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Changes in the Planktonic System of the Nuclear Power Plant Cooling Pond Related to the Invasion of Dreissenidae (Mollusca: Bivalvia)

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Abstract: The introduction of mussels of the family Dreissenidae into the cooling pond of one of the nuclear power plants (NPP) of Ukraine, the Khmelnitsky NPP (north-western region), has caused significant changes both in the contour and in the pelagic parts of the techno-ecosystem. The following three periods were considered: (1) before the introduction of *Dreissena polymorpha*, (2) during the peak of its population development and (3) after the introduction of a second species of *Dreissena* and declining of abundance of Dreissenidae. We recorded a decrease in taxonomic richness and abundance of phytoplankton with the increase of the effect of *D. polymorpha.* No such changes were registered for the zooplankton community. The relationship between the biomass of phytoplankton and zooplankton were quite complex. In addition, the relations of diversity indicators of the phyto- and zooplankton communities were different during the three study periods: negative in the first, positive in the second and none in the third period. We concluded that the invasion of Dreissenidae into the water bodies and its effect on the ecosystems should be considered not only from the standpoint of their direct influence on the water transparency and phytoplankton abundance; this invasion could affect all the components of the pelagic and contour subsystems.

Key words: *Dreissena polymorpha, Dreissena bugensis*, phytoplankton, zooplankton, biomass, NPP cooling pond, contuorisation.

Introduction

The mussel species of the family Dreissenidae usually form communities of consortial type with strong influence on aquatic ecosystems because of their large numbers and biomass in the benthos and periphyton communities (Zebra Mussels 1992), high filtration activity and ability to increase quickly the density and biomass of their populations after establishing in new water bodies (Protasov 2006). These mussels can be attributed to the so-called ecosystem-engineer species (Karatayev et al. 1997). They cause benthification of water bodies (Zhu et al. 2006, Ostapenia et al. 2011, Cuhel & Aguilar 2013), also known as contourisation (Protasov 2014, Protasov & Sylaieva 2014). The effect of contourisation was probably described first by Liakhnovich et al. (1983) based on materials from the Lake Lukomsky (Belarus). The invasion of zebra mussel *Dreissena polymorpha* (Pallas, 1771) entails important changes not only in the benthos and periphyton of water bodies (Karatayev & Burlakova 1993, Karatayev et al. 1997, Terziyski et al. 2018) but also in the life of whole ecosystems (Smith et al. 1998, Zhu et al. 2006). The diversity of the colonised water bodies has not been studied thoroughly. The processes of the re-contourisation and ‘return’ of the ecosystems to a state close to that preceding the invasion have also been insufficiently examined.

According to Beshkova et al. (2014), due to the invasion of *D. polymorpha* in Zhrebchevo reservoir in Bulgaria, the total phytoplankton biomass did not change significantly, while the total abundance increased significantly. At the same time, in the post-invasion period the average individual volume of algae cells decreased, which indicated that *D. polymorpha* could contribute to switching of the phytoplankton communities to r-strategy. However, it should be noted that settlements of *D. polymorpha* and the main habitats of the phytoplankton are spatially distant (close to the bottom area and mainly in the near-surface layers of the water column, respectively), while the phyto- and zooplankton both occupy the water column.

In this work, we analyse our long-term data on a cooling pond ecosystem. The periods of the study of the reservoir before the introduction of *D. polymorpha* as well as the period of the beginning of contourisation were partially elucidated in our previous works (Protasov et al. 2011, Protasov & Sylayeva 2014). This paper presents the comparative results of all three periods, including new data from the period after the contourisation and the introduction of the second species of dreissenids. We aimed at defining the changes in the pelagic subsystem of a nuclear power plant (NPP) cooling pond ecosystem (based on the example of the Khmelnitsky NPP in Ukraine) during the invasion of Dreissenidae. We recognised three periods in this process: (1) before the introduction of the zebra mussel, (2) during the peak of its population development, and (3) after the introduction of a second species of *Dreissena* and decline in abundance of Dreissenidae.

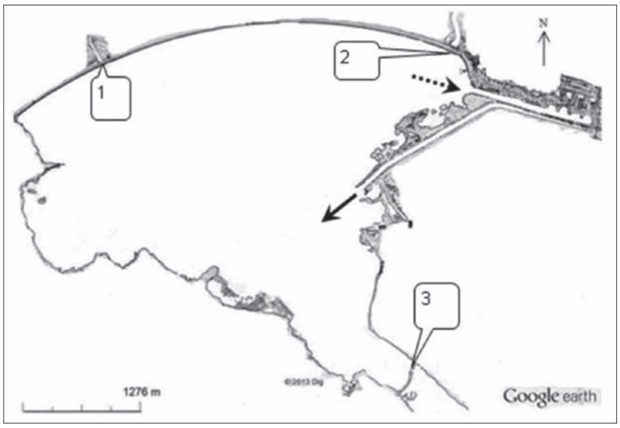

Fig. 1. Map of the cooling pond at the Khmelnitsky Nuclear Power Plant. The solid arrow indicates the hot water input from the discharge canal to the pond, while the dashed arrow indicates the cold-water output in the intake canal. 1 – Flood discharge and return of water filtrate through the dam; 2 – Water pumping from the Goryn River; 3 – Inflow of the Gniloy Rog River.

Materials and Methods

The Khmelnitsky Nuclear Power Plant (KhNPP) cooling pond (CP) is a reservoir filled by water from the Gniloy Rog and Goryn Rivers. It is located in the north-western part of Ukraine. The water surface of the reservoir is 15.4 km^2, while its volume is about 150 million m^3. In the north, the reservoir is restricted by a concrete embankment dam with a length of 6.85 km and a depth of 7–8 m. There is a concreted intake canal (IC), 1.60 km long, and a discharge canal (DC), 3.90 km long, in the eastern part of the reservoir. The water volume of the IC is about 0.8 million m^3, while this of the DC is 0.4 million m^3 (Fig. 1).

The cooling pond and the channels of the NPP, together with the water technical supply systems are considered as a unit techno-ecosystem. We consider it as a system of biotopes of natural and techno-anthropogenic nature, with their living population, united by a system of flows of matter and energy, changing in space and time (Protasov et al. 2011). This concept was established by Tansley (1935) who recognised the existence of both exclusively natural ecosystems and ecosystems that depend on humans to varying degrees. The study was conducted during three periods. In 1998–2001 (hereafter referred to as the first study period, I), only one unit of the NPP was operating. In 2004, the second power unit started operation, while the cooling pond was most probably infested with the zebra mussel in 2002–2003 (Protasov et al. 2011). In the second period (II), the studies were carried out in 2005–2008. In the third period (III), the studies were conducted in 2010–2015. Another species of the family Dreissenidae, the quagga mussel *Dreissena bugensis* Andrusov, 1897 was recorded for the first time in the cooling pond in 2012.

