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Estimation of the Zonal Distribution of Species of Bottom Communities in Lowland Rivers of the Middle and Lower Volga River Basin

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Abstract—A comparative analysis of the variability of the species structure of macrozoobenthos communities in small and medium rivers of the Middle and Lower Volga river basin has been carried out. The statistically significant influence of the natural climatic zone, where the watercourse is located, and manifestation of the latitudinal gradient of biodiversity are shown. A list of indicator species has been made for each geographical zone identified using different criteria of biotopical distribution. Based on the analysis, the indicator value (IndVal) index, which takes into account the zonal distribution of both the occurrence frequencies of a species and its abundance ratios, was recognized as the most adequate. Association rules that contain combinations of species that most frequently occur together in hydrobiological tests have been formulated using the Apriory algorithm.

Keywords: small rivers, macrozoobenthos, structure of bottom communities, altitudinal gradient, species indicator value, association rules

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INTRODUCTION

Analysis of the patterns of the spatial and temporal distribution of hydrobionts is a fundamental problem of ecology and hydrobiology. The transformation of the species composition of communities along the latitudinal gradient determined by the succession of natural climatic zones is substantiated by various hypotheses (*Community Ecology*, 1986), which prioritize factors of evolutionary history or biotic processes that are associated with immigration, colonization, competition, predation, production volume, etc.

The bottom communities of lowland rivers are primarily characterized by changes in the species composition along the longitudinal gradient from the sources to the mouth; i.e., they represent a continuous sequence of local cenotypes with a natural succession of dominant complexes (Shitikov and Zinchenko, 2014). At the same time, a significant part in this distribution is formed by the species exchange between neighboring watercourses on the basis of the emergence of dipteran imagoes, which makes it possible to identify relatively stable subsets of central species that are characteristic of quite vast regions. In both cases, the heterogeneity of environmental conditions and the features of the natural landscape, undoubtedly, lead to the emergence of isolated niches and barriers; the geometry of species ranges takes on the complex mosaic pattern of the spatial distribution of individual taxa.

The identification of the subset of diagnostic species for each type of biotope and the further ecological interpretation of these species are an important stage in the classification of communities or habitats. This is usually performed on the basis of indices that quantify the extent to which the frequency of occurrence of each species from the group of biotopes under study exceeds the occurrence of the other groups or types of communities. One such index called *biotopical distribution* was proposed by Yu.A. Pesenko (1982). The development of the concept of species fidelity by the phytosociological group from Brno University has resulted in substantiation of different measures of association (Chytrý et al., 2002). P. Legendre et al. considered the statistical patterns of the spatial distribution of species in detail (He and Legendre, 2002) and proposed *indicator value* indices (Dufrene and Legendre, 1997) and other parameters that estimate the degree of association between a species and a certain type of habitat (De Caceres and Legendre, 2009).

Based on the generalization of long-term data of hydrobiological studies in the watercourses of the Middle and Lower Volga river basins, this article carries out a comparative analysis of the spatial variability in the species composition of bottom communities in small and medium rivers in five natural climatic zones. The use of the three above-mentioned methods of assessing the regional distribution of species was tested, and groups of statistically significant diagnostic taxa were identified.

MATERIALS AND METHODS

The hydrobiological survey of bottom organisms was performed in small and medium lowland rivers (91 rivers) and tributaries of the Kuibyshev, Saratov, and Volgograd reservoirs, as well as in six rivers of the arid region of the basin of Lake. Elton The research was carried out within the framework of hydrobiological monitoring in different months of the vegetation period from 1990 to 2015. Macrozoobenthos samples were collected in the ripal and medial zone of the rivers using an Ekman–Bergy grab or a hydrobiological scraper, followed by recalculation of individuals per m^2 (Zinchenko et al., 2014). The fixation of organisms and the further laboratory treatment of the collected material were performed according to generally accepted methods. In total, $S = 709$ benthos species and taxa above the level of species were identified.

The boundaries of the landscape zones were determined in three stages.

