotic oxygenic phototrophs and heterotrophic protists, are present.

However, there are many lakes with low concentrations of both sulfates and transition metals; the peculiarities of anoxia and the vertical distribution of plankton in them remain insufficiently studied.

In June 2019, we studied several lakes on the border of the Rep. Tatarstan and Mari El, five of which were characterized by low to moderate water color (<40ºPt) and low sulfate content (<0.1 mm).

2. Material and methods

2.1. Study area

The studied lakes are located in the basins of the river Sumka (Lakes Raifskoe and Yurtushinskoe), its tributary, river Ser-Bulak (Osinovo), and the upper tributary of the Ilet' river, Petyalka (Kara-kul' and Elan-Er). Lake Raifskoe is located on the territory of the Volga-Kama State Natural reserve; Lake Elan-Er is to be included into the projected Mari El republican natural reserve "Sotnur Upland" [11]. Other lakes are included in the list of natural monuments of the Republic of Tatarstan. Morphometric characteristics of the lakes are shown in table 1.

The catchment areas of the lakes except for the Lake Yurtushinskoe are populated; the settlements directly border with the water area of the Raifskoe and Osinovo lakes. All the lakes are used for fishing, recreation and tourism.

| Lake          | Latitude, N | Longitude, E | Area (ha) | Max depth (m) | Length (m) | Source     |
|---------------|-------------|--------------|-----------|---------------|------------|------------|
| Raifskoe      | 55.9063     | 48.7274      | 32        | 19.6          | 1296       | [3, 12]    |
| Osinovo       | 55.8778     | 48.8759      | 8,2       | 24            | 778        | [3]        |
| Yurtushinskoe | 56.0250     | 48.9522      | 8,6       | 26            | 630        | [13]       |
| Kara-Kuša     | 56.1155     | 48.9800      | 10,7      | 11            | 850        | [13]       |
| Elan-Er       | 56.1450     | 48.8724      | 7,9       | 15,6          | 475        | [3]        |

The lake consists of two parts close in area, connected by a channel; the southwestern part is shallow and formed after damming the stream flowing from the lake. The length of the deep northeastern part of the lake is 420 m.

2.2. Sampling

The study was carried out on July 4-9, 2019, during a period of intense cyclonic circulation in the region. Samples were taken with a thin-layer pump sampler with a step of 1-2-5 m. In the area of thermo- and redoxcline, the sampling step was reduced to 0.1-0.5 m. The values of physicochemical parameters (temperature, pH, Eh, O2 concentration) were measured in flowing regime in a stream of
water from a sampling hose. The Eh values in the text are corrected to the potential of a standard hydrogen electrode. From each horizon, 1.5 L of water was taken for subsequent biological, pigment and chemical analysis, and separately, two 10 ml aliquots for analysis for sulfide sulfur and total phosphorus, iron and manganese. Aliquots were fixed with 0.1 ml of 10% zinc acetate and 0.1 ml of dilute (1:3, ~ 4.7 M) sulfuric acid, respectively.

2.3. Chemical and pigment analysis
In the laboratory, 0.2-0.5 L samples were filtered through glass filters with nominal particle retention of 1.2 μm. The filters were air dried in the dark and stored in the dark at a reduced temperature; the filtrates were saved for basic ion chemical analysis. The methods of chemical analysis used and calculations of water density and stratification criteria are listed in [14].

To determine pigment concentrations, the filters were extracted overnight with 90% (v/v) aqueous acetone saturated with MgCO₃. The spectra of extracts in the range of 350-850 nm were recorded on a Specord M-40 spectrophotometer, then the samples were acidified by adding a drop of 6 N HCl and the spectra of pheophytinized extracts were recorded. Pigment concentrations were determined using previously published formulas [15] or, if the spectra indicate possible presence of BChl e, by the method of spectral reconstruction of differential pheophytinization spectra, as described in [16].

3. Results

3.1. Temperature, electrical conductivity and stratification
During the period of our study, at the beginning of July 2019, active cyclonic phenomena with precipitation and strong winds were observed in the region; the maximum daytime temperatures did not exceed 23 °C, and at night they dropped to 11-16 °C. The temperature of the surface layer in the lakes ranged from 18 to 21 °C.