In this article, we deal with three groups of hydrobionts. The first one is benthos, or a group of different organisms, mobile or sedentary, living on friable substrates in the bottom area. The second one is periphyton, or a group of organisms living on the section of solid substrate and water, attached and/or mobile, of various sizes – from microorganisms to macroforms such as molluscs, sponges, bryozoans, etc. (Behning 1928, Bigs 2000, Skalskaya 2005, Sharapova 2007, Protasov 2011). The third is the plankton or a group of organisms living in the water column, under conditions of laminar water flow around them (Aleev 1986, Protasov 2011). The first two groups refer to contour groups living at the boundaries of biotopes (Zaitsev 1986, 2015). The third group lives in relatively homogeneous conditions inside the biotope (Protasov 2011).

The hydrobiological studies were carried out according to standard methods (Arslan et al. 2006, Protasov et al. 2011). The transparency was measured using a Secchi disk with a diameter of 30 cm. The hydro-facilities and the bottom of the cooling pond were explored using light diving equipment (Protasov et al. 1982). The periphyton samples were taken at the slopes of the dam, at the intake canal and from the stones in the southern area, at the inflow of the Gniloy Rog River. The zoobenthos was sampled by diving and by a sectional bottom grab SDCh-100 (capture area of 0.01 m^2) throughout the water part of the cooling pond. The mollusc filtration rate was determined based on the amount of consumed oxygen (Alimov 1981). The zooplankton filtration was defined based on the relationship between the biomass and the filtration rate according the approach of Gutelmacher (1986), considering the entire zooplankton community as a single filtration system. The phyto- and zooplankton samples were taken in the pelagic part of the cooling pond from 0.05–0.50 m from the surface, using a Patalas bathometer. In addition, at some stations, the zooplankton was collected using an Apstein's net (mesh size 80 μm) from a depth of 3 m to the water surface.

The hydrochemical data were received from the Ecological and Chemical Laboratory of the KhNPP.

The term 'the lowest determined taxon' (LDT), which denotes taxa of both species and higher rank defined in accordance with the identification capabilities, was used after Bakanov (1997) to describe the taxonomic richness and diversity of algae and invertebrates. The nomenclature and systematic affiliation of phytoplankton taxa were according to the Algaebase (Guiry & Guiry 2019). The phytoplankton species identification and indication of the trophic condition followed the recommendations of Barinova et al. (2006, 2019).

We used published phytoplankton data for 1998–2010 and zooplankton, zoobenthos and zooperiphyton data for 1998–2012 (Protasov et al. 2011, Protasov & Sylaieva 2014, Protasov & Novoselova 2015). The new data used in the present study are those about phytoplankton in 2011–2015 and about zooplankton, zoobenthos and zooperiphyton in 2013–2017.

A coefficient of variation (CV) was used to assess the heterogeneity of distribution of the plankton and zoobenthos indicators over the water area (Plokhinsky 1970). The species diversity based on abundance and biomass was calculated using the Shannon index (Pesenko 1982). The taxonomic diversity was estimated using the same index, considering the distribution of the LDT or the species in algal divisions (Protasov 2002). The relationship between the algal community and environmental variables was determined using CCA plots constructed in the CANOCO 4.5 Program.

Results

Physical and chemical parameters

During the first study period, the average water transparency in the cooling pond in summer varied from 1.03±0.03 m in June 1998 to 1.33±0.17 m in July 1999. After the introduction of *D. polymorpha* (study period II), the transparency changed significantly (Fig. 2). The highest average values within the water body, i.e. 3.02±0.23 m, were detected in September 2008 in the intake canal where, in the temporary absence of flowage (both units did not operate during the study period because of preventive maintenance), the colonies of *D. polymorpha* were found all over the covering concrete (Fig. 2). In some parts, the transparency reached up to 4 m.

In period I, the average annual content of calcium ions (Ca^{2+}) varied from 49.71 to 54.85 mg/dm^3, while the concentration of sulphate ions (SO_4^{2-}) was between 41.25 and 95.67 mg/dm^3. The average sum of ions in the cooling pond was 352.58 mg/dm^3, which corresponded to a relatively low mineralisation.

Period II was characterised by a gradual increase in the content of bicarbonate ions and chlorine ions and the total mineralisation was up to 438.7 mg/dm^3. During this period the trend of decreasing concentration of calcium ions continued (the average values in 2006–2010 were 44.86 mg/dm^3, reaching 38.0 mg/dm^3 in August – September 2006), along with the increasing concentrations of sulphate ions and phosphate ions. In period II, the average content of phosphate ions in the water of the cooling pond increased from 0.028 to 0.066 mg P/dm^3. The ratio between the nitrogen and the phosphorus changed, being 9:1 in the first study period and 5:1 in the second one.

In period III, the transparency decreased to about 1.5–2.0 m. The concentration of calcium ions in the

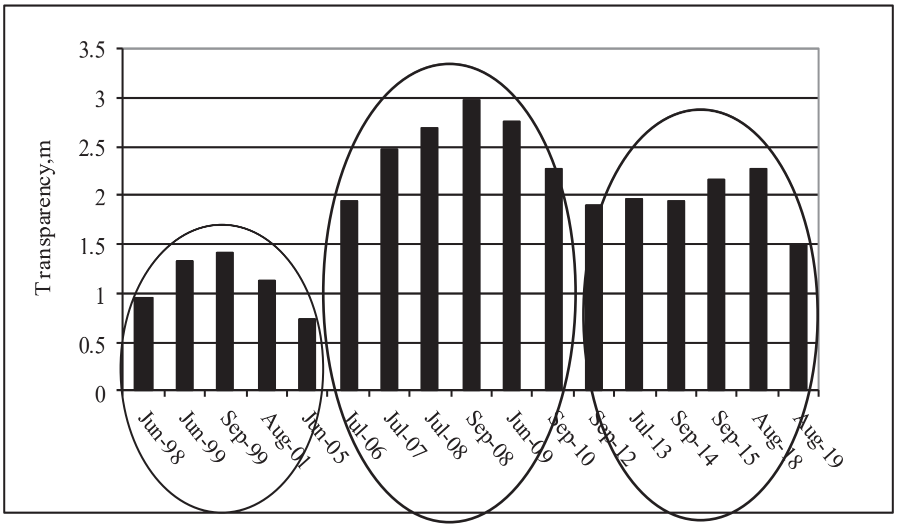

Fig. 2. Changes of water transparency in the cooling pond of the Khmelnitsky NPP (1998-2019).

water increased to 52.85 mg/dm^3 in 2014 and to 55.85 mg/dm^3 in 2015 (average annual values). The average content of sulphate ions in the mentioned years was 90.36 mg/dm^3 and 100.95 mg/dm^3, respectively. The indicators of mineralisation continued to increase to 566.80 mg/dm^3 on average in 2015. The entire studied period (from 1998 and onwards) was marked by an increase in the content of phosphate ions. In period III, their average annual concentration reached 0.228 mg P/dm^3 in 2014 and 0.263 mg P/dm^3 in 2015. The ratio between the nitrogen and the phosphorus changed to 2:1 in this study period.

