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AQUATIC ECOSYSTEMS

Plankton and Bottom Communities in the Saline Rivers of Lake Elton Basin: Statistical Analysis of Dependences

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Abstract—Hydrological, hydrochemical, and hydrobiological data for five saline rivers of the arid Lake Elton region were analyzed. We found that interactions between plankton and benthic communities, in particular, between macrozoobenthos, meiobenthos and zooplankton, created mixed ecological groups of species. Abundances of plankton and bottom communities significantly correlated, which indicated that there is a close relationship between them due to biotic interactions and their similar responses to the effects of environmental factors. Multidimensional scaling and cluster analyses, the construction of hierarchical trees and species diversity models, the spatial correlation Mantel test, etc., were used to study the structure of communities in strongly disbalanced ecosystems of highly mineralized rivers. Indicator species were established by the TWINSPAN procedure. Our results demonstrated that plankton and bottom communities of the saline rivers can be represented as specific consortia or structural units of the river ecosystems.

Keywords: saline rivers, zooplankton, macrozoobenthos, meiobenthos, community structure, statistical analysis
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INTRODUCTION

The saline rivers of the hyperhaline Lake Elton basin (49°07'30" N, 46°30′40″ E, Volgograd Region, arid zone of the desert steppes) attracted our attention due to their high salinity gradient and variable hydrological regime (Zinchenko et al., 2017). The lotic ecosystems of Lake Elton basin are unstable as a result of global and regional climatic fluctuations, including anthropogenic impact. Aquatic species dwell under very specific conditions in different river areas, at low river speed, shallow depth, and high trophic status. These are the most productive zones, where migratory birds commonly gather for fattening (Zinchenko et al., 2014). The contact zones "river–hypersaline lake" refer to dynamically nonequilibrial systems with constantly variable and unpredictable abiotic conditions (tidal movements of saline water from the lake to the river estuaries, surface, and bottom flows of saline water). Under the conditions of stochastic fluctuations of climatic, hydrological, hydrochemical, and hydrophysical factors, the taxonomic structure of aquatic communities exhibited annual and long-term changes (Zinchenko et al., 2017).

In shallow saline rivers and lakes, there is no clear distinction between plankton and benthic communities: the most abundant species occur equally, both on the bottom and in the water column (Anufrieva and Shadrin, 2012; Lazareva, 2017; Kolesnikova et al., 2008; Spaccesi et al., 2009). Therefore, the spatial distribution of these communities should be studied in similar habitats under conditions of variable abiotic factors, which is important for general analysis of the structural organization of aquatic ecosystems.

The plankton, meiobenthos, and macrozoobenthos communities of the unique ecosystem of the basin of hypersaline Lake Elton are still not well studied. They are affected by the salinity gradient and habitat variability. Shallow habitats of saline rivers can be regarded as dynamic macro- and microbiotopes in which aquatic organisms are distributed throughout all spatial scales (Abood and Metzger, 1996). However, the representatives of macrozoobenthos, meiobenthos, and plankton in such habitats are well adapted to variable conditions, which is shown by their high levels of species richness, abundances, and biodiversity (Lazareva, 2017, Lazareva et al., 2013; Zinchenko et al., 2017). As a result, each river section is distinguished by a variety of structural option of these communities, which led us to study the mechanisms for their distribution and functioning.

We studied the mechanisms of the transformation of the community taxonomic structure and assessed the ranges of the tolerance of individual species and the potential of biological processes that help organisms adapt to the limiting environmental factors under conditions of arid aquatic ecosystems (Zinchenko et al., 2014). Therefore, we studied communities under conditions in which the role of environmental factors affecting the structural organization of communities is very significant, while interspecies interactions are not obvious.

Our goal was to carry out a comparative analysis of changes in the taxonomic structure of bottom and plankton communities of saline rivers in the basin of the hypersaline Lake Elton under conditions of extreme environmental factors based on different methods of multidimensional statistical analysis.

