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BIOPHYSICS OF COMPLEX SYSTEMS

The Divergence of Chlorophyll Dynamics in the Naroch Lakes

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Abstract—We present the results of an analysis of the long-term chlorophyll *a* dynamics in the Naroch lakes. It was shown that an increase in nutrient load in the 1970s resulted in progressive eutrophication of the Naroch lakes. Then, starting from the mid-1980s, the water transparency began to increase and the concentration of phosphorus and nitrogen began to decrease due to the implementation of an environmental improvement program. In the 1980s, the Naroch lakes experienced an invasion by the zebra mussel (*Dreissena polymorpha* Pallas). Our analysis showed that the responses of all three lakes to the intensive nutrient load and a further decrease in the nutrient concentration as a result of the environmental-protection measures are correlated. At the same time, the invasion of the zebra mussel *Dreissena polymorpha*, which causes significant transformation of ecosystem processes, led to divergence in the chlorophyll dynamics; this was manifested as a drastic decline in the correlation between the fluctuations in the chlorophyll concentration in each lake.

Keywords: chlorophyll, long-term dynamics, correlation, time series, biological invasion, *Dreissena polymorpha*
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INTRODUCTION

The Naroch lakes are a system that consists of three different trophic water bodies with a common catchment area, which are connected through channels. As a result of long-term monitoring observations, a number of external factors that largely determined the stages of evolution of ecosystems of the Naroch lakes and their current status have been identified [1]. Active agricultural production and, as a consequence, an increased nutrient load on the catchment area have led to progressive eutrophication of these water bodies. Later, due to the purposeful reduction of the nutrient load as a result of the implementation of a program of environmental rehabilitation of the Naroch lakes, the concentrations of nitrogen and phosphorus significantly decreased. In addition, all three lakes are affected by another strong external factor, viz., the invasion and mass-scale reproduction of the Ponto-Caspian water-filtering mollusk, the zebra mussel *Dreissena polymorpha* Pallas.

One of the main parameters of the hydroecological characteristics of water bodies is the concentration of chlorophyll *a*, which characterizes the level of development of planktonic primary producers and is therefore one of the main criteria of the degree of nutrient load and the trophic status of a water body [2] Our assessment of the chlorophyll concentration in the Naroch lakes reflects the entire time period during which significant changes in the functioning of each of the three lake ecosystems occurred. This makes it possible to evaluate the similarities and differences in the impact of drastic external factors on individual lakes of the Naroch group. Given the pivotal role of primary planktonic producers in the evolution of lake ecosystems, the analysis of the chlorophyll dynamics is particularly relevant.

In this paper, we describe the results of the analysis of long-term data on the concentration of chlorophyll *a* in the Naroch lakes. The results of the analysis suggest a similar effect on the chlorophyll dynamics of anthropogenic eutrophication and environmental protection measures, as well as the divergence in the chlorophyll dynamics in the lakes as a result of invasion of the water-filtering mollusk *Dreissena polymorpha*.

MATERIALS AND METHODS

This study was performed in the period from 1978 to 2013 in three lakes of the Naroch group: Batorino, Myastro, and Naroch. The lakes are located in the northwest of Belarus (Fig. 1), are polymictic, and differ in morphometric and hydrological parameters (Table 1).

Samples were taken at the site of regular observations in the deep zone of lakes using a 2-L Ruttner bathometer one to three times a month during the

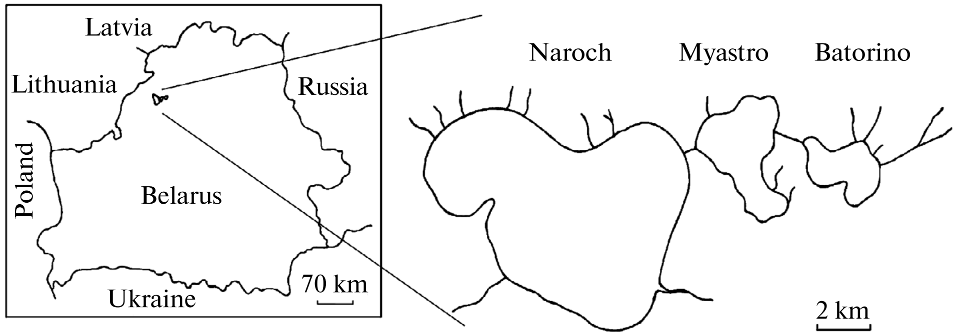

Fig. 1. The system of the Naroch lakes.

