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Article

Interannual changes in zooplankton of the canals of the Volga delta in the spring-summer period

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Abstract. Research conducted in 2011–2014 revealed the main trends in structural and quantitative changes in zooplankton in the Volga delta channels in low-water years compared to middle-water years. It has been shown that in dry years, zooplankton is characterized by a decrease in species richness and high quantitative development of juvenile stages of Copepoda. In a mid-water year, zooplankton is characterized by a high total and specific species richness, an average individual mass of Crustacea, in the spring – a high biomass of Cladocera, in the summer – a decrease in the abundance and biomass of Cladocera, an increase in the quantitative characteristics of Rotifera, and among ecological groups – the proportion of floating organisms. The formation of zooplankton is influenced by a complex of factors, among which, at different times, are the volume of runoff, water level, the rate of its rise, the period of standing and the value of the maximum level, temperature conditions, the duration of the flood, the water content of the floodplain, control by juveniles fish.

Keywords: hydrological regime, weather conditions, control of juvenile fish, species richness, quantitative characteristics, ecological groups of invertebrates

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Научная статья

Межгодовые изменения зоопланктона протоков дельты Волги в весенне-летний период

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Аннотация. Проведенные в 2011–2014 гг. исследования выявили структурные и количественные изменения зоопланктона протоков дельты Волги в маловодные годы по сравнению со средневодным. Показано, что в маловодные годы зоопланктон характеризуется снижением видового богатства и высоким количественным развитием ювенильных стадий Copepoda. В средневодный год зоопланктон отличается высоким общим и удельным видовым богатством, средней индивидуальной массой ракообразных, весной – высокой биомассой ветвистоусых ракообразных, летом – снижением численности и биомассы Cladocera, повышением количественных характеристик Rotifera, а среди экологических групп – доли плавающих организмов. Показано, что на формирование зоопланктона оказывает влияние комплекс факторов, среди которых в разное время выделяются объем стока, уровень воды, скорость его подъема, сроки стояния и величина максимального уровня, температурный режим, продолжительность половодья, обводненность поймы, контроль со стороны молоди рыб.

Ключевые слова: гидрологический режим, погодные условия, контроль сверху, видовое богатство, количественные характеристики, экологические группы

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Introduction

Within the deltas of large rivers there are unique and at the same time vulnerable ecosystems (Alekseevskii et al., 2016), which is explained by the genesis of water bodies – redistribution and significant transformation of physical, chemical and biological characteristics of runoff, interaction of river and sea waters (Alekseevskii et al., 2014; Mikhailov, 1997, 1998; Nigamatzyanova et al., 2015). The delta of the Volga River is one of the largest in the world; it is characterized by a complex hydrographic net with specific ecological conditions (Astrakhansky zapovednik, 1991; Chuikov et al., 1996; Gorbunov, 1976). Volga water enters the sea through channels that occupy about 6.5% of the delta area (Gorbunov, 1976). The channels have a trough-shaped cross-section, with prevailing depths ranging from 1–4 to 10–15 m and widths reaching several tens of meters (Chuikov et al., 1996).

The Volga Delta channels serve as habitats for riparian fishes (gouster *Blicca bjoerkna* Linnaeus, 1758, rod *Aspius aspius* Linnaeus, 1758, pikeperch *Sander lucioperca* Linnaeus, 1758, perch *Perca* spp. Linnaeus, 1758, silver carp *Carassius auratus* Linnaeus, 1758) and migration routes for semi-anadromous species (roach *Rutilus rutilus caspicus* Jakowlew, 1870, bream *Abramis brama* Berg, 1949, carp *Cyprinus carpio* Linnaeus, 1759) (Astrakhansky zapovednik, 1991). The current flood regime and anthropogenic intra-annual redistribution of flow in the Volga Delta largely do not meet the interests of fisheries, contribute to changes in the conditions of biodiversity formation, quantitative characteristics of biological resources, and reduce the biological runoff (Gorbunov, 1976; Gorbunova, 2005; Koblitskaya, 1992; Litvinov and Podolyako, 2014; Taradina and Chavychalova, 2017). This leads to partial loss of fish spawning grounds, disruption of conditions for its reproduction and formation of a food base for young fish and, as a result, to a decrease in the efficiency of natural reproduction (especially of roach and bream) (Gorbunov, 1976; Kizina and Ponomareva, 2009; Levashina and Ivanov, 2014; Litvinov and Podolyako, 2014; Taradina and Chavychalova, 2017; Vetlugina, 2012;). Especially strong depressing effects on fish reproduction in the delta are observed in years with low-water flow of the Volga and regression of the Caspian Sea (Alekhina and Finaeva, 2001; Katunin, 1971; Kizina, 1999; Litvinov, 2018; Podolyako, 2013, 2018; Taradina and Chavychalova, 2017; Taradina et al., 2008; Vasilchenko, 1977) that continues at present.

Zooplankton are among the main elements of trophic networks of diverse water bodies (Derevenskaya et al., 2012; Gliwicz, 2003; Gutelmacher et al., 1988; Kryuchkova, 1989, Stolbunova and Stobunov, 2010). Characteristics of zooplankton are widely used as indicators of ecological processes and condition of water bodies (Fedyaeva and Fedyaev, 2022; Lin et al., 2014; Trindade et al., 2018). In floodplain reservoirs and watercourses, the main factor influencing the formation of its communities is the hydrological pulse (periodic inundation of the floodplain with water during floods) (Fashchevsky, 2007; José de Paggi et al., 2014; Schöll et al., 2012). Fluctuations in the level of the main river determine the degree to which it is connected to the floodplain and have a significant impact on zooplankton (Frutos et al., 2006). Prolonged periods of extreme low-water years act as a stressor for aquatic organisms (José de Paggi et al., 2014) and influence changes in water quality (Lake, 2003).

Zooplankton in the Volga Delta water bodies have been studied for a long time – since the mid 19th century (Baer, 1856; Benning, 1924; Ivlev, 1940; Kosova, 1957, 1958, 1960; Skorikov et al., 1903; Zinoviev, 1947, 1970, et al.). Much attention was paid to studying the influence of river flow regulation on the species composition, seasonal dynamics and ecology of the planktonic invertebrates of typical water bodies of the Volga delta and their role in the nutrition of young fish (Kosova, 1965a, b, 1968a, b, 1970). It was noted that as a result of flow regulation, processes of biocenosis structure reorganization and adaptation of organisms to new conditions began: sharp level fluctuations, late and short floods, changes in thermal regime and transparency (Kosova, 1970). In the channels in the first years after regulation, the number of species increased due to phytophilic, benthic and penetrated northern species, and the number of zooplankton also increased (up to 85.6–549.8 thous. ind./m^3) (Astrakhansky zapovednik, 1991; Kosova, 1970). In the late 1960s – early 1970s, during the period of flow reduction, a decline in zooplankton development was observed; its maximum abundance in the delta channels was in the range of 28.5–67.5 thous. ind./m^3 (Astrakhansky zapovednik, 1991). A number of hydrobiological studies in the conditions of the Caspian Sea level rise from the late 1970s to the late 1990s showed that there was an increase in the proportion of rheophiles, expansion of the area of distribution of species of the Caspian brackish-water complex and penetration of northern invertebrate species, as well as an increase in the zooplankton abundance of the channels up to 630.7–977.6 thous. ind./m^3 (Astrakhansky zapovednik, 1991; Gorbunov and Kosova, 1991; Gorbunov et al, 1996, 1999, 2003; Kosova and Gorbunov, 1989; Kosova et al., 1989). Beginning in 2006, the modern stage of the low-water period was observed;

the years we studied included low-water years, which differed among themselves by parameters of weather and hydrological conditions, as well as mid-water years. At the same time, the available studies insufficiently describe structural changes in zooplankton of the channels under conditions of years of different water content.

Therefore, the aim of this work was to analyze interannual changes in the zooplankton structure of the Volga Delta flow zone in spring and summer depending on weather conditions and hydrological regime.

Materials and methods

Primary material was collected in the spring-summer period (April–August) 2011–2014 at the Obzhorovsky site of Obzhorova channel (N 46.304796 E 48.986697), and at the Damchiksky site of Bystraya channel (N 45.790011 E 47.888501) and Lotosny erik (N 45.782200 E 47.879360) of the Astrakhan State Reserve.

