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WATER QUALITY AND PROTECTION:
ENVIRONMENTAL ASPECTS

Statistical Analysis of Structural Variations of Benthic Communities and Testing the Hypothesis of River Continuum

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Abstract—Statistical methods for assessing the spatial distribution of benthic communities in different parts of watercourses have been considered as applied to lowland rivers of the Lower Volga region. The applicability domains are described for different response models, gradient analysis, and random skewers methods, which are used to analyze the distribution of aquatic organisms in bottom sediments. Stationarity and autocorrelation criteria for the description of generalized characteristics of macrozoobenthos communities are analyzed. The problems of identification of statistically significant isolated zones at whose boundaries the succession change of the species composition of aquatic organisms are discussed. The results of nonparametric dispersion analysis of species similarity matrices, the formation of dendrites, and the search for barriers between individual areas are given (based on Delaunay triangulation and Monmonier's maximal-diversity algorithm).

Keywords: river continuum, patch dynamics, macrozoobenthos communities, spatial distribution, identification of characteristic zones, statistical models

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INTRODUCTION

Assessing the regularities in the distribution of aquatic organism communities along the longitudinal profile of water streams is a fundamental problem of ecology and hydrobiology. The main role in such processes belongs to the regular variation along the river channel of the main hydrological and landscape–topographic factors (primarily, flow velocity), which determine the rate and extent of bank erosion and abrasion, transformation of channels and shallows, accumulation of eroded material, and many other physicochemical characteristics. The watercourse can be considered as an integral ecosystem based on the river continuum concept [27], according to which the species structure of communities is a continuous series of ecomorphs, where a regular change of dominant complexes takes place. The specific set of environmental factors in combination with the features of interspecific competition determine, in each segment of the continuum, the combination of environmental conditions for the formation and development of stable associations of aquatic organisms in accordance with the functions, availability of necessary resources, and the adaptation ability of each species.

At the same time, the general continuum regularity in a watercourse is a background for the development of local biotopic variations (of hydrodynamic regimes, light intensity, soil characteristics, temperature differentials, etc.), which determine the mosaic character of the distribution of aquatic organism populations. The patch dynamics concept [25, 28] emphasizes the dynamic character of such microperturbations and focuses on the significance of stochastic ecological fluctuations, under effect of which the formation of species diversity of riverine communities is largely stochastic. The concept of functional zones [24] is based on the trivial assumption that, based on the combination of hydrological, landscape, hydrochemical, and other factors, isolated hydrogeomorphological domains can be identified in a riverine ecosystem, which determine the species and functional composition of aquatic organism communities.

As far as the existence conditions in the upper, middle, and lower reaches in any river are radically different [1], the studying of specific watercourses commonly involves the acceptance of one of three mutually exclusive scientific hypotheses: (1) the species structure of communities continuously and regularly changes from the source to the mouth; (2) the distribution of species along the river is random; and (3) detached process domains [18], each having a homogeneous species composition but significantly differing from the others, can be identified in the river. The notion of hypothesis is used here in the statistical context, i.e., both the deterministic and stochastic components of variability of communities are assumed present in any river to some extent [2]. However, it is of importance to establish whether the established specific regularities differ (overall and with statistically significance) from a random process of formation of communities [10]. Another hypothesis to be checked, which is associated with the assessment of the spatial heterogeneity of the community, determines the barriers (or boundaries) between watercourse segments at which the species composition of aquatic organisms shows abrupt characteristic changes.

The verification of the above assumptions consists of the generalization of representative sets of empirical data and the analysis of combinations of factors and conditions that determine the taxonomic organization of communities. Unfortunately, the publications mentioned here fail to propose a clear procedure for the selection and processing of key characteristics, and one of a few attempts of statistical assessment of the dependence of species diversity of macrozoobenthos communities on the intensity and frequency of perturbations [26] is not convincing.

This study gives a detailed review of various statistical methods for the analysis of the spatial structuredness of aquatic ecosystems and illustrates the applicability and soundness of such methods by the case of benthic organisms community of a typical medium-size lowland river in the forest-steppe zone in the Lower Volga region. The notion of *ecological succession* is introduced, which is to be understood as a "series of sections" of the ecosystem's state along the longitudinal profile of the river from its source to estuary. In a hydrographic network, such successions can have a complex hierarchical structure (unlike the conventional linear cenotopoclines, which are used in gradient analysis). The proposed analysis of successions for watercourses differs from spatial biogeographic models by the directed character of the identified sections when considered in the direction from the source to the mouth.

MATERIALS AND METHODS

The spatial and hydrological heterogeneity of aquatic ecosystems is often governed by the geometric characteristics of the channel network. According to the network dynamics hypothesis [8], small and medium-size rivers are to be studied in the context of the totality of individual streams, which interact at their confluence, where abrupt differentials in water level, sediment accumulations, and other perturbations may occur. To assess the effect of this factor, the Sok R. and its tributary, the Baitugan R. were chosen as a study object.

The Sok R. (375 km in length) is a typical free-flowing lowland river with water of II–IV quality classes, which empties into the Saratov Reservoir upstream of Samara. The Baitugan (22 km in length) is a spring-fed river of piedmont type, which originates in the spurs of Bugul'minsko-Belebeevskaya upland, empties into the Sok R. (in its upper reaches), and belongs to reference watercourses in terms of its water quality. The examined river system incorporates a wide diversity of biotopic and landscape elements.

The objects of study are macrozoobenthos communities, whose individual taxa show recognized bioindication properties and are known to be the most stable and diverse components of lothic ecosystems [4]. The source material includes benthos samples taken at 22 permanent observation stations in summer in 1990–2007. The results of processing 147 hydrobiological samples were used to choose 375 species and taxonomic groups of benthic organisms for statistical analysis [5].