growing season. Depending on the weather conditions, the first samples were taken in April or May, and the last sample was taken in October. Water samples were taken from six horizons (0.5, 3, 6, 8, 12, and 16 m) in Lake Naroch, four horizons (0.5, 4, 7, and 9 m) in Lake Myastro, and three horizons (0.5, 3, and 5 m) in Lake Batorino. Water from all horizons was mixed to obtain an integrated sample that was representative of the average composition of the lake water. The volume of water from each horizon in the integrated sample was proportional to the fraction of the given layer in the total water volume of the lake and in accordance with the bathymetry data.

The slurry for the determination of the chlorophyll *a* content (without correction for the presence of pheopigments) was collected on Synpor filters (1978–1981) and Nucleopor nuclear filters (1982–2013) with a pore diameter of 1.5 μm. Analysis was performed spectrophotometrically after the extraction of pigments in 90% acetone. The chlorophyll *a* concentration was calculated as described in [3]. The water transparency was determined using a white Secchi disk 30 cm in diameter. The total nitrogen content was determined in the unfiltered water by wet combustion by the Kjeldahl method or by oxidation of samples with potassium persulfate in an autoclave. The total phosphorus content was determined by oxidation of samples with potassium persulfate in an acidic medium in a water bath [4, 5].

Since many data did not fit the normal distribution, the degree of cohesion of traits was estimated using the Spearman rank correlation coefficient.

RESULTS

In general, the dynamics of the chlorophyll concentrations in each of the three lakes were similar throughout the entire study period (1978–2013) (Fig. 2). The correlation coefficients between the changes in the chlorophyll concentration in different lakes for the entire period of observations were 0.67–0.70 at a significance level of less than 0.001. The correlation coefficients between the average seasonal concentrations were even higher (0.77–0.87).

The trend lines shown in Fig. 2 and their coefficients of determination (Table 2) indicate that three periods could be clearly distinguished in the dynamics of the chlorophyll concentration in each lake. An almost complete absence of both ascending and descending trends in the 1978–1983 and 1991–2013 periods can be seen. A much more pronounced direction in the changes in the chlorophyll concentration was observed in the 1984–1990 period. The coefficients of determination increased by several orders of magnitude in 1984–1990 compared to 1978–1983 and decreased again nearly to the baseline level in 1991–2013 (Table 2). The 1978–1983 interval can be considered as a period that preceded the response of the ecosystem to the implementation of the environmental-improvement program for the Naroch lakes. In the 1984–1990 period the chlorophyll concentration tended to decrease under the influence of external factors in all three lakes, and in the 1991–2013 period the fluctuations in the chlorophyll concentration in the ecosystem were non-directional with no clear trend.

We will consider the dynamics of the chlorophyll concentration in each of the above periods in greater

Table 1. The main characteristics of the studied lakes

Indices	Lake Batorino	Lake Myastro	Lake Naroch
Water surface area, km^2	6.3	13.1	79.6
Water mass volume, million m^3	18.7	70.1	710.0
Depth, m (average/maximum)	2.4/5.5	5.4/11.3	8.9/24.8
Water exchange time, year	1.0	2.5	10–11

