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# Zooplankton of macrophyte thickets of different types in kultuk zone of the Volga River Delta in the spring-summer period

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*Abstract.* The peculiarities of the zooplankton communities of plant associations of kultuk zone of the Volga River Delta are described for the spring-summer period. In mixed thickets and in the thickets of true aquatic plants, zooplankton is characterized by high biomass and abundance, and in the thickets of submerged plants, by low values. The factors influencing the formation of zooplankton community include, but not limited to, migration and feeding of juvenile fish, plant population density, water temperature, and rate of organic matter destruction. Shifting of the leading role of each factor during the spring-summer period is discussed.

*Keywords*: plankton, plant associations, juvenile fish.

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## Introduction

Specific conditions have been formed due to a decrease in the flow of the Volga River and the low-water period in the Volga River Delta since 2006, exhibited in a depth decrease and an increase in weediness. Within such conditions, the use of floodplain water bodies in the lower part of the delta as spawning grounds by semi-anadromous and local fish species is limited; their reproduction and development are possible only in kultuk (local name for a shallow water body formed in the Volga River Delta (Kaspiyskaya enciclopediya, 2004)) zone and the island zone of the Volga River Delta (Litvinov, 2018; Podolyako, 2013; Taradina et al., 2008). Taking these changes into account, the studies of the zooplankton community are of primary importance, since main characteristics of the species richness are important indicators of ecological processes and the state of the environment (Lin et al., 2014; Trindade et al., 2018). It is known that in the littoral area of kultuk zone and in the Volga River Delta, the zooplankton abundance and biomass are many times higher than in the sublittoral (Kosova, 1958, 1965, 1968). In the thickets of macrophytes, there are favorable conditions for the habitation of a large number of various planktonic organisms (Chernyaeva and Krivenkova, 2013; Krylov, 2005; Mukhortova, 2007;). Phytophilic zooplankton actively participates in the allochthonous organic matter cycle, consuming detritus, bacterio- and phytoplankton; it acts as the main component of the fish food supply; finally, it is an important agent of water self-purification. There has been reported on the asynchronous nature of the quantitative development of zooplankton (dominance of different complexes in certain plant associations), which is associated with different growth rates of macrophytes, their morphological features, and uneven fish pressure (Gavrilko, 2017; Naumova, 1992). Earlier, a correlation between the weediness of kultuk zone in the Volga River Delta and the quantitative indicators of planktonic invertebrates has been found (Litvinova and Fedyaeva, 2016).

The study aims to analyze the structure of zooplankton community in different types of macrophyte thickets of kultuk zone in the Volga River Delta with varying weediness during the spring-summer period.

## Materials and methods

The material was collected in 2012–2013 in the Obzhorovsky site of the Astrakhan Nature Reserve in kultuk zone near the mouth of the Kutum Channel and Blinov Island; the sampling period lasted from the beginning of the growing season of macrophytes (May) to the beginning of destructive processes (August). The Volga River near Volgograd city was classified in 2012 as low-water (the runoff volume was 240 km$^3$ per year), in 2013, it was considered to be medium-water (271 km$^3$ per year).

The sampling was carried out in three types of plant associations: submerged vegetation (16 samples), true aquatic vegetation (8 samples), and mixed thickets of amphibious and true aquatic vegetation (15 samples). Areas with submerged vegetation were located in the bunchin zone[1], mixed thickets, closeby (1–2 m), and associations of true aquatic plants, at a distance of 15–20 m. When sampling, 100 L of water was filtered through an Apstein plankton net (mesh size of 64 μm), sample processing was performed using standard methods (Metodicheskie..., 1982). At the same time, water temperature and dissolved oxygen were measured using a thermal oximeter (Ecotest-2000-T, Russia).

According to N.V. Litvinova and L.A. Fedyaeva (2016), amphibious vegetation at the site of the mouth of the Kutum Channel combines tall grass formation (common reed *Phragmites australis* (Cav.) Trin.ex Steud, 1841 and narrowleaf cattail *Typha angustifolia* Linnaeus, 1753) and low-grass formation (bur-reed *Sparganium erectum* Linnaeus, 1753). The reed-cattail-bur-reed association is coenosis-forming for the shallow-water section of kultuk zone. The true aquatic vegetation here includes water caltrop *Trapa natans* Linnaeus, 1753, tape grass *Vallisneria spiralis* Linnaeus 1753, sago pondweed *Potamogeton pectinatus* Linnaeus, 1753, floating fern *Salvinia natans* Linnaeus, 1753, duckweeds (genus *Lemna*), including greater duckweed *L. polyrrhiza* Linnaeus, 1753, frogbit *Hydrocharis morsus-ranae* Linnaeus, 1753, and coontail *Ceratophyllum demersum* Linnaeus, 1753. Tall-grass amphibious vegetation at the northeastern tip of Blinov Island is represented by the two most widespread species, common reed and narrowleaf cattail. The thickets of true aquatic vegetation in this area includes water caltrop, white water-lily *Nymphaea alba* Linnaeus, 1753, shining pondweed *Potamogeton lucens* Linnaeus, 1753, floating fern, duckweeds, frogbit, greater duckweed, and coontail. The submerged vegetation at both study sites is represented by coontail. During the study, the projective vegetation cover (weediness) has been assessed (Greig-Smith, 1983). The zooplankton community has been characterized by relative species richness (*S*), abundance (*N*), biomass (*B*), Sörensen similarity index (Sörensen, 1948), and Shannon-Weaver diversity index in regard to biomass (Shannon and Weaver, 1949). In addition to the usual zooplankton groups, the quantitative indicators of Protista have been taken into account as well. The species with share exceeding 10% of total abundance and biomass were considered dominant.

Statistical processing of the data was carried out using parametric methods (ANOVA, Student's *t*-test) in Excel and STATISTICA 10 software packages (Khalafyan, 2007).

## Results

During the study period, the maximum number of invertebrate species was noted in mixed thickets of amphibious and true aquatic plants (109 species), including Rotifera (49), Copepoda (20), Cladocera (33), and Protista (7 species). The thickets of true aquatic plants were distinguished by the minimum species richness of invertebrates (80 species), including Rotifera (35), Copepoda (13), Cladocera (25), and Protista (7 species). In the thickets of submerged plants, 95 species of planktonic invertebrates were recorded, including Rotifera (44), Copepoda (19), Cladocera (25), and Protista (7 species).

In May, the weediness was less than 50%. The water temperature was higher among submerged plants ($F = 7.2$; $p = 0.04$), and dissolved oxygen varied slightly in different types of thickets (Table 1). The similarity of the species composition of zooplankton among submerged plants and among mixed thickets of amphibious and true aquatic plants was 20.5%.

Most of the quantitative indicators of zooplankton were significantly higher in mixed thickets comparing to associations of submerged plants; the differences in the total abundance and biomass, as well as in the share of Rotifera in the total abundance were statis-

[1] Bunchin is a local term for the channel depressions in the Volga River Delta. Bunchin is a channel prolongation, formed by a water stream; it has no continuous above-water banks, and it may change its location. Over time, narrow, strongly elongated islands and spits are formed along bunchins. This is the initial stage of the formation of a delta channel in the lower reaches of the Volga River; they are the runoff hollows in a mild depressions, where a pronounced water flow appears after showers (Belevich, 1958; Kaspiyskaya enciklopediya, 2004).