In the analysis of hydrobiological survey data, the examined river system was divided into 13 ecologically homogeneous areas (4 areas were in the Baitugan R.) with sample numbers of 10–14. The taxonomic composition of macrozoobenthos in the areas was evaluated by three characteristics: the species diversity, the occurrence frequency in samples, and the mean logarithm of the abundance of organisms of each species. The effect of environmental factors was assessed with the use of mean median values of hydrological and Hydrochemical characteristics for each area, as well as their biotope characteristics (Table 1).

GRADIENT ANALYSIS AND RANDOM SKEWERS METHOD

Direct gradient analysis is based on statistical methods for the search of an unknown function f, describing the dependence of species abundance Y on the characteristics of the influencing factors X_i:

$$Y = f(X_i) + \varepsilon,$$

where ε accounts for the effect of random perturbations. The conventional model of response Y implies a symmetric shape of the Gaussian bell curve (GAUS), thus allowing the ecological optimum μ and the tolerance range $\pm 2\sigma$ (or the niche volume) to be determined for each species and the strategy of its adaptation to the ambient conditions to be assessed.

The modern studies [13, 19] extended the knowledge about the character of these relationships and provided procedures for flexible choice of best models of response curves. These include generalized linear (GLM) and generalized additive (GAM) regression models, of which the Gaussian model is a particular case. Of particular interest is Huisman–Olff–Fresco (HOF) model [14], an example of hierarchical combination of five models with increasing complexity: (I) a plateau (no response); (II) monotonic growth; (III) monotonic growth with a plateau; (IV) response (in the form of a Gaussian); (V) asymmetric unimodal response.

Single-factor gradient analysis based on a single environmental parameter is an anachronism. The values of a complex spatial gradient X, which generalizes the entire set of parameters describing changes in the environmental conditions in the medial and rithral zones of watercourses, can be obtained with the use of principal component method [5, 6, 9], which forms a

Table 1. Results of the analysis of the principal components of environmental factor (set in bold are the factors that show a statistically significant correlation with principal components)

Raw characteristics	Relative loads of Raw variables in the principal components	
	component 1	component 2
Stony substrate share	**0.154**	0.027
Elevation a.s.l.	**0.149**	0.116
Depth at the sampling site	**–0.148**	0.038
Percentage of silty substrates	**–0.149**	–0.034
Nitrite nitrogen	**–0.132**	0.046
Water temperature	**–0.157**	0.041
Bottom water pH	–0.112	–0.018
Mineral phosphorus	–0.123	**–0.226**
Flow velocity	0.078	**–0.312**
Watershed area	0.014	**–0.332**
Bichromate oxidability	–0.016	**–0.291**
Oxygen content	–0.050	**0.276**
The share of overall variations of characteristics accounted for by the component, %	49.4	18.9

small number of optimal orthogonal axes, oriented in the direction of maximal statistical variability of original variables. The new latent factors can have some internal unity, allowing some biological meaning to be attributed to them.

The principal component method was used to generalize 12 different hydrological, geomorphological, and Hydrochemical characteristics of the Baitugan–Sok ecosystem and to show that the passage to two factor axes leads to a loss of not more than 32% of the original information, which mostly represents stochastic noise. The first factor (Table 1) is obviously associated with the spatial variability of conditions and combines the elevation above sea level, as well as water depth and temperature at the sampling site, soil variability, etc. The geographic distribution of the observation stations can be superimposed, almost unchanged, on the scale of factor 1 (Fig. 1a), a fact that determines the choice of this axis as a complex longitudinal gradient *X*. The second factor, after the removal of spatial variations, determines the local fluctuations of organic pollution and water saturation with oxygen. Of great importance here is also the area of the watershed as a source of organic matter.

Various response models (GAIUS, HOF, GLM, GAM) were used to assess the character of variations of the abundance of organisms for each type of zoobenthos on the scale of complex spatial gradient *X*. Simultaneously, the statistical significance of this correlation was verified using Monte-Carlo procedure, which restores the distribution of all possible values of Kendall coefficient of rank correlation τ between the ecological characteristics of benthic communities and factor 1. Only 43 macrozoobenthos species out of 375 (16.8%) are shown to have statistically significant correlation with the longitudinal gradient of the watercourse. For a considerable number of species with rare occurrence, the distribution along the gradient cannot be considered at all, because their occurrence is of local or episodic character.

Analysis of models of longitudinal distribution of aquatic organisms in the watercourse revealed their fundamental distinction from the main concepts of gradient analysis, which is conventionally oriented to geobotanic notions. The classical unimodal shape of the response curve with a maximum in the middle of the scale of longitudinal gradient *X* was found to be characteristic only for a set of species, which has a wide range of tolerance to abiotic factors; this set of species is few in number and of little interest in terms of bioindication. Gaussian model with different degrees of asymmetry can be accepted only for seven macrozoobenthos species (Polypedilum nubeculosum, Paratendipes albimanus, Cricotopus gr. sylvestris, etc.). In some cases, different response models yielded radically different diagnostics (Paracladius conversus) or the obtained distribution had indefinite, multimodal shape (Baetis rhodani, Fig. 1b).

