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HYDROCHEMISTRY, HYDROBIOLOGY, ECOLOGICAL ASPECTS

Regularities of Spatiotemporal Dynamics of Chironomid Communities (Chironomidae, Diptera) in the Kuibyshev Reservoir

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Abstract—The dynamics of benthic communities of various reaches of the Kuibyshev Reservoir over a long-term observation period 1966 to 2016 has been has been statistically analyzed. The results of a comparison of the spatial-temporal distribution of structural indicators of chironomid (Chironomidae) communities, including the species diversity and abundance of 48 taxa based on hydrobiological survey data in nine large parts of the reservoir for different years, are presented. Nonparametric analysis of variance revealed a high statistical significance of the variability of the species composition of benthic communities under the influence of temporal and spatial factors. Using multidimensional ordination and generalized Procrustes analysis, the dynamics of the distribution of ecosystem objects (individual species and areas) in the coordinates of two latent axes of maximum variation is shown. A geometric analysis of the multidimensional trajectories of changes in the community of aquatic organisms in individual reaches for different periods of time is carried out. Similar developmental processes of chironomid communities were revealed in a longitudinal succession of reaches on the former channel and sunken floodplain, while similar structural characteristics of the Kamskiy reach and eutrophic Cheremshanskiy Bay are specific. The priority role of chironomids as the most important indicator group necessary for biotic assessment of long-term (50 years) changes in the ecological state of a large reservoir is considered.

Keywords: Kuibyshev Reservoir, bottom community, chironomid species (Chironomidae, Diptera), spatiotemporal dynamics, multidimensional statistical analysis, trajectories of changes in communities

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INTRODUCTION

The Kuibyshev Reservoir is the largest reservoir of the Volga cascade, actively used for the needs of electric energy generation, regulation of seasonal water supply, agricultural irrigation and fishing [4]. The reservoir is a powerful accumulator of surface runoff from a large area and a sink of contaminated anthropogenic wastewater. All this necessitates comprehensive monitoring of all components of the ecosystem, and such monitoring was carried out continuously from 1957 to 1992.

Large body of accumulated information is available. This actualizes the activity on mathematical analysis and the development of expert forecasts of the state of the reservoir ecosystem under different scenarios of economic development of the territory, anthropogenic loads and climatic changes [1]. The main results of mathematical processing of monitoring data on the Kuibyshev Reservoir are published in [5], where the correlation links between the hydrobiological and hydrochemical characteristics of the ecosystem are analyzed in detail. The identified mechanisms of the formation of the structure of zoobenthos communities under the influence of long-term processes of eutrophication of the reservoir were discussed earlier [2, 19]. The reservoir has a rather complex configuration with alternating lake-like expansions and narrows. This is why, the problem of identifying areas that are relatively homogeneous throughout the complex of the considered indicators is relevant. In order to solve it, a procedure for dynamic zoning of the Kuibyshev Reservoir is proposed in [7]. This procedure proposes to perform zoning based on the combination of abiotic and biotic factors using the methods of multidimensional statistics and GIS technologies.

One of the main tasks in the field of aquatic ecology is the analysis of the dynamics of ecosystems in the long-term aspect, including changes in the stability and diversity of biotic communities; speed and direction of structural deformations; identification of the leading factors determining such changes [17]. However, until recently, there were no generally accepted methods for modeling the spatiotemporal trend of ecosystems with a sufficiently large number of components (taxa, sites, and time periods). Various multidimensional methods have been proposed [13], representing the dynamics of ecosystems using ordination diagrams, on which the dots represent the taxonomic

Table 1. Distribution of average indices of species diversity of chironomid (Chironomidae) community in the reaches of the Kuibyshev Reservoir for different observation periods (*n* is the number of species; *H* is the Shannon diversity index, bits/specimen; *N* is the abundance, specimens/m^2)

