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ZOOPLANKTON, ZOOBENTHOS, AND ZOOPERIPHYTON

On One Invariant in the Centuries-Old Dynamics of the Species Structure in Freshwater Zooplankton

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Abstract—Dynamics of the species structure of Cladocera based on the materials on bottom sediments has been studied for 3000- and 6000-year periods in two lakes. The community of one of these lakes has reached a dynamic climax, and the community of the other lake is at the stage of directing succession. The species structure of both communities is approximated well by the Motomura–Whittaker equation (i.e., model of geometrical series). For each of the studied lakes, the main parameter of this model (the coefficient of geometrical progression) does not differ significantly from its theoretically derived value equaled to $1 - \exp(-1) = 0.632$. A stable relationship is found between species diversity of the community, the rate of ecological succession, and the coefficient of geometrical progression.

Keywords: geometric progression, model of Motomura–Whittaker, succession rate, species diversity, Cladocera

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INTRODUCTION

A simple mathematical model predicting the species structure of a community consisting of a small number of competing species was developed by Sukhanov [3, 5–7]. According to this model, the species structure is characterized by a certain invariant, i.e., a constant value which turns out to be the same for many communities. This model is being tested with various communities. In the current paper, we discuss one of the tested communities, namely, the species structure of freshwater zooplankton, or, more specifically, cladocerans, from two typical lakes in European Russia. The material used in the model was taken from the published data [4].

The originator of the above type of models is Motomura [10], who found that the list of species in the sample arranged according to their abundance in descending order, $x_1, x_2, \ldots x_S$, commonly represents the correct geometric progression $x_i = x_1 q^{(i-1)}$, where x_i is the abundance of the species i, $x_1 = \text{const}$ is the abundance of the dominant species, and $q = \text{const}$ is the coefficient of progression (which is less than 1). For over half a century, this model has been actively used in quantitative biocenology, including research into communities of freshwater zooplankton [8].

Whittaker [14] suggested a hypothetical mechanism for establishing the above geometric progression, which was called "preferential occupation." This mechanism is relevant only to communities with competitive interspecies interactions. The size of the certain species niche may be defined as the share of the common resource that this species can utilize. Therefore, if the most competitive species captures the U share of the common resource, less lucky species can exploit only the remaining part. The second species utilizes the same U share; however, it is of the remaining part of the common resources left after the first species. The third species uses the U share of what is left after the first and second species, and so on. If the abundance of each competing species in the community is proportional to the amount of the resource captured by this species, such resource allocation among species leads to a geometric progression of the distribution of species abundances with the coefficient equaled $q = 1 - U$.

The model of the geometric series can also be represented in another form:

$$p_i = CU(1 - U)^{(i-1)}, \tag{1}$$

where p_i is the abundance of the species i in the ranked series, represented as a share of the total community abundance. The parameter $U = 1 - q$ is the share of the captured resource, $C = 1/[1 - (1 - U)^S]$ is the correction on the number of species (S) in the sample, and $i = 1, 2, \ldots, S$. We used the normalized form of the model.

The development of Whittaker's ideas led to the hypothesis of "stochastic residue" [5]. According to this hypothesis, the population of each species aims to use its share of the common resource as much as possible so that its requirements coincide exactly with its available abundance. However, stochastic fluctuations of the environmental conditions continuously disrupt this regulation of population abundance. As a result, in some places there is an excess; in others there is scarcity of individuals relative to the ideally appropriate level of their abundance. Simple calculations based on the probabilistic Poisson distribution enables us to make an important conclusion resulting from a hypothesis of "stochastic residue"; namely, the share of captured resource in the Motomura–Whittaker model is $U = 1 - \exp(-1) = 0.632$.

The goal of this study is to verify this hypothesis on the materials on freshwater cladocerans.

MATERIALS AND METHODS

To test the hypothesis of the "stochastic residue," we used data on the species structure of the taxocene of the cladocerans from Lake Nero (Yaroslavl oblast) and Lake Poletskoe (Moscow oblast) [4]. As follows from the original source, the abundance of crustaceans of each species was determined by carcinological analysis of lake sediments. The samples of sediments were collected from the drilled columns of the ground; 1 m of lake sediments corresponds to a time period of ~1000 years [9]. The depth of the column of the ground taken from Lake Nero was 6 m; that from Lake Poletskoe was 3 m.