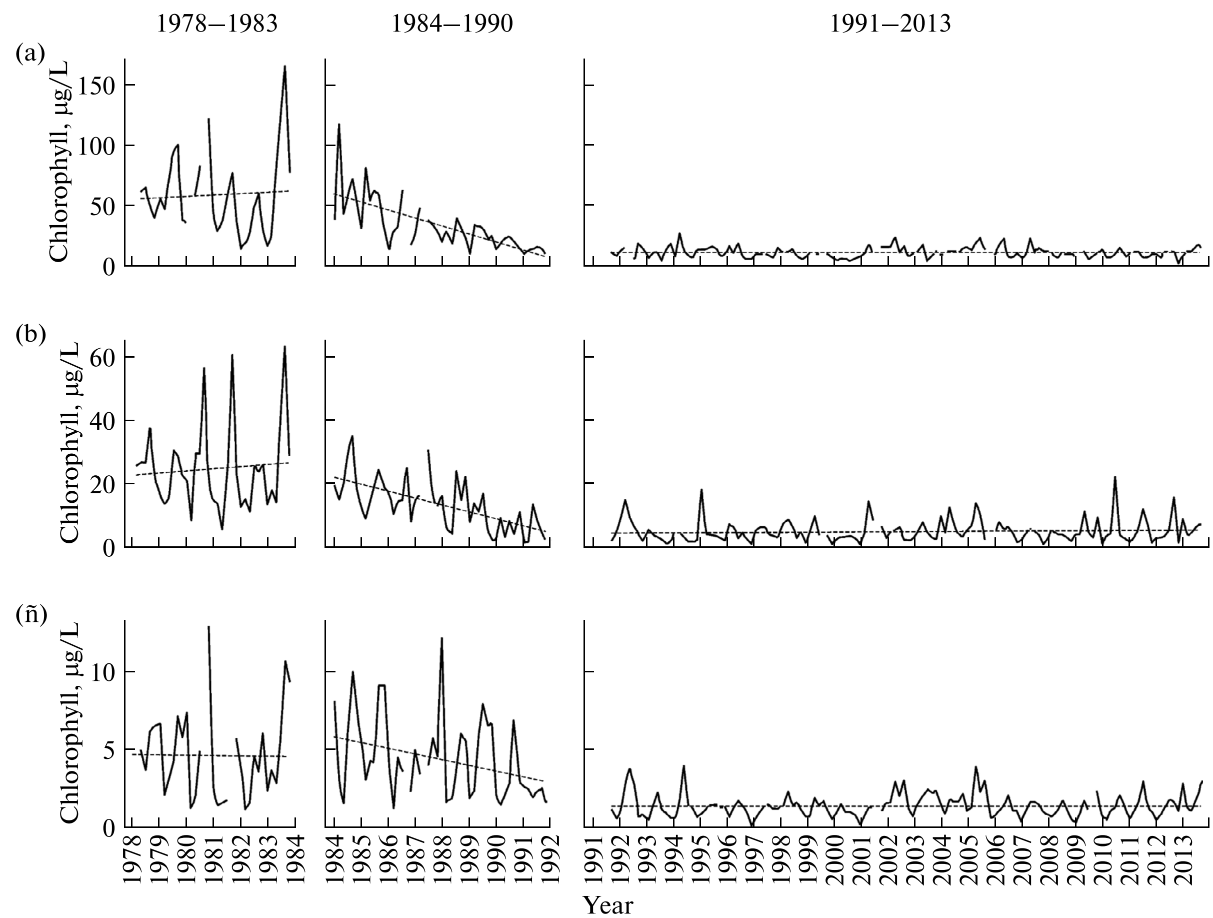

Fig. 2. The dynamics of the chlorophyll *a* concentration in the Naroch lakes in certain periods. The coefficients of determination of the trend lines shown in the figure are summarized in Table 2. Designations: (a), Lake Batorino, (b), Lake Myastro, (c), Lake Naroch.

detail. For this purpose, estimate the changes in the correlation between the fluctuations in the chlorophyll concentration in the lakes of the Naroch group. In the 1978–1983 period, the dynamics of the changes in the chlorophyll concentration in the water of each of the three lakes were clearly similar. The correlation coefficients (Fig. 3) varied from 0.44 to 0.66 and were significant at $p < 0.05$. The correlations between the data for lakes Naroch and Myastro and lakes Myastro and Batorino were significant, even at $p < 0.001$. The values of the correlation coefficients calculated for the average seasonal data, abolishing the intraseasonal fluctuations, were somewhat higher than for the monthly average values; however, due to the small sample ($n = 6$), the significance of the coefficients was relatively low (Fig. 3). The smoothing lines that were built using a local weighted regression [6] show that the dependence was nearly linear (Fig. 3).

