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Long-Term Dynamics of Biological Diversity in Water Basins

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Abstract—The structural complexity of communities of living organisms can be assessed in various ways, including diversity indices. For these purposes, the Shannon index (*H*) was used in the present study. Based on the scarce available published data and our own data, the rates of changes in the number of species and complexity of the community structure of aquatic organisms were determined with reference to macrobenthos communities. The considered changes were described by equations of specific functions that were mathematically analyzed. It was suggested that, in a temperate climate and the absence of strong contamination or eutrophication of water bodies, 12–14 years on average are required for the formation of a complex structure (3–4 bits) of benthic animals under favorable conditions. The complex structure of communities formed in polluted waters remains rather constant. Longer studies (at least 20–30 years) than those used in the present work are necessary to verify and refine the above assumptions

Keywords: change in number of species, structure of macrobenthic communities, Shannon index

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In the hydrobiological literature, there are extensive data from long-term studies of species composition, biomass, and abundance of organisms in communities of planktonic and benthic animals. Unfortunately, they are mostly fragmentary and incomplete and are represented as diagrams, broken lines in plots, or in tables, at best. Since they are not analyzed, they remain quantitative exactly because they are expressed in digits. However, such data are insufficient for quantitative assessment of the structure and, even more so, functioning of biological communities. Long-term determinations of rates of change of particular system parameters are necessary. It may be said that there is almost no such data.

Biological diversity, as a part of general diversity in nature, is related to living organisms and to the biological systems of the supraorganism level. The problem of biological diversity of natural communities is discussed in numerous descriptions and theoretical studies (Margalef, 1997; Alimov, 2000; *Geographiya i monitoring...*, 2002; Protasov, 2002).

The structural complexity of communities of living organisms may be described in various ways, including by diversity indices. At present, about 30 diversity indices are proposed. the Shannon information index is widely used in ecological studies. In this index entropy (uncertainty) is taken as a measure of diversity. The value of this index hardly depends or depends much less than similar indices on the sample size and is characterized by a normal distribution (Odum, 1953), allowing the use of the usual statistic methods. The Shannon entropy is a realistic estimation of diversity (Puzachenko et al., 1999); it depends on the number of analyzed species and on the distribution of abundance of species. The essential merits of the Shannon index are its complete independence from the biocenotic similarity of the compared communities and the possible assessment of the diversity of each cenose separately (Bakanov, 2000).

The Shannon function (*H*) combines two components of diversity—diversity and equitability—into a general diversity index. According to Margalef (1997, p. 145), "There is no sense to separate two indices—diversity and nonequilibrium. They both reflect the general basic quality."

In the present study the change rates of the number of species and complexity of structure of hydrobionts are calculated based on scarce published data and some original material with reference to macrobenthos communities. With this goal, the considered changes were described by equations of concrete functions, which were then analyzed mathematically.

Functions of concrete dependencies ($y = f(x)$) were approximated by polynomials of different powers. The obtained linear, square, and cubic equations were investigated by means of derivatives. To determine the extrema (max, min) and inflection point, the derivatives were set equal to zero, the proper equations were solved (the inflection point was determined by solution of the second derivative), and their roots were found. In all cases, the observation times (t_1) were counted from the moment (t_0) beginning of observa-

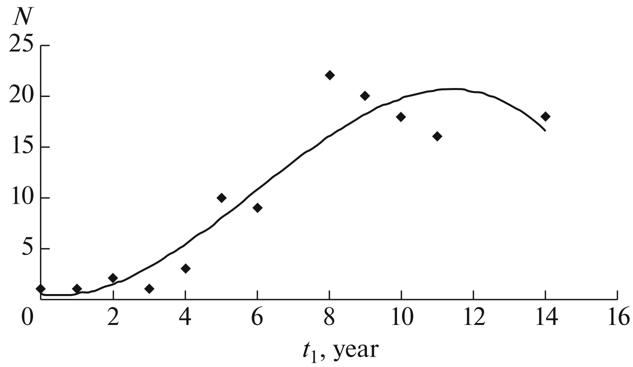

Fig. 1. Dynamics of change of the number of macrozoobenthos (N) species in Shchuchii Bay of Lake Ladoga.

tions in every particular case. Astronomical time (t) was calculated from equation $t = t_0 + t_1$. The mean values of rates of change of the corresponding functions were calculated by means of definite integrals for particular time periods.

