ISSN 1995-0829, Inland Water Biology, 2021, Vol. 14, No. 4, pp. 415–426. © Pleiades Publishing, Ltd., 2021.
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ZOOPLANKTON, ZOOBENTHOS, ZOOPERIPHYTON

Long-Term Dynamics of Zooplankton in the Kama and Votkinsk Reservoirs

E. M. Tselishcheva[a] **and V. I. Lazareva**[b, *]

[a] *Russian Federal Research Institute of Fisheries and Oceanography, Perm Branch, Perm, Russia*
[b] *Papanin Institute for Biology of Inland Waters, Russian Academy of Sciences, Borok, Nekouzskii raion, Yaroslavl oblast, Russia*
**e-mail: lazareva_v57@mail.ru*

Received May 28, 2020; revised December 1, 2020; accepted December 28, 2020

Abstract—The summer (July–August) zooplankton of the Kama and Votkinsk reservoirs on the Kama River was studied for six years (2014–2019). A total of 106 crustacean and rotifer species were recorded; ten of them are invaders mainly of southern origin. It has been revealed that 70% of invaders in both reservoirs were recorded from 2012 to 2016. The cladoceran *Diaphanosoma orghidani* and Ponto-Caspian copepods *Eurytemora caspica* and *Heterocope caspia* have become common species; they annually occur in over 30% of samples and locally form up to 30% of the number of crustaceans. An increase in the density (up to 24–30% of the abundance of crustaceans) of the thermophilic copepod *Thermocyclops crassus,* which was previously not abundant, has been revealed. The average abundance of zooplankton for 2014–2019 (>150 thousand ind./m^3) was generally 1.7–2.0 times higher in the littoral zone than in the pelagic zone in both reservoirs. The summer biomass of zooplankton was high (1.1–1.7 g/m^3) throughout the water area of the reservoirs. The biomass level was 2.5–3 times higher in 2014–2019 than in the 1950–1960s.

Keywords: Kama River, reservoirs, zooplankton, structure, abundance, dynamics
DOI: 10.1134/S1995082921040118

INTRODUCTION

The Kama River is the largest (>2000 km) and most high-water tributary of the Volga River; the average long-term water discharge in its lower reaches is over 4000 m^3/s (*Volga* ..., 1978). The cascade of Kama reservoirs was created in 1954–1979; the regulated part of the river is below the mouth of the Vishera River and includes three reservoirs: Kama, Votkinsk, and Nizhnekamsk (Edel'shtein, 1998). The trophic status of all Kama reservoirs in terms of chlorophyll a concentration in plankton is determined as eutrophic; in terms of the amount of chlorophyll and pheopigments in bottom sediments, the Kama Reservoir is eutrophic, while the Votkinsk Reservoir is mesotrophic (Belyaeva et al., 2018).

The zooplankton of the Kama and Votkinsk reservoirs has been studied since 1956 and 1965, respectively (Ulomskii, 1961; Udalova, 1968; Serkina, 1971, 1975; Poskryakova, 1977; Kortunova and Zueva, 1979; Kortunova and Serkina, 1980; Kortunova, 1983; Kortunova and Galanova, 1988; Kostitsyn et al., 2011; Krainev and Kuznetsova, 2013; Presnova and Khulapova, 2015; Seletkova, 2015). The state of the community is monitored by the Perm Branch of the Russian Federal Research Institute of Fisheries and Oceanography (PermNIRO). It is shown that the abundance of zooplankton in the Kama River is characterized by increasingly large fluctuations year after year (Kortunova, 1983; Kortunova and Galanova, 1988; Seletkova, 2015).

In 2016, a large group of invasive species, including brackish-water Ponto-Caspian crustaceans, was identified in the Kama reservoirs (Lazareva, 2020). The features of the structure and dynamics of the community abundance, taking into account the influence of invaders, have not been discussed in recent years.

The purpose of this research was to analyze the structure and dynamics of the abundance and biomass of summer zooplankton in the Kama and Votkinsk reservoirs for the period of 2014–2019 and determine the features of invader colonization.

MATERIALS AND METHODS

Pelagic and littoral zooplankton was collected at a depth of 5–13 and 1–3 m, respectively, in three parts of both reservoirs (upper (I), central (II), and near-dam (III) parts) in July–August in 2014–2019 according to the standard scheme of sections (stations) and sampling points of the Perm Branch of the Russian Federal Research Institute of Fisheries and Oceanog-

Abbreviations: N_{zoo}—zooplankton abundance, B_{zoo}—zooplankton biomass, N_{rot}—number of rotifers, N_{cr}—number of crustaceans raphy (Fig. 1). Eighteen sections were established in the two reservoirs. Crustaceans and rotifers were recorded in total zooplankton samples, which were collected using a Juday net with a mouth diameter of 12 cm and a mesh sieve of 100 μm. Samples were fixed with 4% formalin and examined at the laboratory under LOMO MSP-2 and BIOLAM 70 microscopes (LOMO-Micro, St. Petersburg).

The abundance and biomass of each identified species from the samples were determined and the total values of these parameters were calculated for four large taxonomic groups (Cladocera, Cyclopoida, Calanoida, and Rotifera) and the whole community. The dominants included species with an abundance of over 10% of the total number of crustaceans or rotifers.

The similarity of the structure of the dominant complexes was determined by the Czekanowski–Sorensen index for quantitative data (I_{CzS}) (Pesenko, 1982):

$$I_{CzS} = \Sigma_{\min} p_i,$$

where p_i is the proportion of the species in the total zooplankton abundance.

Changes in the zooplankton biomass in the Kama and Votkinsk reservoirs over the period from the beginning of the research to 2019 (the whole period of the existence of the water bodies) were analyzed using the literature sources and archival materials from the Russian Federal Research Institute of Fisheries and Oceanography, Perm Branch.

The average number of species in the sample, their abundance and biomass, and error of the mean were calculated.

RESULTS

Species richness and dominants. In 2014–2019, 100 species were identified in the Kama Reservoir and 69 species were found in the Votkinsk Reservoir (106 species in both reservoirs). Most of them (40–45%) were represented by Rotifera; the proportion of Cladocera was 35–40% and that of Copepoda was less than 20%. The species density (number of species in the sample) was high in all observation years. On average, 21 ± 3 species were found in samples from the pelagic zone of the Kama Reservoir and 18 ± 3 species were recorded in samples from the Votkinsk Reservoir; there were slightly fewer species in the coastal areas of both reservoirs (17 ± 2 species from each reservoir). Seven rotifer species, *Keratella serrulata* (Ehrenberg, 1838); *Notholca acuminata* (Ehrenberg, 1832); *Euchlanis lyra* Hudson, 1886; *Mytilina mucronata* (O.F. Müller, 1773); *Synchaeta oblonga* Ehrenberg, 1831; *S. stylata* Wierzejski, 1893; and *Filinia brachiata* (Rousselet, 1901) and two crustacean species, *Alonella nana* (Baird, 1843) and *Ilyocryptus agilis* Kurz, 1878, which were not indicated in the review list of (Lazareva, 2020), were identified in 2012 to 2014. Most of these species were found in the Kama Reservoir. Four species, *E. lyra, Notholca acuminata, Synchaeta oblonga,* and *Alonella nana,* were recorded in the Votkinsk Reservoir.

