

Analysis of the Structure of the Metacommunity of Plankton and Bottom Organisms in Rivers of the Lake Elton Basin

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Abstract—A statistical analysis was performed on hydrochemical and hydrobiological data obtained from samples of macrozoobenthos, meiobenthos, and zooplankton in 2013 and 2018 from different biotopes of the five highly mineralized rivers of the basin of the hyperhaline Lake Elton. The general trends in the formation of the species structure of the metacommunity of aquatic organisms are considered based on the Lybold-Mikkelsen concepts. Randomized null models are used to test hypotheses on the consistent occurrence of species (*coherence*), the formation of compact species associations (*boundary clumping*), and the regular change in the species composition along environmental gradients (*turnover*). The nature of changes in biotic diversity were determined to be nonstationary and intermittent, and the taxonomic structure was highly mosaic, which is characteristic of stochastic-type ecosystems. A close correlation was established within individual mixed associations of benthic and planktonic species due to biotic interactions and the coordinated response of organisms to environmental factors. Statistical models Random Forest and subsequent multivariate analysis were used to identify groups of species by the degree of tolerance to external abiotic influences, and the sets of factors having a significant impact were established.

Keywords: saline rivers, zooplankton, macrozoobenthos, meiobenthos, metacommunity structure, indicator species, private correlation network, factor analysis

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INTRODUCTION

Prieltonye is one of the most unique, natural-territorial complexes of the Lower Volga basin. The meso-, poly- and hyperhaline river systems located in it function under stochastic and often extreme climatic disturbances characteristic of arid zones, which causes sharp fluctuations in the number of individual populations hydrobionts (Zinchenko et al., 2017). Thus, the study of the interdependence of biotic elements within the planktonic and bottom communities of the rivers of the region is relevant and of genuine interest.

We performed a statistical analysis of the taxonomic structure of hydrobionts of saline rivers basin of Lake Elton earlier using various multidimensional methods. This made it possible to highlight nonstationary species associations of the consortium type that formed dynamically, with allowance for the adaptive capabilities of individual taxa (Zinchenko et al., 2018). It was found that that there is no obvious, clear separation of the life forms of planktonic and bottom communities for the studied ecosystems, i.e., the transition of benthic animals to a planktonic way of life was noted, and this leads to a high proportion of interpenetrating ecological groups. The method to assess canonical correlations was used to analyze the severity

of such associative intrasystem connections; a close statistical relationship was found for macrozoobenthos, meiobenthos, and zooplankton (Zinchenko et al., 2019a). Comparison of the results of long-term hydrobiological observations in saline rivers showed both the presence of high structural consistency and stable patterns of spatial distribution, as well as a regular change in the leading types of communities (Zinchenko et al., 2019b). Multivariate ordinal analysis made it possible to establish the nature of mutually coordinated reactions of species to changes in the conditions of the aquatic environment and to identify the complexes of hydrochemical factors that have the most significant effect.

Analysis of the patterns of the species structure of communities and the identification of the mechanisms that generate its characteristic patterns are classic tasks of ecology. The modern views of the study of ecosystems are based on the concept of *metacommunity* (Leibold and Mikkelsen, 2002), which refers to the totality of ecological communities in different areas united by certain patterns of the distribution of the species composition. These laws are based on gradients of environmental factors, various mechanisms of the mutually coordinated coexistence of organisms, and the ability of various species to settle. This results in patterns, such as the formation of multispecies clus-

ters along ecological gradients, the positive or negative joint occurrence of species, and nestedness of the taxonomic structure (Shitikov and Zinchenko, 2011).

The first step in the study of the potential mechanisms for the formation of the metacommunity is to test the statistical hypothesis of the correspondence of the model based on observations and standard patterns that are typical for certain conditions (Connor and Simberloff, 1979). As a reference model, a particular zero model is usually chosen, i.e., the species distribution over sites is random and chaotic, clusters do not form, there is no influence of environmental gradients, and no consistent relationships between species are found (Sanderson, 2004; Hausdorf and Hennig, 2007).

In this article, we present an additional analysis of the structure of the macrozoobenthos, meiobenthos, and zooplankton communities in different parts of the five saline rivers of the Lake Elton basin and propose approaches to the solution of the following urgent problems of a theoretical and practical nature:

1. An analysis of general trends in the formation of the species structure of the studied metacommunity, including the testing of hypotheses about the consistent occurrence of species (*coherence*), the formation of compact species associations (*boundary clumping*), and the regular change in the species composition along environmental gradients (*turnover*);
2. The selection of a set of indicator species, the abundance of which is statistically significantly related to the ecological gradient;
3. The construction of a correlation network that defines high-priority, intrasystem connections.

