Spatial distribution of planktonic ciliates in autumn at the Priplotinny Reach of the Kuibyshev Reservoir, the Volga River, Russia

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Abstract. Spatial distribution of planktonic ciliates at the Priplotinny Reach of the Kuibyshev Reservoir (The Volga River, Russia), including the Usinsky Bay, was studied in detail at a vast station grid in the early-autumn period. The species diversity, species richness, abundance, biomass, and production of ciliates at the Priplotinny Reach were quite low, in contrast to those at the Usinsky Bay. At the Priplotinny Reach, the number of species per sample ranged as 3-23 species, abundance, as 18-356 cells L⁻¹, and biomass, as 0.13-17.94 μg L⁻¹. In the Usinsky Bay, these parameters were 17-38 species, 360-2284 cells L⁻¹, and 5.2-61.4 μg L⁻¹, respectively. Despite relative homogeneity of the hydrophysical conditions at the reach, a high variability in the quantitative characteristics of ciliate community was observed, probably due to local hydrological conditions. On the one hand, the peaks in the ciliates abundance coincided with the period of decrease of the water inflow, i.e., they were associated with the operating mode of hydroelectric power station, and on the other hand, they were caused by the direct influence of water masses of a large tributary. The structural organization of the ciliate community, in contrast to the general quantitative characteristics, was determined by local environment. An increasing role of bacteriovorous and histophagous ciliates was recorded in that areas characterized by high level of organic matter, particularly, in the area of conditional wastewater discharge, bridge construction, and tributary confluence. In general, the distribution of plankton ciliates at the Priplotinny Reach of the Kuibyshev Reservoir was largely influenced by the Usa River, which affected the redistribution of quantitative characteristics of the ciliate communities between the deep-water and shallow-water zones of the reach.

1. Introduction
The upstream zones of dams of hydroelectric power stations in water reservoirs differ from other areas by a number of hydrological and hydrophysical characteristics, by the degree of influence on their water area and coastal zone from waterworks. The Kuibyshev Reservoir is the largest valley reservoir both in the Volga-Kama Cascade and in Europe [1]; the Priplotinny Reach is one of its lake-like extensions. Unlike other sites of reservoir, it has a relatively small area (398 m²), a significant volume of water (6.8 km³), great depths (down to 32 m), and a maximum water retention [2-4]. These features of the Priplotinny Reach cause a later warming up in spring and slow cooling in autumn. Water transparency here is usually higher than in the upper reaches of the reservoir [3]. Silts, rich in organic matter, accumulate here more intensively. At the Priplotinny Reach, the depth increases evenly from the left low flat bank to the higher right bank as at most lake-like extensions of the Kuibyshev...
Reservoir. This is also reflected in the flow rates: they are noticeably lower along the left bank on the flooded floodplain, compared to the deep-water part on the flooded riverbed. In addition, reverse currents (5-6 cm/s) are observed here [3]. The operation cycle of hydroelectric power station (HPS) has the greatest impact on water level fluctuations particularly at the Priplotinny Reach, when the range of water level fluctuation upstream of the dam may reach 25-35 cm during the day, increasing during a storm to 50-60 cm, which is significantly higher than that observed in the reaches located upstream [3]. In addition, wave effect is quite pronounced during the water discharge from hydroelectric power station, leading to even more frequent water level fluctuations in shallow water zone (by 10-50 cm) with a periodicity of 15-60 minutes [5]. These water discharge events lead also to the destruction of the banks at a distance of more than 10 km up from the waterworks [5]. The vibrational (microseismic) impact of a hydroelectric power station also causes destruction of coastal hillsides, being another important factor that has not been studied previously [6]. A large industrial center of Toglyatti, health camps, yacht clubs, a river port, a channel for dumping conditionally clean and storm drains on the left bank, etc. are located along the shores. In the area of Klimovsky narrowness, construction of a bridge crossing has been underway since 2019. On the right bank, the Priplotinny Reach is characterized by numerous large and small bays in ravine and river valleys: the Usa River mouth, bays in the area of the Abalonnev ravine, the villages of Zhiguli, Usolye, etc. The Usinsky Bay, formed as a result of the reservoir water retention and stretching for almost 70 km, is defined by some researchers as a separate area [1, 7], while others consider it as part of the Priplotinny Reach [8, 9]. The unique biocenoses of the Zhiguli Mountains on the right bank of the Kuibyshev Reservoir suffer due to the operation of the Zhigulevsky cement plant. Thus, the Priplotinny Reach of the Kuibyshev Reservoir, like no other area, is influenced by a huge variety of natural and anthropogenic factors.