MATERIALS AND METHODS

Samples were collected during a long-term hydrobiological survey of macrozoobenthos, meiobenthos, and zooplankton in five saline rivers (Khara, Bolshaya Samoroda, Chernavka, Lantsug, Solyanka) belonging to the Lake Elton basin. The mineralization in these rivers varied in a wide range, from 6 to over 41.1 g/L. The locations of the sampling sites, sampling methods, and sample processing are described in Zinchenko and Golovatyuk (2010), Gusakov et al., (2012) and Lazareva (2017). Simultaneously, hydrophysical and hydrochemical analyses of water samples, including measurements of temperature, mineralization, pH, suspended matter, chlorophyll a, dissolved oxygen, cation concentration, anions, and nutrients, were conducted (Zinchenko et al., 2017). For a multidimensional statistical analysis of data collected during the hydrobiological survey in August, 2013, we constructed a matrix of 15×88 T (ind./m^2) of individual taxa groups at 15 sites of five saline lakes, including 28 species of zooplankton, 24 species of macrozoobenthos, and 36 species of meiobenthos. We transformed the matrix values into a unified interval scale and, on the basis of the transformed data, we calculated symmetrical 15×15 distance matrices D consisting of the Bray-Curtis distance coefficients, both between the compositions of the plankton and benthic communities and relative to the total number of species.

The objectives of our statistical analyses were the following:

(a) verification of the null hypothesis about the independence of community functioning with the Mantel matrix correlation method;

(b) analysis of the profiles of the three components of species diversity (α, γ and β) ^qD with respect to the order of the q Hill numbers for the three communities (De'ath, 2012);

(c) cluster analysis of biotopes based on the hierarchical classification (average linkage) and the method of fuzzy k-means;

(d) establishment of indicator species during RQ-diagonalization of the original matrix T by the optimization procedure TWINSPAN (Two-Way INdicator SPecies ANalysis);

(e) ordination of species and biotopes to arrange a graphical order of taxa of plankton and benthic communities along the gradient of environmental factors based on canonical correspondence analysis (CCA) and method of nonmetric multidimensional scaling (NMDS);

(f) identification of priority physical and chemical factors regulating the transformation of aquatic communities based on models of multivariate regression trees (MRT).

We used R software (version 3.02) for statistical calculations. Short descriptions and bibliographic sources for all of the above methods, as well as examples of scripts for calculations, are presented elsewhere (Shitikov et al., 2012; Shitikov and Rosenberg, 2014; Legendre and Legendre, 2012).

RESULTS

Analysis of the plankton species distribution indicated that most species belong to the benthic plankton and are associated with the substrate by trophic relations (Krylov, 2005). The species names that dwell in particular river sections and the frequency of their occurrence in the sampling sites are given in Table 1. Euplankton taxa accounted for 20% of the total number of species and was represented by copepods and rotifers. Benthic plankton were represented by 45% of taxa, whereas the eurytopic and meroplankton species accounted for 15% of the fauna. It is noteworthy is that, in all of the rivers, Harpacticoida and Ostracoda taxa predominated in the meiobenthos, characterizing it as eumeiobenthos or benthic plankton. The zooplankton of polysaline rivers (the Solyanka and Chernavka) was mostly represented by eurytopic species (>50% of the total abundance), whereas mesosaline rivers (the Hara, Lantsug and Bolshaya Samoroda) were mainly inhabited by benthic plankton or euplankton (Lazareva, 2017). Such halophilic species of macrozoobenthos as the larvae of Diptera *Cricotopus salinophilus* (Zinchenko et al., 2009), *Chironomus aprilinus* (Meigen, 1838), *Ch. salinarius* (Kieffer, 1915), *Microchironomus deribae* (Freeman, 1957), *Palpomyia schmidti* (Freeman, 1957) etc. were typical of both communities, i.e. zooplankton and meiobenthos.

For a comparative analysis of the species diversity ^qD, we found the dependence of the three components of the diversity, α, β and γ, on the order of the Hill numbers q (Fig. 1). It was evident that the general variability of the species structure of communities between biotopes measured by β- and γ-diversity decreases in the order macrozoobenthos—zooplankton—meiobenthos at all *q* levels. This means that the taxonomic composition of the macrozoobenthos is more sensitive to environmental conditions than other communities, and it also has a much wider set of species which under certain conditions appear dominant. This conclusion is supported by the construction of rank models of dominance/diversity (Shitikov et al., 2012).