Of much greater importance in terms of bioindication were found to be the species of benthic fauna with maximal occurrence at both ends of the scale of gradient *X*, their response models showing a specific sigmoidal character. Sigmoids with maximums in the right part of the scale *X* encompassed structure-forming taxa (Prodiamesa olivacea, Eukiefferiella gr. gracei, Parametriocnemus lundbecki, Eukiefferiella claripennis, Odontomesa fulva, Parametriocnemus sp.), typical of a reophilic complex of benthic communities

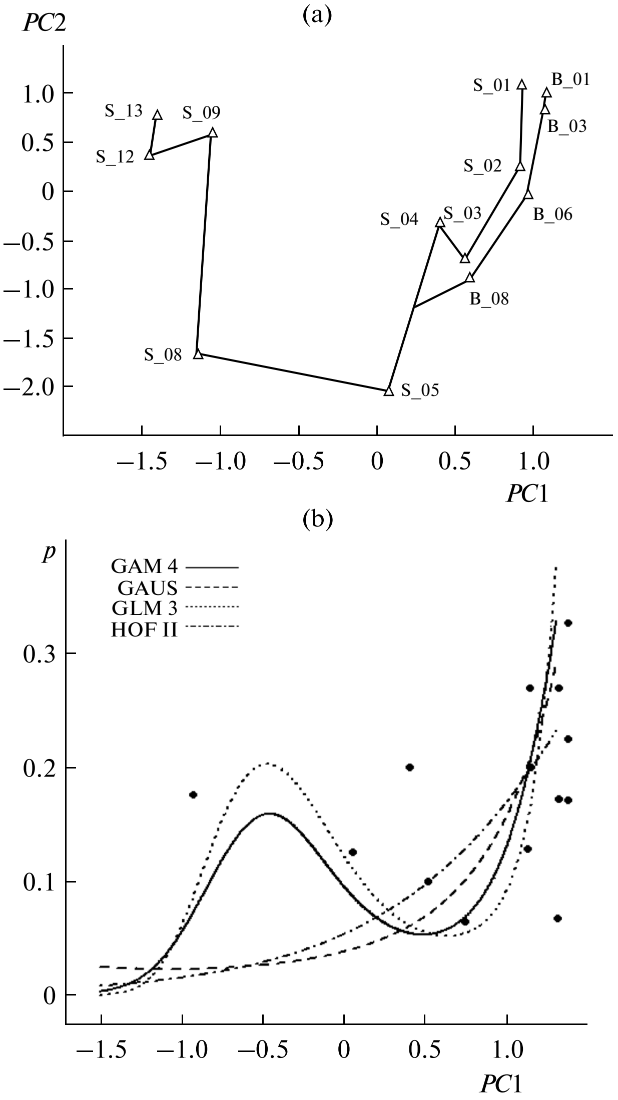

Fig. 1. (a) Location of the areas of the Sok and Baitugan rivers in the space of two principal components *PC*1 and *PC*2 and (b) models of occurrence probability distribution *p* of chironomids Baetis rhodani on the scale of complex spatial gradient *PC*1; here and in Fig. 3, labels for areas of the Sok R. are given with prefix "S," and those for the Baitugan R., with prefix "B."

of the Baitugan R. and the upper reaches of the Sok R. On the other hand, an S-shaped curve with a maximum in the left part of scale X was typical of pelophilic and limnophilic species (Chironomus obtusidens, Pisidium amnicum, Microchironomus tener, Ablabesmyia monilis, Dicrotendipes nervosus, Euglesa henslowana, Dikerogammarus haemobaphes), a feature, which is attributed to the effect of factors of decreasing flow and silting of the Sok R. in its lower reaches.

Pielou **random skewers method** [20, 21] provides an objective assessment of the statistical significance of the deterministic tendency in changes in the structure of the community as a whole along the examined spatial gradient. The results of monitoring are represented in the form of a table, whose lines correspond to *s* detected species and columns, to *m* identified segments of the watercourse, the cells containing the mean abundance of each species. Each column is assigned an ordinal number or rank, r_i ($i = 1, 2, ..., m$), which determines the position of the are on the gradient from the source to the mouth in accordance with Fig. 1a. The data in the table are interpreted as a cloud of *m* points in the *s*-dimensional space of species.

A skewer, penetrating this $s \times m$-dimensional structure, is an arbitrarily oriented vector with random coordinates. Each *i*th empirical point is projected onto the straight line induced by this random vector, and the order of the obtained projections p_i ($i = 1, 2, ..., m$) is determined. Kendall's rank correlation coefficient τ between number sets r_i and p_i is determined: if its value is close to 1 (or −1), the conclusion is made that some multidimensional profile of the benthic community, determined by the skewer direction, is regularly ordered along the longitudinal gradient of the watercourse.

Pielou random skewers test was applied to data on the occurrence of 129 macrozoobenthos species recorded in three or more areas (Fig. 2a) and, separately, for 66 taxa, belonging to chironomid family (Fig. 2b). The procedure of skewering of the set of points was repeated 300 times, and the frequency distribution of all obtained values of the coefficient of rank correlation τ was formed. The null hypothesis tested consisted in that the obtained unimodal distribution has an expectation $\tau \cong 0$ (implying that the cloud of points has no enough directions with respect to which the empirical data are arranged along the examined gradient). The calculated confidence intervals for the τ distribution centers did not include the value 0 (Fig. 2), allowing the null hypothesis to be rejected for both communities under study.

ANALYSIS OF ECOLOGICAL SUCCESSIONS

The ecological succession can be interpreted as a directed series of independent variables *Y*(*r*), taking random values in discrete points of space *r*. Important parameters of the succession, as well as any random process, are expectation $m_Y(r)$, variance $D_Y(r)$, and autocovariation. The focus of analysis of successions is to test a stationarity hypothesis for the process, in which case, the above probabilistic characteristics remain unchanged all along the trajectory of points, and data variations in the series is determined by a random component ε_r of the type of white noise.

