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Spatiotemporal Distribution of Planktonic Ciliates in the Kuibyshev Reservoir in the Area of Klimovskaya Narrowing

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Abstract—An attempt was made to link changes in the quantitative characteristics of the community of free-living planktonic ciliates and the nature of their vertical distribution with the operation mode of the hydroelectric power plant in the reservoir. The low values of the abundance (8000–1 560 000 cells/m^3) and biomass (0.1–66.9 mg/m^3) of ciliates in the water column and the rather wide range of their variation in the reservoir are probably due to the oscillatory nature of the hydrological regime in the regulated river conditions. The vertical distribution of free-living planktonic ciliates in the near-dam section of the Kuibyshev Reservoir was studied at all times of the day on different days of the week. The species were distributed throughout the water column to the bottom with some preference for the surface (0–2 m) and medium (4–10 m) layers. There was no distinct confinement of particular species to certain layers in the conditions of homothermy. The preference for certain horizons is due to some biological characteristics of the species (for example, peritrichs on the coenobia of algae in the surface layers), escape from "blooming spots," etc. Data on vertical migrations or "turbulent transport" are still not available. The effect of the weekly regime of regulation of the Zhiguli HPP operation, at which the fluctuation amplitude of many hydrological parameters probably decreases at the end of the working week, is manifested in an increase in the abundance and biomass of planktonic ciliates at this time. The nature of the daily change in the average ciliate abundance in the water column was the same for the community on working days and was in antiphase with the change in the community abundance on weekends, namely, the maximum number on working days and on weekends was recorded in the evening (8 p.m.) and in the daytime (2 p.m.), respectively.

Keywords: ciliates, vertical distribution, daily and weekly dynamics, hydroelectric power plant (HPH) operation mode, reservoir

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INTRODUCTION

Study of the spatial distribution of hydrobionts in reservoirs is often restricted to studying their distribution along the longitudinal profile and does not always take into account the pattern of their distribution in the water column. Studies of diurnal changes in the vertical distribution pattern of planktonic ciliates in reservoirs (Mamaeva, 1979; Zharikov and Rotar, 1994) are very rare. The data on the vertical distribution of ciliates are usually presented as a result of single studies which, in the best case, take into account seasonal features (Paranjape, 1987; Feng et al., 2014) and were conducted, as a rule, in seas (Agamaliev, 1983, 2017; Olli et al., 1998; Perez et al., 2000; Fenchel and Juwel Hansen, 2006) or stratified lakes (Rossberg and Wickham, 2008). Studies of the change in the diurnal vertical distribution of ciliates were carried out in large lakes, like Lake Baikal (Obolkina, 2015) and Lake Sevan (Zharikov, 2010), during different seasons. Notwithstanding the conclusions, the mechanisms of formation of the vertical distribution of planktonic organisms, especially protozoa, in natural waters are still "in the realm of suppositions" (Obolkina, 2015, p. 80).

In the Volga reservoirs, the vertical distribution pattern of ciliates was studied only in the Rybinsk and Kuibyshev reservoirs (Mamaeva, 1979; Zharikov, 2000). In the Rybinsk Reservoir, the preference of species for different horizons and the dependence of their distribution on wind-induced waves, solar insolation, etc., is shown (Mamaeva, 1979). In the Kuibyshev Reservoir, "the distribution of ciliates in the water column under conditions of homothermy is similar to that in lakes with temperature stratification, regardless of the season of the year" (Zharikov, 2000, p. 68). At the same time, the diurnal pattern of the vertical distribution of the ciliates was determined "not by the

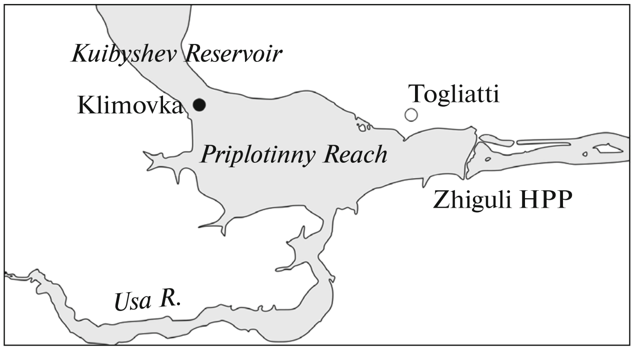

Fig. 1. Schematic map of the location of sampling stations.

temperature or biological migrations, but by turbulence-driven transport." V.V. Zharikov showed the presence of "turbulent hydrological stratification," which is determined by the water capture of the hydroelectric power plant from a depth of 10 m and at which three layers of water are distinguished in the Kuibyshev Reservoir (0–4 m, 4–10 m, and from 10 m to the bottom), "moving at different velocities and in different directions relative to each other, at the boundary of which sharp gradients of the hydrological parameters are developed" (i.e., the velocity and direction of the current) (Zharikov, 2000, p. 68).

