Vertical Distribution and Migration of Algae under Thermal Stratification in Small Water Bodies of the Forest-Steppe Volga Region

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Abstract. In this article the author presents some study results of taxonomic composition, distribution and migrations of algae under thermal stratification in small water bodies of the forest-steppe Volga region. The author considers the main factors influencing the formation of heterogeneity of the structure of algocoenoses: vertical temperature gradients, water density and the content of basic biogenic substances. The composition of vertically migrating common species is discovered. The nature of species distribution during the day is shown, when samples are taken with an interval of 3 hours. The predominance of mobile mixotrophic phytoflagellates is a feature of the taxonomic composition of algae in water bodies with a pronounced vertical heterogeneity of populations of dominant species. The clearest picture of distribution and migration in plankton is demonstrated by Pandorina morum, Mallomonas caudata, Dinobryon divergens, Cryptomonas curvata, and a number of other large-cell flagellar forms. Of the species without active movement, vertical distribution was constantly observed in Westella botryoides, Botryococcus braunii, Dictyosphaerium pulchellum, Koliella longiseta, Woronichinia naegeliana, and some species of the genus Anabaena. The author notes the connection between the maximums of the abundance of some common species with changes in the content of nutrients within the photic zone. Vertical heterogeneity of taxonomic and quantitative indicators in algocoenoses is considered as an adaptive strategy to the heterogeneity of the habitat in highly eutrophic water bodies with a high density of algae in plankton.

1. Introduction
The study of the structural and functional organization of algae communities, as an essential element of the biota of aquatic ecosystems, is necessary for solving fundamental and applied issues of modern hydroecology. The functional state of phytoplankton is of great importance for the life of aquatic organisms and the development of biological processes in the reservoir [1,2]. One of the characteristics of algae communities is the seasonal periodicity of their development and the spatiotemporal heterogeneity of distribution in the reservoir. This is due to hydrodynamic conditions, illumination gradients, temperature, as well as the content of nutrients, competition for resources, and zooplankton devouring [3-5]. In particular, the vertical distribution and migration of species in algocoenoses indicate physicochemical and biological processes in the water column, which determine the features of the location of their populations. For example, the temperature regime is one of the most important abiotic factors affecting the ecosystem of a water body, and the phenomenon of thermal stratification largely deter-
mines the structure and dynamics of planktonic communities. Research in this area is of interest not only for studying the ecology of phytoplankton. Stratified water bodies are complex heterogeneous ecosystems, since thermal stratification forms the difference in physical and chemical parameters, provides a pronounced heterogeneity of the habitat in the water column [4-6]. This, in turn, determines the peculiarities of the composition and distribution of plankton organisms, strategies for the growth, survival and coexistence of species, efficiency of the transformation of matter and energy [1,2]. In practice, data on the distribution of species in depth, on the effect of the vertical structure of the water column on the composition and productivity of aquatic organisms are applicable, for example, for assessing the food supply in fishing ponds [7].

The aim of this research is to consider and analyze the composition and structure of phytoplankton in different types of small eutrophic thermally stratified water bodies under conditions of vertical inhomogeneity of the environment.

2. Environmental conditions in the research small water bodies

Researchers of the Institute of Ecology of the Volga Basin studied phytoplankton of small water bodies located on the border of the forest-steppe and steppe zones of the southeast of the European part of Russia, within the framework of complex hydrobiological studies. The studies included the research of the composition, structure, functional characteristics of aquatic organisms in reservoirs and watercourses of the Middle Volga Integrated Biosphere Reserve (MVIBR), different in origin, position in landscapes, hydrological and hydrochemical conditions [8-10]. One of the features of water bodies is their temperature regime, in particular, the existence of a stable summer thermal stratification of water masses at depths of more than 2 m (figure 1). This is associated with vertical differences in the content of dissolved gases, nutrients and water salinity [11-13]. Studies have shown that stratification limits the convective uplift into the surface horizons of nutrients, carbon dioxide, products of incomplete oxidation of organic matter entering the hypolimnion as a result of sedimentation of seston, that is, it leads to the formation of secondary gradients of "biologically significant substances" [12]. For example, the concentrations of phosphorus, ammonium and iron in the hypolimnion significantly increase in comparison with the overlying layers of thermo- and chemocline [12, 13]. Under conditions of stratification and daytime warming, we observe an increase in the thermal stratification of the water mass, a rapid depletion of oxygen in the hypolimnion to anaerobic conditions in the bottom layers of the deepest lakes. The factors of stratification formation are the following: protection from wind mixing, in some lakes a small area and a relatively high relative depth, conditions that create shading (cover of duckweed, algal bloom). In small rivers of MVIBR, thermal conditions in the water column are more uniform and the presence of temperature gradients is possible locally in areas with low flow rates (backwaters, backwater zones in estuaries).