By the observation periods				By the reservoir parts (reaches)				
years	*n*	*H*	*N*	reaches	code	*n*	*H*	*N*
1966	9.67	1.54	677	Volzhskiy	V	9.14	1.71	1014
1975	8.22	1.22	788	Volgo-Kamskiy	VK	6.57	1.23	601
1984	8.00	1.17	1828	Kamskiy	K	6.57	1.47	350
1992	3.56	1.03	1028	Tetyushinskiy	T	7.14	1.40	662
2002	7.67	1.65	1360	Undorskiy	UN	7.71	1.61	2128
2009	7.44	2.01	1752	Ulyanovskiy	UL	5.71	1.29	1576
2016	4.11	1.60	481	Novodevichskiy	N	8.43	1.82	1832
Average	6.95 ± 0.43	1.46 ± 0.08	1131 ± 143	Priplotinnyi	P	6.43	1.76	1140
				Cheremshanskiy Bay	Ch	4.86	0.83	873

structure of communities observed on the sites at different times. Methods of geometric analysis of trajectories were used to compare the parameters of the state of the ecosystem in different conditions by calculating the Mantel correlation between the corresponding matrices of distances [9]. And only recently, multidimensional autoregressive models and functions of joint distribution of populations have been proposed, which can be used to directly model the interaction of species and the dynamics of communities [14, 16].

The present paper examines the results of using various of the above statistical methods to identify the main regularities of the long-term (50 years) temporal dynamics of chironomid species (Chironomidae; Diptera) as indicators of the ecological state of the Kuibyshev Reservoir [3].

MAERIALS AND MEHODS

To carry out a statistical analysis, a representative sample of the abundance of various Chironomidae (Diptera) species belonging to seven time points for the period 1966–2016 was formed from the entire array of hydrobiological data concerning the state of Kuibyshev Reservoir ecosystem. The choice of the object of study was determined by long-term taxonomic and structural studies of the chironomid cenosis as indicators of waterbodies state [2], which adequately respond to the integral "environmental quality".

To ensure the homogeneity of the data and the equivalence of the sampling effort, for each of the nine sections of the reservoir ("reaches") and each of the seven time periods, four hydrobiological samples were randomly selected, in which the abundance of each species was averaged. A total of 48 chironomids species and taxa were found. The main characteristics of the reaches and the spatial-temporal distribution of the indices of species diversity are presented in Table 1 and Fig. 1.

The initial 7 × 9 × 48 table of species abundance was preliminarily transformed using the χ^2-transformation [12], which makes it possible to best take into account both the specific influence of dominant taxa with a high population density and the undoubted role of the complex of rare species in the community. The Bray – Curtis formula was used to calculate the **D** 63 × 63 matrix of distances between each pair of observations in the multidimensional species space.

The statistical analysis including fulfilling of the following tasks:

nonparametric analysis of variance npMANOVA [8], which was used to assess the statistical significance of variability in the species composition of benthic communities under the influence of temporal and spatial factors;

projection of the entire data array of the performed observations, represented by the distance matrix **D**, onto the ordination plane with two axes of the principal coordinates [13];

generalized canonical correlation analysis of the species space [15] and building on its basis a consensus Procrustes configuration [11], which compares the spatial distributions of chironomid taxa in the studied time periods;

geometric analysis of the trajectories of changes in CTA communities (*Analysis of Community Trajectories* [10]), performed for separate reaches for different periods of time.

All calculations were performed using the R version 3.06 programming environment and its additional packages vegan, mixOmics, RVAideMemoire, vegclust, and qgraph.

