Karst Lakes of Mari Chodra National Park: stratification and vertical distribution of phototrophic plankton

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

E-mail: myugor1960@gmail.com

Abstract. The characteristics of micro-scale vertical heterogeneity of physicochemical parameters, photosynthetic pigments’ content and populations of phototrophic microbial plankton in four karst lakes of the Mari-Chodra NP (rep. Mari El), the Bolshoy Kichier, Cherny Kichier, Shungaldan and the Blue Oxbow, are presented on the basis of summer surveys of 2006, 2007 and 2009. According to our data, two lakes, Shungaldan and Cherny Kichier are, meromictic waterbodies of crenogenic type; the Lake Bolshoy Kichier is holomictic with stable summer stratification and anoxic hypolimnion. The Lake Blue Oxbow occupies an intermediate position, and, apparently, is irregularly mixing. The physicochemical conditions and composition of the phototrophic plankton communities of the chemocline zone of the two previously studied lakes, Bolshoy and Cherny Kichier, have remained stable over the past 20-35 years. Significant development of anoxygenic phototrophic bacteria was found in two lakes in which data on their development were previously absent. In the bacterial plates of meromictic lakes, the concentration of bacteriochlorophyll d, the pigment of green phototrophic bacteria, reaches some mg per liter.

1. Introduction
The features of the circulation and thermal structure of the water mass, and, first of all, the presence and duration of stratification are the most important physical characteristics of water bodies. By suppressing mixing, stratification affects the thermal characteristics of lakes and their ability to accumulate heat, as well as the distribution of biogenic elements entering the lake both from the catchment area and from bottom sediments, and thereby significantly influence planktonic habitats [1]. The isolation from gas exchange with the atmosphere, combined with light deficit in the deep layers, leads to the development of oxygen deficiency and, ultimately, to the formation of anoxic conditions and the accumulation of reduced compounds in the bottom water mass [2]. Chemical gradients in the contact zone of oxic and anoxic waters create new ecological niches for specific clinobiont planktonic organisms, both eukaryotic [3] and prokaryotic, including anoxygenic phototrophs [4] and various lithoautotrophs.

National Park Mari Chodra is located in the southeastern part of Mari El Republic, on the southern edge of the Vyatka Uval elevation and belongs to one of the largest karst provinces in the Volga region, the Volga-Vyatka karst region [5]. On its territory, highly soluble lower Permian carbonate and sulfate rocks approach the surface [6], determining the wide distribution of karst phenomena including karst lakes. Most of the lakes have significant depth, relatively low productivity and high water transparency, and are stably stratified in the summer [7]. Although the lakes in Mari El Republic...
generally have low-mineralized (<200 mg L\(^{-1}\)) calcium-hydrocarbonate water [8], surface layer mineralization of 200-500 mg L\(^{-1}\) is more typical for the lakes at the Mari Chodra National Park [7]. Besides, highly mineralized sulfate-rich waters from deep Paleozoic aquifers participate in the inflow of some lakes along with groundwater and surface runoff [9]. This may lead to suppression of mixing at the periods of homothermy and to the establishment of meromixis [10]. In a significant part of the lakes, the hypolimotic oxygen deficiency reaches the stage of its complete depletion. In the presence of sulfates, the development of anaerobiosis occurs mainly through the accumulation of hydrogen sulfide, leading to the formation of eutinic near-bottom water layers and to the development of sulfate community.

In this paper, we present a description of the vertical heterogeneity of physicochemical parameters, photosynthetic pigments concentrations and phototrophic microbial plankton populations in four karst lakes of Mari-Chodra National Park (Mari El republic): lakes Bolshoy and Cherny Kichier, Shungaldan and Blue Oxbow.

2. Study area, materials and methods

2.1. Lakes' characteristics.
Lake Kichier (56.07036N, 48.34592E) is located on the left-bank floodplain terrace of the Ilet River, and is formed by three large karst dips. The northernmost of them, named Cherny (Black) Kichier (56.07606N, 48.34060E), is separated from the rest of the lake by a shallow strait (figure 1a). Although Cherny Kichier and the rest of the water area, Bolshoy (Big) Kichier, have a common epilimnion, they are often considered as separate lakes due to the sharply different hydrological regime and chemical composition of the waters of hypolimnion.