During sampling, 100 liters of water were filtered through a plankton net with a mesh size of 64 μm, and desktop processing was carried out using standard methods (Metodicheskie rekomendatsii..., 1982). The zooplankton condition was assessed by species richness (number of species encountered), specific species richness (number of species in the sample), abundance, biomass, ratio of species number, abundance and biomass of taxonomic groups of invertebrates, dominant species, Shannon index of abundance and biomass, average individual mass of crustaceans, share of ecological groups in total abundance and biomass. Ecological groups were identified on the basis of invertebrate classifications based on a feeding type and a mode of locomotion (Krivenkova, 2018; Chuikov, 1981a, b).

Information on water level and temperature was obtained from the data of water gauging stations of the Astrakhan State Reserve on the Bystraya channel[1], the volume of the Volga River flow near Volgograd was obtained from Rosgidromet data[2].

Statistical analysis was carried out using parametric indices in normal distribution (ANOVA) and nonparametric methods in the reverse case (Kruskal–Wallis H-Test), and normality test – by the Shapiro-Wilk test. The Pearson correlation coefficients ($p \leq 0.05$) (in case of normal distribution) and Spearman correlation coefficients ($p \leq 0.05$) of abiotic factors and zooplankton indicators were determined in Microsoft Excel 2010 and STATISTICA 10 programs (Khalafyan, 2007). Statistical methods were used to establish the reliability of differences between zooplankton indicators in years with different water availability, as well as to identify its dependence on abiotic factors.

Characteristic of weather and hydrological conditions in 2011–2014

A detailed description of the hydrological regime during the study period is given in a number of works[1] (Litvinov, 2018; Litvinov and Podolyako, 2014; Podolyako, 2013, 2018). Based on the average annual runoff of 252 km^3, 2011, 2012, and 2014 are classified as low-water years (runoff in these years was 201, 240, and 224 km^3 per year, respectively), and 2013 to medium-water (271 km^3) (Podolyako, 2018). The maximum amount of precipitation in spring was in 2011 (143.7 mm), while in 2012–2014 its total was significantly lower (29.5–26.5 mm). In summer, the highest amount of precipitation was recorded in 2013 – 68.2 mm, in 2011–2012 – 48.9 and 46.1 mm, and in 2014 this indicator was the lowest – 10.4 mm.

Low-water years were characterized by a number of features. In 2011, the lowest runoff volume (92 km^3) and a short flood (68 days) were recorded. Besides, a significant decrease in water level before the flood – in March–April (−23 cm) and its subsequent sharp rise (by 109 cm), a large difference in the level on the date of the beginning of the flood and the date of the maximum level (138 cm), the lowest maximum level (289 cm) and a short duration of its standing (8 days) were noted. This year was also characterized by prolonged cold weather, low air and water temperatures in spring, and a late transition through +4 °C mark (April 6). In June, the water level drop was sharp (−63 cm) and in July more gradual (−15 cm). Among the low-water years, 2012 was characterized by the highest spring runoff volume (114 km^3), water level decrease before the flood (−46 cm), maximum level (309 cm) and duration of its standing (21 days). In addition, in this year the level rise occurred in two stages. First, there was a sharp rise in the flood, the greatest difference in levels on the date of the beginning of the flood and the date of

[1] Letopis' prirody Astrkhanskogo zapovednika [Annals of Nature of the Astrakhan State Reserve], 2011–2014.

[2] Federal Service for Hydrometeorology and Environmental Monitoring (Roshydromet), 2022. Web page. URL: https://www.meteorf.gov.ru / (accessed: 02.09.2022).

its maximum value (145 cm), the latest dates of maximum level standing (May 24), late dates of water temperature transition through +4 °C (April 6). Then a sharp rise in temperatures to maximum values in April. Stabilization of high water levels and late establishment of low water levels were observed in June, but in July there was a sharp decrease (to −62 cm). In 2014, a low volume of runoff for the flood period (101 km^3), late (April 27) and short flood (68 days) were recorded. However, compared to other low-water years, the highest and most stable water level before the onset of the flood was registered, there were no fluctuations during 3 months (February–April). This contributed to smooth level rise, minimal difference of levels on the date of flood onset and the date of its maximum value (92 cm), early (May 14) but short standing period (12 days) of the maximum level (298 cm). In addition, early dates of water temperature transition through +4 °C (March 26) and smooth temperature rise were recorded. In June, a significant decrease in the level (up to −63 cm) was noted, which continued in July (−31 cm).

The mid-water year 2013 was characterized by early (28 March), high (317 cm) and long flood (123 days) with a large volume of runoff (140 km^3) and a long period of maximum level standing (41 days). Before the onset of flooding, a decrease in March (–16 cm) and a high level in winter were noted, although the difference in level at the onset of flooding and at the period of maximum level was not as high (126 cm). Also, this year was characterized by early dates of water temperature transition through +4°C (March 26), late, but the sharpest decline of the flood in July (−83 cm).

The findings showed the direct relationships between the volume of runoff during the flood period and water temperature in May (r = 0.74), water level in April-July (r = 0.81–0.99), maximum water level (r = 0.96), the difference in water levels in June–May and April–March (r = 0.87; 0.63), the number of days of standing maximum level (r = 1.00), flood duration (r = 0.98), flood end date (r = 0.76), juvenile fish yield (r = 0.85) and water level at the beginning of the flood (r = 0.45), as well as negative relationships with total precipitation (r = −0.68), May–April water level difference (r = −0.56), including the date of water temperature transition through +4 °C (r = −0.51). The end date negatively (r = −1.0) and duration of flooding (r = 0.73), water temperature in July (r = 0.64), and water level in June and July (r = 0.62 and 0.75) directly correlated with summer precipitation.

Results

During the study period, 147 invertebrate taxa were recorded in the zooplankton composition of the channels, including Rotifera – 71, Copepoda – 40, and Cladocera – 36. Also in the samples Protista species (10) and representatives of Ostracoda, Oligochaeta, Nematoda, Arachnidae, Chironimidae, Coleoptera, Plecoptera, Ephemeroptera, Simuliidae, Gastropoda, Larvae Pisces, Dreissena veligera, Hydra sp. were noted. The lowest species richness of zooplankters was recorded in 2011–2012 and the highest – in 2013 (Table 1).

Spring

Every year in 2012–2014, 4 species were consistently (75–100% of samples) found in the zooplankton composition, in 2011 was 1. Among them, only *Keratella quadrata* (Müller, 1786) was present throughout the study period. In 2012–2014 *Brachionus calyciflorus* (Pallas, 1766) was present, in 2012–2013 it was *Coronatella rectangula* (Sars, 1862), in 2013–2014 *Chydorus sphaericus* (Müller, 1785), in 2012 *Euchlanis dilatata* (Ehrenberg, 1832), and in 2014 *Bosmina longirostris* (Müller, 1785).

Specific species richness ranged from 13.5 ± 6.9 to 24.0 ± 13.0, with the highest recorded in 2013 and the lowest in 2011 and 2012, but differences were not confirmed statistically (Fig. 1). The number of species in the sample was directly related to total level change (r = 0.64), water level in February (r = 0.43) and water temperature (r = 0.57).

The basis of specific species richness was rotifers, with the maximum number of rotifers recorded in 2012 and 2013 and the minimum in 2011 (Table 2). In 2013 and 2014, zooplankton was characterized by the highest specific species richness of Copepoda and Cladocera, although only the number of Copepoda species differed statistically significantly.

Specific species richness of Rotifera, Copepoda and Cladocera was positively correlated with water level (r = 0.65; 0.62 and 0.58), Rotifera was also positively correlated with water temperature (r = 0.61). At the same time, negative correlations of specific species richness of Copepoda and Cladocera with total precipitation (r = −0.46 and −0.45), including Cladocera with the date of water temperature transition through +4 °C (r = −0.44), were found.

Table 1. Species richness of zooplankton in the channels of the Volga Delta in 2011–2014.