At the *first stage* of the analysis, the level of variability in the species composition of bottom communities and the statistical significance of factors determining this variation were estimated using the nonparametric multivariate analysis of variance (NPMANOVA) (Anderson, 2001). The total, T, from 1158 samples taken for analysis was reduced to five geographical regions that were combined by the similarity of natural climatic conditions on the basis of classification (Safronova and Yurkovskaya, 2015):

(1) Kuibyshev Reservoir, forest–steppe zone (Kuib): 131 samples, 270 species;

(2) Saratov Reservoir, forest–steppe zone (Sar/fs): 261 samples, 493 species;

(3) Saratov Reservoir, steppe zone (Sar/st): 474 samples, 389 species;

(4) Volgograd Reservoir, desert steppe (Volg): 60 samples, 179 species; and

(5) Elton Lake, desert steppe (Elt): 232 samples, 79 species.

The geographical and hydrological characteristics (date, river type, station coordinates, current velocity, biotope, etc.) were additionally taken from the database.

At the *second* stage, the indices of zonal distribution were estimated using the general table of species abundances for samples with dimension of 1158 × 709. For this purpose, the following special parameters of organism abundance were used:

t_{ik} and n_{ik}, the frequency of occurrence and total number of the *i*th species in samples belonging to the *k*th group (the geographical region in the case under consideration), $i = 1, 2, ..., S$; $k = 1, 2, ..., 5$;

T_i and N_i, the frequency of occurrence and the total abundance of the *i*th species in all samples;

T_k, the number of samples from the total number, T, covered by the *k*th group; and

N_k and N, the total numbers of all species in samples that were covered by the *k*th group and the total number of specimens in all samples (T).

Using these notations, we calculated the following species indicator value indices for each region.

Level of biotopical distribution (Pesenko, 1982):

$$F_{ik} = \frac{n_{ik}N - N_iN_k}{n_{ik}N + N_iN_k - 2n_{ik}N_k}, \quad (1)$$

which varies from −1 (the species is absent in the *k*th sample group) to +1 (the species occurs only in the *k*th group).

Coefficient of association (Chytrý et al., 2002):

$$\Phi_{ik} = \frac{t_{ik}T - T_iT_k}{\sqrt{T_iT_k(T - T_k)(T - T_i)}}, \quad (2)$$

which corresponds to the Pearson coefficient of correlation between two binary vectors and also varies from −1 to +1.

Indicator value index (Dufrêne and Legendre, 1997):

$$B_{ik} = \frac{t_{ik}}{T_k}, \quad A_{ik} = \frac{n_{ik}/T_k}{\sum_k n_{ik}/T_k}, \quad \mathrm{IndVal}_{ik} = B_{ik}A_{ik}, \quad (3)$$

where B_{ik} is the fraction of the number of samples from the *k*th group that includes the *i*th species; A_{ik} is the ratio of the average abundance of the *i*th species in the *k*th group to the sum of its average abundances in all groups. The IndVal_{ik} value is also 1 if the specimens of species *i* occur in all samples of one group alone.

The calculation according to formulas (2) and (3) took into account the correction for unequal volumes of groups (Tichý and Chytrý, 2006). Each species was considered the indicator of the group for which the indicator value criterion being used took on its maximum value.

The statistical significance of the indicator indices was estimated using the randomization procedure (Shitikov and Rozenberg, 2014); for this purpose, the samples were chaotically mixed 1000 times within the groups identified. During resampling, the I^* index was distributed, given the validity of the null hypothesis on the casual relationship between species and habitat

Table 1. Nonparametric analysis of the variance of matrix of distances between macrozoobenthos samples under the effect of three factors: geographical zone (Region), type of river (small/medium) (TypRiver), and observation period (spring/summer/autumn) (Period)

Factors and their interactions	Degree of freedom	Sum of squares	Mean squares	*F*-test	Estimate of *p* value
Region	4	32.02	8.00	18.2	0.002
TypRiver	1	3.78	3.78	8.6	0.002
Period	2	1.54	0.769	1.75	0.002
Region : *TypRiver*	4	7.44	1.86	4.23	0.002
Residuals	1146	504.2	0.44		
Total	1157	548.9			

groups. The statistical significance obtained, *p*, was calculated as the share of I^* values that exceeded the index value based on real data. If the *p* value was over 0.05, the respective species was considered background.