Lakes Shungaldan (56.14880N, 48.44195E) and Blue Oxbow (a conditional name, “Golubaya Staritsa” in Russian, proposed in [7]) (56.15489N, 48.40886E) are located in the area of the Klenovaja Gora ("Maple Hill") upland. Lake Shungaldan bed consists of single karst funnel of ~150 m diameter (figure 1b, table 1) located in a narrow strip of the left-bank floodplain between the Ilet River and the steep slope of the upland. The Lake Blue Oxbow (figure 1c, table 1) is located on an extended stretch of the left-bank floodplain of Ilet River, and is a remnant of old river meander, complicated by two karst dips [9].

2.2. Sampling
Sampling was carried out in July 2006 (Cherny and Bolshoy Kichier, Shungaldan), in August 2007 (Shungaldan, Blue Oxbow) and in June 2009 (Cherny and Bolshoy Kichier, Blue Oxbow) in the region of maximum depth. In 2006, in the lakes Bolshoy Kichier and Blue Oxbow, the samples were taken by a Ruttner bottle with a step of >1 m. It should be noted that sampling from meta- and hypolimnion using vertical bathometers may give a somewhat distorted results due to a large width of the sampling layer. In other cases, a thin-layer pump sampler similar to that described in [11] was used; in the epi- and hypolimnion samples were taken with increment of 0.5-2 m depending on the total thickness of the layer. In the metalimnion the sampling step was reduced to 0.1-0.25 m.

2.3. Determination of environmental parameters
The temperature was measured with a thermistor sensor except for the Lake Bolshoy Kichier in 2006, where a submersible mercury thermometer was used. Water pH and the redox potential were determined at the time of sampling by portable instruments; electrical conductivity by portable conductivity meter in less than 3-5 hours after sampling. Chemical analyzes were performed by micromodifications of standard methods [12]. In 2006-2007, the main ions concentrations were not determined, so the total mineralization was calculated from conductivity data by the correlation equation \(N = 34; R = 0.998\) according to data obtained in 2009. The water density was calculated using the equations in [13]. The contribution of the meromictic component to the overall stability of the water column was estimated as the ratio of the difference of the water density between the bottom
and surface layers at 4.2°C temperature and the actual mineralization to the difference of the water density under current conditions [14]. Wind speed required to destroy the stratification was calculated as $U = 800\frac{h_{max}(\Delta \rho g/\rho L)^{1/2}}{L}$ [15], where $L$ is the lake length, $h_{max}$ its maximal depth, $\Delta \rho$, the difference of water density ($\rho$) at the bottom and the surface layer, and $g$, acceleration of gravity.

For the photosynthetic pigments’ determination, a certain sample volume, 50-500 ml, was filtered through membrane or glass fiber filter, which was then dried in the dark, and delivered to the laboratory. Pigments were extracted from filters with 5 ml of 90% buffered aqueous acetone overnight at 4°C. In 2006, concentrations of chlorophyll $a$ and bacteriochlorophyll $a$ and $d$ in extracts was determined using the previously published equations [16]. In 2007-2009, a modification of the spectral reconstruction method [17-18] was used to determine the pigment concentrations. In contrast to original method, difference spectra before and after pigment phaeophytinization (by acidification with small volume of HCl) were analyzed. Anoxygenic phototrophic bacteria (APB) were observed, identified and enumerated on acetyl cellulose membrane filters with a pore diameter of 0.2 μm [19].

### Table 1. Some morphometric characteristics of the investigated lakes

| Lake             | Area (ha) | Length (m) | Width (m) | Depth Mean (m) | Max. (m) | Relative (%) |
|------------------|-----------|------------|-----------|----------------|----------|--------------|
| Bolshoy Kichier  | 5.40      | 310        | 220       | 3.8            | 11       | 3.5          |
| Cherny Kichier   | 50.2      | 1210       | 485       | 4.7            | 16.5     | 1.4          |
| Shungaldan       | 1.02      | 130        | 100       | 6              | 13.5     | 10.4         |
| Blue             | whole lake| 4.80       | 1200      | 1.4            | 8        | 0.7          |
| Oxbow            | karst funnel | 0.85       | 100       | 3.6            | 8        | 8.0          |

### Figure 1.
Bathymetric diagram of the Kichier lake (A, after [10]) and satellite photos of lakes Shungaldan (B) and Blue Oxbow (C).