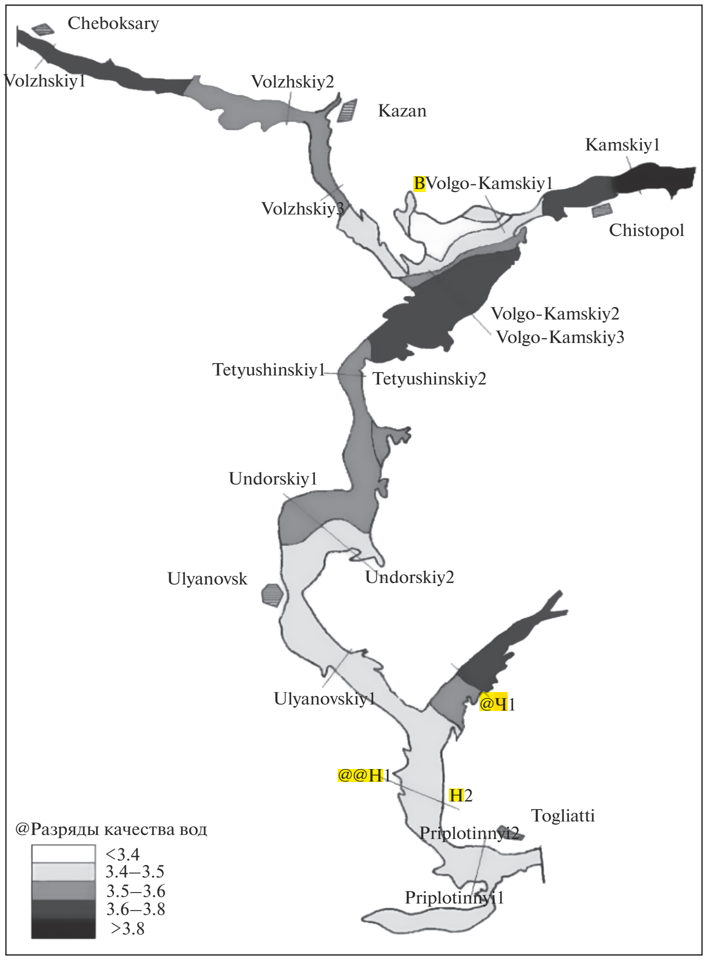

Fig. 1. Schematic map of the spatial zoning of the territory of the Kuibyshev Reservoir based on the set of ten hydrochemical and hydrophysical indicators, recalculated into a generalized category of water quality [8]; Legend of reaches—see table 1.

RESULTS

The statistical significance of the influence of spatiotemporal factors on the taxonomic structure of the chironomid complex was assessed using a nonparametric two-factor analysis of variance. To do this, the multivariate variance, enclosed in the distance matrix **D**, was decomposed by the levels of the "Period" and "Reach" factors with the selection of random residuals; the *p*-values were estimated using randomization algorithms. It was shown that the variation in the data explained by each of the factors significantly exceeds the random observation error: when comparing time periods, $F = 2.79$, $p = 0.002$, when grouped by reaches, $F = 1.61$, $p = 0.002$.

The distance matrix **D** was used for optimal projection of points corresponding to the observations made from the multidimensional space of views onto the ordination plane with two axes of the principal coordinates PC_1–PC_2 [13]. On the diagram (Fig. 2) the distances between the centroids allowed to assess the severity of changes in the average level of species similarity of benthic communities during the considered time period, while the variation of points relative to their common center of gravity reflects the dynamics of the comparative β-diversity of chironomid communities corresponding to each reach. We colud note the relative structural similarity of the chiromid cenoses in 1975–1992 and some specificity of the species composition in 1966 and during the research period in 2002–2009. At that time the rheophilic complex of chironomids was replaced by phytophilic and pelophilic cenoses with a predominance of *Dicrotendipes nervosus, Polypedilum bicrenatum, Cryptochironomus defectus*, *Cladotanytarsus mancus*, etc.

To project the coordinates of individual chironomid species, a generalized analysis of the principal components was performed with regularization for each time period, after which all seven obtained partial ordinations were combined using Procrustes transformations. The diagram in Fig. 3 shows how the "center of gravity" of the abundance of analyzed taxa changes over time and relative to certain reaches. The variation

