Ecological Role of *Cyprideis torosa* and *Heterocypris salina* (Crustacea, Ostracoda) in Saline Rivers of the Lake Elton Basin: Abundance, Biomass, Production, Fatty Acids

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Saline rivers are highly productive ecosystems in arid regions. The meiobenthic community (bottom meiofauna) and its dominant representatives are one of the least studied components of these aquatic ecosystems. Ostracods *Cyprideis torosa* and *Heterocypris salina* are major consumers among the species of bottom meiofauna in saline rivers flowing into the hyperhaline Lake Elton (Volgograd Region, Russia). We estimated the abundance, biomass and production of *C. torosa*, the dominant species at the mouth of the polyhaline Chernavka River (average salinity is ~30 g l^{-1}) and *H. salina*, the dominant species at the mouth of the mesohaline Bolshaya Samoroda River (~13 g l^{-1}) in Spring (May) and Summer (August). Additionally, we studied the composition and content of fatty acids of the ostracods and their potential food sources (bottom sediments with bacterial-algal mats). We found that the abundance and biomass (wet weight with shells) of *C. torosa* in the Chernavka River and *H. salina* in the Bolshaya Samoroda River reached 3.5×10^6 ind. m^{-2} and 117 g m^{-2}, and 1.1×10^5 ind. m^{-2} and 12 g m^{-2}, respectively. The first species formed on average about 85% of the total abundance and 96% of the total biomass of the meiobenthos, and the second one, about 13% and 31%, respectively. The daily production of *C. torosa* and *H. salina* can reach 249 and 36 mg m^{-2} ash-free dry weight, respectively. The results indicate a potentially high role for

these species in the total flow of matter and energy in the studied habitats. Based on the fatty acid (FA) composition of the ostracods and their food sources, it was found that *C. torosa* mainly consumed diatoms, while *H. salina* preferred bacteria, cyanobacteria, and green algae. Differences between the species were greater than differences between the bottom sediments from the rivers. It may mean that the ostracods selectively consumed different food items that may be related to different nutrient requirements of the species. Seasonal changes in FA compositions of the ostracods were higher than in their food sources (bottom sediments), which also indicates selective feeding of the species.

Key words: Saline rivers, Ostracods, Diet, Fatty acid markers.

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BACKGROUND

Nematodes, turbellarians, oligochaetes, ostracods, harpacticoid copepods are commonly the most diverse and abundant metazoan groups of bottom meiofauna (meiobenthos) inhabiting different non-marine saline habitats, including streams. Roundworms are usually the main representatives, but under specific conditions, other taxa may also dominate (Giere 2009). In inland saline rivers, the predominance of the first larval instars of halophilic chironomid species has been noticed (Gusakov and Gagarin 2012; Gusakov 2019). It is known that in a small and stable range of changes in the salinity level, common factors (*e.g.*, temperature, ionic composition, oxygen and nutrient content, flow rate, characteristics of bottom sediments, degree of overgrowth with macrophytes, etc.) can have a noticeable effect on the distribution, diversity, and structure of halophilic communities. At the same time, in some habitats, periodic or sudden abrupt (in a wide range) salinity changes are of paramount importance (Williams 1998; Soetaert et al. 1995; Ingole and Parulekar 1998; Coull 1999; Giere 2009; Lazareva et al. 2010; Zinchenko and Golovatyuk 2010). Under such conditions, the reduction of species richness of meiobenthic communities occurs, since many halophilic and halobiont animals can survive in a wide salinity gradient, but successful reproduction of populations of a considerable number of species is apparently possible only in a relatively narrow range (Ingole and Parulekar 1998; Coull 1999). Against the background of low species richness, a mass development of a few (sometimes only one-two) of the most tolerant species is often observed. Castel (1992) categorized similar biotopes as extreme for meiofauna. One

of the typical examples of water bodies with an unstable salinity regime are small highly mineralized rivers, which are exposed to precipitation and floods, and their mouths are additionally subject to tidal and wind surges, in general, of more saline waters from receiving basins.

Saline rivers are widespread in arid and semiarid regions of the world. The study of these aquatic ecosystems is of considerable importance for comprehending the diversity, ecology and biology of halophilic and halobiont species, trophic interactions, and the transfer of organic matter and energy from the aquatic to terrestrial ecosystems (Williams 1987; Ballinger and Lake 2006; Velasco et al. 2006; Zinchenko et al. 2014). Among the various groups of aquatic organisms living in saline rivers, the quantitative role of bottom meiofauna is still poorly studied. Until now, most researches of the meiobenthic community and its major members in the salinity gradient have been carried out in coastal lagoons and estuaries of fresh rivers flowing into the sea, while data from isolated athalassic saline basins are scarce (Castel 1992; Soetaert et al. 1995; Coull 1999; Giere 2009; Gusakov 2019).

In the southeast of the European part of Russia (the Volgograd Region), on the boundary between the steppes and semi-deserts, there is a closed basin of the hyperhaline Lake Elton with several inflowing rivers differing in salinity. As preliminary studies have shown, organisms of bottom meiofauna, in particular, ostracods *Cyprideis torosa* (Jones, 1850) and *Heterocypris salina* (Brady, 1868) are important components of the bottom communities of these aquatic ecosystems. *Cyprideis torosa* is a common species in all rivers, but most abundant in polyhaline habitats. *Heterocypris salina* is one of the dominant species in mesohaline rivers, while in polyhaline ones it is not found at all (Gusakov and Gagarin 2012; Zinchenko et al. 2018; Gusakov 2019).

The Ostracoda (seed shrimps) is the most species-rich class of Crustacea. They are widely distributed in various biotopes around the world, from the deep sea to temporary ponds and ground-waters. A diverse fauna of ostracods inhabits athalassic saline aquatic ecosystems, sometimes reaching high abundances (Heip 1976a; De Deckker 1981; Rodríguez-Pérez and Baltanás 2008; Giere 2009). In his review, De Deckker (1981) lists more than 40 ostracod species known from saline waters (> 3‰) of Europe. Due to their mobility and behaviour, ostracods belong to the main bioturbators among meiobenthic animals and have a considerable impact on the structure and geochemistry of sediments. In the habitats where these crustaceans are abundant, their empty shells can form a major part of the bottom sediments. Since shells of many species are preserved well in bottom sediments, fossil ostracods are successfully used to indicate environmental conditions and allow climatic reconstructions in paleolimnological investigations (Heip 1976a; De Deckker 1981; Meisch 2000; Martens et al. 2008; Karanovic 2012; Mischke et al. 2012).

In some saline habitats, ostracods are likely the top of the trophic chains (Heip 1976a), and some species can consume up to half of the total food intake of the examined meiofauna (Ólafsson

et al. 1999). However, data on the feeding spectra of ostracods, especially of those inhabiting saline rivers, are practically absent. Furthermore, most of the known studies on the ostracod diet are generally based on two traditional methods: direct examination of gut contents under a microscope and laboratory observations on feeding behavior of animals (Smith 2020). Both approaches have some disadvantages (Nielsen et al. 2018). Examination of gut contents does not always allow identification of food objects because they are destroyed during feeding, especially if the crustacean is an active predator, scraper or grinder (Smith 2020). In addition, not all consumed objects are digested and assimilated. For instance, some microalgae remain viable after passing through the guts of aquatic invertebrates (Porter 1976; Gladyshev et al. 2000). On the other hand, in laboratory experiments, it is possible to estimate the ability of organisms to consume only limited food sources, but feeding behavior and trophic interactions of organisms in the natural environment are much more flexible, diverse, and determined by many factors that cannot be replicated in artificial conditions.

In addition to those described above, there are other approaches for studying the food spectra of Ostracoda. One of them is fatty acid (FA) analysis. In contrast to traditional methods, FA analysis indicates food assimilated by the animal and discloses its diet under natural conditions. FAs can be used to study animal diets because many organisms synthesize specific FAs characteristic only to them. Bacteria, algae, plants, and some animal taxa synthesize specific FAs, which are transferred through the food web and accumulated in lipids of animals at the higher trophic levels. FA markers of various taxa have been published elsewhere (*e.g.*, Kelly and Scheibling 2012; Makhutova et al. 2013). Numerous data on trophic relationships in aquatic ecosystems were successfully obtained by tracking the transfer of specific FAs in food webs (*e.g.*, Desvilettes et al. 1997; Sushchik et al. 2003; Taipale et al. 2009; Whiles et al. 2010; Makhutova et al. 2013; Sauvanet et al. 2013; Galloway et al. 2015; Golovatyuk et al. 2018; Guo et al. 2018). Besides the use of FAs as food markers, some FAs, namely, arachidonic (ARA, 20:4n-6), eicosapentaenoic (EPA, 20:5n-3), and docosahexaenoic (DHA, 22:6n-3) acids, are physiologically essential compounds required for normal growth and development of animals, including humans, and used as indicators of food quality (Gladyshev et al. 2013).

The aim of the present work was to estimate the abundance, biomass, and production of *C. torosa* and *H. salina* in two saline rivers of Lake Elton basin and to assess the role of these ostracods in the ecosystem food webs by studying the food sources of the species using fatty acids markers.

MATERIALS AND METHODS

Study area

Lake Elton (catchment area 1365 km^2, water surface area ~180 km^2) is the largest hypersaline lake of Europe. It is located in the southeast of the European territory of the Russian Federation within the northern part of the Caspian Depression (the Volgograd Region, 110 km east of the Volga River) (Fig. 1). The main landscape surrounding the lake is a desert steppe. The climate is continental and dry with the annual average air temperature of +7°C, the lowest in January (down to -36.1°C) and the highest in August (up to 41.1°C). The average amount of precipitation is 280–300 mm year^{-1}, which is 2.0–2.5 times less than the evaporation from an open water surface. The lake has seven small (~2.4–59 km long) inflows (Fig. 1). The inflows are typical lowland rivers with asymmetrical valleys, meandering beds, and slow water flow. The rivers are mainly filled from two sources: atmospheric precipitation (80–90%) and groundwater. In the catchment area, salt-bearing and carbonate sedimentary rocks predominate. A significant mineralization gradient (commonly from 6 to ~40 g l^{-1}) is characteristic of these rivers. Detailed description of the research area and saline rivers of the Lake Elton basin is given elsewhere (Lazareva et al. 2010; Golovatyuk et al. 2018; Zinchenko et al. 2011 2019).

The study was carried out at the mouths of two rivers: the polyhaline Chernavka River and the mesohaline Bolshaya Samoroda River (hereinafter referred to as the B. Samoroda River) (Fig. 1). The main characteristics of the rivers and habitats studied are given in table 1. The data on the water chemistry were kindly provided by the Center for Monitoring the Aquatic and Geological Environment, Ltd. (Samara, Russia), which has a Federal license for chemical analyses of surface waters.