A systematic studies of biological and environmental parameters of the area have been carried out since the establishment of the Kuibyshev Biological Station at the Volga River. During the first years, these were regular expeditions covering entire reservoir, but the sampling in the Priplotinny Reach was performed monthly only at two standard stations for a long time (1965-1984); later, seven floodplain micro-polygons have been studied [4, 7, 10]. In 1989-1991, observations were carried out every ten days at the station located opposite the IEVB RAS in addition to the standard stations. At the Priplotinny reach, hydrochemistry, hydrology, and bottom sediments were studied at a more vast grid of stations (15-16 stations) [9, 11]. However, in general, the detailed studies, aimed on assessing heterogeneity of the environment and its effect on aquatic communities, are rare [12]. Studies of ciliates, an ecologically important group of Protozoa, as are generally rare. Except random expeditions in different years [13], systematic studies of the Kuibyshev Reservoir in general and the Priplotinny Reach in particular started only at mid-1980s. Within the framework of the expeditions of the Institute of Ecology of the Volga River Basin of the Russian Academy of Sciences performed at the Kuibyshev Reservoir, ciliates were studied monthly (from May to October) in 1988-1989 and for three hydrological seasons (May, July, September) in 1990 and 1992 [14]. After a considerable period of break of these studies, the research has been renewed in certain months of 2009 and 2010 [15, 16], and later, during the “transit” expeditions of the I.D. Papanin Institute for Biology of Inland Waters of the Russian Academy of Sciences along the Volga River in 2016-2019 [17]. However, the samples for studying ciliates were taken only at one or two stations; a detailed study of the spatial distribution of ciliates in the Priplotinny Reach was not carried out.

The study aims to analyze spatial distribution of ciliates and the degree of the community heterogeneity across the entire Priplotinny Reach, including the Usinsky Bay, taking into account the morphometric, morphological, hydrological and other environmental parameters; and to assess the influence of natural and anthropogenic factors, such as large industrial center, the construction of a bridge, a cement plant, the mouth of a large tributary, the mode of operation of hydroelectric power stations, etc., on the distribution of planktonic ciliates.
2. Materials and Methods
The planktonic ciliate communities were studied at 21 stations at the Priplotinny Reach water area from September 17 to October 3, 2020 and at 6 stations in the Usinsky Bay on October 6, 2020 (figure 1). The water was sampled with a Dyachenko’s bathometer simultaneously with the sampling for hydrophysical and hydrochemical parameters. Integrated samples were analyzed for the Priplotinny Reach, and the samples obtained from surface water layer, for the Usinsky Bay. Integrated sample was obtained by combining the same volumes of water from different water layers in one bottle. Samples were taken every 1 m from the surface down to a 5-m-depth, then every 2.5 m down to a 10-m depth, and every 5 m down to the bottom. The volume of the combined sample was 250-500 mL, depending on the abundance of ciliates and the amount of the suspended matter. The ciliates were counted on the slides glass after preliminary concentration by gravity of the sample on the membrane filters and fixation with mercury (II) chloride. Species were defined out both on slides glass and alive. The taxonomy is given according to the system proposed by E. Small and D. Lynn [18]. The trophic groups corresponded to [19], with some modifications, when mixotrophs ("phototrophs", according to [19]) were not considered as a trophic group, but as a special ecological group of ciliates with different trophic preferences. Species diversity was evaluated using standard (Shannon’s and Pielou’s) indices.

When analyzing the data obtained, we combined the stations into the following groups: (a) stations located along the left bank of the Priplotinny Reach on a flooded floodplain; (b) on a flooded riverbed; (c) along the right bank, and (d) in the Usinsky Bay (table 1, figure 1). In this paper, we adopt a zoning scheme, where the Usinsky Bay is part of the Priplotinny Reach [8], but when we compare and average the data, the Priplotinny Reach ("Reach", except the bay) and the Usinsky Bay ("Bay") are considered. When analyzing the ciliate communities along the longitudinal axis of reservoir, the data was averaged for six transects: transect I – stations nos. B3, B6, B7, H7; transect II – stations nos. 2-4, 6, 39; transect III – stations nos. 1, 5, 7; transect IV – stations nos. 8, 10, 11, 12, 34; transect V – stations nos. 13, 14; transect VI – stations nos. 15, 16 (figure 1).