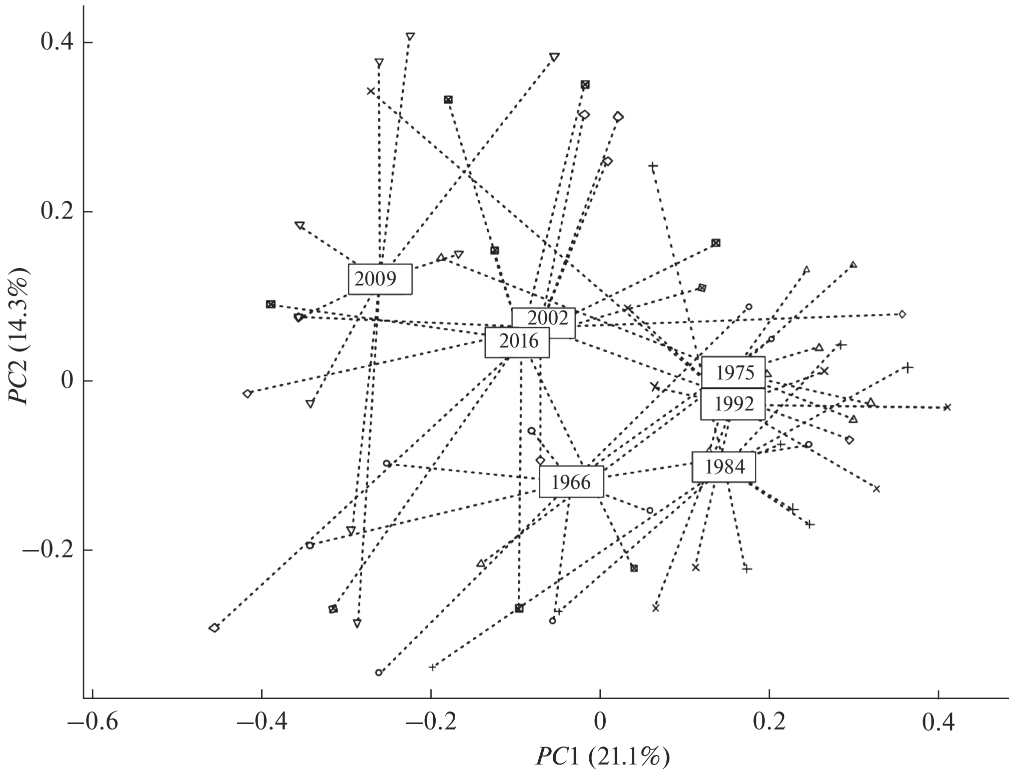

Fig.2. Ordination diagram of the chironomid community in different periods of time. Here and in Figs. 3–4 along the abscissa and ordinate axes are the values of the first two principal coordinates *PC*1 and *PC*2. The scatter of points corresponding to observations in the reaches of the Kuibyshev Reservoir is shown with respect to the projections of centroids by years, represented by numbers in rectangles.

of groups of points relative to each of their centroids reflects the range of ecological conditions in which each species lives, emphasizing the extent of their eurybiontness.

The ordination algorithms presented above are based on local comparisons of sets of repeated observations at the same sites. At that, the analysis is limited to their projections onto the two main axes of variation, which in this example explain only 35–38% of the total variance. An alternative method for trajectory analysis STA [10] formally considers community dynamics as an interconnected sequence of points in a multidimensional space that describes the similarity of species structures without using the procedures of variables reduction. A key aspect of the method is the possibility to assess the generalized geometric consistency of trajectories, which allows quantitative analysis and comparison of the expression of structural changes in each studied region. Unfortunately, the STA method does not allow direct visualization of multidimensional trajectories, but it is possible to perform their approximate projection onto the plane of two principal coordinates (Fig. 4), if the nature of the data makes it possible to neglect the information that is accumulated in the other axes.

Such important geometric components of the trajectory as the length and angle of rotation of individual segments, the rate of change and general direction, as well as the proximity of the starting and ending points, may explain the succession cycles of communities, etc. The procedures are proposed that allow calculating the indicators of divergence/convergence for any pair of observed communities, i. e. to consider how synchronously the directionality of the two trajectories changes over time [10]. The Mann–Kendall test was used to assess the validity of the hypothesis of such a monotonous trend; for example, we found that the dynamics of changes in the community of chironomids in the Volzhskiy and Undorski reaches has a character that is synchronous in form.