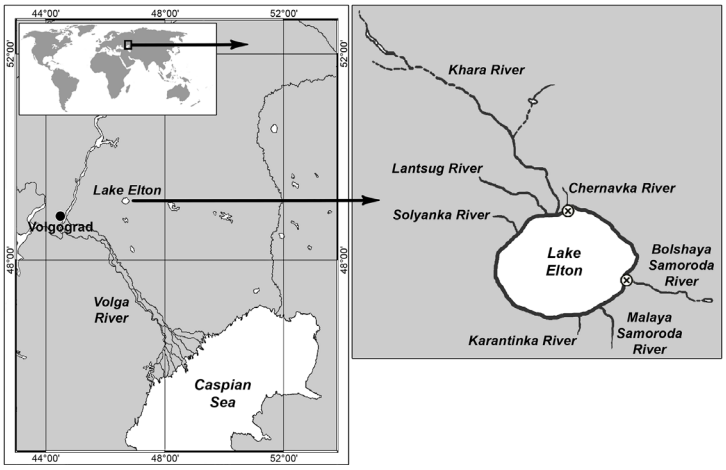

Fig. 1. Map of the study area and a scheme of location (points with crosses) of the sampling stations. The exact coordinates of the stations are given in table 1.

Table 1. Values of the physical and chemical parameters (min-max) in mouths of the Chernavka and B. Samoroda rivers during the study period

Parameter	Chernavka River	B. Samoroda River
Length, km	5.2	24.3
Catchment area, km^2	18.4	130.0
Location of the stations	N 49°07.620', E 46°46.969'	N 49°12.599', E 46°40.702'
Riverbed width, m	3.5	25.0
Depth, m	0.05–0.10	0.10–0.15
Current velocity, m s^{-1}	0.05–0.20	0.01–0.05
Temperature, °C	20.0–28.0	22.0–29.6
pH	7.4–8.2	8.0–8.9
O_2, mg l^{-1}	5.9–18.6	6.7–13.0
Total mineralization, g l^{-1}	26.5–31.0	9.8–16.0
Na^++K^+, g l^{-1}	7.98–9.43	2.80–4.54
Ca^{2+}, g l^{-1}	0.92–1.44	0.28–0.67
Mg^{2+}, g l^{-1}	0.68–0.89	0.32–0.58
Cl^-, g l^{-1}	15.62–17.27	4.26–7.28
SO_4^{2-}, g l^{-1}	0.83–1.92	1.26–3.58
HCO_3^-, g l^{-1}	0.23–0.31	0.34–0.54
PO_4^{3-}–P, mg l^{-1}	0.39-1.70	0.44-1.20
NH_4^+–N, mg l^{-1}	4.90–30.00	0.18–8.25
NO_3^-–N, mg l^{-1}	0.03–0.10	0–0.10

Sampling

Samples of bottom meiofauna were collected at the mouth of the Chernavka River in May 2019 and in August 2009, 2017–2019, and at the mouth of the B. Samoroda River in May 2015, 2019 and in August 2013, 2014, 2018, and 2019. At each sampling event, three cores of the bottom sediments and near-bottom water (about 5 cm each) were taken using a plastic tube with diameter of 34 mm (capture area ~9 cm^2) and pooled in one sample. The samples were fixed with 4% formaldehyde. In the laboratory, they were filtered through a sieve with a mesh size of 82 μm. The sieved residues were examined using a Bogorov counting chamber under a stereomicroscope. *Cyprideis torosa* and *H. salina* were selected from the chamber manually (with a pipette). Measurement of selected ostracod specimens was performed using an eyepiece micrometer. Their individual weights were calculated using length-weight equations:

$W = 0.189\ L^{3.091}$

for *C. torosa* (Ankar and Elmgren 1976), and

$W = 0.15\ L^3$

for *H. salina* (Kurashov 2002), where W is the wet weight with shells (mg), L is the body length (mm).

Calculation of production

The production characteristics of the *C. torosa* and *H. salina* populations were evaluated by the physiological method (Winberg 1971). Only larval stages of the crustaceans (there are eight of them in both species) were used in the calculations. The possible daily increase of biomass of eggs developing in some females was neglected.

Daily production was calculated as follows:

$P = R\,K_2 / (1–K_2)$,

where P is the production (cal m^{-2} day^{-1}), R is the metabolic rates (cal m^{-2} day^{-1}), K_2 is the coefficient of efficiency of assimilated food energy used for growth, whose value for ostracods (with shells) is 0.38 (Kurashov 2002 2007).

Values of R were determined using the formula:

$R = 4.86\,Q\,N$,

where 4.86 is the oxycaloric coefficient (cal ml^{-1} O_2), Q is the rate of daily oxygen consumption (ml O_2 $ind.^{-1}$ day^{-1}), N is the abundance (ind. m^{-2}) (Winberg and Lavrentieva 1984; Kurashov 2007).

The values of Q were obtained from the equations of the relationship between oxygen consumption per hour and animal body weight, taking into account the temperature of the study periods:

$Q = 0.3096\,W_{av}^{1.049}\,q_t\,24$

for *C. torosa* and

$Q = 0.0478\,W_{av}^{0.746}\,q_t\,24$

for *H. salina* (Kurashov 2007), where W_{av} is the average weight of one individual (g wet weight with shells), q_t is the temperature correction. The q_t value was estimated using the constant Q_{10} = 2.25 as:

$q_t = 2.25^{(t–20/10)}$,

where t is the temperature (°C) (Winberg 1983).

To convert the calculated production from the energy units to the biomass equivalent, the following values for ostracods were used: 450 cal per 1 g wet weight with shells (Sherstiuk 1971), and 6000 cal per 1 g ash-free dry weight (Ankar and Elmgren 1976).

Fatty acid analysis

In May and August 2019, mature and premature instars of *C. torosa* and *H. salina* were sampled in the Chernavka and B. Samoroda rivers, respectively. At each sampling point, samples of the surface layer of bottom sediments were collected (using a net with a mesh size 82 μm) in a 2.0-

liter container partially filled with water from the studied biotope. In the laboratory, the ostracods were withdrawn with a pipet under a stereoscopic microscope and transferred to a Petri dish containing a filtered water from the respective habitat. This procedure was repeated three times: the individuals were transferred from one dish to another every hour to remove contaminants adhering to the shells and for emptying of their guts. Finally, the crustaceans were washed one more time in a dish with distilled water, gently wiped with filter paper until the wet spots disappeared, and weighed. Immediately after weighing, the animals were placed in a vial with chloroform-methanol mixture (2:1, v/v), which then were kept at -20°C until further analysis. In total, 1500 individuals of *C. torosa* and 760 of *H. salina* were collected in three replicates for each species in each season. Besides, bottom sediments with bacterial-algal mats were collected from the studied habitats. Benthic invertebrates present in the sediments were removed under a stereomicroscope. Then, the samples were dried at room temperature until the disappearance of surface moisture. Their weighing, preservation and storage were carried out as described above for ostracods.

The samples of ostracods (with shells) and bottom sediments were homogenized, and lipids were extracted with chloroform and methanol (2:1, v/v). Dry lipids were then supplemented with 0.8 ml of sodium methylate solution in methanol (8 g l^{-1}). The mixture was heated for 10 min at 90°C. The tubes were cooled for 5 min at room temperature, supplemented with 1 ml of methanol: H_2SO_4 (97:3, v/v), and methylated for 10 min at 90°C. The fatty acid methyl esters (FAMEs) were extracted from the mixture with 2 ml hexane and washed three times with 5 ml of saturated NaCl solution. The hexane extract containing FAMEs was dried by passing it through a layer of anhydrous Na_2SO_4, and then the layer of anhydrous Na_2SO_4 was washed with 6 ml of hexane. Hexane was evaporated on a rotary vacuum evaporator. FAMEs were resuspended in 0.03 to 0.1 ml hexane prior to chromatographic analysis. Analysis of FAMEs was conducted using a gas chromatograph with a mass spectrometric detector (Model 7000 QQQ, Agilent Technologies, U.S.), which was equipped with a 30 m capillary HP-FFAP column with the internal diameter of 0.25 mm. The conditions of the analysis were as follows: the velocity of the helium carrier gas was 1.2 ml min^{-1}; the temperature of the injection port was 250°C; the temperature of the heater was programmed from 120 to 180°C at a rate of 5°C min^{-1} for 10 minutes isothermally, then to 220°C with a rate of 3°C min^{-1} for 5 min isothermally, and then to 230°C at a rate of 10°C min^{-1} for 20 min isothermally; the temperature of the chromatography/mass interface was 270°C; the temperature of the ion source was 230°C and that of the quadrupole was 180°C; the ionization energy of the detector was 70 eV; and scanning was performed in the range of 45–500 atomic units with a rate of 0.5 sec per scan (Makhutova et al. 2017). The data were analyzed and counted by the MassHunter Software (Agilent Technologies). The peaks of FAMEs were identified by the mass spectra obtained. The content of fatty acids in the biomass was quantified based on the peak value of the

internal standard, methyl nonadecanoate (Sigma-Aldrich, U.S.), a certain amount of which was supplemented to the samples before the extraction of lipids.

Statistics

To compare the mean values of percentages and contents of each FA in the biomass of ostracods and the bottom sediments, ANOVA, pre-checked with Kolmogorov-Smirnov one-sample test for normality, and Tukey HSD *post hoc* tests were used. To evaluate putative differences in the overall FA composition of ostracods and sediments, multivariate correspondence analysis (CA) was done. Percentages of 32 FAs (see the list below in Results with 20 FAs, plus 16:1n-9 and 16:1n-5) were used as variables, and cases corresponded to sediment (number of samples, $n = 12$) and ostracod samples ($n = 12$). The above statistical tests were performed according to Legendre and Legendre (1998), using STATISTICA software (ver. 9.0, StatSoft Inc. Tulsa, OK, U.S.).

RESULTS

Species composition of the bottom meiofauna

The species richness of the meiobenthos varied between 5 and 10 taxa (7 ± 1 on average) in the Chernavka River and between 7 and 18 taxa (12 ± 2) in the B. Samoroda River. In total, 15 and 26 taxa were identified respectively in these rivers. There were three species of ostracods among them (Appendix 1). *Cyprideis torosa* was the only species of ostracod found in the Chernavka River. It was one of the most common species of the meiofauna in the study habitats. Together with the nematode *Monhystrella parvella* (Filipjev, 1931), it was present in all samples from both rivers. Besides, in the Chernavka River, the harpacticoid copepod *Cletocamptus retrogressus* (Schmankewitsch, 1875) and chironomid larvae of *Cricotopus salinophilus* (Zinchenko, Makarchenko et Makarchenko, 2009) were dominant species. In the B. Samoroda River, the ostracod *H. salina*, the harpacticoid copepod *Cletocamptus confluens* (Schmeil, 1894), and chironomid larvae of *Tanytarsus kharaensis* (Zorina et Zinchenko, 2009) had high frequencies of occurrence (Appendix 1).

