ISSN 1995-0829, Inland Water Biology, 2017, Vol. 10, No. 4, pp. 384–398.

ZOOPLANKTON, ZOOBENTHOS, AND ZOOPERIPHYTON

Macrozoobenthos in Saline Rivers in the Lake Elton Basin: Spatial and Temporal Dynamics

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Received July 14, 2016

Abstract—The data on seasonal and interannual changes in the taxonomic, structural, and quantitative characteristics of macrozoobenthos communities in rivers with a high salinity gradient are given. A total of 91 benthic invertebrate taxa have been revealed, which were dominated by *Cricotopus salinophilus*, *Chironomus salinarius*, *C. aprilinus*, *Tanytarsus kharaensis*, *Microchironomus deribae*, *Glyptotendipes salinus* (Diptera: Chironomidae), *Culicoides (M.) riethi*, *Palpomyia schmidti* (Diptera: Ceratopogonidae), *Paranais simplex* (Oligochaeta), and *Ephydra* sp. (Ephydridae) in different years. The fauna of benthic communities is mainly represented by eurybiontic halotolerant species with different ranges of resistance to salinity. The taxonomic composition and diversity of macrozoobenthos communities are closely correlated with water salinity in the range from 4 to 41 g/L; the complex of hydrological and hydrophysical factors (depth, overgrowing, water temperature, pH, etc.) control the distribution and abundance of species.

Keywords: saline rivers, Lake Elton, macrozoobenthos, spatial and temporal dynamics, abundance, biomass, species diversity, abiotic factors

DOI: 10.1134/S1995082917040125

INTRODUCTION

Benthic organisms are permanent components of the total diversity of the ecosystem of the high-mineralized rivers of hypersaline Lake Elton. The most characteristic feature of the Elton Lake region is its important role as the largest migration route in Eurasia, where high-productive water bodies maintain enormous aggregations of transient swimming and semiaquatic bird species and serve as a place for their fattening and a source of the formation of organomineral mud with high balneological value [5]. The development of scientific foundations for maintaining the stable development of unique biota habitats is a component of the general strategy of conservation of the biological diversity of Elton Natural Park. Faunistic and biocenotic studies of saline rivers in the Lake Elton region are particularly important; here, "... the water is the main factor that determines the ecological characteristics of the area ..." [5, p. 3]. Some results of research into the saline rivers were previously presented in works [4, 6, 7, 18, 29, 30].

The objective of this research was to study interannual and seasonal changes in the taxonomic composition, abundance, and biomass of benthic communities in the saline rivers of the Lake Elton region, which are associated with the effect of abiotic factors under salinity gradient conditions.

MATERIAL AND METHODS

In terms of hydrographic characteristics, the unique natural–territorial complex of the Lake Elton region (49°07′30″ N, 46°30′40″ E) belongs to the Caspian closed basin with poor development of the river network. The area is characterized by a high level of aridity, as well as by precipitation deficit and active wind conditions. The temperature regime is distinguished by a high amplitude of extreme values: an absolute air-temperature minimum in January (–36.1°C) and a maximum in August (41.1°C) [5]. The hydrographic network of the Lake Elton region is mainly formed by the minor lowland rivers of the Elton basin. The main channel of the Khara, Lantsug, Bolshaya Samoroda (B. Samoroda), Chernavka, and Solyanka rivers has a perennial stream in the middle and lower reaches and is intermittent in the upper reaches during dry years (Fig. 1). The hydrological and hydrographic and chemical parameters of the rivers are significantly determined by the geological structure of the water catchment basin, with the dominance of saliniferous and carbonate sediments, as well as by other factors (climate, topography, etc.) against the background of clearly pronounced seasonal variations in the water level in the rivers, which result in mineralization changes (Tables 1, 2). The rivers are generally fed by atmospheric precipitation and underground waters [5], which create a high salinity gradi-

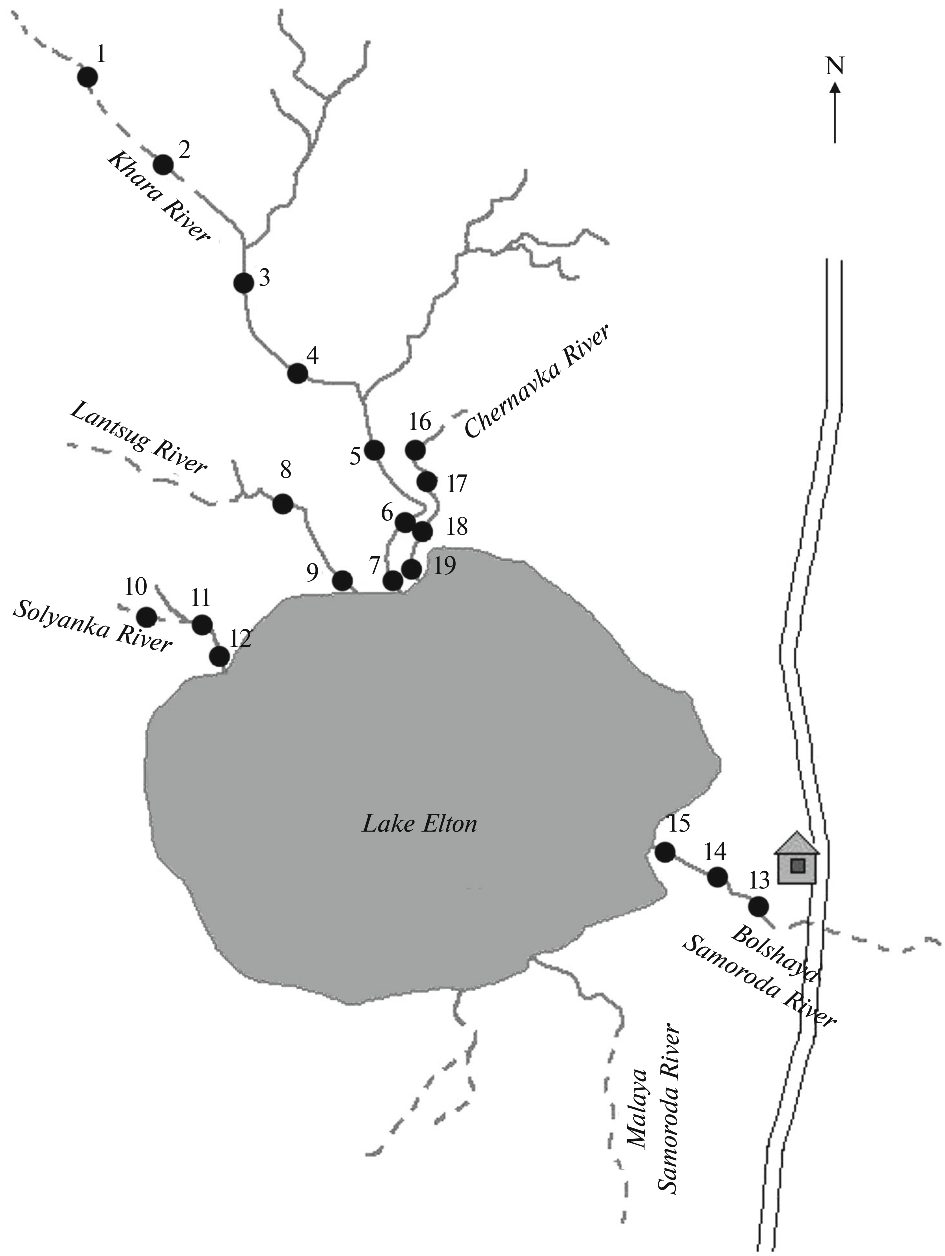

Fig. 1. Schematic map of the study area: (1–19) numbers of sampling stations.

ent. In the lower reaches, the salinity level can be over 100 g/L during the discharge of saline underground aquifers and periods of surge wind currents from Lake Elton. With respect to the salinity value, the rivers are classified as brackish or mesohaline (salinity level less than 25 g/L) and saline or polyhaline (salinity level over 25 g/L) watercourses of the arid area [1]. The length of the rivers varies from 5.2 (the Chernavka River) to 46.4 km (the Khara River). The current velocity is no more than 1.1 m/s. The water temperature varied from 12 to 33.1°C during the sampling period. In the upper and middle reaches, the rivers are overgrown with higher aquatic vegetation. The area of the coverage with common reed *Phragmites australis* (Cav.) is approximately 90% in the middle reaches. In some areas, the riverside is characterized by the development of *Enteromorpha intestinalis* (L.). In the mouth reaches that are free of macrophyte thickets, the primary stable lower layers of the substrate represent submerged layers of cyanobacterial mats.