MATERIALS AND METHODS

The source material was obtained from hydrobiological surveys of macrozoobenthos, meiobenthos, and zooplankton in 13 different sections of five saline rivers of the Lake Elton basin (49°07'30" N, 46°30'40" E), which have a significant mineralization gradient (from 6 to 50.1 g/L). A detailed description and scheme of the research area and the methods used for hydrobiont sampling and cameral processing of the collected material were presented earlier in the works (Zinchenko et al., 2017, 2018, 2019a, 2019b). The environmental factors, including measurements of the hydrological parameters of watercourses (depth, flow velocity, etc.), indicators of water quality, and the content of the main chemical components, were monitored at the same stations in parallel. In the aggregate of the latter, each observation station was assigned to one of three gradations of mineralization.

The results of hydrobiological surveys in August 2013 and 2018 on the same fixed sections were used for the statistical analysis. An abundance table of 136 taxa was compiled. It included 36 species and genera of macrozoobenthos, 50 species of meiobenthos (ind./m²), and 50 species of zooplankton (ind./m³). For correct joint data processing, the abundance values were trans-

formed into a single point scale from 0 to 6 and a generalized taxonomic abundance matrix with a dimension of 26 × 136.

An analysis of the three main elements of the metacommunity structure (consistency, turnover, and concentration of species; Leibold and Mikkelsen, 2002) was carried out to determine the pattern type that best reflects the species distribution along the main axis of the variation of environmental factors. An ordered incidence matrix was constructed based on empirical data. With the use of the proposed statistical criteria (Presley et al., 2010), the matrix was compared with randomized null matrices formed with the method *r1*, i.e., the species richness of the sites was considered to be unchanged, and the probabilities of species detection were proportional to their common frequencies. The significance of the structural elements was evaluated as a result of multiple repetitions of the Monte Carlo simulation process.

The clustering test, which tests the hypothesis of the existence of positive species associations, was carried out based on the parametric bootstrap of the distance matrix between the plots with the Kulchitsky quantitative measure. A statistical criterion that takes into account the ratio of the total distances inside and between the clusters was used (Hennig and Hausdorf, 2004). The simplest *unconstrained* null model assumed that all biotopes are equally suitable or accessible for all species, regardless of the habitats in which they were found. In limited models, a certain correlation structure was additionally set in the form of a matrix of distances between individual sections on the scale of the analyzed gradient (environmental, spatial, or temporal).

The index was previously used (Zinchenko et al., 2018, 2019a, b) to rank species by the degree of their indicator valence relative to the Dufrene-Legendre salinity gradient *IndVal*. In the present work, the Boruta algorithm (Kursa and Rudnicki, 2010), which evaluates the informational content of each species in the form of a partial forecast error caused by the exclusion of this species from the model, was used in this work. The algorithm tests the null hypothesis using a randomization method based on a highly efficient ensemble of Random Forest models.

The tightness of the statistical relationship between the selected species was evaluated with the “graphical lasso” method (Friedman et al., 2007), which was used to find the maximum likelihood estimate of the matrix of partial correlation coefficients Σ based on the regularization algorithm (i.e., with allowance for the penalty for the sum of absolute values Σ^{-1}). The resulting matrix graph was displayed in the format of an optimized correlation network.

The statistical analysis was performed with the R programming environment, version 3.06, and *its additional packages*: *metacom*, *prabclus*, *Boruta*, *huge*, and *qgraph*.

Table 1. Statistical significance of various hypotheses regarding the taxonomic structure of the metacommunity of aquatic organisms in the rivers of the Lake Elton basin

Testable Hypotheses	Statistics	<i>p</i> -value
1. Elements of metastructure (Leibold, Mikkelsen, 2002):		
—species <i>coherence</i>	−9.89	≈0
—species turnover	0.88	0.37
—presence of boundary clumping	1.71	0.000001
2. Severity of associations of species under various restrictions (Hennig and Hausdorf, 2004):		
—unlimited model		0.143
—geolocation model		0.286
—model assuming localization along rivers		0.0495
—model taking into account the relationship with the salinity gradient.		0.0594

RESULTS AND DISCUSSION

Table 1 presents the results of tests of statistical hypotheses regarding the laws of the taxonomic structure of the metacommunity. The negative value of the *Z*-criterion and the significance of statistics for the test for species consistency indicates the predominance of a “chessboard” pattern: species compositions have more continuity gaps (*embedded absences*) than a random structure contains. The significance of species turnover according to the *Z*-criterion confirms that numerous unpredictable occurrences or exclusions of species are stochastic in nature. The test χ^2 for the presence of condensations rejects the null hypothesis of the absence of clustering. All of these features occur when the dominant gradient of the medium is absent, and the species distribution forms under the influence of several, in a sense, multidirectional external factors.