In general, in reservoirs where the functioning of the ecosystem depends on the operation of hydroelectric power plants, in addition to the action of a complex of physical, chemical, and biotic factors, hydrological factors most likely play a key role in the distribution of organisms in the water column, namely, the velocity, direction of water flow, level, and factors related to the operation mode of the hydroelectric power plants. The weekly and daily regulation of the Zhiguli HPP operation assumes that, during the peak electrical load (daytime and working days), it develops increased power compared to night hours and weekends and increased water intake from the upstream reach, which can lead to an increase in the velocity, a decrease in the water level in the upstream reach, and other consequences.

The aim of this work is to identify changes in the quantitative parameters of the ciliate community in the water column and the pattern of their diurnal vertical distribution on different days of the week in the reservoir with a weekly and daily type of HPP operation mode.

MATERIALS AND METHODS

The vertical distribution of ciliates was studied in the area of the Klimovskaya narrowing of the Kuibyshev Reservoir (village of Klimovka) (Fig. 1) at six-hour intervals on July 19–20, 2011, and August 23–28, 2012. In 2012, samples were collected for three days (every other day) at the end of the working week (the first 24 hours, August 23–24, 2012), on the weekend (the second 24 hours, August 25–26, 2012), and the beginning of the working week (the third 24 hours, August 27–28, 2012). Samples were collected in the channel part of the reservoir with a Dyachenko bathometer from the surface to the layer of 10 m, every 2 m; and after 10 m to the bottom, with an interval of 5 m. The depth at the sampling stations was 15 m in 2011 and 18–20 m in 2012.

The species were identified and counted using preparations fixed in mercuric chloride (Rotar, 1995). The water temperature, pH, oxygen content, and oxygen saturation were measured with a DS5X multiprobe (Hach Environmental, United States). The species diversity and similarity of the species composition were assessed using the Shannon diversity index and the Sorensen similarity coefficient. The dendrogram of differences in the species composition of ciliates was constructed using the Euclidean distance; grouping was performed by Ward's method. The statistical analysis (primary statistics, means, ranges (min–max); correlation analysis) and graphics were made using the Excel 15.0 (Microsoft Office, 2013), SigmaPlot 12.5 (Systat Software, 2013), and Statistica 12 (Statsoft, 2014) software packages.

RESULTS AND DISCUSSION

Abiotic conditions. In July 2011, the weather was clear and windless. In August 2012, the weather was, on the contrary, windy the first two days, and calm on the third day contributing to the preservation of large patches of cyanobacteria in the surface layer formed due to wind-induced effects (clearly expressed by 8 a.m. in the morning). The temperature regime was characterized by homothermy in almost the entire water column of (24–25.5°C in July 2011 and 21–22°C in August 2012). In August 2012, by the third day of observation, the average temperature in the water column decreased by almost a degree (from 22.23 to 21.37°C). The water transparency during the study period in 2011 was 0.6–0.7 m, and in 2012 it varied between 1.4 and 2.4 m (on average, about 2 m). The oxygen content in the water column ranged from 7.2 to 9.1 mg/L, which is quite favorable for hydrobionts.

Due to the lack of detailed (hourly) data on the operating mode of the Zhiguli HPP for 2012, the graph (Fig. 2a) presented in the work of A.V. Rakhuba (2012) was used as a model. Assuming that the cyclic operation of the HPP was maintained in 2012, it is possible to get an approximate idea of the water discharge through turbines. It was maximum in the evening