Benthic and periphytic communities

The dynamics of the benthic and periphyton stages of the populations of *Dreissena* spp. had their own characteristics. In 2005–2007, the average biomass of *D. polymorpha* in the reservoir and in the intake canal (periphyton) was from 6181.2±5492.4 g/m² to 14827.2±9894.7 g/m², respectively (Table 1). The high values of CV, up to 88.9%, indicated an uneven distribution of the biomass, which naturally increased at a depth of 4–6 m, when the samples were taken along the transect from the surface to the bottom. The maximum biomass value of 20.4 kg/m² was registered in 2005 in the intake canal (Table 1). The minimum biomass was observed in 2012, when *D. bugensis* was introduced into the reservoir; its biomass had values from 42.0±58.5 g/m² to 354±731.1 g/m² in the intake canal and at the dam, respectively.

At the bottom, *D. polymorpha* was distributed practically along the entire water area of the cooling pond, including the deeper silted parts (in the study period II). Subsequently, its distribution was reduced to the isobaths of 2–5 m. The colonies had patchy distribution and both individual small colonies and massive settlements were recorded. This determined the significant variability in the recorded biomass. For example, in July 2006, at the individual stations the absolute minimum biomass was 0.18 g/m^2, while the maximum was 9722.61 g/m^2.

After the appearance of *D. bugensis* in the cooling pond in 2012, the total biomass of dreissenids did not increase and its values remained rather low (169.45 ± 347.73 g/m^2). In 2013–2017, the biomass of Dreissenidae showed a large range of values (from 12.05 ± 8.78 g/m^2 up to 1612.69 ± 2767.0 g/m^2) and there was no clear trend of decrease or increase.

Planktonic communities

Changes in the pelagic part of the ecosystem occurred during the studied periods. According to the data from June 1998, 72 LDT of algae were recorded, while in June 1999 they were 94 LDT. The community was characterised by predominance of species of green algae. In total, algae from eight divisions were recorded (Fig. 3). In period II, considerable changes took place in the phytoplankton: the representatives of five divisions disappeared, while in period III they returned in a reverse order of their disappearance.

In the zooplankton community, the quantitative dominance of any of the groups was not well expressed. In the four main groups (Cladocera, Copepoda, Rotifera, larvae of Dreissenidae) there was a certain trend of decreasing richness.

The distribution of the phytoplankton in the three periods was characterised by a decrease in the abundance and biomass within period II. Thus, the average abundance was reduced by several orders of magnitude from 112.45 million cells/dm^3 in the

Table 1. Biomass of Dreissenidae in the benthos and periphyton of the Khmelnitsky NPP cooling pond (averaged data ± SD). CV – coefficient of variation.

Date (year/month)	Average biomass, (pond) benthos, g/m²	Average biomass (dam), periphyton, g/m²	Average biomass (intake canal), periphyton g/m²	CV % benthos	CV % periphyton (dam)	CV% periphyton (inflow canal)	Maximum biomass, benthos, g/m²	Maximum biomass, (dam), periphyton, g/ m²	Maximum biomass, (intake canal), periphyton g/ m²
2005	1584.7± 2270.5	14412.2± 5591.2	14827.2± 9894.7	143.3	38.8	66.7	8201.8	19900.5	20370.4
2006	2118.7± 2765.0	6181.2± 5492.4	7950.5± 6311.5	130.5	88.9	79.4	14639.5	16889.0	18400.0
2007	1620.7± 2028.8	6878.4± 3867.6	12169.9± 4525.5	125.2	56.2	37.2	7257.2	14418.2	21303.0
2008/07	1712.1± 1789.6	2195.8± 1806.3	10823.7± 3231.1	104.5	82.3	29.9	5427.1	4921.4	14708.2
2008/09	—		5681.0± 5200.8			91.5			14911.0
2010	451.8± 823.4	4930.2± 5900.9	5877.5± 4721.7	182.3	119.7	80.3	2613.2	11742.0	12518.0
2012	169.5± 347.7	354.3± 731.1	42.0± 58.5	205.2	206.4	139.4	1022.6	1661.0	129.5
2013	1021.0± 718.8	6822.1± 7062.0	3236.0± 4047.6	70.4	103.5	125.1	1914.6	20335.1	8900.0
2014	243.9± 506.8		3063.7± 3286.4	207.8		107.3	1274.0		8018.0
2015	1612.7± 2767.0		904.9± 1939.3	171.6		214.3	7011.0		5244.0
2016	12.0±8.8		795.8± 854.8	72.9		107.4	19.2		7333.0
2017	608.2± 807.0	0.4±0.8	7789.1± 8993.9	132.7	197.7	115.5	1977.0	1.6	15731.5

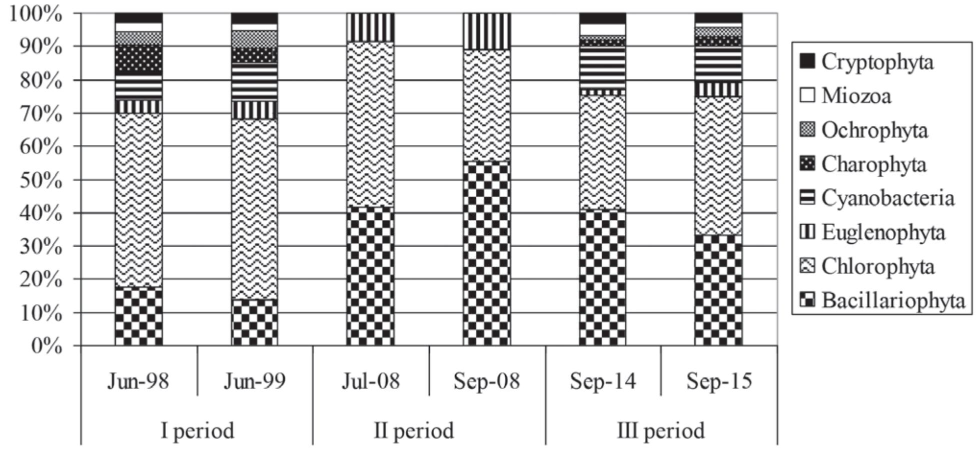

Fig. 3. Taxonomic richness (%) of algae in the three periods of study.