Another geometric characteristic of the ecosystem is the Haussdorf distance *r* between all paired trajectories. On the basis of the calculated matrix of *r* distances and using the methods of cluster analysis, a dendrogram was plotted (Fig. 5). This dendrogram, shows that relatively homogeneous processes of development of communities took place in pairs of the Undorskiy and Novodevichiy, Ulyanovskiy and Priplotinniy, Volzhskiy and Volgo-Kamskiy reaches, while the dynamics of the Kamskiy reach and Cheremshanskiy bay exhibits a specific character.

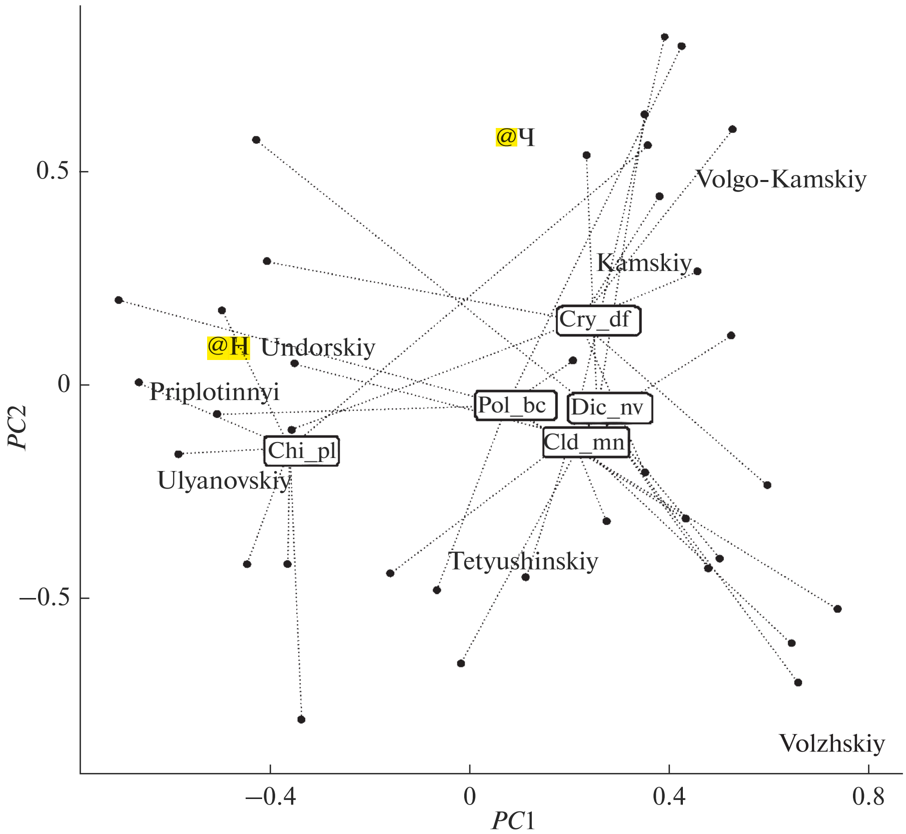

Fig. 3. The projections of the centroids of the coordinates of individual reaches, designated by letter abbreviations from Table 1, and a diagram of the generalized Procrustes analysis of the temporal dynamics of the main species of chironomids. Shown is the scatter of points corresponding to observations for different years, relative to the projections of the centroids of the species, represented by codes in rectangles (Chi_pl—*Chironomus plumosus;* Cld_mn—*Cladotanytarsus mancus*; Cry_df—*Cryptochironomus defectus*; Dic_nv—*Dicrotendipes nervosus*; Pol_bc—*Polypedilum bicrenatum*).