The nonstationarity of ecological data commonly has the character of random walk $y_r = \rho y_{r-1} + \varepsilon_r$, random walk with a drift $y_r = \alpha + \rho y_{r-1} + \varepsilon_r$, or a combination of random walk with a linear trend $y_r = \alpha + \rho y_{r-1} + \mu r + \varepsilon_r$. The null hypothesis for Dickey–Fuller test [11] consists in that the series is not station-

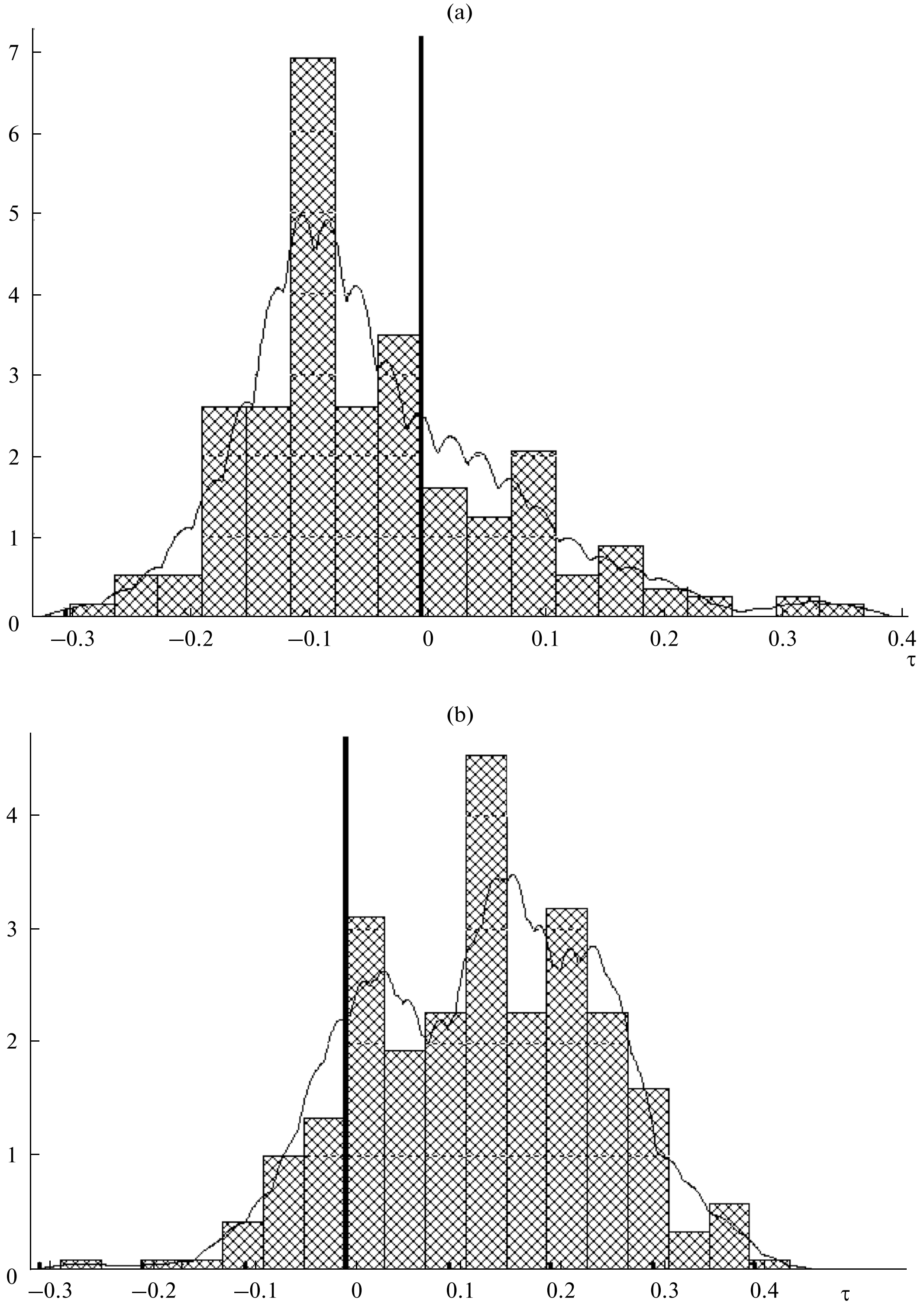

Fig. 2. Histogram of the distribution of Kendall rank correlation coefficient τ, obtained in 300 iterations by random skewers method, including: (a) for 129 macrozoobenthos species (the right confidence boundary of the mean $m + ts_m = -0.04 + 1.96 \times 0.0065 = -0.027$, m is the mean, s_m is the error of the mean, t is Student test value at 5% significance level), (b) for 66 Chironomidae taxa (left confidence boundary of the mean $m + ts_m = 0.13 - 1.96 \times 0.0067 = 0.119$).

Table 2. Estimates of correlation and stationarity of series of benthic community characteristics in the areas in the Sok–Baitugan riverine ecosystem (numbers in square brackets are the values of p-probability, corresponding to the statistic being tested; given in bold are the case when the null hypothesis was rejected)