Table 2. The coefficients of determination (R^2) of the trend lines for the time series of the chlorophyll *a* concentration in the Naroch lakes (regression lines are shown in Fig. 2)

Lakes	Years		
	1978–1983	1984–1990	1991–2013
Naroch	0.000005	0.11*	0.0006
Myastro	0.0077	0.41	0.0080
Batorino	0.0039	0.52	0.0021

* In the 1984–1993 period, R^2 is 0.26.

The correlation coefficients between the chlorophyll concentrations that were calculated on the basis of the monthly average values for the different lakes in the 1984–1990 period decreased (cf. Figs. 3a and 4a). The correlation coefficient between the monthly average values of the chlorophyll concentration in lakes Naroch and Batorino was only 0.25 and was statistically insignificant (Fig. 4a). For the average seasonal values, the correlation coefficients between the data on the chlorophyll concentration dynamics in lakes Naroch and Myastro, as well as in lakes Naroch and Batorino, were also reduced compared to the previous period (cf. Figs. 3b and 4b). However, the correlation of data for lakes Batorino and Myastro increased in

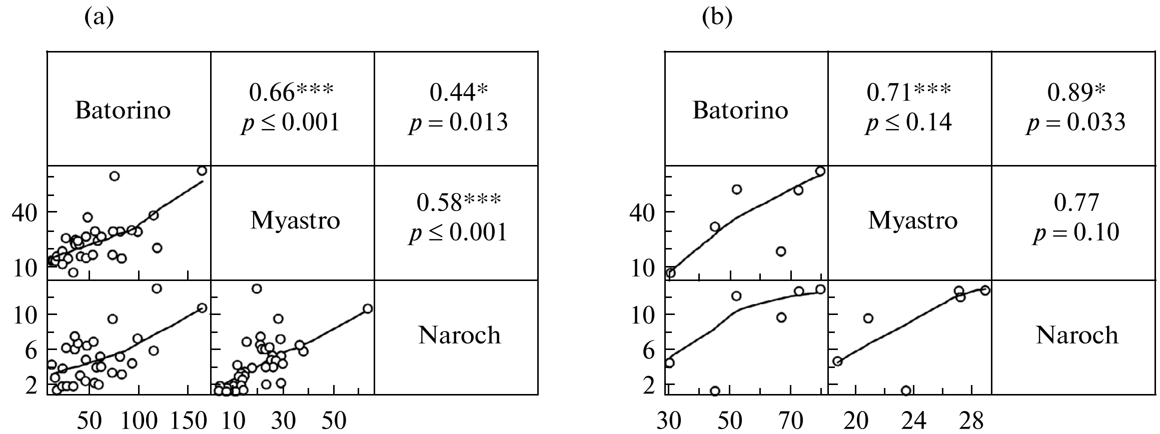

Fig. 3. Correlation coefficients and smoothing lines on scatterplots that were calculated on the basis of (a) monthly and (b) mean seasonal values of the chlorophyll *a* concentration in the Naroch lakes for the 1978–1983 period. The level of significance was $^*p < 0.05$ and $^{***}p < 0.001$. The axes of the scatterplots show the chlorophyll concentration in μg/L. The smoothing lines are represented as a weighted local regression obtained by the LOWESS curve-fitting method [6].