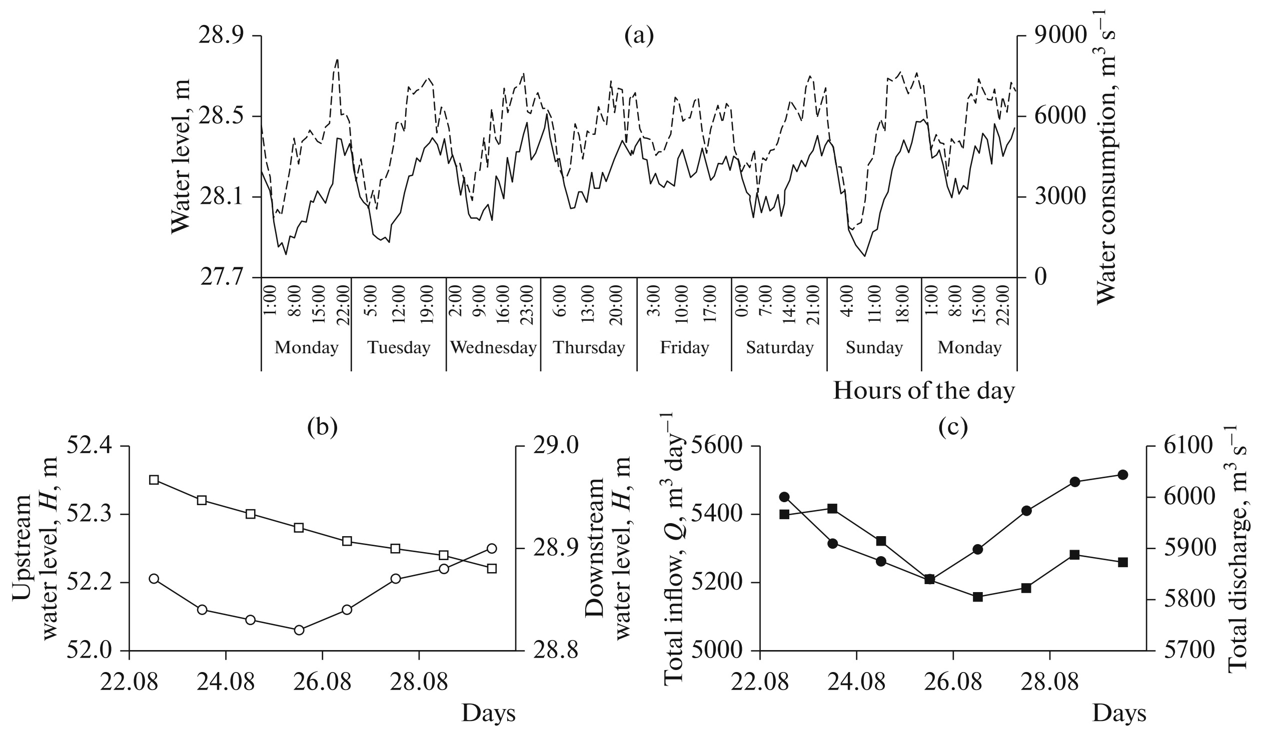

Fig. 2. Hydrological parameters of the Kuibyshev Reservoir in the area of the Zhiguli HPP: (a) an example of the dynamics of water flow (- - -) and water level (–) downstream of the Zhiguli HPP from August 1, 2011 (Monday) to August 8, 2011 (Tuesday) (according to: Rakhuba, 2012, with changes); (b) average daily water level in the upper (□) and lower (○) reaches; (c) total water inflow (■) and discharge (●) for the period from August 22, 2012 till August 29, 2012, Kuibyshev hydrological post (Available at: http://gis.vodinfo.ru/).

(8:00 p.m.) and decreased by the morning hours (4:00–6:00 a.m.). It is noteworthy that, by the end of the working week (Thursday–Friday), the amplitude of the water discharge fluctuation and, accordingly, the level decreased (Fig. 2a). Directly during the surveyed period on August 23–28, 2012, the water level in the upper reach gradually decreased (Fig. 2b), probably due to a decrease in the inflow, which decreased by the weekend. The water discharge decreased by the end of the week and increased again by the beginning of the week (Fig. 2c).

General characteristics of the planktonic ciliate community in July 2011 and August 2012. During the study period, the number of ciliates was small and varied between 8000 and 1560000 ind./m^3, and the biomass ranged between 0.1 and 66.9 mg/m^3. In the study period for three full days in 2012, there was a declining trend in the average daily parameters of abundance and the species richness, and, on the contrary, a decreasing trend in the species diversity (Table 1). In general, in July, when the entire water mass warmed up greatly, the average abundance was twice, and the biomass was three times higher than in August. The species diversity in 2011, on the contrary, significantly decreased compared to 2012, with a rather similar number of species identified for the 24-hour survey in both years (see Table 1).

A total of 23 species were identified in July, and from 19 to 26 species were found in August on some days (35 species in total for three days). Despite the seasonal and annual differences, the similarity according to the Sorensen index between the communities in 2011 and 2012 was rather high and amounted to 66%. Significant differences were found for the dominant complex of species. In July 2011, compared to August 2012, the contribution of ciliates of the family Vorticellidae (60 and 17% of the total abundance, respectively) was higher. In August 2012, on the contrary, the ciliates of the genus *Rimostrombidium* (45% of the abundance) were more developed compared to 2011 (14%). The "classic" Volga dominant *Tintinnopsis cylindrata* was part of the dominant complex (10% of the abundance in 2011), and was a subdominant (7–8%) in 2012. *Epistylis procumbens* Zacharias, 1897 was absent in August 2012, but in July 2011, it formed 12% of the abundance and 71% of the biomass.

