

Phytoplankton in the Zhrebchevo Reservoir (Central Bulgaria) before and after invasion of *Dreissena polymorpha* (Mollusca: Bivalvia)

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Abstract: Species composition and abundance of the phytoplankton and its relation with the main nutrients in the Zhrebchevo Reservoir before (1978-1980) and after (2009-2010) *Dreissena polymorpha* invasion were compared. The changes in the species composition concerned mainly Cyanoprokaryota (lowest similarity) and were primarily expressed by the increase in the number of chroococcalian species. Changes in the dominant composition were established at the levels of division (dominance of Cryptophyta), order (dominance of Chlorococcales instead of Volvocales) and genus (dominance of *Aphanocapsa*, *Aphanothece* and *Woronichina* instead of *Microcystis*, and *Cyclotella* instead of *Stephanodiscus*). The total phytoplankton biomass did not change statistically significantly, while the total abundance increased significantly. At the same time, the average individual volume decreased in the post-invasion period, which indicates that the zebra mussel might contribute to switching of phytoplankton assemblages to r-strategy. We found that the zebra mussel might cause an underestimation of the trophic status, assessed by the phytoplankton biomass in comparison with that assessed by the phosphorous concentration.

Key words: *Dreissena polymorpha*, zebra mussel, phytoplankton, reservoir

Introduction

The zebra mussel (*Dreissena polymorpha*) is among the highly invasive species (invaders) that have infested many water basins across Eurasia and North America during the past and recent decades (HIGGINS, ZANDEN 2010). By both direct (consumption) and indirect impact (altered nutrient availabilities and increased competition), it can cause great changes in ecosystem functioning as a whole and, in particular, in the phytoplankton assemblages. Different aspects concerning the relations between *Dreissena* spp. and the phytoplankton composition and abundance were studied but the results are often ambiguous and sometimes even controversial (CONROY *et al.* 2005). Most of these results showed a significant increase in water transparency as a consequence of the filtering activity or changes in water chemistry caused by *Dreissena* spp. (KALCHEV

et al. 2014, BARBIERO *et al.* 2006). However, this effect is not always related to significant reduction in the phytoplankton biomass, plankton primary production, and resulting trophic status (IDRISI *et al.* 2001, MILLER, WATZIN 2007, NICHOLLS *et al.* 2002, ZHANG *et al.* 2008). A lot of works focused on the relationship between zebra mussel and abundance of Cyanoprokaryota, in particular of *Microcystis*, as one of the main harmful taxa, potentially producing toxin. Some authors reported an increase in cyanoprokaryota dominance (DE STASIO *et al.* 2008, CARACO *et al.* 2006, MILLER, WATZIN 2007) and stimulating effect on *Microcystis* by zebra mussel (VANDERPLOEG *et al.* 2001, NICHOLS *et al.* 2002, BYKOVA *et al.* 2006, FISHMAN *et al.* 2010), especially at low nutrients (RAIKOW *et al.* 2004, SARNELLE *et al.* 2005, KNOLL *et al.* 2008).

Most of the studies concern the natural water bodies – mainly great lakes and rivers, while the reservoirs as specific aquatic ecosystems, with their considerable water level fluctuations and shorter hydraulic residence time seemed to have been neglected (DZIALOWSKI, JESSIE 2009, KALCHEV *et al.* 2013). The aim of this work is to compare the phytoplankton species composition and abundance in the Zhrebchevo Reservoir before and after *Dreissena* invasion, as well as to evaluate the changes in phytoplankton in relation to certain physical and chemical characteristics of pre- and post- invasion periods. We also compare some phytoplankton characteristics of the Zhrebchevo Reservoir with those of two other reservoirs – Ogosta (infested with *Dreissena*) and Koprinka (uninfested).

Material and Methods

The Zhrebchevo Reservoir is one of the largest reservoirs in Bulgaria built in the valley of the Tundzha River. It was studied during the period 1978-1980 (NAIDENOV 1981, SAIZ 1981) long before the invasion with *Dreissena*. The data about the phytoplankton in that pre-invasion period (SAIZ 1981) were compared with our results for the period 2009-2010 when the reservoir was already infested with *Dreissena* (post-invasion period). The morphometric characteristics of the Zhrebchevo Reservoir, as well as of the other two reservoirs – Koprinka and Ogosta, are shown in Table 1.