Taxa	Year			
	2011	2012	2013	2014
Rotifera	40	40	49	41
Copepoda	17	19	29	23
Cladocera	21	17	25	25
Total number of species	78	76	103	89
Others	11	13	12	13

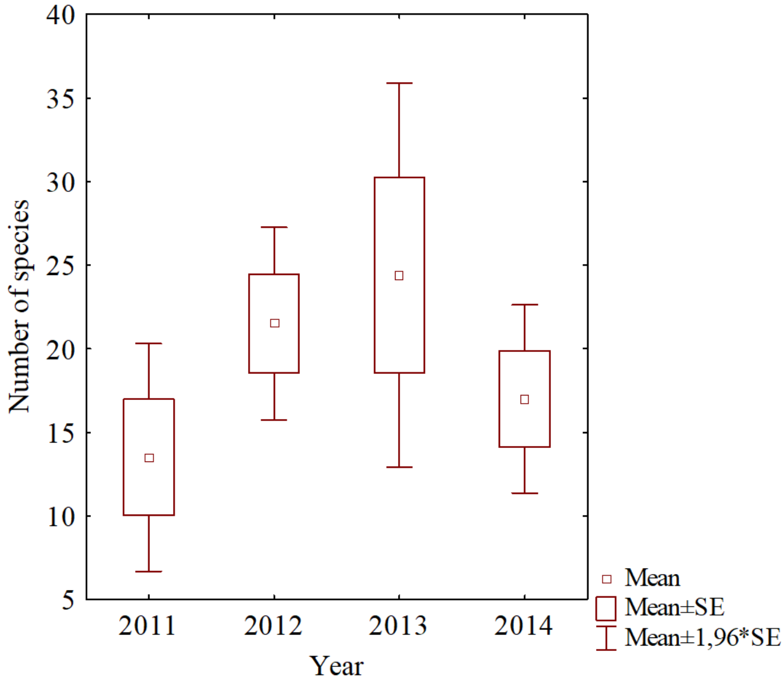

Fig. 1. Specific species richness of zooplankton in the channels of the Volga Delta in the spring of 2011–2014.

Zooplankton abundance ranged from 0.9 ± 1.5 to 10.0 ± 6.3 thous. ind./m^3 and biomass from 2.5 ± 4.9 to 40.2 ± 36.0 mg/m^3 (Fig. 2). Minimum abundance and biomass were recorded in 2011, maximum density in 2012, and biomass in 2012–2013, but the differences were not statistically significant. However, in 2012, the quantitative characteristics of Rotifera and Copepoda were statistically significantly higher than the data obtained in other years; maximum abundance of Cladocera was recorded in 2014, and biomass – in 2013 (Table 2).

Positive correlations of zooplankton abundance (r = 0.56), zooplankton biomass (r = 0.44), Rotifera abundance and biomass (r = 0.46; 0.53), Copepoda abundance (r = 0.63) with water temperature in April were found. Copepoda abundance was negatively related to spring precipitation (r = −44), positively to the date of flood onset (r = 0.44), and Cladocera abundance to water level at the onset of flooding (r = 0.47). Similar to abundance and biomass of Rotifera (r = 0.48; 0.67), Copepoda (r = 0.53; 0.53) and Cladocera (r = 0.67; 0.48). total abundance and biomass were related to water temperature dynamics (r = 0.68; 0.57).

In 2012–2013, Rotifera formed the basis of abundance (Table 2) due to the dominance of *Euchlanis dilatata* (2012–2013), *Brachionus quadridentatus* (Hermann, 1783) (2012), *B. calyciflorus* (2012–2014), *Keratella quadrata* (2013). In 2011, Copepoda prevailed with the dominance of juvenile Cyclopoida, which were among the dominants throughout the study period. In 2014, the basis of abundance was formed by Cladocera at the expense of *Bosmina longirostris*. Due to the dominance of the same species

Table 2. Structural and quantitative indicators of zooplankton of the Volga Delta ducts in the spring of 2011–2014. Here and further: S – specific species richness, mean; N – abundance, median, thousand ind./m^3; % N – the proportion in the total abundance, mean; B – biomass, median, mg/m^3; % B – the share in the total biomass, mean; H_N – the Shannon abundance index, mean, bits/ thous. specimen; H_B – the Shannon biomass index, mean, bits/g; w_{Crust} – the mean individual mass of crustaceans, mg; F – Fisher's test, $H_{K–W}$ – Kruskal–Wallis test, *p* – significance level; [a–d] – significant differences ($p \le 0.05$) between years, in pairwise comparisons; significant differences between years are indicated in bold.

Index		Year 2011[a]	2012[b]	2013[c]	2014[d]	F	$H_{K–W}$	*p*
S	Rot	6.2 ± 4.6	10.8 ± 5.2	10.4 ± 5.7	8.0 ± 3.5	0.9	–	0.41
	Cop	2.5 ± 1.3[c,d]	4.1 ± 1.9	6.6 ± 2.8[a]	6.0 ± 2.4[a]	**3.1**	–	**0.05**
	Clad	0.7 ± 1.5[c]	3.6 ± 2.6	6.0 ± 5.0[a]	4.1 ± 2.4	2.0	–	0.14
N / % N	Rot	0.3 ± 1.3[b] / 38.4 ± 30.5	4.6 ± 5.7[a] / 53.9 ± 24.5	0.7 ± 2.1 / 47.4 ± 20.9	1.2 ± 0.6 / 36.6 ± 25.1	0.6	5.6	0.13 / 0.61
	Cop	0.4 ± 0.3[b] / 61.8 ± 33.7[c]	2.9 ± 2.1[a] / 39.9 ± 25.3	0.5 ± 1.1 / 26.8 ± 11.7[a]	0.8 ± 0.4 / 29.6 ± 25.3	1.8	**8.7**	**0.03** / 0.17
	Clad	0.03 ± 0.01 / 1.8 ± 3.7	0.3 ± 0.5 / 6.0 ± 7.7	1.3 ± 1.9 / 25.7 ± 28.4	1.9 ± 2.9 / 33.6 ± 34.4	2.1	6.6	0.08 / 0.12
B / % B	Rot	0.9 ± 4.3 / 41.5 ± 31.2	26.1 ± 40.9 / 71.4 ± 22.8[c]	1.7 ± 9.7 / 30.9 ± 24.0[b]	2.6 ± 11.2 / 33.5 ± 27.4	2.9	6.2	0.09 / **0.05**
	Cop	0.8 ± 0.8 / 52.5 ± 33.1[b]	4.1 ± 3.5 / 17.4 ± 12.2[a]	4.8 ± 5.4 / 30.7 ± 25.3	3.8 ± 6.2 / 31.4 ± 27.8	1.5	5.7	0.12 / 0.22
	Clad	0.2 ± 0.5[c] / 5.6 ± 11.3	0.7 ± 3.4[c] / 10.6 ± 17.1	19.6 ± 29.7[a,b] / 37.4 ± 36.3	10.7 ± 13.6 / 34.6 ± 29.8	1.9	5.0	0.16 / 0.15
H_N		2.9 ± 0.3[d]	2.4 ± 0.7	3.2 ± 0.6[d]	2.1 ± 0.4[a,c]	**3.9**	–	**0.02**
H_B		2.6 ± 0.6	3.0 ± 0.6	3.1 ± 0.7	2.2 ± 0.6	1.2	–	0.32
w_{Crust}		0.001 ± 0.001	0.006 ± 0.01	0.009 ± 0.01	0.003 ± 0.0016	0.8	–	0.47

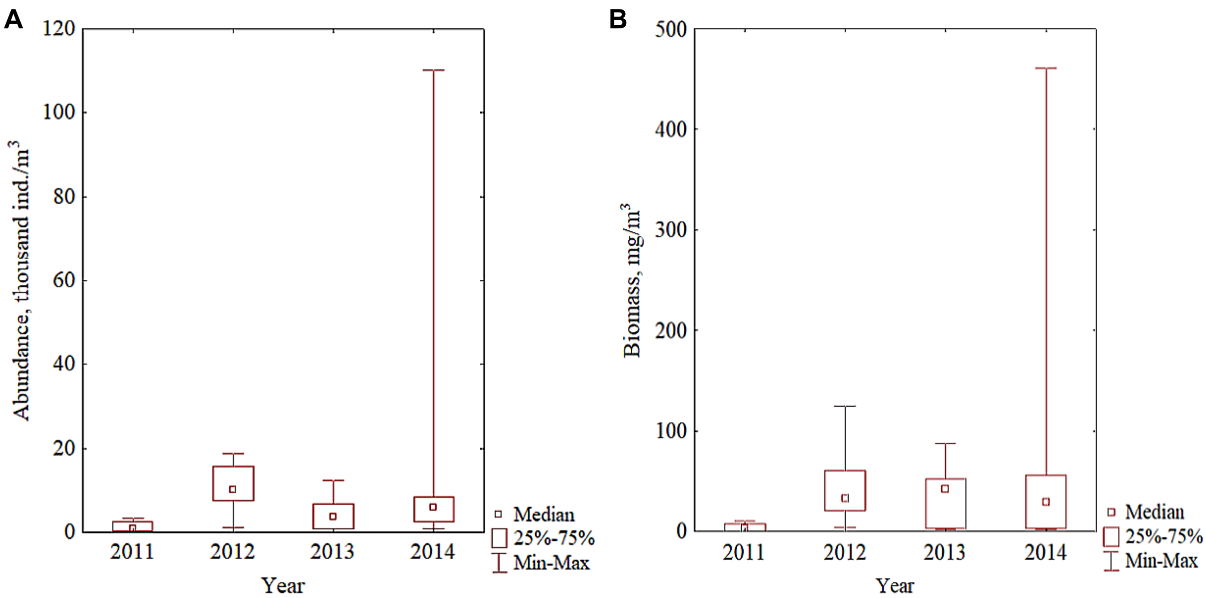

Fig. 2. Abundance (**A**) and biomass (**B**) of zooplankton in the channels of the Volga Delta in the spring of 2011–2014.