The composition of abundant rotifer species in the upper part of the **Kama Reservoir** significantly differed from their composition in its other two parts (Fig. 2a). It was often dominated here by *Asplanchna priodonta* Gosse, 1850 (10–60% N_{rot}); *Brachionus angularis* Gosse, 1851 (25–50% N_{rot}); and *Synchaeta pectinata* Ehrenberg, 1832 (30–40% N_{rot}). In the central and near-dam parts, the main contribution to the N_{rot} value was made by *Kellicottia longispina* (Kellicott, 1879) (20–90%); *Euchlanis dilatata lucksiana* (Hauer, 1939) (10–90%); *Keratella quadrata* (O.F. Müller, 1786) (10–20%); and *Polyarthra major* Bruckhardt, 1900 (10–20%).

The abundance of crustaceans throughout the water area of the reservoir was formed mainly by three species (Fig. 2b). These are the copepods *Mesocyclops leuckarti* (Claus, 1857) (10–70% N_{cr}) and *Thermocyclops crassus* (Fischer, 1853) (10–64% N_{cr}) and cladoceran *Daphnia galeata* Sars, 1864 (10–60% N_{cr}). In the littoral zone of the upper part, 10–23% of N_{cr} was formed by *Bosmina* (s. str) *longirostris* (O.F. Müller, 1785). On the whole, the pelagic and coastal communities in each part of the reservoir were characterized by a similar ratio of main dominants (Figs. 2a, 2b).

B_{zoo} was formed mainly by a large (body length up to 2.0 mm) cladoceran, *Daphnia galeata,* throughout the water area of the reservoir. Its contribution to the biomass varied from 10 to 90% during the 6 years of observations (on average, 55 ± 15% in the pelagic zone and 40 ± 10% in the littoral zone) (Fig. 3a). Rotifers of the genus *Asplanchna* significantly contributed in the upper part of the reservoir (on average up to 20% B_{zoo} and up to 50% B_{zoo} in some years).

The structure of the dominant complexes of zooplankton in different parts of the reservoir was characterized by a relatively low level of similarity (generally <50%). This is due to “outbreaks” of the abundance of species (up to 15–40% N_{rot} and 10–30% N_{cr}) in some years which were not numerous in other years (e.g., *Keratella cochlearis* (Gosse, 1851), *Ploesoma truncatum* (Levander, 1894), *Chydorus sphaericus* (O.F. Müller, 1785), and *Bosmina (Eubosmina)* cf. *crassicornis* (Lilljeborg, 1887)) or are untypical for the biotope (*Brachionus quadridentatus* Hermann, 1783 in the pelagic zone and *Eurytemora caspica* Sukhikh et Alekseev, 2013 in the littoral zone). The highest values of the index of similarity in the community structure were recorded between the central and near-dam parts; they reached 60–70% in the pelagic zone and 65–75% in the littoral zone. The similarity in the zooplankton structure did not exceed 60% in the pelagic zone and 40% in the littoral zone over a number of years (from 2014 to 2019). It was the highest (50–60%) between years (2014 and 2019 and 2015, 2017, and 2019) with low summer heating of water (17 ± 2°C), while the maximum differences (similarity <35%)

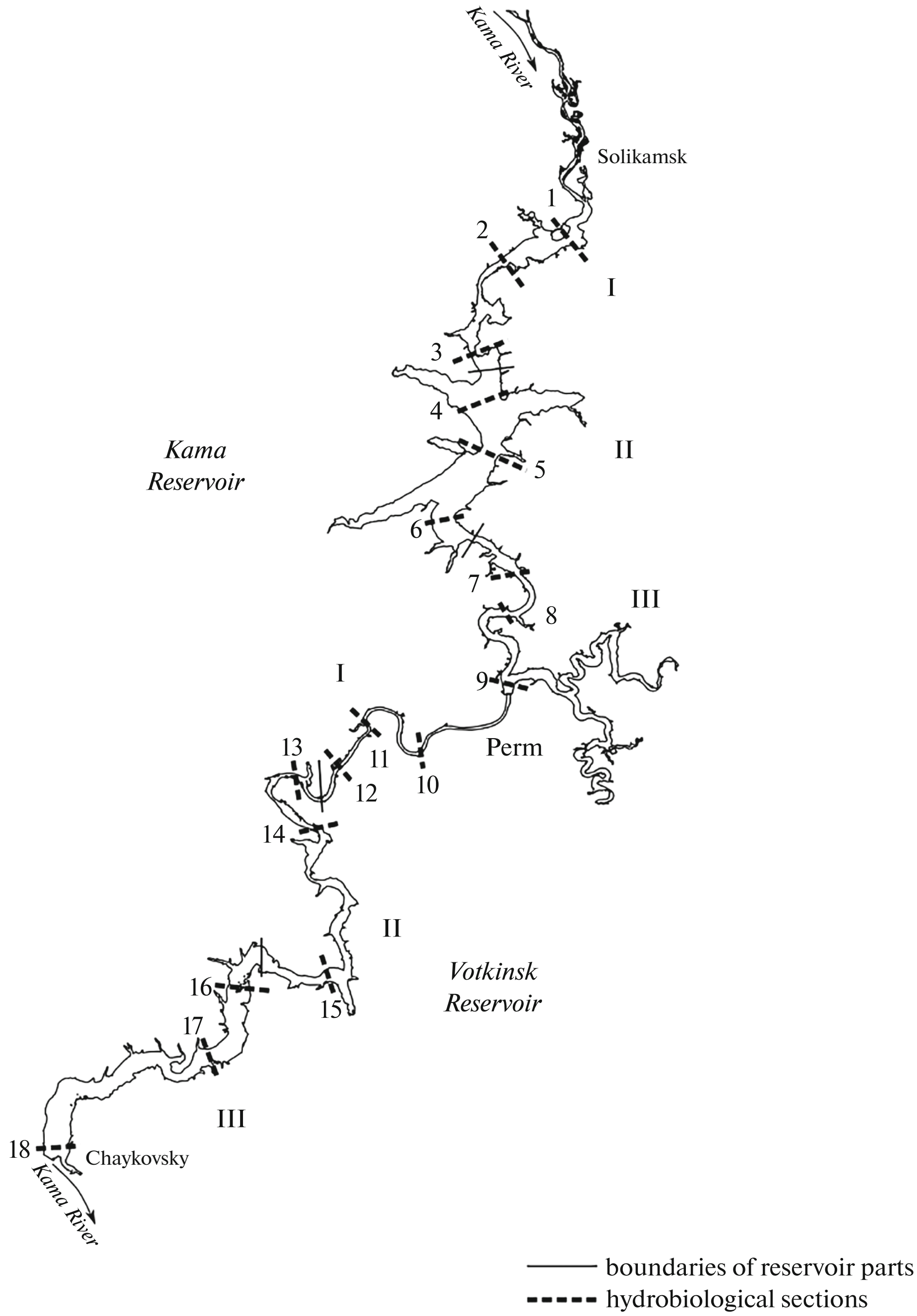

Fig. 1. Scheme and zoning of the Kama and Votkinsk reservoirs. Reservoir parts: (I) upper part, (II) central part, and (III) near-dam part.

were observed between 2016 and 2018, when the water heating was high (22 ± 2°C).

Rotifers *Euchlanis dilatata lucksiana* and *Kellicottia longispina* were almost annually abundant throughout the pelagic zone of the **Votkinsk Reservoir** (15–95 and 10–80% N_{rot}, respectively) (Fig. 2c). Crustaceans were dominated by the copepods *Mesocyclops leuckarti* (30–80% N_{cr}) and *Thermocyclops crassus* (10–35% N_{cr}), which together formed up to 75% N_{cr} (Fig. 2d). In some years (2014–2015), *Daphnia galeata* was a common species (25–26%).