DISCUSSION

Analysis of the long-term dynamics of chironomids (Chironomidae, Diptera) community from 1966 to 1975 in all reaches of the Kuibyshev Reservoir revealed the stabilization of the taxonomic composition against the background of a general increase in the abundance of benthos (Table 1). Starting from 1975, which was the hottest and least-water year, there has been an outbreak of the development of the entire benthos, and while the mass species remained in the chironomid community, innumerous species *Microchironomus tener, Harnischia fuscimana, Polypedilum scalaenum*, etc., were started to be recorded at low occurrence. Further analysis of the ecological indicators of chironomid communities during the period of eutrophication of the reservoir (1985–1992) showed a decrease in species diversity [3] with a simultaneous increase in the total abundance due to one or two dominant species (*Chironomus plumosus, Procladius ferrugineus*). After 1992, a period of successive restoration of the reservoir ecosystem began, which continues to the present.

Statistical analysis of the spatiotemporal dynamics of the distribution of the species of the chironomid community made it possible to carry out a quantitative comparison of the severity of structural changes in each reach of the reservoir. Against the background of a significant stochastic drift caused by multifactorial fluctuations of natural-climatic and anthropogenic nature, pronounced deterministic tendencies were revealed. In particular, on the former channel and the sunken floodplain of the Kuibyshev Reservoir itself, the distribution of species diversity and abundance of chironomid communities is relatively homogeneous, as opposite to the water masses of the parts of the Kamskiy Reach and Cheremshanskiy Bay, where these indicators are considerably lower (Table 1). The taxocenosis of pelophilous species, which determine the structural features of the distribution of chironomids, has been identified. Thus, during all periods and in all regions, two taxa were dominant in numbers—*Procladius ferrugineus* and *Chironomus plumosus*. The larvae of these species particularly determine the features of interannual changes in the abundance and biomass of the reservoir benthos.

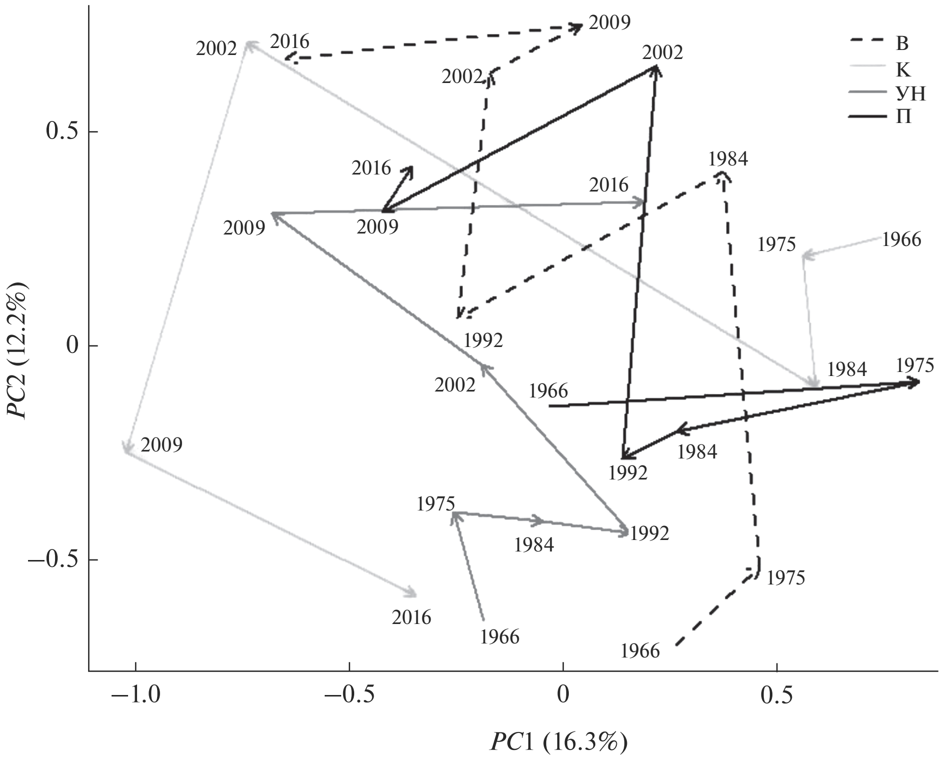

Fig. 4. The projection onto the ordination plane of the dynamic trajectories of the species structure of chironomids along the reaches, the legend is from Table. 1. At the nodes of broken lines, straight numbers represent the years of observations.