Chloride-sulfate waters prevail with respect to the principal anion ratio; in terms of the cation composition, the mineralization is mainly formed by the sodium, sodium–magnesium, and magnesium groups. There is a seasonal spread of the values of the content of principal ions against the background of the

Table 1. Hydrological and geographical characteristics of the rivers in the Lake Elton basin (April to September 2006–2013)

Parameter	Rivers				
	Khara	Lantsug	Chernavka	Solyanka	B. Samoroda
Geographical coordinates (the mouth reach), N, E	49°12′, 46°39′	49°12′, 46°38′	49°12′, 46°40′	49°10′, 46°35′	49°07′, 46°47′
Altitude of the source, m	21	21	8	18	21
Altitude of the mouth above sea level, m	–21	–20	–20	–19	–22
Slope, ‰	0.91	2.06	5.38	5.52	1.77
Length, km	46.4	19.9	5.2	6.7	24.3
Width, m	2.0–59.0	1.5–45.0	1.0–8.0	1.0–5.0	3.5–35.0
Water catchment area, km^2	177.0	126.0	18.4	17.8	130.0
Current velocity, m/s	0.01–1.1	0.04–0.23	0.05–0.4	0.02–0.4	0.03–0.25
Flow rate in May (mouth), m^3/s	0.22	0.36	0.06	0.02	0.20
Depth, m	0.05–3.0	0.05–1.6	0.05–0.8	0.05–0.8	0.05–1.0
Overgrowing, %	0–90	0–70	30–50	40–60	10–90
Soil type	G, S, B	P, G, B	G, B, S	G, S	G, S, B, P

The limits of fluctuations and the calculated values of the parameters are given. Soil: G, gray silt, B, black silt, P, plant residues, S, sand.

Table 2. Physicochemical characteristics of the water in the rivers flowing into Lake Elton (April to September, 2006–2013)

Parameter*	Rivers				
	Khara	Lantsug	Chernavka	Solyanka	B. Samoroda
pH	6.8–10.0	6.9–8.9	6.5–8.4	6.9–8.4	7.4–8.8
O_2, mg/L	3.4–31.3	1.8–46.0	2.9–33.8	2.9–35.0	6.2–31.0
Water temperature, °C	12.0–33.0	14.9–33.1	12.5–33.1	15.1–30.2	12.3–31.1
Total salt content, g/L	6.6–41.4	4.6–30.0	17.2–31.7	25.1–29.0	4.0–26.3
$Na^+ + K^+$, g/L	1.71–12.31	1.19–9.07	3.43–10.53	7.59–9.41	1.12–5.50
Ca^{2+}, g/L	0.16–1.20	0.20–0.80	0.30–1.60	0.72–1.22	0.18–0.60
Mg^{2+}, g/L	0.15–1.59	0.13–1.17	0.04–1.22	0.51–0.96	0.04–2.60
Cl^-, g/L	1.78–22.40	2.06–18.64	10.24–19.17	15.13–17.40	1.48–15.98
SO_4^{2-}, g/L	1.72–12.11	0.55–4.27	0.40–0.96	0.09–0.84	0.41–4.02
HCO_3^-, g/L	0.02–3.81	0.16–0.44	0.21–0.45	0.09–0.41	0.34–0.72
PO_4^{3-}-P, mg/L	0.003–1.678	0.002–1.520	0.001–0.168	0.007–0.241	0.318–1.494
P_{total}, mg/L	0.119–2.412	0.144–2.773	0.053–0.250	0.131–0.421	1.057–1.995
NH_4^+-N, mg/L	0.18–13.31	0.42–10.63	30.80–45.92	13.10–45.30	0.18–2.33
NO_3^--N, mg/L	0.01–2.14	0.01–1.13	0.14–2.38	0.39–6.58	0.06–1.06
DO, mg/L	15.0–18.0	31.0–32.0	22.0–26.0	16.0–32.0	20.0–24.0

* The hydrochemical water samples were analytically treated by the accredited hydrochemical laboratory of OOO Tsentr monitoringa vodnoi i geologicheskoi sredy (the Center for Monitoring Water and Geological Environments), city of Samara. DO, dichromate oxidability; the limits of factor fluctuations are shown.

high amplitude of salinity variation. The content of total phosphorous and mineral nitrogen is characteristic of eutrophic waters.

The material was collected at 19 permanent stations (Fig. 1) in the ripal and medial zones of the middle and lower reaches of mesohaline (B. Samoroda, Khara, and Lantsug) and polyhaline (Chernavka and Solyanka) rivers. Due to the periodic absence of the runoff in the upper reaches of the rivers, the data of one-time benthos collections at stations 1, 2, 10, 13, and 16 are not given.

We selected 238 quantitative soil samples in different months over the period from 2006 to 2013. The methods of material sampling and treatment and the

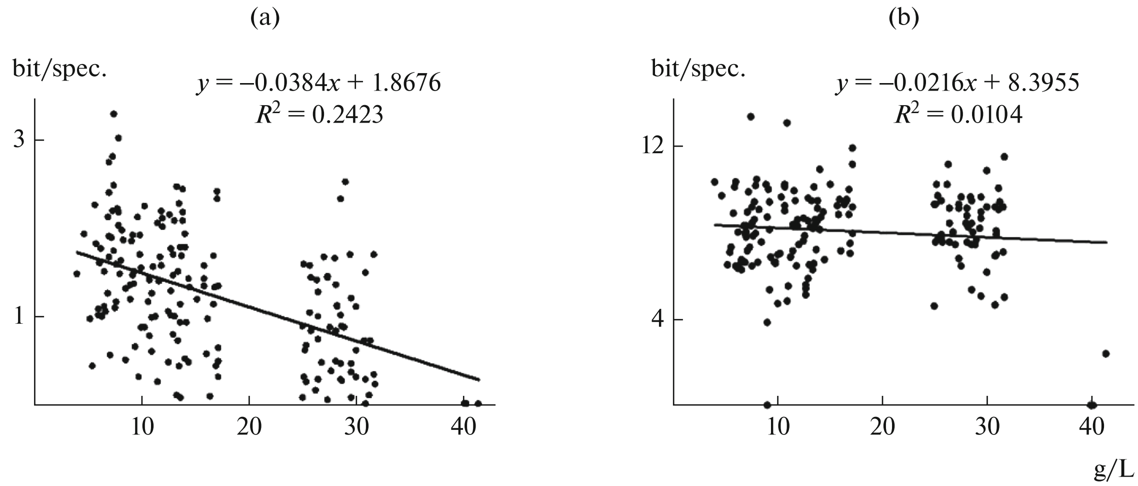

Fig. 2. Relationship between the values of Shannon's index (bit/spec.) and water salinity (a) and between the abundance of macrozoobenthos communities and water salinity (b) in the rivers.

list of publications that were used for determining the species composition of macrozoobenthos communities were previously described [18, 29, 30]. The benthic communities were assessed using the number of species, their abundance (spec./m^2) and biomass (g/m^2), and the species and taxon occurrence rate (%) and Shannon's index of species diversity. The seasonal dynamics of the abundance and biomass of zoobenthos communities was studied in 2013 based on the example of the B. Samoroda River (stations 14 and 15).