Hourly changes in the average water column parameters of the ciliate communities on different days of the week. On workdays, the maximum ciliates abundance was recorded at 7–8 p.m. at the minimum water level

Table 1. Characteristics of ciliates communities (and ranges of their fluctuations) in the water column per day in July 2011 and August 2012

Date	Abundance, cells L^{-1}	Biomass, μg L^{-1}	Number of species	Shannon index
Jul. 19–20, 2011	443 / 60–1560	19.5 / 0.7–66.9	23	1.95
Aug. 23–24, 2012	218 / 20–828	4.9 / 0.4–16.8	26	2.88
Aug. 25–26, 2012	101 / 8–480	4.0 / 0.1–15.2	24	3.00
Aug. 27–28, 2012	97 / 8–588	4.7 / 0.5–27.9	19	3.13

The average in the numerator, min–max in the denominator.

in the upper reaches due to the maximum water discharge; the morning decrease in electricity consumption leads to a decrease in the abundance of ciliates too. On weekends, with low electricity consumption by industrial enterprises, the ciliates abundance increases in the morning, reaching the maximum at 2 p.m. Quite often, the species diversity indicators change in the opposite phase with changes in abundance or biomass: for example, in 2012, the abundance increased, and the Shannon index decreased by 8 p.m. (see Fig. 3).

Hourly change in the vertical distribution of ciliates. There was no distinct pattern of ciliate distribution in the water column depending on the time of the day and the day of the week. The only thing that can be noted is the rather frequent occurrence of the maximum abundance of ciliates in the water layer of 4–10 m in August 2012 and in the lower horizons in July 2011 (Fig. 4), probably due to the more intense bloom of cyanobacteria and their concentration near the surface during this period. With all the diversity of the ciliate distribution over the horizons at different times of the day on working days, the maximum abundance was recorded in the evening (8 p.m.) in the water layer of 2–4 m, and on weekends, in the afternoon (2 p.m.) on the surface (Fig. 4).

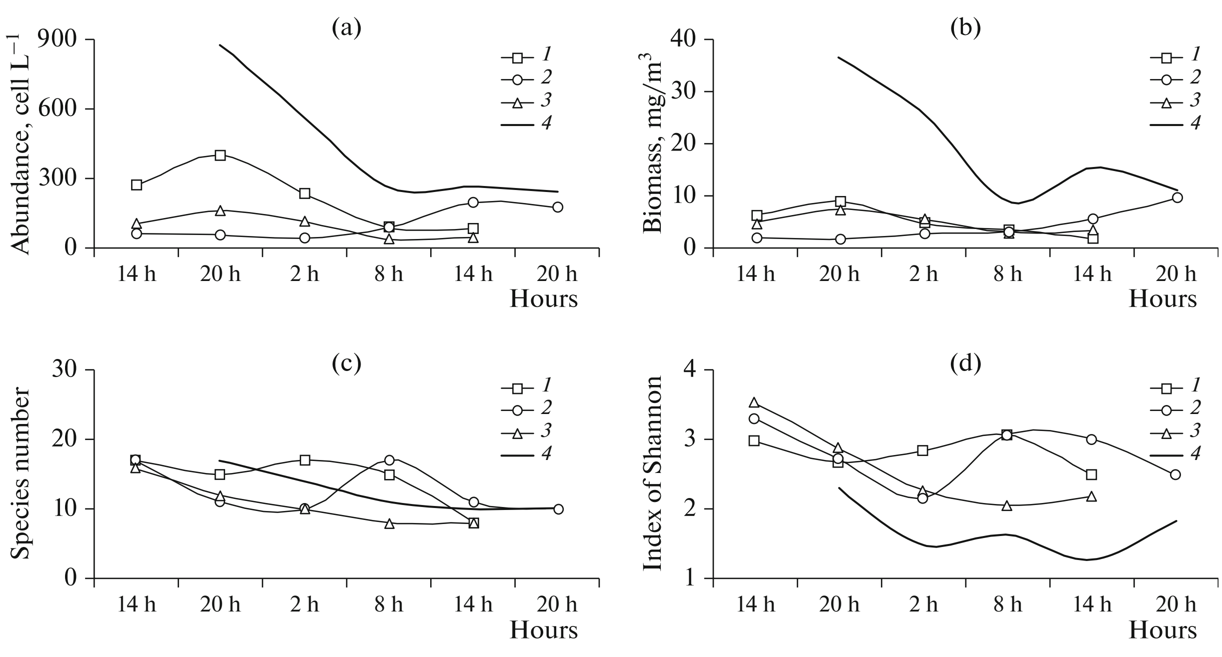

Fig. 3. Hourly change in the average water column abundance (a), biomass (b), species richness (c) and species diversity (d) of ciliates on all days of the week of August 23–28, 2012 (*1–3*) and July 19–20, 2011 (*4*): (*1*) Thursday–Friday, (*2*) Saturday–Sunday, (*3*) Monday–Tuesday, (*4*) Tuesday–Wednesday.