Abundance, biomass and production of the ostracods

Cyprideis torosa was the dominant taxon of the bottom meiofauna in the Chernavka River

during the entire study period. Its abundance and biomass in some of the samples reached very high values, up to 3.5×10^6 ind. m^{-2} and 117 g m^{-2}, rarely recorded in the meiofauna or for ostracod populations (Appendix 1, Table 2). On average, *C. torosa* accounted for about 85% of the total abundance and 96% of the total biomass of all meiobenthos taxa in the samples. The average proportion of adults in its population was about 17% of abundance and 60% of biomass (Table 2). Females ranged from 44% to 77% of the adult individuals.

The abundance and biomass of *H. salina* in the B. Samoroda River in some samples exceeded 111×10^3 ind. m^{-2} and 12 g m^{-2}. In some periods, percentages of *H. salina* reached 20–30% of the total abundance and 50–60% of the total biomass of the entire community, and the average values were about 13% and 31%, respectively. The average proportion of adult females in the *H. salina* population (the species reproduce by parthenogenesis, males are not known) was 40% of abundance and 68% of biomass (Appendix 1, Table 2).

The production characteristics of the populations of *C. torosa* and *H. salina* are given in table 2. The average production of *C. torosa* was substantially higher than that of *H. salina*. The daily production of the both species varied considerably during the studied period. Its maximum values for each of the crustaceans were found in August, while close to minimum ones were registered both in May and August (Table 2).

Table 2. Quantitative characteristics of the populations of *Cyprideis torosa* and *Heterocypris salina* in the Chernavka and B. Samoroda rivers: N – abundance; $N_{\%}$ – relative abundance of total meiobenthos; B – biomass; $B_{\%}$ – relative biomass of total meiobenthos; $N_{AD\%}$ – relative abundance of adults in the population; $B_{AD\%}$ – relative biomass of adults in the population; P – daily production in calories; P_{WW} – daily production in wet weight with shells; P_{AFDW} – daily production in ash-free dry weight

	Cyprideis torosa (Chernavka River)							
Date	20.08.09	16.08.17	17.08.17	18.08.17	19.08.18	16.05.19	16.08.19	Average ± SE
N, 1×10^3 ind. m^{-2}	552.0	3503.5	1927.0	3093.2	1303.6	483.2	1607.7	1781.5 ± 476.2
$N_{\%}$, %	90.8	85.1	79.7	86.0	76.6	78.8	94.9	84.6 ± 2.7
B, g m^{-2}	33.2	117.4	87.0	94.9	85.3	47.9	49.3	73.6 ± 12.4
$B_{\%}$, %	96.8	99.0	98.3	98.5	93.5	94.8	93.1	96.3 ± 1.0
$N_{AD\%}$, %	18.2	9.8	15.6	7.7	22.7	37.4	9.1	17.2 ± 4.3
$B_{AD\%}$, %	59.3	48.3	51.2	68.3	71.3	66.2	56.0	60.1 ± 3.6
P, cal m^{-2} day^{-1}	267.7	1495.4	1072.2	1404.8	322.2	261.7	366.2	741.5 ± 229.1
P_{WW}, mg m^{-2} day^{-1}	594.9	3323.0	2382.6	3121.8	716.1	581.5	813.7	1647.7 ± 509.0
P_{AFDW}, mg m^{-2} day^{-1}	44.6	249.2	178.7	234.1	53.7	43.6	61.0	123.6 ± 38.2
	Heterocypris salina (B. Samoroda River)							
Date	14.08.13	16.08.14	29.05.15	19.08.18	15.05.19	16.08.19	Average ± SE	
N, 1×10^3 ind. m^{-2}	13.3	17.8	1.1	111.1	20.0	71.4	39.1 ± 19.1	
$N_{\%}$, %	4.1	4.1	0.5	7.3	28.4	32.5	12.8 ± 6.2	
B, g m^{-2}	2.6	2.3	0.2	1.6	4.1	12.6	3.9 ± 2.0	
$B_{\%}$, %	25.8	28.9	4.3	4.7	54.2	66.8	30.8 ± 11.4	
$N_{AD\%}$, %	66.7	43.8	33.3	1.2	51.9	40.9	39.6 ± 9.8	
$B_{AD\%}$, %	86.6	75.1	65.5	25.6	83.8	72.6	68.2 ± 9.9	
P, cal m^{-2} day^{-1}	19.4	46.9	4.7	86.9	38.2	218.5	69.1 ± 35.0	
P_{WW}, mg m^{-2} day^{-1}	43.1	104.3	10.4	193.2	84.9	485.5	153.6 ± 77.9	
P_{AFDW}, mg m^{-2} day^{-1}	3.2	7.8	0.8	14.5	6.4	36.4	11.5 ± 5.8	

Fatty acid composition and content

Using correspondence analysis, the species of ostracods and the river bottom sediments were represented in a two-dimensional space according to their percentages of fatty acids (Fig. 2). The first dimension explained 70.23% of inertia of the data set, and the second one 14.70%. Chi-square values for both dimensions and the total Chi-square were significant ($p < 0.0001$). The first dimension showed large differences between ostracods and sediments. These differences were mostly related to the relative composition in 18:2n-4, 22:5n-3, 22:6n-3, 22:5n-6, 18:0, 20:4n-6, 20:5n-3 and 18:1n-9, on the one hand, and 24:0, i15:0, 16:3n-3, 16:1n-7, and bacterial FAs (Sum13-17), on the other. Indeed, significant differences were found in the contents of these FAs between ostracods and sediments (Table 3). Additionally, *H. salina* had significantly higher percentages of 18:3n-6 compared to the bottom sediments from the B. Samoroda River. By contrast, *C. torosa* had significantly lower percentages of 14:0, 20:0, and i17:0 compared to the bottom sediments from the Chernavka River (Table 3).

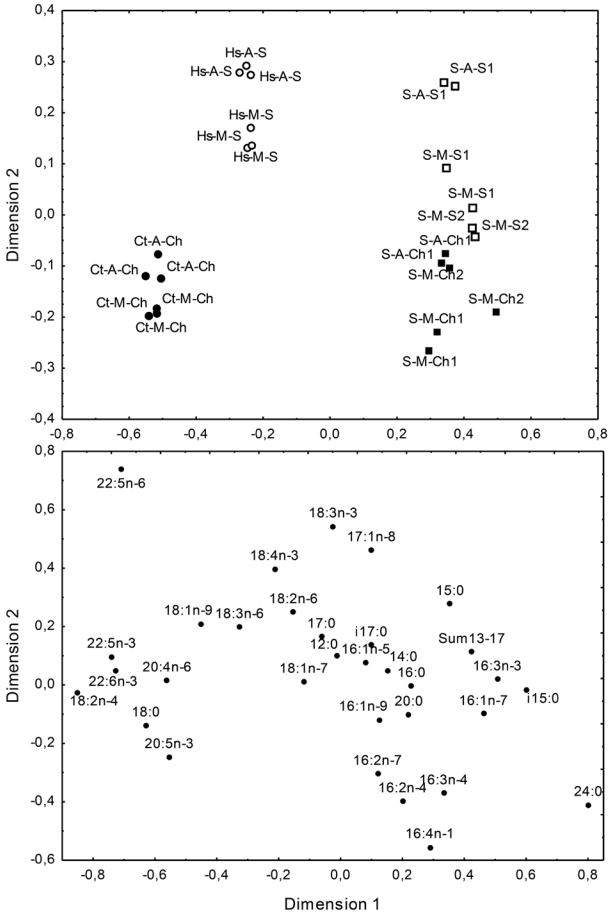

Fig. 2. Results of correspondence analysis of *Cyprideis torosa*, *Heterocypris salina*, bottom sediments from the B. Samoroda River and the Chernavka River in May and August, 2019 and fatty acids (% of the total according to Table 3) represented in a two-dimensional space reproducing 85%

of total inertia. Ct-A-Ch – *C. torosa* from the Chernavka River in August; Ct-M-Ch – *C. torosa* from the Chernavka River in May; Hs-A-S – *H. salina* from the B. Samoroda River in August; Hs-M-S – *H. salina* from the B. Samoroda River in May; S-A-S – bottom sediments from the B. Samoroda River in August; S-M-S – bottom sediments from the B. Samoroda River in May; S-A-Ch – bottom sediments from the Chernavka River in August; S-M-Ch – bottom sediments from the Chernavka River in May.

Table 3. Average values of quantitatively and qualitatively prominent fatty acids (% of total fatty acids ± standard error SE), and sum content of fatty acids and contents of 20:5n-3 and 22:6n-3 (mg g^{-1}, wet weight) in bodies of *Heterocypris salina* from the B. Samoroda River and in bodies of *Cyprideis torosa* from the Chernavka River, and in bottom sediments of the B. Samoroda River and the Chernavka River in May and August, 2019, in the basin of Lake Elton, Russia