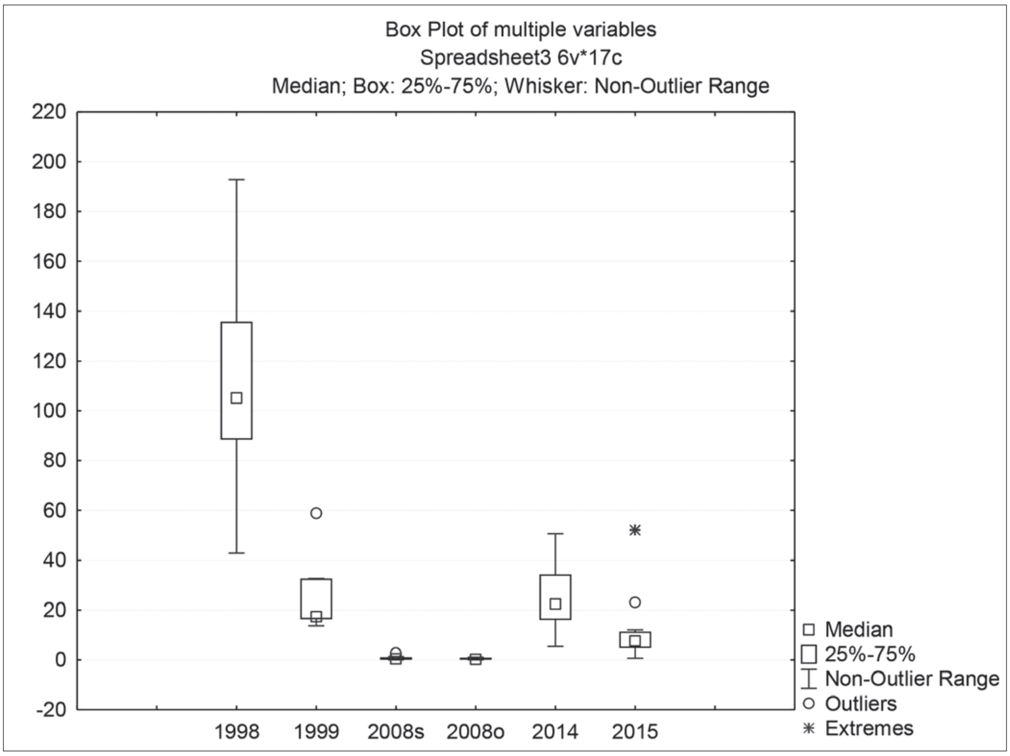

Fig. 4. Dynamics of the phytoplankton abundance (million cells/dm^3) in the three periods of study.

summer of 1998 to 0.46 million cells/dm^3 in the autumn of 2008 (Fig. 4).

The values of the relative abundance of the phytoplankton phyla had similarities during periods I and III (Fig. 5). The cyanobacteria had the highest abundance, while diatoms, cyanobacteria and green algae – the highest biomass. During period III, the pattern in the dominance among the groups returned to that of period I. In period II, the diatoms predominated significantly in terms of abundance and biomass (Fig. 5).

The zooplankton biomass decreased during period II (Fig. 6). However, in the first period high biomass values were observed only in 2001, followed by relatively large biomass of cladocerans (Fig. 6).

Phyto- and zooplankton interrelations

The general relationship between the phytoplankton and zooplankton biomass were quite complex (Fig. 7). In period I, the phytoplankton biomass varied between 12.04 mg/dm^3 and 45.37 mg/dm^3. Dominant by biomass were the following species: *Stephanodiscus hantzschii* Grunow (Bacillariophyta) (12.0–80.8% of the total biomass), the large-celled *Ceratium hirundinella*

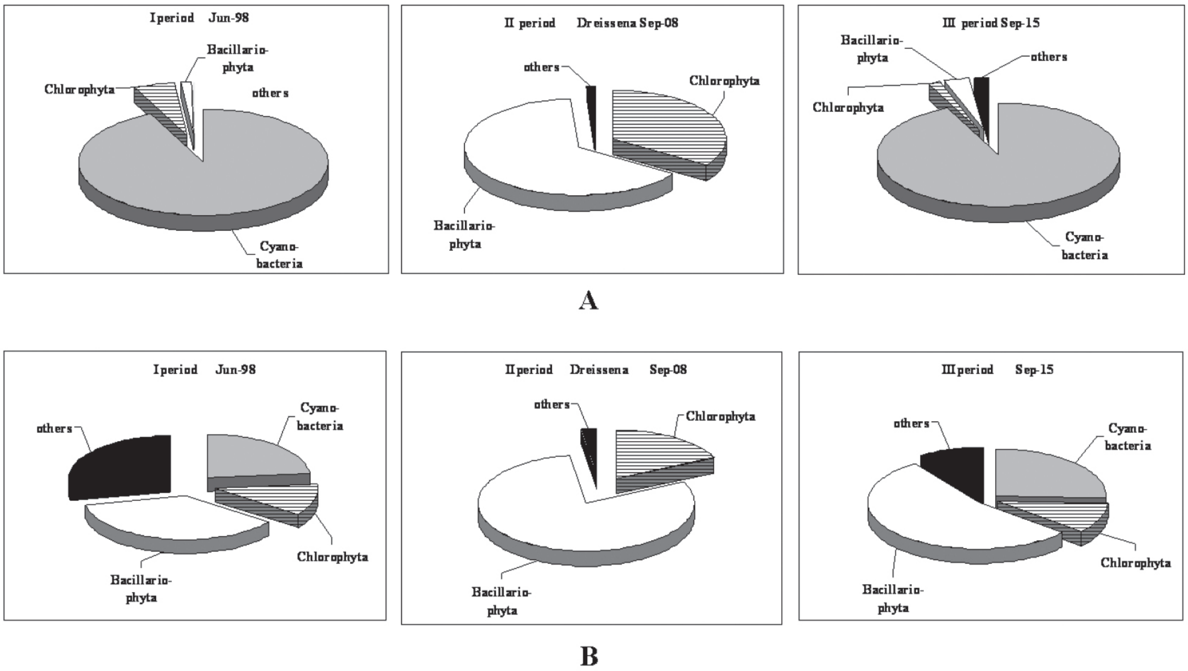

Fig. 5. Relative abundance (A) and biomass (B) of the phytoplankton phyla during the three periods of study.