**Table 1.** Indicators of water temperature (WT) and dissolved oxygen (DO) in the thickets of vegetation.

| Type of vegetation | DO, mg/L | | | | WT, °C | | | |
|---|---|---|---|---|---|---|---|---|
| | May | June | July | August | May | June | July | August |
| Submerged plants | 5.8 ± 2.0 | 7.4 ± 1.8 | 4.0 ± 2.0 | 5.5 ± 1.3 | 20.6 ± 1.1 | 25.1 ± 3.3 | 26.1 ± 0.8 | 24.1 ± 0.6 |
| Mixed thickets | 5.6 ± 2.9 | 6.0 ± 0.1 | 2.6 ± 0.6 | 5.9 | 16.7 ± 2.3 | 24.4 ± 3.6 | 26.1 ± 1.7 | 25.2 |
| True aquatic plants | – | 5.4 ± 0.3 | 3.3 ± 0.9 | 3.8 | – | 27.2 | 27.9 ± 2.2 | 26.1 |

tically significant (Table 2). At the same time, in the associations of submerged plants, the share of Cladocera and Protozoa in the total abundance and the share of Protozoa in the total biomass of zooplankton were significantly higher; a slightly higher value of the Shannon index was noted as well. In mixed thickets, *Euchlanis dilatata* (Hauer, 1930), *Trichothria truncata* (Whitelegge, 1889), and Cyclopoida nauplii dominated by abundance; in the thickets of submerged plants, these were *Euchlanis dilatata, Diflugia corona* (Wallich, 1864), *D. oblonga* (Ehrenberg, 1838) nauplii Cyclopoida; by biomass, these were *Euchlanis dilatata, Brachionus calyciflorus* (Pallas, 1766), *Chydorus sphaericus* (Müller, 1785), and *Euchlanis dilatata, Diflugia corona, Bosmina longirostris* (O.F. Müller, 1785), respectively.

In June, weediness at all study sites exceeded 50%. The highest water temperature was noted in the thickets of true aquatic plants, the lowest, in mixed thickets; the maximum dissolved oxygen was found in the thickets of submerged plants (Table 1). The zooplankton communities of mixed thickets and of the thickets of true aquatic plants were distinguished by the greatest species similarity (51%); the similarity between the thickets of submerged and of true aquatic plants, as well as between submerged and mixed thickets, was much lower (28.0 and 25.7%, respectively).

Among submerged plants (weediness of 50–75%), Rotifera and Protista prevailed quantitatively in zooplankton community, Cladocera dominated by biomass (Table 3). *Diflugia oblonga, D. corona*, Cyclopoida, and *Euchlanis dilatata* copepodites dominated by abundance, *Euchlanis dilatata*, Cyclopoida copepodites, *Eucyclops serrulatus* (Fischer, 1851), and *Scapholeberis mucronata* (O.F. Müller, 1776), by biomass. In mixed thickets of amphibious and true aquatic plants (weediness of 50–75%), Rotifera prevailed by abundance, *Euchlanis dilatata, Diflugia obloga*, and juvenile Cyclopoida predominated. Cladocera made up most of biomass due to *Simocephalus (Crownocephalus) serrulatus* (Koch, 1841), *Scapholeberis mucronata,* and *Eurycercus lamellatus* (O.F. Müller, 1776). As weediness increased up to 75–100%, relative species richness of zooplankton increased too, the Shannon index decreased, and the bulk of the population was represented by Protista, and *Arcella discoides* (Ehrenberg, 1843), *Centropyxis aculeata* (Ehrenberg, 1838), and Cyclopoida nauplii dominated. Cladocera dominated by biomass due to *Simocephalus (Crownocephalus) serrulatus* and *S. vetulus* (O.F. Müller, 1776), *Eurycercus lamellatus*, and *Megacyclops viridis* (Jurine, 1820). In the thickets of true aquatic plants (weediness of 50–75%), all taxonomic groups of invertebrates were characterized by high quantitative characteristics, but Copepoda prevailed over other groups. Cyclopoida nauplii, *Arcella vulgaris* (Ehrenberg, 1830), and *Euchlanis dilatata* dominated by abundance. Cladocera (represented mostly by *Eurycercus lamellatus*) dominated by biomass. In mixed thickets (weediness of up to 75–100%) and among true aquatic plants, the total abundance and biomass of invertebrates, as well as the abundance of Crustacea and Protozoa were significantly higher comparing to those in other types of thickets (Table 3). In addition, the maximum relative species richness and maximum share of Cladocera in the total biomass of zooplankton were noted here, accompanied by minimum share of Rotifera and the lowest Shannon-Weaver index. In thickets of true aquatic plants, the abundance and biomass of Rotifera was significantly higher, as well as the share of Copepoda and Cladocera in the total abundance of zooplankton. In the mixed thickets, as weediness increased to 75–100% relative to other areas, absolute abundance and biomass of Rotifera, and their share in the total abundance sharply decreased, but the abundance of Protista and Cladocera increased significantly.

**Table 2.** Parameters of zooplankton ($m \pm SD$) in May in the thickets of submerged plants (I) and in mixed thickets of amphibious and true aquatic plants (II), weediness of up to 50%. Here and in Tables 3—5: *N* is abundance, thousand ind./m$^3$; *N* (%), share of taxonomic group in total abundance; *B*, biomass, mg/m$^3$; *B* (%), share of taxonomic group in total biomass; *S*, the number of species in the sample; $H_B$, Shannon-Weaver index calculated in terms of biomass; *F*, Fisher's test; *p*, significance (statistically significant differences are highlighted in bold).

| Parameter | | I | II | *F* | *p* |
|---|---|---|---|---|---|
| *N* | Total | 4.0 ± 0.7 | 19.2 ± 10.2 | **6.1** | **0.047** |
| | Rotifera | 1.1 ± 0.3 | 13.8 ± 9.2 | 5.2 | 0.06 |
| | Copepoda | 1.1 ± 0.6 | 3.6 ± 1.9 | 4.5 | 0.07 |
| | Cladocera | 0.4 ± 0.3 | 0.9 ± 1.4 | 0.3 | 0.55 |
| | Protista | 1.2 ± 0.4 | 0.7 ± 0.6 | 0.3 | 0.55 |
| *N* (%) | Rotifera | 30.1 ± 14.0 | 66.6 ± 21.6 | **6.6** | **0.04** |
| | Copepoda | 27.9 ± 13.1 | 24.9 ± 23.2 | 0.0 | 0.84 |
| | Cladocera | 10.8 ± 5.2 | 4.0 ± 4.2 | 4.0 | 0.08 |
| | Protista | 31.1 ± 4.0 | 4.2 ± 4.5 | **69.3** | 0.0001 |
| *B* | Total | 8.2 ± 4.2 | 79.9 ± 30.8 | **15.0** | **0.008** |
| | Rotifera | 1.6 ± 0.9 | 38.9 ± 30.6 | 4.1 | 0.087 |
| | Copepoda | 1.07 ± 0.7 | 28.5 ± 42.8 | 1.1 | 0.32 |
| | Cladocera | 2.85 ± 2.1 | 7.2 ± 9.1 | 0.6 | 0.45 |
| | Protista | 2.6 ± 2.2 | 1.3 ± 1.2 | 0.2 | 0.92 |
| *B* (%) | Rotifera | 24.4 ± 14.9 | 50.4 ± 37.0 | 1.2 | 0.3 |
| | Copepoda | 15.9 ± 15.6 | 28.8 ± 32.9 | 0.3 | 0.55 |
| | Cladocera | 32.0 ± 7.6 | 10.7 ± 13.0 | **6.4** | **0.04** |
| | Protista | 28.2 ± 12.7 | 1.8 ± 1.5 | **23.6** | **0.002** |
| S | | 22.3 ± 8.6 | 32.0 ± 6.2 | 3.5 | 0.10 |
| $H_B$ | | 3.2 ± 0.9 | 2.9 ± 0.9 | 0.2 | 0.67 |