### 3. Results

All lakes were thermally stratified at the sampling dates. The highest temperatures of the surface layer were recorded in the Lake Kichier (> 28°C). In the Lake Shungaldan the temperature of the surface layer was 3-4°C lower in both years; in the Lake Blue Oxbow, under a mat of duckweed and filamentous algae, it did not exceed 20°C. The temperature of the bottom layer in all lakes was 5.3-6.5°C, except for the Lake Blue Oxbow in August 2007 where it reached 8.6°C (table 2).

The stratification by mineralization was also noted in all lakes in addition to the thermal one. In the lakes Cherny Kichier and Shungaldan the difference of mineralization between the surface and bottom layers was 650-1050 mg L$^{-1}$; in the Lake Blue Oxbow, mineralization stratification was less pronounced (300-400 mg L$^{-1}$), and in Lake Bolshoy Kichier it did not exceed 100 mg L$^{-1}$ (table 2). The bottom layer of the lakes was anoxic and strongly reductive, except for Lake Bolshoy Kichier. In the latter lake Eh was weakly positive in 2007, which apparently reflects a low concentration of sulfides compared to other lakes and their partial oxidation until the moment of measurement.

The meromictic component of the density gradient in the lakes Shungaldan and Cherny Kichier exceeds 0.6 g L$^{-1}$ (table 3). Considering the small size of these water bodies, it was sufficient to prevent their holomixis, according to the calculations by the method [20]. In the Lake Shungaldan, the
Chemocline separating low- and highly mineralized water masses practically coincides with the center of the thermocline, and was located at the 3-4 m depth. In the Lake Cherny Kichier, thermocline positioned at depths of 2 to 4 m, chemocline was located at its lower boundary, at 3.8-5.0 m (figure 2). Noteworthy, the chemocline position in the Lake Cherny Kichier was close to the maximum depth of the strait connecting it with the rest of the Lake Kichier.

**Table 2. Physicochemical characteristics of the surface and bottom layers of studied lakes**

| Lake              | Data       | Surface layer |                  | Bottom layer |                  |
|-------------------|------------|---------------|-----------------|--------------|-----------------|
|                   |            | T (°C)        | TDS (mg L⁻¹)    | pH | Eh | T (°C) | TDS (mg L⁻¹) | pH | Eh |
| Bolshoy Kichier   | 15.07.2006 | 27.0          | 113             | –  a | – | – | 189 | – | – |
|                   | 16.06.2009 | 26.5          | 108             | 8.08 | +410 | 6.1 | 203 | 6.4 | +60 |
| Cherny Kichier    | 15.07.2006 | 27.1          | 113             | 9.3  | +255 | 6.3 | 865 | 6.8 | -185 |
|                   | 17.06.2009 | 28.0          | 109             | 8.64 | +300 | 6.5 | 763 | 6.35 | -125 |
| Shungaldan        | 20.07.2006 | 23.8          | 900             | 7.5  | +280 | 6.5 | 1650 | 6.75 | -195 |
|                   | 08.08.2007 | 23.3          | 780             | 7.9  | +290 | 6.5 | 1840 | 7.0 | -145 |
| Blue Oxbow        | 08.08.2007 | 18.6          | 2390            | –    | – | 8.6 | 2600 | – | – |
|                   | 18.07.2009 | 17.1          | 2210            | – | +380 | 5.3 | 2630 | – | -110 |

*a* here and in other tables “-” indicate that parameter was not determined

**Table 3. Difference of water density (Δρₜₘ) between the surface and bottom layers, its meromictic component (Δρₘₑₙ), and the wind speed (Uₗ) required to mix lake completely during homothermy.**

| Lake              | Date       | Δρₜₘ (kg m⁻³) | Δρₘₑₙ (kg m⁻³) | % of Δρₜₘ | Uₗ (m s⁻¹) |
|-------------------|------------|---------------|----------------|-----------|------------|
| Bolshoy Kichier   | 15.07.2006 | 3.33          | 0.072          | 2.17 | 8.4 |
|                   | 16.06.2009 | 3.37          | 0.081          | 2.40 | 9.4 |
| Cherny Kichier    | 15.07.2006 | 4.05          | 0.61           | 14.97 | 26.7 |
|                   | 17.06.2009 | 4.28          | 0.61           | 14.12 | 27.3 |
| Shungaldan        | 20.07.2006 | 3.33          | 0.72           | 21.61 | 59.3 |
|                   | 08.08.2007 | 3.34          | 0.87           | 25.78 | 70.5 |
| Blue Oxbow        | 08.08.2007 | 1.55          | 0.17           | 10.86 | 22.3 |
|                   | 18.07.2009 | 1.68          | 0.39           | 22.99 | 33.1 |

In the Lake Bolshoy Kichier, a mineralization component of general stability was an order of magnitude lower than in the Lake Cherny Kichier (table 3). Regarding the significantly higher length of the lake and, therefore, higher wind load, the suppression of mixing during the autumn isothermy is unlikely. Chemocline in this lake is indistinct.