To the date of sampling, all lakes were already thermally stratified. In lakes Raifskoe and Elan-er, the isothermal surface layer had a thickness of 2 m, in other lakes – 3 m. The maximums of stability were located in the depth range of 4.25-4.75 m, except for in the Lake Raifskoe (3.75 m).

Water mineralization estimated from the electrical conductivity was the smallest in the Lake Yurtushinskoe and the largest in the Lake Elan-Er. While in lakes Yurtushinskoye and Osinovo the difference of conductivity between the surface and bottom layers did not exceed 15 μSm cm⁻¹, in lakes Kara-Kul and Elan-Er it was more than 100 μSm cm⁻¹. Lake Raifskoe had intermediate position (44 μSm cm⁻¹) by this parameter. Except for the Lake Osinovo, the depth interval of mineralization increase, if any, lay within or overlapped the thermocline zone. Calculations show that in none of the lakes did the vertical gradient of mineralization significantly increase lake stability.

The water in all the studied lakes was of calcium-hydrocarbonate type; the share of sulfates has been always less than 10%. The TDS was less than 250 mg/L in lakes of the headwater parts of the watershed (Yurtushinskoe and Osinovo) and much higher in three other water bodies (table 2). The total content of iron and manganese in the surface layers was low. However, they and also total phosphorus accumulated in noticeable amounts in the anoxic layers (table 2).

The average value of Eh in the surface aerated zone in the Lake Yurtushinskoe was 268 mV, in the Lake Kara-Kul, 370 mV, and in other lakes it was close to 400 mV. The bottom layer of all lakes was aphyotic and anoxic. In lakes Raifskoe and Kara-Kul, oxygen was depleted in the middle part of the thermocline (figure 1); in the thermocline of other lakes, on the contrary, a weak deep-water maximum of oxygen was observed, and its depletion position was located at the lower boundary of the thermocline or even (in Lake Yurtushinskoe) in the middle part of the hypolimnion. The report [3] indicated oxygen presence in the lakes Raifskoe, Osinovo and Elan-Er down to the bottom; apparently, this was due to oxygen contamination during sampling, low reducing buffering of lake water, and interferences of the iodometric method of oxygen analysis.
Table 2. Mean hydrochemical water composition and parameters of lakes' stratification

|                     | Elan-Er | Kara-Kul' | Osinovo | Raifskoe | Yurtushinskoe |
|---------------------|---------|-----------|---------|----------|--------------|
| TDS (mg L\(^{-1}\)) | 370.2   | 289.4     | 143.3   | 334.0    | 93.0         |
| Sum of anions (meq) | 4.625   | 3.688     | 1.845   | 4.318    | 1.171        |
| \(\text{HCO}_3^-\) | 0.979   | 0.913     | 0.843   | 0.820    | 0.915        |
| \(\text{SO}_4^{2-}\) | 0.011   | 0.054     | 0.042   | 0.072    | 0.061        |
| Cl\(^-\)            | 0.009   | 0.033     | 0.115   | 0.108    | 0.024        |
| \(\text{Ca}^{2+}\)  | 0.723   | 0.606     | 0.580   | 0.684    | 0.683        |
| \(\text{Mg}^{2+}\)  | 0.159   | 0.224     | 0.145   | 0.112    | 0.137        |
| \(\text{Na}^+ + \text{K}^+\) | 0.080 | 0.156     | 0.247   | 0.185    | 0.158        |
| Fe + Mn total       | 0.037   | 0.014     | 0.028   | 0.019    | 0.022        |

- Mean concentrations (mg L\(^{-1}\))
  - Whole water column
    - \(P_{\text{min}}\) 0.002
    - \(P\) 0.066
    - Fe 2.866
    - Mn 1.945
  - Mixing layer
    - \(P\) 0.018
    - Fe 0.265
    - Mn 0.144

- Stratification parameters
  - Conductivity (µSm cm\(^{-1}\))
    - Surface 339
    - Bottom 442
  - \(\Delta E_h\) (mV)
    - 430
  - Transparency (m)
    - 4
  - Depth (m) of
    - Thermocline 5
    - O\(_2\) maximum 4.5
    - O\(_2\) depletion 7.5
    - Redoxcline 9.3
    - Halocline 6–12

A distinct redox transition zone was found in three of the studied lakes, Osinovo, Kara-Kul' and Elan-Er; the \(\Delta E_h\) amplitude in them exceeded 400 mV, and the \(E_h\) values in the bottom layers were negative, indicating the presence of strong reducing agents. In lakes Raifskoe and Yurtushinskoe \(\Delta E_h\) was about 80 and 160 mV, respectively. In this work, in contrast to previous studies, we measured the redox potential in a flow-through cell; this allows obtaining results that are close in accuracy to those obtained by submersible probes and, therefore, to the true values \textit{in situ}.