The relationship between the population density of macrozoobenthos species and environmental factors was analyzed using the method of direct gradient analysis (the canonical correspondence analysis (CCA)) [24] on the basis of data from 19 stations collected in August 2006–2013. The benthos composition was estimated taking into account the average values of the number of individuals of each species in logarithmic form. The interpretation of CCA diagrams is based on the consideration of patterns using two-dimensional projection [30]. The data were statistically processed using Microsoft Excel electronic worksheets and the Canoco 4.5 software package.

RESULTS

The diverse taxonomic composition of benthic communities in the rivers is structurally determined by euryhaline species of several ecological groups that were distinguished according to the level of their multiyear frequency of occurrence in sites with different salinity levels (Table 3). We found 91 macroinvertebrate taxa, which were usually identified to the species level and belonged to one of the five large systematic groups (Oligochaeta, Malacostraca, Branchiopoda, Insecta, and Arachnida). Insects were dominant with respect to the species abundance—68 species and taxa. The dipteran larvae are represented by 41 taxa, of which 25 are formed by the species of the Chironomidae family. We recorded 18 oligochaete species and 18 beetle larvae, as well as 6 bug species, 3 dragonfly species, and 2 crustacean species. Sixty-five hydrobiont species were revealed in the saline rivers for the first time compared to the published data [6] (Table 3). The number of taxa in the mesohaline rivers (Khara, Lantsug, and B. Samoroda) varied from 48 to 58, and 22 to 25 species were found in the polyhaline rivers (Solyanka and Chernavka).

The most common nine species and taxa are oligochaetes *Paranais simplex*; bugs *Sigara* sp.; beetles *Hygrotus enneagrammus*; and dipterans *Palpomyia schmidti*, *Culicoides* (*M.*) *riethi*, *Chironomus salinarius*, *Cricotopus salinophilus, Odontomyia* sp., and *Ephydra* sp. (Table 3).

Representatives of the Ceratopogonidae and Chironomidae families inhabit the mesohaline rivers with a frequency of occurrence of over 30%: *Culicoides riethi*, *Cricotopus salinophilus,* and *Chironomus salinarius*, while the polyhaline rivers have a high frequency of occurrence of species *Cricotopus salinophilus*, *Palpomyia schmidti*, and *Ephydra* sp. (the family Ephydridae). The salinity level that allows the species to steadily inhabit saline rivers is in the range from 4.0 to 41.4 g/L. However, some species (*Artemia salina*, *Cricotopus salinophilus*, and *Ephydra* sp.) also occur in the river–lake area at a salinity level of over 100 g/L. A significant linear decrease in the number of benthic species is recorded at a salinity level of over 14 g/L (Fig. 2a).

Shannon's index of macrozoobenthos species diversity varied from 0.05 to 3.29 bit/spec. over the study period (Fig. 2a). The low values of Shannon's index (0.05–0.5 bit/spec.) are characteristic of benthos communities in the mouth reach of the polyhaline Solyanka River (stations 12 and 19, May 2011–2012), while the maximum values (3.0–3.29) are char-

Table 3. Taxonomic composition, frequency of occurrence (%), and ecological groups (EGs) of macrozoobenthos communities

Code	Taxon	Rivers					
		Kh (68)	L (44)	BS (59)	Ch (39)	S (28)	EG
	Oligochaeta						
OlEnh.a	*Enchytraeus albidus* Henle, 1837*	1.5	–	–	–	–	ER, EPH
OlEnh.i	*E. issykkulensis* Hrabě, 1935*	3.0	–	–	7.5	–	HP, HL
OlHen.s	*Henlea stolli* Bretscher, 1900*	–	–	–	2.5	–	ER, EPH
OlHom.n	*Homochaeta naidina* Bretscher, 1896*	–	4.7	–	–	–	ER, EPH
OlLim.c	*Limnodrilus claparedeanus* Ratzel, 1868*	–	2.3	–	–	–	ER, EPH
OlLim.g	*L. grandisetosus* Nomura, 1932*	–	4.7	–	–	–	ER, EPH
OlLim.h	*L. hoffmeisteri* Claparede, 1862*	9.1	4.7	7.7	–	–	ER, HL
OlLim.p	*L. profundicola* (Verril, 1871)*	1.5	9.3	19.2	–	–	ER
OlLim.s	*L.* sp.	1.5	9.3	–	–	–	ER
OlLim.u	*L. udekemianus* Claparède, 1862	–	9.3	–	–	–	ER
OlLid.d	*L. dnieprobugensis* Jaroschenko 1948 = *Potamothrix caspicus* (Lastockin,1937)*	–	–	3.8	–	–	ER, EPH
OlLum.l	*Lumbriculus lineatus* (Müller, 1771)	–	–	1.9	–	–	ER, EPH
OlNai.c	*Nais communis* Piguet, 1906*	9.1	7.0	1.9	–	–	ER
OlNai.e	*N. elinguis* Müller, 1773*	10.6	2.3	17.3	–	–	ER
OlNai.p	*N. pseudoobtusa* Piguet, 1906*	–	7.0	–	–	–	ER, EPH
OlPar.s	*Paranais simplex* Hrabe, 1936*	12.1	21.0	32.7	7.5	7.7	HP, ER
OlPot.b	*Potamothrix bedoti* (Piguet, 1913)*	1.5	–	–	–	–	ER, EPH
OlUnc.u	*Uncinais uncinata* (Oersted, 1842)*	6.1	9.3	–	–	–	ER, HL
	Malacostraca						
AmGam.l	*Gammarus lacustris* Sars, 1863	9.1	20.9	44.2	–	–	ER
	Branchiopoda						
BrArt.s	*Artemia salina* (Linnaeus, 1758)	–	–	–	–	1.5	HB
	Insecta						
	Odonata						
OdAes.s	*Aeschna* sp.	1.5	–	–	–	–	ER
OdIsc.e	*Ischnura elegans* (Vander Linden, 1820)*	6.1	2.3	3.8	–	–	ER
OdSym.p	*Sympetrum* sp.	–	2.3	1.9	–	–	ER
	Heteroptera						
HeCal.g	*Callicorixa gebleri* (Fieber, 1848)*	–	2.3	–	–	–	ER, EPH
HePar.c	*Paracorixa concinna* (Fieber, 1848)*	–	–	17.3	–	–	ER
HeSig.n	*Sigara nigrolineata* (Fieber, 1848)*	–	–	–	5	–	HB, EPH
HeSig.a	*S. assimilis* (Fieber, 1848)*	–	–	–	22.5	3.8	HP, HB
HeSig.l	*S. lateralis* (Leach, 1817)*	–	7.0	17.3	–	3.8	ER, HP
HeSig.p	*S.* sp.	10.6	21.0	1.9	10	15.4	ER, HP
	Coleoptera						
CoAnc.p	*Anacaena* sp.	–	2.3	–	–	–	ER, EPH
CoBer.b	*Berosus bispina* Reiche, Saulcy, 1856*	–	2.3	–	20	3.8	ER, HP
CoBer.f	*B. fulvus* Kuwert, 1888*	–	7.0	9.6	5	19.2	ER, HP
CoBer.r	*B.* (*Enoplurus*) *frontifoveatus* Kuwert 1888*	–	–	–	5	–	HP, EPH
CoBer.p	*B.* sp.	13.6	4.7	7.7	7.5	–	ER, HP
CoCym.m	*Cymbiodyta marginella* (Fabricius, 1792)*	–	–	1.9	–	–	ER, EF
CoDon.p	*Donacia* sp.	1.5	–	–	–		ER, EPH

Table 3. (Contd.)