In the Lake Blue Oxbow, the sampling was performed only in the northern karst funnel. In 2009, the mineralization difference between the bottom and surface layers was twice as high as in 2007 (table 2), but about a half of the difference was concentrated in the surface layer (figure 2), protected from mixing by a layer of macrophyte-algal bacterial mats, completely covering the surface of the karst funnel. In 2007, the near-surface mineralization gradient was absent.

In the Lake Shungaldan a narrow peak of the biomass of phototrophic organisms, the so-called "microbial plate", was located in the contact zone between aerobic and anaerobic water masses (figure 3). *Chlorobium clathratiforme* and *Chl. limicola* dominated among the green sulfur bacteria (Chlorobiaceae) (figure 4). Among purple sulfur bacteria (Chromatiaceae), *Allochromatium vinosum* morphotype prevailed in 2006. It formed large flat aggregates at the biomass peak and represented by single motile cells below. *Thiocapsa* spp. and *Thiodiction bacillus* were less common. In 2007, *Thiocapsa roseopersicina* became the dominant morphotype, and slightly larger gas-vacuolated *Tea. rosea* was the subdominant by biomass (figure 4).
Above, in mixolimnion, the concentration of photosynthetic pigments was low, corresponding to oligotrophic conditions, as the phytoplankton development was limited by the lack of nutrients. Below 4-m depth, the development of all phototrophic organisms was suppressed presumably by both high sulfide concentration of (>150 mg L\(^{-1}\) in the bottom layer) and low illumination.

**Figure 2.** Vertical distribution of temperature (1), TDS (2), water density (3), general (\(N^2\), 4) and meromictic stability (\(N^2\), 5) in lakes Shungaldan (a), Cherny Kichier (b), Bolshoy Kichier (c) and Blue Oxbow (d).

The concentration of the main photosynthetic pigment of Chlorobiaceae, bacteriochlorophyll (Bchl) \(d\), exceeded in maximum 2 mg L\(^{-1}\); the concentration of Bchl \(a\), the main light-harvesting pigment of Chromatiaceae, minor in Chlorobiaceae, reached 253 μg L\(^{-1}\), exceeding the concentration of chlorophyll (Chl) \(a\). The ratio of Bchl \(d\)/Bchl \(a\) was less than 10, indicating a significant development of purple bacteria, since the ratio of these pigments in green bacteria is typically >50.

The Lake Cherny Kichier was similar to the Lake Shungaldan by morphology and chemocline position (at 3.75 m depth). However, the connection of its mixolimnion with the epilimnion of a larger eutrophic basin (Lake Bolshoy Kichier) resulted in significantly worse light conditions in the chemocline zone. In 2006, due to the strong cyanobacterial bloom, Chl \(a\) maximum was located at the surface; its concentration reached 69.2 μg L\(^{-1}\). The maximal Bchl \(d\) concentration was slightly less than in the Lake Shungaldan (1.64 mg L\(^{-1}\)), but Bchl \(a\) concentration was only 50.9 μg L\(^{-1}\) (figure 3). The Chlorobiaceae were represented by *Chl. clathratiforme*, *Chl. luteolum* and *Ancalochloris perflivelii*, as
well as consortia *Chlorochromatium aggregatum* and *Pelochromatium roseum* (in order of biomass decrease). *Tiocapsa roseum* and several other species of purple bacteria were also present (Figure 4).

![Figure 3](image1.png)

**Figure 3.** Vertical distribution of photosynthetic pigments in the lakes: Shungaldan, August 2007 (a), Cherny Kichier, June 2009 (b), Bolshoy Kichier, June 2009 (c) and Blue Oxbow, June 2009 (d).