While some data on simplification of the community structure under the influence of environmental factors are available, there are almost no data on complication of the community structure in the course of restoration after their destruction by economical or wasteful activities. Such data are extremely important. In this respect, the long-term studies of Shchuchii Bay (Lake Ladoga) ecosystem made by the team of the Limnology Institute, Russian Academy of Sciences (RAS), are unique and have no parallel cases. The data on Shchuchii Bay macrozoobenthos (Raspopov et al., 1998, 2003; Ignat'eva and Barbashova, 2003) were used to determine of the rate of secondary succession in communities of benthic animals.

Shchuchii Bay (area 0.4 km^2, mean depth 2 m, maximum depth 3.7 m) is situated in the northwestern part of Lake Ladoga. Its ecosystem suffered from wastewater discharge from the Priozersk Pulp and Paper Mill for over two decades. As a result, the bay has turned into a dead zone. Priozersk Mill closed in 1986. Since this time the experts of the Limnology Institute RAS started long-term monitoring of the formation of a new bay ecosystem. The process of bay self-purification started immediately once the bay pollution ended. This was favored by the intensive water exchange between the bay and Lake Ladoga due to long and gently sloping waves that may occur up to 29 times a year. The intensity of self-purification increased with time.

In the first year of observations, i.e., immediately after discontinuation of wastewater discharge from the mill, the Shchuchii Bay macrobenthos was represented only by scarce larvae of *Chironomus plumosus* L. The formation of benthic animal communities and the bay ecosystem began in the late 1980s and the early 1990s. The following animals appeared: oligochaetes, Baikalian gammarid *Gmelinoides fasciatus* Stebb., mollusks, caddis worms. The new bay system continued to form until the end of 1990s. The daily primary production in the bay was 190 mg C/m^3.

Monitoring showed that that the average quantity of benthic animals for the bay gradually increased, attaining maximum values, and then somewhat decreased (Fig. 1).

The number of species in communities of benthic animals (N) increased with time (t_1):

$$N = (-0.031 \pm 0.012)t_1^3 + (0.553 \pm 0.2) \times t_1^2 - (0.481 \pm 0.171)t_1 + (0.468 \pm 0.22), \quad (1)$$
$$R^2 = 0.89.$$

The rate of increase of the number of species (V_N) or the first derivative of equation (1) is:

$$V_N = dN/dt_1 = -0.093t_1^2 + 1.106t_1 - 0.481.$$

From the equation (on the condition that $V_N = 0$), it was found that the maximum species number was attained up to $t_1 = 11$ years after the start of monitoring, or up to 1997. The inflection point of this function, which corresponds to $t_1 = 4$ years and was attained by 1990, was determined from the equation of the secondary derivative. Thus, the number of species from the beginning of observations increased with an increasing rate until 1990; the rate was slower up to the end of observations and reached the maximum of 20 species by 1997. The species number then decreased somewhat. However, it is not yet possible to assess the rate of decrease, since there are no data after 2001. In the considered period, the mean rate of increase of the species number was two species per year.

The increase in the structural complexity of benthic communities as estimated by the diversity index (H) during the time (t_1) of restoration of bay ecosystem (Fig. 2) may be described by the equation

$$H = (-0.003 \pm 0.001)t_1^3 + (0.039 \pm 0.025) \times t_1^2 + (0.242 \pm 0.12)t_1 - (0.299 \pm 0.132), \quad (2)$$
$$R^2 = 0.92.$$

The rate of change of the structural complexity (V_H), or the derivative of equation (2), would then be

$$V_H = dH/dt_1 = -0.009t_1^2 + 0.078t_1 + 0.242.$$

Assuming that the first derivative of equation (2) is equal to zero, the function maximum was calculated; it was attained by $t_1 = 12$ years, or 1999. The Shannon index was 3.6 bits/specimen. The inflection point of the function corresponded to $t_1 = 3$ or 1990 ($H = 0.23$ bit/year). Thus, during the first three years, the rate of community complexity (V_H) increased and then gradually increased until the end of observations. The structural complexity of benthic animal communities increased at a mean rate of ~0.3 bit/year.

It may be concluded that, for the Shchuchii Bay example, the rate of secondary succession of animal communities was calculated for the first time. On average for the studied period, the rate is 0.3 bit per year and two species per year. The species number and structural complexity of benthic animal communities increased during the observation period, but their change rates slowed after 1990. The increase in the complexity of community structure in one year by one species corresponds 0.15 bits of information.