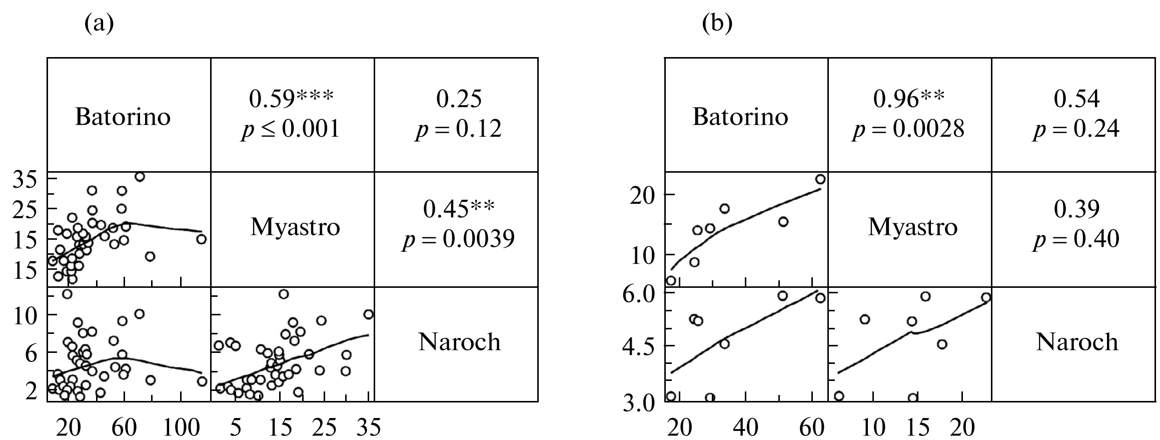

Fig. 4. The correlation coefficients and smoothing lines on scatterplots that were calculated on the basis of (a) monthly and (b) mean seasonal values of chlorophyll *a* concentration in the Naroch lakes for the 1984–1990 period. The level of significance was $^{**}p < 0.01$ and $^{***}p < 0.001$. The axes of the scatterplots show the chlorophyll concentration in μg/L. The smoothing lines are represented as a weighted local regression obtained by the LOWESS curve-fitting method [6].

this case (cf. Figs. 3b and 4b) and was statistically significant at $p < 0.01$. This indicates a greater contingency of the chlorophyll concentration dynamics in these lakes in the 1984–1990 period.

The correlation between chlorophyll concentrations calculated on the basis of monthly average values for different lakes in the 1991–2013 period continued to decrease (cf. Fig. 5a and Figs. 3a, 4a). The relatively higher levels of significance of the correlations for the monthly average values can be explained by the relatively longer duration of this period and, consequently, a larger sample. Compared with the 1978–1983 period, the correlations in the 1991–2013 period decreased by a factor of 1.3–2.4. The correlations for the average seasonal values decreased by a factor of 1.6–3.9. This may mean that in 1991–2013 the ecosystems of individual Naroch lakes were exposed to factors that influenced each of these water bodies differently. Interestingly, the significant difference in the correlations in these two periods (1978–1983 and 1991–2013) is observed in the absence of trends in the chlorophyll concentration dynamics in each of these periods.

Note that the ratio between the upper and lower quartiles for the chlorophyll *a* concentration in all lakes in both periods (1978–1983 and 1991–2013) changed insignificantly; it was 1.79–2.74. Therefore, the accidental changes in correlations due to the difference in the data scatter can be excluded with certainty. If we consider important hydroecological parameters, such as the contents of total phosphorus and nitrogen in the water and the water transparency during the above two periods (Table 3), we can see that the greatest changes occurred in Lake Myastro. The