Table 2. Role of the main structure-forming ciliate species in several water layers over the entire study period

Species	Frequency of occurrence, %			Abundance, cells L^{-1}			Contribution to the total abundance, %		
	Layers, m								
	0–4	4–10	>10	0–4	4–10	>10	0–4	4–10	>10
Askenasia volvox (Eichwald, 1852)	14	14	3	1	1	0	0.3	0.5	0.1
Balanion planctonicum (Foissner, Oleksiv et Müller, 1990)	24	22	22	10	7	2	3.0	3.7	1.3
Epistylis procumbens Zacharias, 1897	30	24	14	22	14	7	6.7	7.0	3.9
Limnostrombidium viride (Stein, 1867)	22	32	38	3	4	6	0.9	2.3	3.3
Pelagostrombidium mirabile (Penard, 1916)	20	17	22	2	2	2	0.8	0.9	1.2
Rimostrombidium lacustris (Foissner, Skogstad & Pratt, 1988)	88	79	76	25	16	20	7.9	8.0	11.8
Rimostrombidium spp.	86	76	81	45	41	46	14.0	20.6	27.1
Tintinnopsis cylindrata Kof. & Cam., 1892	76	71	54	30	18	17	9.2	9.4	10.1
Urotricha spp.	38	36	38	6	9	8	1.8	4.5	4.6
Vorticella spp.	92	82	84	153	71	52	47.6	35.9	30.5
Hypotricha spp.	52	35	24	10	3	2	3.2	1.7	1.1

Rimostrombidium spp. = *R. humile* (Penard, 1922) + *R. hyalinum* (Mirabdulaev, 1985); *Urotricha* spp. = *U. farcta* Clap. et Lachmann, 1859 + *U. furcata* Schewiakoff, 1892.

Vertical distribution of species and particular groups of species. There is no clear preference or confinement of species to certain layers, as is characteristic of stratified water bodies. The preference for certain layers is due to the biological parameters of the species (peritrichs on the cenobia of algae), avoidance of "blooming spots," etc. With a few exceptions, the frequency of the most common species, *Vorticella* sp. on the coenobia of algae, the small *Rimostrombidium* spp., and the large *Rimostrombidium lacustris* and *T. cylindrata*, was above 75% in all distinguished zones (0–2 m, 4–10 m, and below 10 m) and decreased slightly toward the bottom (Table 2). In general, the species are present in the entire water column under the conditions of homothermy. A greater preference for the surface (0–2 m) and medium (4–10 m) layers in terms of the contribution of ciliates to the total abundance is typical for the species *E. procumbens*, *Balanion planctonicum*, *Vorticella* sp., *Askenasia volvox*, and hypotrich. The increase in the contribution of species belonging to the genera *Rimostrombidium*, *Limnostrombidium*, *Pelagostrombidium*, and *Urotricha* to the lower layers is rather surprising (Table 2).

As for the change in the distribution of certain species at different times of the day, only *R. lacustris* showed a more or less clear distribution: during the daytime it concentrated in the surface and near-surface horizons, and at night, it was in the near bottom horizons. Other choreotrichs concentrated near the surface mostly by 8 p.m. (Fig. 5). The vertical displacement of the peaks of the abundance of urotrichs (order Prorodontida) during the day may slightly resemble migrations: during the day they concentrated near the surface and in the middle layers at a depth of 5 m, and at night, at a depth of 10 m or more (Fig. 5). Tintinnids were more or less evenly distributed in the water column in the evening and at night, and by the morning on weekdays their abundance had decreased; at night and in the morning on the weekends, they were absent in the water column, and in the afternoon they concentrated near the surface, and in the evening, near the bottom.

The complete absence of a species in the water column for some time may indicate either its low abundance (trace amounts) with a sufficiently uneven distribution, or synchronous cyst formation (which is unlikely), or a sharp change in water masses, etc.