Data on the species abundances were taken from the enlarged graph [4, Fig. 2] with the help of Grafula 2 freeware program tracer (wesik@comset.net). In this case, the absolute error in the estimation of the species abundance was a constant, and the relative error for rare species was noticeably greater than for abundant species. To meet the homocedasticity condition, parameter U was calculated not by means of a simple formula, but by a nonlinear adjustment procedure [1]. The geometric progression model (1) was used to approximate the whole series of shares $p_1, p_2, \ldots, p_S$ for all S species found in a particular sample collected from a specific location in the ground column. Although the total number of species in the sample occasionally reached ten, the total abundance of the first three most abundant species averaged 88% of the total taxocene population. In Figs. 1 and 2, for simplicity, only the first three dominant species are represented mainly determining the shape of the whole community.

One of the most important characteristics of the species structure of the community is its species diversity. Our focus in the current study was on this parameter. Species diversity is commonly estimated by the Shannon index taken by ecologists from information theory. This index was especially popular in the 1970s. We suggest that species diversity should be estimated by the Simpson index in the interpretation of Gibson [2], which is expressed by the simple formula $D = 1/\sum_{i=1}^{S} p_i^2$.

The advantage of the Simpson index over the Shannon index becomes obvious if we imagine a community where all the species have the same abundance; i.e., each species share equals $p_i = 1/S$. Then the species diversity D found by the Simpson index will be equal to species richness S. This is a result of the equality of all species in the community. The Shannon index does not give such a result.

The rate of changes observed in the species structure of the community was estimated as $V = v(t)/dt$. Here $t = (t_j + t_{j+1})/2$ is the arithmetic mean between adjacent j and $(j + 1)$ time moments, $dt = (t_{j+1} - t_j)$ is the interval between these time moments, and $v(t) = -\ln(R_{j,j+1})$ is the characteristic of the differences in the species structure of the community between times j and $j + 1$ [12]. $R_{j,j+1} = \sum_{i=1}^{S} p_{i,j} p_{i,j+1} \Big/ \sum_{i=1}^{S} p_{i,j}^2 \sum_{i=1}^{S} p_{i,j+1}^2 p$ is the correlation coefficient between species structures at times j and $(j + 1)$ [11], where $p_{i,j}$ and $p_{i,j+1}$ are the shares of species i in the total biomass of the community at times j and $(j + 1)$, respectively. $V = v(t)/dt$, characterizing the rate of ecological succession, is estimated in unit [time^{-1}].

RESULTS

Lake Nero. The adjustment of the model of the geometric series to the species structure of the cladocerans from this lake proved to be quite admissible; i.e., the coefficient of determination for all samples averaged 0.89 ± 0.01. As follows from L.M. Sushchenia et al. [8], the approximation of the species structure of the cladocerans by the model of the geometric series is more accurate for data from lakes with more transparent water. Since the high transparency of water is usually associated with the oligotrophy of the lake, with the shortage of food resources and, as a consequence, with intensive competitive interactions, such a relationship becomes quite clear. The more intense the competitive relations between species in the community are, the better the conditions of the hypothesis of "preferential occupation" are met, which is necessary for a model of the geometrical series. In this case, the model becomes more adequate and the approximation of real data with the help of this model proves to be higher.

The dynamics of the relative abundance in the three most abundant species from this taxocene is shown in Fig. 1a. The dominant species *Chydorus sphaericus* (O.F. Müller, 1776) maintained its leadership throughout the study period. The second and third most important species (*Bosmina sp.* and *Alona* sp.)