According to published records, the Zhrebchevo Reservoir was invaded by zebra mussel, *Dreissena polymorpha* (Pallas, 1771), in the 2000s (HUBENOV 2005, TRICHKOVA *et al.* 2009), the Ogosta Reservoir – by zebra mussel, *D. polymorpha*, and quagga mussel, *Dreissena rostriformis bugensis* Andrusov, 1897, in the 1990-2000s (HUBENOV 2002, TRICHKOVA *et al.* 2009), while the Koprinka Reservoir was uninfested by *Dreissena* spp. during the period of study (KALCHEV *et al.* 2014).

During the pre-invasion period in the Zhrebchevo Reservoir, two spring, five summer and three autumn samplings were conducted (SAIZ 1981). The quantitative samples were collected by means of 1L Friedenger sampler and fixed with formaldehyde (up to 4%). During the post-invasion period we sampled the reservoir five times – once in spring, two in summer, and two in autumn. Samples of 0.5L were taken from the epilimnion, metalimnion and the hypolimnion, using 1.7 L Hydro-Bios Plastic Water Sampler (NISKIN Type), at four sampling sites along the reservoir (Fig. 1 after KALCHEV *et al.* 2013), and fixed with Lugol solution. The location of sampling

Table 1. Location and morphometric characteristics of the Zhrebchevo, Ogosta and Koprinka reservoirs

Characteristics Reservoir	Zhrebchevo	Ogosta	Koprinka
Geographical coordinates	N 42°63' E 25°86'	N 43°23'35" E 23°12'16"	N 42°36'51" E 25°19'05"
Altitude, m a.s.l	273	186	390
Length, km	16	6,26	7
Volume, m ³ x 10 ⁶	400	506	67,85
Maximum depth, m	52	56	36

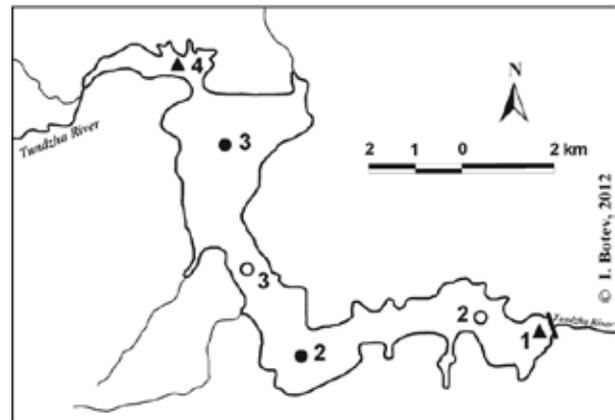


Fig. 1. Schematic map of Zhrebchevo reservoir with locations of sampling sites before ○ (Saiz (1981)), after ● *Dreissena* invasion and sites common for both periods ▲

sites 1st and 4th was the same in the pre- and post-invasion period; therefore, only the data from these stations were used to conduct comparative analyses. Qualitative samples were taken by an Apstein plankton net and preserved with formaldehyde up to 4% concentration.

In the pre-invasion period the phytoplankton counting was done by using a chamber of 10 cm³ and inverted microscope of Utermoehl (SAIZ 1981). In the post-invasion period two methods of counting were combined depending on the cell size: Bürker hemocytometer chambers and a straight light microscope were used when the small species dominated in the samples. Hydro-Bios tubular chambers and an inverted microscope were used for large species sedimentation and enumeration. The algal biovolume was estimated by means of geometrical approximation method (ROTT 1981). The abundance of phytoplankton was presented by both the number of individuals per cubic meter (numerical abundance, numbers) and by grams per cubic meter (biomass). The statistical significance of differences between both periods with regard to the numbers, biomass and average volume of phytoplankton was checked

by means of rank M & W U test (PAST software, HAMMER *et al.* 2001). The degree of species similarity in both periods was estimated by the Sørensen coefficient (RUSEV 1993), calculated both for all species and separately for Cyanoprokaryota, Chlorophyta and Bacillariophyta as the most species-rich groups. Only taxa of species and subspecies ranks were used for calculation. The relation between the numbers and biomass of the phytoplankton, on the one hand, and the main nutrients (inorganic soluble forms of nitrogen and phosphorous, N:P ratio), on the other, was estimated by means of Pearson linear correlation and regression analysis and non parametric correlation test of Spearman (PAST software).