Fatty acids	Marker	B. Samoroda River				Chernavka River			
		Heterocypris salina		Sediments		*Cyprideis torosa*		Sediments	
		May, $n = 3$	August, $n = 3$	May, $n = 4$	August, $n = 2$	May, $n = 3$	August, $n = 3$	May, $n = 3$	August, $n = 3$
12:0, %		0.7 ± 0.0^{A}	0.3 ± 0.0^{B}	0.6 ± 0.1^{AC}	0.4 ± 0.0^{BC}	0.4 ± 0.1^{BC}	0.3 ± 0.0^{B}	0.3 ± 0.0^{B}	0.3 ± 0.0^{BC}
14:0	diatoms	3.4 ± 0.1^{AC}	4.1 ± 0.1^{AB}	4.0 ± 0.1^{AB}	4.6 ± 0.2^{B}	2.8 ± 0.1^{C}	2.4 ± 0.1^{C}	4.2 ± 0.3^{AB}	5.0 ± 0.1^{B}
15:0	bacteria	1.7 ± 0.0^{AE}	1.4 ± 0.0^{ADE}	2.1 ± 0.3^{A}	3.8 ± 0.1^{B}	0.5 ± 0.0^{C}	0.7 ± 0.0^{CD}	1.4 ± 0.1^{E}	2.0 ± 0.0^{A}
16:0		13.1 ± 0.7^{A}	14.9 ± 0.2^{A}	20.5 ± 0.2^{B}	24.3 ± 0.3^{B}	12.3 ± 0.1^{A}	12.6 ± 0.2^{A}	21.7 ± 1.1^{B}	20.9 ± 0.0^{B}
17:0	bacteria	1.0 ± 0.0^{A}	1.0 ± 0.0^{A}	0.7 ± 0.1^{BC}	1.0 ± 0.0^{A}	0.6 ± 0.0^{BD}	0.8 ± 0.0^{AC}	0.6 ± 0.1^{B}	0.8 ± 0.0^{ACD}
18:0	detritivory	5.0 ± 0.1^{A}	5.3 ± 0.1^{A}	1.2 ± 0.2^{B}	2.6 ± 0.1^{C}	9.1 ± 0.1^{D}	9.9 ± 0.2^{D}	2.5 ± 0.4^{C}	3.1 ± 0.1^{C}
20:0	detritivory	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.4 ± 0.0^{B}	0.2 ± 0.0^{A}	0.2 ± 0.0^{A}	0.3 ± 0.0^{B}	0.3 ± 0.0^{B}
24:0	detritivory	0.1 ± 0.0^{A}	0.0 ± 0.0^{A}	0.2 ± 0.0^{A}	0.4 ± 0.1^{B}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.9 ± 0.1^{C}	0.7 ± 0.0^{C}
i15:0	bacteria	0.9 ± 0.0^{A}	0.8 ± 0.0^{A}	1.5 ± 0.2^{A}	3.0 ± 0.1^{B}	0.3 ± 0.0^{A}	0.3 ± 0.0^{A}	2.8 ± 0.2^{B}	2.8 ± 0.1^{B}
i17:0	bacteria	0.6 ± 0.0^{A}	0.7 ± 0.0^{A}	0.3 ± 0.0^{BC}	0.6 ± 0.0^{A}	0.3 ± 0.0^{B}	0.2 ± 0.0^{B}	0.7 ± 0.1^{A}	0.5 ± 0.0^{AC}
Sum13-17	bacteria	5.3 ± 0.1^{A}	4.8 ± 0.1^{A}	7.4 ± 0.3^{B}	12.1 ± 0.3^{C}	2.0 ± 0.1^{D}	2.3 ± 0.1^{D}	8.1 ± 0.4^{BE}	9.2 ± 0.3^{E}
16:1n-7	diatoms	10.5 ± 0.3^{A}	8.5 ± 0.1^{A}	26.9 ± 0.9^{B}	15.6 ± 0.0^{C}	7.1 ± 0.1^{A}	6.6 ± 0.3^{A}	21.8 ± 1.5^{D}	20.9 ± 0.0^{D}
17:1	bacteria	1.4 ± 0.0^{A}	1.7 ± 0.0^{B}	1.1 ± 0.1^{C}	2.4 ± 0.1^{D}	0.4 ± 0.0^{E}	0.7 ± 0.1^{EF}	0.6 ± 0.0^{E}	0.9 ± 0.0^{CF}
18:1n-9		12.0 ± 0.9^{A}	11.9 ± 0.1^{A}	3.9 ± 1.0^{B}	4.7 ± 0.0^{B}	9.5 ± 0.1^{A}	9.8 ± 0.6^{A}	3.1 ± 0.4^{B}	4.1 ± 0.3^{B}
18:1n-7		15.5 ± 0.3^{AC}	14.0 ± 0.2^{AB}	11.6 ± 0.7^{B}	15.4 ± 0.2^{AB}	15.6 ± 0.2^{AC}	17.0 ± 0.4^{A}	12.2 ± 1.3^{BC}	14.0 ± 0.0^{ABC}
16:2n-7	diatoms	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.2 ± 0.0^{AB}	0.1 ± 0.0^{A}	0.2 ± 0.0^{AB}	0.2 ± 0.0^{AB}	0.3 ± 0.1^{B}	0.3 ± 0.0^{AB}
16:2n-4	diatoms	0.7 ± 0.0^{AB}	0.6 ± 0.0^{A}	1.1 ± 0.2^{ABC}	0.6 ± 0.0^{A}	1.3 ± 0.1^{BC}	0.9 ± 0.1^{ABC}	2.2 ± 0.2^{C}	1.6 ± 0.0^{C}
16:3n-4	diatoms	1.2 ± 0.1^{AB}	0.7 ± 0.0^{A}	1.4 ± 0.3^{AB}	0.7 ± 0.0^{A}	1.0 ± 0.1^{A}	0.6 ± 0.0^{A}	2.8 ± 0.7^{B}	2.3 ± 0.0^{AB}
16:3n-3	green algae	0.1 ± 0.0^{A}	0.1 ± 0.0^{A}	0.3 ± 0.0^{B}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.0 ± 0.0^{A}	0.1 ± 0.1^{A}	0.0 ± 0.0^{A}

16:4n-1	diatoms	0.3 ± 0.0^{AC}	0.0 ± 0.0^{B}	0.5 ± 0.0^{A}	0.0 ± 0.0^{BC}	0.5 ± 0.0^{A}	0.3 ± 0.0^{AC}	0.9 ± 0.1^{D}	0.5 ± 0.0^{A}
18:2n-6	cb+green algae	2.5 ± 0.1^{AC}	2.6 ± 0.0^{A}	2.3 ± 0.5^{AC}	1.6 ± 0.0^{AB}	1.4 ± 0.0^{AB}	2.3 ± 0.1^{AC}	0.9 ± 0.1^{B}	1.2 ± 0.1^{BC}
18:2n-4	m/s bacteria	1.1 ± 0.0^{A}	0.8 ± 0.0^{B}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	1.4 ± 0.0^{D}	0.9 ± 0.0^{B}	0.2 ± 0.0^{E}	0.2 ± 0.0^{CE}
18:3n-6	cb+green algae	0.9 ± 0.0^{A}	0.7 ± 0.0^{B}	0.4 ± 0.0^{C}	0.3 ± 0.0^{CE}	0.5 ± 0.0^{D}	0.6 ± 0.0^{BD}	0.2 ± 0.0^{E}	0.4 ± 0.0^{CD}
18:3n-3	cb+green algae	2.2 ± 0.1^{A}	4.4 ± 0.1^{B}	2.2 ± 0.2^{A}	3.0 ± 0.1^{C}	1.1 ± 0.0^{D}	1.1 ± 0.0^{D}	1.0 ± 0.1^{D}	0.9 ± 0.0^{D}
18:4n-3	dinoflagellates	1.5 ± 0.0^{AC}	2.5 ± 0.1^{B}	1.0 ± 0.2^{AE}	2.0 ± 0.2^{BC}	1.3 ± 0.0^{A}	1.1 ± 0.0^{AE}	0.5 ± 0.1^{D}	0.6 ± 0.0^{DE}
20:4n-6		3.4 ± 0.2^{A}	2.9 ± 0.1^{A}	1.3 ± 0.2^{B}	0.9 ± 0.0^{B}	3.1 ± 0.1^{A}	4.9 ± 0.2^{C}	0.9 ± 0.0^{B}	1.3 ± 0.0^{B}
20:5n-3	diatoms	10.0 ± 0.4^{A}	9.7 ± 0.2^{A}	4.4 ± 0.4^{BD}	2.3 ± 0.2^{B}	19.9 ± 0.4^{C}	17.2 ± 0.5^{C}	7.1 ± 1.5^{AD}	5.7 ± 0.3^{AB}
22:5n-6		0.2 ± 0.0^{A}	0.5 ± 0.0^{B}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}	0.1 ± 0.0^{C}	0.2 ± 0.0^{A}	0.0 ± 0.0^{C}	0.0 ± 0.0^{C}
22:5n-3		0.8 ± 0.0^{A}	0.5 ± 0.0^{B}	0.1 ± 0.0^{C}	0.1 ± 0.1^{C}	0.5 ± 0.0^{B}	0.7 ± 0.1^{AB}	0.1 ± 0.1^{C}	0.0 ± 0.0^{C}
22:6n-3	dinoflagellates	2.0 ± 0.1^{A}	2.1 ± 0.0^{A}	0.3 ± 0.0^{B}	0.2 ± 0.0^{B}	2.5 ± 0.1^{C}	1.8 ± 0.0^{A}	0.4 ± 0.1^{B}	0.2 ± 0.0^{B}
20:5n-3, mg g^{-1} ww		1.5 ± 0.4^{A}	1.5 ± 0.0^{A}	0.1 ± 0.0^{B}	0.0 ± 0.0^{B}	2.6 ± 0.1^{C}	1.3 ± 0.2^{A}	0.1 ± 0.0^{B}	0.1 ± 0.0^{B}
22:6n-3		0.3^{A}	0.3^{A}	0.0^{A}	0.0^{A}	0.3^{A}	0.1^{A}	0.0^{A}	0.0^{A}
Σ FAs		14.8 ± 3.4^{A}	15.0 ± 0.2^{A}	2.9 ± 0.6^{BC}	0.6 ± 0.0^{B}	13.0 ± 0.4^{AC}	7.8 ± 1.0^{C}	1.3 ± 0.1^{B}	1.0 ± 0.0^{BC}

Means in lines labeled with the same letter are not significantly different at $P < 0.05$ after Tukey HSd post hoc test (normal distribution, standard errors are given) or Kruskal-Wallis test with multiple comparisons of mean ranks (non-normal distribution, standard errors are omitted). Sum13-17 – sum of i13:0, ai13:0, 13:0, i15:0, ai15:0, ai15:1, 15:0, i17:0, ai17:0, ai17:1, 17:0. m/s bacteria – methanotrophic bacteria or symbiotic bacteria. cb – cyanobacteria.

The second dimension, although comparatively less substantial, was also significant, indicating that the largest differences between *H. salina* (especially in August) and the bottom sediments from the Chernavka River in May were primarily due to 22:5n-6 and 16:4n-1. Regarding both dimensions and FA percentages of ostracods and sediments, there were differences between *H. salina* and *C. torosa*, mostly associated with the difference in the percentages of 22:5n-6 and 20:5n-3, and differences between the sediments of the B. Samoroda River and those from the Chernavka River, mostly associated with the percentages of 18:3n-3 and 17:1, on the one hand, and 16:4n-1 and 24:0 on the other hand (Fig. 2, Table 3). Additionally, *H. salina* had significantly higher percentages of Sum 13-17, 17:1 and 18:3n-3, and lower percentages of 18:0 than *C. torosa* (Table 3).