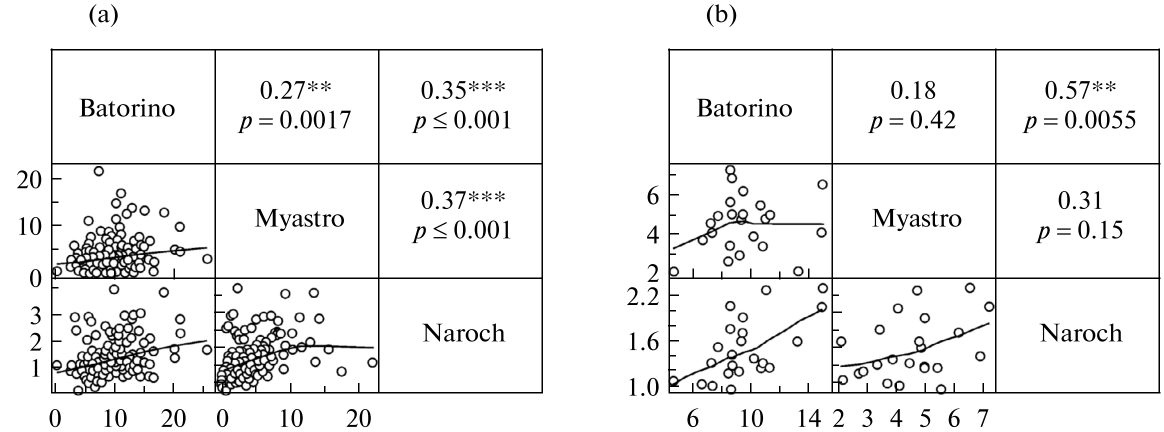

Fig. 5. The correlation coefficients and smoothing lines of scatterplots that were calculated on the basis of (a) monthly and (b) mean seasonal values of the chlorophyll *a* concentration in the Naroch lakes for the 1991–2013 period. The level of significance was $^{**}p < 0.01$ and $^{***}p < 0.001$. The axes of the scatterplots show the chlorophyll concentration in μg/L. The smoothing lines are represented as a weighted local regression obtained by the LOWESS curve-fitting method [6].

total phosphorus concentration in the 1991–2013 period decreased by 41% compared to the 1978–1983 period and the water transparency increased by a factor of 2.5. For Batorino and the Naroch lakes, qualitatively similar changes in these parameters were found.

DISCUSSION

The strong correlations between the fluctuations in the chlorophyll *a* concentrations in the Naroch lakes for the entire considered period (1978–2013) indicate that the lakes as a whole function as parts of a single system.

One of the main indicators of anthropogenic impact is the external nutrient load, i.e., the entry of nutrients with the atmospheric precipitation falling in this water area, as well as from the local sources and with the channel and diffuse runoff from the catchment area [7]. The presence of a correlation (Fig. 3) between the chlorophyll content in the lakes during the anthropogenic eutrophication in 1978–1983, which preceded the response of the ecosystem to the measures that were taken within the environmental-improvement program, suggests that the changes in the anthropogenic load on each of the Naroch lakes were largely comparable. As a result, the fluctuations in the chlorophyll concentration dynamics during the considered period were similar (Fig. 2).

Starting from 1984, the chlorophyll concentration clearly tended to decrease, which is apparently due to the implementation of the environmental-improvement program and the reduction in the nutrient load

Table 3. Changes in the hydroecological parameters of the Naroch lakes (mean ± standard deviation) in 1991–2013 compared to 1978–1983

Lake	Indices	Time period		% of initial value
		1978–1983	1991–2013	
Batorino	TP, mg/L	0.089 ± 0.031	0.036 ± 0.010	40
	Transparency, m	0.759 ± 0.301	1.230 ± 0.460	162
	TN, mg/L	1.597 ± 0.775	1.057 ± 0.492	66
Myastro	TP, mg/L	0.059 ± 0.021	0.035 ± 0.014	59
	Transparency, m	1.575 ± 0.403	3.970 ± 1.080	252
	TN, mg/L	1.096 ± 0.496	0.824 ± 0.426	75
Naroch	TP, mg/L	0.034 ± 0.011	0.015 ± 0.004	43
	Transparency, m	5.198 ± 1.172	6.781 ± 1.221	130
	TN, mg/L	0.710 ± 0.382	0.629 ± 0.313	89