The taxocene of crustaceans in the shore zone of this reservoir actually did not differ from that in the pelagic one (Fig. 2d). Along with common rotifer species, *Polyarthra major* and *Synchaeta pectinata* were relatively abundant species (up to 35 and 30% N_{rot}, respectively) throughout the water area in the littoral zone of the central part (Fig. 2c).

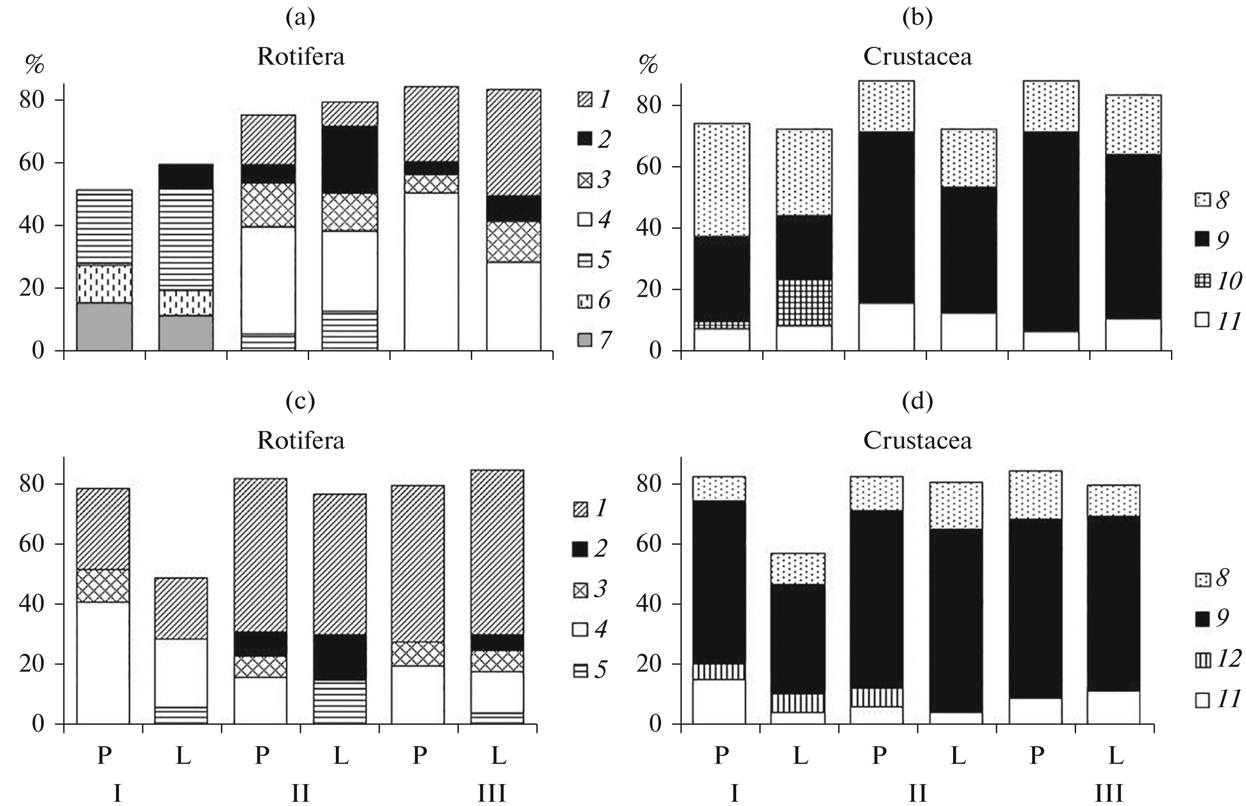

Fig. 2. Ratio (%) of the number of main dominants in the groups of rotifers (a, c) and crustaceans (b, d) in the pelagic (P) and littoral (L) zones of the Kama (a, b) and Votkinsk (c, d) reservoirs in 2014–2019 (average for 6 years). Reservoir parts: (I) upper part, (II) central part, and (III) near-dam part. Rotifera: (*1*) *Euchlanis dilatata lucksiana,* (*2*) *Polyarthra major,* (*3*) *Keratella quadrata,* (*4*) *Kellicottia longispina,* (*5*) *Synchaeta pectinata,* (*6*) *Brachionus angularis,* and (*7*) *Asplanchna priodonta*. Crustacea: (*8*) *Thermocyclops crassus,* (*9*) *Mesocyclops leuckarti,* (*10*) *Bosmina longirostris,* (*11*) *Daphnia galeata,* and (*12*) *Bosmina* cf. *crassicornis*.

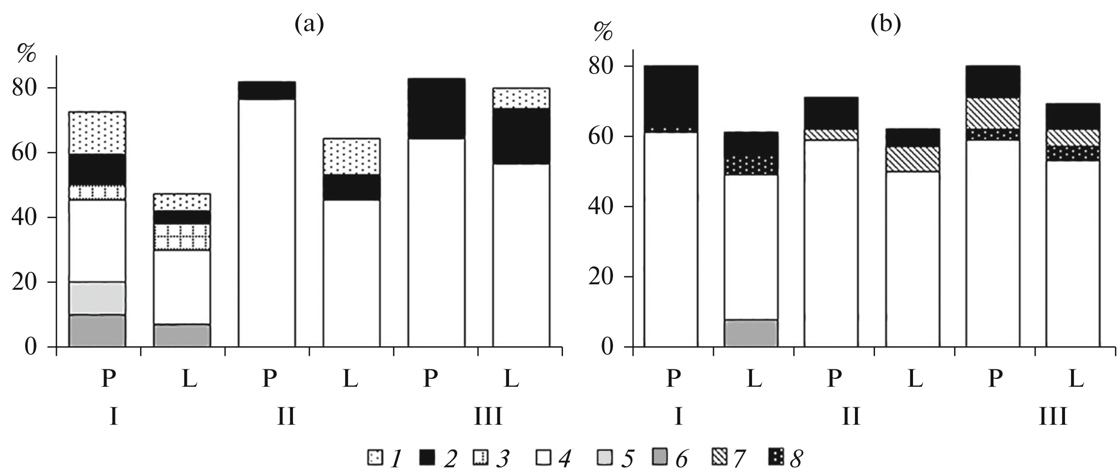

Fig. 3. Ratio (%) of the biomass of the main dominants of zooplankton in the pelagic (P) and littoral (L) zones of the Kama (a) and Votkinsk (b) reservoirs in 2014–2019 (average for the six years). Reservoir parts: (I) upper part, (II) central part, and (III) near-dam part. (1) *Thermocyclops crassus*, (2) *Mesocyclops leuckarti*, (3) *Diaphanosoma orghidani*, (4) *Daphnia galeata*, (5) *Asplanchna herricki*, (6) *A. priodonta*, (7) *Heterocope caspia*, and (8) *Eurytemora caspica*.

Almost the entire biomass of zooplankton (up to 85%) throughout the water area of the reservoir was formed by the cladoceran *Daphnia galeata* (Fig. 3b). In the pelagic zone, 40% B_{zoo} was formed by *Mesocyclops leuckarti*. On the whole, the ratio of the biomass of the main dominants did not significantly differ between the pelagic zone and shore zone of the reservoir.