3. Results and Discussion

3.1. Abiotic conditions of the study area
The studies were carried out during the beginning of the autumn cooling, when the water temperature dropped to 15 °C; homothermy was observed in the entire water column (table 1). Probably, due to the large volume of water, the water cooling here was slower than at other reaches, so Cyanobacteria bloom lasted almost until October at the Priplotinny Reach, which affected the development of other aquatic organisms. In the first half of the sampling period, the weather was rainy and windy; Cyanobacteria were evenly distributed in the water column. On the contrary, in the second half of the study period, it was sunny and often calm, so the "blooming spots" were concentrated near the water surface. In general, the ranges of some abiotic parameters in the water area of the entire reach (CV, %) are small (table 1), this indicates relatively homogeneous conditions for aquatic organisms in terms of temperature and pH. The waters of the Usinsky Bay differed only in their lower water transparency.

3.2. Species composition, taxonomic and species diversity
During the study period, about 70 species were identified at the Priplotinny Reach (including the Usinsky Bay): 53 species in the water area of the reach, and 49 species, in the Usinsky Bay. The similarity of the ciliate fauna of the reach and the bay was 66%. Taxonomic diversity was higher at the Priplotinny Reach: the species composition was represented by a large number of taxa (7 classes), compared to that in the Usinsky Bay (5 classes) (table 2). The ciliates belonging to species-rich taxa were similar at the Reach and in the Bay, these were three classes (Spirotrichea, Litostomatea, and Oligohymenophorea) characterized by the greatest number of species. However, the functional role of representatives of the same classes at the Reach and in the Bay was different. Thus, Spirotrichea clade dominated in the ciliates community of the Reach, followed by Prostomatea clade; in the Bay, these were representatives of Oligohymenophorea (dominated also by biomass) (table 2).
Table 1. Characteristics of sampling stations in the Priplotinny Reach of the Kuibyshev Reservoir in autumn 2020

| Zone                  | Station no. | Parameter      | Depth, m | Water surface temperature, °C | Near-bottom temperature, °C | Transparency, m | pH  |
|-----------------------|-------------|----------------|----------|------------------------------|-----------------------------|-----------------|-----|
| Left bank on a flooded | B6, B7, H7, | min-max        | 9.6      | 15.4                         | 15                          | 3.11            | 8.42|
| floodplain            | 1, 2        | mean           | 6.0-16   | 14.7-16.2                    | 14.5-16.0                   | 2.10-4.30       | 8.24-9.55|
| Flooded riverbed      | B3, 3, 11,  | min-max        | 15.2     | 15.4                         | 15.3                        | 3.35            | 8.37|
|                       | 34, 14      | mean           | 6.32     | 15.0-16.1                    | 15.3-16.2                   | 3.10-3.60       | 8.27-8.47|
| Right bank            | 4, 5, 12    | min-max        | 15.5-15.8| 15.3-15.8                    | 2.80-3.20                   | 8.30-8.47       |     |
| Priplotinny Reach     | All, except | mean           | 53.8     | 3.0                          | 3.5                         | 14.5            | 1.1 |
|                       | Y1-Y6       | min-max        | 7.0-16   | 15.7-15.8                    | -                           | 2.10-2.70       | 8.38-8.53|
|                       | CV, % a     |                | 29.8     | 0.3                          | -                           | 8.4             | 0.6 |

*Here and in table 4, CV is coefficient of variation

Table 2. Taxonomic structure of the ciliate communities of the Priplotinny Reach and the Usinsky Bay according to the number of species (n, %), abundance (N, %), and biomass (B, %)

| Class              | Near-dam zone (Priplotinny Reach) | Usinsky Bay |
|--------------------|----------------------------------|-------------|
|                    | n  | N % | B   | n  | N % | B   |
| Nassophorea        | 1.4 | 0.04 | 0.03 | 0  | 0   | 0   |
| Heterotrichea      | 2.8 | 0.05 | 1.7  | 0  | 0   | 0   |
| Litostomatea       | 21.1| 8.9  | 28.5 | 26.8 | 11.6 | 29.6 |
| Oligohymenophorea  | 21.1| 3.5  | 12.7 | 17.9 | 27.9 | 39.8 |
| Philopharyngea     | 4.2 | 0.3  | 0.1  | 5.4 | 0.9 | 0.3 |
| Prostomatea        | 18.3| 22.4 | 6.2  | 14.3 | 17.3 | 11.7 |
| Spirotrichae       | **31.0**| **64.8** | **50.7** | **35.7** | **42.3** | **18.6** |