TP, total phosphorus, TN, total nitrogen content.

in the catchment area of the Naroch lakes [7]. The correlation coefficients (Fig. 4) indicate that in the 1984 to 1990 period the changes in the chlorophyll concentration in lakes Batorino and Myastro were most similar. The weaker correlations in the fluctuations of the chlorophyll concentration in Lake Naroch compared to the other two lakes of the Naroch groups indicate that a disproportion in the changes in the nutrient load and, therefore, in the development of chlorophyll-containing organisms in the water column of each lake in this period compared to the 1978–1983 period began to occur. Lake Naroch is the last and the largest in the group of the Naroch lakes: approximately half of the surface runoff flows into Lake Naroch after passing through lakes Batorino and Myastro [8]; it is characterized by the longest period of water exchange (Table 1). This may cause a delay of the response of the ecosystem of Lake Naroch to external impacts (the reduction in the nutrient load on the catchment area of the Naroch lakes). In general, however, both the presence of the trend and the changes in the numerical values of correlation coefficients indicate a similar response of all of the Naroch lakes to the implementation of the environmental rehabilitation program of the catchment area in 1984–1990 (Fig. 4).

The 1991–2013 period is characterized by a divergence of the chlorophyll concentration dynamics in the Naroch lakes, which manifests itself as a distinct decrease in the correlations (cf. Figs. 3, 5) between the fluctuations in the chlorophyll concentration in individual lakes as compared to the 1978–1983 period (i.e., the period when, as in 1991–2013, there was no long-term trend in the chlorophyll concentration dynamics (Fig. 2)). This divergence may indicate the impact of a strong external factor that affects each of the three lakes differentially. It is noteworthy that this factor is not directly related to the reduction in the nutrient load on the catchment area of the lakes, which clearly manifested itself in 1984–1990 as a marked trend to a decrease in the chlorophyll concentration (Fig. 2) in each Naroch lake. This external factor could be the biological invasion of the Naroch lakes by the mollusk *Dreissena polymorpha*.

The invasion by the zebra mussel causes complex and diverse rearrangements in the structure and functioning of lake ecosystems [9–11]. The impact of the zebra mussel is primarily associated with its ability to form extremely dense populations, its strong breeding potential, and the filtering type of feeding. The zebra mussel exerts a significant impact on the nutrient regime due to the accumulation of the reserve nitrogen and phosphorus in the biomass. This leads to a partial withdrawal of these elements from the turnover for a fairly considerable period of time, equal to the sum of the lifespan of *Dreissena* and the time that is required for the decomposition of the soft tissue and shells of dead mollusks [1]. The decomposition time strongly varies depending on hydrochemistry (in particular, the calcium content) and the water mass movement [12]. An equally important factor that affects the turnover of matter in the lake ecosystem is the filtration activity of mollusks, their involvement in the destruction of organic matter, the excretion of bioavailable forms of nutrients during metabolism, the substrate-forming role of the zebra mussel in periphyton development, and the influence of this mollusk on early sedimentogenesis [1].

In Lake Myastro, the zebra mussel was first encountered in 1984 [13]. The first findings of the zebra mussel in Lake Batorino were made approximately at the same time [14]. In Lake Naroch, the first zebra mussels were found in 1989 [15]. The main factors that determine the development of zebra mussel populations are the amount of available substrate for colonization, the morphometry, and the trophic status of lakes [16]. The differences in the timing of zebra mussel invasion and certain differences in biotic and abiotic factors of the lakes could determine the differential impact of the life activities of the zebra mussel on individual Naroch lakes.