The structure of zooplankton was relatively homogeneous and characterized by a high level of similarity (>50%) in different parts of the reservoir. The highest

Table 1. Occurrence and abundance of invasive species in the Kama and Votkinsk reservoirs in 2014–2019

Species	Year of the first find	Source	Observation period					
			2014	2015	2016*	2017	2018	2019
Kama Reservoir								
Pompholyx sulcata	1980s	*1*	14/0.9	8/0.01	46–90/12.0	33/11.0	26/6.0	17/0.4
Brachionus diversi-cornis (Daday, 1883)	2002	*3*	14/0.5	–	13–40/0.8	–	–	–
Brachionus budapes-tinensis Daday, 1885	2003	*3*	2/0.5	–	25/0.8	6/0.6	–	–
Kellicottia bostoniensis	2012	*4*	2/0.1	69/0.6	–	17/1.6	–	28/1.1
Eurytemora capsica	2012	*1*	62/2.0	31/16.0	46–75/0.8	83/7.5	37/0.8	56/0.5
Conochiloides coenobasis	2013	*1*	10/7.1	–	25/21.0	–	8/10.0	6/1.8
Asplanchna henrietta	2016	*2*	–	–	25/1.6	–	–	–
Diaphanosoma orghidani	2016	*2*	–	–	52–60/21.0	94/8.4	81/31.0	67/3.5
Cercopagis pengoi	2016	*2*	–	–	40/0.05	8/0.04	4/0.05	6/0.01
Heterocope caspia	2016	*2*	74/5.9	–	79–90/5.0	72/3.3	63/1.9	72/0.5
Votkinsk Reservoir								
Pompholyx sulcata	1980s	*1*	–	7/3.4	27–100/5.0	17/0.8	–	6/0.2
Brachionus diversicornis	2002	*1*	22/2.4	44/4.1	27–40/9	–	4/1.8	–
Brachionus budapestinensis	2003	*1*	–	–	9–40/3.0	–	–	–
Eurytemora capsica	2012	*1*	100/2.8	100/4.9	73–100/3.0	67/4.6	22/1.1	78/1.3
Conochiloides coenobasis	2016	*2*	–	–	70/10	–	4/1.8	–
Asplanchna henrietta	2016	*2*	–	–	60/14	–	–	–
Diaphanosoma orghidani	2016	*2*	–	–	91–100/3.0	50/1.4	63/0.2	17/0.01
Cercopagis pengoi	2016	*2*	–	–	15/0.02	–	–	–
Heterocope caspia	2016	*2*	56/1.7	85/4.5	82–100/19.0	83/6.6	81/28.3	72/1.9

Occurrence is above the line (%) and maximum number is below the line (thousand individuals/m^3); dash indicates that the species was absent in the samples. *Eurytemora capsica*, determined as *E. affinis* (Poppe, 1880) until 2016. Source: (*1*) Archive from the Perm Branch of the Russian Federal Research Institute for Fisheries and Oceanography, (*2*) (Lazareva, 2020), (*3*) (Seletkova, 2015), (*4*) (Krainev et al., 2018). Data from source 2 were additionally used for 2016.
*—additionally, the data of the work (Lazareva, 2020) are given.

Table 2. Abundance (thousand ind./m^3) and biomass (g/m^3) of zooplankton in the Kama Reservoir in 2014–2019

Taxon	2014	2015	2016	2017	2018	2019
Pelagic zone						
Cladoceran	18 ± 5 / 1.10 ± 0.34	2 ± 1 / 0.29 ± 0.08	30 ± 8 / 1.25 ± 0.24	18 ± 4 / 0.71 ± 0.16	29 ± 11 / 1.54 ± 0.30	7 ± 2 / 0.48 ± 0.13
Cyclopoida	38 ± 8 / 0.22 ± 0.05	21 ± 7 / 0.04 ± 0.01	106 ± 6 / 0.28 ± 0.03	65 ± 9 / 0.23 ± 0.05	75 ± 23 / 0.20 ± 0.13	33 ± 4 / 0.13 ± 0.05
Calanoida	1.0 ± 0.2 / 0.03 ± 0.01	1.0 ± 0.5 / 0.01 ± 0.001	1.0 ± 0.5 / 0.02 ± 0.01	1.0 ± 0.1 / 0.03 ± 0.01	1.0 ± 0.6 / 0.01 ± 0.001	1.0 ± 0.5 / 0.02 ± 0.01
Rotifera	17 ± 3 / 0.03 ± 0.01	6 ± 2 / 0.01 ± 0.001	46 ± 13 / 0.24 ± 0.10	29 ± 6 / 0.04 ± 0.01	80 ± 2 / 0.14 ± 0.01	22 ± 8 / 0.25 ± 0.13
N_{zoo}/B_{zoo}	76 ± 9 / 1.38 ± 0.37	31 ± 8 / 0.35 ± 0.09	184 ± 20 / 1.79 ± 0.16	114 ± 8 / 1.01 ± 0.20	191 ± 30 / 1.90 ± 0.41	64 ± 7 / 0.88 ± 0.04
Dreissena veliger	1.0 ± 0.2 / <0.01	1.0 ± 0.5 / <0.01	1.0 ± 0.5 / <0.01	1.0 ± 0.2 / <0.01	6 ± 1 / 0.01 ± 0.001	1.0 ± 0.5 / <0.01
Littoral zone						
Cladocera	54 ± 5 / 2.64 ± 0.67	3 ± 1 / 0.73 ± 0.39	45 ± 9 / 0.81 ± 0.27	48 ± 11 / 1.22 ± 0.30	42 ± 14 / 1.76 ± 0.25	5 ± 1 / 0.29 ± 0.05
Cyclopoida	44 ± 6 / 0.34 ± 0.08	48 ± 24 / 0.07 ± 0.03	175 ± 51 / 0.51 ± 0.18	137 ± 23 / 0.58 ± 0.13	111 ± 17 / 0.32 ± 0.08	14 ± 3 / 0.03 ± 0.001
Calanoida	1.0 ± 0.2 / 0.03 ± 0.01	17 ± 8 / 0.3 ± 0.14	1.0 ± 0.2 / 0.01 ± 0.001	3 ± 1 / 0.09 ± 0.02	2.0 ± 0.4 / 0.05 ± 0.02	1.0 ± 0.1 / 0.02 ± 0.01
Rotifera	36 ± 10 / 0.05 ± 0.01	22 ± 6 / 0.02 ± 0.001	61 ± 15 / 0.11 ± 0.03	44 ± 2 / 0.08 ± 0.01	165 ± 50 / 0.21 ± 0.08	7 ± 1 / 0.03 ± 0.01
N_{zoo}/B_{zoo}	139 ± 5 / 3.07 ± 0.69	90 ± 36 / 1.13 ± 0.56	283 ± 67 / 1.44 ± 0.47	233 ± 30 / 1.97 ± 0.41	323 ± 71 / 2.33 ± 0.38	28 ± 3 / 0.36 ± 0.06
Dreissena veliger	4 ± 1 / <0.01	0	1.0 ± 0.5 / <0.01	1.0 ± 0.3 / <0.01	3.0 ± 1.0 / <0.01	1.0 ± 0.2 / <0.01

Here and in Table 3, abundance is above the line and biomass is below the line; N_{zoo} and B_{zoo} are the total abundance and biomass of Cladocera, Cyclopoida, Calanoida, and Rotifera.

values (60–70%) of the similarity index were recorded between the complexes of dominants in the central and near-dam parts. In some years (2018 and 2019), the similarity of the zooplankton structure reached 80% in the pelagic zone, while littoral communities differed very markedly during all six observation years (the similarity was less than 45%). As in the Kama Reservoir, a mass development (60–70% N_{rot} and 13–60% N_{cr}) of usually small-numbered species (e.g., *Brachionus angularis, Asplanchna priodonta, Bosmina longirostris, Eurytemora caspica,* and *Heterocope caspia* Sars, 1897) were locally recorded here in some years. The similarity of the structure of zooplankton in the Votkinsk Reservoir did not exceed 60% year by year; it was closest to 60% (54–60%) in 2014, 2015, 2016, and 2018, while the maximum differences (the similarity was less than 35%) were recorded between 2014 and 2019 and 2016 and 2019. In the intracascade Votkinsk Reservoir, no clear correlation was observed between the community structure and thermal water regime.