Code	Taxon	Rivers					
		Kh (68)	L (44)	BS (59)	Ch (39)	S (28)	EG
CoEnh.q	*Enochrus quadripunctatus* (Herbst, 1797)*	1.5	4.7	11.5	15	–	ER, HP
CoEnh.f	*E.* (*Lumetus*) *fuscipennis* (Thomson, 1884)*	–	–	1.9	–	–	ER, EPH
CoEnh.p	*E.* sp.	–	4.7	11.5	2.5	19.2	ER, HP
CoHel.o	*Helochares* (*Helochares*) *obscurus* (Müller, 1776)*	1.5	–	–	2.5	–	ER, HL
CoHyr.f	*Hydrobius fuscipes* Leach, 1815*	–	–	3.8	–	–	ER, EPH
CoHyg.e	*Hygrotus enneagrammus* (Ahrens, 1833)*	1.5	9.3	26.9	10	11.5	ER, HP
CoHyg.f	*H.* (*Coelambus*) *flaviventris* (Motschulsky, 1860)*	–	–	1.9	–	–	ER, EPH
CoOch.m	*Ochthebius* (*Ochthebius*) *marinus* (Paykull, 1798)*	–	4.7	1.9	–	–	ER
CoOch.p	*O.* sp.	–	–	1.9	2.5	–	ER, HP
CoPar.a	*Paracymus aeneus* (Germar, 1824)*	4.5	4.7	3.8	–	7.7	ER, HP
CoPel.c	*Peltodytes caesus* (Duftschmid, 1805)*	–	–	3.8	–	–	ER, EPH
	Diptera						
	Psychodidae						
PsPsy.p	*Psychoda* sp.	1.5	7.0	9.6	–	3.8	ER, HP
	Culicidae						
CuAed.p	*Aedes* sp.	–	–	1.9	2.5	3.8	ER, HP
CuCux.p	*Culex* sp.	–	4.7	9.6	–	11.5	ER, HP
	Ceratopogonidae						
CeCul.s	*Culicoides* (*Monoculicoides*) *riethi* Kieffer, 1914*	42.4	44.2	46.2	5	3.8	ER, HP
CeDas.p	*Dasyhelea* sp.	–	4.7	5.8	–	–	ER
CeMal.p	*Mallochohelea* sp.	1.5	2.3	1.9	–	–	ER
CePal.p	*Palpomyia schmidti* Goetghebuer, 1934*	6.1	4.7	9.6	82.5	73.1	ER, HB
CeSph.p	*Sphaeromias miricornis* (Kieffer, 1919)*	–	7.0	21.2	–	–	ER
	Chironomidae						
ChCor.p	*Corynoneura* sp.	–	4.7	–	–	–	ER
ChCri.c	*Cricotopus* (*C.*) *caducus* Hirvenoja, 1973*	3.0	–	–	–	–	ER, EPH
ChCri.o	*C.* (*C.*) *ornatus* (Meigen, 1818)*	–	–	51.9	–	–	HL, ER
ChCri.f	*C. salinophilus* Zinchenko, Makarchenko et Makarchenko, 2009*	53.0	67.4	34.6	97.5	96.2	ER, HP
ChCri.s	*C.* gr. *Sylvestris*	31.8	32.6	23.1	–	–	ER
ChCri.p	*C.* sp.	15.2	14.0	7.7	–	–	ER
ChGly.g	*Glyptotendipes glaucus* (Meigen, 1818)*	–	4.7	–	–	–	ER, EPH
ChGly.p	*G. paripes* (Edwards, 1929)*	3.0	7.0	1.9	–	–	ER
ChGly.s	*G. salinus* Michailova, 1987*	34.8	32.6	40.4	–	3.8	ER, HP
ChChi.a	*Chironomus aprilinus* Meigen, 1838*	34.8	34.9	21.2	–	–	ER
ChChi.p	*Ch.* gr. *Plumosus*	12.1	16.3	7.7	–	–	ER
ChChi.s	*Ch. salinarius* Kieffer, 1915*	48.5	55.8	30.8	40	30.8	ER, HP
ChCld.l	*Cladopelma* gr. *Lateralis*	4.5	4.7	–	–	–	ER
ChCld.m	*Cladotanytarsus* gr. *mancus*	4.5	–	1.9	–	–	ER
ChDic.n	*Dicrotendipes notatus* (Meigen, 1818)*	3.0	–	–	–	–	ER, EPH
ChMch.d	*Microchironomus deribae* (Freeman, 1957)*	25.8	27.9	40.4	–	–	ER
ChPtt.i	*Paratanytarsus inopertus* (Walker, 1856)*	3.0	4.7	–	–	–	ER
ChPtt.p	*P.* sp.	–	9.3	–	–	–	ER

Table 3. (Contd.)

Code	Taxon	Rivers					
		Kh (68)	L (44)	BS (59)	Ch (39)	S (28)	EG
ChPas.p	*Parasmittia* sp.	–	2.3	–	–	–	ER, EPH
ChPol.n	*Polypedilum* (*P.*) *nubeculosum* (Meigen, 1804)	–	2.3	–	–	–	ER
ChPrc.p	*Procladius* sp.	–	4.7	–	–	–	ER
ChPse.p	*Psectrocladius* sp.	1.5	–	–	–	–	ER
ChTan.p	*Tanypus punctipennis* Meigen, 1818*	–	4.7	–	–	–	ER
ChTar.k	*T. kharaensis* Zorina et Zinchenko, 2009*	33.3	7.0	46.2	–	–	ER, HL
ChTar.p	*Tanytarsus* sp.	1.5	4.7	–	–	–	ER
	Stratiomyidae						
StNem.p	*Nemotelus* sp.	3.0	7.0	1.9	7.5	–	ER, HP
StOdn.s	*Odontomyia* sp.	1.5	11.6	1.9	12.5	15.4	ER, HP
StStr.p	*Stratiomys* sp.	1.5	–	–	2.5	3.8	ER, HP
	Tabanidae						
TaTab.p	*Tabanus* sp.	3.0	–	–	–	–	ER
	Dolichopodidae						
Dl	Dolichopodidae gen. sp.	3.0	–	5.8	–	–	ER
	Ephydridae						
EbEdr.p	*Ephydra* sp.	12.1	25.6	23.1	30	50	ER, HP
EbPar.p	*Parydra* sp.	–	2.3	–	–	–	ER, EPH
	Muscidae						
MuLis.p	*Lispe* sp.	3.0	–	1.9	2.5	–	ER, HP
	Arachnida						
Ar	*Aranei* gen. sp.	–	–	3.8	–	–	ER
HcHyp.f	*Hydryphantes* (*Polyhydryphantes*) *flexuosus* Koenike, 1885	–	–	1.9	–	–	ER
HcHyp.o	*H. octoporus* (*P.*) Koenike, 1896	–	–	1.9	–	–	ER

ER, euryhaline species; HP, halophilic species; HB, halobionts; HL, haloxenes; and EPH, ephemeral species in the saline rivers of the Lake Elton region. *Recorded for the first time in the region; "–" indicates the absence of taxa. Kh, Khara; L, Lantsug; BS, B. Samoroda; S, Solyanka; and Ch, Chernavka. The number of soil samples is in brackets.

acteristic of the upper and middle reaches of the mesohaline Lantsug and B. Samoroda rivers (stations 8, 13, and 14, May and August, 2009 and 2012). There is a rather close and statistically significant relationship between the values of Shannon's index and the salinity level (Fig. 2a) ($r = -0.489$, $F = 57.08$, $p = \sim 0$). The peculiarity of the macrozoobenthos fauna is determined by the formation of several ecological groups that differ from each other with respect to the salinity level; among them, rare ephemeral populations of species forming them were also recorded (Table 3). The fauna is also characterized by the specificity of species distribution in the rivers in terms of adaptation to environmental conditions [30]. Thus, during the study period, oligochaetes *Henlea stolli* were abundant only in the Chernavka River, *Nais pseudoobtusa* and *Homochaeta naidina* were abundant in the Lantsug River, *Enchytraeus albidus* was abundant in the Khara River, and *Potamothrix caspicus* and *Lumbriculus lineatus* were abundant in the B. Samoroda River. The habitation of beetles *Enochrus fuscipennis* and *Hydrobius fuscipes* is confined to the sites of the mesohaline B. Samoroda River that are characterized by overgrowth, while the species *Berosus frontifoveatus* is characteristic only of the saline waters of the Chernavka River (Table 3). The instability of the habitat creates conditions for the development of species with a life strategy of extreme activity, which have an unlimited food resource but are characterized by a habitation, the periodicity of which depends on changes in the salinity level. It was previously determined that chironomid and ceratopogonid larvae, which selectively feed on diatoms and bacteria, mainly develop in benthic communities in highly productive saline rivers [18, 23, 29]. It is appropriate to note that the pattern of trophic chains in river communities requires better understanding, since there is no clear boundary in the distribution of plankton and benthos organisms in saline water bodies [10, 26]; this allows euryhaline animals to have a significant range of arrangement in the space of abiotic factors [3, 29].