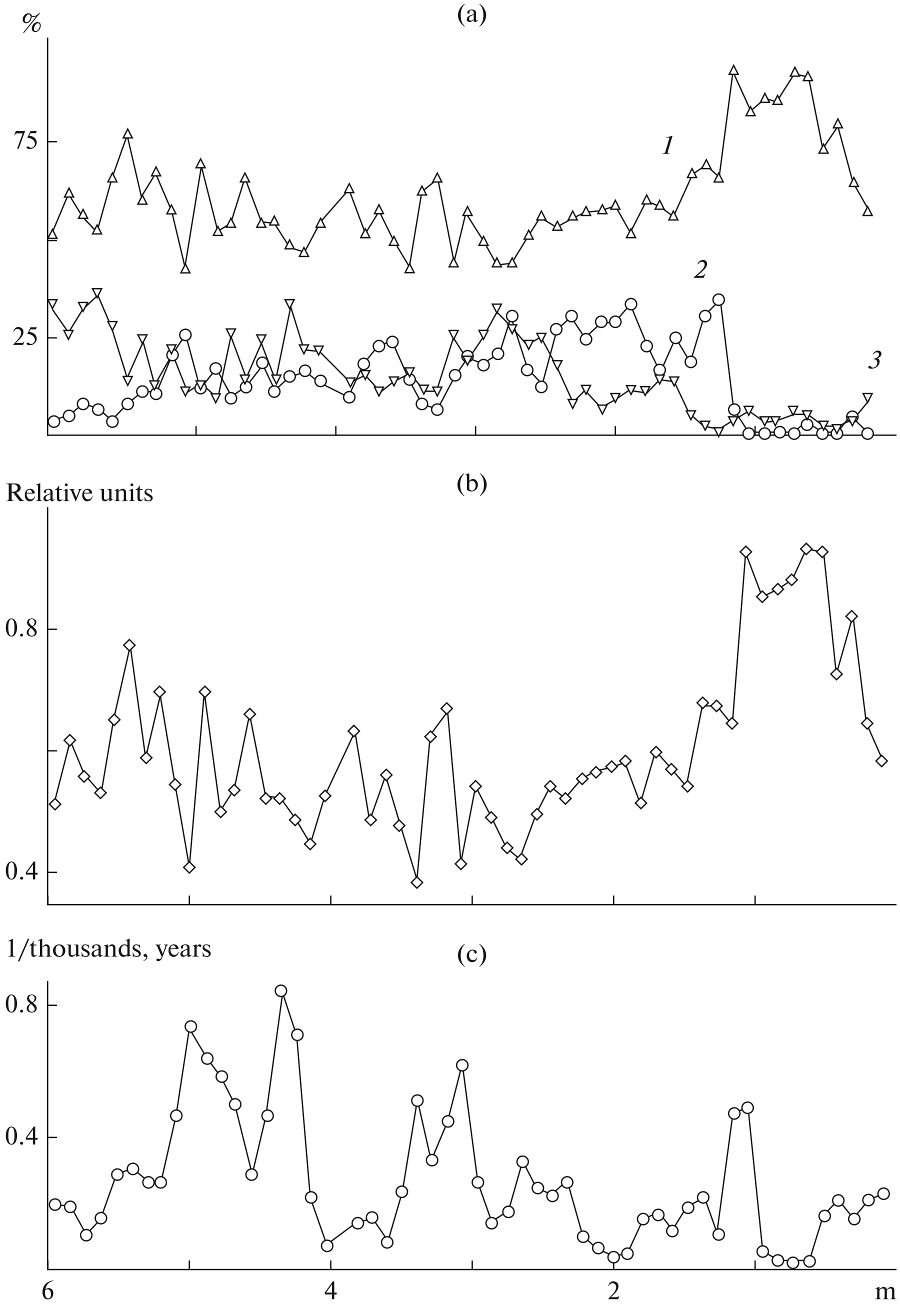

Fig. 1. Dynamics of the species structure in the cladoceran community from Lake Nero: (a) the share of the species in the total abundance, (b) the share of the captured resource, and (c) the succession rate; (*1*) *Chydorus sphaericus*, (*2*) *Bosmina* sp., and (*3*) *Alona* sp. The *x* axis represents the thickness of the bottom sediments.

alternately replaced each other being in the roles of subdominants.