Compared to the data obtained in May, the total abundance and biomass of zooplankton, the share of Rotifera and Protista in the total abundance, and the share of Rotifera in the total biomass increased in the thickets of submerged plants (Fig. 1, Tables 2, 3). In mixed thickets, as weediness increased up to 50–75%, the zooplankton abundance slightly decreased, but the share of Crustacea and Protozoa increased, and the zooplankton biomass increased due to Cladocera (Fig. 2, Tables 2, 3). As weediness of mixed thickets increased up to 75–100%, the abundance of zooplankton increased significantly as well due to an increase in the abundance of Crustacea and Protozoa, and the biomass, due to Cladocera.

In July, weediness of all areas was 75–100%. The maximum water temperature was observed in the thickets of true aquatic plants; minimum temperature and maximum dissolved oxygen, in the thickets of submerged plants (Table 1). The similarity of the species composition of zooplankton between mixed thickets and thickets of submerged plants was 31.4%, submerged and true aquatic plants, 34.6%, mixed and true aquatic plants, 48.3%.

Copepoda formed the basis of the abundance and biomass of zooplankton both in submerged plants and in mixed thickets (Table 4). In the thickets of submerged plants, juvenile Cyclopoida, *Arcella vulgaris, Trichocerca rattus* (Müller, 1776), and *Lecane bulla* (Gosse, 1851) dominated by abundance; by biomass, these were Cyclopoida copepodites, *Euchlanis dilatata*, and *Macrocyclops, albidus* (Jurine, 1820). In mixed thickets, the dominant species by abundance were the nauplii Cyclopoida, *Coronatella rectangula* (Sars, 1861), *Lecane bulla, Trichocerca rattus,* and *Mytilina ventralis* (Ehrenberg, 1830); in terms of biomass, copepodites Cyclopoida, *Macrocyclops albidus*, *Simocephallus (Crownocephalus) serrulatus,* and *Eurycercus lamellatus*. Copepoda also formed the bulk of the abundance in the thickets of true aquatic plants, but Cladocera prevailed by biomass. Juvenile Cyclopoida dominated in terms of abundance; *Simocephallus*

**Table 3.** Parameters of zooplankton ($m \pm SD$) in June in the thickets of submerged plants, weediness of 50–75% (I), amphibious and true aquatic plants, weediness of 50–75% (II) and of 75–100% (III), and true aquatic plants, weediness of 50–75% (IV). Letter indices mark significant differences between the indicators. Designations are similar to Table 2.

| Parameter | | I$^{\text{а}}$ | II$^{\text{б}}$ | III$^{\text{в}}$ | IV$^{\text{г}}$ | F | p |
|---|---|---|---|---|---|---|---|
| N | Total | 10.0 ± 3.1$^{\text{в, г}}$ | 17.7 ± 9.9$^{\text{в, г}}$ | 117.4$^{\text{а, б, г}}$ | 74.8$^{\text{а, б, в}}$ | 94.2 | 0.0003 |
| | Rotifera | 3.5 ± 2.0$^{\text{г}}$ | 5.9 ± 2.3$^{\text{г}}$ | 1.5$^{\text{г}}$ | 18.9$^{\text{а, б, в}}$ | **13.2** | **0.015** |
| | Copepoda | 2.3 ± 1.5$^{\text{в, г}}$ | 5.0 ± 2.5$^{\text{в, г}}$ | 22.8$^{\text{а, б}}$ | 26.8$^{\text{а, б}}$ | **51.2** | **0.001** |
| | Cladocera | 0.8 ± 0.7$^{\text{в, г}}$ | 1.7 ± 1.2$^{\text{в, г}}$ | 11.1$^{\text{а, б, г}}$ | 15.8$^{\text{а, б, в}}$ | 90.7 | 0.00039 |
| | Protista | 3.2 ± 3.1 | 4.9 ± 3.9 | 81.9$^{\text{а, б, г}}$ | 13.2$^{\text{а, б, в}}$ | **153.3** | **0.0001** |
| *N* (%) | Rotifera | 41.8 ± 27.1 | 35.5 ± 6.8 | 1.3 | 25.3 | 0.7 | 0.56 |
| | Copepoda | 21.8 ± 11.4 | 29.2 ± 2.3 | 19.5 | 35.8 | 0.5 | 0.69 |
| | Cladocera | 7.5 ± 4.1 | 9.2 ± 1.7 | 9.4 | 21.1 | 3.2 | 0.13 |
| | Protista | 28.7 ± 18.0 | 26.0 ± 7.3 | 69.7 | 25.3 | 2.0 | 0.25 |
| *B* | Total | 35.3 ± 30.6$^{\text{в, г}}$ | 121.5 ± 89.5$^{\text{в, г}}$ | 1420$^{\text{а, б}}$ | 1651.0$^{\text{а, б}}$ | **262.4** | **0.00004** |
| | Rotifera | 8.2 ± 5.7$^{\text{г}}$ | 22.9 ± 22.1$^{\text{г}}$ | 0.6$^{\text{г}}$ | 105.6$^{\text{а, б, в}}$ | **17.2** | **0.009** |
| | Copepoda | 7.0 ± 7.1$^{\text{в, г}}$ | 17.0 ± 15.2$^{\text{в, г}}$ | 201.8$^{\text{а, б}}$ | 194.5$^{\text{а, б}}$ | **156.2** | **0.00013** |
| | Cladocera | 18.2 ± 27.5$^{\text{в, г}}$ | 91.4 ± 67.5$^{\text{в, г}}$ | 1160.6$^{\text{а, б}}$ | 1338.0$^{\text{а, б}}$ | **264.3** | **0.00004** |
| | Protista | 1.9 ± 1.6 | 2.7 ± 2.2 | 57.5$^{\text{а, б, г}}$ | 12.9$^{\text{а, б, в}}$ | **270.7** | **0.00004** |
| *B* (%) | Rotifera | 41.1 ± 35.2 | 15.4 ± 4.1 | 0.01 | 6.4 | 0.4 | 0.74 |
| | Copepoda | 17.5 ± 14.4 | 12.0 ± 1.7 | 14.2 | 11.7 | 0.06 | 0.97 |
| | Cladocera | 35.8 ± 30.6 | 70.5 ± 5.9 | 81.7 | 81.0 | 0.6 | 0.62 |
| | Protista | 5.6 ± 0.5 | 2.0 ± 0.0 | 4.0 | 0.7 | 0.8 | 0.52 |
| S | | 25.7 ± 2.5 | 33.0 ± 1.4 | 35.0 | 41.0 | 2.4 | 0.2 |
| $H_B$ | | 3.1 ± 0.5 | 3.0 ± 0.7 | 2.3 | 2.3 | 1.4 | 0.35 |

*(Crownocephalus) serrulatus*, *Coronatella rectnagula*, *Eurycercus lamellatus,* Cyclopoida copepodites, and *Macrocyclops albidus,* by biomass.