as in terms of abundance, most biomass in 2011 provided Copepoda, in 2012 – Rotifera, in 2013 and 2014 – Cladocera (Table 2).

Positive correlations with water level were found with the proportion of Cladocera in total zooplankton abundance and biomass (r = 0.46 and 0.53), while negative – with the proportion of Copepoda (r = −0.79 and −0.53). In addition, the proportion of Cladocera in total abundance and biomass positively correlated with water level at the beginning of the flood (r = 0.52 and 0.48), whereas negatively - with the date of water temperature transition through +4 °C (r = −0.51 and −0.49), and the proportion in total biomass was correlated with water level in April (r = 0.46). The proportion of Rotifera in total biomass was positively related to the date of water temperature transition through +4 °C (r = 0.47) and negatively - to water temperature in March and April (r = −0.57 and −0.57). The proportion of Copepoda in total abundance decreased with decreasing water temperature in spring (r = −0.51), but increased with increasing precipitation (r = 0.45).

Among the invertebrate ecological groups, swimming organisms formed the basis of abundance in 2013 and 2014, with a statistically significantly higher proportion of verticators in 2013, and primary dominant fine and coarse filter feeders in 2014 (Table 3). Floating-crawling organisms also formed a high proportion of the total abundance in all years, but their maximum abundance was observed in 2012 and 2013 at the expense of verticators, and in 2013 also at the expense of secondary filter feeders, scrapers

Table 3. The share (in %) of ecological groups of invertebrates in the total abundance of zooplankton in the channels of the Volga Delta in the spring of 2011–2014. I – free-swimming organisms, II – associated with the substrate, III – attached to the substrate and the surface film of water, IV – a mixed group of juvenile copepods; 1, 2 – verticators; 3 – fine filtrators; 4 – coarse filtrators; 5, 6 – primary, fine and coarse filtrators; 7 – secondary filtrators, scrapers and detritophages; 8 – collectors, omnivores; 9 – active predators, omnivores copepods; 10 – grabbing predators with an incudate type of mastax; 11 – Copepoda predators; 12 – attaching verticators; 13 – copepods filtrators and predators; F – Fisher's test; [a–d] – statistically significant (p ≤ 0.05) differences between years at pairwise comparisons; significant differences between years are indicated in bold.

Ecological group		Year					
By movement and relation to the substrate	By nutrition	2011[a]	2012[b]	2013[c]	2014[d]	F	*p*
I	1	8.8 ± 2.9[c]	9.5 ± 6.0[c]	22.3 ± 14.2[a, b, d]	5.2 ± 5.5[c]	**4.2**	**0.02**
	6	0.9 ± 1.8[d]	2.9 ± 5.2[d]	10.4 ± 15.6	33.1 ± 36.0[a, b]	2.7	0.07
	9	0	2.4 ± 4.0	1.9 ± 2.0	1.0 ± 1.3	0.8	0.47
	10	2.9 ± 2.8	3.6 ± 7.3	1.6 ± 3.2	0.3 ± 0.5	0.6	0.60
	13	0	0.008 ± 0.02	0.02 ± 0.06	0.01 ± 0.05	0.4	0.75
	Total	12.7 ± 3.5[d]	18.6 ± 8.8	36.4 ± 11.7	39.7 ± 32.7[a]	2.3	0.10
II	2	24.9 ± 30.3	40.5 ± 26.5	23.4 ± 13.8	25.5 ± 20.0	0.6	0.57
	7	0.9 ± 1.8	2.5 ± 2.0	14.0 ± 26.8	2.0 ± 2.2	1.0	0.38
	8	5.3 ± 6.8[b]	0.5 ± 0.6[a]	1.6 ± 1.3	1.7 ± 1.9	1.9	0.16
	11	0.1 ± 0.2	0.1 ± 0.2	0.8 ± 1.1	1.0 ± 1.7	0.9	0.43
	12	0	0	0	0	–	–
	Total	31.3 ± 30.9	43.7 ± 25.1	39.8 ± 21.6	30.2 ± 20.3	0.4	0.75
III	5	0	0.5 ± 1.1	1.2 ± 2.5	0.1 ± 0.3	0.7	0.55
IV	3	50.3 ± 36.7[c]	31.7 ± 24.3	14.6 ± 9.4[a]	24.4 ± 22.9	1.7	0.23
	4	1.9 ± 3.3	4.9 ± 2.9	8.6 ± 5.8	10.4 ± 14.6	0.9	0.40
	Всего	52.3 ± 35.3	36.6 ± 24.8	23.2 ± 14.8	34.8 ± 22.3	1.0	0.42

Table 4. Share (in %) of ecological groups of invertebrates in the total biomass of zooplankton in the channels of the Volga delta in the spring of 2011–2014. Designations as in Table 3.

Ecological group		Year					
By movement and relation to the substrate	By nutrition	2011[a]	2012[b]	2013[c]	2014[d]	F	*p*
I	1	6.4 ± 6.1	23.8 ± 35.1	3.3 ± 2.9	1.7 ± 5.0	1.6	0.22
	6	1.9 ± 3.8	3.6 ± 6.7	17.0 ± 24.1	29.4 ± 34.3	1.8	0.18
	9	0	8.1 ± 9.1	9.1 ± 6.8	7.8 ± 9.9	0.9	0.46
	10	5.8 ± 4.8	11.5 ± 22.9	8.3 ± 17.4	8.7 ± 18.9	0.07	0.97
	13	0	0.06 ± 0.1	0.1 ± 0.3	0.2 ± 0.4	0.3	0.78
	Total	14.2 ± 2.4	47.2 ± 28.9	38.0 ± 30.3	46.6 ± 37.4	1.2	0.33
II	2	26.3 ± 33.0	35.5 ± 30.2	20.6 ± 25.1	18.6 ± 25.1	0.4	0.73
	7	1.8 ± 3.6	4.8 ± 5.7	8.8 ± 14.1	4.4 ± 3.6	0.6	0.62
	8	8.4 ± 9.9	1.4 ± 2.2	3.6 ± 6.4	12.0 ± 16.2	1.2	0.32
	11	1.9 ± 3.8	0.4 ± 0.6	5.9 ± 8.5	7.1 ± 11.2	1.0	0.40
	12	0	0	0	0	–	–
	Total	38.5 ± 33.8	42.2 ± 28.5	38.9 ± 22.6	42.3 ± 31.0	0.02	0.99
III	5	0	2.4 ± 5.8	11.6 ± 21.2	1.8 ± 3.9	1.0	0.37
IV	3	44.6 ± 39.5[b, c, d]	3.9 ± 3.1[a]	1.3 ± 1.3[a]	4.6 ± 6.1[a]	**6.3**	**0.004**
	4	1.6 ± 2.8[c]	3.9 ± 2.2	10.8 ± 8.8[a]	6.0 ± 5.7	2.3	0.11
	Всего	46.3 ± 38.0[b, c, d]	7.9 ± 3.7[a]	12.1 ± 9.2[a]	10.8 ± 8.8[a]	**4.7**	0.01

and detritophages. In low-water years, a mixed group of juvenile Copepoda by type of movement and feeding reached high abundance, where fine filter-feeders dominated, the share of which in 2011 was statistically significantly higher than in other years.