At the *third stage*, the most frequently occurring paired, triple, and higher combinations of macrozoobenthos taxa were identified using the Apriori algorithm (Hahsler et al., 2005) forming sets of association rules of the following type:

$$\text{if } \langle \mathscr{A} \rangle, \text{ then } \langle \mathscr{C} \rangle,$$

where $\mathscr{A}$ is the combination of co-occurring species that is characteristic of communities in a specific region, $\mathscr{C}$. The informative value and usefulness of each *j*th rule being formed was estimated using the occurrence frequency criteria, such as *support* and *confidence*. The $\mathscr{A} \rightarrow \mathscr{C}$ rule has a support (Sup) if it is true for T_{jk} samples from their total number, T: $\text{Sup}_j = T_{jk}/T$. The confidence (Conf) of the rule shows the level of probability with which the final part of the rule follows from the conventional part: $\text{Conf}_i = T_{jk}/T_i$.

The calculations were made using the R 3.3 statistical environment and its software packages: *vegan*, *indicspecies* and *arules*.

RESULTS AND DISCUSSION

A preliminary statistical analysis showed that the values of the abundance of separate species in samples had a wide range of variations; in addition, their distribution clearly represented the Zipf hyperbole. Starting from the maximum value of 412800 spec./m^2, which was due to the local irruption of *Potamothrix caspicus* oligochaetes, the rank distribution curve was characterized by a long right-hand tail, in which over 50% of species had an abundance of less than 80 spec./m^2. Under these conditions, the abnormally high values of abundance of individual species may distort both the results of analysis of variance and the estimates of the indicator value, (1) and (3). To compensate for this distortion, the initial data table was preliminarily transformed using the χ^2-transformation (Legendre and Gallagher, 2001), resulting in the most reasonable balance of abundance in taxocenes, which takes into account the specific influence of taxa with a high population density, as well as giving increased attention to the complex of rare species.

It should also be noted that bottom communities are characterized by the no less significant heterogeneity of the frequency of occurrence, T_i, of individual species; the rank distribution of this occurrence is also hyperbolic. Specifically, the most dominant species, *Polypedilum nubeculosum*, was revealed in 374 samples (32% of their total number), while 312 species (44%) were found only in one to two samples.

The matrix of taxonomic distances, D, with dimension of 1158 × 1158 between each pair of samples was calculated according to the Bray–Curtis formula of the reduced sum of minima, taking into account the transformed abundance of individuals of each species. Using the nonparametric multivariate analysis of variance (NPMANOVA) (Anderson, 2001), we decomposed the multivariate dispersion included in the distance D matrix according to the degrees of influence of impact factors. The statistical significance, *p*, of the variance fraction, F, which is explained by these factors or their interactions, was estimated using randomizing algorithms.

It was assumed that the differences in the species composition of samples may be determined by three factors: the identified geographical zones, the type of river (small/medium), and the observation period (spring/summer/autumn). The results of the analysis of variance presented in Table 1 show the high significance of all these factors; the highest share of the

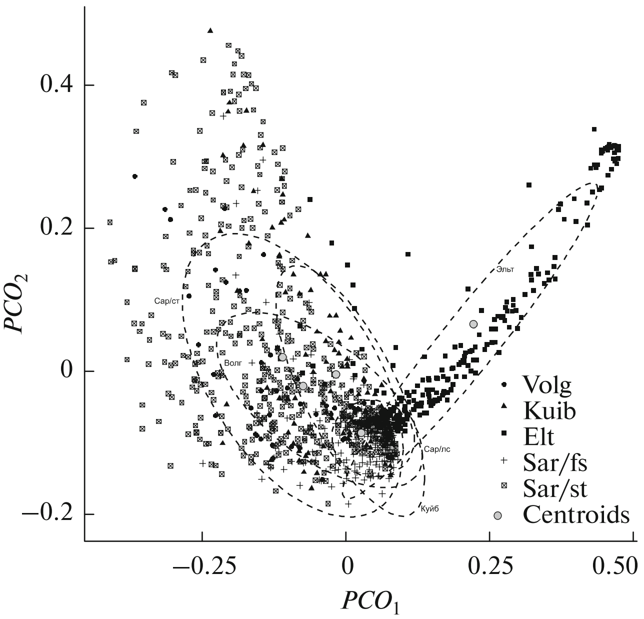

Fig. 1. Ordination of macrozoobenthos samples using the principal coordinate method; the gray circles indicate the coordinates of centroids for separate geographical zones and the dashed lines present 80% confidence ellipses based on the multidimensional *t*-distribution.

explained variance is characteristic of geographical zone groupings. We did not assess the effect of the long-term dynamics, since sampling in different periods was usually performed in not more than four to five replications.