The generalization of the multiyear dynamics (2006–2013) of the abundance of macrozoobenthos communities shows that the benthic population density in rivers with different salinity levels varies in a wide range without clearly pronounced regularities. A significant range of multiannual and intra-annual variations in the abundance of benthic organisms is recorded in May and August (Fig. 3), which is characteristic of the benthos in all the rivers. The seasonal and interannual variability in the state of benthic communities is usually determined by mass outbreaks of separate species. For instance, the abundance of benthic species reached 598000 spec./m^2 in the middle reaches of the Lantsug River (May 2011) at a salinity level of 7.5 g/L on the basis of eurybiontic chironomids *Cricotopus salinophilus* and *Paratanytarsus* sp. (Fig. 3). In the B. Samoroda River (August 2010) at a salinity level of 10.9 g/L, the peak zoobenthos abundance (461200 spec./m^2) is determined by the development of the population of ephemeral oligochaetes *Potamothrix caspicus* and halophile chironomids *Glyptotendipes salinus*. In the mouth reaches of the Khara (st. 7) and Chernavka (st. 19) rivers at a salinity level of 14 and 32.7 g/L, respectively, the high benthos density in May 2011 and 2012 was provided by the larvae of chironomids *Cricotopus salinophilus* (123600 spec./m^2). Summer increases in the abundance in different years are generally determined by the development of halophilic species. For instance, in 2007, chironomids *Tanytarsus kharaensis* were abundant in the Khara River (28600 spec./m^2); in 2009 and 2010, oligochaetes *Paranais simplex* and chironomids *Cricotopus salinophilus* were abundant in the Lantsug River (26000 spec./m^2); and in 2013, the benthos abundance reached 35000 spec./m^2 in the mouth of the Chernavka River on the basis of *Cricotopus salinophilus*, *Chironomus aprilinus, C salinarius*, and *Palpomyia schmidti*. When the salinity level increased to 20 g/L (August 2012) in the benthos of the middle reaches of the Khara River, larvae of beetles *Berosus bispina* and *B. fulvus* and of chironomids *Chironomus salinarius* were revealed.

In different years, the values of the average abundance and biomass can be different in the mesohaline Khara, Lantsug, and B. Samoroda by 8–21 and 14–26 times, respectively, while in the polyhaline Chernavka and Solyanka rivers, they can differ by 12–28 and 10–30 times (Fig. 3). Under these conditions, the statistical relationship between the total number ($\ln N$) of benthic communities and the salinity level (Fig. 2b) was not so pronounced ($r = -0.16$, $F = 4.7$, $p = 0.0315$).

Analysis of long-term changes (2006–2013) in the ratio between the abundance and biomass of different taxonomic groups revealed spatial differences in the structural organization of benthic communities (Fig. 3). In some years, the mass development of ceratopogonids, crustaceans, beetle larvae, oligochaetes, dipterans, and other taxa were recorded in the middle reaches of the rivers (Lantsug, 2007, B. Samoroda, 2008 and 2012, and Solyanka, 2008, 2011, and 2013); here, they find refugia and additional food sources among macrophyte thickets. The highly eutrophic mouth areas of the meso- and polyhaline rivers are characterized by the development of communities dominated by halophilic oligochaetes, beetle larvae, chironomids, or ceratopogonids in different years (their share is from 70 to 100% of the total number and biomass of benthic communities (Fig. 3)).

The composition of dominant species is significantly different. In particular, representatives of the infauna were dominant in number in the mesohaline rivers during different years: *Nais pseudobtusa* (2009), *Uncinais uncinata* and *Homochaeta naidina* (2007 and 2009), and *Limnodrilus grandisetosus* (2009 and 2010) in the Lantsug River; *Enchytraeus albidus* (2007), *E. issykkulensis* (2007 and 2008), and *Nais communis* (2006–2009) in the Khara River; and *N. communis* (2009), *N. elinguis* (2011), and *Lumbriculus lineatus* (2012) in the B. Samoroda. In 2013, an increase in the abundance and biomass of freshwater shrimps *Gammarus lacustris* was recorded in the reedy biotopes of the middle reaches (st. 14) of the B. Samoroda River (Fig. 3), while the larvae of chironomids *Microchironomus deribae*, *Tanytarsus kharaensis*, and *Glyptotendipes salinus*; ceratopogonids *Culicoides* sp.; and oligochaete *Potamothrix caspicus* were abundant in the mouth reach. Representatives of ephemeral species occurred in the river fauna only in some years. Thus, small (175 spec./m^2) oligochaete species, *Henlea stolli* (2009) and *Enchytraeus issykkulensis*, were found in the Chernavka River; their abundance was 1760 spec./m^2 in 2007 (Fig. 3). The distinctive feature of benthic communities in the mouth reaches of high-mineralized rivers is the development of monodominant communities of chironomids *Cricotopus salinophilus* or ceratopogonids *Palpomyia schmidti* in some years; their share in the total number can reach 98% (2010 and 2011).

The seasonal dynamics of the abundance and biomass of benthic communities (based on the example of the B. Samoroda River) is associated with the biotopical spatial variability. In the middle reaches of the river, the increases in the abundance in late June and the second decade of August at a high water temperature (23–26°C) are due to the development of crustaceans *Gammarus lacustris* and oligochaetes *Paranais simplex*, *Limnodrilus hoffmeisteri*, and *Potamothrix caspicus* (Fig. 4). In the mouth reaches (st. 15), the peak abundance and biomass of dipterans (July, August, September, and November) are due to the abundance of *Cricotopus ornatus*, *Microchironomus deribae*, *Tanytarsus kharaensis*, *Glyptotendipes salinus*,