We found positive correlations of the share of floating organisms in the total zooplankton abundance, floating primary fine and coarse filter-feeders with water level at the beginning of the flood (r = 0.54 and 0.50), floating verticators with water level in March (r = 0.44). In addition, the proportion of floating verticators in total abundance negatively correlated with the date of flood onset (r = −0.63) and the March–February water level difference (r = −0.58). The proportion of primary fine and coarse filter feeders positively correlated with spring water temperature (r = 0.56), and the proportion of verticals - negatively with water temperature (r = −0.46).

The basis of biomass among ecological groups of zooplankton in 2012–2014 was formed by floating organisms (Table 4), with the dominance of primary fine and coarse filter feeders in 2013 and 2014, and verticators in 2012, as well as predator-omnivores and incudate mastax predators. Swimming-crawling organisms had a high proportion in all years at the expense of verticators, in 2013 due to secondary filter feeders, scrapers and detritophages, and in 2011, 2014 – collectors and omnivores organisms. In 2011, the proportion of the mixed group of juvenile Copepoda by feeding and movement type was statistically significantly higher than in the other years.

This group demonstrated strong correlations with total precipitation in spring (r = 0.73) and negative – with water level in January. The proportion of fine filter feeders negatively correlated with water levels in January–April (r = −0.44 and −0.72), while coarse filter feeders positively with water levels in January and April (r = 0.53 and 0.53). The group of juvenile copepods and fine filtrators mixed in feeding and movement patterns negatively correlated with water temperature in spring (r = −0.50 and −0.46), while the proportion of floating primary fine and coarse filtrators positively correlated with water temperature (r

= 0.53). Negative correlations were found between the proportion of primary fine and coarse filterers and the date of water temperature transition through +4 °C (*r* = −0.45), and the proportion of free-swimming verticators through +10 °C (*r* = −0.46).

The Shannon index values for abundance in 2011 and 2013 were statistically significantly different from those in 2014; for biomass, the highest values were found in 2012–2013. Mean individual crustacean masses were not statistically significantly different between years, but the highest indicators were found in 2013, whereas the lowest – in 2011 and 2014 (Table 2).

Summer

Each year, 3 consistently occurring species were recorded in the composition of zooplankton, in all years – 2 species *Brachionus calyciflorus* and *Bosmina longirostris.* Also, *Asplanchna priodonta* (Gosse, 1850) were present in 2012–2013, *Coronatella rectangula* – in 2011 and 2014, and *Thermocyclops oithonoides* – in 2012 (Sars, 1863).

Specific species richness ranged from 18.8 ± 3.8 to 23.0 ± 6.6. The maximum number of species in the sample was recorded in 2013 due to Rotifera and Copepoda, while the minimum number of species was recorded in 2011. The highest number of Cladocera species was noted in 2014, although the differences were not confirmed statistically (Fig. 3, Table 5). The specific species richness of Rotifera was found to be directly correlated with water levels in May and June (*r* = 0.61 and 0.47), number of flood days (*r* = 0.53).

Zooplankton abundance ranged from 6.8 ± 2.7 to 14.7 ± 9.2 thous. ind./m^3 and biomass ranged from 19.8 ± 40.5 to 49.6 ± 43.7 mg/m^3. Zooplankton abundance and biomass were the highest in 2014 and the lowest in 2012, 2013, although these differences were not statistically significant (Fig. 4). The maximum abundance of Rotifera was recorded in 2013, the minimum in 2011, Copepoda – in 2011, 2013, and Cladocera – in 2014 and 2011–2012 (Table 5). A direct correlation was revealed between Cladocera abundance and water temperature dynamics (*r* = 0.51).

Rotifera formed the basis of abundance in 2013, Copepoda - in 2011 and 2014; these groups were equally represented in 2012 (Table 5). The dominant species included *Brachionus calyciflorus* (2011–2014), *Asplanchna priodonta* (2013), and juvenile Copepoda (2011–2014).

Direct correlations of Copepoda proportion in total zooplankton abundance with water temperature in June were found (*r* = 0.52). The proportion of Rotifera was positively correlated with the maximum water level and the date of its establishment (*r* = 0.47 and 0.49). There was an inverse correlation of

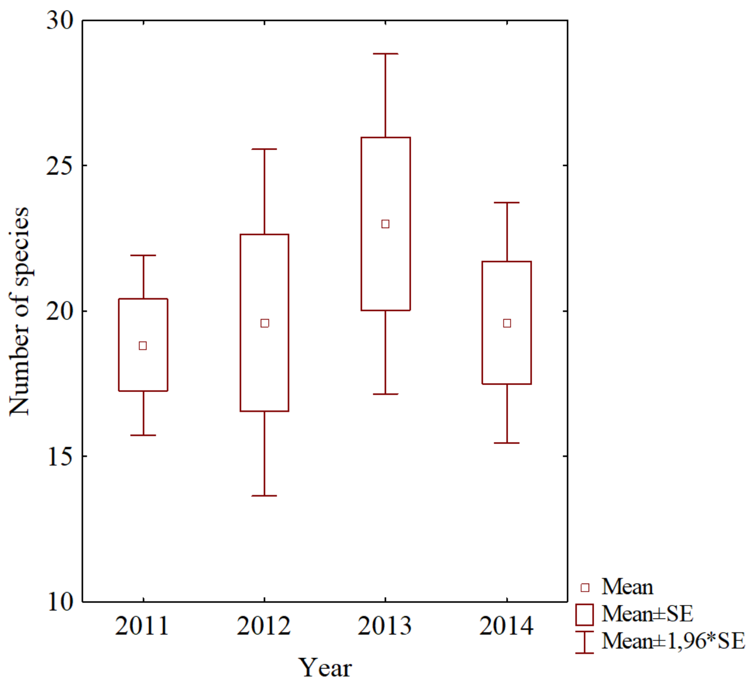

Fig. 3. Specific species richness of zooplankton in the channels of the Volga Delta in the summer of 2011–2014.

Table 5. Quantitative indicators of zooplankton in the Volga delta channels in the summer of 2011–2014. Designations as in Table 2.

Index		Year 2011^{a}	2012^{b}	2013^{c}	2014^{d}	F	$H_{K–W}$	p
S	Rot	7.0 ± 3.4	7.1 ± 4.1	10.5 ± 3.2	6.5 ± 3.0	1.6	–	0.20
	Cop	4.5 ± 2.1	4.6 ± 1.6	6.1 ± 1.4	5.7 ± 1.6	1.4	–	0.24
	Clad	5.8 ± 3.3	4.0 ± 2.1^{d}	5.3 ± 1.5	6.5 ± 2.3^{b}	1.6	–	0.20
N / % N	Rot	1.5 ± 2.3 28.1 ± 22.3	3.4 ± 4.2 41.6 ± 14.1	4.4 ± 1.7 53.2 ± 16.3	2.4 ± 3.8 27.4 ± 25.0	1.8	2.5	0.47 0.16
	Cop	6.1 ± 4.1 55.3 ± 23.0^{c}	5.6 ± 4.0 48.2 ± 17.9	1.8 ± 1.1 22.9 ± 8.5^{a}	3.7 ± 8.8 46.6 ± 24.8	2.4	3.8	0.30 0.09
	Clad	0.8 ± 1.5 15.6 ± 9.9	0.9 ± 1.5 9.1 ± 6.2	1.3 ± 1.1 22.9 ± 20.3	2.3 ± 2.4 25.6 ± 19.6	1.0	2.9	0.40 0.37
B / % B	Rot	5.1 ± 4.7 34.2 ± 23.3	4.4 ± 10.9 33.5 ± 19.0	12.9 ± 10.2 50.4 ± 27.5	8.1 ± 15.5 33.2 ± 30.0	0.9	1.5	0.24 0.45
	Cop	11.6 ± 14.6 38.1 ± 20.3	11.8 ± 20.1 51.4 ± 16.8^{c}	7.7 ± 4.2 23.0 ± 13.1^{b}	6.6 ± 12.5 32.1 ± 27.3	1.6	0.6	0.62 0.21
	Clad	8.7 ± 29.9 36.6 ± 26.5	4.4 ± 9.7 16.6 ± 10.2	4.4 ± 8.8 26.0 ± 25.4	22.4 ± 10.5 34.5 ± 26.7	0.8	0.5	0.64 0.50
H_N		2.4 ± 0.8	2.6 ± 0.5	2.9 ± 0.6	2.5 ± 0.4	0.5	–	0.66
H_B		2.4 ± 0.8	3.2 ± 0.6	3.1 ± 1.0	2.8 ± 0.7	0.7	–	0.51
w_{Crust}		0.004 ± 0.002	0.003 ± 0.001	0.005 ± 0.001	0.003 ± 0.001	1.6	–	0.20

Copepoda proportion (r = −0.52) and a direct one of Rotifera proportion (r = 0.47) with the number of flood days. The proportion of Copepoda also negatively correlated with water level in April–June (r = −0.46 and −0.55), while the proportion of Rotifera and water level in May and June (r = 0.46 and 0.49) showed positive correlations.