Fluctuations of the species structure of the community are reflected in the changes of the rate of ecological succession (Fig. 1c). The succession rate showed a sharp increase in those periods when a subdominant and a sub–subdominant replaced each other in the ranking list of their abundances. Such processes were observed during the periods from 5000 to 4000 years ago and ~3000 and ~1000 years ago.

The share of resources captured by cladoceran species in Lake Nero was $U = 0.603 \pm 0.018$. The deviation from the theoretically calculated value 0.632 was only 4.6%, and it was statistically insignificant, because, according to Student's test, the level of significance for the null hypothesis was $P = 0.09$, which

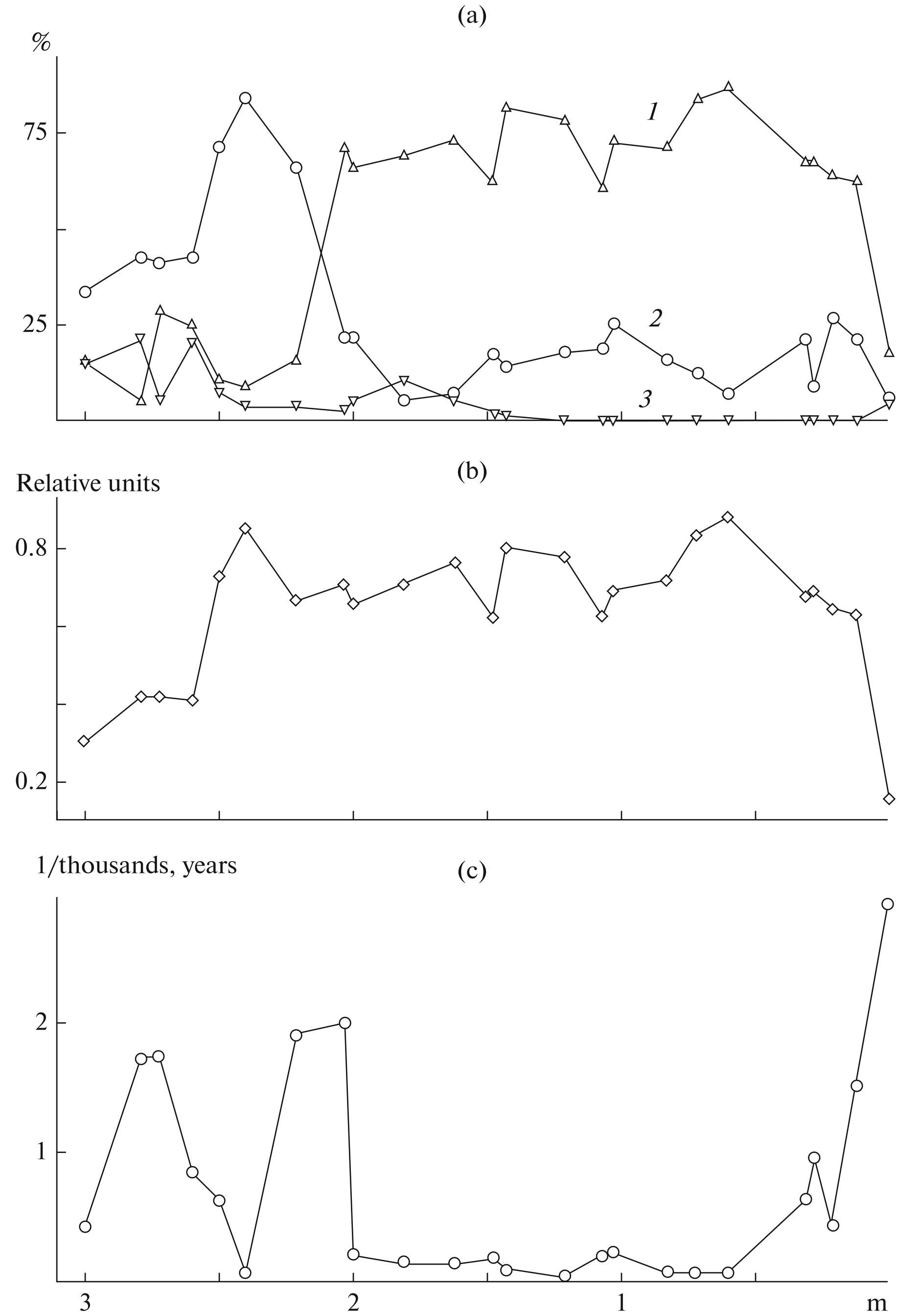

Fig. 2. Dynamics of the species structure in the cladoceran community from Lake Poletskoe: (*1*) *Chydorus sphaericus*, (*2*) *Alona affinis*, and (*3*) *Alonella nana*. The rest of the symbols are the same as in Fig. 1.