Results and Discussion

Differences in the phytoplankton species composition and dominant species before and after *Dreissena polymorpha* invasion in the Zhrebchevo Reservoir

A total of 77 phytoplankton taxa before the invasion (SAIZ 1981) and 95 taxa after the invasion by *D. polymorpha* in the Zhrebchevo Reservoir has been reported (Table 2). Regarding the number of species the leading group in both periods was Chlorophyta, followed by Bacillariophyta and Cyanoprokaryota. The Sørensen coefficient of similarity in both periods, calculated on the basis of the complete taxonomical lists, was 0.42, but separately for single algal divisions amounted to 0.22 for Cyanoprokaryota, 0.48 for Chlorophyta, and 0.57 for Bacillariophyta. These differences indicate that not all phytoplankton divisions change equally, which was also reported by NICHOLLS *et al.* (2002). Obviously, the main changes in the species composition (lowest similarity) concern mainly the division of Cyanoprokaryota. We observed an increase in chroococcalian species and disappearance of some Nostocales after the invasion of *D. polymorpha* (Table 2). This result is in accordance with observations of some authors that report an increase in the importance of chroococoid Cyanoprokaryota caused by the zebra mussel (MAKAREWICZ *et al.* 1999, NICHOLLS *et al.* 2002). Unfortunately, we did not have data about the relative biomass of Cyanoprokaryota in the pre-invasion period, which did not allow us to reveal some tendency in the abundance of this group after the invasion. Other changes after *D. polymorpha* invasion refer to the dominant species mainly in summer and autumn (Table 3). The spring data are not very representative because in the post-invasion period the sampling was done a month later, at more advanced stratification in comparison with the pre-invasion

period. *Microcystis aeruginosa* was reported by SAIZ (1981) as one of the main dominant species in summer and autumn during the pre-invasion period. After the invasion of *D. polymorpha* we found *Aphanocapsa holsatica*, *Aphanothece clatrata* and *Woronichina naegeliana* to dominate instead (Table 3). According to RAIKOW *et al.* (2004) and SARNELLE *et al.* (2005), the relation between *D. polymorpha* and *Microcystis* is strongly influenced by the concentration of nutrients, and the stimulating effect by *D. polymorpha* may exist only when the total phosphorous (TP) concentration is low (under 25 mg m⁻³ according to RAIKOW *et al.* 2004). In the Zhrebchevo Reservoir, a high TP concentration (over 25 mg m⁻³) was recorded (KALCHEV *et al.* 2013), and according to our results, a negative effect of *D. polymorpha* on *Microcystis* was observed, which is in congruence with the literature sources.

We also registered differences in the dominant species within the Chlorophyta division before and after the invasion of *D. polymorpha*. In the pre-invasion period the dominating chlorophytes belonged to orders Volvocales and Desmidiiales, while during the post invasion period the Chlorococcales species prevailed (Table 3). In contrast to this, the differences within the division of Bacillariophyta were not significant. The same dominant diatoms were encountered before and after the invasion, with the exception of *Stephanodiscus hantzshii* available only before the invasion and *Cyclotella ocellata* registered after the invasion (Table 3). A similar decline of *Stephanodiscus* after the arrival of zebra mussel was also reported by other authors (NICHOLLS *et al.* 2002).