Despite approximately the same number of species in the combined list of ciliates of the Reach and the Bay, the average number of species in the samples from the Usinsky Bay was higher (25 vs. 10). The average value of the Shannon index (α-diversity, H) in the Usinsky Bay was also higher (3.17 in the bay versus 2.54 at the Reach) by abundance and 2.43 versus 1.74 by biomass, respectively. This may be partly explained by the constant mixing of the water masses of the reservoir and the river, which led to an increased diversity at the border area. However, the β-diversity of the ciliate community at the Reach (total area) was higher (H = 4.16) than that in the Bay (H = 3.54). This was probably due to the larger area of the Reach and its greater spatial heterogeneity associated with the diversity of local environmental conditions. The basis of the abundance and biomass of ciliates at the Reach and in the Bay communities was formed by the species presented in table 3.

During the study period, Tintinnopsis cylindrata, Rimostrombidium hyalinum, and R. lacustris (frequency of occurrence of 90%, 86%, and 57%, respectively) were recorded most often at the Reach; in the Bay, in addition, these were Histiothalantium bodamicum, Tintinnidium flaviatile (Stein, 1863), and small urotrichs (table 3). Limnostrombidium pelagicum and Pelagostrombidium mirabile, usually common in summer, were found in only one or two samples (frequency of occurrence was 5-10%), and P. fallax, rare in summer, was recorded in every fourth sample (24%). About 20 species (Placus luciae, Leptopharinx costatus, Sphaerophrya sp. Staurophrya elegans and others) were recorded only once at the Priplotinny Reach. A rather rare Tintinnidium ephemeridum was an interesting finding in the Usinsky Bay. T. cylindrata dominated absolutely by abundance both at the Reach and in the Bay, followed by Rimostrombidium lacustris and R. hyalinum (at the Reach) and H. bodamicum and Coleps hirtus viridis (in the Bay). R. lacustris and Paradileptus conicus dominated by biomass at the Reach,
Pelagodileptus trachelioides and Stokesia vernalis, in the Bay (table 3). It should be noted that dominance of H. bodamicum has been observed in the Kuibyshev Reservoir for the first time.

Table 3. Major structure-forming species at the Priplottinny Reach and in the Usinsky Bay, September 17—October 7, 2020; the species are arranged by the density index \(\sqrt{NB}\) in descending order