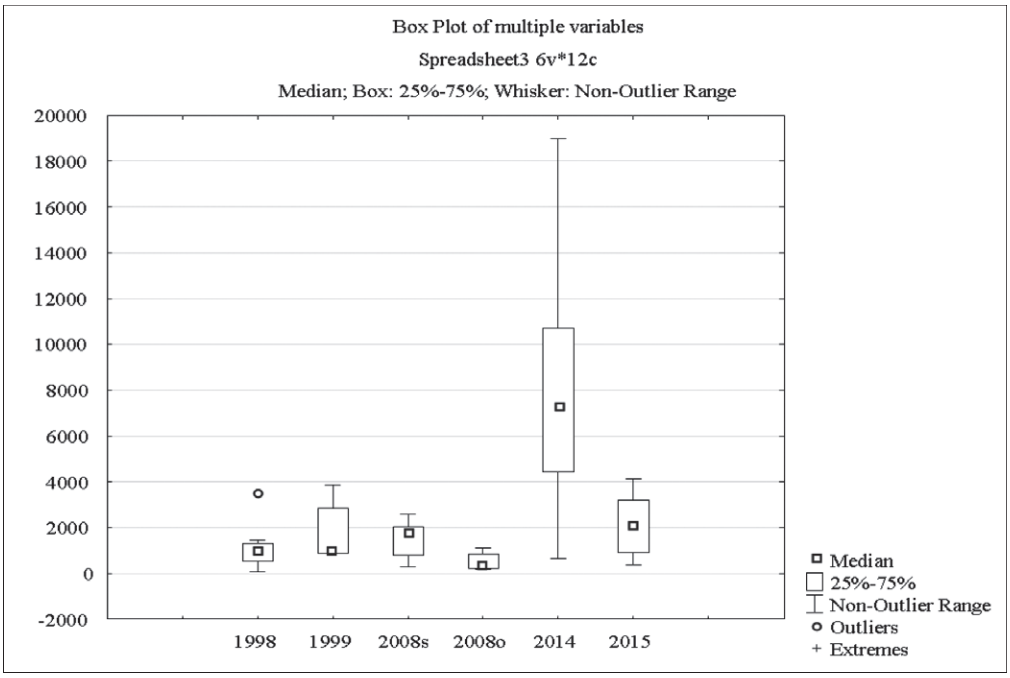

Fig. 6. Dynamics of the zooplankton biomass (mg/m^3) in the three periods of study.

(O. F. Müller) Dujardin (Miozoa) (26.0–44.7%) and *Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault (6.4–25.9%) and *Microcystis aeruginosa* (Kützing) Kützing (12.8%) (Cyanobacteria). The proportion of Chlorophyta in the total phytoplankton biomass ranged from 3.3% to 20%.

In period II, the minimum biomass of zooplankton was registered with the biomass of phytoplankton being low. The representative of Bacillariophyta, *Aulacoseira ambigua* (Grunow) Simonsen (79.9%) and *Aulacoseira granulata* (Ehrenberg) Simonsen (72.6%), as well as of Chlorophyta, *Monactinus simplex* (Meyen) Corda (54.0%), dominated the biomass.

During the period of the maximum zooplankton biomass, the phytoplankton biomass was 1.11–1.55

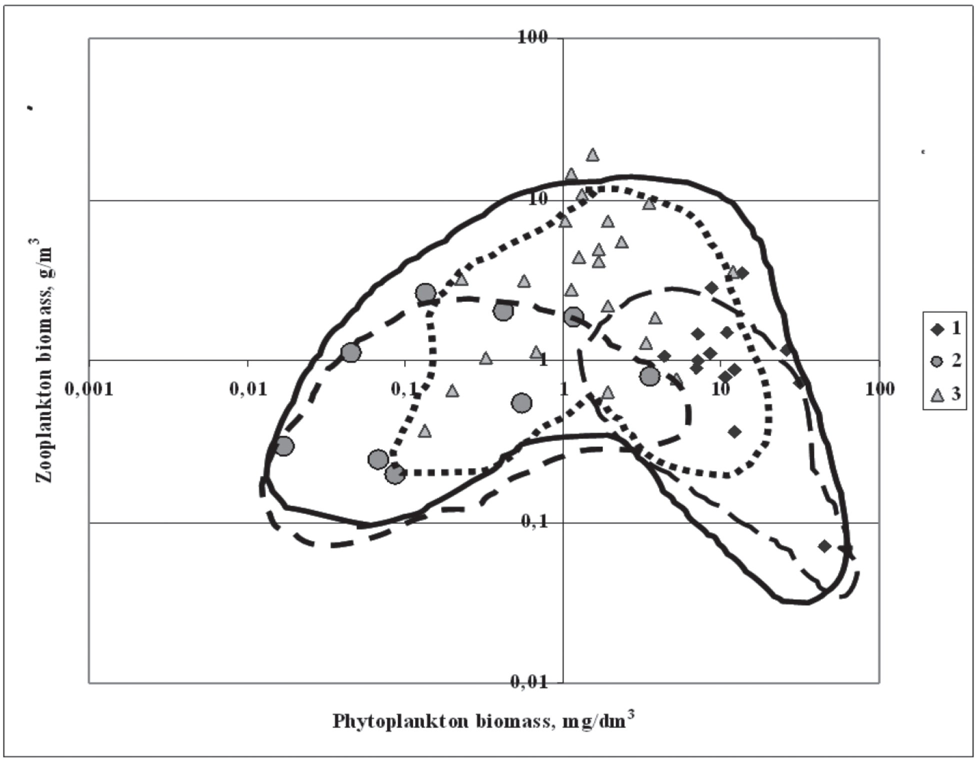

Fig. 7. Relationship between phyto- and zooplankton biomass in the three study periods: 1 – period I; 2 – period II and 3 – period III. The fields of points that belong to the three study periods are delineated.

mg/dm^3. The taxa *M. aeruginosa* (32.6–45.3%), *A. granulata* (18.2) and *Peridinium* sp. dominated in period III. The highest values of the zooplankton biomass (10.7–18.9 g/m^3) were due to the dominance of *Daphnia longispina* (O. F. Müller), accounting from 60% to 78% of the total biomass.

Complex interactions between the phytoplankton and zooplankton took place presumably along with the increased influence of Dreissenidae.

The composition and structure of the phytoplankton communities were different for each period (Table 2).

The average mass of phytoplankton cells in period I varied between 1.24x10^{-7} and 4.32x10^{-7} mg. The average cell mass among the main divisions of algae was 0.13x10^{-7}–4.33x10^{-7} mg for Cyanobacteria, 1.30x10^{-7}–4.60x10^{-7} mg for Chlorophyta, 34.3x10^{-7}–97.3x10^{-7} mg for Bacillariophyta. The average cell mass in period II was slightly higher (2.19x10^{-7} – 7.12x10^{-7} mg) than in period I.