Significant difference was found regarding the status of the Cryptophyta division in the phytoplankton community before and after the invasion. During the pre-invasion period, the cryptophytes were poorly presented both qualitatively and quantitatively, while after the invasion some of them appeared as dominants (Table 3), reaching sometimes very high relative abundance. NADAFI *et al.* (2007) defined cryptophytes as a good diet for *D. polymorpha*. According to these authors, not only the nutritional quality of algae but also its size is important and *D. polymorpha* seems to avoid too large (>50 µm) and too small (≤7 µm) algae. Some experimental findings showed that *D. polymorpha* selectively removes cryptophytes from the water (LAVRENTYEV *et al.* 1995), but NICHOLLS *et al.* (2002) found that biovolumes of *Cryptophyceae* do not change significantly after the invasion of *D. polymorpha*. On analysing literature data from different freshwater ecosystems (rivers and lakes), HIGGINS,

Table 2. Lis of phytoplankton taxa before (SAIZ, 1981) and after *Dreissena* invasion

Taxon	Period	Before invasion	After invasion
Cyanophyta			
<i>Anabaena flos-aquae</i> (LYNGB.) BRÉBISSON		+	
<i>A. sheremetievi</i> ELENKIN		+	
<i>A. spiroides</i> KLEBAHN		+	+
<i>Aphanizomenon flos-aquae</i> (L.) RALFS			+
<i>Aphanocapsa holsatica</i> (LEMMERMANN) CRONBERG et KOMÁREK		+	+
<i>Aphanothece clathrata</i> WEST et G.S. WEST			+
Chroococcus sp.			+
Merismopedia sp.			+
<i>Microcystis aeruginosa</i> (KÜTZING) KÜTZING		+	
<i>M. wesenbergii</i> (KOMÁREK) KOMÁREK			+
<i>Oscillatoria limosa</i> AGARDH ex GOMONT		+	
Phormidium sp.			+
Planktolyngbia sp.			+
Pseudanabaena sp.			+
<i>cf. Rhabdogloea linearis</i> (GEITLER) KOMÁREK			+
<i>Woronichinia naegiliana</i> (UNGER) ELENKIN			+
Chlorophyta			
<i>Actinastrum hantzschii</i> LAGERHEIM		+	+
<i>Ankyra ancora</i> (G.M.SMITH) FOTT			+
<i>A. judayi</i> (G.M.SMITH) FOTT		+	+
<i>A. lanceolata</i> (KORSHIKOV) FOTT			+
<i>A. ocellata</i> (KORSHIKOV) FOTT			+
<i>Botryococcus braunii</i> KÜTZING		+	
<i>Carteria globosa</i> KORSHIKOV		+	+
Chlamydomonas sp.			+
<i>Closterium aciculare</i> T. WEST		+	+
<i>Cl. acutum</i> v. <i>variable</i> (LEMMERMANN) WILLI KRIEGER			+
<i>Cl. moniliferum</i> (BORY) EHRENBERG ex RALFS		+	
<i>Cl. parvulum</i> NÄGELI		+	
<i>Cl. setaceum</i> EHRENBERG ex RALFS		+	
<i>Coelastrum astroideum</i> DE NOTARIS			+
<i>C. microporum</i> NÄGELI		+	
<i>C. polychordum</i> (KORSHIKOV) HINDÁK			+
<i>C. reticulatum</i> (P.A.DANGEARD) SENN			+
Cosmarium sp.			+
<i>Crucigenia lauterbornii</i> (SCHMIDLE) SCHMIDLE		+	
<i>C. quadrata</i> MORREN		+	+
<i>Crucigeniella apiculata</i> (LEMMERMANN) KOMÁREK		+	
Crucigeniella sp.			+
<i>Dictyosphaerium anomalum</i> KORSHIKOV		+	
<i>D. ehrenbergianum</i> NÄGELI sensu SKUJA		+	
<i>D. pulchellum</i> WOOD		+	
Didymocystis sp.			+
<i>Elakatothrix genevensis</i> (REVERDIN) HINDÁK			+
<i>Eudorina elegans</i> EHRENBERG		+	+
<i>Eutetramorus fotii</i> (HINDÁK) KOMÁREK			+