The taxonomic structures of plankton sufficiently correlate with those of benthic communities, which

Table 1. Distinctive species in zooplankton (ZP), meiobenthos, (MB) and macrozoobenthos (ZB); the sampling sites of the saline rivers of Lake Elton basin were grouped in accordance with hydrochemical indicators.

Communities	Species, river, sites, factors	Occurrence, %	IndVal	*p*-value
Group 1: Khara River – sites 4, 5, 6 Content O_2<153.5%; Content Mn>0.23 mg/L; mineralization <18.7 g/L				
MB	***Oncholaimus rivalis***	20	**0.750**	**0.069**
ZP, MB	***Brachionus calyciflorus***	80	**0.750**	**0.051**
ZP, MB	***Acanthocyclops americanus***	33	**0.750**	**0.009**
MB, ZB	*Glyptotendipes salinus*	13	0.500	0.146
ZB	*Chironomus plumosus*	13	0.500	0.154
MB ZP, ZB	*Chironomus aprilinus*	13	0.250	1
ZB, MB	*Nais elinguis*	20	0.250	1
Group 2: Solyanka River – site 10; Chernavka River – site 16 O_2<153.5%; Mn>0.23 mg/L; mineralization>18.7 g/L				
ZP, MB ZB	***Palpomyia schmidti***	27	**0.667**	**0.046**
ZB	*Berosus fulvus*	7	0.500	0.269
MB, ZB	***Culicoides riethi***	47	**0.486**	**0.089**
Group 3: Lantsug River – site 8; Bolshaya Samoroda River – sites 14, 15 O_2<153.5%; Mn<0.23 mg/L; mineralization <19.4 g/L				
MB	***Heterocypris salina***	20	**1.000**	**0.003**
ZB	***Sphaeromias* sp.**	13	**0.667**	**0.048**
ZB	***Limnodrilus profundicola***	13	**0.667**	**0.06**
ZP, MB	***Eucyclops serrulatus***	13	**0.667**	**0.049**
ZP, MB	*Cletocamptus confluens?*	20	**0.667**	**0.046**
ZP, MB ZB	*Sigara lateralis*	13	**0.667**	**0.05**
ZB	*Gammarus lacustris*	27	**0.620**	**0.085**
MB	*Candona* spp.	20	**0.580**	**0.091**
ZB, ZP	*Paracorixa concinna*	13	0.333	0.468
ZB	*Limnodrilus udekemianus*	13	0.333	0.455
ZP	*Ceriodaphnia reticulata*	7	0.333	0.462
Group 4: Lantsug River – site 9; Khara River – site 7 O_2>153.5%; mineralization <18.7 g/L				
MB, ZP	***Cletocamptus retrogressus***	53	**0.621**	**0.011**
ZB, ZP, MB	***Chironomus salinarius***	33	**0.593**	**0.067**
ZP	*Cletocamptus retrogressu*s	20	**0.545**	**0.097**
ZP	*Diacyclops bisetosus*	7	0.500	0.283
ZP	*Arctodiaptomus* (*Rh.*) *salinus*	7	0.500	0.283
MB	*Monhystrella parvella*	80	0.314	0.482
MB, ZP	*Megacyclops viridis*	20	0.300	0.58
Group 5: Solyanka River – sites 2, 3; Chernavka River – sites 1, 2 O_2>153.5%; mineralization >19.4 g/L				
ZB, ZP, MB	***Palpomyia* sp.**	53	**0.667**	**0.011**
ZP, MB	***Apocyclops dengizicus***	40	**0.556**	**0.072**
MB, ZP	***Cyprideis torosa* var. *littoralis***	67	**0.552**	**0.006**
ZP, MB, ZB	*Ephydra* sp.	27	0.500	0.156
MB, ZB, ZP	*Cricotopus salinophilus*	67	0.447	0.143

IndVal—indicator index (Legendre and Legendre, 2012). Bold font denotes species that are statistically significant as indicator species for α=0.1.