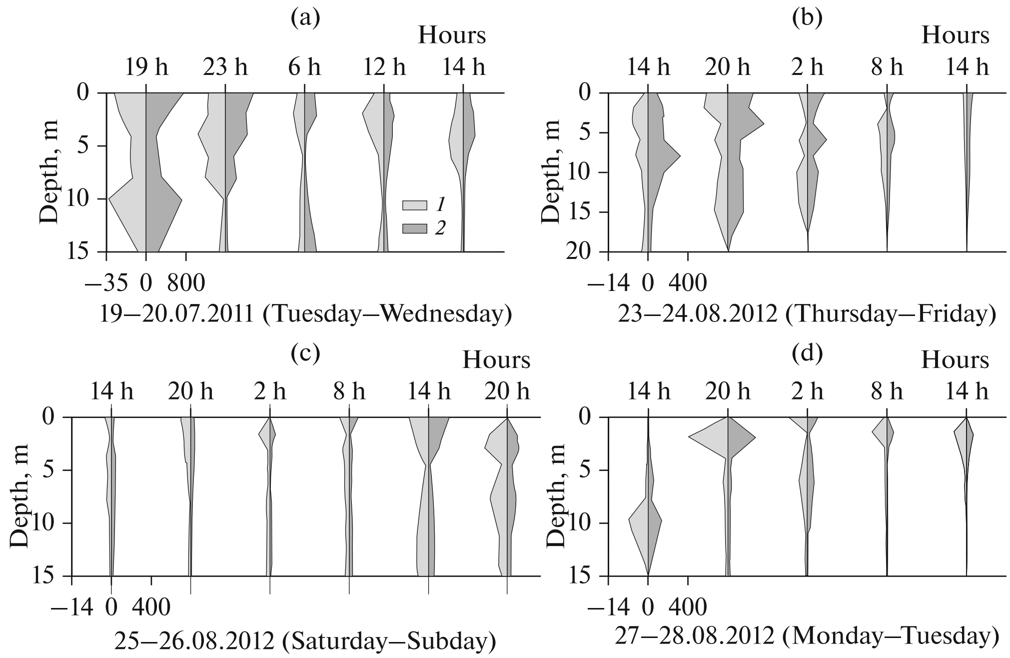

Fig. 4. Vertical distribution of the abundance and biomass of ciliates in July 2011 (a) and August 2012 (b–d): (*1*) abundance, *N*, cells L^{-1}; (*2*) biomass, *B*, mg m^{-3}.

DISCUSSION

There are numerous speculations about particular patterns of the vertical distribution of hydrobionts in water bodies and their causes. It is considered that the vertical distribution, for example, of zooplankton as a whole is “the result of active and passive migrations of animals, which are adaptations to the heterogeneity of distribution and dynamic changes in abiotic and biotic environmental factors” (Drobotov, 2014). Light and temperature as factors directly regulating the abundance of phytoplankton, the first link in the food chain, and indirectly, the abundance of zooplankton play an important role in these migrations. Since these factors are subject to seasonal and diel rhythms, the vertical migrations of hydrobionts are also characterized by periodicity (Kiprushina, 2009). The distribution of phototrophic protists (dinoflagellates, phototrophic ciliates *Mesodinium rubrum*) and the factors regulating their migration behavior are associated with the light and feeding conditions, but the final reason for this strategy is not clear (Olli et al., 1998; Fennel et al., 2006; Jephson, 2012).

It is shown that ciliates in Lake Baikal (Obolkina, 2015) concentrate at a depth of 20–25 m during the daytime on sunny days in spring, and in the near-surface layers (0–1, 0–5 m) at night and in the early morning hours. In the opinion of L.A. Obolkina, (2015, p. 88), the distribution of ciliates during this period is associated “with water mixing and reflects different stages of spring plankton settling.” During the ice period, accumulations of ciliates in the daytime are often found in the surface water layer, and light and hydrodynamics are the main factor regulating their distribution; temperature probably does not play a special role (Eggert, 1973; Obolkina, 2015). V.M. Kaplin (1970) considered that nutrition and hydrodynamics play a decisive role in the distribution of ciliates. It has been suggested (Eggert, 1973) that the diurnal vertical migrations of ciliates are passive under the effect of diurnal convection and horizontal currents. The vertical distribution of ciliates in Lake Sevan is characterized by the avoidance of the surface water layer (0–3 m) by ciliates during daytime hours, which is due to the negative impact of UV rays under conditions of high water transparency in a high-altitude water body (Zharikov, 2010). In stratified lakes with a higher trophic status (than Lakes Baikal and Sevan), ciliates occupy such a layer in the water column of the reservoir that meets the ecological requirements of the species in terms of temperature, gas regime, nutrient level, and the possibility to shelter from predators (Zingel, 2005; Fennel, 2012; Bykova, 2015).

The studies concerning possible mechanisms by which the nonrandom distribution of planktonic ciliates in the water column is maintained are not available in the literature, with a few exceptions (Jonsson, 1989). For example, tintinnids in marine systems often accumulate close to the surface (Agamaliev, 1983; Jonsson, 1989; Paranjape, 2011; Feng et al., 2014). Jonsson (1989) suggested that gravity is the ultimate