The concentration of sulfides in the lakes was low. In lakes Raifskoe and Yurtushinskoe, they were below the detection limit. In the Elan-Er, Osinovo and Kara-Kul' lakes, the maximum concentration of sulfides was 0.06, 0.55 and 0.83 mg L\(^{-1}\), respectively. It is characteristic that the maxima of sulfides were recorded in the lower part of the redoxcline, while in the bottom layer the concentrations were 1.5-2.5 times lower. According to our results, high concentrations of total iron and manganese are present in the anaerobic layer of the lakes (table 2). This indirectly indicates that the main reducing agent in the layers below the redoxcline appears to be Fe (II), although we did not measure it directly.

Mean total phosphorus concentrations (table 2) in lakes are characteristic of mesotrophic (Yurtushinskoe, TSI\(_p\)=39.8) to eutrophic state (Osinovo and Elan-Er, TSI\(_p\)=64.2 and 64.7, respectively); however, TSI\(_p\) in surface mixing layer is much lower (36.4-46.4), and indicate mesotrophic state.
3.2. Photosynthetic pigments

In the surface mixed layer of all lakes, Chl a concentration corresponded to the mesotrophic level of productivity, from 3 nM in Lake Yurtushinskoe to 8.8 nM in the lake Kara-Kul'. In these lakes, Chl a distribution of in the isothermal layer was noticeably uneven (figure 1); in the rest, its concentration within this layer was approximately constant. Starting from the depth of oxygen depletion down to the redoxcline, Chl a concentration increased markedly, and bacteriochlorophylls of anoxygenic phototrophic bacteria were detected. The exception was the lake Yurtushinskoye, in which chlorophyll concentrations decreased from 4 m to the bottom and only traces of Bchl a were recorded among bacteriochlorophylls. In other lakes the pigments of green sulfur bacteria were present, namely Bchl d in lakes Raifskoe, Elan-Er and Kara-Kul' and Bchl e in Lake Osinovo.

The lowest mean Chl a concentration in a whole water column was found in the Lake Yurtushinskoe; the second lowest one was detected in the lake Raifskoe. In these two lakes only traces of Bhl a were found; small concentration of Bchl d was also found in the lake Raifskoe. In the other three lakes, the average concentration of Bchl d or Bchl e was 2-5 times higher than the concentration of Chl a, and noticeable concentrations of Bchl a were also detected (table 3). The highest Bchl d concentration was found in the lake Elan-Er; where the most significant deep phytoplankton maximum was also developed. In general, this lake turned out to be the most biologically heterogeneous among the studied.

Table 3. Average photosynthetic pigments concentrations (nM) and position of maxima

|          | Elan-Er | Kara-Kul' | Osinovo | Raifskoe | Yurtushinskoe |
|----------|---------|-----------|---------|----------|--------------|
| Chl a    | 4.45    | 8.77      | 6.77    | 6.93     | 2.98         |
| Chl a    | 23      | 8.69      | 5.65    | 3.07     | 1.71         |
| Bchl d   | 101.3   | 24.8      | 10.4 a  | 0.24     | 0            |
| Bchl a   | 4.83    | 2.82      | 1.26    | 0.01     | 0.02         |
| Pigment maxima position (m) | | | | | |
| Chl a    | 8; 9.5-10 | 0; 5; 6.5 | 7.5 | 4 | 1; 3 |
| Bchl d   | 9.5     | 6.5       | 9.5-13 a | 4 | na |
| Bchl a   | 9.5     | 6         | 9       | 4.5      | 20           |

- Bchl e

Deep-water maximum of Chl a was observed at 4 m depth in Lake Raifskoe (figure 1b). Its concentration exceeded the surface one by more than twice; at the same depth, the maximum Bchl d was found. Bchl d concentration (~ 4.3 nM), however, was three times less than of the Chl a at this depth. In the underlying horizons, the Chl a concentration decreased, and only traces of BChl d were found. Bchl a concentration in the lake was below the detection limit at most of depths; this obviously indicates the absence of purple phototrophic bacteria.