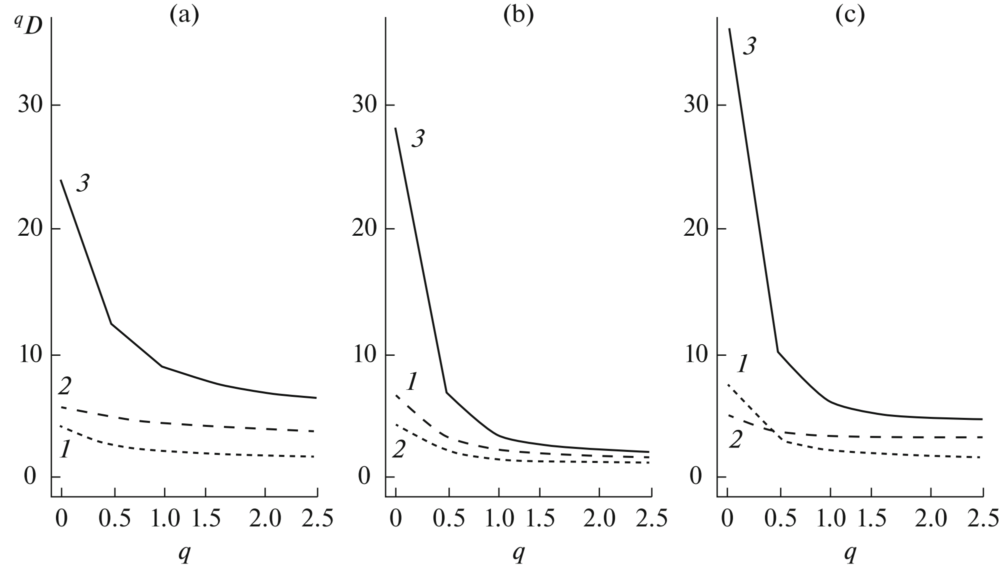

Fig. 1. Dependence of components of α (1), β (2) and γ (3) species diversity ^qD on Hill numbers q for three aquatic communities: macrozoobenthos (a), zooplankton (b), and meiobenthos (c).

indicates a close relation between them. Mantel matrix correlation analysis (Fig. 2) supported the hypothesis about the direct or indirect interactions between aquatic communities (macrozoobenthos, meiobenthos and zooplankton) that are created as a result of their mutual response to abiotic factors and interspecies interactions: $R_m = 0.56 / 0.68$, $p < 0.05$. The degree of interactions between the species structure of communities and hydrochemical indicators represented as a matrix of standardized Euclidean distances appeared to be lower: R_m = 0.39/0.44, $p < 0.05$. The difference between the coefficients of matrix correlation R_m can be related to different biotic relationships between communities and, mainly, to similar trophic response of species.

Since there is a statistically significant synchronicity between the changes in species composition between communities, we can distinguish sustainable taxa associations connected with individual types of biotopes with homogeneous environmental conditions. The associations of species composition of any ecological communities can be distinguished on the basis of two different approaches: (a) clustering without consideration of environmental factors and based only on the species composition in a given habitat and (b) habitat classification on the basis of environmental factors with respect to the distances between the vectors of hydrochemical indicators in Euclidean space; afterwards, the species included in a given cluster were combined into an individual group.

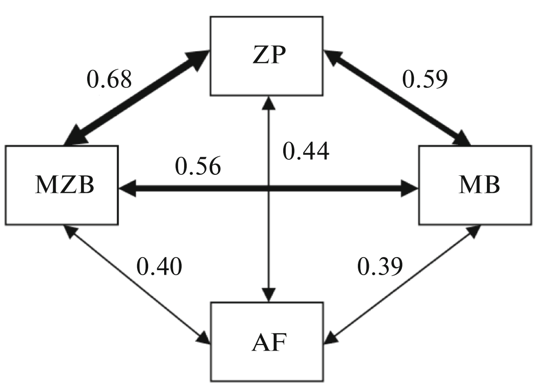

Fig. 2. Mantel correlation between distance matrices D based on abiotic factors (AF) and the transformed numbers of species individuals in macrozoobenthos (MZB), zooplankton (ZP), and meiobenthos (MB).