Ostracods and sediments showed seasonal tendencies in the two-dimensional space. Samples of *H. salina* collected in May were closer to each other than to *H. salina* collected in August (Fig. 2). Indeed, *H. salina* collected in May had significantly higher percentages of 12:0, 16:4n-1, 18:2n-4, 18:3n-6 and 22:5n-3 but significantly lower percentages of 17:1, 18:3n-3, 18:4n-3 and 22:5n-6 than in August (Table 3). A similar tendency was observed for *C. torosa* (Fig. 2). This species collected in May had significantly higher percentages of 18:2n-4 and 22:6n-3 but significantly lower percentages of 17:0, 20:4n-6 and 22:5n-6 than in August (Table 3). Some differences between sediments collected in May and August were also found but they were less considerable compared to animals (Fig. 2). The bottom sediments from the B. Samoroda River collected in May had significantly higher percentages of 16:1n-7, 16:3n-3 and 16:4n-1 but significantly lower percentages of 15:0, 17:0, 18:0, 20:0, 24:0, i15:0, i17:0, Sum13-17, 17:1, 18:3n-3, 18:4n-3 than in August. The bottom sediments collected from the Chernavka River in May had significantly higher percentages of 16:4n-1 but significantly lower percentages of 15:0, 17:1 and 18:3n-6, than in August (Table 3).

The average contents (mg g^{-1} of wet weight) of the sum of FAs in the biomass of *H. salina* in May and August and *C. torosa* in May did not differ significantly (Table 3). However, the average content of the sum of FAs in the biomass of *C. torosa* in August was significantly lower compared to *H. salina* in May and August. The FAs content in the ostracod biomass was approximately one order of magnitude higher than in sediments (Table 3). The sum of FAs in the sediments did not differ significantly between rivers.

The average content of the physiologically important eicosapentaenoic acid (20:5n-3, EPA) in the biomass of *H. salina* in May and August and *C. torosa* in August did not differ significantly (Table 3). However, the average content of EPA in the biomass of *C. torosa* in May was significantly higher. The average content of another physiologically important fatty acid, namely, docosahexaenoic acid (22:6n-3, DHA) in the biomass of both ostracods did not differ significantly

between them. The average content of EPA and DHA in sediments was similar in both rivers (Table 3).

DISCUSSION

Distribution and ecology of *Cyprideis torosa* and *Heterocypris salina*

In the Lake Elton basin *C. torosa* (Syn.: *C. littoralis* (Brady, 1870), *C. padaschenkoi* (Daday, 1909), *C. aegyptiaca* (Daday, 1910)) is known since the first studies of its aquatic fauna (Ermakov et al. 1933; Bronstein 1947). More recent surveys have shown that this crustacean is one of the most common and abundant members of the meiobenthos in the rivers flowing into the lake. Hitherto, it is the only species of Ostracoda registered in the polyhaline Solyanka and Chernavka rivers (see Fig. 1), the salinity of which is usually 25–32 g l^{-1}. The highest frequencies of the species (89–100%) in the area have been recorded in these two rivers and also in the mesohaline B. Samoroda River (Gusakov and Gagarin 2012; Gusakov 2019; see Appendix 1, Table 2).

Currently, *C. torosa* is perhaps one of the best-known and well-studied living and fossil representatives of the Ostracoda (De Deckker and Lord 2017). The species has a wide geographical distribution. Its present range covers Europe, Western, Central and South Asia, and Africa, from the polar and temperate to subtropical and tropical regions. It is a euryhaline species and populates a wide spectrum of habitats, from fresh to hypersaline waters, but it is most common in shallow marine lagoons, estuaries, coastal marshes, ponds, lakes, and different athalassic brackish and saline water bodies (Bronstein 1947; Shornikov 1974; Heip 1976a; De Deckker 1981; Meisch 2000; Pint and Frenzel 2016; Wouters 2017). According to various sources, the upper limit of the salinity tolerance of *C. torosa* reaches 96–150 g l^{-1} (De Deckker 1981; Neale 1988; Bodergat et al. 1991; Plotnikov 2016). The species is also able to tolerate a wide range of temperatures, oxygen depletion, high sulfide concentration and a variety of substrates (Gamenick et al. 1997; Mezquita et al. 2000; De Deckker and Lord 2017). In addition to the general adaptation to high salinity, *C. torosa* easily tolerates abrupt changes in salt content, as it can reach high abundances in biotopes with considerable salinity fluctuations (Shornikov 1974). This is the likely reason why this species dominates at the mouths of some tributaries of Lake Elton, in particular, in the Chernavka River, where wind surges of brine from the lake area are often observed.

The second ostracod species we studied, *H. salina*, has been found in the study area only in the mesohaline Lantsug, Khara, and B. Samoroda rivers (see Fig. 1), in biotopes with a salinity not higher than 16.3 g l^{-1}. The species was most commonly found (in 90% of the samples) in the B.

Samoroda River (Gusakov 2019; see Appendix 1, Table 2). *Heterocypris salina*, has a "rich" taxonomic history. Since its original description, this ostracod has repeatedly been rediscovered as a new species. Therefore, at least nine synonyms of this species are now known (Meisch 2000; Karanovic 2012). In previous studies from the tributaries of the Lake Elton, *H. salina* had been known by the name *Cyprinotus salinus* (Brady, 1868) (Ermakov et al. 1933; Bronstein 1947; Lazareva et al. 2010; Gusakov and Gagarin 2012). Its biogeographic distribution corresponds basically to the Holarctic, although its range partially enters the southern hemisphere. At present, most of the known findings of the species are concentrated in Europe, West Asia, and North Africa (Meisch 2000; Henderson 2002). *Heterocypris salina* inhabits water bodies of different types, from freshwater springs and wells to the littoral zones of seas, but it prefers the slightly saline coastal and continental waters, thus being a halophilic species. According to various observations, *H. salina* can be found in sites with salinity up to 20–35 g l^{-1}, but the optimal conditions for its development are in the range of 5–10 g l^{-1} (Löffler 1961; Ganning 1971; Meisch 2000; Perçin-Paçal et al. 2017). It can tolerate some harsh environmental conditions, such as low oxygen and high sulfide concentrations, high temperature, a high degree of organic pollution and is also found in intermittently drying pools (Mezquita et al. 1999; Meisch 2000; Henderson 2002; Kubanç et al. 2007; Perçin-Paçal et al. 2017).

Abundance, biomass and production

The abundance and the biomass of ostracods in the Chernavka River were significantly higher than those in the B. Samoroda River due to the distinct dominance of *C. torosa* in the bottom meiofauna of the former river (see Appendix 1, Table 2). It is well known that *C. torosa* can dominate the benthic communities of saline water bodies, sometimes reaching extremely large abundances (Heip 1976a; Herman and Heip 1982; Gamenick et al. 1997). Previously, the maximum abundance and biomass of the species was found by Heip (1976a) in a brackish pond on the Baltic coast: up to 1.8×10^6 ind. m^{-2} and 48.9 g m^{-2} of dry weight (with shells). These data are in a good agreement with maximum values found in our study. Herman and Heip (1982) assumed a wet/dry weight ratio in *C. torosa* of 4/1. In conformity with this, the maximum biomass of this species at the mouth of the Chernavka River corresponded to approximately 30 g m^{-2} of dry weight (August 16, 2017; see Table 2). However, *C. torosa* abundance in the same sample was significantly higher, which can be explained by the predominance of early age stages. The number of adults in the population from the Chernavka River was less than 10% of the total, while in a study by Heip (1976a), it reached 18%. Very high abundances of *C. torosa* may be associated with local aggregations of this species at the bottom, as was shown in another work by Heip (1976b).

Despite the lower abundance and the biomass of *H. salina* in the B. Samoroda River, in some periods this species accounted for more than a quarter of the total abundance and biomass of meiobenthos (see Appendix 1, Table 2). This ostracod is considered as a typical, frequently occurring, and abundant species of various brackish ecosystems (Ganning 1971; De Deckker 1981; Mezquita et al. 1999; Meisch 2000; Henderson 2002; Valls et al. 2014; Perçin-Paçal et al. 2017). However, no quantitative data on the abundance and biomass of *H. salina* in other water bodies were reported in the available literature. At the same time, it is known that other of its congeners inhabiting moderately saline biotopes can also dominate among other ostracods in such habitats, reaching a comparatively high density. For instance, the maximum abundance of *H. exigua* (Gauthier et Brehm, 1928) in a coastal Mediterranean shallow oligohaline lake was found to be up to 200×10^3 ind. m^{-2}, and attaining a mean annual production of 28.7 g of dry weight (with shells) m^{-2} $year^{-1}$ (Rodríguez-Pérez and Baltanás 2008).

Data on the production of *C. torosa* and *H. salina* are scarce. For *H. salina*, they are apparently absent altogether. We used the physiological method, which is not accurate enough and is usually employed for preliminary assessment of the species production (Kurashov 2002 2007). In addition, we had only a small number of scattered observations. Nevertheless, the calculations performed indicate a potentially high role of these ostracods in the transformation of matter and energy in the studied biotopes, at least in the spring and summer periods (Table 2). For *C. torosa*, more detailed studies on this topic were carried out earlier by Herman et al. (1983) in a shallow brackish coastal pond in Belgium. They used two production models: the first was based on the age-distribution of shells preserved in the sediment and the second was based on the analyses of the size and frequency of living ostracods of different developmental stages. In both cases, the results were similar: 9.7 and 9.2 g of shell-free dry weight m^{-2} $year^{-1}$, respectively. Recalculated per day, production of *C. torosa* obtained by Herman et al. (1983) was approximately 25–27 mg m^{-2} of shell-free dry weight. De Deckker and Lord (2017) in their review noted that the values found by Herman et al. (1983) are impressive and clearly emphasize the important role of the species in trophic chains. Unfortunately, the study by Herman et al. (1983) is still, apparently, the only example of a thorough analysis of the productivity of *C. torosa*, despite the wide distribution of this species.

As estimated in our study, the production of *C. torosa* and *H. salina* (see Table 2) is quite comparable with the previously obtained data on the production of dominant representatives of the macrobenthos from the respective rivers. Thus, Zinchenko et al. (2014) calculated that the average production of the dominant chironomid larvae in the Chernavka River in August was 490 mg of dry weight m^{-2} day^{-1}, and Golovatyuk et al. (2018) found that analogous values for the larvae of dominant biting midges in the river of 156 mg of dry weight m^{-2} day^{-1} in May and 30 mg of dry

weight m^{-2} day^{-1} in August. According to data of Golovatyuk et al. (2020), the daily production of three chironomid species prevailing in the macrofauna at the mouth of the B. Samoroda River amount about 42–135 mg of dry weight m^{-2}. All in all, the comparison once again emphasizes the importance of the studied ostracod species in the total benthic energy flow in the examined saline habitats.