In Lake Naroch an abrupt increase in the zebra mussel population was observed. For example, in 1990, the average biomass of the zebra mussel in Lake Naroch was 1.5 ± 0.6 g/m^2, whereas in 1993 it reached 99 ± 30 g/m^2. This biomass value remained almost unchanged up to 1997. In lakes Myastro and Batorino, the average biomass of the zebra mussel in 1993 was 402 ± 187 and 79 ± 13 g/m^2, respectively. In 1995, the biomass of the mollusk in Lake Myastro slightly decreased (288 ± 118 g/m^2), whereas in Lake Batorino, conversely, it increased (100 ± 36 g/m^2) [16]. Since the zebra mussel biomass in lakes Naroch and Batorino in 1993 did not differ significantly, whereas in Lake Myastro it was several times higher than in the other two lakes [16], it can be concluded that Lake Myastro was the most suitable object for the invasion of this invasive species. Study results have shown that the greatest quantity of the zebra mussel biomass in Lake Myastro compared with the other two lakes may be due to the presence of relatively large amounts of a stable substrate for colonization (non-silted sand and stones) and, consequently, a better survival of mollusks and the preservation of large individuals in the population [16].

The correlations between the average seasonal concentrations of chlorophyll in 1991–2013 (Fig. 5) show that the decrease in the correlation between the changes in the chlorophyll concentration in time between the individual lakes were most characteristic of Lake Myastro, whose ecosystem experienced the zebra mussel invasion most significantly. Of the three lakes, the greatest increase in the water transparency and decrease in the concentration of total phosphorus in 1991–2013 compared to 1978–1983 was detected in Lake Myastro (Table 3), which was probably due to the relatively strong impact of the zebra mussel on the ecosystem of this lake [17]

The decrease in the total nitrogen concentration in Lake Myastro was less pronounced than the decrease in the water transparency and the total phosphorus concentration and, in general, did not differ from the changes in the nitrogen concentration of the other two lakes. The ratio between the nitrogen and phosphorus concentrations was, on average, 47 : 1 for Lake Naroch, 27 : 1 for Lake Myastro, and 31 : 1 for Lake Batorino (Table 3). Taking the fact into account that phosphorus becomes a limiting factor at a nitrogen-to-phosphorus ratio greater than 7 [18] or, according to other sources, greater than 12–17 [19, 20], it can be postulated that the limiting nutrient element in the development of primary producers in the Naroch lakes is phosphorus. In Lake Myastro, the zebra mussel biomass accumulated 37% of the phosphorus and 10.5% of the nitrogen from its reserve in water in 1978–1990 versus 14–16 and 3–5%, respectively, in lakes Naroch and Batorino [17]. The slurry deposition rate by the zebra mussel was also greatest in Lake Myastro, which provided the reserve particulate matter turnover of 24 $season^{-1}$ versus 10 and 16 $season^{-1}$ in lakes Naroch and Batorino, respectively. At the same time, the photosynthetic activity of the sediments deposited by the mollusks was much lower than that of the slurry that was deposited gravimetrically (0.64 ± 0.09 versus 0.89 ± 0.16 mg O_2/L per day) due to partial inactivation and assimilation of algae by the mollusks [17].

It should be noted that the relationship between the nitrogen and phosphorus content in the water and the chlorophyll concentration is unidirectional (i.e., the contents of these nutrients determine the chlorophyll concentration), whereas the relationship between the chlorophyll concentration and water transparency is bidirectional. A change in the water transparency leads to a change in the photic zone and, therefore, in the productive capacities of the phytoplankton. The phytoplankton and chlorophyll as its component are an integral part of the particulate matter, which determines the water transparency to the greatest extent. This determines the intricate mechanism of the response in the development of chlorophyll-containing organisms in the water column to the functioning of a population of such a potent water-filtering organism as *Dreissena polymorpha*.

Thus, our analysis showed that the responses of all three lakes to the intensive nutrient load and its subsequent decrease due to the implementation of the environmental-improvement measures were correlated. The subsequent divergence in the chlorophyll dynamics that was identified in this study was caused by different degrees of influence of the mollusk *Dreissena polymorpha*, whose life activities can significantly transform ecosystem processes, on each lake of the Naroch group. The differences in the impact intensity were determined primarily by the geomorphology of the lakes and the presence of a suitable stable substrate for colonization by the zebra mussel.

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