![Figure 4](image2.png)

**Figure 4.** Vertical distribution of the APB morphotypes in chemocline zone of the lakes: Shungaldan, August 2007 (a), Cherny Kichier, June 2009 (b), Bolshoy Kichier, June 2009 (c): 1 - *Tcp.*rosea; 2 - *Tcp.*roseopersicina; 3 - other Chromatiaceae; 4 - *Chl.*limicola; 5 - *Chl.*clathratiforme; 6 - *Chl.*luteolum; 7 - *Anc.* perfilievi; 8 - *Chl.*pheobacteroides; 9 - consortia.

In 2009, spectral reconstruction pigment analysis method was applied, that allowed to distinguish different bacteriochlorophylls of green sulfur bacteria (chlorobium-chlorophylls). It was found that the
maximum of Chl a was at 3.6 m, Bchl d maximum was found at 3.9 m and common maximum of Bchls a, c, and e was located at 4 m depth (figure 3). Although Bchl d was the predominant, the concentration of Bchl c was also high. The sum of Bchls c-e ("chlorobium-chlorophylls") was slightly less than the content of Bchl d in 2006.

In the Lake Bolshoy Kichier, the concentration of Chl a in 2006 was the highest (54.5 μg L⁻¹) at 1 m depth. The position of the chemocline maximum was not determined with accuracy as the sampling in the chemocline zone were performed with a 1 m step. Maximal concentrations of bacteriochlorophylls were at 4 and 5 m depth (3.03 and 3.15 μg L⁻¹ of Bchl a and 75.0 and 72.8 μg L⁻¹ Bchl d at 4 and 5 m, respectively). Therefore, their true maxima were located somewhere within this depth range. In 2009, Chl a maximum was located at 3.8 m depth, and the maxima of all bacteriochlorophylls, at 4.85 m depth (figure 3). Noteworthy, bacteriochlorophylls’ concentrations were significantly lower in both years comparing to that in the Lake Cherny Kichier, but the APB composition was similar (figure 4); however, the proportion of consortia was higher in the Lake Bolshoy Kichier.

In 2007, samples were taken from only four horizons at the Blue Oxbow. According to the data obtained, the redoxcline was located between 3 and 6 m. The development of phytoplankton and APB in this lake was weak. This could be due to the skip of the “microbial plate” zone at sampling; however, more likely, it was a result of the shading by floating plants and filamentous algae. Purple sulfur bacteria were present in the studied horizons in low abundance. Among green sulfur bacteria, several Chlorobium species dominated, including brown-colored ones. The content of photosynthetic pigments was also small, in comparison with the lakes Shungaldan and Cherny Kichier (table 4). The maxima of Chl a, Bchl a and Bchl d were found at 6 m depth; maximum of Bchl e, in the bottom layer. In 2009, the concentrations and positions of the maxima have changed a bit, but general pattern remained the same.

**Table 4.** The maximal concentrations (μg L⁻¹) of tetrapyrrrole photosynthetic pigments in the water column of the studied lakes. The depth of maxima is shown in parentheses.

| Lake          | Year | Chl a   | Bchl a | Bchl c | Bchl d   | Bchl e |
|--------------|------|---------|--------|--------|----------|--------|
| Bolshoy Kichier | 2006 | 54.5 (1.0) | 2.0 (4.0) | - | 75.0 (5.0) | - |
|               | 2009 | 27.2 (3.8) | 1.99 (4.75) | 29.1 (4.75) | 154.5 (4.75) | 12.2 (4.75) |
| Cherny Kichier | 2006 | 69.2 (0) | 31.6 (3.75) | - | 1641 (3.75) | - |
|               | 2009 | 108.4 (3.6) | 8.2 (4.0) | 354.3 (4.0) | 485.2 (3.9) | 51.3 (4.0) |
| Shungaldan     | 2006 | 140.1 (3.5) | 157.3 (3.5) | - | 2116 (3.5) | - |
|               | 2007 | 882.9 (3.5) | 289.2 (3.5) | 88.5 (3.4) | 4243 (3.5) | 9.9 (4.0) |
| Blue Oxbow     | 2007 | 19.7 (6.0) | 14.6 (6.0) | 0 | 157.1 (6.0) | 20.9 (8.5) |
|               | 2009 | 33.1 (5.8) | 9.2 (6.0) | 20.4 (5.75) | 222.7 (6.0) | 45.7 (6.0) |

**4. Discussion**

Stratification, i.e. the suppression of complete mixing of the water mass in the lakes, is associated with a vertical gradient of water density, which depends on the temperature and content of impurities, primarily dissolved salts (with some influence of dissolved gases, organics, colloids and submicrometer-size particulate matter). During isothermal periods, the vertical density distribution may be treated as determined only by the difference in TDS, which, if sufficient, prevents the mixing of water bodies even under isothermy, and leads to the establishment of meromixis [21].