Feeding spectra

Among the ostracod FAs, we found trophic markers and other FAs that apparently play an important role as structural compounds or which accumulate for further use in various metabolic processes. The percentages of most physiologically important FAs did not differ between the species studied, except 18:0 and 20:5n-3 (see Table 3). The two-fold increase in the level of 18:0 in *C. torosa* compared to *H. salina* may indicate a lower Δ9 desaturase activity in the former species. On the other hand, a high level of 18:0 is usually associated with detritivory (Hama 1999). However, together with 18:0, the increasing levels of bacterial FAs and long-chain SFAs are usually found under detritivory (Makhutova et al. 2013). In contrast to *H. salina*, *C. torosa* had a low level of bacterial FAs; thus, a high level of 18:0 in *C. torosa* can hardly be associated with detritivory. At the same time, the two-fold increase in the level of 20:5n-3 in *C. torosa* appears to be associated with diatoms. FA markers of diatoms, namely, 16:2n-7, 16:2n-4, 16:3n-4, 16:4n-1, and 20:5n-3, were abundant in the bottom sediments from the Chernavka River; therefore, diatoms could be the food source for *C. torosa*. The FA markers of diatoms were found in both ostracods, which confirms the presence of diatoms in their diets.

The previously studied invertebrate species inhabiting saline rivers of the basin of Lake Elton, including the Chernavka River, were found to be selective feeders (Zinchenko et al. 2014; Golovatyuk et al. 2018). The FA composition of bottom sediments in the Chernavka River, sampled in different years in the habitats of different invertebrate species, varied significantly. Bottom sediments confined to the habitat of *Palpomyia schmidti* Goetghebuer, 1934 (Ceratopogonidae) and *Cricotopus salinophilus* (Chironomidae) were poor in microalgae FA markers but rich in decomposed organic matter and detritus (Zinchenko et al. 2014; Golovatyuk et al. 2018). In contrast, bottom sediments confined to the habitat of *C. torosa* were rich in microalgae FA-markers, especially FA markers of diatoms. However, all investigated invertebrate species inhabiting the Chernavka River had a high level of FA markers of diatoms, including physiologically valuable EPA, and FA markers of green microalgae/cyanobacteria. The proportions of FA markers of diatoms and FA markers of green microalgae/cyanobacteria in different invertebrate species differed, which indicates the selectivity of feeding of the species. The heterogeneity of the bottom

sediment composition is obvious: there were places where microalgae, preferably consumed by invertebrates, developed abundantly and places with a high content of detritus and decomposed organic matter, which were obviously less attractive for invertebrates.

Bottom sediments from the B. Samoroda River confined to the habitat of *H. salina* were rich in microalgae FA markers, but, in contrast to the Chernavka River, FA markers of green microalgae/cyanobacteria were more abundant. According to FA composition of *H. salina*, this species consumed more green microalgae/cyanobacteria than *C. torosa*. Both ostracods seemed to consume flagellates, since their FA markers, namely, 18:4n-3 and 22:6n-3, were found in their bodies.

The ostracods had several FAs that were absent in the bottom sediments or were there in trace amounts (see Table 3). One of such FAs was an unusual isomer, 18:2n-4. This FA was strongly associated with ostracods and had seasonal features: both species contained higher percentages of 18:2n-4 in May than in August. Some PUFAs of n-4 and n-7 families, such as 16:2n-4, 18:2n-4, 18:2n-7, 18:3n-4, 18:3n-7, and 20:3n-7, are considered as markers of methanotrophic bacteria or symbiotic bacteria, which were found in vent mussels and some other animals (Saito 2011). In addition to 18:2n-4, the ostracods studied here contained traces of 18:3n-4 and 18:2n-7. Some symbiotic (intestine) bacteria might be the source of these polyunsaturated fatty acids (PUFAs) in ostracods. Other, previously studied, invertebrate species from the Chernavka River did not contain either 18:2n-4 or 18:3n-4 in substantial quantities (Zinchenko et al. 2014; Golovatyuk et al. 2018). Kanapatskiy et al. (2018) identified bacteria belonging to 20 phyla, including methanotrophic bacteria, in the bottom sediments of the Chernavka River and the B. Samoroda River. Thus, the bacterial origin of these specific FAs, 18:2n-4, 18:3n-4, and 18:2n-7 in ostracods is possible, but more research is needed to clarify this issue.

Thus, the FA markers indicated that the basis of *C. torosa* diet were diatoms, while the diet of *H. salina* included bacteria, cyanobacteria/green algae, flagellates (maybe cryophytes), and also diatoms. The feeding habits of *H. salina* differed between seasons: in May, it consumed diatoms in greater proportions than in August, but in August, it consumed more bacteria, cyanobacteria/green algae, and flagellates. Its feeding behavior reflected seasonal changes in the bottom sediments in the B. Samoroda River. *Cyprideis torosa* also tended to have seasonal differences in its diet, but they were less marked than those of *H. salina*.

According to the literature, the majority of species of ostracods are likely generalists. Depending on the conditions and possibilities, they can use various sources of food: organic detritus, bacteria, algae, fungal hyphae, dead and living plants, dead animals and their feces, etc. Certain species can be classified as facultative predators. They consume not only small animals, such as protozoans, rotifers, nematodes, small crustaceans, etc., but also relatively large ones, namely

daphnids, non-biting midge and mosquito larvae, oligochaetes and polychaetes, and even fish fry by attacking them in groups (Bronstein 1947; Liperovskaya 1948; Rossi et al. 2011; Karanovic 2012; Smith 2020). In laboratory experiments with *Heterocypris incongruens* (Ramdohr, 1808), Rossi et al. (2011) found that cannibalism could also be a feeding strategy of ostracods. One of the important food sources of ostracods is algae-microbial mats (biofilms) (Gerdes et al. 1985; Lawrence et al. 2002). Biofilms are formed in large amounts in some biotopes, in particular, in small saline rivers, such as the tributaries of Lake Elton (Gerdes et al. 1985; Lawrence et al. 2002; Kanapatskiy et al. 2018). Some quantitative studies show that ostracods may be the main consumers in the community of bottom meiofauna. Thus, at the Baltic Sea coastal area, four ostracod species accounted for half of the ^{14}C uptake of the entire meiobenthos. In that case, the share of one species, *Candona neglecta* Sars, 1887, was 46% (Ólafsson et al. 1999).

Previous studies of *C. torosa* and *H. salina* diets are scarce. Liperovskaya (1948) classified *C. torosa* as a group of silt-feeding species because silt prevailed in their guts while algae (diatoms) were found sporadically. Heip (1976a), based on observations in a small brackish-water pond on the Baltic coast, identified this species as a detritivore, which probably consumes bacterial biomass that develops on organic matter. It was also noted that *C. torosa* is evidently on top of the food chain in this water body due to low diversity of aquatic fauna and the absence of potential predators (Heip 1976a). Later, *C. torosa* was identified as a selective deposit feeder, but it was problematic to distinguish between feeding on bacteria and feeding on other organic material, when the species consumes the detritus (Herman and Heip 1982). Gerdes et al. (1985) ranked *C. torosa* with a group of benthic primary consumers that feed mainly on diatoms and coccoid cyanobacteria, which are abundant in the top layers of the biofilms. Our analysis of the FA content of the species in the Chernavka River is in good agreement with the suggestion made by Gerdes et al. (1985) about the predominately diatom diet of this crustacean.

A study by Ganning (1971), which was conducted at Baltic brackish-water rockpools, demonstrated that *H. salina* mainly consumed algae. Microscopic analysis of gut content and laboratory observations of feeding behavior revealed that this ostracod preferred small green algae, such as desmids and did not consume particles of animal origin. In summer, green algae constituted 50 to 90% of its gut contents (Ganning 1971). Yousef and Hegab (2017) established that a laboratory culture of *H. salina* successfully grows and develops on a diet of live and dried green alga *Chlorella vulgaris*. Thus, the species is probably algophagous. However, data on *H. salina* diet are still limited and do not take into consideration the possibility of switching to alternative food sources when required. For example, the results obtained in our study based on the FA analysis confirmed the algae diet of this species but added some new food sources for it, namely, bacteria.

Differences in FA composition between the two studied ostracod species were more explicit

than differences between the bottom sediments from both rivers analysed (see Table 3, Fig. 2). It may mean that ostracods selectively consumed different food items. There can be many reasons for selective feeding. One of the reasons may be different nutrient requirements of the species, which are determined by the phylogenetic factor. Such feeding habits enable the species to inhabit the same aquatic ecosystem. Indeed, both *H. salina* and *C. torosa* were found in the B. Samoroda River (see Appendix 1). The key importance of the phylogenetic factor for FA composition of invertebrates from species to order or phylum has been revealed elsewhere (Kraffe et al. 2008; Makhutova et al. 2011 2016; Lau et al. 2012; Gladyshev et al. 2015). It is well known that other small aquatic crustaceans, namely, Cladocera and Copepoda, exhibit taxonomic differences in the contents of long-chain PUFAs. Cladocera are characterized by the high level of EPA (up to 22%) and a negligible level of DHA and other C22 PUFAs, or their complete absence, while Copepoda are characterized by a lower level of EPA (less than 13%) and the high level of DHA (up to 26%) (Gladyshev et al. 2015). The ostracods studied here were closer to Cladocera by these parameters: they had a high level of EPA (up to 20.6%) and a low level of DHA (less than 2.6%), like Cladocera. However, in contrast to Cladocera, DHA was found in all samples of Ostracoda.

CONCLUSIONS

The present study shows that the ostracods *Cyprideis torosa* and *Heterocypris salina* are the dominant species of the bottom meiofauna community in the saline tributaries of Lake Elton, reaching a considerable abundance and biomass here. *Cyprideis torosa* forms the basis of the community at the mouth of the polyhaline Chernavka River, and *H. salina* is one of the dominant species at the mouth of the mesohaline B. Samoroda River. Our preliminary estimate indicates potentially high productivity of these species in the studied rivers, at least in spring and summer.

Due to the high abundance and productivity, both ostracods are an important component of the food chains of the studied habitats. The fatty acid analysis revealed that *C. torosa* mainly consumed diatoms, while the basic constituents of the *H. salina* diet were bacteria and cyanobacteria/green algae. Differences between both ostracod species were greater than differences between the bottom sediments from the two studied rivers. It may mean that the ostracods selectively consumed different food items that may be related to different nutrient requirements of the species. Seasonal changes in the FA composition of ostracods were much higher than in their main food sources – bottom sediments, which also indicates selective feeding of the species. The studied ostracods were closer to Cladocera than to Copepoda in EPA and DHA percentages.