| Species | Abundance (cells L\(^{-1}\)) | Biomass (mg m\(^{-3}\)) | Abundance (%) | Biomass (%) | Frequency of occurrence (%) |
|---------|-------------------------------|--------------------------|---------------|-------------|----------------------------|
| **Near-dam (except Usinsky Bay)** |                               |                          |               |             |                            |
| Rimostrombidium lacustris (Foissner, Skogstad et Pratt, 1988) | 11.5 | 1.43 | 12.0 | 43.8 | 57 |
| Tintinnopsis cylindrata Kof. & Cam., 1892 | 32.6 | 0.09 | 34.0 | 2.7 | 90 |
| Vorticella sp. (<25 μm) | 4.3 | 0.30 | 4.5 | 9.3 | 48 |
| Paradileptus conicus Wenrich, 1929 | 2.8 | 0.37 | 2.9 | 11.2 | 43 |
| Rimostrombidium hyalinum (Mirabdullaev, 1985) | 11.4 | 0.05 | 11.9 | 1.5 | 86 |
| Urotricha venatrix Kahl, 1935 | 0.7 | 0.16 | 0.7 | 5.0 | 24 |
| Pelagodileptus tracheliole (Zacharias, 1894) | 0.3 | 0.26 | 0.3 | 8.1 | 10 |
| Tintinnidium fluviatile (Stein, 1863) | 2.4 | 0.03 | 2.5 | 0.9 | 33 |
| Pelagostrombidium fallax (Zach., 1895) | 0.8 | 0.07 | 0.8 | 2.2 | 24 |
| Urotricha spp. (U. furcata Clap. & Lachmann, 1859+ U. furcata) | 3.6 | 0.01 | 3.7 | 0.4 | 48 |
| Schewiakoff, 1893) | 1.7 | 0.02 | 1.8 | 0.6 | 33 |
| Hypotrichia spp. | 1.4 | 0.02 | 1.5 | 0.7 | 33 |
| Stokesia vernalis Wenrich, 1929 | 0.2 | 0.05 | 0.2 | 1.5 | 10 |
| Codonella cratera (Leidy, 1887) | 1.2 | 0.02 | 1.3 | 0.6 | 14 |
| Rimostrombidium humile (Penard, 1922) | 2.1 | 0.01 | 2.2 | 0.3 | 29 |
| Histiobalantium bodamicum Krainer et Muller, 1995 | 1.0 | 0.02 | 1.1 | 0.5 | 24 |
| Uronema sp. | 2.0 | 0.01 | 2.1 | 0.2 | 19 |
| Vorticella sp. (<25 μm) | 1.3 | 0.01 | 1.4 | 0.2 | 29 |
| Balanion planctonicum (Foissner, Oleksiv & Müller, 1990) | 2.3 | 0.00 | 2.4 | 0.1 | 38 |
| **Usinsky Bay** |                               |                          |               |             |                            |
| Histiobalantium bodamicum Krainer et Muller, 1995 | 218 | 3.51 | 24.7 | 10.7 | 100 |
| Tintinnopsis cylindrata Kof. & Cam., 1892 | 241 | 0.77 | 27.3 | 2.3 | 100 |
| Coleps hirtus viridis Ehrenberg, 1831 | 116 | 1.50 | 13.1 | 4.6 | 83 |
| Pelagodileptus tracheliole (Zacharias, 1894) | 13 | 12.33 | 1.5 | 37.6 | 50 |
| Paradileptus conicus Wenrich, 1929 | 16 | 2.12 | 1.9 | 6.5 | 83 |
| Stokesia vernalis Wenrich, 1929 | 5 | 4.42 | 0.6 | 13.5 | 33 |
| Rimostrombidium lacustris (Foissner, Skogstad et Pratt, 1988) | 13 | 1.65 | 1.5 | 5.0 | 83 |
| Tintinnidium fluviatile (Stein, 1863) | 43 | 0.51 | 4.9 | 1.5 | 100 |
| Urotricha venatrix Kahl, 1935 | 9 | 2.10 | 1.0 | 6.4 | 50 |
| Limnostrombidium pelagicum (Kahl, 1932) | 31 | 0.51 | 3.5 | 1.6 | 100 |
| Urotricha pelagica Kahl, 1935 | 14 | 0.33 | 1.6 | 1.0 | 83 |
| Enchelys simplex Kahl, 1926 | 6 | 0.57 | 0.6 | 1.7 | 67 |
| Askensia volvox (Eichwald, 1852) | 14 | 0.19 | 1.5 | 0.6 | 100 |
| Monodinium chlorelligerum Krier, 1995 | 9 | 0.21 | 1.0 | 0.7 | 83 |
| Tintinnidium fluviatile f. minima Mamaev, 1979 | 22 | 0.03 | 2.5 | 0.1 | 100 |
| Rimostrombidium hyalinum (Mirabdullaev, 1985) | 13 | 0.05 | 1.5 | 0.2 | 83 |
| Urotricha spp. (U. furcata Clap. & Lachmann, 1859+ U. furcata) | 11 | 0.04 | 1.2 | 0.1 | 100 |
| Schewiakoff, 1893) | 10 | 0.08 | 1.2 | 0.2 | 50 |

3.3 Spatial heterogeneity of quantitative characteristics of the ciliate communities

Generally, during the study period, the abundance of ciliates at the Priplottinny Reach was quite low in contrast to that in the Usinsky Bay (table 4). However, the species richness, abundance, and biomass almost fell within the long-term range, except the year of 2017 (table 5). This particular year was characterized by an increased inflow (especially in the summer low water) [20], as a result, the bloom
was reduced; in turn, this led to high abundance and biomass of ciliates at the compared stations. According to some authors [13, 14], the abundance, biomass, and production of planktonic ciliates usually decrease in the Kuibyshev Reservoir from its upstream reaches downstream to the dam. That is why the development of ciliates in the Priplotinny Reach is very low. However, according to the same data [13], these differences disappear in autumn.