Ideally, both versions of the grouping should coincide. Indeed, in our case both, clustering methods and the indirect approach of TWINSPAN-ordination gave qualitatively identical results similar to that obtained by the MRT tree. The divisions of habitats and analyzed communities into five clusters via the construction of hierarchical trees are presented in Table 1. We combined them in associated groups on the basis of an analysis of the autecological and synecological properties of individual species (Lazareva, 2017; Zinchenko et al., 2017).

For each jth species from $s = 88$, the indicator indices d_{jk} are calculated (Table 1), which were equal to the product of the relative frequency and the relative average population density of each species for the samples from the group k (Legendre and Legendre, 2012). The index of indicator significance $\text{IndVal}_j = \max [d_{jk}]$ takes the maximum value (100%) if individuals of species j are present in all the samples from the group k and the corresponding value of p reflects the statistical significance of each species as an indicator of particular communities or environmental conditions.

Direct ordination performed by the method of nonmetric multidimensional scaling distinguished

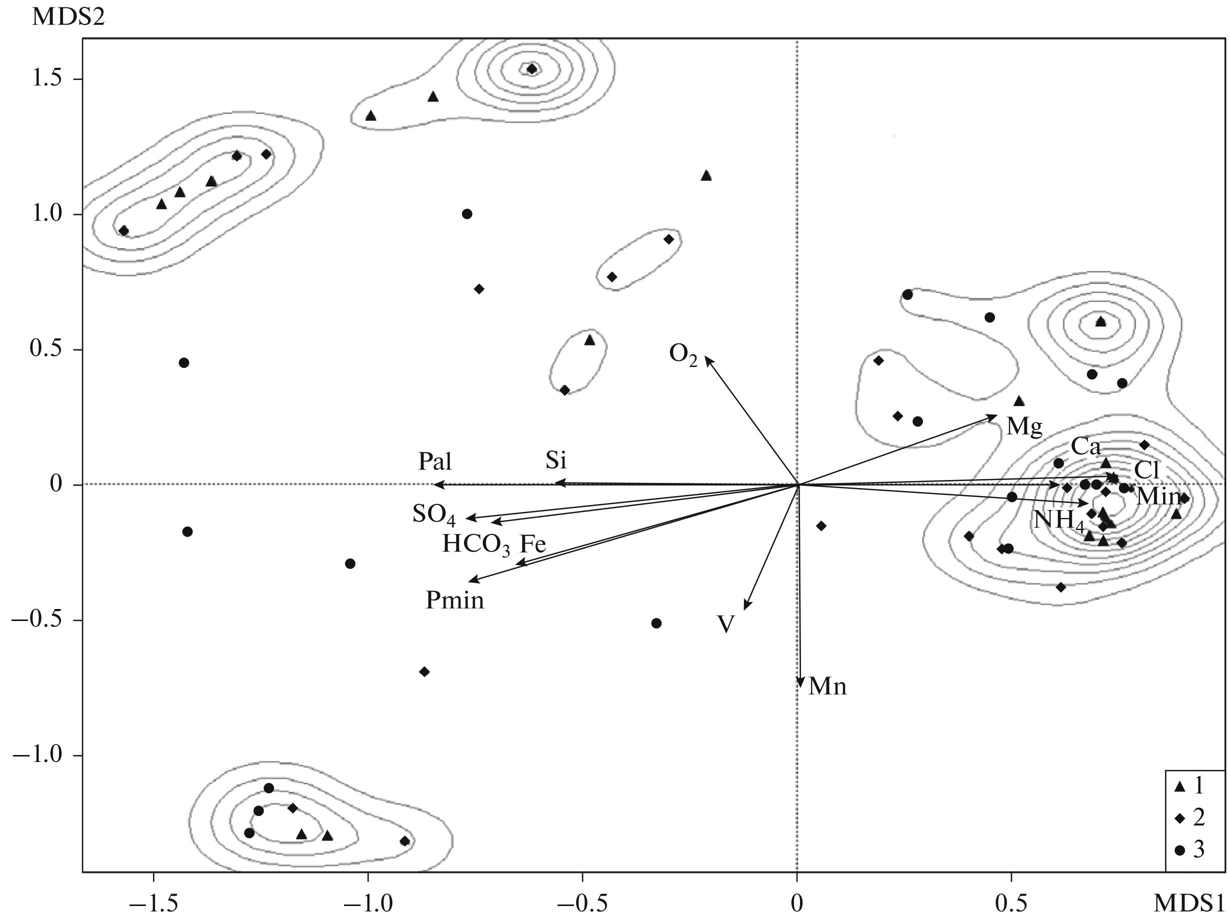

Fig. 3. Ordination diagram of species distribution of macrozoobenthos (1), zooplankton (2), and meiobenthos (3) based on non-metric multidimensional scaling. *Legend:* the arrows indicate additional axes of the main environmental factors: calcium content (Ca), manganese (Mn), magnesium (Mg), iron (Fe), silicon (Si), ammonium nitrogen (NH_4), mineral (Pmin) and total phosphorus (Pal), dissolved oxygen (O_2), sulfates (SO_4), chlorides (Cl), bicarbonates (HCO_3), suspended solids (V) and total mineralization (Min).

associations of species and habitats, assessing the statistical significance of the impacts of each environmental factor on the transformation of the communities' species compositions. Figure 3 shows that most of the hydrochemical indicators are highly correlated; they have identical (or diametrically opposite) trends and degree of influence. The axes of such important specific factors as the content of manganese ions, oxygen (for meiobenthos), and suspended substances (for macrozoobenthos) are orthogonal to the main multicollinear structure.

DISCUSSION

The spatial structure of the aquatic communities of any taxa mainly depends on the hydrological and hydrochemical factors and habitat features in the rivers, which, in turn, determine the total production and energy processes (Alimov et al., 2013). However, the high seasonal variability of environmental conditions in the saline rivers of the arid ecosystems determines the specific character of the structuring and transformation of communities