The zooplankton of the mixed thickets was characterized by the highest abundance of Rotifera, as well as the highest abundance and biomass of Copepoda, comparing to other sites (Table 4). In the thickets of true aquatic plants, the maximum abundance and total biomass of Cladocera and Protista, as well as the highest biomass of Rotifera, were recorded. In the sequence “thickets of submerged plants → mixed thickets → thickets of true aquatic plants”, the abundance and biomass of zooplankton, the abundance and biomass of Cladocera and Protista, the biomass of Rotifera, the share of Cladocera in the total abundance, and relative species richness increased, but the share of Rotifera in the total abundance and biomass and Shannon-Weaver index decreased.

Compared to the data obtained in June, the total abundance and biomass of zooplankton of all taxonomic groups, except Copepoda, decreased in the thickets of submerged plants (Figs. 1–3, Tables 3, 4). In mixed thickets, relative species richness, the total abundance and biomass of zooplankton decreased due to decreasing share of Cladocera and Protista, but Shannon-Weaver index and the share of Copepoda in the total abundance increased. In thickets of true aquatic plants, relative species richness and biomass of zooplankton decreased, the Shannon-Weaver index increased, the share of Copepoda in the total biomass and abundance of zooplankton slightly increased due to Crustacea and Protozoa.

In August, the water temperature was slightly lower in the thickets of the submerged plants; here, dissolved oxygen was higher comparing to other areas. In the thickets of true aquatic plants, the highest water temperature and the lowest dissolved oxygen were noted (Table 1). The similarity of the species composition of zooplankton between mixed thickets and thickets of submerged plants was 28.2%, mixed thickets and true aquatic plants, 29.6%, submerged plants and true aquatic plants, 34.1%.

In the thickets of submerged plants, Copepoda and Rotifera absolutely dominated by abundance, Cladocera, by biomass (Table 5), followed by

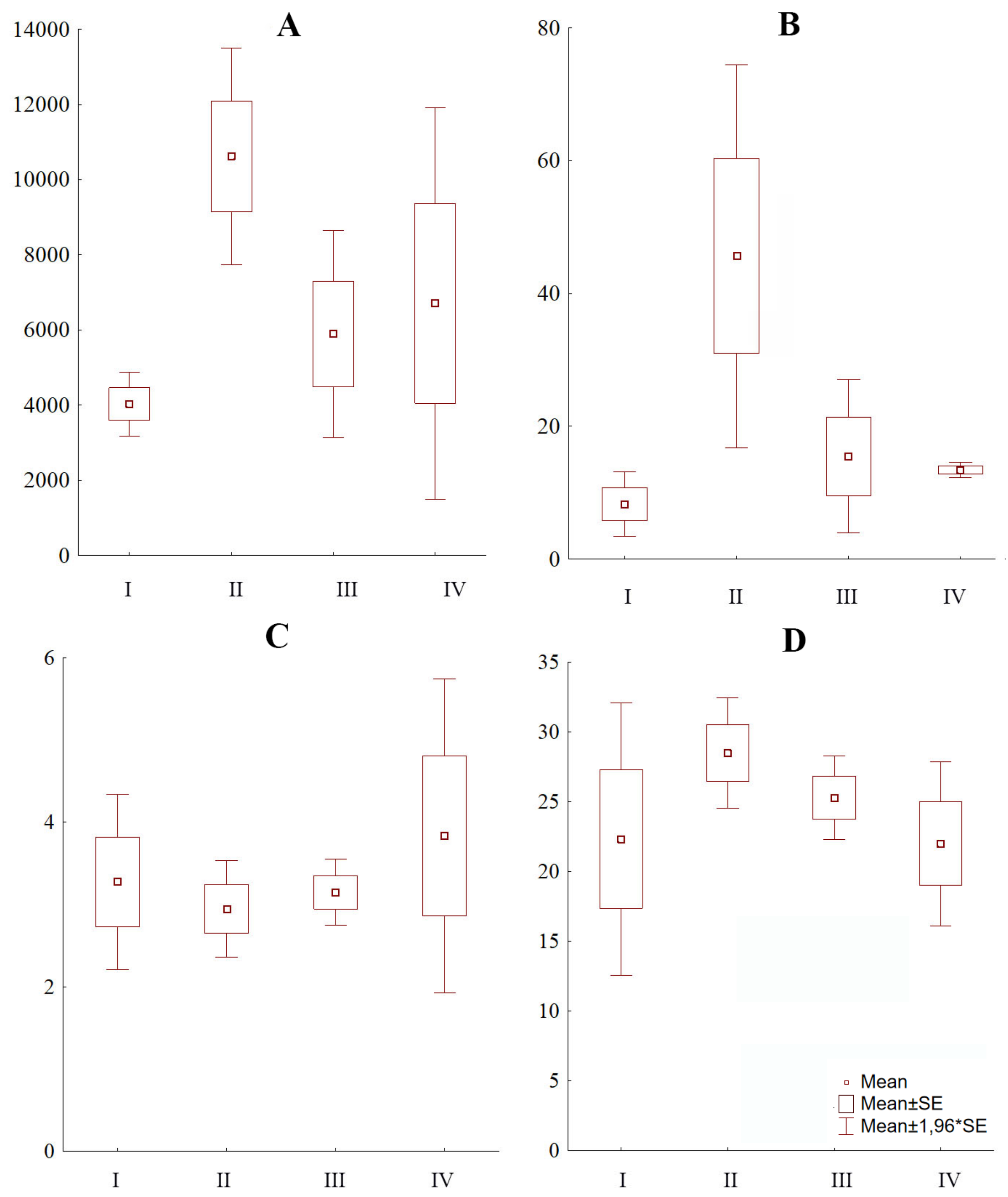


**Fig. 1.** Abundance, ind./m³ (**A**), biomass, mg/m³ (**B**), Shannon-Weaver index, bit/mg (**C**), and relative species richness (**D**) of zooplankton in the thickets of submerged plants. I – May (weediness of up to 50%); II – June (50–75%); III – July (75–100%); IV – August (75–100%).