### Table 4. Communities of planktonic ciliates of the Priplotinny Reach and the Usinsky Bay, the Kuibyshev Reservoir, on September 17—October 7, 2020

| Area                      | Parametersa | n   | H     | N     | B       | P       | P/B    | W       |
|---------------------------|-------------|-----|-------|-------|---------|---------|--------|---------|
| Priplotinny Reach         | mean        | 10  | 2.58  | 96    | 3.05    | 1.21    | 0.47   | 0.032   |
|                           | min-max     | 3-23| 1.44-3.95 | 18-356 | 0.2-18.0 | 0.1-6.5 | 0.29-0.79 | 0.005-0.100 |
|                           | CV, %       | 59  | 27    | 96    | 130     | 120     | 31     | 74      |
| Usinsky Bay               | mean        | 25  | 3.17  | 883   | 32.82   | 12.15   | 0.40   | 0.044   |
|                           | min-max     | 17-38| 2.69-3.52 | 360-2284 | 5.2-64.0 | 3.1-22.7 | 0.28-0.60 | 0.014-0.105 |
|                           | CV, %       | 32  | 10    | 84    | 66      | 64      | 29     | 74      |
| Reach + Bay               | mean        | 14  | 2.71  | 271   | 9.66    | 3.64    | 0.45   | 0.034   |
|                           | min-max     | 3-38| 1.00-3.95 | 18-2284 | 0.16-64.0 | 0.12-22.7 | 0.28-0.79 | 0.005-0.105 |
|                           | CV, %       | 66  | 25    | 175   | 167     | 162     | 31     | 74      |

*aAbbreviations: n – number of species per sample, H – Shannon index (by abundance), N – abundance (cells L⁻¹), B – biomass (mg m⁻³), P – production (mg m⁻³ day⁻¹), P/B – daily P/B-coefficient, W – average cell weight (µg)

### Table 5. Comparative characteristics of the ciliate communities at two stations of the Priplotinny Reach (opposite the Usa River estuary and at the dam) in different years

| Year      | Month   | Number of species | Abundance (cells L⁻¹) | Biomass (mg m⁻³) | Reference |
|-----------|---------|-------------------|-----------------------|------------------|-----------|
| 1989      | June - Octobera | -                | 20-968               | 39               | [9]       |
| 2009      | Augustb  | 13                | 8-170                | -                | [16]      |
| 2010      | July     | 5-6               | 26-48                | 1.07-1.60        | [17]      |
| 2016      | June     | 23-35             | 554-628              | 28.6-86.1        |           |
| **2017**  | **August** | **23-26**        | **1060-1104**        | **44.4-57.9**    | **Our data** |
| 2018      | August   | 12                | 172                  | 2.9              |           |
| 2019      | August   | 6                 | 76-120               | 0.7-4.9          |           |
| 2020      | September-October | 13-23            | 112-356              | 3.9-5.6          |           |

a – average for the Priplotinny Reach

In contrast to the Usinsky Bay, a greater heterogeneity of the spatial distribution of the characteristics of the ciliate communities in the autumn period in the Priplotinny Reach is evidenced by the greater variability in the ciliate abundance, biomass, and production (coefficients of variation are 96-130%) (table 4), which are largely influenced by the volume of water inflow (figure 1).

If one compares the distribution of ciliates by defined zones, no unambiguous patterns in the formation of ciliate communities would be found, from the shallow left bank to the deep right bank. The ciliate abundance increases along this transect (table 6). Biomass and production are the highest in the central part, at the flooded riverbed of the Volga River, due to the development of a large active swimming ciliate Rimostrombidium lacustris (24% of the total abundance), able to withstand strong currents. Near the coast, smaller Tintinnopsis cylindrata dominates (28% and 47% of the total abundance). Accordingly, daily P/B-coefficient, which indicates the rate of production processes, is higher in the communities along both right and left banks (table 6). In general, low species richness, abundance, biomass, and production of ciliates near the left bank are probably due to unstable conditions in shallow waters during this period of the year. Shallow waters are more susceptible both to faster water cooling and to sharp difference of night and day air temperature. In addition, when the
water level is low in autumn, its fluctuations associated with the operation of hydroelectric power station are more pronounced here [3, 5, 6]. However, a greater variety of ecotopes in shallow waters along the left bank contributes to a higher β-diversity accompanied by low α-diversity in certain samples (tables 4, 6). The Shannon index was 4.07 for entire ciliate community along the left bank, while for the community of the old riverbed of the Volga River and along the right bank, it was 3.84 and 3.10, respectively.