Role of invaders in the community. Nine to ten invasive species were recorded in the zooplankton of the studied reservoirs; they were identified here for the first time mainly in the 2010s (Table 1). Most of them (except *Kellicottia bostoniensis* (Rousselet, 1908)) are represented by southern thermophilic species. Three of them (the cladoceran *Cercopagis pengoi* (Ostroumov, 1891) and copepods *Heterocope caspia* and *Eurytemora caspica*) are brackish-water Ponto-Caspian forms. Three of the ten invaders—the cladoceran *Diaphanosoma orghidani* Negrea, 1982 and copepods *Eurytemora caspica* and *Heterocope caspia*—have become common in both reservoirs (they annually occur in more than 30% of samples).

The maximum abundance of most southern rotifers did not exceed 10 thousand ind./m^3; only some of the species were locally dominant in the zooplankton of the reservoirs in some years. Thus, the abundance of *Conochiloides coenobasis* Skorikov, 1914 reached 20 thousand ind./m^3 (22% N_{rot}) and that of *Pompholyx*

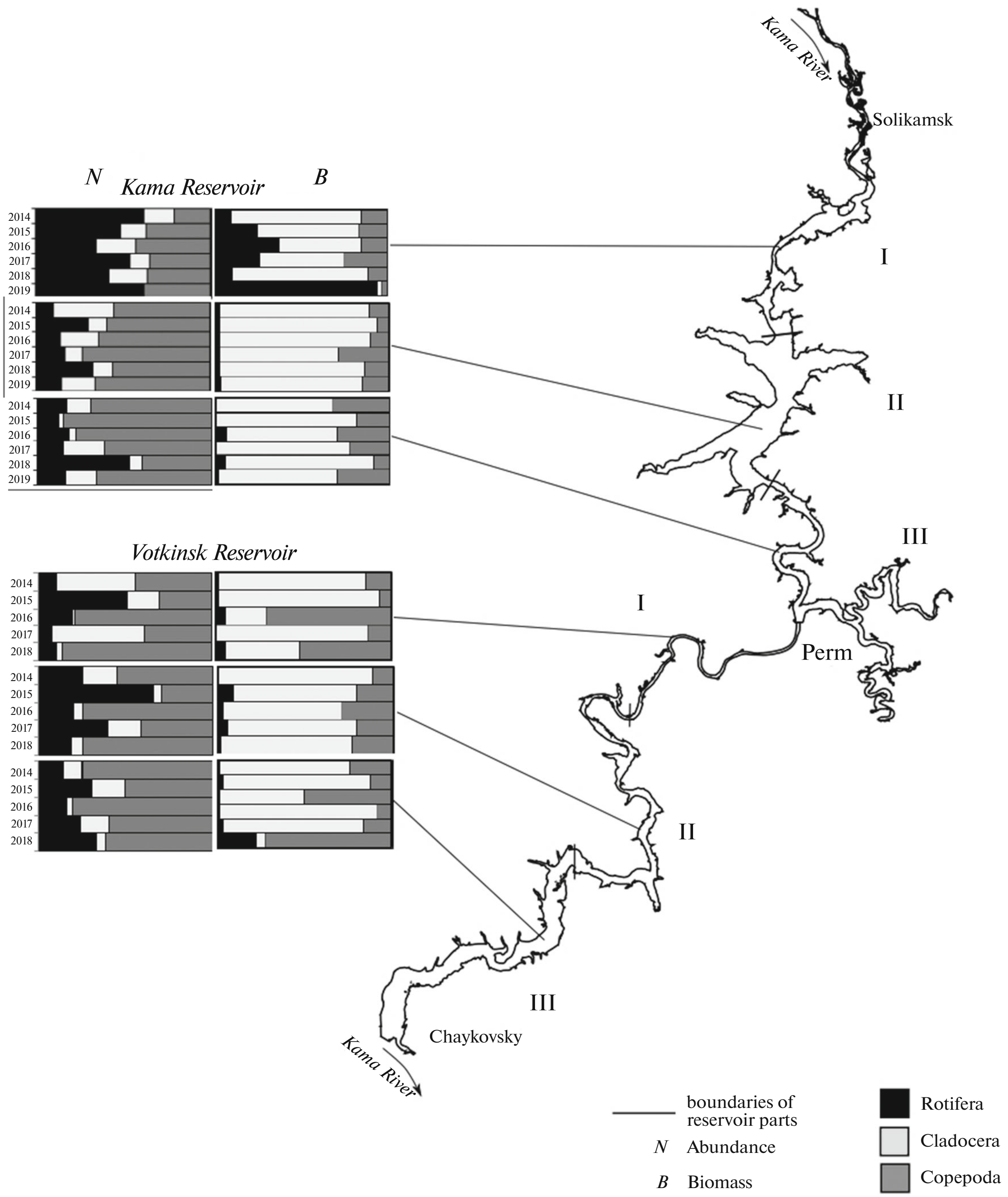

Fig. 4. Ratio (%) of large taxonomic groups of zooplankton in different parts (I, upper part; II, central part; and III, near-dam part) of the Kama and Votkinsk reservoirs in 2014–2019.

sulcata Hudson, 1885 was 12 thousand ind./m^3 (24% N_{rot}) in the upper part of the Kama Reservoir in August 2016. The abundance of *Asplanchna henrietta* Langhaus, 1906 was 14 thousand ind./m^3 (11% N_{rot}) in the central part of the Votkinsk Reservoir near the mouth of the Ocher River in 2016.

A significantly greater contribution to the N_{cr} value was made by southern crustaceans; among them, large species also contributed greatly to B_{zoo}. The copepod *Eurytemora caspica* in the shore zone was highly abundant (up to 16 thousand ind./m^3) in the central and near-dam parts of the Kama Reservoir in 2015 (25–30% N_{cr}) and throughout the water area of the Votkinsk Reservoir in 2019 (13–17% N_{cr}). The contribution of this species to B_{zoo} reached 25–40% in the littoral zone of the Kama Reservoir and 10–23% in the littoral zone of the Votkinsk Reservoir. The proportion