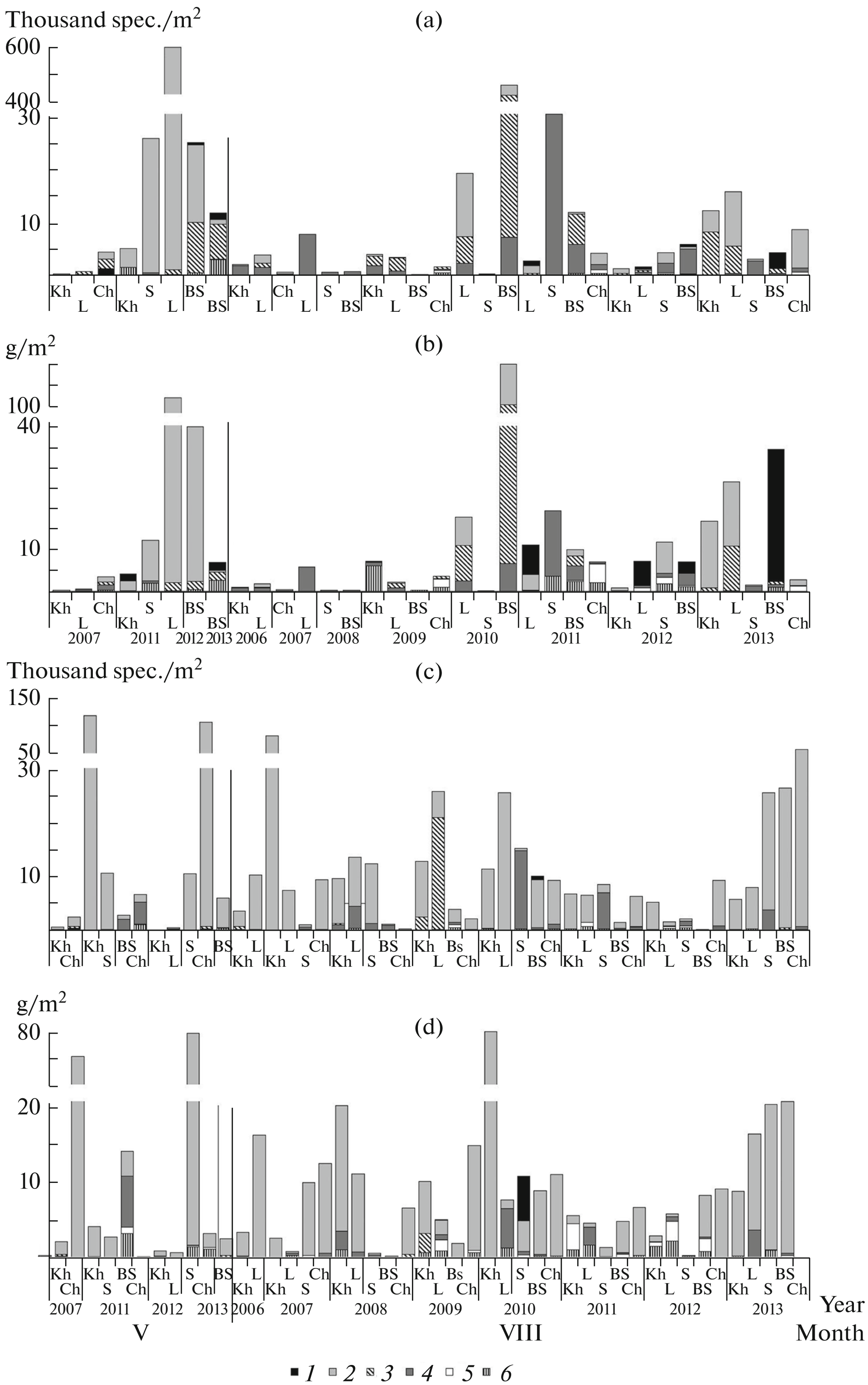

Fig. 3. Multiyear changes in the ratio between the abundance ((a, c), thousand spec./m^2) and biomass ((b, d), g/m^2) of different taxonomic groups at the stations of the middle (a, b) and lower (c, d) reaches of the rivers: (*1*) Amphipoda, (*2*) Chironomidae, (*3*) Oligochaeta, (*4*) Ceratopogonidae, (*5*) Coleoptera, and (*6*) others (Odonata, Heteroptera, Psychodidae, Ephydridae, Stratiomyidae, Tabanidae, Dolichopodidae, Muscidae, and Arachnida). Rivers are shown along the abscise axis: Kh, Khara; BS, Bolshaya Samoroda; L, Lantsug; S, Solyanka; and Ch, Chernavka.

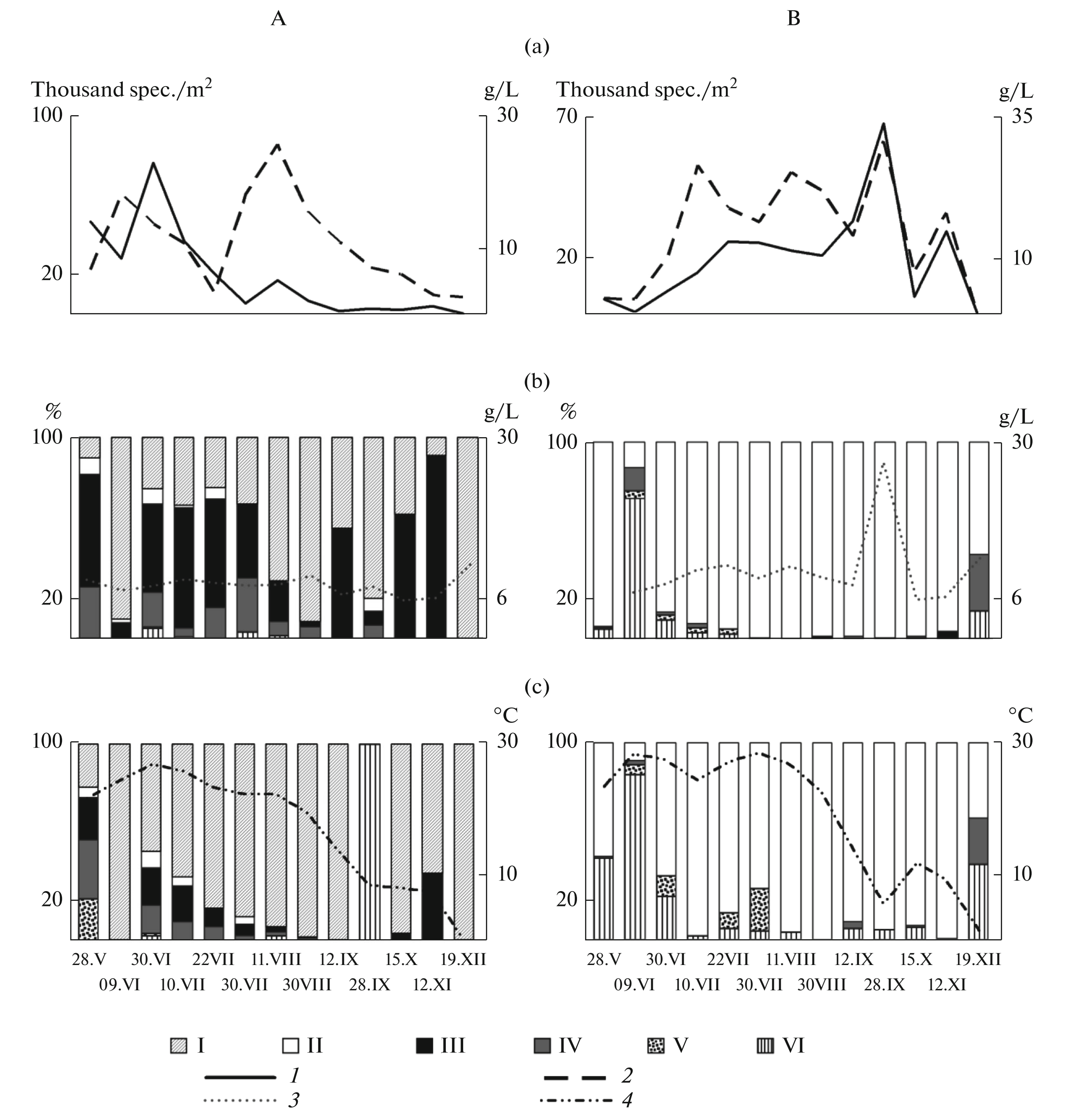

Fig. 4. Seasonal dynamics of the abundance ((*1*) thousand spec./m^2) and biomass ((*2*) g/m^2) of benthic communities (a) at stations in the middle ((A) st. 14) and lower ((B) st. 15) reaches of the B. Samoroda River and the share (%) of taxonomic benthos groups in the total number (b) and biomass (c) along the salinity ((*3*) g/L) and water temperature ((*4*) °C) gradient in 2013: (I) Amphipoda, (II) Chironomidae, (III) Oligochaeta, (IV) Ceratopogonidae, (V) Coleoptera, and (VI) others.

Culicoides sp., and *Spaeromids* sp., whose relation with environmental factors is not evident throughout the season. At the same time, there is no doubt that changes in the hydrological and hydrochemical characteristics of watercourses lead to the rearrangement of all processes of functioning of saline river ecosystems, including structural changes in the benthic fauna [3, 21, 29]. This is particularly characteristic of mouth reaches, where the crucial role is played by the formation of primary products and by the influence of the development of cyanobacterial mats [25] and green filamentous algae on biota (the area of their coverage is up to 39 to 70% in the lower reaches) on the one hand, and by the intensity of consumption of mass larvae of chironomids, ephydrids, and other animals by birds on the other [9].