Ecological and statistical characteristics	Total species	Mean number of species in a sample	Shannon diversity index	Number of organisms of all species (ln)	The share of predator–seizers, %	The share of Diamesinae + Orthocladiinae (d_D), %
Minimal value area	49 (S_01)	4.23 (B_08)	3.07 (B_08)	127 (S_01)	7.2 (B_03)	4.0 (S_12)
Maximal value area	102 (B_03)	8.91 (S_04)	4.80 (B_03)	343 (B_06)	28.8 (S_05)	35.7 (S_02)
Pearson correlation coefficient	0.13 [0.66]	0.144 [0.63]	–0.075 [0.8]	0.164 [0.59]	–0.333 [0.26]	0.915 **[≅0]**
Kendall rank correlation coefficient	0.156 [0.46]	0.09 [0.66]	0.077 [0.71]	0.18 [0.39]	–0.384 [0.07]	0.59 **[<0.01]**
Dickey–Fuller test (drift model)	–2.33 [0.178]	–2.67 [0.108]	–3.51 [**0.028**]	–2.57 [0.124]	–0.703 [0.809]	–3.36 [**0.035**]
Dickey–Fuller test (linear trend)	–2.08 [0.498]	–2.52 [0.314]	–3.29 [0.119]	–2.32 [0.393]	–1.87 [0.602]	–4.25 [**0.032**]
Dickey–Fuller test (first differences)	–3.26 [**0.044**]	–4.39 [**0.008**]	–4.55 [**0.006**]	–3.47 [**0.031**]	–6.34 [**0.0005**]	–4.26 [**0.009**]
Ljung–Box Q-statistics	1.55 [0.21]	0.467 [0.494]	0.090 [0.764]	0.713 [0.398]	0.043 [0.835]	7.30 [**0.007**]

ary and has a single unit root H_0: $\rho = 1$, $\mu = 0$. The hypothesis is tested by evaluating a criterion $t = (\rho - 1)/s_{\varphi}$, which is compared with tabulated critical values t_{crit} obtained by Monte-Carlo method: when the t-statistics is not significant and the corresponding p value is >0.05, the null hypothesis is accepted and the series is declared nonstationary.

To check the autocorrelation of ecological successions, Ljung–Box Q-statistics [15] was used: when its sample value was in excess of the 95% quantile of $\chi^2(m)$ distribution, the succession $Y(r)$ is declared to have autocorrelation (up to the mth order). Parallel to that, the share of spatial covariation in empirical data was evaluated by Moran's I index, widely used in biogeography [23] and, similar to the correlation coefficient, varying within –1 to +1. The greater I, the more similar are the ecological objects located near one another in the space with the similarity level decreasing with increasing distance.

To illustrate the river continuum theory and patch dynamics, their authors commonly used generalized indices, related to structural–functional characteristics of the communities: species diversity, coefficient P/B, the relationships between individual taxonomic or trophic groups, etc. in the analysis of succession of areas for the Baitugan and Sok rivers, the dynamics of variations of six major generally accepted characteristics of the state of benthic communities was assessed (Table 2).

In the context of conventional correlation analysis, Pearson's linear correlation coefficients and Kendall's rank correlation coefficients τ were evaluated between the generalized characteristics and the longitudinal gradient scale *PC*1 (Fig. 1a) and p-values were evaluated, reflecting the significance of the divergence of those coefficients from the values simulated by bootstrap method at a random distribution of observation data over the watercourse. Statistically significant deterministic relationship with the longitudinal gradient was found to exist only for the share d_D of chironomids of Diamesinae + Orthocladiinae in the total number of benthic organisms, which gradually decreases from the source to the mouth. For other characteristics, null hypothesis is accepted, implying the absence of dependence of the entire community as a whole on the spatial factor.

Analysis of stationarity with respect to steady drift with the use of Dickey–Fuller test has shown (Table 2) that four series of presented characteristics out of six correspond to random walk model, suggesting the absence of any spatial ecosystem regularities. However, the dynamics of two series (Shannon diversity index and the share d_D of chironomids Diamesinae + Orthocladiinae) was found to be stationary, while the statistically significant value of t-criterion relative the function of linear trend for d_D suggests this relationship to have a relatively smooth monotonic shape. The same relationship for Shannon index is of quasiperiodic character, as can be seen from the nonstationarity of this series relative to linear trend. Dickey–Fuller test for series composed of first-order differences clearly shows them to be stationary, a fact that rejects the hypothesis regarding the existence in the watercourse of abrupt differentials and patch dynamics with respect to characteristics of macrozoobenthos communities.

Analysis of Ljung–Box statistics and autocorrelograms of Moran index revealed the absence of autocorrelation for five series of generalized ecological characteristics. Only the autocorrelation spectrum of the share of chironomid taxa d_D was found to have a high statistical significance and moderate curvature, characteristic of monotonic relationships.

ANALYSIS OF SPECIES STRUCTURE WITH THE USE OF SIMILARITY METRICS

The continuity of the spatial structure of communities along the watercourse corresponds to the null hypothesis, suggesting that the community is homogeneous and has no statistically significant barriers (boundaries) separating isolation zones. More precisely, the values of the occurrence frequency of a complex of species in nearby river segments, taken together, show no statistically significant differences. Conversely, the alternative hypothesis will suggest that abrupt changes in the species composition can take place at the boundaries of such segments.

The following statistical procedures were implemented with the use of Bray–Curtis metrics, evaluating the distance between two species compositions s and i in an s-dimensional space as j: $d_{ij} = \dfrac{\sum_{k=1}^{s} |a_{ik} - a_{jk}|}{\sum_{k=1}^{s} a_{ik} + \sum_{k=1}^{s} a_{ik}}$, where s is the total number of species, a_{ik} and a_{jk} are the logarithms of the abundance of the kth species, $k = 1, 2, ..., s$. Two distance matrices were formed: D_p with a size of 147 × 147 for each pair of hydrobiological samples and D_r with a size of 13 × 13 for the pairwise comparison of watercourse segments.

Nonparametric multidimensional dispersion analysis (npMANOVA) [7] provides statistical estimate of the effect of the spatial factor of habitat grouping for areas with the use of species similarity matrix D_p. In this case, the distribution centers of the values of d_c within each group and their between-group contrasts are found with the use of Monte-Carlo methods. The null hypothesis, regarding the absence of the effect of the grouping factor, is also tested in the process of randomization of matrix D, whose elements have been many times randomly mixed relative the identified groups.