The average mass of algae cells in period III was the lowest for the whole period of the study (0.62x10^{-7}–0.69x10^{-7} mg). After their disappearance in period II, Cyanobacteria dominated again in the phytoplankton and prevailed in abundance (up to 94.3%). The mass of their cells (0.24x10^{-7}–0.30x10^{-7}) was still smaller than in period I, while that of Chlorophyta (2.01x10^{-7}–3.89x10^{-7}) did not change in comparison with the same in period II and that of Bacillariophyta (28.9x10^{-7}–34.6x10^{-7}) increased by an order of magnitude.

Figure 8 indicates a complex relationship between the average cell mass of the phytoplankton and the zooplankton biomass. Within the range of zooplankton biomass 5–15 g/m^3, the average mass of algae cells decreased almost twice, while for the zooplankton biomass of less than 5 g/m^3 the decrease was almost ten times. In parallel with the increase in the zooplankton biomass, the phytoplankton communities included more and smaller forms.

Diversity in the pelagic communities. The diversity of phyto- and zooplankton communities (including both the degree of dominance or evenness and species richness) varied in the three periods (Fig. 9). In period I, with the increase of the diversity of phytoplankton, the diversity of zooplankton (both in abundance) decreased. In period II, that relationship was reverse. In period III, these ratios did not return to their previous values and no clear trends were found.

Dynamics of algae species as indicators of trophic status. Along with the changes in the trophic parameters of the cooling pond, such as transparency, concentration of nutrients and their ratios, there were also changes in the composition and number of

Table 2. The dominance structure of the phytoplankton (PPL) at extreme values of the zooplankton (ZPL) biomass. LDT – the lowest determined taxon.

Zooplankton extremum / phytoplankton extremum	Period	Richness of phytoplankton LDT	Total phytoplankton biomass mg/dm^3	Diversity of phytoplankton abundance, bit/ind	Diversity of phytoplankton biomass, bit/mg	Evenness of phytoplankton abundance	Evenness of phytoplankton biomass	Dominant species	Biomass of dominant phytoplankton, %
ZPLmin / PPLmax	I	24	12.04	1.986	2.382	0.43	0.52	*Stephanodiscus hantzschii*	27.9
								Ceratium hirundinella	26.0
								Aphanizomenon flosaquae	25.9
ZPLmin / PPLmax	I	28	31.29	2.315	2.691	0.48	0.56	*Ceratium hirundinella*	44.7
								Microcystis aeruginosa	12.8
								Stephanodiscus hantzschii	12.0
								Phacotus coccifer	11.6
								Aphanizomenon flosaquae	6.4
ZPLmin/ PPLmax	I	40	45.37	2.531	1.319	0.48	/0.25	*Stephanodiscus hantzschii*	80.8
ZPLmin / PPLmin	II	4	0.017	1.039	1.006	0.52	0.50	*Aulacoseira ambigua*	79.9
ZPLmin / PPLmin	II	2	0.087	0.679	0.995	0.68	1	*Monactinus simplex*	54.0
ZPLmin /PPL min	II	2	0.068	0.984	0.847	0.98	0.85	*Aulacoseira granulata*	72.6
ZPLmax/ PPLaverage	III	16	1.11	0.947	2.621	0.24	0.07	*Microcystis aeruginosa*	45.3
								Aulacoseira granulata	18.2
ZPLmax / PPLaverage	III	11	1.58	1.267	2.531	0.37	0.73	*Microcystis aeruginosa*	32.6
								Peridinium sp.	20.8

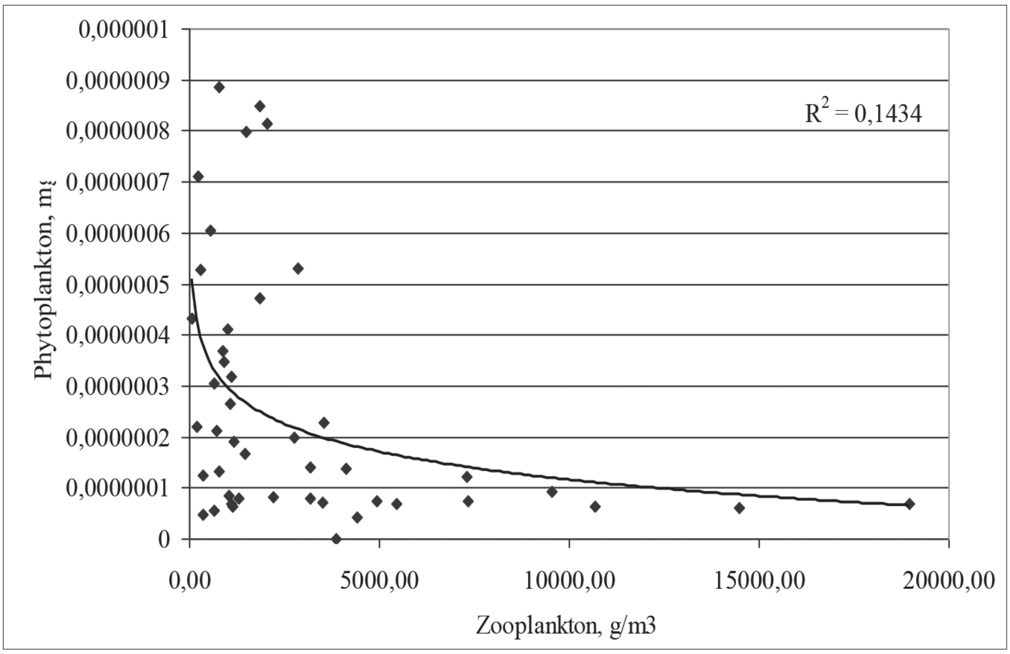

Fig. 8. Relationship between zooplankton biomass and phytoplankton average cell mass for the whole study period.