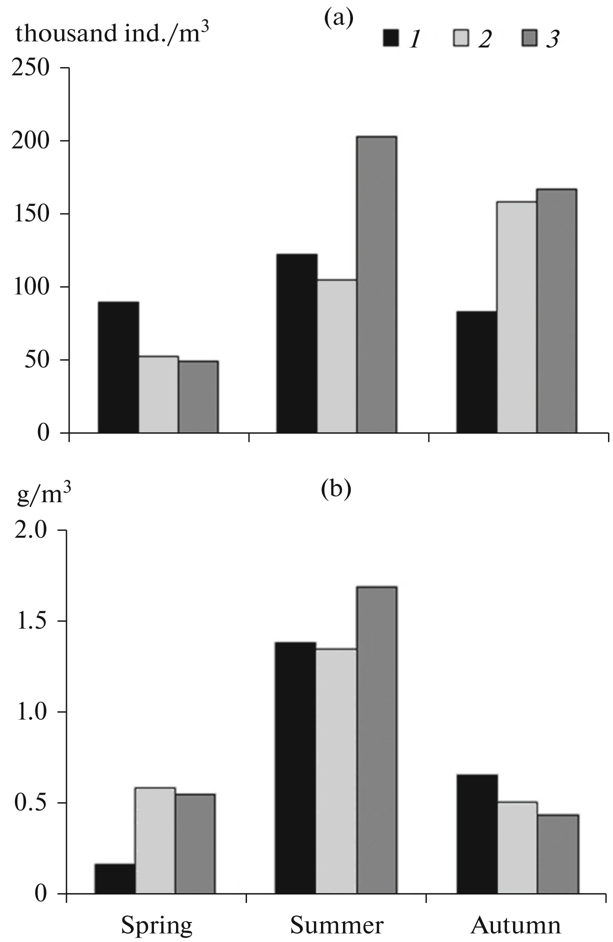

Fig. 5. Seasonal variation in the abundance (a) and biomass (b) of zooplankton in the Kama Reservoir in 2016. (*1*) Upper part (I), (*2*) central part (II), and (*3*) near-dam part (III).

of *E. caspica* was 14–16% B_{zoo} in the pelagic zone of the Votkinsk Reservoir.

Two other species made a significant contribution only to B_{zoo}. In 2016 and 2018, the abundance of *Diaphanosoma orghidani* reached 20–30 thousand ind./m^3 in the upper part of the Kama Reservoir, or 13–17% B_{zoo} in the pelagic zone and 15–18% in the littoral zone. In the central part of the reservoir, the species was dominant only in the littoral zone (up to 14% B_{zoo} in 2019). In 2019, the copepod *Heterocope caspia* formed 12–40% B_{zoo} in the littoral zone and up to 55% B_{zoo} in the pelagic zone of the near-dam part in the Votkinsk Reservoir.

Abundance and biomass. In the pelagic zone of the Kama Reservoir, the total abundance of zooplankton varied from 30 to 190 (on average, 110 ± 27) thousand ind./m^3 and 0.4 to 1.9 (on average, 1.2 ± 0.2) g/m^3 in the summer of 2014 to 2019 (Table 2). The greatest contribution to the community abundance (>50%) was made by Cyclopoida (>20%) and Rotifera (30%); the biomass was formed mainly by Cladocera (>70%). In the central and near-dam parts, the ratio of the main taxa of zooplankton was stable for all 6 years of observations, while it varied greatly in the upper part from year to year (Fig. 4). The maximum (up to 60%) contribution of rotifers to the abundance of the community was observed here. The amount of meroplankton, represented by veligers of mollusks of the genus *Dreissena,* was very low in all years (on average, 1.0 ± 0.5 thousand ind./m^3) at a biomass of less than 0.01 g/m^3.

The seasonal variation of the development of pelagic zooplankton was studied in the Kama Reservoir in 2016; it was characterized by an increase in abundance from spring (May) to summer (August) and a slight decrease in autumn (September–October) (Fig. 5a). In the central part of the reservoir, the number of zooplankton even slightly increased in autumn. On the contrary, the seasonal dynamics of the biomass was characterized by a clearly pronounced summer maximum typical for all parts of the reservoir (Fig. 5b). The biomass was minimal in spring and maximal in autumn in the upper part of the reservoir when compared to other parts.

In the pelagic zone of the Votkinsk Reservoir, the abundance of zooplankton varied from 13 to 107 (on average, 76 ± 15) thousand individuals/m^3) and biomass was 0.1–1.4 (on average, 1.0 ± 0.2) g/m^3) in summer from 2014 to 2019 (Table 3). The greatest contribution to the community abundance was made by copepods (~60%) and rotifers (>25%); the biomass was formed mainly by cladocerans (~80%). The ratio of the abundance of the main zooplankton taxa was unstable from year to year in all three parts of the reservoir; variations were observed in the proportion of both rotifers and copepods (Fig. 4). Variations in the biomass structure were determined mainly by fluctuations in the abundance of Cyclopoida. The average number of veligers of mollusks of the genus *Dreissena* was 4 times higher in the Votkinsk Reservoir (4.0 ± 0.5 thousand ind./m^3) than in the Kama Reservoir; however, their biomass did not exceed 0.01 g/m^3.

In both water bodies, the abundance of littoral zooplankton significantly exceeded the abundance of pelagic zooplankton by 1.7–2.0 times (Fig. 6a). On average, it reached 183 ± 47 thousand ind./m^3 in the Kama Reservoir and 155 ± 33 thousand ind./m^3 in the Votkinsk Reservoir. The littoral community of the Kama Reservoir was dominated by copepods (60% of the community); the community of the Votkinsk Reservoir was dominated by copepods and rotifers (42 and 36%, respectively). The biomass of coastal zooplankton was high in both water bodies (1.5–1.7 g/m^3) and did not significantly differ from that observed in the pelagic zone during the same period (1.1–1.4 g/m^3) (Fig. 6b).

The average amount of pelagic zooplankton in 2014–2019 was 20–30% higher in the Kama Reservoir than in the Votkinsk Reservoir (Fig. 6); however, these

Table 3. Abundance (thousand ind./m^3) and biomass (g/m^3) of zooplankton in the Votkinsk Reservoir in 2014–2019