The distance D matrix was used for the optimal projection of the performed observations in the multidimensional space of species onto the ordination plane with two axes of principal coordinates, PCO_1 and PCO_2 (P. Legendre and L. Legendre, 2012; Shitikov et al., 2012). The distances between the points of centroids of each geographical zone in the diagram (Fig. 1) make it possible to estimate the average level of species similarity between the groups, while the size of confidence ellipses, which included 80% of samples from each group, allowed us to estimate their comparative β-diversity. Figure 1 shows the clear specificity of the species composition of the totality of samples from the small rivers of the basin of Elton Lake, while between the other zones, these differences are not as clear. One can also note a significantly higher β-diversity of samples that were taken in the steppe part of the Saratov and Volgograd reservoirs than that from the forest–steppe zone, which can be interpreted as the manifestation of the latitudinal gradient phenomenon.

Lists of diagnostic species from the entire set of taxa were determined for each of the five geographical zones using different indices of fidelity (1–3). The most significant of them are given in Table 2, which also provides an important indicator value, such as the fraction of the frequency of occurrence of each *i*th species in samples of the *k*th group, n_{ik}/T_i.

It is believed that, if the level of Pesenko biotopical distribution of F_{ik} exceeds +0.7, the *i*th species clearly prefers the *k*th biotope. However, since the frequencies of occurrence are not used in formula (1), the maximum fidelity point, $F_{ik} = +1$, was automatically assigned to all 184 species, which occurred only once in samples of the entire database. The maximum index was also gained by most of the species that occurred only in two to three samples. Such exaggerated attention to rare and casual species led to the conclusion that the direct use of the index of biotopical distribution, F_{ik}, for sampling diagnostic species is inappropriate in our conditions and this index is given in Table 2 only in comparison with other indices.

Using the indicator value indices, $IndVal_{ik}$, for which the *p*-values were less than 0.05, we identified 240 species, relating each of them to one of the geographical zones (see Table 2). The number of statistically significant indicator species for each zone varied from 16 (Sar/st) to 87 (Volg). To assess the specificity of the species composition of the communities being studied, we calculated the coverage indicator C

Table 2. Number of statistically significant indicators and their coverage indicator in habitat zones

Tributaries, geographical zone	Number of indicators	Coverage of group
Kuibyshev Reservoir, forest–steppe zone	42	0.916
Saratov Reservoir, forest–steppe zone	71	0.957
Saratov Reservoir, steppe zone	16	0.845
Volgograd Reservoir, desert steppe	87	1.0
Lake Elton, desert steppe	24	1.0

(De Caceres et al., 2012), i.e., the fraction of samples from each zone where at least one indicator species was revealed. Its use made it possible to establish that the taxocenes of Lake Elton and the Volgograd Reservoir are more localized (C = 1) than those of the steppe zone of the Saratov Reservoir (C = 0.845).

The coefficients of association, F_{ik}, which were calculated for these species and based only on the frequencies of occurrence, largely showed similar results: the Pearson coefficient of correlation between IndVal and F was $R = 0.927$. However, there were also some differences in the results (approximately 10%) and the coefficients of association were statistically insignificant ($p > 0.05$) or indicated different geographical distributions in this case. The article by De Caceres et al. (De Caceres et al., 2012) discusses the causes of such differences and provides recommendations on conditions in which it is reasonable to use a certain fidelity criterion.