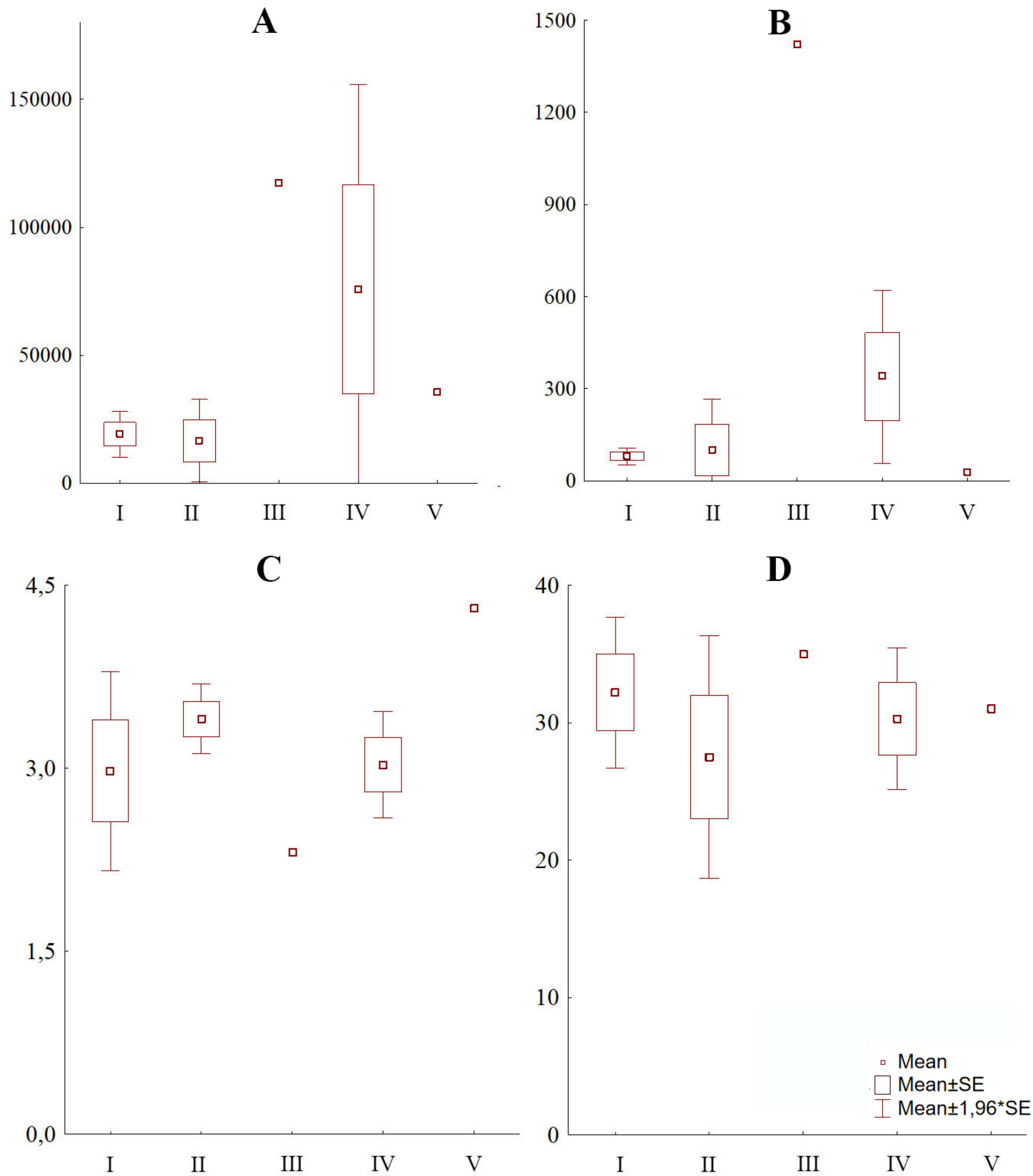


**Fig. 2.** Abundance, ind./m$^3$ (**A**), biomass, mg/m$^3$ (**B**), Shannon-Weaver index, bit/mg (**C**), and relative species richness (**D**) of zooplankton in the mixed thickets of amphibious and true aquatic plants. I – May (weediness of up to 50%); II – June (50–75%); III – June (75–100%); IV – July (75–100%); V – August (75–100%).