Four models of taxon distribution over river sections were constructed to verify the assumption of spatial autocorrelation of the species composition (Table 1). Two models are based on the hypothesis that the probability of the formation of repeated associations of species is greater in areas that are close to each other (within the same river or belonging to the same gradation of salinity). For them, a statistically significant level of taxon clustering was revealed ($p = 0.05$ – 0.06). For models that assume that there is no spatial autocorrelation or that it is based only on the proximity of the geographical coordinates of the points, the hypothesis about the random nature of the detected clusters is not rejected.

To clarify the particular species that form interconnected associations, we constructed the network graph shown in Fig. 1a. The obtained correlation pleiades were formed from combinations of species, the frequent joint occurrence of which is due to both biotic interactions and a mutually coordinated response to changes in aquatic factors. The use of partial correlation coefficients, which are usually three to four times lower in absolute value than traditional Pearson coefficients, made it possible to evaluate the “pure” effects of pairwise interaction between two specific network nodes after the elimination of the combined effect of

all other nodes, which thereby drastically reduces the false or induced correlation effect.

To assess the close connection between the species of aquatic organisms and the ecological gradient, 99 iterations of the construction of “random forest” models consisting of 500 hierarchical trees were performed. The importance of each species was calculated with the algorithm “Boruta” according to the *Z*-criterion, which estimates the decrease in the response prediction error when an empirical abundance vector is replaced with a random vector. It was found (Table 2) that only 16 taxa of the 136 initial species have a statistically significant relationship with the water-mineralization factor; thus, the presence of other species at any point in the studied hydraulic system is random and equally probable.

Note that some species, such as *Cricotopus salinophilus* (Zinchenko, et al., 2009) *Microchironomus deribae* (Freeman, 1957), and *Apocyclops dengizicus* (Lepeshkin, 1900), are often found simultaneously in planktonic and benthic samples. These phyto- and bacteriophages play an important ecological role in both environments due to the specific distribution of food resources in the hypereutrophic sections of rivers, including cyanobacterial mats.

The main components of the initial matrices are analyzed in order to evaluate the specific abiotic characteristics of biotopes that affect the existence of individual species. Figure 1b shows a bipartite correlation graph showing the relationships between the first 25 taxa from Table 2 and the three latent factors that determine the main axes of multidimensional data variation. Factor 1 includes a set of indicators that determine the water salinity: the content of chloride ion, calcium, and all three forms of nitrogen (positive correlation +), as well as sulfate ion and the depth of the stream (negative correlation −). Factor 2 is closely related to the oxygen content and pH level (+) and the concentration of manganese and iron (−). Factor 3 is associated with the content of chlorophyll “a” and magnesium and the water temperature (+), as well as phosphates and bicarbonates (−).

Table 2. Taxa of zooplankton (ZP), meiobenthos (MeB), and macrozoobenthos (MaB), which are of the greatest importance in the construction of models of the dependence of species composition on the salinity gradient in saline rivers