Figure 1. Vertical temperature profiles of some of the studied water bodies: I and II - closed lakes (Gudronnoe 2, Maloye Karstovoe), III – pond (Zhiguli village), IV - floodplain lake (Kamennoye), V - small river (Tisherek river). Data is for July.
A high content of phosphorus and nitrogen in water with an increase in their amount to the bottom is typical for most water bodies. The concentration of total phosphorus is often higher than 0.1 mg/L, the maximum values in the surface water horizon in some lakes reached 1.4–2.6 mg P\text{\textsubscript{tot}}/L; the content of mineral nitrogen, represented mainly by the ammonium ion, varies from 0.2 to 11.3 mg N\text{\textsubscript{min}}/L, on average it is about 1 mg N\text{\textsubscript{min}}/L [8, 11, 13]. The content of dissolved organic matter in most lakes is high; water bodies are distinguished by its vertical distribution and the amount of easily oxidized fraction [10, 13].

3. Materials and Methods

The study of the vertical distribution of phytoplankton is a part of the algological studies carried out on reservoirs and watercourses of MVIBR [3, 14, 15]. In this study, the authors consider the vertical structure of phytoplankton in water bodies with a different composition of mass forms of algae and their distribution. The methodology for collecting and processing samples corresponds to that adopted for algological studies; dominants and subdominants are classified as mass species, forming, respectively, from 5 to 10% and more than 10% of the total abundance or biomass of phytoplankton [16]. We used the Spearman's rank correlation coefficient to assess the relationship between phytoplankton indicators and environmental factors.

4. Results and discussion

4.1. General vertical distribution of phytoplankton

We observed vertical distribution of algae in most of the stratified water bodies of MVIBR. Figure 2 shows the dynamics of temperature, oxygen content, abundance and biomass of algae during the open water period using the example of one of the lakes of the Zhigulevsky Reserve. As can be seen, by the beginning of sampling (the first ten days of May), the upper water horizon warms up in the reservoir and stratification formation begins; the quantitative distribution of phytoplankton over depth is uniform (figure 2). In June, the value of the vertical temperature gradient reached 7.8 deg/m - in the layer between 1-2 m, and in July-August its values were 3.6-3.8 deg/m throughout the water column. The surface horizon of the studied lake in summer correspond to mesotrophy. The concentration of biogenic substances (phosphate and total phosphorus, mineral nitrogen) increases to deeper layers, several times in hypolimnion - to hypertrophy; the photic zone in the lake is almost to the bottom ... The vertical change in the content of chlorophyll-a (Chl-a) has a similar character, and the Chl-a maxima are noted in summer at a depth of 2 m in the pycnocline zone, which is formed under direct temperature stratification and increased mineralization to the bottom [17].

![Figure 2](image_url)

**Figure 2.** Seasonal dynamics of t - water temperature (t, °C), O\textsubscript{2} - oxygen concentration (mg O/L) according to: [13, 17], N - abundance (million cells/L), B - biomass (mg/L) of phytoplankton in a thermally stratified reservoir ("Strelnoe 5").
The distribution of phytoplankton corresponded to the heterogeneity of physical and chemical parameters. High concentrations of algae during the period of summer stratification were at a depth of 1–2 m; the seasonal maximum of abundance was noted in July (figure 2). The dynamics of oxygen content also indicates the highest activity of phytoplankton in the subsurface horizon (figure 2). This type of vertical distribution is especially well pronounced in June-July and may reflect the known ability of species to extract nutrients in places of their greater concentration, with depletion in the epilimnion: the relationship between the dynamics of the abundance of mass species correlates \( R = 0.87; p < 0.0025 \) with a change in nutrient content within the photic zone. On the other hand, we do not exclude the sedimentation effect of passively planktonic species to the limit of changes in water density, as well as the eating of algae by zooplankton. Thus, in August, we observed a reduction of algae (figure 2), while the samples showed a large number of zooplankton organisms (Cladocerans and Copepods) at a depth of 1 to 2 m. Herbivorous zooplankton often have a distribution similar to phytoplankton. With a shortage of resources at the surface of the reservoir, it migrates into deeper layers beyond the maximum abundance of algae into meta- and hypolimnion; at the same time, it enriches the water with nutrients available to phytoplankton and is associated with it with the nutrient cycle [4, 18]. By autumn, water temperature dropped and thermal stratification was destroyed. Despite this, the development of algal populations in the photic zone continued, and phytoplankton abundance remained high (figure 2). In September-October, during the period of autumn thermal mixing, the removal of nutrients from the underlying horizons contributes to the maintenance of the abundant growth of algae species: their abundance in these months is comparable to that in summer (figure 2).