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REFERENCES

Ankar S, Elmgren R. 1976. The Benthic Macro- and Meiofauna of the Askö-Landsort Area (Northern Baltic Proper). A Stratified Random Sampling Survey. Contributions from the Askö Laboratory **11:**1–115.

Ballinger A, Lake PS. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food

webs. Mar Freshwater Res **57:**15–28. doi:10.1071/MF05154.

Bodergat A-M, Rio M, Andréani A-M. 1991. Composition chimique et ornementation de *Cyprideis torosa* (Crustacea, Ostracoda) dans le domaine paralique. Oceanologica Acta **14:**505–514.

Bronstein ZS. 1947. Ostracoda of fresh waters. Publishing House of Academy of Sciences of USSR, Moscow, Leningrad. (in Russian)

Castel J. 1992. The meiofauna of coastal lagoon ecosystems and their importance in the food web. Vie Milieu **42:**125–135.

Coull BC. 1999. Role of meiofauna in estuarine soft-bottom habitats. Aust J Ecol **24:**327–343. doi:10.1046/j.1442-9993.1999.00979.x

De Deckker P. 1981. 10. Ostracods of athalassic saline lakes. A review. Hydrobiologia **81:**131–144. doi:10.1007/BF00048710.

De Deckker P, Lord A. 2017. *Cyprideis torosa*: a model organism for the Ostracoda? Journal of Micropalaeontology **36:**3–6. doi:10.1144/jmpaleo2016-100.

Desvilettes C, Bourdier G, Amblard C, Barth B. 1997. Use of fatty acids for the assessment of zooplankton grazing on bacteria, protozoans and microalgae. Freshwater Biol **38:**629–637. doi:10.1046/j.1365-2427.1997.00241.x.

Ermakov NV, Krapin V, Popova A. 1933. On some biocenoses of the salty rivers of Lake Elton. Journal of the Bio-Zoological Cycle of UAS **3(7):**85–110. (in Ukrainian)

Galloway AWE, Brett MT, Holtgrieve GW, Ward EJ, Ballantyne AP, Burns CW, Kainz MJ, Müller-Navarra DC, Persson J, Ravet JL, Strandberg U, Taipale SJ, Ahlgren G. 2015. A fatty acid based Bayesian approach for inferring diet in aquatic consumers. PLoS ONE **10:**e0129723. doi:10.1371/journal.pone.0129723.

Gamenick I, Rethmeier J, Rabenstein A, Fischer U, Giere O. 1997. Effects of anoxic and sulfidic conditions on cyanobacteria and macrozoobenthos in shallow coastal sediments of the Southern Baltic Sea. Arch Hydrobiol **140:**465–490. doi:10.1127/archiv-hydrobiol/140/1997/465.

Ganning B. 1971. On the ecology of *Heterocypris salinus*, *H. incongruens* and *Cypridopsis aculeata* (Crustacea: Ostracoda) from Baltic brackish-water rockpools. Mar Biol **8:**271–279. doi:10.1007/BF00348009.

Gerdes G, Spira Y, Dimentman C. 1985. The Fauna of the Gavish Sabkha and the Solar Lake – a Comparative Study. *In*: Friedman GM, Krumbein WE (eds) Hypersaline Ecosystems. The Gavish Sabkha. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo. doi:10.1007/978-3-642-70290-7_18.

Giere O. 2009. Meiobenthology. The microscopic motile fauna of aquatic sediments. Springer-Verlag, Berlin, Heidelberg. doi:10.1007/978-3-540-68661-3.

Gladyshev MI, Emelianova AY, Kalachova GS, Zotina TA, Gaevsky NA, Zhilenkov MD. 2000. Gut content analysis of *Gammarus lacustris* from a Siberian lake using biochemical and biophysical methods. Hydrobiologia **431:**155–163. doi:10.1023/A:1004036111433.

Gladyshev MI, Makhutova ON, Sushchik NN. 2013. Production of EPA and DHA in aquatic ecosystems and their transfer to the land. Prostaglandins and other Lipid Mediators **107:**117–126. doi:10.1016/j.prostaglandins.2013.03.002.

Gladyshev MI, Sushchik NN, Dubovskaya OP, Buseva ZF, Makhutova ON, Fefilova EB, Feniova IY, Semenchenko VP, Kolmakova AA, Kalachova GS. 2015. Fatty acid composition of Cladocera and Copepoda from lakes of contrasting temperature. Freshwater Biol **60:**373–386. doi:10.1111/fwb.12499.

Golovatyuk LV, Zinchenko TD, Sushchik NN, Kalachova GS, Gladyshev MI. 2018. Biological aspects of the associations of biting midges (Diptera: Ceratopogonidae) in two saline rivers of the Elton Lake Basin, Russia. Mar Freshwater Res **69:**906–916. doi:10.1071/MF17125.

Golovatyuk LV, Zinchenko TD, Nazarova LB. 2020. Macrozoobenthic communities of the saline Bolshaya Samoroda River (Lower Volga region, Russia): species composition, density, biomass and production. Aquat Ecol **54:**57–74. doi:10.1007/s10452-019-09726-z.

Guo F, Bunn SE, Brett MT, Fry B, Hager H, Ouyang X, Kainz MJ. 2018. Feeding strategies for the acquisition of high-quality food sources in stream macroinvertebrates: Collecting, integrating, and mixed feeding. Limnol Oceanog **63(5):**1964–1978. doi:10.1002/lno.10818.

Gusakov VA. 2019. Bottom Meiofauna of Highly Mineralised Rivers in the Eltonsky Nature Park (Russia). Nature Conservation Research **4:**37–63. doi:10.24189/ncr.2019.004. (in Russian)

Gusakov VA, Gagarin VG. 2012. Meiobenthos Composition and Structure in Highly Mineralized Tributaries of Lake El'ton. Arid Ecosystems **2:**232–238. doi:10.1134/S2079096112030067.

Hama T. 1999. Fatty acid composition of particulate matter and photosynthetic products in subarctic and subtropical Pacific. J Plankton Res **21:**1355–1372. doi:10.1093/plankt/21.7.1355.

Heip C. 1976a. The life-cycle of *Cyprideis torosa* (Crustacea, Ostracoda). Oecologia **24:**229–245. doi:10.1007/BF00345475.

Heip C. 1976b. The spatial pattern of *Cyprideis torosa* (Jones, 1850) (Crustacea: Ostracoda). J Mar Biol Assoc UK **56:**179–189. doi:10.1017/S002531540002052X.

Henderson PA. 2002. Freshwater Ostracods: Keys and notes for the identification of the species. Pisces Conservation Ltd., Lymington.

Herman PMJ, Heip C. 1982. Growth and Respiration of *Cyprideis torosa* Jones 1850 (Crustacea Ostracoda). Oecologia **54:**300–303. doi:10.1007/BF00379996.

Herman PMJ, Heip C, Vranken G. 1983. The production of *Cyprideis torosa* Jones 1850 (Crustacea,

Ostracoda). Oecologia **58:**326–331. doi:10.1007/BF00385231.

Ingole BS, Parulekar AH. 1998. Role of salinity in structuring the intertidal meiofauna of a tropical estuarine beach: Field evidence. Indian J Mar Sci **27:**356–361.

Kanapatskiy TA, Samylina OS, Plotnikov AO, Selivanova EA, Khlopko YA, Kuznetsova AI, Rusanov II, Zakharova EE, Pimenov NV. 2018. Microbial Processes of Organic Matter Production and Decomposition in Saline Rivers of the Lake Elton Area (Volgograd Oblast, Russia). Microbiology **87:**66–78. doi:10.1134/S0026261718010095.

Karanovic I. 2012. Recent Freshwater Ostracods of the World: Crustacea, Ostracoda, Podocopida. Springer-Verlag, Berlin, Heidelberg. doi:10.1007/978-3-642-21810-1.

Kelly JR, Scheibling RE. 2012. Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser **446:**1–22. doi:10.3354/meps09559.

Kraffe E, Grall J, Le Duff M, Soudant P, Marty Y. 2008. A striking parallel between cardiolipin fatty acid composition and phylogenetic belonging in marine bivalves: a possible adaptative evolution? Lipids **43:**961–970. doi:10.1007/s11745-008-3219-9.

Kubanç N, Özulug O, Kubanç C. 2007. The ontogeny of appendages of *Heterocypris salina* (Brady, 1868) Ostracoda (Crustacea). Hydrobiologia **585:**255–272. doi:10.1007/s10750-007-0642-5.

Kurashov EA. 2002. The role of meiobenthos in lake ecosystems. Aquatic Ecol **36:**447–463. doi:10.1023/A:1016535921472.

Kurashov EA. 2007. Methods and approaches for quantitative investigation of freshwater meiobenthos. *In*: Gusakov VA (ed) Actual problems of the study of micro-, meiozoobenthos and phytophilous fauna of fresh water bodies. Vector TiS, Nizhny Novgorod. (in Russian)

Lau DCP, Vrede T, Pickova J, Goedkoop W. 2012. Fatty acid composition of consumers in boreal lakes – variation across species, space and time. Freshwater Biol **57:**24–38. doi:10.1111/j.1365-2427.2011.02690.x.

Lazareva VI, Gusakov VA, Zinchenko TD, Golovatyuk LV. 2010. Mesofauna of salt rivers of the El'ton Lake basin (Volgograd region). *In*: Krylov AV, Rivier IK, Shcherbina GKh (eds) Ecology and morphology of invertebrates of continental waters. Nauka DNC Press, Makhachkala. (in Russian)

Lawrence JR, Scharf B, Packroff G, Neu TR. 2002. Microscale Evaluation of the Effects of Grazing by Invertebrates with Contrasting Feeding Modes on River Biofilm Architecture and Composition. Microb Ecol **43:**199–207. doi:10.1007/S00248-001-1064-y.

Legendre P, Legendre L. 1998. Numerical ecology. Elsevier Science, Amsterdam.

Liperovskaya ES. 1948. On the feeding of freshwater ostracods. Zoologicheskii Zhurnal **27:**125–136. (in Russian)

Löffler H. 1961. Beiträge zur Kenntnis der Iranischen Binnengewässer. II. Regional limnologische

Studien mit besonderer Berücksichtigung der Crustaceenfauna. Internationale Revue der gesamten Hydrobiologie und Hydrographie **46:**309–406. doi:10.1002/iroh.19610460304.

Makhutova ON, Sushchik NN, Gladyshev MI, Ageev AV, Pryanichnikova EG, Kalachova GS. 2011. Is the fatty acid composition of freshwater zoobenthic invertebrates controlled by phylogenetic or trophic factors? Lipids **46:**709–721. doi:10.1007/s11745-011-3566-9.