DISCUSSION

The results of the analysis of published data on the interannual dynamics of macrozoobenthos communities in the saline rivers indicate that hydrobionts inhabiting them have adapted to the evolutionarily hydrological variability and extreme effects of high mineralization [11, 13, 17, 20, 22]. There are known taxa with significant variations in the range of resistance to salinity [16, 18, 28]. Although species that inhabit rivers with a high salinity gradient and a high rate of salinity variation are poorly resistant to some environmental factors [13], their euryhalinity provides a rather stable diversity of benthic communities. The distinctive features of benthic communities in the rivers of arid areas are spatial and temporal and structural and functional changes in the conditions of abnormal situations [12, 27], which leads to the permanent rearrangement of hydrosystems under salinity gradient conditions.

In the course of multiyear studies, the revealed high taxonomic wealth and abundance of insects, including scientifically new species, are characteristic of saline rivers in other arid regions of the world [15]. The presented list of taxa cannot be considered complete, since we continue to identify some species (e.g., *Chironomus* gr. *plumosus*, *Dicrotendipes notatus*, *Microchironomus deribae*, etc.) at all metamorphosis phases. It should be noted that Diptera larvae are mostly not identified to the species level in a rather extensive literature, although the distribution of many species is associated with salinity changes [8, 18, 22]. The identification of mass species of Chironomidae, Coleoptera, and Ceratopogonidae made it possible to avoid many errors during the assessment of the taxonomic abundance and biological features of species in the saline rivers [18, 22, 29]. In addition, a special study is required for peripheral biotopes and creeks (after spring flood), which seem to play the role of recolonization areas populated by a specific flora and fauna in accordance with the osmoregulatory capabilities of species forming them [2]. During the study period, the taxonomic abundance increased 1.6 times for the Khara River alone on the basis of ephemeral species from local biotopes belonging to different ecological groups.

The results of the analysis indicate that the faunistic diversity of macrozoobenthos communities is generally due to euryhaline species, among which four more or less different ecological groups can be distinguished, taking into account the frequency of occurrence of species and their density in rivers with different salinity levels. Haloxenes (GL) (Table 1) can be absent in habitats for several years; however, they never disappear from the composition of the fauna of brackish rivers. For instance, being previously abundant in the mouth reaches of the Khara River, the endemic species of chironomids *Tanytarsus kharaensis* has not been recorded in this river since 2010, but is characteristic of the mesohaline Lantsug and B. Samoroda rivers. In addition, oligochaetes *Limnodrilus hoffmeisteri* were not revealed in the Lantsug and Khara rivers in 2013, which were previously numerous here, while in the B. Samoroda River their abundance was 3240 spec./m^2 in the upper reaches in 2013. It can be assumed that it is quite possible to find other eurybiontic haloxenes (e.g., chironomids *Tanytarsus kharaensis*, oligochaetes *Enchytraeus issykkulensis*, etc.) under the conditions of the “island” isolation of the Lake Elton region in the future, which are less competitive than halophiles such as *Cricotopus salinophilus* and *Chironomus salinarius*. The complex of halophilic (HP) species includes resident taxa, i.e., constant species for the region (10 species), which reach their mass development both in the mesohaline (~16 g/L) and polyhaline (~32 g/L) rivers over long-term periods. They can maintain self-contained populations, which is exemplified by the constant recording of juvenile and mature individuals. For instance, while occurring in various biotopes, oligochaetes *Paranais simplex*; beetles *Berosus bispina*, *Enochrus quadripunctatus*, and *Hygrotus enneagrammus*; and chironomids *Cricotopus salinophilus* and *Chironomus salinarius* are regularly present in the rivers even during surging periods, thereby having adapted to salinity variations in different ways (deepening into the soil, a short life cycle, one-time emergence, and air breathing). The typical halobionts (HBs) can include small crustaceans *Artemia salina*, which exist at a salinity of over 100‰; bugs *Sigara nigrolineata*; beetles *Berosus frontifoveatus*; and ceratopogonids *Palpomyia schmidti* [23]. The complex of ephemeral (occasional) taxa (EPH) is represented by species whose survival seems to depend on the dynamism of the salinity level in microbiotopes or undetermined factors. Thus, species that were recorded in different years—oligochaetes *Enchytraeus albidus*, *Henlea stolli* (2009, the Chernavka River), *Homochaeta naidina*, *Limnodrilus grandisetosus* (2009, the Lantsug River), and *Potamothrix caspicus*; beetles *Enochrus fuscipenis*, *Hygrotus flaviventris*, and *Anacaena* sp. (2011, the B. Samoroda River); chironomids *Cricotopus caducus*; and ephydrids *Parydra* sp., which are associated with a salinity level of up to 16 g/L, were not found in further studies. For instance, the abundance of *Potamothrix caspicus* could reach 412800 spec./m^2 in macrophyte thickets. It is possible that these species cannot maintain self-contained populations in saline water (mature individuals, juvenile stages, etc., were found).

It is assumed that competitive interactions may also be involved in the process of succession of one species by another. The displacement of freshwater oligochaetes *Limnodrilus hoffmeisteri* by more tolerant *L. profundicola* is recorded in the mesohaline rivers;

the species *Paranais simplex*, which lives at a salinity of up to 41 g/L, displaces *Nais communis* (the Lantsug and Khara rivers); in the biotopes of the B. Samoroda River that are subject to overgrowth, the larvae of chironomids *Glyptotendipes salinus* were displaced (replaced) by amphipods *Gammarus lacustris*. In addition, we recorded the coexistence of "replaceable" species of the same genus or family, e.g., *Nais elingues* and *Paranais simplex*, in similar biotopes (in the B. Samoroda River). At the same time, it is rather difficult to reveal the competitive advantages of certain species in a salinity gradient. For instance, the replacement of euryhaline oligochaetes *Uncinais uncinata* by *Paranais simplex* and *Limnodrilus grandisetosus* (2009, 2010, and 2013) in the mesohaline Lantsug River is presumably due to different adaptations of species to changes in salinity and temperature rather than to direct competition. Based on the example of the development of oligochaetes, the differential fertility of species may increase the differences in the population size even more significantly during high and low salinity phases. For example, this is characteristic of the distribution of oligochaetes *L. profundicola* and *Paranais simplex* in the soil column that is also associated with cyclical seasonal variations in the interstitial salinity gradient [14].

The pattern of observed multiyear changes in the benthos abundance is due to the emergence of hardly explicable population peaks of some animal species (Figs. 3, 4) under the conditions of different scenarios of fluctuations in climatic, hydrological and hydrochemical, and biotic factors. The previously obtained data on the resistance of some species to salinity explain the dynamism of their development [7, 8, 14, 19, 20]. The colonization by some pioneer species (*Henlea stolli*, *Homochaeta naidina*, and *Limnodrilus grandisetosus*) that is accompanied by cyclical variations in their abundance shows that this process is a rather casual event under the conditions of the dynamic functioning of saline rivers. One can agree with the opinion of researchers who acknowledge the thesis on the "active diversity" of a small number of species ("implemented biodiversity") and so-called "dormant biodiversity" (dormant stages), which is characteristic of communities under the conditions of extreme factors [3, 10]. Presumably, the ecocrisis combinations of ever-changing climatic, hydrological and hydrochemical, and biotic factors (e.g., due to solar activity outbursts) may lead to the bifurcation state of the system that sharply changes the species ratio in the community [12, 17, 21].

The results of ordination of the assessment of the influence of abiotic factors on mass benthic species in the studied saline rivers revealed changes in the species composition of benthic communities in the gradient of ecological habitat conditions (Fig. 5). One can state the formation of a specific cenosis of euryhaline species, which is associated with a rather low mineralization of 3 to 6 g/L (the Khara, B. Samoroda, and Lantsug rivers), as well as with hydrological and hydrochemical factors (R, P_{total}, pH, and SO_4^- vectors). The species of oligochaetes *Limnodrilus profundicola* (OlLim.p), chironomids *Chironomus aprilinus* (ChChi.a), and crustaceans *Gammarus lacustris* (AmGam.l) are characteristic of muddy biotopes with shallow depths, low overgrowing by macrophytes, and a high content of biogenic substances. The high productivity of the rivers leads to the mass development of euryhaline species *Paranais simplex* (OlPar.s), *Glyptotendipes paripes* (ChGly.p), *G. salinus* (ChGly.s), and *Limnodrilus profundicola* (OlLim.p). Some species of chironomids and oligochaetes are associated with pH and the content of sulfate ions in the water. These are *Microchironomus deribae* (ChMch.d), *Tanytarsus khaerensis* (ChTar.k), *Nais elinguis* (OlNai.e), etc. (Fig. 5).