In the Lake Kara-Kul' (figure 1c), the zone of deep-water phytoplankton development, judging by Chl a distribution, had two maxima, at 5 and 6.5 m. The upper peak corresponded to the depth of oxygen depletion, and the lower one, to the position of the maximal Eh gradient. Between these maxima, a relatively significant maximum of Bchl a was found. Maximum of Bchl d was 10 cm below the lower maximum of Chl a; Bchl d concentration in its peak, 160 nM, was nearly an order higher than the concentration of Chl a.

Even more complex vertical distribution of Chl a was detected in Lake Elan-Er (figure 1d). A small maximum was found in the thermocline region, at 5 m, and two more significant ones, at 8 m (about 80 nM) and 9.5-9.8 m (117 nM). According to preliminary data, the maximum at 8 m was associated
with the development of red-colored filamentous cyanobacteria. At 9.5 m, narrow main maximum of Bchl $d$ was located. Its concentration at the peak reached 1860 nM. Nearly ten times smaller secondary maximum was observed at 9 m.

Finally, in Lake Osinovo, a single Chl $a$ maximum was found at ~7.5 m depth, and even there its concentration did not exceed 17 nM (figure 1e). At 8 m, pigments of anoxygenic phototrophic bacteria were already found, but, unlike other lakes, this lake was dominated by Bchl $e$ instead of Bchl $d$. The wide area of this maximum was located in the depth range of 9.5-13 m; Bchl $e$ concentration varied here from 20 to 31 nM; below it decreased by 3-5 times. A peak of Bchl $a$ (6.8 nM) was detected between the maxima of Chl $a$ and Bchl $e$.

![Figure 1](image_url)

**Figure 1.** Vertical distribution of physical and chemical parameters and the concentrations of photosynthetic pigments. Lake Yurtushinskoe (a) and Lake Raifskoe (b).
Figure 1. (continued). Lake Kara-Kul’ (c), Lake Elan-Er (d) and Lake Osinovo (e).
4. Discussion

At the time of our observations, all the studied lakes were thermally stratified, and the low temperature of the bottom layer indicates the rapid formation and stability of the stratification. Active cyclonic phenomena with precipitation and strong wind, observed in the Middle Volga region during our study, created conditions for intensive wind and convection mixing of the waterbodies. However, these meteorologic peculiarities resulted only in the absence of a daytime surface thermocline and the formation of a significant isothermal surface layer. The position of the thermocline and the depth of the maximum stability layer did not correlate with the morphometric characteristics of the lakes as predicted in [17, 18]. For example, in Lake Raifskoe, despite its largest size, the thermocline was located much higher than in other, smaller lakes. This may be caused by the replenishment of its hypolimnion by the cold waters of the tributaries.

After establishment of stratification, hydrological isolation between the epilimnion and the hypolimnion of lakes leads to the development of hypolimnetic oxygen deficit. In water bodies with sufficient productivity and/or external organic load, oxygen in the hypolimnion is completely exhausted, but in less productive lakes, it often remains in noticeable amounts down to the bottom [19].

Despite their different trophic state, in all the studied lakes oxygen deficiency in bottom water mass by the time of our study reached the stage of its complete depletion. In most of them, oxygen was absent in the whole hypolimnion, and only in the least productive Lake Yurtushinskoe the anoxic zone occupied only its small lower part. The metalimnion of the lakes, except for the Lake Raifskoe, remained at least microaerobic, and in lakes Elan-Er and Osinovo, noticeable hypolymnic maxima of oxygen were recorded in the thermocline (figure 1).