Procedure npMANOVA was applied to check the significance of the spatial grouping factor in three variants: (a) the entire watercourse was divided into 13 segments; (b) the segments were combined to form three large fragments of the ecosystem (two parts of the Sok R. in its upper and lower reaches and, separately, the Baitugan R.); (c) a scheme of hierarchical two-factor analysis, including both grouping levels mentioned above was used. In this case, a statistically significant variations of the species composition were found to exist both between the replications at both levels and between the segments within individual large areas. However, the use of multiple comparison method (between-group contrasts) showed that the variation of species structure is mostly determined by variations of benthic communities for pairs of segments most remote from one another within each watercourse area.

Graph-analytical method [5] utilizes a representation of matrix D in the form of a dendrite (adjacency graph with maximal weights), whose nodes correspond to watercourse areas and edges correspond to the values of Bray–Curtis metrics d_{ij} for each pair i and j of adjacent nodes of the graph. If the passage from one point of the ecological succession to another is accompanied by the replacement of a considerable number of species by other taxa and the distance d_{ij} is large, it is reasonable to assume that structural changes of succession character take place in the community [12]. The possible gaps in the continuities were found with the help of a randomization procedure [5], which evaluates, for each graph edge, the statistical significance (p_{ij}) of the excess of d_{ij} over the analogous value in the case of a random distribution of species over the areas.

The analysis of dendrite components for the simulated watercourse has shown that the species composition of adjacent areas mostly showed no significant differences, though three characteristic gaps were recorded at the inflow site of the Baitugan R., as well as at stations in the upper {S_01–S_03} and lower {S_09–S_12} reaches of the Sok R.

Barrier detection algorithm [16] also belongs to the class of problems of isolation by distance, but it uses geometric approaches applied in biogeography, which evaluate variations of the community species structure in real geographic coordinates. With this in view, the spatial configuration of the areas was approximated by a triangular network with the use of Delaunay triangulation and each link of the network was associated with the values of the matrix of species distances D, calculated by the data of hydrobiological survey. The boundary of domains along which the distance between nearby pairs of ecological objects are maximal was found by the Monmonier maximal-diversity trial-and-error search algorithm [16], which evaluates the statistical significance of the evaluated barriers based on a randomization test.

The boundaries of the characteristic zones in the system of watercources found with the use of Monmonier algorithm does not contradict the results obtained by the graph-analytical method. The first main boundary (Fig. 3) separates the part of the watercourse upstream of station S_5 from areas situated further downstream in the Sok R. (the mean boundary distance $d = 0.674$). The boundary ranking second, isolates as a characteristic zone the entire domain of the Baitugan R. ($d = 0.635$). The position of the third

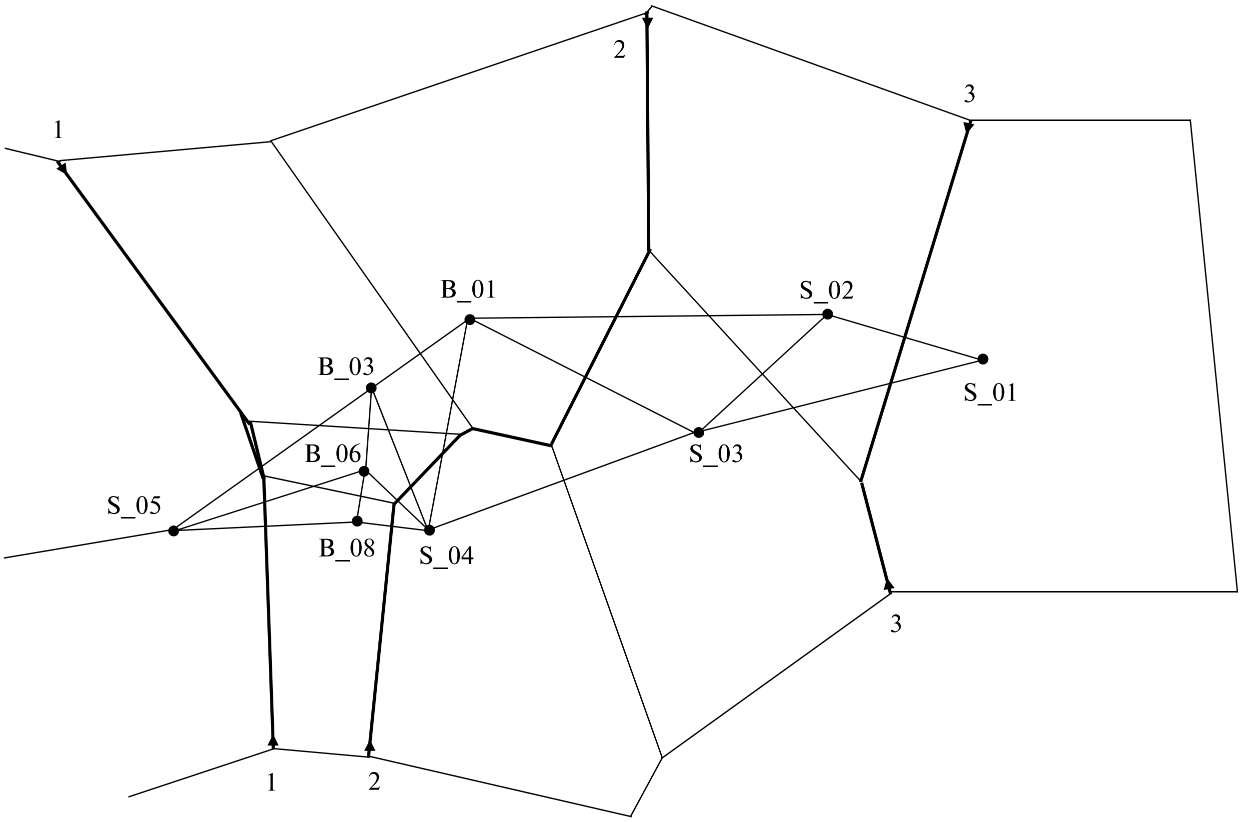

Fig. 3. Identification of barriers (thick lines with ordinal digital denotations) between individual isolated parts of benthic communities for the Baitugan–Sok ecosystem with the use of Delaunay triangulation and Monmonier algorithm.

boundary emphasized the specific biotopic conditions at shallows in the area S_1 of the Sok R.