was almost twofold greater than the standard critical level of 0.05. Thus, the key parameter of the species structure in the taxocene of the cladocerans from this lake actually coincides with the constant of the proposed model.

The dynamics of parameter U in the cladoceran community for ~6000 years demonstrated abrupt and high fluctuations relative to the average level (Fig. 1b). In general, the nature of these fluctuations indicated a classical dynamic climax when the species structure of the taxocene irregularly fluctuates close to its stationary state.

It should be noted that fluctuations of the share of captured resource in the total abundance of the cladoceran species almost completely coincided with the fluctuations of the corresponding share (p_1) of the dominant species *Chydorus sphaericus*. It would not be so striking if we return again to the equation of the geometric series (1). The correction C on the number of species in the sample became actually equal to 1 at sufficiently large value $U \geq 0.6$ and at the species richness of the sample $S \geq 4$. Then the values of the parameters U and p_1 appeared indistinguishable from each other, provided that in the worst case this difference is 3%.

For cladocerans from Lake Nero, the correlation coefficient between the series U and p_1 reached 0.997. The averages for these series equaled, respectively, 0.603 ± 0.018 and 0.603 ± 0.017; i.e., there was no difference between them. Therefore, this property of the model of the geometric series allows us to use the easily determined share p_1 of the dominant species in the taxocene as an express estimate for share U of the captured resource.

Lake Poletskoe. The adjustment of the model of the geometric series (1) to the cladoceran species structure from this lake was also quite admissible. On average for all samples, the determination coefficient equaled 0.85 ± 0.02. The share of captured resource was 0.640 ± 0.036. The deviation from the model constant equaling 0.632 reached 1.3% and, as in Lake Nero, was statistically insignificant, since the level of significance for the null hypothesis was $P = 0.83$. Thus, the main parameter of the species structure in the taxocene of cladocerans from Lake Poletskoe also fully corresponded to the model requirements.

Dynamics of the share of captured resources in Lake Poletskoe for about 3000 years is shown in Fig. 2b. As in Fig. 1b, there are high oscillations of this parameter relative to the average level there. However, in contrast to the community of Lake Nero, the species structure in the taxocene of cladoceran species demonstrated regular directing changes along the time scale. A little over 2000 years ago, there was a change in the leading species in this community, namely, the dominant *Alona affinis* (Leydig, 1860) sharply reduced its abundance and its place was occupied by the previously subdominant *Chydorus sphaericus*. Therefore, the dynamics of the species structure of this community illustrates an evident case of classical directing ecological succession.

The dynamics of the abundance of the first three most abundant species is shown in Fig. 2a. Subdominant species *Chydorus sphaericus* and *Alona affinis* exchanged places with each other in the ranking list of species abundances almost 3000 years ago. At that time, the first jump in the rate of ecological succession was registered (Fig. 2c). The dominant and subdominant species (*Alona affinis* and *Chydorus sphaericus*, respectively) exchanged their positions in the community with each other a little over 2000 years ago. Afterwards, the second powerful jump in succession rate happened. The third, and the last, most recent jump in succession rate was caused by a sharp decrease in the abundance of dominant and subdominant species.

Fluctuations in the share of the captured resource in the taxocene of Lake Poletskoe, like in Lake Nero, mirrored the oscillations of the share of the dominant species (no matter which). The correlation coefficient between these two time series was also high (0.996). Estimates of the arithmetic means for the parameters U (0.640 ± 0.036) and p_1 (0.633 ± 0.034) differed by 1.1%, which overlaps with standard errors of the means and is statistically insignificant.