Following oxygen depletion, anaerobic biogeochemical processes lead to the formation of a number of secondary vertical gradients (redox, biogenic elements, etc.). In general, these gradients can be located in any part of the stagnant anoxic zone with low turbulent diffusion. In our lakes the redox zone, i.e., transition from oxidizing to reducing conditions, was in all cases located 2 m or more below the point of oxygen depletion. In the least productive lakes, Yurtushinskoe and Raifskoe, the amplitude of the redox potential step is small so the redox conditions remained oxidizing even in the bottom layer, and sulfides were not detected. In other lakes sulfides were found, albeit in very small quantities and the Eh value in the bottom layer reached negative values. However, total Fe concentrations were always higher than those of $\text{S}^2-$ (table 2), and since Fe (III) is incompatible with sulfides, we assume that the predominant redox component in anoxic layers of all studied lakes was Fe (II), although it was not directly determined in this study. Most of the sulfides were obviously bound into particulate FeS, but nevertheless their traces in the water reduced its Eh to negative values.

According to the Chl a concentration, the development of phytoplankton in the epilimnion of the lakes was weak. However, deep Chl a maxima were observed in the thermocline zone or above the redoxcline, except for Lake Yurtushinskoe. The phytoplankton species composition at these maxima has not yet been determined; in the Lake Elan-Er, judging by the intense red color of the seston of this zone, phycoerythrin-containing cyanobacteria prevailed. In this lake, the deep Chl a maximum was pronounced (up to 117 nM); it was the smallest in the Lake Raifskoe (11 nM).

In three lakes, Raifskoe, Kara-Kul and Elan-Er, BChl d, typical pigment of planktonic “green” strains, prevailed among pigments of Chlorobiaceae. However, in the Lake Osinovo, the development of brown forms synthesizing BChl e and diaromatic carotenoid, isorenieratene, was observed. Brown Chlorobiaceae strains are believed to develop predominantly on a deeper redoxcline than green Chlorobiaceae [20-22]. However, the chemocline in the Lake Elan-Er was located almost at the same depth as in the Lake Osinovo (table 2, figure 1 d, e), but the pigment composition of the Chlorobiaceae populations were nevertheless, radically different. We believe that in the case of the Lake Osinovo dominance of brown forms with Bhl e was associated with the lowest water color (13ºPt) compared to all other lakes (about 30ºPt). As result, more light energy of the spectral range of 450-530 nm, the area of the blue maximum of these bacteria in vivo, reached its deep layers. Similar idea on the water color effects ecological success of green or brown Chlorobiaceae populations have been made earlier [23].
Although the difference between the two least productive and three more productive lakes is evident (table 2, 3), the correlation between the mean water column concentrations of total phosphorus and Chl a (0.75) is insignificant. A significant positive correlation is, however, found between the average concentrations of chlorophyll a and the sum of bacteriochlorophylls. This may indicate that the development of populations of both oxygenic and anoxygenic phototrophs in the zones of deep maxima depends on the same factors, and that the competition between these two groups is small, otherwise one would expect a negative correlation between these values.

The presence of individual maxima of Bchl a indicates the existence of distinct zones of development of purple bacteria in the redoxcline, at least in lakes Kara-Kul and Osinovo. The presented data do not give an unambiguous answer to the question of which species of anoxygenic phototrophic bacteria develop in the studied lakes. In the Lake Raifskoe, the presence of Chloronema giganteum (Chloroflexales: Chloroflexi) was previously found, and in Lake Osinovo, where Bchl e dominates, the synthesis of which by Chloroflexaceae is unknown, evidently contains brown strains of Chlorobiaceae. All these issues will be discussed in subsequent studies.

5. Conclusion.
Karst lakes with low to moderate TDS, low sulfate content and water color are widespread in the Middle Volga region. The article presents the results of our research of the features of the water column stratification in several karst lakes on the territory of the Volga-Vyatka karst province, the largest karst region in the Middle Volga basin [1]. The data obtained show that in most lakes, after the establishment of summer stratification, anoxic conditions are developed in the hypolimnion, and, despite the low concentrations of sulfides and reduced forms of iron and manganese, deep chlorophyll and bacteriochlorophylls maxima are formed in most of the lakes in the redoxline zone, indicating the presence of microbial plankton maxima consisting of both oxygenic and anoxygenic phototrophs.

Besides these common features, the presented data demonstrate a high diversity of peculiarities of both chemical stratification and vertical distribution of phototrophic organisms in the studied lakes, which are probably due to small differences in the limnological characteristics of lakes, their water chemistry, and their history.

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