Copepoda (2011–2012), Rotifera (2013) and Cladocera (2014) formed the basis of biomass. Juvenile Copepoda (2011–2014), *Brachionus calyciflorus* (2011–2014), *Asplanchna priodonta* (2013), *Megacyclops viridis* (Jurine, 1820) (2012), *Bosmina longirostris* (2011–2014) dominated. The proportion of Copepoda in total biomass positively correlated with the May–April water level difference (r = 0.44) and the date of maximum level (r = 0.48).

Among the ecological groups, swimming-crawling organisms formed the basis of zooplankton abundance in 2012–2013, while in 2011 and 2014, the proportion of the mixed group of juvenile Copepoda by mode of movement and feeding increased statistically significantly (Table 6). The maximum proportion of swimming organisms due to primary fine and coarse filter feeders and predators with mastax incudate type were recorded in 2013. The proportion of mixed group of juvenile copepods and fine filter feeders by mode of movement and feeding were found to be negatively correlated with the yield of juvenile fish on the spawning grounds (r = −0.53 and −0.56), duration of flood (r = −0.53 and −0.54), water level in May (r = −0.49 and −0.48) and June (r = −0.50 and −0.54). The proportion of floating-crawling organisms and floating-crawling verticators positively correlated with maximum water level (r = 0.43 and 0.44), and floating organisms - negatively with the date of flood onset (r = −0.47).

Throughout the study period, the biomass-dominant ecological groups included floating organisms at the expense of primary fine and coarse filter feeders, with the maximum proportion observed in 2011 and 2014 (Table 7). In addition, in 2011 and 2014, the mixed group of juvenile Copepoda by

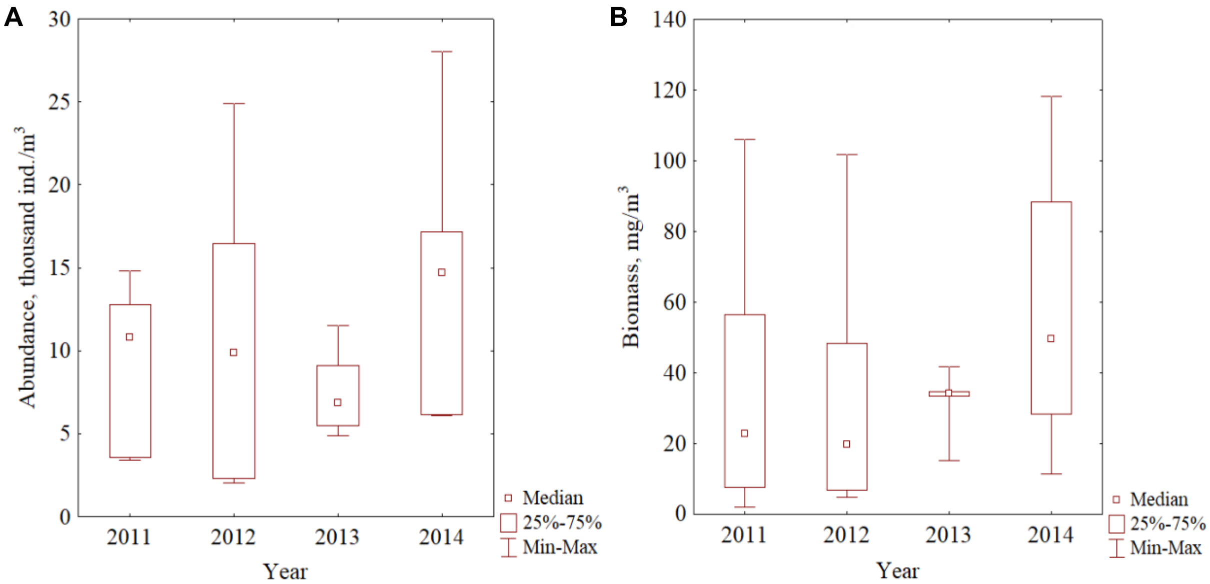

Fig. 4. Abundance (**A**) and biomass (**B**) of zooplankton in the channels of the Volga Delta in the summer of 2011–2014.

modes of locomotion and feeding had a high proportion, with maximum abundance in 2011. In 2013, the proportion of predators with incudate mastax type statistically significantly increased, and the proportion of swimming-crawling organisms also was growing due to verticators, with maximum reached in 2012.

Positive correlations of the share of swimming-crawling organisms in the total biomass with water temperature were found in April and May (r = 0.47 and 0.47), and for mixed by mode of movement and feeding of juvenile copepods – in June (r = −0.50). Negative correlations were noted for predators with incudate type of mastax and mixed group of juvenile Copepoda with the date of maximum water level establishment (r = −0.45 and −0.50) and for the latter group also with the duration of flooding (r = −0.45). The proportion of swimming-crawling organisms was negatively correlated with spring precipitation (r = −0.56).

The Shannon index values were not statistically significantly different, although the highest were for indices calculated for abundance in 2013, biomass in 2012–2013, and the lowest – in 2011 (Table 5). Interannual differences in mean individual crustacean masses were also not confirmed statistically, with the maximum value found in 2013 and the minimum in 2012 and 2014 (Table 5).

Discussion

The studies conducted in 2011-2014 in the Volga Delta showed that in low-water years the specificity of environmental conditions is associated with a decreased runoff during floods, late rise in levels, low levels, and their early recession. This contributes to the reduction of inundated floodplain areas, the short duration of floodplains, the decrease in the intensity of organisms entering the channels and organic matter from floodplain areas, including the increased role of abiotic factors in the development of zooplankton (Beaver et al., 2013; Frutos et al., 2006; José de Paggi et al., 2014; Zalocar de Domitrovic, 2002). As a result, we note (confirmed by correlation coefficients) the decreased zooplankton species richness and increased proportion of juvenile Copepoda at the expense of fine filter feeders previously found in the kultuk zone of the Volga Delta (Fedyaeva and Fedyaev, 2020; Shtepina, 2013) and under similar conditions in other regions (Frutos et al., 2006; José de Paggi et al., 2014; Keckeis et al., 2003). Floodplain pools are known to act as a source of biota diversity for the main river channel (José de Paggi et al., 2014; Schöll et al., 2012). The decrease in mean individual crustacean mass may be related to an increase in the proportion of juvenile Copepoda, less input of large crustaceans and organic matter from the floodplain.

In summer of low-water years, the specific species richness of zooplankton at the expense of Rotifera and Copepoda decreased when the volume of runoff, duration of flooding and amount of allochthonous organic matter decreased, and water level fluctuations occurred. The abundance and biomass of Rotifera, the average individual mass of crustaceans, and the Shannon index of abundance also

Table 6. Share (in %) of ecological groups of invertebrates in the total abundance of zooplankton in the channels of the Volga delta in summer in 2011–2014. Designations as in Table 3.