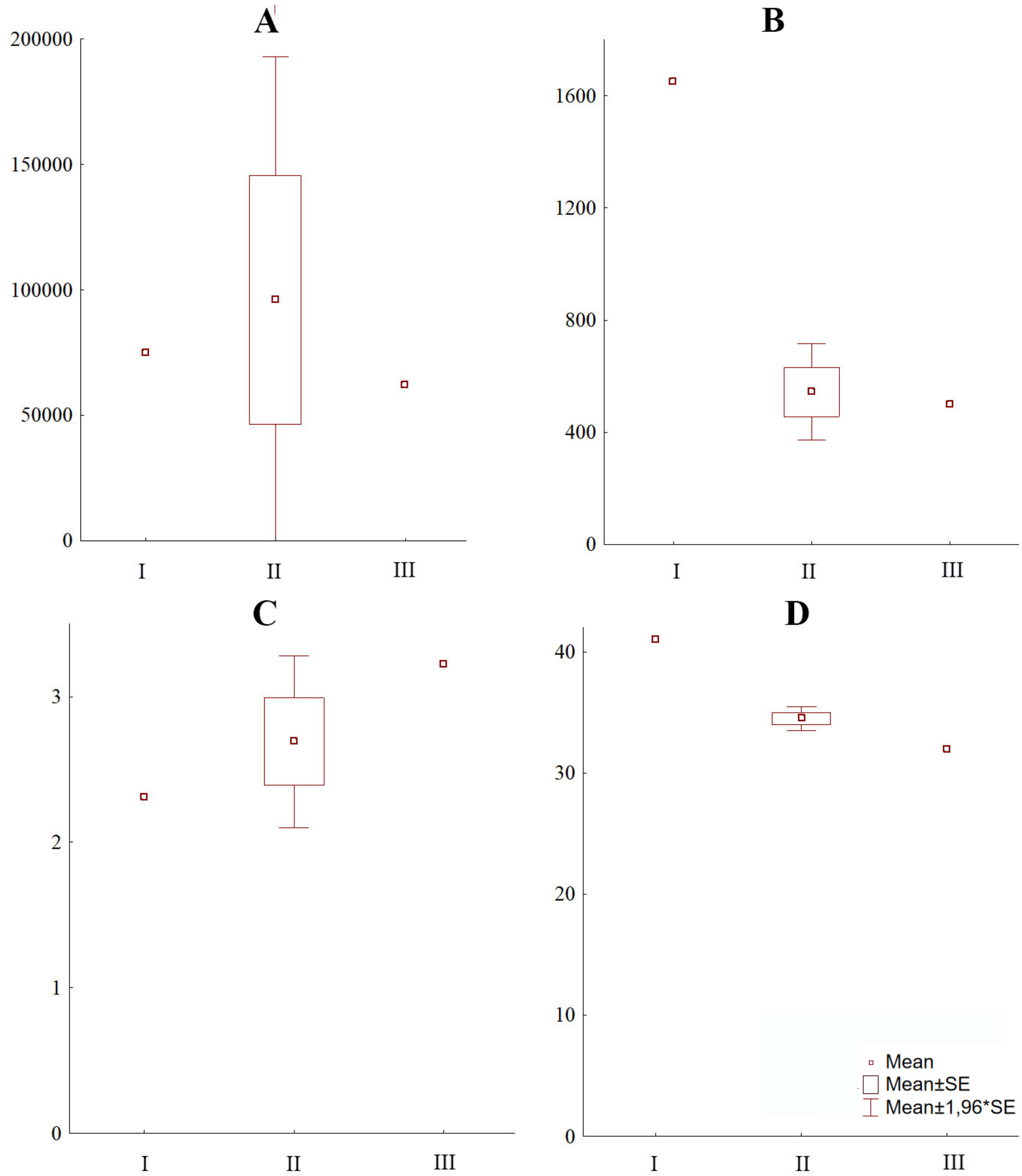


**Fig. 3.** Abundance, ind./m$^3$ (**A**), biomass, mg/m$^3$ (**B**), Shannon-Weaver index, bit/mg (**C**), and relative species richness (**D**) of zooplankton in the thickets of true aquatic plants. I – June (weediness of 50–75%); II – July (75–100%); III – August (75–100%).

juvenile Cyclopoida (abundance) and juvenile Cyclopoida and *Euchlanis dilatata* (biomass). In mixed thickets, Rotifera prevailed by abundance and biomass, followed by *Arcella discoides, Lecane luna* (Müller, 1776), *Euchlanis dilatata*, and Cyclopoida nauplii (abundance), and *Lecane luna* and *Euchlanis dilatata* (biomass). In the thickets of true aquatic plants, Crustacea formed the basis of abundance and biomass; followed by juvenile Cyclopoida, *Coronatella rectangula*, and *Pleuroxus aduncus* (Jurine, 1820) in terms of abundance and *Simocephallus (Crownocephalus) serrulatus* and *Macrocylops albidus* in terms of biomass.

The minimum abundance and biomass of zooplankton were recorded in the thickets of submerged plants, maximum, in the thickets of true aquatic plants (Table 5). In the mixed thickets, Rotifera and Protista had the highest abundance and biomass, Cladocera, the lowest; in the thickets of true aquatic plants, the highest abundance and biomass were noted for Copepoda and Cladocera. The maximum Shannon-Weaver index for zooplankton was observed in mixed thickets of plants, the minimum, in true aquatic plants.

Comparing to July, relative species richness and biomass of zooplankton slightly decreased in the thickets of submerged plants, but abundance and the Shannon-Weaver index increased (Figs. 1–3, Tables 4, 5). At the same time, the share of Rotifera in the total abundance increased, but the share of Copepoda decreased; considering total biomass, the share of Cladocera increased, but the share of Copepoda descreased. In the mixed thickets, the abundance and biomass of Rotifera and the Shannon-Weaver index increased, but the total abundance and biomass of zooplankton decreased. In the thickets of true aquatic plants, relative species richness, abundance and biomass of zooplankton slightly decreased, but the abundance of Rotifera and their share in the total abundance, biomass and share in the total biomass of Copepoda, as well as the Shannon-Weaver index, increased.

## Discussion

Zooplankton community of mixed thickets of amphibious and true aquatic plants is characterized by the highest species richness, the thickets of true aquatic plants, by the lowest. These differences may be associated with the habitat peculiarities; in particular, mixed thickets are characterized by the greatest heterogeneity of environmental conditions. However, relative species richness of zooplankton is slightly higher in the thickets of true aquatic plants, which may be preconditioned by the species composition of macrophytes, weediness, popualtion density, and biomass of plants (Cheruvelil et al., 2002; Conde-Porcuna, 2000; Gavrilko, 2019; Kuczyńska-Kippen et al., 2009; Scheffer, 2001). This indicates that the differences in species richness are more likely associated with the difference in the volume of zooplankton sample.

Relatively low level of similarity between thickets of different types evidences on its significant role in the formation of the qualitative composition of zooplankton, weediness, population density, and biomass of macrophytes. At the same time, differences in the composition of invertebrate species emerging from the latent stages, as well as the amount of accumulated organic matter, both play a significant role, as evidenced by the least similarity of communities in May. Increasing weediness, decreasing flow, and the presence of a large number of common plant species in zones of mixed thickets and thickets of true aquatic plants contribute to an increase in the similarity of the species composition of zooplankton between them in June and July. At the same time, the degree of similarity between other sites, differing by the plant composition the most, is noticeably lower. In August, a decrease in the similarity of the species composition may be associated with differences in destruction processes, changes in the qualitative composition of invertebrates, and changes in environmental conditions during the period of shallowing and drying of the coastal zone (Kosova, 1958, 1965; Sadchikov and Kudryashov, 2004).

Shifts in the leading role of different environmental factors during the spring-summer period are also evidenced by the quantitative characteristics of communities. In May, the most specific conditions are formed in mixed thickets of amphibious and true aquatic plants, where the highest quantitative indicators of zooplankton are noted along relatively weak development of vegetation. K.V. Gorbunov (1976) notes that allochthonous organic matter is of primary importance in the biological productivity of the lower reaches of the Volga River Delta in comparison with autochthonous organic matter. It is obvious that a large amount of organic matter of macrophyte thickets accumulates in these areas. The harvest of these plants, which are converted by bacteria into nutrient detritus or dissolved organic matter, is the main source of energy for non-predatory invertebrates, plankton and benthos in the water bodies of the Volga River Delta (Gorbunov, 1976). The presence of a large amount of organic matter is confirmed by the predominance of Rotifera, in particular, *Brachionus calyciflorus,* which is an indicator of highly trophic waters, as well as by the minimum Shannon-Weaver index. The organisms at dormancy (including Rotifera eggs) stages before flooding may have a certain contribution to high zooplankton abundance and biomass, as it has been reported earlier (Kosova, 1958).

In June, on the contrary, minimum quantitative characteristics of invertebrates are found in mixed

**Table 4.** Parameters of zooplankton (*m* ± *SD*) in July in the thickets of submerged plants (I), mixed thickets of amphibious and true aquatic plants (II), and true aquatic plants (III), weediness in all cases is 75–100%. Letter indices mark significant differences between the indicators. Designations are similar to Table 2.