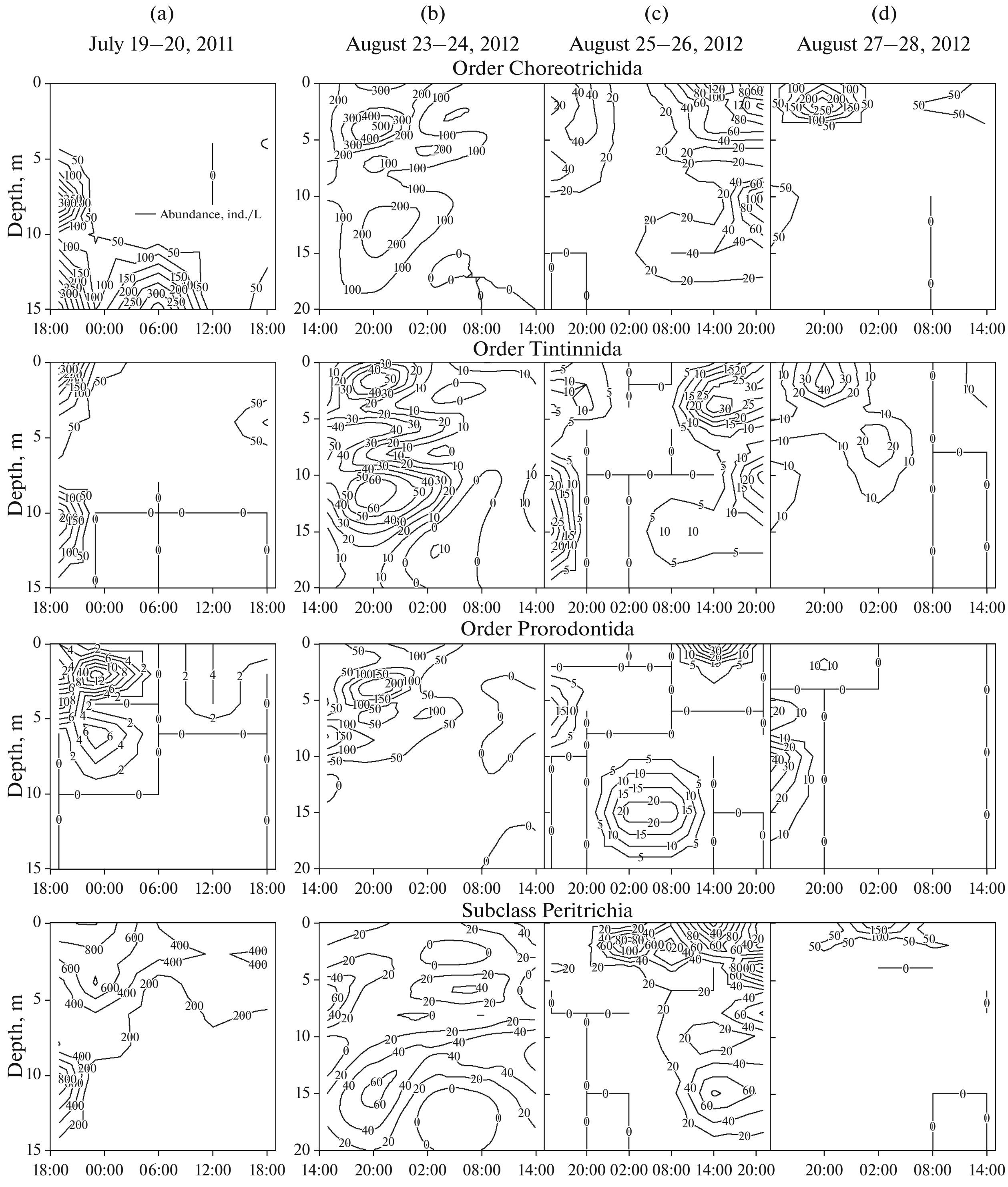

Fig. 5. Changes in the diurnal vertical distribution of the abundance of certain ciliate taxa on all days of the week: (a) July 20, 2011; (b–d), August 23–28, 2012.

cause for directed swimming of ciliates towards the surface. At the same time, negative geotaxis (upward swimming) results from interactions between the sinking velocity of the organism, swimming velocity, tumbling and jumping rates, body shape, or density asymmetry of the cell, etc. Thus, the distribution of ciliates in the water column is the resulting value of the vertical swimming and sinking velocities and the turbulence

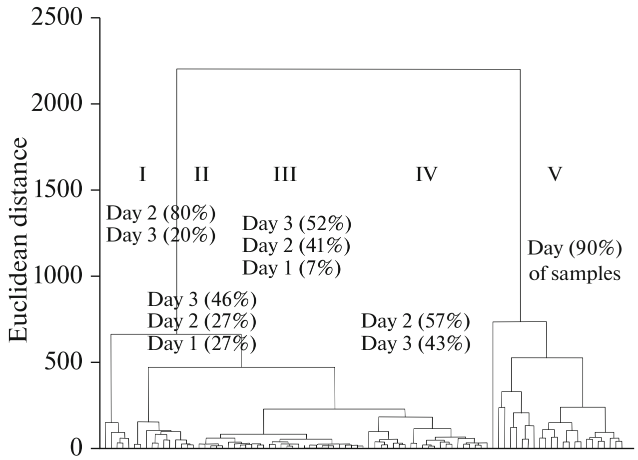

Fig 6. Clustering of data by the Ward method (I–V are cluster numbers). The percentage of samples in each cluster related to certain days is shown in parentheses

velocity (Jonsson, 1989). This is a rather important conclusion, since in the literature many authors do not take into account hydrological factors, which become of primary importance in the conditions of regulated rivers.