Thus, in a community that is in a stationary climax state, as well as in a community experiencing regular, directing succession changes, the average values of parameter U are not significantly different from the invariant $1 - \exp(-1)$. In this case, both estimations of the share of the captured resource can be averaged. With an increase in the sample size, the standard error of the mean decreases and the null hypothesis falls into the more rigid testing conditions. The average value over both lakes was $U = 0.614 \pm 0.017$. It differed from the theoretical constant 0.632 by only 2.8%, and this difference was statistically insignificant (the level of significance for the null hypothesis was $P = 0.29$).

However, all this is true only for the averaged values. Some particular samples can significantly differ in parameter U from the value $1 - \exp(-1)$ in the direction of one or the other side.

Species diversity. It should be noted that the share of the captured resource U is clearly related to the species diversity of the community D. This relationship can be justified. Simple calculations lead to the following conclusion. For geometric progression (1) describing the ideal distribution of species abundance in the community, such a relationship is described as $D = K(2 - U)/U$, where $K = [1 - (1 - U)^S]^2/[1 - (1 - U)^{2S}]$ is the correction of the number of species S in the sample. In this particular case, because of the rather large values of U and S, this correction does not actually differ from 1. Then, the discussed relationship becomes quite simple: $D = (2 - U)/U$. This ratio generates a monotonically decreasing dependence of D on U, which can be interpreted as follows: the larger U is, the smaller the geometric progression coefficient $q = 1 - U$ is; i.e., the greater the inequality of abundance between species is, the more pronounced the level of monodominance of the community and the lower its species diversity.

The relationship between the species diversity in the cladoceran communities and the share of captured resource is shown in Fig. 3a. The empirical data for both lakes are irregularly mixed so that there are no differences between the climax community and the community at the state of directing succession; i.e., both communities are subject to the same trend. It should be noted that all empirical data, except one, corresponds well to the theoretically derived curve $D = (2 - U)/U$. Moreover, this curve does not have any adjustment empirical coefficients, which is quite rare for environmental studies.