Figure 1. Spatial distribution of abundance and biomass of ciliates at the Priplotinny Reach of the Kuibyshev Reservoir (including the Usinsky Bay) in September-October 2020

Table 6. Major characteristics of ciliate communities in different zones of the Priplotinny Reach; values outside the brackets indicate the mean, inside the brackets, the maximum

| Parameters                                      | Left bank | Flooded (old) riverbed | Right bank |
|------------------------------------------------|-----------|------------------------|------------|
| Number of species per sample                   | 9 (21)    | 10 (21)                | 11 (23)    |
| Shannon index (by abundance)                   | 2.57 (3.95) | 2.64 (3.33)          | 2.32 (3.28) |
| Shannon index (by biomass)                     | 1.63 (3.17) | 1.68 (2.43)          | 2.28 (3.20) |
| Abundance, cells L⁻¹                           | 71 (188)  | 104 (278)             | 147 (356)  |
| Biomass, mg m⁻³                                | 1.88 (5.77) | 5.14 (18.03)         | 2.55 (4.37) |
| Production, mg m⁻³                             | 0.74 (2.25) | 1.95 (6.52)          | 1.19 (2.06) |
| Daily P/B-coefficient                          | 0.48 (0.76) | 0.47 (0.78)          | 0.53 (0.79) |
| Average cell weight, μg                        | 0.024 (0.050) | 0.036 (0.065)      | 0.035 (0.100) |

When studying the spatial distribution of ciliates along the longitudinal axis of the reservoir, there was a decrease in the average for transects characteristics of species diversity and quantitative development of plankton ciliates towards the downstream along the reach, bellow the Klimovskaya narrowness to the middle of the reach (until the zone of conditionally clean drains), and their further increase due to the restructuring of the community under the influence of the Usa River (figure 2). This effect was evidenced by almost fourfold increase in the number of ciliate species per sample.
increased downstream the confluence of the Usa River; abundance has increased in 7.8 times, biomass, 6.3 times; this led to a redistribution of the quantitative characteristics of the ciliate communities between the deep and shallow parts of the reservoir (figure 1).

Upstream the confluence of the Usa River, abundance and biomass of ciliates at the stations located along the left bank of reach was higher than those along the right bank. On the contrary, downstream the confluence of the Usa River, in the channel of the deep-water part, the communities of ciliates were more abundant and diverse comparing to those along the left, shallower, bank (figure 1). There were also changes in the composition of the dominant complex under the influence of the Usa River: for example, there was a replacement of the third most important dominant (Tintinnidium fluviale, 12.5% of the total abundance) with Rimostrombidium hyalinum (9.1%). In general, the similarity of the ciliate fauna at the stations along the right bank of the reach upstream and downstream the confluence of the Usa River was only 35%. The basis of the trophic structure of the community remained almost unchanged: omnivorous ciliates (54% of the total abundance upstream the confluence and 51.5% downstream the confluence of the Usa River) and phytogrophes (38% and 34%, respectively) still dominated. However, the contribution of bacterio-detritivorous (from 4.2% to 8.3%) and predator (from 4.2% to 6.4%) ciliates increased as indicated in the brackets.

**Figure 2.** Dynamics of species richness and species diversity (left panel) and abundance and biomass of ciliates (right panel) along transects in the Priplotinny Reach

**3.4. Influence of the hydrological features of the Priplotinny Reach on the heterogeneity of the ciliates distribution**

Although there is a seemingly chaotic pattern of ciliate abundance at the reach, there is a dependence of this parameter on the hydrological conditions (figure 3). When the samples are arranged in chronological order, approximately equal peaks no. 1 and no. 3 (N = 188 cells L⁻¹ and N = 168 cells L⁻¹) are observed at stations nos. 39 and B7, which differ greatly in many parameters: by depth (15 m and 2 m, respectively), by location (near the shore and on the floodplain closer to the flooded riverbed), by the bloom degree (a powerful spot of cyanobacteria at station no. B7), by the impact of anthropogenic factors (station no. B7 locates near the bridge under construction), etc. However, they are similar by the sampling time (weekends), when the water flow is reduced, which is associated with the weekly operation mode of both the Zhigulevskaya HPS and other HPSs located upstream (figure 3). The abundance peaks nos. 2 and 4 were recorded at stations no. 12 (N = 356 cells L⁻¹) and no. 14 (N = 278 cells L⁻¹), located downstream the confluence of the Usa River, where the ciliate abundance was higher almost an order of magnitude. Thus, both operation mode of the Zhigulevskaya HPS and the volume of water inflow have a significant impact on the dynamics of the ciliate abundance in the HPS backwater.
3.5. Features of the structure of the ciliate communities of the Priplotinny Reach and the Usinsky Bay

In general, the ciliate communities of the Reach and the Bay differed significantly. This was evidenced by a significant role of histophagous *C. hirtus viridis* in the Usinsky Bay (36% by abundance, 13% by biomass), especially in its upstream part (station no. Y2). In addition, bacterio-detriforovorous ciliates contributed more to the total abundance and predator ciliates, to the total biomass, in the Bay, comparing to those at the Reach, due to the reduced role of herbivorous ciliates (figure 4c).