| Parameter | | I[а] | II[б] | III[в] | *F* | *P* |
|---|---|---|---|---|---|---|
| *N* | Total | 5.8 ± 3.7 | 75.7 ± 10.8 | 96.0 ± 69.9 | 1.9 | 0.18 |
| | Rotifera | 1.9 ± 2.0 | 15.5 ± 16.8 | 5.3 ± 5.0 | 2.4 | 0.12 |
| | Copepoda | 2.4 ± 3.6 | 47.5 ± 8.4 | 38.7 ± 19.9 | 1.1 | 0.35 |
| | Cladocera | 0.4 ± 0.2[в] | 6.9 ± 6.8[в] | 32.8 ± 35.6[а, б] | **6.8** | **0.009** |
| | Protista | 1.0 ± 1.3[в] | 5.7 ± 6.5[в] | 19.0 ± 19.3[а, б] | **5.1** | **0.02** |
| *N* (%) | Rotifera | 36.7 ± 25.2 | 26.2 ± 11.3 | 10.1 ± 12.6 | 1.6 | 0.23 |
| | Copepoda | 32.0 ± 25.4 | 45.2 ± 15.2 | 44.6 ± 11.7 | 0.8 | 0.46 |
| | Cladocera | 8.1 ± 4.5 | 15.4 ± 16.5 | 28.1 ± 16.6 | 2.1 | 0.16 |
| | Protista | 23.0 ± 25.5 | 13.1 ± 4.2 | 17.0 ± 7.7 | 0.5 | 0.61 |
| *B* | Total | 15.5 ± 15.6[б, в] | 339.0 ± 380.1[а] | 544.3 ± 124.3[а] | **4.4** | **0.0034** |
| | Rotifera | 2.7 ± 2.3[б, в] | 13.2 ± 11.7[а] | 20.6 ± 23.4[а] | **3.0** | **0.08** |
| | Copepoda | 7.9 ± 9.9 | 185.0 ± 337.3 | 127.7 ± 39.8 | 1.05 | 0.37 |
| | Cladocera | 3.0 ± 4.5[б, в] | 130.8 ± 103.0[а, в] | 408.0 ± 185.1[а, б] | **17.3** | **0.00021** |
| | Protista | 1.7 ± 2.7 | 10.1 ± 13.1 | 13.6 ± 8.2 | 1.9 | 0.17 |
| *B* (%) | Rotifera | 22.9 ± 19.3 | 10.9 ± 12.4 | 3.4 ± 3.5 | 1.6 | 0.22 |
| | Copepoda | 37.9 ± 22.0 | 41.8 ± 21.9 | 24.9 ± 13.0 | 0.4 | 0.62 |
| | Cladocera | 20.7 ± 15.4[в] | 45.9 ± 27.5 | 72.9 ± 17.3[а] | **5.1** | **0.02** |
| | Protista | 14.9 ± 14.7 | 4.7 ± 4.2 | 2.7 ± 2.1 | 2.0 | 0.16 |
| | S | 25.2 ± 4.0 | 30.3 ± 7.0 | 34.5 ± 0.7 | 2.7 | 0.09 |
| | $H_B$ | 3.1 ± 0.5 | 3.0 ± 0.6 | 2.7 ± 0.4 | 0.5 | 0.59 |

thickets (weediness of 50–75%), as well as in the thickets of submerged plants. It is possible that the decrease in abundance and biomass of zooplankton is caused by the influence of juvenile fish (Bartell and Kitchell, 1978; Gilyarov, 1987; Hrbaček, 1962; Stenson et al., 1978, Zhang et al., 2019), since this period is characterized by their mass migrations from both the floodplain spawning grounds and kultuk zone (Koblitskaya, 1958). It is known that juveniles of roach *Rutilus caspicus* (Yakovlev, 1870) at the early stages of development feed mainly on Rotifera, juveniles of silver bream *Blicca bjoerkna* (Linnaeus, 1758), on Cladocera (Gorbunov, 1958; Gorbunov and Kosova, 1961). Food spectrum and stomach fullness index of the fry reflect the qualitative composition of the zooplankton and zoophytos of vegetation (Strelnikova, 2013). In kultuk zone, not only on juveniles of commercial fish feed on zooplankton, but also the fry of silver bream, rudd, and bleak (Khoroshko, 1956). The gut contents of juvenile bream *Abramis brama* (Linnaeus, 1758) in kultuk zone comprises more than 50% of zooplankton, these fish are also characterized by higher stomach fullness index comparing to the specimens sampled in the upstream canals (Khoroshko, 1956).

In addition, increasing grazing pressure by juvenile fish may be influenced by the location of the area of submerged and mixed plants near the bunchins and in the areas with pronounced water flow. According to A.F. Koblitskaya (1958), the first peak of fish fry migrations is well-pronounced, most of the fish are transported with the current. The largest number of juveniles migrates to kultuk zone during overflow in late May–mid-June. Juveniles migrating from the upstream floodplain water bodies and lakes ("ilmens") in kultuk zone feed here for some time and gradually migrate downstream; for example, the maximum abundance of juvenile roach was observed in late May–mid-June (Zhidovinov, 1985; Koblitskaya, 1958; Khoroshko, 1956). According to E.V. Nikitin (2013), as well as D.G. Taradina and N.I. Chavychalova (2017), young roach predominate in the downstream migration (at different water content, its share varies as 60–90%) during the period of maximum water level in June in kultuk zone. The total number of larvae and juveniles of local origin, migrating to kultuk zone from

**Table 5.** Parameters of zooplankton ($m$ ± $SD$) in July in the thickets of submerged plants (I), mixed thickets of amphibious and true aquatic plants (II), and true aquatic plants (III), weediness in all cases is 75–100%. Letter indices mark significant differences between the indicators. Designations are similar to Table 2.

| Parameter | | I$^{\text{а}}$ | II$^{\text{б}}$ | III$^{\text{в}}$ | *F* | *P* |
|---|---|---|---|---|---|---|
| *N* | Total | 6.7 ± 3.7 | 35.2 | 62.0 | 75.1 | 0.08 |
| | Rotifera | 2.8 ± 1.5 | 26.8 | 13.2 | 82.7 | 0.077 |
| | Copepoda | 2.4 ± 1.1 | 3.8 | 21.9 | 110.9 | 0.06 |
| | Cladocera | 1.3 ± 0.9$^{\text{б, в}}$ | 0.05$^{\text{а, в}}$ | 22.4$^{\text{а, б}}$ | **184.3** | **0.05** |
| | Protista | 0.1 ± 0.1$^{\text{б, в}}$ | 4.5$^{\text{а}}$ | 4.3$^{\text{а}}$ | **514.9** | **0.03** |
| *N* (%) | Rotifera | 42.1 ± 0.7$^{\text{б, в}}$ | 76.1$^{\text{а, в}}$ | 21.3$^{\text{а, б}}$ | **1400.1** | **0.01** |
| | Copepoda | 38.1 ± 4.7 | 10.9 | 35.4 | 11.4 | 0.2 |
| | Cladocera | 18.5 ± 4.1 | 0.1 | 36.2 | 18.6 | 0.16 |
| | Protista | 1.1 ± 1.3 | 12.7 | 6.9 | 25.7 | 0.13 |
| *B* | Total | 13.4 ± 0.8$^{\text{б, в}}$ | 28.6$^{\text{а, в}}$ | 499.7$^{\text{б, в}}$ | **124870.6** | **0.002** |
| | Rotifera | 3.5 ± 1.9 | 23.3 | 9.2 | 33.1 | 0.12 |
| | Copepoda | 3.2 ± 3.8$^{\text{в}}$ | 3.6$^{\text{в}}$ | 227.2$^{\text{а, б}}$ | **1293.7** | **0.01** |
| | Cladocera | 5.8 ± 2.7$^{\text{в}}$ | 0.3$^{\text{в}}$ | 257.7$^{\text{а, б}}$ | **3175.1** | **0.01** |
| | Protista | 0.4 ± 0.5 | 1.3 | 5.6 | 34.8 | 0.11 |
| *B* (%) | Rotifera | 26.2 ± 13.4 | 81.6 | 1.8 | 9.5 | 0.22 |
| | Copepoda | 25.1 ± 30.3 | 12.7 | 45.4 | 0.3 | 0.79 |
| | Cladocera | 42.8 ± 18.2 | 1.1 | 51.5 | 2.3 | 0.42 |
| | Protista | 2.9 ± 3.7 | 4.6 | 1.1 | 0.2 | 0.83 |
| | *S* | 22.0 ± 4.2 | 31.0 | 32.0 | 2.5 | 0.4 |
| | $H_B$ | 3.8 ± 1.3 | 4.3 | 3.22 | 0.2 | 0.87 |