Significance	Group	Species code	Taxa	Occurrence	Z-criterion	p-value	
High	ZB	Pal_sh	<i>Palpomyia schmidti</i>	11	10.75	1.00	
	MeB	Apo_dn	<i>Apocyclops dengizicus</i>	8	6.92	1.00	
	MaB	Apo_dn	<i>Apocyclops dengizicus</i>	9	8.60	1.00	
	Zp	Cri_sf	<i>Cricotopus salinophilus</i>	19	7.15	0.99	
	Zp	Aca_sp	<i>Acanthocyclops americanus</i>	4	3.73	0.75	
	ZB	Cri_sf	<i>Cricotopus salinophilus</i>	16	3.65	0.73	
	Zp	Bra_pl	<i>Brachionus plicatilis</i>	22	3.53	0.71	
	MB	Het_sl	<i>Heterocypris salina</i>	5	3.31	0.69	
	Average	Zp	Cle_cn	<i>Cletocamptus confluens</i>	4	3.29	0.63
		ZB	Gam_lc	<i>Gammarus lacustris</i>	6	3.11	0.60
MB		Mic_db	<i>Microchironomus deribae</i>	3	3.06	0.57	
MB		Chi_sl	<i>Chironomus salinarius</i>	11	2.77	0.51	
MB		Pal_sh	<i>Palpomyia schmidti</i>	7	2.29	0.38	
Zp		Meg_vr	<i>Megacyclops viridis</i>	7	2.18	0.37	
MB		Cyp_tr	<i>Cyprideis torosa</i>	17	2.32	0.36	
MB		Cri_sf	<i>Cricotopus salinophilus</i>	15	2.07	0.12	
Weak		Zp	Cru_rf	<i>Cricotopus rufiventris</i>	3	1.43	0.05
		ZB	Gly_sl	<i>Glyptotendipes salinus</i>	4	1.56	0.03
	Zp	Dia_bs	<i>Diacyclops bisetosus</i>	3	1.09	0.03	
	ZB	Chi_ap	<i>Chironomus aprilinus</i>	4	0.35	0.02	
	MB	Nai_el	<i>Nais elinguis</i>	4	1.54	0.02	
	ZB	Tan_kh	<i>Tanytarsus kharaensis</i>	2	1.32	0.01	
	ZB	Mic_db	<i>Microchironomus deribae</i>	8	0.96	0.01	
	MB	Onc_rv	<i>Oncholaimus rivalis</i>	4	0.70	0.01	
	MB	Mo_pv	<i>Monhystrella parvella</i>	23	1.62	0.01	
	ZB	Chi_sl	<i>Chironomus salinarius</i>	10	0.09	~0	
	ZB	Aed_sp	<i>Aedes</i> sp.	3	0.25	~0	
	MB	Net_lc	<i>Nitokra lacustris</i>	3	1.07	~0	
	MB	Par_lt	<i>Paranais litoralis</i>	3	0.95	~0	
	MB	Can_sp	<i>Candona</i> spp.	3	0.88	~0	
	MB	Dip_dl	<i>Diplolaimelloides delyi</i>	5	0.72	~0	
	ZB	Ber_sp	<i>Berosus</i> sp.	3	0.72	~0	
	MB	Cal_sl	<i>Calodorylaimus salinus</i>	3	0.42	~0	
	Zp	Euc_sr	<i>Eucyclops serrulatus</i>	3	0.02	~0	
	MB	Tu	<i>Turbellaria</i> spp.	4	0.00	~0	
	ZB	Cul_sp	<i>Culicoides</i> sp.	3	-0.08	~0	
	Zp	Cyp_tr	<i>Cyprideis torosa</i>	6	-0.40	~0	
	Zp	Gam_lc	<i>Gammarus lacustris</i>	3	-0.44	~0	
	ZB	Odn_sp	<i>Odontomyia</i> sp.	3	-0.45	~0	
	ZB	Sig_sp	<i>Sigara</i> sp.	4	-0.50	~0	
	ZB	Eph_sp	<i>Ephydra</i> sp.	4	-0.56	~0	
	Zp	Cyc_np	<i>Cyclopoidea nauplii</i>	12	-0.63	~0	
	Zp	Col_ad	<i>Colurella adriatica</i>	3	-0.72	~0	
Zp	Bde	<i>Bdelloidea</i> spp.	4	-0.80	~0		
Zp	Cyc_cp	<i>Cyclopoidea copepodit</i>	8	-0.81	~0		
Zp	Bra_cl	<i>Brachionus calyciflorus</i>	3	-1.72	~0		

CONCLUSIONS

(1) The studied river ecosystem is characterized by a high degree of stochasticity of natural and climatic changes, such as the surge phenomena of water in the river—hyperhaline lake system, the drying up and regulation of the river bed, a high mineralization gradient,

the overgrowth of biotopes by macrophytes, etc. This led to a generally unsteady character of the hydrobiont metacommunity, which is expressed by an intermittent gradient of biotic diversity, a highly mosaic taxonomic structure, the absence of nesting, and other continuum patterns of species turnover (Table 1).