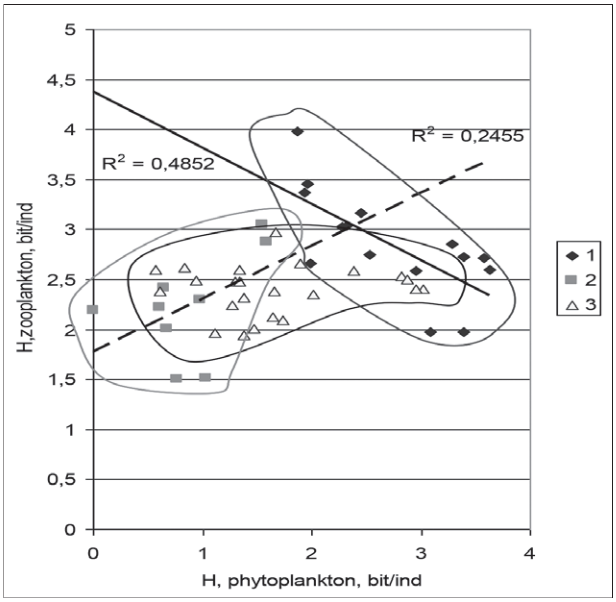

Fig. 9. Relationship between the diversity in abundance of phyto- (X-axis, bit/ind.) and zooplankton communities (Y-axis, bit/ind.) in the three study periods: 1 – period I; 2 – period II and 3 – period III.

the phytoplankton species trophic indicators (Table 3). The indicators of meso- and eutrophic conditions prevailed. In period II, matching the impoverished total composition, the number of indicator species from all groups naturally decreased and their ratio changed. After the restoration of the phytoplankton total richness and its composition at the level of phytoplankton groups (period III), there was an increase in the quantity of the trophic indicator species.

Relationship with environmental parameters. In period I, the environmental variables had diverse influence on the phytoplankton community (Fig. 10A). The permanganate oxidisability, nitrates and ammonia influenced the biomass positively. The water transparency was negatively associated with the biomass of phytoplankton in period II, while ammonia was positively associated. The permanganate oxidisability had a positive effect on the structural variables and species richness of the phytoplankton. The nitrates and water transparency stimulated the structural variables and species richness of the phytoplankton in period III, whereas the algal biomass was influenced positively by the ammonia and negatively by the water transparency and permanganate oxidisability. The CCA analysis suggested no association between the phytoplankton abundance (*Abund*) and any of the studied variables for the three study periods (Fig. 10).

Filtration activity of Dreissenidae and zooplankton. Our estimate of the total quantity of filtrators in the cooling pond showed that the mass of Dreissenidae was one or two orders of magnitude higher than the mass of zooplankton (Table 4). The total amount of *D. polymorpha* in the pond reached 12,800 tons (2005). In 2007 and 2014, the total mass of zooplankton exceeded 1000 tons, while in the other years it was considerably lower. However, the intensity of filtration per unit mass of zooplankton was elevated, i.e. two orders of magnitude higher than that of Dreissenidae in the periphyton and benthos. According to our calculations, this indicator for *D. polymorpha* was 0.00126 dm^3/mg of biomass per day.

Table 3. Dynamics of the number of indicator species for trophic levels within the floristic spectrum of the phytoplankton in the different periods of study.

Periods→	**I**	**I**	**II**	**II**	**III**	**III**
Trophic levels↓	**VI.1998**	**VI.1999**	**VII.2008**	**IX.2008**	**IX.2014**	**IX.2015**
Oligotrophy	5	2	2	0	2	5
Mesotrophy	8	10	2	1	11	11
Eutrophy	7	7	0	1	12	9
Total sum	20	19	4	2	25	25

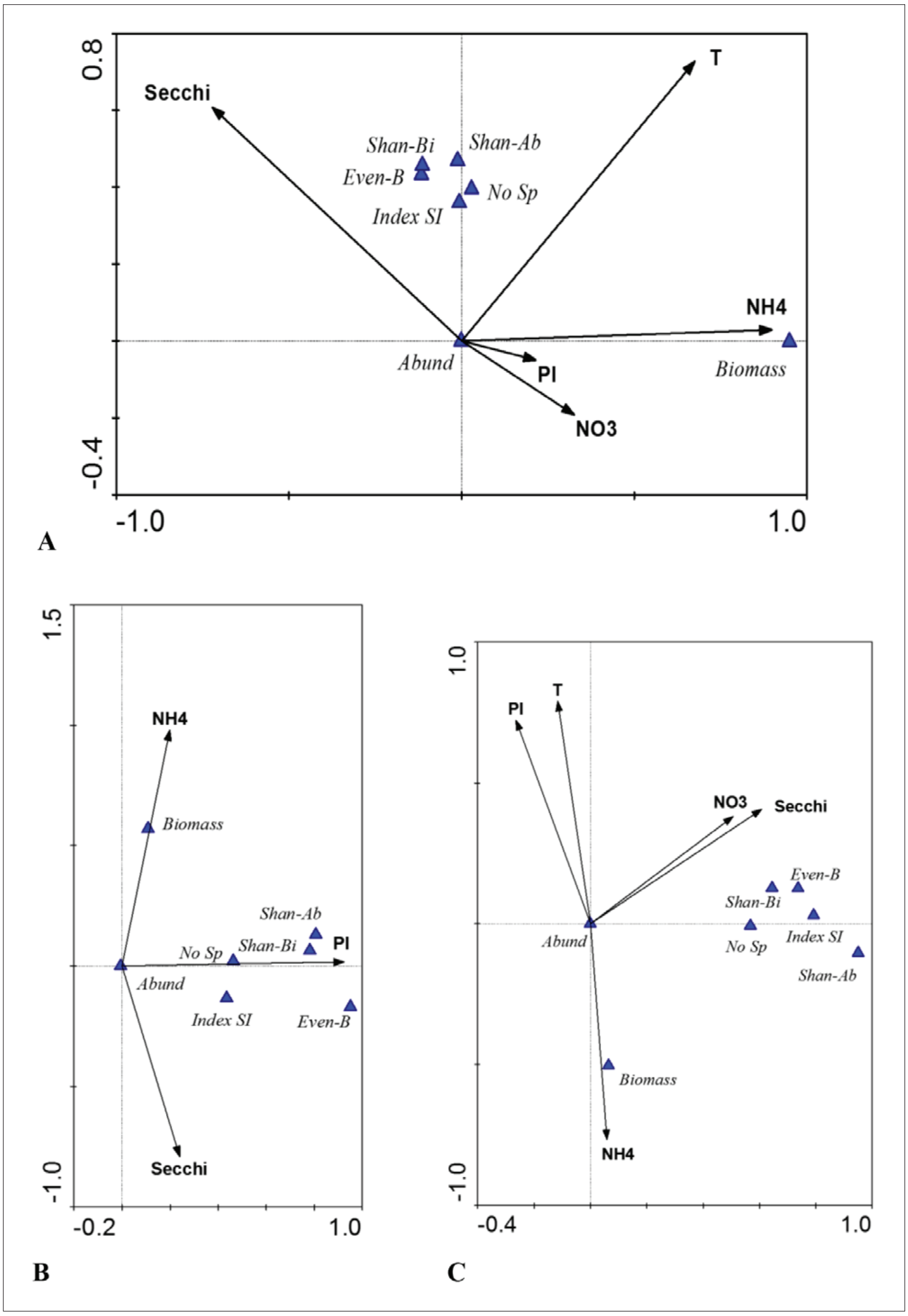

Fig. 10. CCA plots for the relationship between the algal community and environmental variables in each of the three study periods: **A** – Period I (Monte Carlo Test of significance: eigenvalue = 0.009, P-value = 0.002); **B** – Period II (Monte Carlo Test of significance: eigenvalue = 0.009, P-value = 0.616); **C** – Period III (Monte Carlo Test of significance: eigenvalue = 0.001, P-value = 0.012). PI – permanganate oxidisability.