To separate the true diagnostic species of one zone from the species that are simultaneously related to several zones, we implemented the brute force algorithm of combining them into groups from two, three, or four species and recalculated the indicator value indices, IndVal, for each variant of sample separation. This scheme of calculations revealed that 86 species should be considered as species that are characteristic of different combinations of zones. For instance, *Procladius choreus* is a significant indicator of a combination of two zones, Sar/fs + Sar/st ($p = 0.003$), although it is statistically insignificant for each of them ($p > 0.053$).

The IndVal-based lists of diagnostic species and their spatial distribution in the small and medium rivers of the Middle and Lower Volga basin significantly correspond to their ecological characteristics, which was previously described in detail (Zinchenko, 2011).

During the implementation of the Apriori algorithm, we set the threshold values of $\mathrm{Sup}_0 = 0.01$ and $\mathrm{Conf}_0 = 0.6$; i.e., each species combination being identified should occur in at least 12 samples taken from the respective zone and this number should be not less than 60% of cases of the total occurrence of the left part of the association rule throughout the set of observation. A total of 8703 association rules met this condition; some of them are given in Table 3. For instance, the paired combination of the species *Monodiamesa bathyphila* and *Prodiamesa olivacea* occurred in $0.031 \times 1158 = 36$ samples from the rivers of the forest–steppe zone of the Saratov Reservoir, which was 92.1% of the total occurrence of this combination. A useful indicator of the rule value is the lift presented in Table 3; it shows how many times the frequency of the combination of species is higher in samples associated with group $\mathcal{C}$ than in all the other samples: $\mathrm{Lift}_j = \mathrm{Conf}_j = \mathrm{T}_k$.

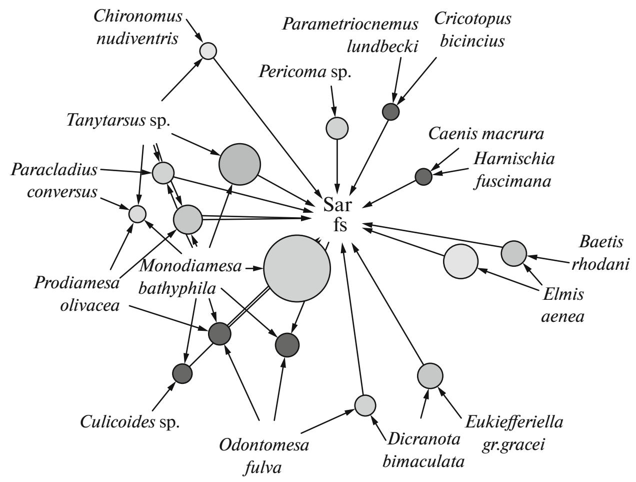

Fig. 2. Visualization of the 16 best rules in the form of a graph that are associated with middle and small rivers of the forest–steppe zone of Saratov Reservoir.

It is convenient to present a set of selected rules that combine the most frequently occurring combinations of species in the form of the oriented graph. An example of this graph for the small rivers of the forest–steppe zone of the Saratov Reservoir is given in Fig. 2. The sizes of circles of each node are proportional to the level of support, Sup_j, of the respective rule and the color depth is proportional to the value of the lift, Lift_j.

It should be noted that each of the zones under consideration, except Lake Elton, has a wide range of local biotopical conditions that determine the set of habitats of different hydrobiont taxocenes. Hydrological and hydrochemical characteristics, such as river width, current velocity, soil type, water quality, and mineralization, vary for many watercourses from different geographical regions. However, it can be assumed that the calculated diagnostic value of the greater part of species is primarily determined by the latitudinal natural climatic gradient. In addition, one cannot disregard that the localization of the occurrence of some taxa may be determined by factors of evolutionary history, landscape features, the presence of barriers to invasions, etc.

We also believe that the identified combinations of the most frequently co-occurring species have a significant statistical value rather than being a result of the biotic relationships between them.

In this study, we calculated diagnostic indices by grouping samples according to the zonal principle. Methodologically, these calculations are also identical for more detailed gradations, which identify separate watercourses or their biotopes.