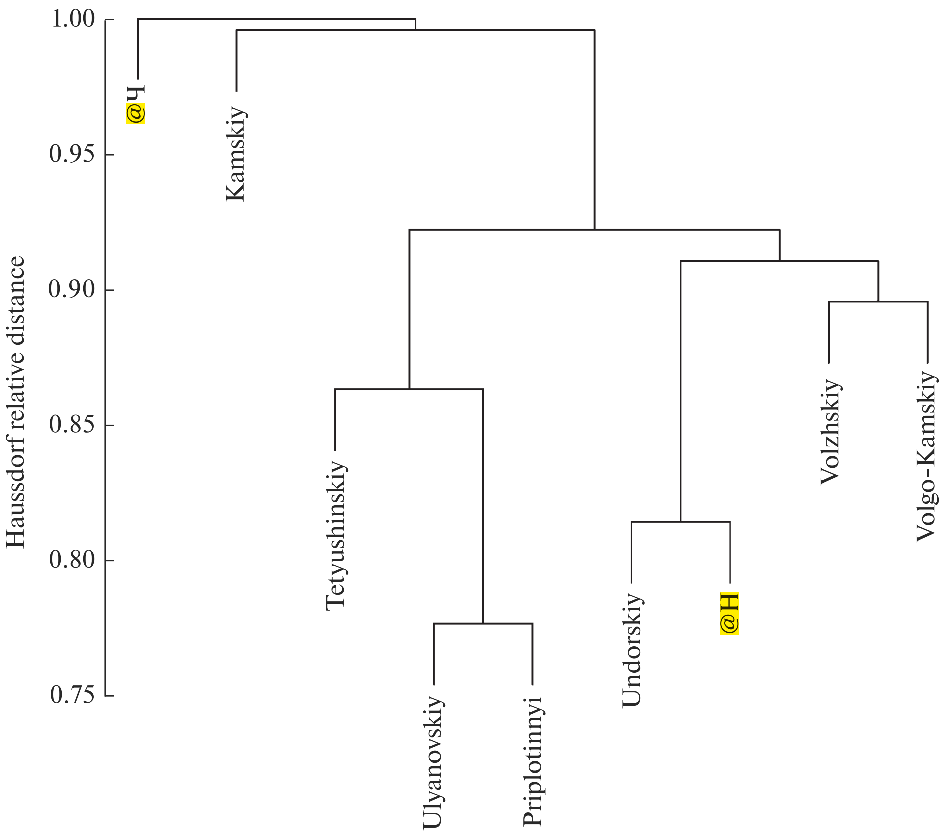

Fig. 5. Cluster dendrogram of the Kuibyshev Reservoir reaches plotted on the basis of the Haussdorf distance measure between the trajectories of the dynamics of chironomid communities for 1966–2016.

Geometric analysis of the trajectories of the dynamics of communities and the use of clustering methods allowed for revealing of the relatively similar processes of development of chironomid communities in pairs of reaches Undorskiy and Novodevichskiy, Ulyanovskiy and Priplotinnyi, Volzhskiy and Volgo-Kamskiy. The long-term dynamics of the structural characteristics of the chironomid community of the Kamskiy Reach and the eutrophic Cheremshanskiy Bay has a specific character, which is associated with a significant heterogeneity of water masses, peculiarities of hydrological conditions and hydrochemical regime.