Table 4. Total mass of Dreissenidae in the cooling pond, filtering activity of Dreissenidae in the periphyton and benthos (excluding the intake canal) and filtering activity of the zooplankton. * – no *Dreissena*; ** – no data.

Year	Total mass of *Dreissena* at the dam (in periphyton), tons	Total mass of *Dreissena* in the intake canal (in periphyton), tons	Total mass of *Dreissena* (in benthos), tons	Total mass of the zooplankton, tons	Filtration of *Dreissena* at the dam (in periphyton), mln m^3/day	Filtration of *Dreissena* in the intake canal (in periphyton), mln m^3/day	Filtration of *Dreissena* (in benthos), mln m^3/day	Filtration of the zooplankton, mln m^3/day
1998	*	*	*	200	*	*	*	30.0
1999	*	*	*	200	*	*	*	30.0
2001	*	*	*	700	*	*	*	110.0
2005	2962	1245	8546	500	3.7	1.6	12.3	90.0
2006	1270	668	8189	350	1.6	0.8	11.7	40.0
2007	1414	1022	3265	1350	1.8	1.3	2.9	60.0
2008	451	909	4410	200	0.6	1.1	2.5	30.0
2009	**	**	2153	400	**	**	2.6	60.0
2010	1013	494	961	70	1.3	0.6	0.4	15.0
2012	73	4	460	**	0.1	0.0	0.2	**
2013	1402	272	1057	**	1.8	0.3	1.1	**
2014	**	257	679	1200	**	0.3	0.4	144.0
2015	**	76	2911	310	**	0.1	1.4	46.1

The share of zooplankton in the total filtration was significantly higher than that of *D. polymorpha*, for example, 74% in 2006 and 99% in 2014 compared to the filtration of zebra mussels in contour groups. In the contour groups, up to 67% (2012) of all the filtration by Dreissenidae were due to *D. polymorpha* of the benthic part of the Dreissenidae populations.

Discussion

The invasion of zebra mussel into the cooling pond has significantly affected both the hydrophysical and hydrochemical parameters and the relationship between the components of the plankton. The mass development of Dreissenidae in the cooling pond was accompanied by changes in the trophic parameters of the water bodies, such as transparency, concentration of nutrients and their ratios.

Previous long-term studies have shown the water transparency is related to the biomass of planktonic algae in this reservoir (Protasov & Novoselova 2015) Thus, the transparency can be a good indicator of contourisation processes, as pointed out by other researchers (Ostapenia et al. 2011, Zhu et al. 2006). Changes of some hydrochemical indicators (decrease in the content of calcium ions in the water) at the beginning of the contourisation processes and the mass development of *Dreissena* also show a significant dependence on the hydrochemical regime, for example through the content of the calcium ions that are used to build their shells.

The entire study period was marked by an increase in the content of the phosphate ions. During period III, their average annual concentration reached 0.228 mg P/dm^3 in 2014 and 0.263 mg P/dm^3 in 2015. This was a result not only of the processes within the cooling pond, but also due to external factors. The reservoir received on average more than 5 million m^3/year of wastewater (Protasov et al. 2011). In 2013–2017, the biomass of Dreissenidae varied greatly and there was no clear trend of decrease or increase.

The influence of Dreissenidae was not the only factor determining the development of phyto- and zooplankton. The relationship between zooplankton and phytoplankton was also important. The phytoplankton reached its maximum abundance in period I. At the stations where minimal zooplankton biomass values were registered, phytoplankton biomass was the highest. Apparently, the large-cell phytoplankton was less accessible to the zooplankton (Kiselev 1980). In period II, the minimum values of the zooplankton biomass were likely associated with competitive trophic relations with *D. polymorpha* as demonstrated by Karatayev et al. (1997). In period III, the maximum zooplankton biomass was observed at stations with an average phytoplankton biomass. The zooplankton was probably the determining factor in the regulation of the dimensional structure of the phytoplankton. Despite the fact that with a relatively large biomass of zooplankton, the sizes of cells of phytoplankton varied, in general, the obtained dependence is consistent with the results of Pomati et al. (2020) that under different conditions in lakes with different trophic state and different biomass of zooplankton, large-sized algae predominate under high pressure of zooplankton.

As noted above, many authors (Liakhnovich al. 1983, Zhu et al. 2006, Ostapenia et al. 2011) report the ability of Dreissenidae to modify the environment through their filtration activity. The transition of the ecosystem to contourisation is associated exactly with biofiltration and increasing water transparency (Ostapenia et al. 2011). However, the intensity of filtration per unit mass of zooplankton was two orders of magnitude higher than that of Dreissenidae in the periphyton and benthos. For zooplankton, a filtration value of 0.1 dm^3/mg biomass per day has been calculated (Gutelmacher 1986). According to our calculations, for *D. polymorpha* this indicator was 0.00126 dm^3/mg biomass per day. In 2005, for example, all *D. polymorpha* in the intake canal filtered a volume of water equal to 1.5 canal volumes per day. Therefore, in the summer of 2008, when both power units were not working temporarily and there was no flow in the canal, the Secchi transparency increased up to 4 m and the quantity of dissolved oxygen reached critically low values. However, it should be considered that the formal comparison of filtration activities cannot always be reliable for generation of concepts and conclusions, because the feeding spectra in different groups of molluscs (Makhutova et al. 2013) and planktonic and counturobiont filtrators might be quite different.

Conclusions

Our results and analyses showed that attention should be paid to the unity of ecosystem processes. We believe there is no a unique direct association between the functioning of the populations of Dreissenidae and the processes occurring in the pelagic subsystem, in particular in the phytoplankton. The invasion of *D. polymorpha* has indirect impact on a whole range of processes, which leads to the phenomena of contourisation. It remains unclear why the introduction of the second species of Dreissenidae, as a rule, does not lead to such processes. The question about the possible cyclical nature of these processes also remains open. The mechanism of the contourisation processes appears to be much more complex than it could be assumed if relying only on the assessment of the role of *D. polymorpha*.

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