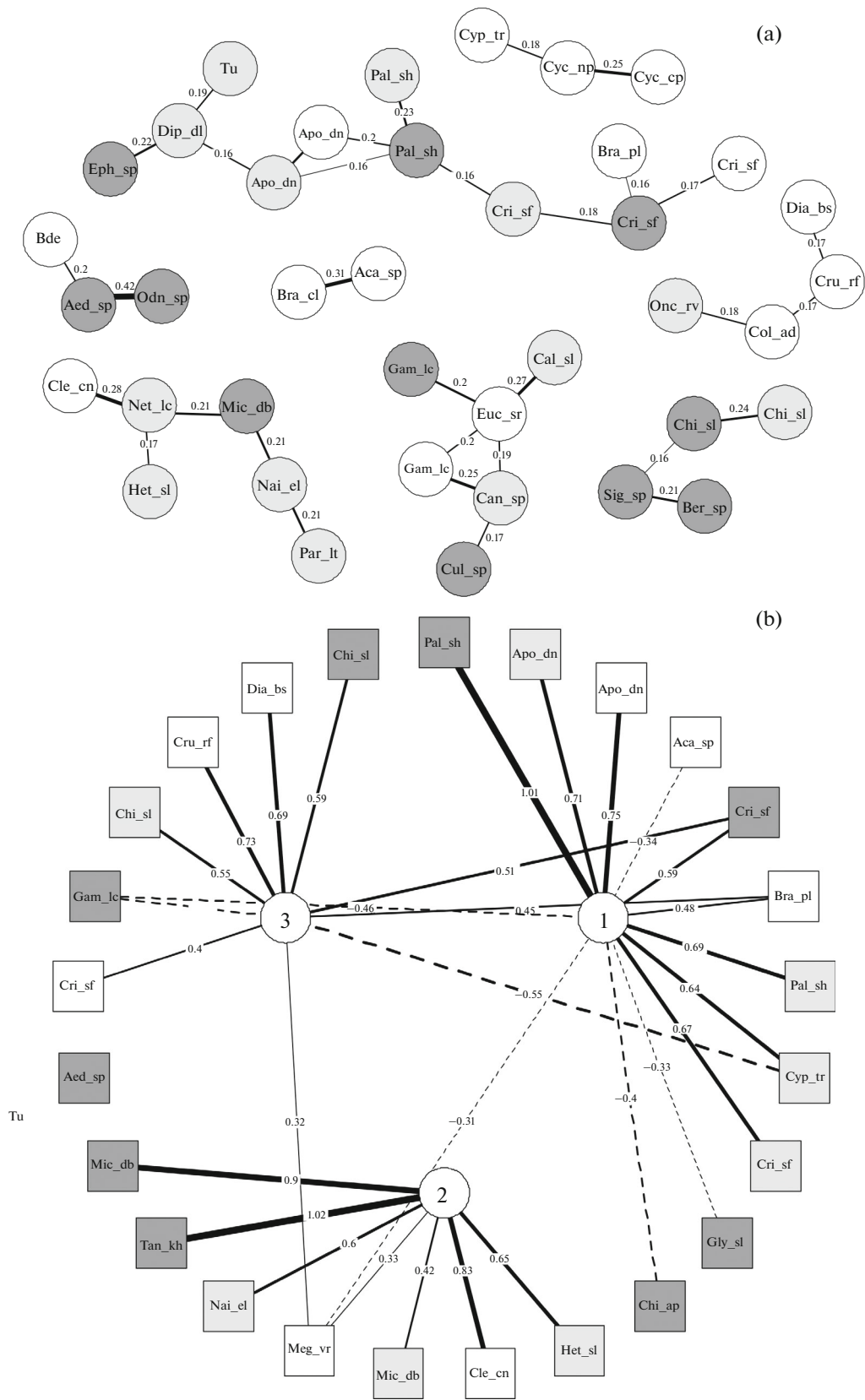


Fig. 1. Graphs of statistical relationships between the components of the metacommunity of aquatic organisms in the rivers of the Lake Elton basin: (a) a private correlation network of interspecific relations, (b) the relationship of the abundance of species with the three main latent variables generalizing abiotic factors. Dark gray, macrozoobenthos taxa; gray, meiobenthos; white, zooplankton. For species codes, see Table 2.

(2) The dynamics of the parameters of the external environment makes a stable state of the ecosystem impossible: there are a number of relatively stable equilibria caused by high-priority factors operating at each point and moment of time. However, the close relationship between the studied planktonic and bottom species of the metacommunity is constantly maintained due to the biotic interactions of phyto- and bacteriophage populations. Correlation analysis demonstrated the formation of mixed consortia of species from different groups of organisms (Fig. 1a).

(3) The spatial species distribution forms under the influence of several, often multidirectional external factors, of which the features of local biotopes and the ionic composition of the aquatic environment are important. A relatively small taxocenosis of truly halophilic species, which are closely correlated with water salinity, was identified (Table 2). However, the most of the species richness is made up of eurybiont species, which are evenly distributed over the ecological gradient and adapted to inhabit the mineralized waters of arid territories (Fig. 1b). Important environmental factors for their resource endowment are the content of phosphates, dissolved oxygen, and chlorophyll “a,” which is typical of eutrophic streams (Zinchenko et al., 2014).

(4) The diversity, adaptation, and sustainability of populations with resource endowment of the types of hydrosystem’s species in the Elton Biosphere Reserve implies the preservation of the natural dynamics of natural habitats.

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COMPLIANCE WITH ETHICAL STANDARDS

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

Statement on the welfare of humans or animals. This article does not contain any studies involving animals performed by any of the authors.

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