Judging by the vertical distribution of abiotic factors and values of general and meromictic stability (tables 2, 3; figure 2), the lakes Cherny Kichier and Shungaldan are meromictic. According to the description given in [9], bottom layers of the Lake Shungaldan are fed by the highly mineralized water from deep springs, while the surface layer receives less mineralized surface influx. The position of the halocline remains stable due to mixing of uprising bottom water with the surface water mass. Such a mechanism is defined as crenogenic meromixis [22]. It is probably true also for the Lake Cherny
Kichier, and the differences between the two lakes are primarily that the latter one has a common epilimnion with a much larger Bols hoy Kichier.

In the Lake Cherny Kichier the chemical composition of water, the chemocline position, and the magnitude of the environmental gradients remained very close to those previously obtained [23-24]. Small differences are most likely the result of seasonal fluctuations. Thus, the meromictic regime of the lake proves to be quite stable. Unfortunately, no comparable long-term data for the Lake Shungaldan are available.

In the Blue Oxbow the difference in mineralization in both study years was also sufficient to prevent mixing during isothermal periods (table 3), but the vertical distribution of mineralization turned out to be highly unstable. This fact, as well as the absence of a stable position of main mineralization step (the halocline), prevent us from attributing it meromictic. However, our data do indicate a high probability of skipping whole lake mixing at least in some periods of isothermy, so the lake is irregularly mixing or at least spring-meromictic [26].

The hydrological regime of the Blue Oxbow has experienced significant changes since 1998 or 2001 [9]. While earlier the lake had high water exchange rate, during our studies the northern karst funnel of the lake looked rather stagnant, and at least a significant part of its surface was covered with a macrophyte-algal mat dominated by duckweeds and filamentous green algae. It is likely that the presence of this layer impeded effective wind mixing of the surface layer, resulting in its desalination (which was evident even in 2009 compared to 2007), and in lifting and flattening of the halocline.

The largest of the investigated lakes, the Lake Bols hoy Kichier, is holomictic. Although mineralized water entering this lake from the chemocline of the Lake Cherny Kichier causes some increase in the mineralization of its bottom layer, it is insufficient for prevention whole lake mixing at homothermic periods. Even moderate wind speed (<10 m s⁻¹) is sufficient for its full overturn. The steeply vertical increase of the water mineralization with depth in the lake supports this conclusion. It should be noted that a distinctly higher value of water conductivity was found at the bottom (at 16 m) in [24] comparing to our results, and the vertical distribution of conductivity was complex and consisted of several steps. These differences may be related to the accumulation of highly mineralized waters during the stratification period, since the data in [24] referred to the second half of September. However, they may also reflect the evolution of the lake's ecosystem over the years.

The hydrodynamic characteristics of the lakes, primarily the duration and severity of stratification, impact significantly the development of phototrophic plankton. Under stratification conditions, plankton species that can resist sedimentation due to their active mobility, small size, or low buoyancy of their cells gain a high environmental advantage in the entire water column [27].

At stable stratification conditions, especially in meromictic lakes, sedimentation transport of organic carbon and nutrients to the bottom layer is not compensated by their return to the surface. Therefore, as a rule, the epilimnion of stratified lakes is markedly nutrient-depleted, while in the aphotic bottom layers they are in excess. Near-bottom oxygen deficit also develops due to of organic carbon respiratory consumption and, after full oxygen exhaustion, reduced inorganic compounds and other products of anaerobic respiration accumulate, often in high quantities [28].