4.2. Vertical distribution of common species
Long-term data analysis of phytoplankton in the water bodies of MVIBR made it possible to identify a group of taxa that, upon stratification, have a pronounced difference in abundance at different horizons in the water column. First of all, these are various phytoflagellates from the divisions Cryptophyta, Chrysophyta, Dinophyta, Euglenophyta and flagellate forms of the division Chlorophyta. Their significant role in the taxonomic and quantitative structure of algal communities is characteristic of the studied water bodies [15, 19]. This is facilitated by factors that control the formation of algocoenoses in a number of lakes. Low pH (less than 6) leads to a direct limitation of algae growth and, also due to a decrease in the availability of nutrients, an increased algal bloom (up to 100-340 oPt), which in turn leads to a reduced transparency and, consequently, the narrowing of the photic zone. Such conditions give an advantage to motile phytoflagellates capable of mixotrophy. They make vertical migrations and can successfully exploit light and trophic resources [20-22]. In addition to phytoflagellates, the heterogeneity of vertical distribution during stratification is demonstrated by a large group of species of the Chlorophyta division (of the order Chlorococcales) and some Cyanoprokaryota. Table 1 shows the composition of common species in the water bodies of MVIBR. In addition, there are species that are locally dominant (in 1-2 water bodies) and have a clear vertical depth distribution under stratification, for example: *Pseudocarteria peterhofiensis* (Kiss.) Ettl, *Gonyostomum semen* (Ehr.) Dies. and some others.
Table 1. Common species composition in thermally stratified water bodies of MVIBR

| Phytoflagellates                                      | Others                                      |
|------------------------------------------------------|---------------------------------------------|
| **Chrysophyta**                                      | **Chlorophyta**                             |
| *Mallomonas caudata* Iwan., species of the genus Dinobryon (D. divergens Imhof, D. sertularia Ehr., D. bavaricum Imhof), species of the genus Synura (S. uvelia Ehr., S. petersenii Korsh.), Chrysococcus biporus Skuja | *Botryococcus braunii Kütz., Westella botryoides (West) De-Wild., species of the genus Scenedesmus (S. armatus Chod., S. acutiformis Schröd., S. acuminatus (Lagerh.) Chod.), species of the genus Dictyospheria (D. pulchellum Wood, D. tetrachotomum Printz, D. chlorelloides (Naum.) Kom. & Perman), species of the genus Monoraphidium (M. contortum (Thuret) Kom.-Legn., M. arcuatum (Korsh.) Hind., M. irregulare (G.M.S.) Kom.-Legn., Lagerheimia genevensis Chod., Ocystis lacustris Chod., species of the genus Coelastrum (C. astroideum De-Not., C. microporum Nag. in A. Br.), species of the genus Nephrichlamys, Koliella longiseta (Visch.) Hind. |
| **Euglenophyta**                                     |                                             |
| *Euglena acus* (O.F.M.) Ehr., *E. polymorpha* Dang., *Trachelomonas hispida* (Perty) Defl., *T. volvocina* Ehr., *T. intermedia* Dang. |                                             |
| **Chlorophyta**                                      |                                             |
| *Pandorina morum* (O.F.M.) Bory, *Eudorina elegans* Ehr., species of the order Chlamydomonadales (Chlamydomonas cingulata Pasch., Chloromonas depauperata (Pasch.) Gerl.) |                                             |
| **Cryptophyta**                                      |                                             |
| species of the genus Cryptomonas (C. curvata Ehr., C. platyris Skuja, C. ovata Ehr., C. marssonii Skuja) |                                             |
| **Dinophyta**                                        |                                             |
| *Ceratium hirundinella* (O.F.M.) Duj., *Peridinium cinctum* (O.F.M.) Ehr., *Peridiniopsis berolinense* (Lemm.) Bourr. |                                             |