It would be instructive to compare the obtained results for benthic animal communities in Shchuchii Bay with long-term structural changes in the benthic communities of other water bodies that have been exposed to a less intensive anthropogenous impact than that of Shchuchii Bay. Unfortunately, there are very few studies recording long-term changes in the structure and complexity of aquatic animal communities. A recent publication contained data from long-term observations of structural changes in benthic communities that formed in some water bodies of Leningrad oblast. For example, in 1991–2005, the structural change in profundal benthic communities of the mesotrophic Lake Krasnoe, Karelian Isthmus was estimated by the Shannon index (Belyakov, 2008). Similar data were obtained in 1994–2004 for benthic communities in the Neva Bay of the Gulf of Finland (Station 14), which is average for this bay and for the tip of the eastern part of the Gulf of Finland (Balushkina, 2008). On average, in 1994–2005, the waters of the Neva Bay were assessed as polluted. In the same period, the waters of the tip of the eastern part of the Gulf of Finland were assessed as polluted—saprobic. Station 14 in the Neva Bay was characterized by slower flowage and slightly polluted waters, and the benthos structure was characterized by developed populations of unionid mollusks. The material on benthic communities of Lake Krasnoe, the Neva Bay, and the tip of the Gulf of Finland was analyzed in the same way as

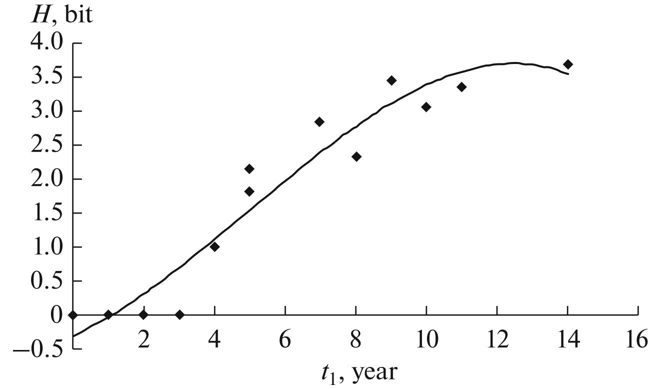

Fig. 2. Dynamics of change of the diversity index (H) in macrozoobenthos animal communities in Shchuchii Bay of Lake Ladoga.

that on Shchuchii Bay benthic communities. The results are shown in Fig. 3 and Table 1.

Figure 3 and Table 1 demonstrate that the community structure of benthic animals in the newly formed Shchuchii Bay ecosystem was much more complicated (H = 3.6 bit/specimen) under the assumed equations than in the communities of the Neva Bay and Lake Krasnoe that formed over a long time and differed little in this index (H = 2.7, 2.87 bit/specimen, respectively). The communities in the most polluted (of those investigated) waters of the tip of the eastern part of the Gulf of Finland were less complexly organized (H = 2.2 bit/specimen). The change in the diversity index dynamics in the Shchuchii Bay and Lake Krasnoe communities manifested cyclicity. The time of rate change (the function inflection point) in Lake Krasnoe was 60%, while it did not exceed 20% of the time to attain the maximal structure complexity in Shchuchii Bay communities, i.e., retardation of the rate of structural community changes in Shchuchii Bay occurred approximately three times earlier. The

Table 1. Change of the Shannon index in different water bodies in the observation period

Water body	H_{max}	t_{1max}	H_{min}	t_{1min}	$t_{1(.)}$	V_H
Shchuchii Bay	3.6	12 (2000)	0	0 (1987)	3 (1990)	0.26
Lake Krasnoe	2.7	16 (2006)	1.3	4 (1995)	10 (2000)	0.021
Neva Bay, Station 14	2.87	10 (2004)	2.45	2 (1995)	–	0.06
Neva Bay (average)	2.8	7 (2001)	2	0 (1994)	–	0.02
Head of Gulf of Finland	2.2	0 (1994)	1.3	7 (2005)	–	–0.085

H_{max} (bit/specimens) is the maximum value of the diversity index; H_{min} (bit/specimens) is the least value of the diversity index; t_{1max} and t_{1min} (years) is the time of attainment of function extrema; $t_{1(.)}$ is the time of attainment of the inflection point of the function curve; V_H (bit/year) is the rate of change in indices in benthic animal communities in the studied water bodies; time t is indicated in parentheses.