In the case of ciliates from the Kuibyshev Reservoir, data clustering using Ward's method showed a greater isolation of the community at the end of the working week (1st day, cluster V), while the communities of weekends (2nd day, clusters I and IV) and the beginning of the week (3rd day, clusters II and III) are combined into one cluster (Fig. 6), despite the fact that the communities developing on work days of the week were generally more similar in terms of the species composition (by 71% according to the Sorensen coefficient).

The isolation of the ciliate community at the end of the work week is probably explained by the smaller amplitude of fluctuations in water discharge and, accordingly, the water level on these days (Fig. 2a). Of course, the conclusions made based on the data obtained in different periods (hydrological in July 2011, and hydrobiological in August 2012) are not quite correct; nevertheless, they make it possible to suggest a reason why the abundance on the first day (Thursday–Friday) is significantly (twice) higher (Table 1, Fig. 6). At the same time, the biomass changes slightly (Table 1) due to the fact that small *R. hyalinum* is replaced by large *R. lacustris* in the dominant complex. The reasons for replacement are not clear, but it can be assumed that this is due to the adaptive advantages of larger species as strong swimmers, able to withstand stronger hydrological disturbances at the beginning of the work week. According to some coinciding hydrological and hydrobiological data of 2012, a significant positive correlation was found between the specific number of ciliate species and the water level in the upstream reach ($r = 0.84$, at $p < 0.05$) and the abundance of ciliates and the total inflow of water (respectively $r = 0.75$ and $r = 0.73$, at a lower level of significance $p < 0.1$). Thus, the weekly regulation of the HPP operation obviously affects the functioning of the ciliate community. The effect of the diurnal cycle of the HPP operation is manifested in the fact that the abundance and biomass increase and the species diversity decreases, as a rule, by 8 p.m. The hydrological features of the reservoir regime affect the abundance of ciliates and, indirectly, through other hydrobionts, for example, cyanobacteria, the mass development of which negatively affects the ciliates and the distribution of which directly depends not only on wind-induced mixing, but also on the turbulence, flow velocity, inflow and water discharge, etc. Thus, the mass accumulation of cyanobacteria in calm conditions caused a sharp decrease in the development of the ciliate community in the morning hours on the third day.

There are no clear patterns in the dynamics of the vertical distribution of ciliates at this stage of the study. A sharp decrease in the total abundance in all horizons, and not just its redistribution over layers during the day and, consequently, a decrease in the average abundance of ciliates in the water column during the studied period, may indicate both the replacement of the community with the waters inflowing from upstream and the insufficient sampling frequency (6 h, and not 4 h; every other day, and not consecutively without interruptions). The absence of a consistent and gradual change in the abundance of certain species/taxa (up to the absence of a species in the water column for some time) (Fig. 5) probably also indicates that their distribution is not the result of vertical migrations, but rather the result of passive transport with water masses. Thus, since the data obtained raise more questions than they give answers, and many conclusions remain at the level of assumptions, the study of the vertical distribution of ciliates in conditions of the reservoir will be necessarily continued. At the same time, in the future, it is necessary to have accurate hydrological data (discharge and water level, water flow velocity at different horizons, etc.), synchronous in time with the collection of hydrobiological samples. Despite the great labor intensity of studies of the dynamics of the vertical distribution of ciliates by hours and days, it probably makes sense to conduct continuous sampling of the material during the entire weekly cycle of the HPP operation.

CONCLUSIONS

The difference shown in the development of ciliate communities on working days and weekends is probably enough to come to a conclusion about the significant, if not decisive, impact of hydrological factors on hydrobionts in the reservoir. The effect of weekly–daily regulation of the HPP operating mode is manifested, in particular, in the fact that the maximum abundance of ciliates on working days is recorded in the evening, and on weekends, in the afternoon. In addition, a decrease in the total inflow and amplitude of fluctuations in the water level and water discharge at the end of the working week probably contributes to the formation of higher average abundance and biomass of ciliates at this time.

It is still early to reach a conclusion about clear and unambiguous patterns of the vertical distribution of ciliates associated with HPP discharges, biological migrations, "turbulent transport," etc.

Nevertheless, the recorded relatively low average abundance and biomass of ciliates in the water column of the reservoir compared to lakes are probably due to the unstable hydrological regime.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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