DISCUSSION OF RESULTS

The concepts of riverine continuum or patch dynamics in the publications of the recent 25 years [2, 24–27] are commonly presented as theoretical substantiations, not accompanied by the processing of large bodies of empirical data based on strict procedures of statistical testing of hypotheses. Since each aquatic organism species has an individual life strategy, ecological optimum, and a tolerance range, hence a specific character of the distribution over the longitudinal profile of the watercourse, it remains unclear which characteristics of communities are to be used for assessing the continuum property: the occurrence dynamics of individual, subjectively chosen species; generalized functional characteristics; complex abundance/diversity criteria; or something other.

The single-factor gradient analysis is informative and reflects a well interpretable spatial probability distribution of the occurrence of individual species over longitudinal river profile (Fig. 1b). Some methodological difficulties in this case are mostly due to the uncertainty of criteria for the choice of the most adequate model [17]. However, when discussing the general regularities of river continuum (or patch dynamics), one has to consider the joint response to changes in the environmental factors for the entire aquatic organism community of the lothic system as a whole, consisting of a complex system of ecologically interrelated components.

A question now is which generalized parameters of ecosystems should be used in this case. The example of benthic communities was used to show that the conventional diversity characteristics of a cenosis (the number of species, Shannon index, etc.) are meaningful only for watercourses that show abrupt changes in their environmental conditions (e.g., powerful local anthropogenic impact). In the trivial case, the use of those indices, based on averaging, is not fully correct: Shannon species diversity index on the four main components of the ecosystem (the Baitugan and Sok rivers in their upper, middle, and lower reaches) vary insignificantly—from 4.26 to 4.8—however, in each case it is based on the radically different species complexes. The limitation of such analysis to individual organism groups with high bioindication properties, e.g., chironomids Diamesinae + Orthocladiinae, can radically change the conclusion regarding the existence of nonrandom regularities in their spatial distribution.

For the same reasons, the application of Pielou random skewers method to the full species space leads to uncertain results as compared with the analysis of individual functional or taxonomic groups [20]. Such conclusion can also be derived from Fig. 2; however, the successive division of the community into groups will sooner or later bring us to the level of a species, at which the random skewers method will turn into a worsened version of gradient analysis.

The present-day biogeography and the theory of time series analysis show considerable achievements in simulating one-dimensional series. However, the development of effective algorithms for structural analysis, assessing the cause and effect cointegration, and goal-oriented selection of models of dynamics of noisy series with large dimension (in this case, the joint population density of 200–300 species in the community under study) for this scientific field is a problem of indeterminate future. This implies the need to develop nontrivial methods and algorithms for assessing ecological successions.

Analysis of species similarity matrices D in combination with up-to-date nonparametric methods for testing hypotheses (npMANOVA, dendtrite formation, the search for “barriers”) provide an objective substantiation of succession changes of species composition and enable the identification of isolated zones in the ecosystem. The further development of those ideas [22] is directed at their integration with ordination methods, which incorporate various procedures of goal-oriented projecting of the multidimensional original cloud of empirical data onto an optimal space with small dimension [3, 5, 6].

The identified gaps in the continuum and the detected barriers (Fig. 3) have a quite explicable ecological meaning. The species composition of macrozoobenthos in the Sok R. in areas S_1–S_4 and throughout the Baitugan R. is typical of the rithral zone of watercourses where the majority of faunistic diversity is due to the relatively small taxa of litho-reophilic larvae of amphibiotic insects (Diptera, Ephemeroptera, Trichoptera). Succession changes of ecoforms takes place in area S_5, and the species structure of the benthic community starts changing due to the development of taxa of eurybiont character. Additional structural features of the macrozoobenthos of estuary S_12, reflecting the domination of limnophilic benthic organisms are largely due to the transformation of the Sok R. by waters of the Saratov Reservoir.

Such phenomenon was characterized as *Anderson M. Jaccented gradient* [20], where a gradual change of the species structure from the source to the mouth is accompanied by local changes in the types of communities, caused by fluctuations of hydrological and hydrochemical characteristics. This model of variations of hydrobiocenoses can be supposed to be typical of the majority of free-flowing lowland rivers with natural hydrological regime.

CONCLUSIONS

An important component of a study of the structural and functional regularities in the formation of aquatic organism communities in lothic ecosystems is an integrated analysis of monitoring data with the use of procedures for testing statistical hypotheses. The application of nonstationarity criteria and autocorrelation of spatial series of generalized characteristics of biodiversity allows one to identify a deterministic component in the cenotic variations of empiric data sets.

Single-factor gradient analysis in combination with multivariate procedures (principal component method, nonparametric dispersion analysis, random skewers, etc.) make it possible to test the hypothesis regarding the random character of the distribution of the species composition of communities along the longitudinal profile of the watercourse.

Graph-analytical method and Monmonier’s algorithm for the search of barriers are proposed to use for the reliable assessment of the spatial heterogeneity of communities and identification of isolated zones on whose boundaries the ecosystem undergoes succession changes.