Figure 3 shows the nature of changes in the abundance of some common species in depth during summer stagnation. As can be seen, in different years, in different water bodies, it is possible to register several types of vertical distribution for the same species. This applies especially to large motile flagellates - *Ceratium hirundinella, Mallomonas caudata, Cryptomonas curvata, C. platyris, Chlamydomonas cingulata, Gonyostomum semen*, as well as colonial forms of phytoflagellates - *Pandorina morum, Eudorina elegans*, species of the genus Synura, Dinobryon. For example, *C. curvata* has the abundance maxima near or below the thermocline (figure 3); *D. divergens, C. hirundinella, M. caudata*, in addition, can form maxima near the surface. The distribution can be more complex when parts of the population of the same species are simultaneously located in different horizons of the water column (*Botryococcus braunii, M. caudata C. hirundinella, Chrysococcus biporus*).

The idea of the vertical species distribution in algocoenoses should be made taking into account their migratory behavior during the day. Thus, the ability of organisms to move around gives them a selective advantage in the nutrient or light-limited conditions. In addition, the nature of the distribution of a species in depth reflects its response to the values of environmental factors. For example, active movement allows the species to occupy a photosynthetically advantageous position in the epilimnion during the day and extract essential nutrients at night, moving down the depth profile [5, 23].
4.3. Diurnal dynamics of the vertical distribution of dominant species
We chose a small eutrophic reservoir to study the diurnal changes in the vertical distribution of species in plankton. In the reservoir, the concentration of nutrients increased in the meta- and hypolimnion. The concentration of total phosphorus ranges from 0.6 to 1.3 mg P_tot/L; mineral nitrogen - 0.3-2.5 mg N_min/L. The water transparency is 1.2 m, pH is 7.9. Temperature gradient in the surface water layer - from 0.6 to 2.7 deg/m; at a depth of 1-2 m there is a layer of maximum temperature difference - from 2.9 to 3.3 deg/m, at 2 m and at the bottom it is close to 2 deg/m. The greatest temperature difference at each of the horizons falls on daytime hours (11-19 hours), the minimum one is at 7 hours in the morning (figure 4). Sampling frequency - in 3 hours. We found 170 species and intraspecific taxa in phytoplankton, of which 60% are phytoflagellates of different taxonomic groups. Vertical migrations are observed in more than a third of species, however, the quantitative structure is determined by 9-11 taxa, significant variability in distribution is observed in 8 species. The following species were dominant: Pandorina morum, Cryptomonas curvata, Chrysococcus sp. and Scenedesmus armatus, the first three species of which are phytoflagellates. In total, the dominants make up to at least 75% of the total phytoplankton abundance; the biomass was dominated by large forms - P. morum and C. curvata, sometimes also Botryococcus braunii, Ceratium hirundinella and some other dinoflagellates.

Figure 3. Types of vertical distribution of some dominant species during stratification in the water bodies of MVIBR. Data is for July; the lines on the graphs represent various water bodies.
Figure 4. Mutual arrangement of populations of dominant species in a thermally stratified reservoir (backwater of the Tisherek river) during the day.

The diurnal dynamics of the dominant species proves their active vertical movement (figure 4). In the daytime (11, 15 o’clock), the maximum number of algae was recorded at different depths. Thus, two species dominate in the epilimnion: the flagellate Chrysococcus sp. and motionless Scenedesmus armatus (figure 4). Apparently, these are the species most sensitive to the light regime: their movement into deeper water layers at the end of the day coincided with a decrease in illumination, but a decrease in the number at noon (15 hours) on the surface and an increase at a depth of 1 m may be associated with the need to avoid photoinhibition. The species may have a mixotrophic feeding strategy judging by the preservation of a part of the Chrysococcus sp. population during the day at a depth of 1–2 m and at nighttime maximum abundance at a depth of 2–3 m (figure 4).