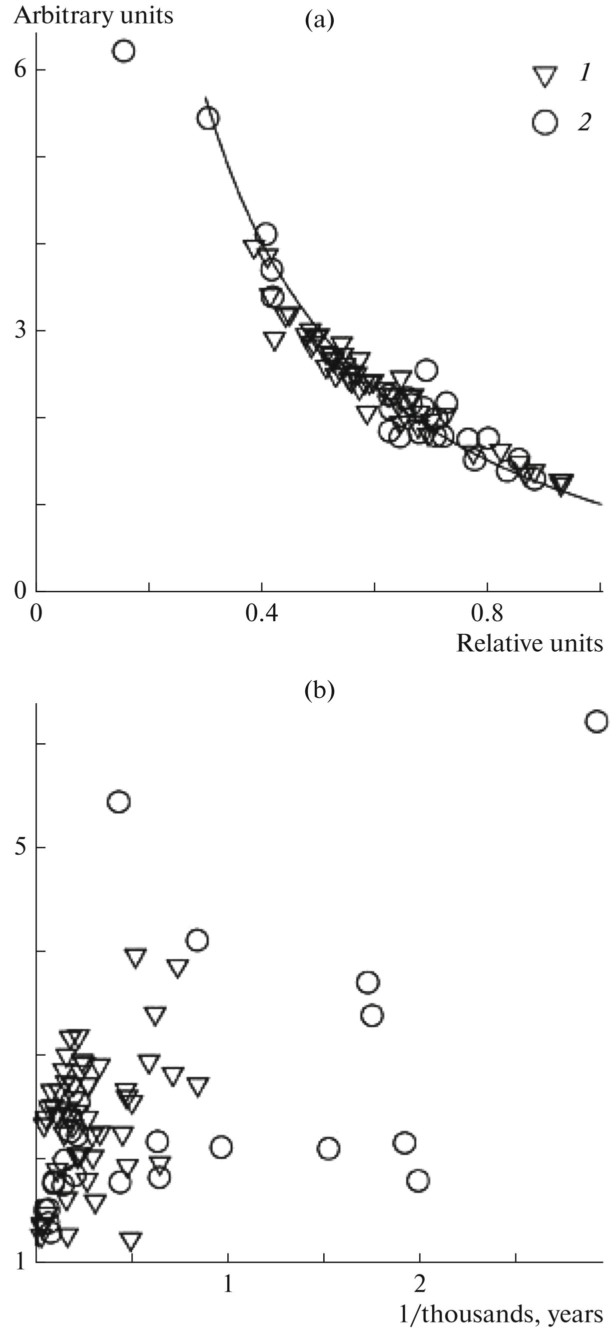

Fig. 3. Relationship of the Simpson index of the species diversity (the y axis) with the share of the resource (a) and with the succession rate (b). Lakes: (*1*) Nero and (*2*) Poletskoe.

The species diversity increased in direct proportion to the rate of ecological succession (Fig. 3b). The correlation coefficient is not very high, but it is significant, equaling 0.474 ± 0.099. The points corresponding to different lakes in the figure are strongly mixed, which indicates a common trend for both lakes. However, the species diversity and rate of succession in Lake Poletskoe are higher than in Lake Nero.

DISCUSSION

In this work, we presented two cases illustrating the rightness of the "stochastic residue" hypothesis. However, we have many more such cases that are in the processes of preparation for publications. In general, we proposed a preliminary hypothesis stating that the species structure of the simple competitive biocenosis is characterized by an invariant, i.e., a certain constant, the mean value of which is the same for different communities.

This hypothesis is unlikely to convince the skeptical reader; however, there is a way to impartially test our hypotheses. In particular, you should use collections of cases collected by independent experts. For our objectives, there is such collection. Almost 30 years ago, it was collected by Sugikhara [13] for testing a different concept. The data collected by Sugikhara includes evidences on simple two- or three-species communities of fish, mollusks, barnacles, and trees, 129 taxocenes in total. A brief summary of the results of this work, a statistical analysis of the hypothesis of a "stochastic residue" on such representative data, did not refute it.

One of the cornerstones of the above model is its requirement that all the species included in the sample would be competitively related to each other and that the number of the species in the samples should not be large. We cannot always prove convincingly that all the species in the sample competitively interact with each other. However, ecologists established some widely accepted principles. In particular, we believe that, if we choose a small subset from the whole community consisting of closely related species that pertain to the same supraspecies taxon, these species are likely to be competitors, due to their common origin, and, therefore, they have similar requirements and similar life strategies. The level of the supraspecies taxon that determines the composition of a certain taxocene should not be too high and full-scale so as not to involve species that fully differed from each other in regards to their life cycles and the nature of interspecific relationships. The low systematic level of the supraspecies taxon almost always involves a small number of species.

CONCLUSIONS

The species structure in the taxocene of the cladocerans from the two lakes did not statistically differ from that predicted by the model. Moreover, the model equally well describes the species structure both in the lake at the state of directing succession and in the lake at the state of dynamic climax. This does not mean that a statistically significant deviation from the model constant value should always evidence against the proposed model. Moreover, the test for the rightness of $U = 0.632$ can be used to classify communities consisting only of a small number of competing species [5].

Communities with a parameter U, on average, close to $1 - \exp(-1)$, are most likely typical of biotopes of temperate latitudes. Such biotopes are characterized by high-frequency, broad, and unpredictable fluctuations of the environmental conditions continuously violating the regulation of species density. The species diversity of communities inhabiting such biotopes is characterized by moderate standard values. If U is significantly <0.632, in accordance with the hypothesis of the "stochastic residue," the community consists of species with low tolerance to unfavorable environmental conditions. The species diversity of such communities is very high and should be typical of the tropics, with comfortable conditions that enable lowly tolerant species to survive. If the mean value of U is significantly >0.632, the community is likely to consist of species with high tolerance to unfavorable environmental conditions. The species diversity of such communities is low due to the larger share of the dominant species. In severe and unfavorable environments (extreme climate, polluted biotope), highly tolerant species that shape monodominant cenoses are more likely to survive. After a comprehensive and rigorous critical test, the criterion $U > 0.632$ could be used in practice for the statistically significant detection of contaminated biotopes.

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