Makhutova ON, Protasov AA, Gladyshev MI, Sylaieva AA, Sushchik NN, Morozovskaya IA, Kalacheva GS. 2013. Feeding spectra of bivalve mollusks *Unio* and *Dreissena* from Kanevskoe Reservoir, Ukraine: are they food competitors or not? Zool Stud **52:**56. doi:10.1186/1810-522X-52-56.

Makhutova ON, Shulepina SP, Sharapova TA, Dubovskaya OP, Sushchik NN, Baturina MA, Pryanichnikova EG, Kalachova GS, Gladyshev MI. 2016. Content of polyunsaturated fatty acids essential for fish nutrition in zoobenthos species. Freshw Sci **35:**1222–1234. doi:10.1086/688760.

Makhutova ON, Borisova EV, Shulepina SP, Kolmakova AA, Sushchik NN. 2017. Fatty acid composition and content in Chironomid species at various life stages dominating in a saline Siberian lake. Contemp Probl Ecol **10:**230–239. doi:10.1134/S1995425517030064.

Martens K, Schoen I, Meisch C, Horne DJ. 2008. Global diversity of Ostracods (Ostracoda, Crustacea) in freshwater. Hydrobiologia **595:**185–193. doi:10.1007/s10750-007-9245-4.

Meisch C. 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag, Heidelberg, Berlin.

Mezquita F, Griffiths HI, Sanz S, Soria JM, Piñón A. 1999. Ecology and Distribution of Ostracods Associated with Flowing Waters in the Eastern Iberian Peninsula. J Crustacean Biol **19:**344–354. doi:10.1163/193724099X00150.

Mezquita F, Olmos V, Oltra R. 2000. Population ecology of *Cyprideis torosa* (Jones, 1850) in a hypersaline environment of the Western Mediterranean (Santa Pola, Alacant) (Crustacea: Ostracoda). Ophelia **53:**119–130. doi:10.1080/00785236.2000.10409442.

Mischke S, Ginat H, Al-Saqarat B, Almogi-Labin A. 2012. Ostracods from water bodies in hyperarid Israel and Jordan as habitat and water chemistry indicators. Ecol Indic **14:**87–99. doi:10.1016/j.ecolind.2011.07.017.

Neale JW. 1988. Ostracods and palaeosalinity reconstructions. *In*: De Deckker P, Colin J-P, Peypouquet J-P (eds) Ostracoda in the Earth Sciences. Elsevier, Amsterdam, New York.

Nielsen JM, Clare EL, Hayden B, Brett MT, Kratina P. 2018. Diet tracing in ecology: Method comparison and selection. Methods Ecol Evol **9:**278–291. doi:10.1111/2041-210X.12869.

Ólafsson E, Modig H, van de Bund WJ. 1999. Species specific uptake of radio-labelled phytodetritus by benthic meiofauna from the Baltic Sea. Mar Ecol Prog Ser **177:**63–72.

doi:10.3354/meps177063.

Perçin-Paçal F, Altinsaçli S, Altinsaçli S. 2017. Distribution, diversity and some ecological characteristics of ostracods (Crustacea: Ostracoda) in Gökçeada (Imbros) Island (Northern Aegean Sea, Turkey). Biologia **72:**774–789. doi:10.1515/biolog-2017-0088.

Pint A, Frenzel P. 2017. Ostracod fauna associated with *Cyprideis torosa* – an overview. J Micropalaeontol **36:**113–119. doi:10.1144/jmpaleo2016-010.

Plotnikov IS. 2016. Long-term changes in the fauna of free-living aquatic invertebrates of the Aral Sea. ZIN RAS, St. Petersburg. (in Russian)

Porter KG. 1976. Enhancement of algal growth and productivity by grazing zooplankton. Science **192:**1334–1336. doi:10.1126/science.192.4246.1332.

Rodríguez-Pérez H, Baltanás Á. 2008. Ecology and production of *Heterocypris exigua* and *Plesiocypridopsis newtoni* (Crustacea, Ostracoda) in an oligohaline hypertrophic shallow lake. Fundamental and Applied Limnology/Archiv für Hydrobiologie **172/1:**13–26. doi:10.1127/1863-9135/2008/0172-0013.

Rossi V, Benassi G, Belletti F, Menozzi P. 2011. Colonization, population dynamics, predatory behaviour and cannibalism in *Heterocypris incongruens* (Crustacea: Ostracoda). J Limno **70:**102–108. doi:10.4081/jlimnol.2011.102.

Saito H. 2011. Characteristics of fatty acid composition of the deep-sea vent crab, *Shinkaia crosnieri* Baba and Williams. Lipids **46:**723–740. doi:10.1007/s11745-011-3549-x.

Sauvanet J, Bourdier G, Jouve L, Bec A, Desvilettes C. 2013. Feeding of pike larvae (*Esox lucius* L.) in an alluvial river backwater: fatty acid as markers of two organic matter flows. Fund Appl Limnol **183:**337–350. doi:10.1127/1863-9135/2013/0440.

Sherstiuk VV. 1971. Caloricity of the feed organisms of the Kremenchug reservoir. Hydrobiological Journal **7:**99–103. (in Russian)

Shornikov EI. 1974. Subclass Ostracoda. *In*: Mordukhai-Boltovskoi FD, Kondakov NN, Markova EL, Romanova NN, Yablonskaya EA (eds) Atlas of Invertebrates of the Aral Sea. Pischevaya promyshlennost', Moscow. (in Russian)

Smith RJ. 2020. Ostracod Research at the Lake Biwa Museum, Japan. Diet. Available at https://www.biwahaku.jp/smith/ostracod_food.html. Accessed 20 Sept. 2020.

Soetaert K, Vincx M, Wittoeck J, Tulkens M. 1995. Meiobenthic distribution and nematode community structure in five European estuaries. Hydrobiologia **311:**185–206. doi:10.1007/BF00008580.

Sushchik NN, Gladyshev MI, Moskvichova AV, Makhutova ON, Kalachova GS. 2003. Comparison of fatty acid composition in major lipid classes of the dominant benthic invertebrates of the Yenisei River. Comparative Biochemistry and Physiology Part B:

Biochemistry and Molecular Biology **134:**111–122. doi:10.1016/S1096-4959(02)00191-4.

Taipale S, Kankaala P, Hamalainen H, Jones RI. 2009. Seasonal shifts in the diet of lake zooplankton revealed by phospholipid fatty acid analysis. Freshwater Biol **54:**90–104. doi:10.1111/j.1365-2427.2008.02094.x.

Valls L, Rueda J, Mesquita-Joanes F. 2014. Rice fields as facilitators of freshwater invasions in protected wetlands: the case of Ostracoda (Crustacea) in the Albufera Natural Park (E Spain). Zool Stud **53:**68. doi:10.1186/s40555-014-0068-5.

Velasco J, Millán A, Hernández J, Gutiérrez C, Abellán P, Sánchez D, Ruiz M. 2006. Response of biotic communities to salinity changes in a Mediterranean hyper stream. Saline Systems **2:**12–15. doi:10.1186/1746-1448-2-12.

Whiles MR, Gladyshev MI, Sushchik NN, Makhutova ON, Kalachova GS, Peterson SD, Regester KJ. 2010. Fatty acid analyses reveal high degrees of omnivory and dietary plasticity in pond-dwelling tadpoles. Freshwater Biol **55:**1533–1547. doi:10.1111/j.1365-2427.2009.02364.x.

Williams WD. 1987. Salinization of rivers and streams: an important environment hazard. Ambio **16:**180–185.

Williams WD. 1998. Salinity as a determinant of the structure of biological communities in salt lakes. Hydrobiologia **381:**191–201. doi:10.1023/A:1003287826503.

Winberg GG (ed). 1971. Methods for the Estimation of Production of Aquatic Animals. Academic Press, London, New York.

Winberg GG. 1983. Vant-Hoff temperature coefficient and the Arrhenius equation in biology. Journal of General Biology **44:**31–42. (in Russian)

Winberg GG, Lavrentieva GM (eds). 1984. Methodical recommendations for the collection and processing of materials in hydrobiological studies in freshwater bodies. Zoobenthos and its production. GosNIORH, ZIN AN SSSR, Leningrad. (in Russian)

Wouters K. 2017. On the modern distribution of the euryhaline species *Cyprideis torosa* (Jones, 1850) (Crustacea, Ostracoda). J Micropalaeontol **36:**21–30. doi:10.1144/jmpaleo2015-021.

Yousef EA, Hegab MH. 2017. Evaluation of Two Novel Feeding Protocols Utilizing Alive and Dried *Chlorella vulgaris* to Grow *Heterocypris salina* (Ostracoda: Crustacea). Journal of Zoological Research **1:**10–15.

Zinchenko TD, Golovatyuk LV. 2010. Biodiversity and macroinvertebrate community structure of saline streams of arid region of the south Russia (Lake Elton's plain). Arid Ecosystems **16:**25–33. (in Russian)

Zinchenko TD, Golovatyuk LV, Vykhristjuk LA, Shitikov VK. 2011. Diversity and structure of macrozoobenthic communities in the highly mineralized Khara River (territory adjacent to Lake Elton). Biol Bull **38:**1056–1066. doi:10.1134/S1062359011100190.

Zinchenko TD, Gladyshev MI, Makhutova ON, Sushchik NN, Kalachova GS, Golovatyuk LV. 2014. Saline rivers provide arid landscapes with a considerable amount of biochemically valuable production of chironomid (Diptera) larvae. Hydrobiologia **722:**115–128. doi:10.1007/s10750-013-1684-5.

Zinchenko TD, Shitikov VK, Golovatyuk LV, Gusakov VA, Lazareva VI. 2018. Plankton and Bottom Communities in the Saline Rivers of Lake Elton Basin: Statistical Analysis of Dependences. Arid Ecosystems **8:**225–230. doi:10.1134/S2079096118030083.

Zinchenko TD, Golovatyuk LV, Abrosimova EV. 2019. Non-Biting Midges (Diptera, Chironomidae) in the Benthic Communities of Saltwater Rivers in the Lake Elton Basin: diversity, salinity tolerance and distribution. Entomological Review **99:**1–16. doi:10.1134/S0013873819060095.

Supplementary materials

Appendix 1. Composition, frequency of occurrence (*F*, %), abundance (*N*, 1×10^3 ind. m^{-2}) and biomass (*B*, g m^{-2}) of the meiobenthos taxa in the Chernavka and B. Samoroda rivers (< 0.5 – small maximal and/or average *N* (less than 500 ind. m^{-2}); <0.01 – small maximal and/or average *B* (less than 10 mg)). (download)