REFERENCES

1. Bukharin, O.V., Zakharov, V.M., Zinchenko, T.D., Nemtseva, N.V., Rozenberg, G.S., and Shitikov, V.K., Methods of biomonitoring for the assessment of state of the anthropogenically-loaded plane river, *Ekologiya I prom-st' Rossii,* 2010, no. 11, pp. 10–15.
2. Zinchenko, T.D., Bioindication role of chironomids (Diptera, Chironomidae) in aquatic ecosystems: problems and perspectives, *Usp. Sovrem. Biol.,* 2009, vol. 129, no. 3, pp. 257–270.
3. Zinchenko, T.D., Long-term formation of zoobenthos of the Kuibyshev Reservoir: dynamics of chironomids (Diptera: Chironomidae) in relation to the processes of eutrophication, *Izv. Samar. NTs RAN,* 2003, special issue 1. pp. 91–101
4. *Kuibyshevskoe vodokhranilishche (nauchno-informatsionnyi spravochnik)* (Kuibyshev Reservoir (scientific-information handbook) Rozenberg, G.S., Vykhristyuk, L.A., Ed., Tolyatti: IEVB RAN, 2008.
5. Menshutkin, V.V., Pautova, V.N., Nomokonova, V.N, Seleznev, V.A., Popchenko, I.I., Zinchenko, T.D., Ivatin, A.V., Vykhristyuk, L.A., Vykhristyuk, M.M., Shitikov, V.K., and Kazantseva, T.I., Statistical relations in the Kuibyshev Reservoir ecosystem, *Gidrobiol. Zh.,* 1998, vol. 34, no. 5, pp. 94–103.
6. Pautova, V.N. and Nomokonova, V.I., *Produktivnost' fitoplanktona Kuibyshevskogo vodokhranilishcha* (Productivity of the Kuibyshev Reservoir phytoplankton), Tolyatti, 1994.
7. Shitikov, V.K., Vykhristyuk, L.A., Pautova, V.N., and Zinchenko, T.D., Multifactor ecological zoning of the Kuibyshev Reservoir, *Vodn. Resur.,* 2007, vol. 34, no. 4, pp. 481–489.
8. Anderson, M.J., A new method for non-parametric multivariate analysis of variance, *Austral. Ecol,* 2001, vol. 26, pp. 32–46.
9. Clarke, K.R., Somerfield, P.J., Airoldi, L., and Warwick, R.M., Exploring interactions by second-stage community analyses, *J. Experimental Marine Biol. Ecol,* 2006, vol. 338, pp. 179–192.
10. De Caceres, M., Coll, L., Legendre, P., Allen, R.B., Wiser, S.K., Fortin, M.-J., Condit, R., and Hubbell, S., Trajectory analysis in community ecology, *Ecological Monographs,* 2019, vol. 89, no. 2.
11. Gower, J.C., Generalized procrustes analysis, *Psychometrika,* 1975, vol. 40, pp. 33–51.
12. Legendre, P. and Gallagher, E., Ecologically meaningful transformations for ordination of species data, *Oecologia,* 2001, vol. 129, pp. 271–280.
13. Legendre, P. and Legendre, L., *Numerical ecology,* Amsterdam: Elsevier Sci. BV, 2012.
14. Ovaskainen, O., Tikhonov, G., Dunson, D., Grotan, V., and Engen, S., https://doi.org/10.1098/rspb.2017.0768
15. Tenenhaus, A. and Tenenhaus, M., Regularized generalized canonical correlation analysis, *Psychometrika,* 2011, vol. 76, pp. 257–284.
16. Thorson, J.T., Ianelli, J.N., Larsen, E.A., Ries, L., Scheuerell, M.D., Szuwalski, C., and Zipkin, E.F., Joint dynamic species distribution models: a tool for community ordination and spatio-temporal monitoring, *Global Ecol. Biogeogr,* 2016, vol. 25, pp. 1144–1158.
17. Vellend, M., *The theory of ecological communities,* Princeton, New Jersey: Princeton Univ. Press, 2016.
18. Vikhristuk, L., Hydrochemical state of the Kuibyshev Reservoir, *Water Resour. Development,* 1996, vol. 12, no. 4, pp. 547–559.
19. Zinchenko, T.D., Long-term (30 years) dynamics of Chironomidae (Diptera) fauna in the Kuibyshev water reservoir associated with eutrophication processes, *Nether. J. Aguat. Ecol,* 1992, vol. 26, nos 2–3, pp. 533–542.

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