Ecological group: By movement and relation to the substrate	Ecological group: By nutrition	2011[a]	2012[b]	2013[c]	2014[d]	F	*p*
I	1	4.9 ± 7.7	5.6 ± 7.6	4.9 ± 8.9	1.3 ± 1.9	0.4	0.70
	6	14.0 ± 11.0	8.7 ± 4.0	19.2 ± 21.6	10.3 ± 16.6	0.6	0.61
	9	1.0 ± 1.6	1.0 ± 1.9	0.4 ± 0.5	1.6 ± 2.8	0.4	0.75
	10	3.0 ± 3.2	3.3 ± 4.2	8.5 ± 8.9	6.6 ± 9.8	0.8	0.49
	13	0.2 ± 0.3	1.4 ± 1.8	2.3 ± 4.1	0.3 ± 0.7	1.2	0.30
	Total	23.3 ± 10.7	20.3 ± 14.0	35.4 ± 19.9	20.3 ± 17.9	1.1	0.36
II	2	20.2 ± 17.0	38.3 ± 16.3	40.1 ± 19.5	22.9 ± 19.8	1.8	0.16
	7	1.0 ± 1.0	1.4 ± 1.3	3.5 ± 6.2	2.9 ± 3.6	0.6	0.57
	8	0.6 ± 1.2	1.6 ± 2.4	0.3 ± 0.3	0.5 ± 0.6	0.9	0.42
	11	3.3 ± 6.9	1.7 ± 2.1	1.0 ± 1.8	1.2 ± 1.3	0.4	0.72
	12	0	0	0	0	–	–
	Total	25.5 ± 21.2	44.6 ± 15.3	47.3 ± 24.8	27.9 ± 19.9	1.8	0.17
III	5	0.02 ± 0.03	0.07 ± 0.1	0.1 ± 0.2	0.4 ± 0.7	1.3	0.28
IV	3	36.0 ± 17.9[в]	22.7 ± 13.8	16.2 ± 6.8[a, d]	40.5 ± 16.0[в]	**3.4**	**0.03**
	4	14.5 ± 15.0	12.7 ± 5.5	4.4 ± 4.0	10.3 ± 9.5	1.1	0.36
	Total	50.6 ± 27.5[в]	35.4 ± 17.4	20.7 ± 8.6[a,г]	50.8 ± 24.1[в]	2.5	0.08

decreased, but the total abundance increased at the expense of juvenile Copepoda. The obtained correlation coefficients indicate the leading role of summer water level, flood runoff volume and water temperature.

An increase in water availability contributed to a number of changes in zooplankton communities. The maximum specific species richness and number of species encountered was recorded in the channels in a mid-water year, as previously noted (Fedyaev and Fedyaeva, 2020; Frutos et al., 2006; José de Paggi et al., 2014). In addition, high zooplankton biomass due to crustaceans, as well as their maximum average individual mass were observed. It is known that in high-water years, the proportion of large cladocerans crustaceans increases in floodplain water bodies, from which they enter the watercourses (Frutos et al., 2006). In the studied channels, this is confirmed by the presence of positive correlations of Cladocera abundance and biomass with water level before and at the beginning of the flood, as well as with water temperature. It is known that in spring in the channels, control from above by fish is minimal, as the main spawning and nursery area for fish in mid-water and high-water years is hollow spawning grounds (Koblitskaya, 1958; 1992; Litvinov and Podolyako, 2014; Podolyako, 2013; Taradina et al., 2008). In addition, in spring of the midwater year, zooplankton was characterized by a maximum share in the total abundance of floating verticators, but a minimum share of a mixed group of juvenile crustaceans of Copepoda – at the expense of fine filter feeders (Fedyaeva and Fedyaev, 2020). Low abundance of juvenile Copepoda in the river in years with high water availability has been described in a number of papers (José de Paggi et al., 2014; Keckeis et al., 2003). The increase in the proportion of floating verticators could be influenced by an increase in the influx of allochthonous organic matter from the floodplain into the channels, the mass of which increases almost 6 thousand times at the flood peak (Bogatov and Fedorovsky, 2017). Substrate and surface water film-associated primary fine and coarse filter feeders, floating-crawling secondary filter feeders, scrapers, and detritophages were also noted

Табл. 7. Share (in %) of ecological groups of invertebrates in the total biomass of zooplankton in the channels of the Volga delta in summer in 2011–2014. Designations as in Table 3.

Ecological group		Year					
By movement and relation to the substrate	By nutrition	2011^{a}	2012^{b}	2013^{c}	2014^{d}	F	*p*
I	1	1.0 ± 2.1	1.6 ± 1.9	1.7 ± 3.3	0.4 ± 0.7	0.4	0.74
	6	31.8 ± 30.7	13.0 ± 6.5	24.5 ± 26.3	16.4 ± 23.8	0.8	0.48
	9	5.2 ± 8.4	5.9 ± 9.1	1.9 ± 2.4	6.3 ± 7.6	0.3	0.78
	10	8.6 ± 13.3	5.3 ± 5.5^{c}	25.0 ± 20.7^{b}	11.4 ± 14.4	2.1	0.12
	13	3.4 ± 5.0	6.9 ± 9.3	4.8 ± 8.1	1.8 ± 4.1	0.6	0.61
	Total	50.3 ± 20.3	32.8 ± 19.7	58.1 ± 19.3	36.5 ± 26.8	1.7	0.19
II	2	12.3 ± 11.6^{b}	33.0 ± 18.6^{a}	21.7 ± 12.7	21.2 ± 23.2	1.5	0.23
	7	1.9 ± 3.0	1.6 ± 1.4	4.0 ± 8.2	4.6 ± 7.3	0.4	0.69
	8	0.6 ± 1.5	3.1 ± 5.0	0.5 ± 0.9	1.5 ± 1.6	0.9	0.42
	11	2.6 ± 2.8	8.7 ± 11.5	3.5 ± 6.3	5.6 ± 6.4	0.7	0.52
	12	0	0	0	0	–	–
	Total	17.5 ± 15.1^{b}	46.4 ± 20.9^{a}	29.9 ± 20.6	33.1 ± 19.5	2.4	0.09
III	5	0.2 ± 0.4	0.3 ± 0.7	1.4 ± 3.1	1.9 ± 2.9	0.9	0.43
IV	3	9.9 ± 8.0^{b}	3.2 ± 2.6^{a}	3.8 ± 3.1	10.4 ± 6.9	**2.8**	**0.06**
	4	21.4 ± 20.3	16.8 ± 9.6	6.2 ± 7.6	16.1 ± 15.8	1.0	0.39
	Total	31.3 ± 20.8^{c}	20.1 ± 11.7	10.0 ± 9.8^{a}	26.6 ± 20.1	1.8	0.19

among the dominant groups. Since many species utilize particulate organic matter as a food source (Wallace et al., 2006), the detection of phytophilic organisms in channels indicates that they come from floodplains with vegetation present (Frutos et al., 2006). The main importance of allochthonous organic matter in the biological productivity of the lower reaches of the Volga delta was pointed out by K.V. Gorbunov (1976). In the water area of the channels, destruction exceeds primary production, which occurs due to translocation and destruction of excess organic matter from the flooded floodplain.

In summer of the mean-water year, an increase in the specific species richness of Rotifera and Copepoda and in quantitative indices of Rotifera was observed. It is known that in high-water years, the number of rotifers in rivers growes (Corrales, 1979; José de Paggi, 1993; Vásquez and Rey, 1989) due to their short generation phases (Gulyas, 2002; Lansac Tôha et al., 2004; Pourriot et al, 1982; Rzóska, 1976), better adaptation to turbulence and high suspended sediment concentrations (Armengol et al., 1983; Bonetto and Corrales de Jacobo, 1985; José de Paggi and Paggi, 2007; José de Paggi et al., 2014; Kirck and Gilbert, 1990). At the end of flooding, the channels are enriched with organic matter due to its removal from the floodplain (Kosova, 1970), which leads to the creation of more favorable trophic conditions conducive to the mass development of rotifers. This, in turn, is confirmed by the positive correlation of specific species richness and the share of rotifers in total abundance with water level, runoff volume, date and magnitude of maximum level, including duration of floods. Decrease in specific species richness and biomass of Cladocera, average individual mass of crustaceans and high values of the Shannon index for abundance and biomass are determined by the increased control by young fish. It is known that Cladocera abundance and biomass drop with increasing control from above (Bartell and Kitchell, 1978; Gilyarov, 1987; Hrbaček, 1962; Stenson et al., 1978; Zhang et al., 2019). Besides, due to the eating of the most conspicuous large-sized and numerous food objects (Gliwicz, 2002; Murdoch, 1969; Murdoch et al., 1975), the Shannon index, especially calculated by biomass, increases. Favorable conditions in floods and provision of food objects were responsible for appearance of a high proportion of predators with incudate type of mastax (Kosova, 1965).