There are many ciliates carrying symbiotic algae (28% of the total number of species) in the ciliate community of the Usinsky Bay. These include large-size ciliates, such as *Pelagodileptus trachelioides* and *Stokesia vernalis*, and the aforementioned *C. hirtus viridis*, which is often found in the lakes along the boundary of oxygen and anoxic zones. The large predator *Pelagodileptus trachelioides* has been found in the estuarine zone (three stations, located in down course of the Bay). In the Volga-Kama Basin, they were often found in the areas of high turbulence [17], in particular, at the confluence of the Volga and Kama rivers (the Volga-Kama Reach) and in the locks of the Lenin Volga-Don Shipping Canal. Average share of mixotrophic ciliates in the Usinsky Bay was 18% by abundance and 60% by biomass, at the Priplotinny Reach, 3% and 17%, respectively. Such an increased contribution is often attributed either to favorable conditions or to a lack of oxygen. In our case, we cannot still provide an explanation for the increased role of mixotrophs in the Usa River.

The structure of the ciliate communities at the reach was largely affected by local conditions. Bacterio-detriforovorous ciliates dominated along the left bank (33% of the total abundance and 41% of the total biomass), herbivorous ciliates, in the central part and along the right bank (52% and 82%, respectively). This was probably due to greater anthropogenic load along the left bank (a large industrial center, the construction of a bridge), enhanced by reduced flow in shallow waters. In general, the maximum share of bacterio-detriforovorous ciliates, reflecting a higher concentration of organic matter, detritus, and bacteria, was recorded in the area of the bridge construction, in the drainage zone (left bank), and in the mouth area of the tributary (right bank) (figures 4a, 4b). Downstream the confluence of the Usa River, the share of bacterio-detriforovorous ciliates to total abundance increased (from 4.2% to 8.3%), but the basis of the trophic structure of the community along the right bank of the reach changed little when comparing the areas located upstream and downstream the confluence of the tributary. In particular, omnivore ciliates (54% of the total abundance upstream the tributary confluence and 52% downstream the confluence) and herbivorous (38% and 34%, respectively) were still dominants.
Regard should be paid to histophagous ciliates of the Priplotinny Reach, they were recorded only at one station, not belonging to the mouth of the Usa River, but in the area of storm drains of the Avtozavodsky District, which indicated active decomposition of organic matter. High contribution of bacterio-detrivorous and histophagous ciliates coincided strongly with the zones of increased water saprobity in the area of the yacht club ($S = 2.44$), the construction of the bridge ($S = 2.25$), and the discharge of conditionally clean effluents ($S = 2.21$). However, it should be noted that general environmental saprobity defined in regard to the ciliate species, serving as indicators of organic pollution, varied insignificantly at the entire water area of the Reach; in addition, the average saprobity at the reach ($S = 2.14$) and in the Bay ($S = 2.11$) was nearly the same, corresponding to the $\beta$-mesosaprobic zone.

4. Conclusion
For the first time, the spatial distribution of ciliates on the vast grid of stations has been studied at the Priplotinny Reach of the Kuibyshev Reservoir in autumn. Frequent strong winds, cloudy and rainy weather are major factors contributing to better mixing of the entire water column and thus to homogenous environment within the entire water column and along the reservoir stream. As a result, in the autumn, the abiotic conditions for aquatic organisms were relatively similar. Nevertheless, the fluctuations of ciliate abundance was quite pronounced in a relatively homogeneous environment due to several hydrological factors: the operation mode of hydroelectric power station and the volume of water of the tributary. The structure of the ciliate community was formed under the influence of local conditions: for example, there was a natural increase of the role of bacteriovorous and histophagous ciliates in the area of conditional wastewater discharge and near the construction of a bridge along the left bank. In addition, due to the greater diversity of ecotopes, high $\beta$-diversity and low $\alpha$-diversity of the ciliate community was a feature of the shallow waters near the left bank. Despite the fact that the reservoir water retention extends almost throughout the entire Usinsky Bay, it may be considered as a...
ecotone zone, where a particular community is formed: the species richness at the inflow stations was higher by 2.5 times on average; the abundance, biomass, and production were higher almost by an order of magnitude; and bacteriderotitorous and histophagous ciliates, actively decomposing of organic matter after pronounced bloom of cyanobacteria in the summer period, played a large role in the bay.

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