that are mainly dependent on the adaptive abilities of individual species. Under such conditions, the structure of communities at each point in space is mostly regulated by a mutually associated response to stochastic and/or extreme levels of environmental factors, while interspecies interactions (mutualism, commensalism, competition) remain not so important. The coexistence of different-sized species groups in meiobenthos, macrobenthos, and zooplankton is justified by the principle of complementarity of ecological niches (Stolyarov and Burkovsky, 2008). The saline river communities, which were described in a few publications, are functionally different from those in Elton region, even in a taxonomic structure that varies in a wide range among saline rivers in the arid regions of the world. Therefore, we are not able to perform comparative analysis between the communities (Spaccesi et al., 2009).

Our studies suggest that the spatial structures (mosaic) of zooplankton, macrobenthos, and meiobenthos communities coincide. Within each biotope, the boundaries and the area occupied by their taxa associations overlap or remain in a state of fluctuating equilibrium. The general trend of all saline rivers is a decrease in the taxonomic diversity of zooplankton, meiobenthos, and macrozoobenthos in the conditions of high levels of trophic status, productivity, and abundance of aquatic taxa (Lazareva, 2017; Zinchenko et al., 2017). Moreover, Nematoda, Ceratopogonidae, and Chironomidae demonstrated the highest resistance to extreme environmental factors.

The concepts of stability and equilibrium in ecology are related to the metaphor of the "ecological balance," which is based on the idea that natural components tend to compensate for the effects of various external disturbances by performing regular fluctuations of population abundances and species composition (Cuddington, 2001). This metaphor plays a fundamental role in understanding the "dynamic balance" of communities of highly mineralized waters in arid regions. Apparently, the high variability and/or unpredictable regimes in saline rivers can create a state of a hypereutrophic system, in which abiotic processes are the main factors determining the structure of lotic system communities. It is possible that the capacity for consortium connections are the dominant factor in the formation of community structures in highly mineralized rivers.

CONCLUSIONS

Our studies of community structure under the conditions of a fluctuating environment in highly mineralized rivers, which were based on different methods of multivariate analysis, suggest that the associated plankton and bottom communities are a kind of consortium representing the structural unit of the ecosystems in saline rivers.

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