The complex of halophile species closely related to principal ions and cations, among which halophile and halobiont species *Berosus fulvus* (CoBer.f), *Psychoda* sp. (PsPsy.p), *Palpomyia schmidti* (CePal.p), and *Cricotopus salinophilus* (ChCri.f) are dominant, was isolated in the left part of the ordination diagram (Fig. 5). During different seasons, this cenosis includes species that are characteristic of the Chernavka and Solyanka rivers (Table 3). In 2006 to 2007, the statistical relationship between ephemeral chironomids *Dicrotendipes notatus* and oxyphilic oligochaetes *Enchytraeus issykkulensis* (OlEnh.i), *Limnodrilus profundicula* (OlLim.p), and *Potamothrix bedoti* (OlPot.b) was observed in the Khara River with the oxygen content. The change in oxygen concentration in the near-bottom horizons was not an environment-forming factor for a number of halophilic species of chironomids of the genera *Chironomus*, *Tanytarsus*, and *Cricotopus*. We did not reveal a clear relationship between the population density and environmental factors for eurybiontic taxa such as *Paratanytarsus inopertus* (ChPtt.i), *Cricotopus* sp. (ChCri.p), *Cladopelma* gr. *lateralis* (ChCld.l), and *Culicoides riethi* (CeCul.s). The ordination analysis showed (Fig. 5) that the taxonomic abundance of saline rivers depends not only on the salinity level itself, but also on factors such as oxygen and phosphorus content. A substantial influence is made by the specificity of the ionic chloride to sulfate ratio. The role of hydrological and hydrophysiological factors (overgrowing with macrophytes, water temperature, and depth) is high; they determine the resource availability for benthic communities [15, 21]. Undoubtedly, knowledge on the life strategies of species and general ecological characteristics under natural conditions makes it possible to exclude a wide range of uncertainties and the erroneous interpretation of the results, which are observed, for example,

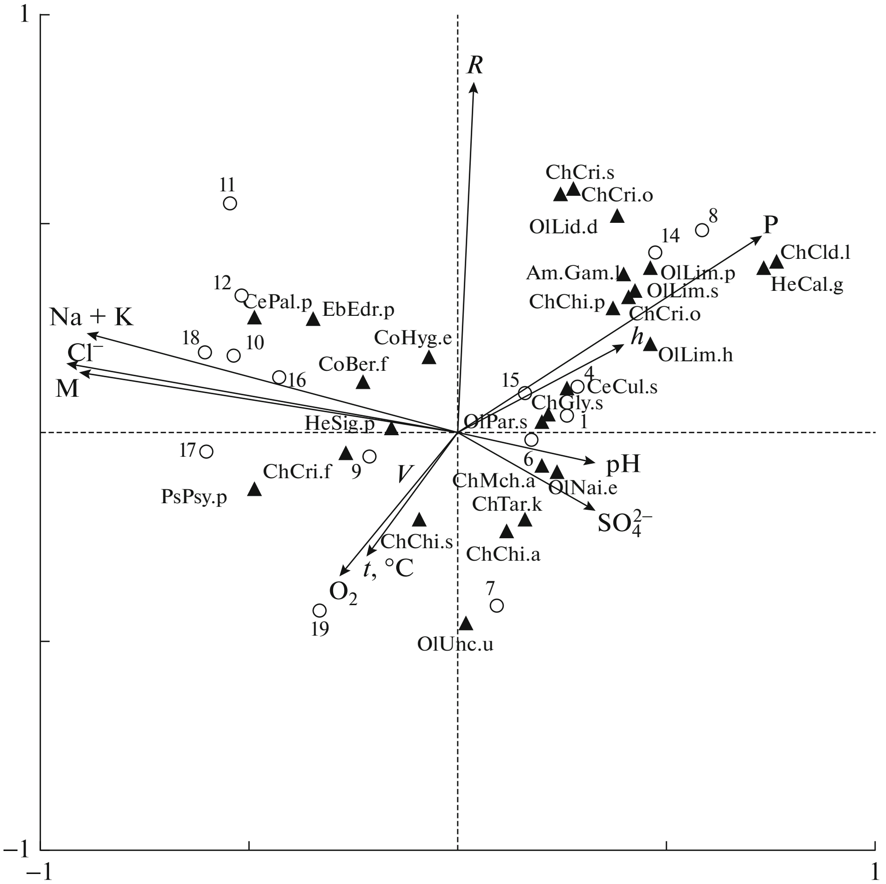

Fig. 5. Ordination of the relationship between the factors of the habitat and species composition of mass species of benthic communities in five saline rivers on the basis of the canonical correspondence analysis (CCA); vectors: t, °C, the water temperature vector during the sampling period; O_2, oxygen content vector (pH); M, water salinity vector; Na + K, SO_4, Cl^-, ion and cation vectors; h, vectors of the river depth in the sampling site; R, overgrowing vector; V, current velocity vector; P, total phosphorus content vector. (1–19) Numbers of stations. See the codes of main taxa (triangles) in Table 3.

during the analysis of interactions between contour and internal communities, taking into account the fact that there is no clear line between plankton and benthos in high-mineralized rivers, as in other saline water bodies [3, 22]. Given the effect of extreme factors such as high salinity and temperature, in combination with a significant level of biogenic substances and high primary production due to different causes, including macrophyte decomposition and the functioning of cyanobacterial mats, the studies should be accompanied by a determination of the role of each of the components in assessing their production. This is important for revealing the features of the development of planktonic and benthic community populations. There is no doubt that the diversity of morphofunctional adaptations also provides the development of hydrobionts in natural surface waters [18].

Under conditions of temporal climatic fluctuations and an increasing anthropogenic load, one can expect different structural associations of the ecosystem of the Lake Elton region; their prediction is possible only on the basis of seasonal monitoring studies.

CONCLUSIONS

Saline rivers with a high salinity gradient should be considered a specific adaptive zone populated by flora and fauna in accordance with the osmoregulatory capabilities of species forming them. The multiyear (2006–2013) studies of high-mineralized rivers (with a gradient from 4 to 41 g/L) made it possible to reveal the conditions of formation of a specific euryhaline benthofauna. Ninety-one taxa were recorded; most of them are new or rare species for the region. An important role is played by changes in the complex of hydrological and hydrochemical, hydrophysical, and biotic factors throughout the season, as well as by their spatial distribution in the rivers. Benthic communities are structured depending on the salinity level and other leading indicators that are associated with their specific biotic structure, adaptations to extreme habitat conditions, and resource availability; however, the differences between cenoses are also determined by the unique ecological features of the river system. Under the influence of global and regional natural and climatic fluctuations, the hydrosystems of the saline rivers in the basin of the hypersaline Lake Elton region function under nonstabilized conditions in the presence of periodic bifurcations, which results in the constant rearrangement of all its structural and functional components. This is also the main cause of fluctuations of the total diversity and composition of benthic communities, which are not characterized by evolutionarily established stabilized conditions.

ACKNOWLEDGMENTS

We are grateful to E.V. Makarchenko, O.V. Zorina (the family Chironomidae), and A.A. Prokin (order Coleoptera).

This study was financially supported by the Russian Foundation for Basic Research, grants nos. 13-04-10119; 13-04-00740; and 15-34-51088, as well as by the Program of Fundamental Research of the Russian Academy of Sciences for Priority Areas "The Biodiversity of Natural Systems."

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Translated by D. Zabolotny