Taxon	2014	2015	2016	2017	2018	2019
Pelagic zone						
Cladocera	10 ± 3 / 0.78 ± 0.23	13 ± 6 / 1.21 ± 0.42	4 ± 1 / 0.45 ± 0.16	14 ± 3 / 1.26 ± 0.45	5 ± 2 / 0.74 ± 0.26	1.0 ± 0.5 / 0.06 ± 0.02
Cyclopoida	33 ± 9 / 0.12 ± 0.03	36 ± 15 / 0.11 ± 0.04	79 ± 12 / 0.28 ± 0.02	36 ± 14 / 0.10 ± 0.02	67 ± 12 / 0.15 ± 0.02	4 ± 1 / 0.02 ± 0.01
Calanoida	1.0 ± 0.1 / 0.02 ± 0.001	2.0 ± 0.5 / 0.06 ± 0.02	2 ± 0.5 / 0.04 ± 0.01	3 ± 1 / 0.06 ± 0.01	2 ± 0.5 / 0.05 ± 0.02	1 ± 0.5 / 0.02 ± 0.01
Rotifera	12 ± 5 / 0.01 ± 0.001	34 ± 8 / 0.04 ± 0.01	20 ± 4 / 0.03 ± 0.01	20 ± 6 / 0.02 ± 0.01	26 ± 10 / 0.02 ± 0.01	6 ± 1 / 0.01 ± 0.001
N_{zoo}/B_{zoo}	60 ± 18 / 0.93 ± 0.26	95 ± 32 / 1.42 ± 0.49	107 ± 18 / 0.80 ± 0.19	74 ± 24 / 1.44 ± 0.49	105 ± 25 / 0.98 ± 0.30	13 ± 2 / 0.11 ± 0.03
Dreissena veliger	5 ± 2 / 0.01 ± 0.001	9 ± 4 / 0.01 ± 0.001	2 ± 1 / 0.01 ± 0.001	1.0 ± 0.5 / 0.01 ± 0.001	5 ± 2 / 0.01 ± 0.001	1.0 ± 0.5 / 0.01 ± 0.001
Littoral zone						
Cladocera	29 ± 15 / 2.97 ± 1.51	32 ± 13 / 1.29 ± 0.64	39 ± 13 / 1.02 ± 0.15	36 ± 9 / 1.43 ± 0.40	10 ± 3 / 0.43 ± 0.09	1.0 ± 0.1 / 0.02 ± 0.01
Cyclopoida	73 ± 26 / 0.24 ± 0.1	46 ± 17 / 0.10 ± 0.03	113 ± 18 / 0.42 ± 0.11	55 ± 15 / 0.11 ± 0.03	68 ± 16 / 0.14 ± 0.04	3.0 ± 0.3 / 0.01 ± 0.001
Calanoida	5 ± 2 / 0.12 ± 0.05	36 ± 19 / 0.13 ± 0.05	2.0 ± 0.5 / 0.05 ± 0.01	3 ± 1 / 0.08 ± 0.04	3 ± 1 / 0.05 ± 0.02	2.0 ± 0.3 / 0.04 ± 0.01
Rotifera	64 ± 17 / 0.04 ± 0.03	80 ± 17 / 0.12 ± 0.03	107 ± 44 / 0.11 ± 0.05	36 ± 10 / 0.06 ± 0.01	50 ± 20 / 0.05 ± 0.02	11 ± 5 / 0.01 ± 0.01
N_{zoo}/B_{zoo}	177 ± 60 / 3.38 ± 0.72	200 ± 61 / 1.65 ± 0.72	262 ± 39 / 1.61 ± 0.20	140 ± 36 / 1.67 ± 0.43	134 ± 37 / 0.67 ± 0.17	18 ± 5 / 0.08 ± 0.01
Dreissena veliger	6 ± 2 / <0.01	7 ± 2 / <0.01	2.0 ± 0.5 / 0.31 ± 0.18	10 ± 3 / 0.01 ± 0.001	4 ± 2 / <0.01	1.0 ± 0.2 / <0.01

differences are insignificant. A similar ratio of the abundance was also observed in the littoral zone, where the abundance and biomass differed by 10–15%.

An analysis of the dynamics of the biomass of zooplankton in the Kama Reservoir for 63 years and Votkinsk Reservoir for 54 years showed significant interannual fluctuations during all study periods and a clear trend towards an increase in biomass in the current period in both reservoirs (Fig. 7). In the Kama Reservoir, the biomass of pelagic zooplankton was almost 2.5 times higher in 2014–2019 (1.2 ± 0.2 g/m^3) than in the first decade of the existence of the reservoir (0.5 ± 0.1 g/m^3). Biomass values comparable to the current ones (1.3 ± 0.1 g/m^3) were observed in the 1970s. In the Votkinsk Reservoir, the zooplankton biomass was relatively low until 2010 (0.6 ± 0.1 g/m^3). A threefold increase in the community biomass (up to 1.9 g/m^3) was recorded in the hot summer of 2010. It usually remained high in subsequent years (until 2018): 1.3 ± 0.2 g/m^3 (on average, two times higher than the biomass before 2010). The biomass of zooplankton in the reservoir sharply decreased to 0.1 g/m^3 in the cold and high-water year of 2019.

DISCUSSION

Over 106 zooplankton species live in the Kama and Votkinsk reservoirs; almost half of them are rotifers. According to the archival data from the Perm Branch of the Russian Federal Research Institute of Fisheries and Oceanography, the species richness of the community exceeds 180 species. The most complete composition of zooplankton in the reservoirs of the Kama River is given in the review by Lazareva (2020). All seven species that supplemented this list in our research were identified in unpublished archival materials from the Perm Branch of the Russian Federal Research Institute of Fisheries and Oceanography. They are usually not numerous in the taiga zone of European Russia (Pidgaiko, 1984); therefore, they were not considered invaders.

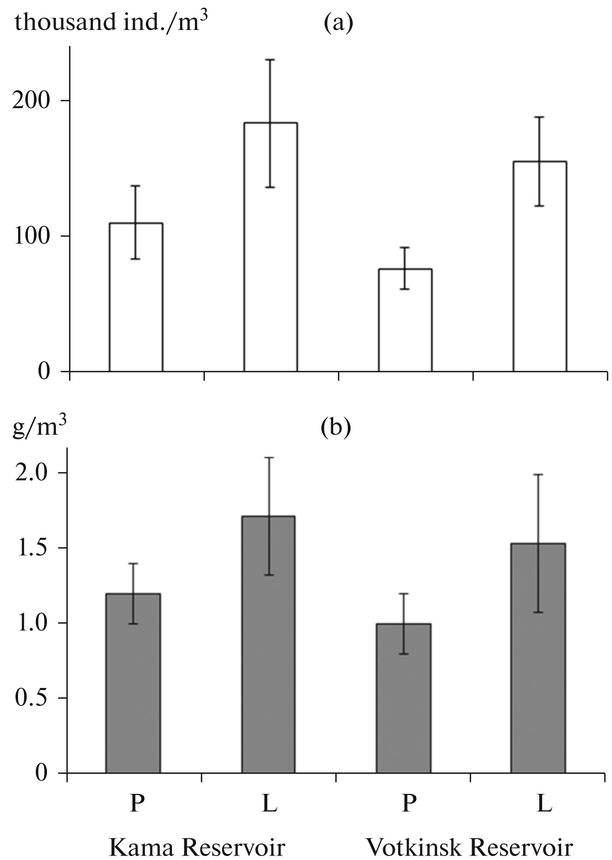

Fig. 6. Abundance (a) and biomass (b) of zooplankton in the pelagic (P) and littoral (L) zones of the Kama and Votkinsk reservoirs in 2014–2019.

The analysis of the archival data from the Perm Branch of the Institute of Fisheries and Oceanography made it possible to establish the dates of appearance of southern thermophilic invasive species, including three brackish-water Ponto-Caspian crustaceans, in the Kama and Votkinsk reservoirs (Table 1). Only one freshwater southern rotifer, *Pompholyx sulcata,* penetrated these water bodies back in the 1980s, two species of the genus *Brachionus* appeared here in the early 2000s, and the other invaders appeared here in the 2010s (Kuznetsova, 2015; Seletkova, 2015; Krainev et al., 2018; Lazareva, 2020).

Of particular interest is the colonization of Ponto-Caspian crustaceans in the Kama River. The copepod *Eurytemora caspica* was recorded in both studied reservoirs for the first time in 2012; at that time, the species was determined as *E.* cf. *affinis* (Kuznetsova, 2015). For comparison, this species was recorded in the Volga River for the first time in the mid-1980s (Timokhina, 2000). Based on morphological and molecular methods (Sukikh et al., 2020), it has now been established that *E. caspica* lives in the reservoirs of the Volga and Kama rivers, while typical *E. affinis* (Poppe, 1880) has not been found anywhere.

The exact habitats of the other two Ponto-Caspian species have been established only since 2016 (Lazareva, 2020). In 2016–2019, the predatory cladoceran *Cercopagis pengoi* was recorded annually, but only in the near-dam part of the Kama Reservoir. The copepod *Heterocope caspia*, which is relatively abundant in the second half of summer, presumably appeared in both reservoirs back in the early 2000s. However, the invader was confused with *H. appendiculata* Sars, 1863, which is common for the taiga zone. *H. caspia* has been abundant in the reservoirs of the Volga River (Volgograd, Saratov, and Kuibyshev reservoirs) since the mid-1960s (*Volga* ..., 1978; Timokhina, 2000).