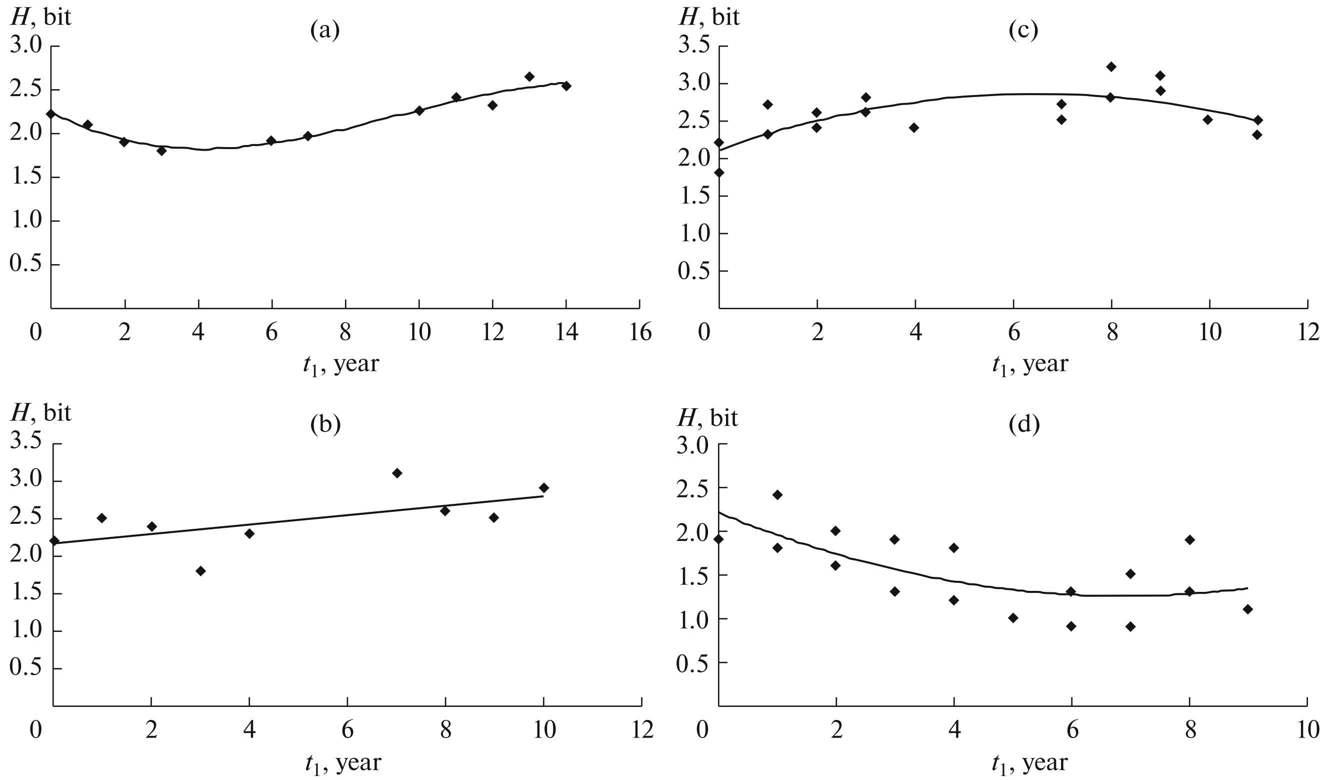

Fig. 3. Dynamics of diversity index in Lake Krasnoe (a) (Belyakov, 2008); in Neva Bay, Station 14 (b), middle (c), and tip of the Gulf of Finland (d) (Bulushkina, 2008).

maximum diversity in the newly formed benthic community in Shchuchii Bay took 12 years. After this, the change rate decreased: from 0.114 bit/year in the 11th year of observations to 0.04 in the 13th year and to 0.021 in the 14th year. The highest diversity of benthic communities was attained in 16 years in Lake Krasnoe and in 7–10 years in Neva Bay after the beginning of observations.

It may be assumed that, at temperate climate and in the absence of strong pollution or eutrophication of water bodies, the formation of a maximally complex structure (3–4 bits) of communities of benthic animals would, on average, require about 12–14 years under favorable conditions. In communities that have already formed in polluted waters, the maximally complex structure remains permanent. Verification of the above assumptions would require longer studies (not less than 20–30 years) than discussed in the present paper. Unfortunately, this most likely will not happen in the foreseeable future.

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