These factors strongly influence the development of APB. Non-sulfur and aerobic APB are capable of developing in aerobic water layers but never reach significant biomass; most common chemocline species, representatives of the families Chromatiaceae, Chlorobiaceae and several planktonic Chloroflexales, require reducing conditions for their growth [4]. They also require light, so as result of the trade-off of these requirements they form their maxima at the top of anoxic layer, where concentration of their photosynthesis donors is quite low. Nevertheless, as their reductant supply is sustained by diffusion, their growth depends from its concentration below. Our data clearly illustrate this pattern in the meromictic lakes with high sulfide content (Shungaldan and Cherny Kichier) where APB development is much higher than in the holomictic Lake Bols hoy Kichier as judged by the maximum concentrations of their pigments (table 4). In full accordance with the peculiarities of its hydrodynamics, Lake Blue Oxbow occupies an intermediate position.
In all studied lakes, green sulfur bacteria dominate, which is manifesting in strong prevalence of Bchl d in the pigment composition of chemocline maxima. Although it is believed that brown forms of Chlorobiaceae preferably develop in lakes with much deeper location of the chemocline [29], their pigment (Bchl e), was found in small quantities in all four studied lakes. Purple sulfur bacteria using only Bchl a require more light for their development; therefore, they are recorded in greatest quantities in the Lake Shungaldan with almost oligotrophic mixolimnion, and to much less degree, in other lakes (table 4, figure 4). Our data indicates the change of purple bacteria dominant species in lake Shungaldan in 2006 and 2007, but it is unclear whether these changes were associated with interannual variations or with seasonal succession.

Noteworthy, the position of the APB maxima and even their species composition in the lakes Cherny and Bolshoy Kichier, have not changed much since 1968 [24], and are generally very similar to the results of another 2006 studies [25]. In 1968, Chl. luteolum dominated, but Chl. clathratiforme was the subdominant.

The species composition of the APB in all four studied lakes is rather similar. Obviously, this can be explained by their territorial proximity, as well as similar euxinic conditions in their anaerobic zone. In the lakes with the ferruginous type of anoxia, other species dominate [30]. The species composition appeared the least diverse in the Lake Shungaldan, which probably reflects a high degree of competition in a very narrow zone of the “microbial plate” in this lake.

Although one could expect some differences in the APB community composition of the meromictic and holomictic water bodies, such as the lakes Cherny and Bolshoy Kichier, they were not detected. This is probably due to the fact that the runoff from the chemocline zone of the Lake Cherny Kichier serves as a bacterial inoculum for the development of anaerobic plankton community in the Lake Bolshoy Kichier.

Both environmental conditions and phototrophic communities’ composition of the chemocline zone of the two previously studied lakes (Bolshoy and Cherny Kichier) have remained stable over the past 20-35 years. Significant APB development was found in two other lakes. In all of them, Bchl d was the dominant chlorobium-chlorophyll, reaching some mg per liter in the bacterial plates of meromictic lakes, but other chlorobium-chlorophylls were detected as well. The Bchl a concentration in different lakes varied from 1% of the sum of chlorobium-chlorophylls (Cherny and Bolshoy Kichier) to 7.5% (Shungaldan); in the latter lake it may exceeds the maximal concentration of Chl a. Noteworthy is the difference in the width of zone of APB development in holomictic and meromictic lakes: in the meromictic lakes Cherny Kichier and Shungaldan it is several times narrower than in holomictic lake Bolshoy Kichier.

References
[1] Gorham E and Boyce F M 1989 Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. J. Great Lakes Res. 15(2) 233-245
[2] Diao M, Huisman J and Muyzer G 2018 Spatio-temporal dynamics of sulfur bacteria during oxic-anoxic regime shifts in a seasonally stratified lake. FEMS Microbiol. Ecol. 94(4) fiy040
[3] Klaveness D and Løvhøiden F 2007 Meromictic lakes as habitats for protists. Algae and Cyanobacteria in Extreme Environments. ed Seckbach J. (Springer) pp 59-78
[4] Overmann J and Garcia-Pichel F 2013 The Phototrophic Way of Life. The Prokaryotes - Prokaryotic Communities and Ecophysiology. eds E Rozenberg et al. (Springer) pp 203-257
[5] Stupishin A V 1967 Lowland Karst and Patterns of Its Development on the Example of the Middle Volga Region. (Kazan, Izd. Kazan. Univ.)
[6] Dedkov A P 2009 Geological and Geomorphological Conditions of Development and Genesis of Karst Lakes of the Middle Volga Region. Biodiversity and Typology of Karst Lakes of the Middle Volga Region. ed N M Mingazova (Kazan, Izd. Kazan. Univ.) pp 19-35
[7] Mingazova N M (ed.) 2009 Biodiversity and Typology of Karst Lakes of the Middle Volga Region. (Kazan, Izd. Kazan. Univ.)
[8] Sorokin I N and Petrova R S (eds.) 1976 Lakes of the Middle Volga Region. (Leningrad, Nauka)