An increase in the abundance of cyclopoid copepods of the genera *Mesocylops* and *Thermocyclops*, in particular, *T. crassus,* as a result of warming was recorded in the reservoirs of the Upper Volga (Lazareva and Sokolova, 2015). Similar changes in plankton were recorded in water bodies of Western Europe (Adrian et al., 2006). Until the mid-2000s, the contribution of Cyclopoida to the biomass of pelagic zooplankton varied from 25 to 50% in the Kama Reservoir and from 8 to 30% in the Votkinsk Reservoir (Poskryakova, 1977; Kortunova, 1983; Kortunova and Galanova, 1988; Presnova and Khulapova, 2015; Seletkova, 2015). In 2014–2019, Cyclopoida formed 10–20% of the biomass in the Kama Reservoir and 7–35% in the Votkinsk Reservoir. Until 2010, *Mesocyclops leuckarti* was mainly dominant in the plankton of both water bodies (Kortunova, 1983; Kortunova and Galanova, 1988; Presnova and Khulapova, 2015; Seletkova, 2015). In 2014–2019, the contribution of *Thermocyclops crassus* reached 24–30% of the crustacean abundance and 20% of the zooplankton biomass in the Kama Reservoir in some years.

The number of zooplankton in both studied reservoirs is characterized by increasingly large fluctuations year after year (Kortunova, 1983; Kortunova and Galanova, 1988; Seletkova, 2015). This pattern is also confirmed by our data for 2014–2019 (Fig. 7). The biomass of zooplankton in the reservoirs has increased in the current period by 2.5–3.0 times compared to the 1950s–1960s. In the Kama Reservoir, its maxima were recorded in the 1970s and 2010s. In the Votkinsk Reservoir, a significant increase in biomass was observed only in the 2010s. An increase in the amount of summer zooplankton in the past decade has also been recorded for other reservoirs of the cascade, in particular, for the reservoirs of the Upper and Middle Volga (Kopylov et al., 2012; Lazareva et al., 2014). This is presumably determined by the eutrophication of the reservoir ecosystems due to global warming.

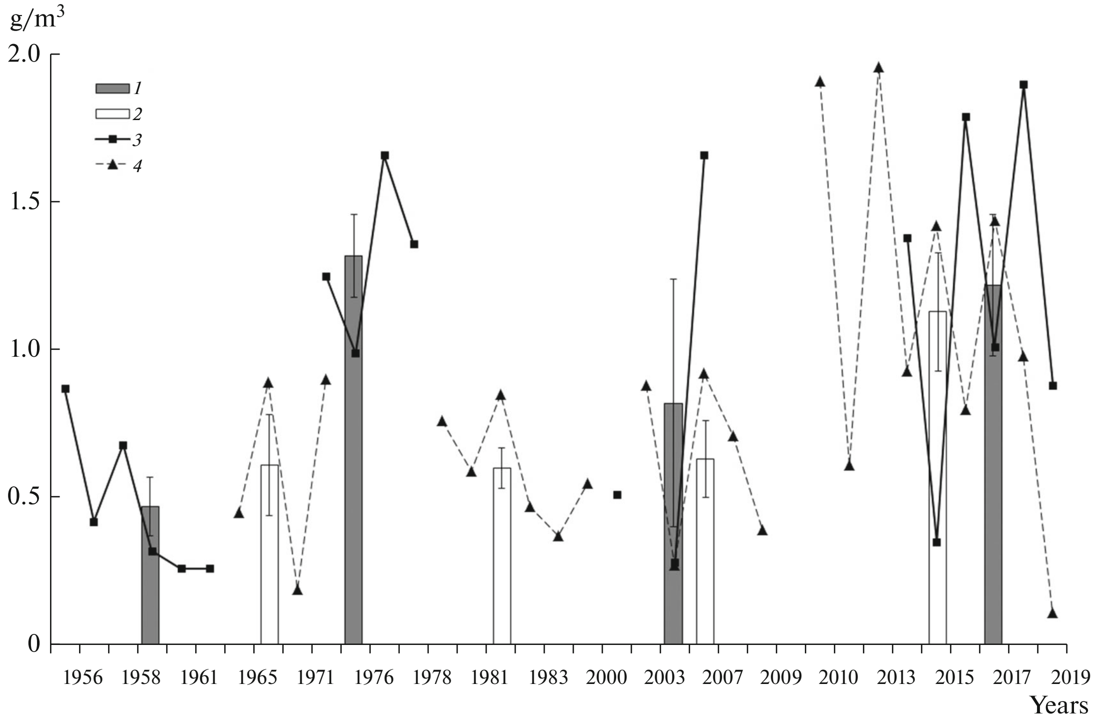

Fig. 7. Long-term changes in zooplankton biomass in the Kama (1956–2019) and Votkinsk (1965–2019) reservoirs. (*1*) Kama Reservoir, average values for the period of 3 to 6 years; (*2*) Votkinsk Reservoir, average for the period of 3 to 9 years; (*3*) average for July–August in each year in the Kama Reservoir; and (*4*) average for July–August in each year in the Votkinsk Reservoir. Source: 1956–1959 (Ulomskii, 1961); 1961–1962 (Kortunova and Serkina, 1980; Serkina, 1971); 1965–1966 (Udalova, 1968); 1971–1975 (Serkina, 1975; Poskryakova, 1977); 1976–1978 (Kortunova and Zueva, 1979; Kortunova and Galanova, 1986); 1979–1982 (Kortunova and Galanova, 1988); 1983–2009 (Kostitsyn et al., 2011; Seletkova, 2015); 2010–2011 (archival data from the Perm Branch of the Russian Federal Research Institute of Fisheries and Oceanography); 2013 (Krainev and Kuznetsova, 2013), and 2014–2019 (this paper).

CONCLUSIONS

A total of 100 and 69 zooplankton species were recorded in the Kama and Votkinsk reservoirs, respectively, over 6 years (2014–2019). The exact dates of the appearance of ten invasive species of southern origin were determined; 70% of them were recorded in both reservoirs from 2012 to 2016. Among them, three crustacean species (the southern cladoceran *Diaphanosoma orghidani* and Ponto-Caspian copepods *Eurytemora caspica* and *Heterocope caspia*) were annually recorded in more than 30% of samples and locally formed up to 30% of the crustacean abundance. Among southern rotifers, *Conochiloides coenobasis, Pompholyx sulcata,* and *Asplanchna henrietta* were abundant in some years (up to 24% N_{rot}). An increase in the contribution of the thermophilic copepod *Thermocyclops crassus* to the community (up to 24–30% of the crustacean abundance) was recorded; this species was not previously dominant here. In 2014–2019, the highest abundance of zooplankton in both reservoirs (>150 thousand ind./m^3) was observed in the shore zone, while it was 1.7–2.0 times lower in the pelagic zone. The biomass of coastal and pelagic zooplankton did not actually differ and varied from 1.1 to 1.7 g/m^3. A clear trend towards an increase in zooplankton biomass was revealed in the reservoirs in the 2010s; the level of biomass became 2.5–3.0 times higher in 2014–2019 than in the 1950s–1960s.

FUNDING

This study was performed as part of State Task AAAA-A18-118012690106-7.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

Statement on the welfare of humans or animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Translated by D. Zabolotny