floodplain water bodies in high-water years is 44.4 × $10^9$ ind. and 107.0 × $10^9$ ind., respectively; in dry years, this parameter ranges from 29.9 × $10^9$ ind. to 112.6 × $10^9$ ind. (Taradina et al., 2008). Limiting role of the fish population in the formation of zooplankton in mixed thickets and in the thickets of submerged plants may also be evidenced by an increase in the Shannon index, when grazing of the most visible and numerous food objects is observed (Gliwicz, 2002; Murdoch, 1969; Murdoch et al., 1975), which, in turn, leads to a decrease of quantitative characteristics of certain species, i.e., its share in total abundance/biomass (Krylov et al., 2020, 2021; Ozero..., 2016;).

At the same time, it is known that thickets of macrophytes play a special role in ensuring the protection of planktonic invertebrates from predators (Burks et al., 2002; Lauridsen and Buenk, 1996; Lewin et al., 2004; Lin et al., 2014). This is probably one of the main reasons for high abundance and biomass of zooplankton due to Crustacea observed alongside with an increase in weediness of mixed thickets up to 75–100%. During this period, abundant zooplankton is also recorded in the thickets of true aquatic plants. This may be due to their remoteness from the банчин, so there are no mass accumulations of juvenile fish during the first migration peak. In addition, maximum water temperature is observed in this particular type of thickets, as well as the minimum oxygen content, which may adversely affect the distribution of juvenile fish.

In July, the second peak of mass migrations of juvenile fish in kultuk zone is observed, although it is less pronounced comparing to the first peak, but there are still a lot of fish juveniles. If fish reproduce in kultuk zone, then juveniles stay at the spawning grounds, fatten, and migrate gradually, starting from stage C (Koblitskaya, 1958). In dry years, kultuk zone is a place of more intensive spawning for many phytophilous fish species (Nikitin, 2013; Podolyako, 2013). For example, the year of 2012 has been characterized by a one-time spawning in shallow channels (“yeriks”), and the second (portional) peak of spawning has been observed in kultuk zone and river delta (Vasil’eva et al., 2016; Litvinov and Podolyako, 2014). In high-water years, kultuk zone is also of great importance for feeding juveniles of phytophilous fish species (Taradina et al., 2008). For example, the year of 2013 has been characterized by favorable hydrological conditions for spawning and feeding of juvenile fish on floodplain spawning grounds, downstream migration of a large number of species (with a predominance of juvenile roach) from floodplain water bodies (Vasil'eva et al., 2016; Litvinov and Podolyako, 2014; Taradina and Chavychalova, 2017). During this period, the influence of juvenile fish on zooplankton has been most clearly manifested in the thickets of submerged vegetation in the bunchins: here, the abundance and biomass of zooplankton was low due to Cladocera, but high Shannon-Weaver index was observed. According to S.A. Podolyako (2014), phytocenoses of both cattail and common reed are the preferred feeding grounds for juvenile roach and silver bream in kultuk zone of the Volga River Delta. E.V. Nikitin (2017) notes that fish fry are distributed during this period over vast feeding grounds and most of semi-anadromous fish species descend to deeper water layers along the estuarine seashore. Obviously, this is also a reason for a decrease in the quantitative characteristics of Cladocera and an increase in Shannon-Weaver index in the mixed thickets near the bunchins. At the same time, the remoteness from the bunchins, high density of thickets of true aquatic plants, their complex spatial structure, and low oxygen concentrations contributed to a decrease in the pressure of juvenile fish. As a result, zooplankton here is characterized by high abundance and biomass due to Crustacea impact, as well as by low values of Shannon-Weaver index, noted earlier (Khoroshko, 1956). It is also important to note that the maximum water temperature is observed in the thickets of true aquatic plants, which may serve a preconditioning factor for composition, quantitative characteristics, and distribution of zooplankton (Kolada, 2014; Yang et al., 2017).

Higher aquatic vegetation in freshwater reservoirs plays an important role in enrichment of water and bottom sediments with various organic and mineral substances, especially by dying off of plant mass and its decomposition (Strelnikova, 2013). Due to small body size, short lifespan, and frequent changes in species ratio, zooplankton communities are very sensitive to physical and chemical variables (Zhang et al., 2019). It is known that the intensity of water self-purification in the littoral exceeds twofold that in the open areas. For example, zooplankton community of the thickets of higher aquatic vegetation in Lake Kenon consumes on average 4.6 tons of suspended organic matter per day (Krivenkova, 2018). In August, when the shores of kultuk zone become shallow and dry due to high air temperature, a high abundance of Rotifera is observed, accompanied by high aboundance of various detritus-feeding and sessile filter-feeding organisms, preconditioned by abundant detritus formed as the remains of higher aquatic plants decompose (Gorbunov, 1976; Kosova, 1958, 1965; Litvinova and Fedyaeva, 2016). An increase in the abundance of Rotifera and Protozoa during this period is observed in almost all of the types of studied thickets. In addition, second peak of fry migration may occur in August (Koblitskaya, 1958; Zhidovinov, 1985), accompanied by feeding of juvenile fish. Our data evidence that juvenile fish play an important role in formation of zooplankton community in the thickets of submerged vegetation and in mixed thickets, tracked by an increase in the Shannon-Weaver index. In the mixed thickets, there is a significant increase of both Rotifera and Protista abundance, accompanied by a decrease in Cladocera abundance; this may be associated both with a higher degree of destruction and with top-down control. In the thickets of true aquatic plants, a minimum content of dissolved oxygen and maximum water temperature are observed, which may precondition low attractiveness of these sites for juvenile fish. This is confirmed by the results of our study, when the zooplankton in these thickets is characterized by the maximum abundance and biomass (including Cladocera), as well as by the minimum Shannon-Weaver index. Similar data were obtained in caltrop thickets, where a decrease in oxygen concentration leads to unfavorable conditions for young fish (age 0+ and 1+), so zooplankton here has a high biomass (Dyachenko et al., 2020).

Therefore, developing of zooplankton community in spring in different types of macrophyte thickets of kultuk zone of the Volga River Delta is influenced the most by the amount of accumulated organic matter and, probably, by the composition of Rotifera species (including dormant stages and/or eggs). In June and July, the grazing pressure by fish is of primary importance, and grazing intensity is preconditioned by the proximity of the sites to the bunchins and the vegetation density, as well as by weediness, temperature conditions, and fish fry grazing pressure.

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