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REFERENCES

1. Alimov, A.F., *Elementy teorii funktsionirovaniya vodnykh ekosistem* (Elements of the Theory of Aquatic Ecosystem Functioning), St. Petersburg: Nauka, 2001.
2. Bogatov, V.V., Combined concept of river ecosystem functioning, *Vestnik DVO RAN*, 1995, no. 3, pp. 51–61.
3. Jongman, R.H.G., ter Braak, C.J.F., and van Tongeren O.F.R., *Analiz dannykh v ekologii soobshchestv i landshaftov* (Data Analysis in Community and Landscape Ecology), Moscow: RASKhN, 1999.
4. Zinchenko, T.D., *Ekologo-faunisticheskaya kharakteristika khironomid (Diptera, Chironomidae) malykh rek basseina Srednei i Nizhnei Volgi (atlas)* (Ecological–Faunistic Characteristic of Chironomids (Diptera, Chironomidae) in Small Rivers in the Basins of the Middle and Lower Volga: Atlas), Tolyatti: Kassandra, 2011.
5. Shitikov, V.K., Zinchenko, T.D., and Rozenberg, G.S., *Makroekologiya rechnykh soobshchestv: kontseptsii, metody, modeli* (Macroecology of Riverine Communities: Concepts, Methods, Models), Tolyatti: Kassandra, 2012.
6. Shitikov, V.K., Rozenberg, G.S., and Zinchenko, T.D., *Kolichestvennaya gidroekologiya: metody, kriterii, resheniya* (Quantitative Hydroecology: Methods, Criteria, Solutions), Moscow: Nauka, 2005.

7. Anderson, M.J., A new method for non-parametric multivariate analysis of variance, *Aust. J. Ecol.*, 2001, vol. 26, pp. 32–46.
8. Benda, L., Poff, L.R., Miller, D., et al., Network dynamics hypothesis: spatial and temporal organization of physical heterogeneity in rivers, *BioScience*, 2004, vol. 54, pp. 413–427.
9. Borcard, D., Legendre, P., Avois-Jacquet, C., et al., Dissecting the spatial structure of ecological data at multiple scales, *Ecology*, 2004, vol. 85, pp. 1826–1832.
10. Connor, E.F. and Simberloff, D., The assembly of species communities: chance or competition?, *Ecology*, 1979, vol. 60, pp. 1132–1140.
11. Dickey, D.A. and Fuller, W.A., Distribution of the estimators for autoregressive time series with a unit root, *J. Am. Stat. Assoc.*, 1979, vol. 74, pp. 427–431.
12. Fisher, S.G., Barnes, J.R., and Minshall, G.W., Succession in streams, in *Stream Ecology: Application and Testing of General Ecological Theory*, New York: Plenum Press, 1983, pp. 7–27.
13. Guisan, A. and Thuillier, W., Predicting species distribution: offering more than simple habitats models, *Ecol. Let.*, 2005, vol. 8, pp. 993–1009.
14. Huisman, J., Olff, H., and Fresco, L.F., A hierarchical set of models for species response analysis, *J. Veget. Sci.*, 1993, vol. 4, pp. 37–46.
15. Ljung, G.M. and Box, G.E.P., On a measure of lack of fit in time series models, *Biometrika*, 1978, vol. 65, no. 2, pp. 297–303.
16. Manni, F., Guerard, E., and Heyer, E., Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by "Monmonier's" "algorithm," *Hum. Biol.*, 2004, vol. 76, no. 2, pp. 173–190.
17. McGill, B.J., Strong and weak tests of macro-ecological theory, *Oikos*, 2003, vol. 102, pp. 679–685.
18. Montgomery, D.R., Process domains and the river continuum concept, *J. Am. Water Resour. Assoc.*, 1999, vol. 35, pp. 397–410.
19. Oksanen, J. and Minchin, P.R., Continuum theory revisited: what shape are species responses along ecological gradients?, *Ecol. Modell.*, 2002, vol. 157, pp. 119–129.
20. Perry, J.A. and Schaeffer, D.J., The longitudinal distributions of or riverine benthos: a river discontinuum?, *Hydrobiologia*, 1987, vol. 148, pp. 257–268.
21. Pielou, E.C., Probing multivariate data with random skewers: a preliminary to direct gradient analysts, *Oikos*, 1984, vol. 42, pp. 161–165.
22. Pillar, V.D., How sharp are classifications?, *Ecology*, 1999, vol. 80, no. 8, pp. 2508–2516.
23. Sokal, R.R. and Oden, N.L., Spatial autocorrelation in biology. 1. Methodology, *Biol. J. Lin. Soc.*, 1978, vol. 10, pp. 199–228.
24. Thorp, J.H., Thoms, M.C., and DeLong, M.D., The riverine ecosystem synthesis: biocomplexity in river networks across space and time, *Riv. Res. & Appl.*, 2006, vol. 22, pp. 123–147.
25. Townsend, C.R., The patch dynamics concept of stream community ecology, *J. North Amer. Benthol. Soc.*, 1989, vol. 8, pp. 36–50.
26. Townsend, C.R., Scarsbrook, M.R., and Dolédec, S., Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness, *J. North Amer. Benthol. Soc.*, 1997, vol. 16, pp. 531–544.
27. Vannote, R.L., Minshall, G.W., Cummins, K.W., et al., The river continuum concept, *Can. J. Fish. Aquat. Sci.*, 1980, vol. 37, pp. 130–137.
28. Yodzis, P., Competition, mortality, and community structure, in *Community Ecology*, Diamond, J. and Case, T., Eds. New York: Harper and Row, 1986.

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