The species Scenedesmus armatus, which is characteristic of eutrophic waters [24], is an indicator of saprobity. It is obvious that it is able to use passive subsidence to move in depth and regulate its specific gravity during the day, effectively using trophic and light resources during the day, which allows it to maintain a high number (figure 4). The main part of the Cryptomonas curvata population is concentrated within the hypolimnion, but during the day at a depth of about 1 m, the number of the species is also maintained at a noticeable level (figure 4). Apparently, the vertical movement of C. curvata and its physiological characteristics allow it to develop successfully and avoid competition...
with other species. In addition, Cryptomonas species are a good food for zooplankton and can use migrations, avoiding being eaten away: in the reservoir under study, planktonic crustaceans were in noticeable numbers at a depth of 0 to 2 m. This is consistent with the ecological and biological characteristics of Cryptomonas as actively motile species that prefer eutrophic waters, are resistant to low light intensity, and are capable of photomixotrophy [2, 4, 20, 25].

The species Pandorina morum is widespread in eutrophic mesosaprobic waters and abundantly growth in the organic-mineral environment [26, 27]. In the studied reservoir, P. morum almost constantly maintains its maximum number in the thermocline zone (figure 4), keeping part of the population at the surface during daylight hours.

The distribution of species with maximum abundance at the border of the meta- and hypolimnion may indicate that these waters are preferable for them. Such distribution should be due to the satisfaction of environmental requirements, for example, it may indicate the consumption of available forms of nutrients in places of their concentration. It is known that different metabolic strategies contribute to a variety of ways of entering matter and energy into algal cells [22, 25]. The vertical temperature gradient in the metalimnion leads to an increase in the density and viscosity of water, diffusion of nutrients and their enrichment in this layer [4, 5, 21]. However, we were unable to establish a significant correlation between the abundance and biomass of the dominant species for the studied eutrophic reservoir with the vertical change in the content of biogenic substances. Apparently, the development of algae is not limited by them. At night (23, 3 o'clock), the vertical distribution of each of the dominant species acquires a similar character: the highest concentrations are observed at a depth of 2-3 m (figure 4).

Studies of the nature of vertical diurnal migration and photosynthetic activity of phytoplankton have led researchers to believe that algal communities manifest themselves as “self-adjusting” systems that absorb solar energy as efficiently as possible [28]. At the same time, photosynthetic reactions occur in the surface layer of water during the day. Dark assimilation and use of metabolites can occur at different times of the day at different depths. In the early morning (7 o'clock), all species, with the exception of C. curvata, change position, rising to the water surface and occupying a position favorable for photosynthesis (figure 4), and in the daytime redistribute their abundance again. It is characteristic that, during the daytime, the abundance maxima of the four dominant species are distributed in different horizons of the water column (figure 4), forming a quantitative structure that allows them to coexist.

Thus, in the reservoir under consideration, the dominant species demonstrates the strategy of organisms for which the light / nutrient ratio is an important condition for maintaining a high abundance. However, it is most likely that the light factor and adaptive habitat strategy for a eutrophic reservoir with a high species density should be considered the main reasons for the migratory behavior of algae. Forms that have a competitive advantage dominate: mixotrophs that regulate the vertical position. This is consistent with the results of studying the phytoplankton of eutrophic water bodies, in which different groups and species of algae, capable of separating photosynthesis and nutrient absorption, reach their maximum density at different depths using different niches [2, 5, 6, 23, 29].

5. Conclusion
Analysis of the vertical structure of phytoplankton in small eutrophic water bodies of the forest-steppe Volga region showed that features of composition and distribution of algae over depth are associated with the vertical stratification of the water column. In water bodies with a pronounced vertical heterogeneity of temperature, physical and chemical parameters, motile large-cell mixotrophic phytoflagellates mainly dominate: Pandorina morum, Mallomonas caudata, Dinobryon divergens, Cryptomonas curvata and other flagellate forms. Vertical distribution is observed in species that do not have active movement: Scenedesmus armatus, Westella botryoides, Botryococcus braunii, Dictyosphaerium pulchellum and a number of others. The most pronounced temperature gradient in June-July leads to a clear differentiation of species populations along the depth profile. In general, the highest density of algae is often noted at a depth corresponding to the metalimnion and the upper boundary of the hypo-
limnion, which in a number of lakes correlates with changes in the nutrient content within the photic zone. The authors found that under conditions not limited by nutrients, populations of common species form density maxima at different depths. We should assume it an adaptive strategy for avoiding interspecific competition during the eutrophication of water bodies.

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