Table 3. Most frequently occurring combinations of species of bottom communities that are associated with geographical regions of the Middle and Lower Volga region

Species name	Sup	Conf	Lift
Kuibyshev Reservoir			
Procladius sp., *Limnodrilus* sp.	0.014	0.941	8.32
Cryptochironomus gr. *defectus*, *Procladius* sp.	0.010	0.846	7.48
Isochaetides michaelseni, *Limnodrilus* sp.	0.010	0.733	6.48
C. gr. *defectus*, *Procladius* sp., *Limnodrilus* sp.	0.010	1.0	8.84
Saratov Reservoir/forest–steppe zone			
Tanytarsus sp., *Dicranota bimaculata*	0.035	0.847	3.66
Paracladius conversus, *Tanytarsus* sp.	0.035	0.709	3.06
Prodiamesa olivacea, *Tanytarsus* sp.	0.035	0.780	3.36
Monodiamesa bathyphila, *P. olivacea*	0.031	0.921	3.97
M. bathyphila, *Tanytarsus* sp.	0.028	0.968	4.18
Cricotopus bicinctus, *Dicranota bimaculata*	0.027	0.833	3.59
Odontomesa fulva, *P. olivacea*	0.023	0.838	3.62
C. bicinctus, *Procladius ferrugineus*, *Tanytarsus* sp.,	0.022	0.735	3.17
Saratov Reservoir/steppe zone			
Chironomus plumosus, *P. ferrugineus*	0.111	0.767	1.90
P. ferrugineus, *Limnodrilus hoffmeisteri*	0.086	0.730	1.8
Ch. plumosus, *Polypedilum bicrenatum*, *P. ferrugineus*	0.080	0.778	1.92
Polypedilum bicrenatum, *Tubifex tubifex*	0.063	0.760	1.88
Ch. plumosus, *P. bicrenatum*, *T. tubifex*	0.063	0.752	1.86
P. ferrugineus, *Tubifex tubifex*	0.061	0.761	1.88
P. bicrenatum, *L. udekemianus*	0.059	0.792	1.96
Ch. plumosus, *L. hoffmeisteri*, *Limnodrilus* sp.	0.059	0.833	2.06
Ch. plumosus, *P. bicrenatum*, *P. ferrugineus*, *L. hoffmeisteri*	0.042	0.779	1.93
Volgograd Reservoir			
Cricotopus gr. *sylvestris*, *Paratanytarsus* sp.	0.019	0.617	11.3
P. nubeculosum, *Caenis robusta*	0.018	0.91	16.62
C. gr. *sylvestris*, *P. nubeculosum*, *Paratanytarsus* sp.	0.016	0.72	13.1
C. gr. *sylvestris*, *P. nubeculosum*, *C. robusta*	0.015	1.0	18.2
Lake.Elton			
Palpomyia schmidti, *Cricotopus salinophilus*	0.059	1.0	5.07
C. salinophilus, *Ephydra* sp.	0.039	1.0	5.07
Microchironomus deribae, *Tanytarsus kharaensis*	0.032	1.0	5.07
Culicoides sp., *C. salinophilus*	0.032	1.0	5.07
Chironomus salinarius, *Ephydra* sp.	0.025	1.0	5.07
P. schmidti, *Ch. salinarius*, *C. salinophilus*	0.025	1.0	5.07
Ch. salinarius, *C. salinophilus*, *M. deribae*, *T. kharaensis*	0.014	1.0	5.07

Sup, support, Conf, confidence, Lift, lift.

CONCLUSIONS

The species composition of bottom communities in small and medium rivers has a clear pattern of variability, depending on the latitudinal gradient of natural climatic conditions. However, its general continuous nature may be sharply disturbed due to the heterogeneity of environmental conditions and natural landscape features. For instance, the isolation and high mineralization of the rivers of the basin of Lake Elton have led to the emergence of bottom communities with a unique taxocene. On the whole, the observed spatial transformation of the species composition against the background of the succession of natural climatic zones can be characterized as a discontinuous (or accentuated) latitudinal gradient.

The use of diagnostic value indices, which take into account different frequencies of species occurrence in different biotopes, is an effective method of estimating the spatial variability in the taxonomic structure of communities. The lists of diagnostic species formed show the natural transition of the cenotic role from some key taxa to others in the sequence of watercourses of the basins of the reservoirs of the Volga cascade.

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