At the same time, changes in zooplankton were also revealed for some low-water years. In spring 2011, zooplankton was characterized by minimal quantitative characteristics. This year was characterized by the lowest volume of runoff, a significant decrease in water level before the flood and then its sharp rise, a large difference between the level on the date of the beginning of the flood and the maximum level, the lowest and shortest period of its standing, prolonged cold weather, late transition of water temperature through +4 °C, low yield of young fish on the spawning grounds (Podolyako, 2014; Taradina and Chavychalova, 2017). As previously indicated by A.A. Kosova (1970) and K.V. Gorbunov (1976), the decrease in zooplankton abundance and biomass was due to the influence of untimely water releases accompanied by a sharp rise and fall of the level. In addition, in years with a later spring, protozoa, small rotifers and naupliuses of Copepoda are the first to develop in mass (Kosova, 1965), which explains the decrease in the number of trophic groups, the predominance of a mixed (by feeding and movement) group of juvenile copepods of fine filter feeders, as well as the low average individual mass of crustaceans, but high Shannon index of abundance. In low-water years, large Cladocera are scarce in the floodplain (Frutos et al., 2006) that explains their low quantitative representation in the channels as well. This is also confirmed by the inverse correlation of Cladocera abundance and specific species richness with the difference between the maximum and initial water level.

In the summer of 2011, during the early low water period and the lowest water level, zooplankton was characterized by low specific species richness, the highest abundance of Copepoda due to juvenile individuals and the lowest number of rotifers. A decrease in rotifer density under low water conditions was also observed in other watercourses (José de Paggi et al., 2014) and associated with reduced inputs of allochthonous organic matter and organisms from the floodplain. Simultaneously, the number of crustacean species, average individual crustacean mass, and biomass of Cladocera (primary fine and coarse filter feeders) increased in the summer of 2011 relative to spring, and the Shannon index of abundance and biomass decreased. Obviously it is explained by the reduced control from above due to low yields of juvenile fish in the floodplain (Podolyako, 2014), as well as the late onset of biological spring due to prolonged cold weather.

Among the low-water years, 2012 was characterized by the largest volume of runoff, maximum decrease in water level before the flood, high difference between the maximum level and the level at the date of the beginning of the flood, sharp water rise, the latest dates of standing maximum levels, the highest and longest maximum level, with late dates of water temperature transition through +4 °C, but then a sharp rise to maximum values in April, one-time spawning of fish on the spawning grounds (Litvinov and Podolyako, 2014). Under these conditions, a rapid and significant increase in the number of species and abundance of Rotifera and Copepoda took place in spring. It is known that outbreaks of mass development of zooplankton in spring are possible when there are sufficient numbers of bacteria and other microorganisms multiplying at the expense of allochthonous organic matter of the previous vegetation period (Gorbunov, 1976; Kosova, 1970). During late and cold spring, outbreaks of mass development of a number of spring species coincide, resulting in a sharp increase in total zooplankton abundance (Kosova, 1970). At the same time, low quantitative characteristics of Cladocera were observed, which, as indicated by correlation coefficients, was associated with the delayed temperature rise in late March and early April, late flooding and low water levels before the onset of flooding.

In the summer of 2012, which differed from other low-water years by stabilization of high water levels in June, late establishment of low water levels, and abrupt rise in two stages, the abundance of Rotifera (floating-crawling verticillators) remained high. In addition, control from above increased in summer, as juvenile fish rolled into channels after feeding on hollow spawning grounds and as water levels dropped (Kizina, 1999; Koblitskaya, 1958, 1966). Simultaneous and late spawning of fish with subsequent rolling of juveniles into channels resulted in the formation of communities characterized by low values of Cladocera abundance and biomass, average individual crustacean mass, and relatively high Shannon index of biomass.

In spring 2014, zooplankton was characterized by the highest quantitative indices of all taxonomic groups of invertebrates in the series of low-water years, as well as increased specific species richness of Copepoda, which was associated with the peculiarities of weather and hydrological conditions: warm and early spring, coincidence of the timing of water level rise and its temperature. According to A.A. Kosova (1970), it is under these conditions that zooplankton is characterized by high average annual abundance and biomass. According to A.A. Kosova (1965), outbreaks of mass development of rotifers coincide in time with the mass appearance of planktonic algae and bacteria, which serve as food for them, and precede the mass reproduction of predatory rotifers. Obviously, the dominance among ecological groups of invertebrate predators with mastax incudate type is related with these factors. At the same time, the low flood level did not lead to enrichment of the channels with organic matter and zooplankters from the water bodies of the flooded areas that contributed to further reduction of specific species richness of zooplankton, the average individual mass of crustaceans and the Shannon index.

In summer, against the background of the upper control reduction due to the low yield of juvenile fish (Taradina and Chavychalova, 2017), zooplankton was distinguished by high abundance and biomass, including at the expense of Cladocera, as well as a decrease in the Shannon index. The influence of the control from above also determined the representation of ecological groups, among which floating primary fine and coarse filter feeders prevailed.

The influence of a number of factors provided similar features of zooplankton organization in some years. Thus, in low-water year 2012 and mid-water year 2013, longer periods of maximum flood levels and duration, and later establishment of low-water period were observed. Due to this, spring zooplankton was characterized by high individual mass of crustaceans due to the input of organisms and organic matter from floodplain water bodies. In summer, relatively high control from above was noted in both years, resulting in a decrease in total zooplankton biomass, number of species and Cladocera biomass, and an increase in the Shannon index.

In 2013 and 2014, in spite of different runoff volume, similarity in temperature regime in March early April, close dates of water temperature transition through +4 °C, higher water level before the beginning of the flood, the smallest difference between the maximum level and the level at the beginning of the flood were also found. Under these conditions, the quantitative characteristics of crustaceans, the proportion of floating organisms increased in spring, and a similar composition of dominant species was formed. In summer, a higher proportion of predators with the incudate type of mastax were observed. It was proved by the correlation of this group with early warming of water in spring and early date of its maximum level.

The extremely low-water years of 2011 and 2014 saw the lowest flows and short floods, low levels, early low water, and reduced yields of juvenile fish on the shelf (Litvinov and Podolyako, 2014; Taradina and Chavychalova, 2017). In spring, a decrease in specific species richness of zooplankton (also indicated by correlations), the Shannon index and the average individual crustacean mass was observed. In summer, the biomass of Cladocera and their specific species richness increased, while Rotifera abundance and Shannon index decreased.

Conclusion

The studies carried out in 2011–2014 are evince of a decrease in the specific species richness of zooplankton, the average individual mass of crustaceans and an increase in the proportion of juvenile Copepoda at the expense of fine filter feeders occurred in low-water years due to the decreased runoff and water levels, the reduced areas of inundated floodplains, low flow of organisms and organic matter from such floodplains into the channels. An increase in maximum levels, duration of flooding, input of allochthonous organic matter and organisms from the floodplain (with the presence of vegetation) into the channels, yield of juvenile fish on the canals, etc. were the key factors in the conditions of water availability increase in the mid-water year. Due to this, the zooplankton contained the maximum number of species encountered, high specific species richness and average individual mass of crustaceans, as well as the minimum proportion of the mixed (by mode of movement and feeding) group of juvenile Copepoda. In spring, there was a high biomass of zooplankton at the expense of crustaceans, a maximum proportion of floating verticators and a dominance of phytophilic groups of Cladocera. In summer, there was an increase in the quantitative indices of Rotifera. However, as compared to spring, the specific species richness and biomass of Cladocera, the average individual mass of crustaceans decreased and the Shannon index increased because of control from above.

The main factors in the series of low-water years were conditions of the lowest flow volume with a significant drop in water level before flooding and then a sharp rise, early low water, prolonged cold weather, low yields of juvenile fish on the spawing grounds, and reduced inputs of allochthonous organic matter and organisms from the floodplain. This led to an increase in Copepoda abundance at the expense of juvenile individuals. In spring, minimal quantitative characteristics of zooplankton but a high Shannon Index of abundance were noted. In summer, this resulted in low specific species richness of zooplankton with a minimum number of rotifers. In contrast to spring, the number of crustacean species, average individual mass of crustaceans, biomass of Cladocera increased, but the Shannon index decreased.

Thus, the leading factors regulating the qualitative and quantitative characteristics of zooplankton were the volume of runoff during the flood, its duration, water levels before the flood onset, height and rate of rise of levels, water temperature in spring and yield of juvenile fish. However, in the channels, water levels and water temperature increased annually in spring, while in summer the closest conditions were formed with the establishment of low water levels and stabilization of high water temperatures. This probably caused changes in the quantitative characteristics and structure of ecological groups of zooplankton in mid- and low-water years mainly at the trend level.

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