Table 2. Continued

Taxon	Period	Before invasion	After invasion
<i>Korshikoviella michailovskoensis</i> (ELENKIN) SILVA			+
<i>Kirchneriella obesa</i> (W. WEST) SCHMIDLE		+	
<i>Lagerheimia genevensis</i> (CHODAT) CHODAT			+
<i>Monoraphidium arcuatim</i> (KORSHIKOV) HINDÁK			+
<i>M. circinale</i> (NYGAARD) NYGAARD			+
<i>M. contortum</i> (THURPIN) KOM.-LEGN.			+
<i>M. komarkovae</i> NYGAARD			+
<i>Oedogonium</i> sp.		+	
<i>Oocystis lacustris</i> CHODAT			+
<i>Oocystis marsonii</i> LEMMERMANN			+
<i>Oonephris obesa</i> (W.WEST) FOTT			+
<i>Pandorina morum</i> (O.F. MÜLLER) BORY		+	+
<i>P. smithii</i> CHODAT			+
<i>Pediastrum boryanum</i> (TURPIN) MENEGH		+	+
<i>P. duplex</i> MEYEN		+	+
<i>P. simplex</i> MEYEN		+	+
<i>P. tetras</i> (EHRENBERG) RALFS		+	+
<i>Phacotus lenticularis</i> (EHRENBERG) STEIN		+	
<i>Planktosphaeria gelatinosa</i> G.M. SMITH			+
<i>Scenedesmus acuminatus</i> (LAGERHEIM) CHODAT		+	+
<i>S. acuminatus</i> v. <i>biseriatus</i> REINHARD		+	
<i>S. arcuatus</i> v. <i>platydiscus</i> G.M. SMITH		+	
<i>S. bijugatus</i> KÜTZING		+	
<i>S. communis</i> HEGEWALD		+	+
<i>S. opoliensis</i> P.G. RICHTER		+	
<i>S. sempervirens</i> CHODAT			+
<i>S. smithii</i> TEILING			+
<i>Staurastrum chaetoceras</i> (CHROED.) G.M. SMITH			+
<i>Staurastrum gracile</i> RALFS		+	+
<i>Tetraedron minimum</i> (A. BRAUN) HANSGIRG		+	+
<i>Volvox aureus</i> EHRENBERG		+	+
Bacillariophyta			
<i>Acanthoceras zachariasii</i> (BRUN) SIMONSEN			+
<i>Amphora ovalis</i> KÜTZING		+	+
<i>Asterionella formosa</i> HASSALL		+	+
<i>Attheya Zachariasii</i> BRUN		+	+
<i>Aulacoseira islandica</i> (O.MÜLLER) SIMONSEN		+	+
<i>A. granulata</i> (EHRENBERG) SIMONSEN		+	+
<i>A. granulata</i> v. <i>angustissima</i> (O. MÜLLER) SIMONSEN		+	+
<i>Ceratoneis arcus</i> (EHRENBERG) KÜTZING		+	
<i>C. arcus</i> v. <i>amphioxys</i> (RABENHORST) BRUN		+	
<i>Cocconeis placentula</i> EHRENBERG			+
<i>Cyclotella meneghiniana</i> KÜTZING			+
<i>C. ocellata</i> PANTOCSEK			+
<i>Cyclotella</i> sp.		+	+
<i>Cymatopleura elliptica</i> (BRÉBISSON) W. SMITH		+	
<i>C. solea</i> (BRÉBISSON) W. SMITH		+	

Table 2. Continued

Taxon	Period	Before invasion	After invasion
<i>Diatoma vulgare</i> BORY		+	
<i>Epithemia zebra</i> (EHRENBERG) KÜTZING		+	
<i>Fragelaria crotonensis</i> KITTON		+	+
<i>F. capucina</i> DEZMAZIÈRES		+	
<i>Gomphonema olivaceum</i> (HORNEMANN) BRÉBISSON		+	+
<i>Gyrosigma acuminatum</i> (KÜTZING) RABENHORST		+	+
<i>Hantzschia amphioxys</i> (EHRENBERG) GRUNOW		+	
<i>Melosira varians</i> C. AGARDH		+	+
<i>Navicula bacillum v. lepida</i> (GREGORY) CLEVE			+
<i>Navicula</i> spp.		+	+
<i>Nitzschia acicularis</i> (KÜTZING) W. SMITH		+	+
<i>N. dissipata</i> (KÜTZING) GRUNOW			+
<i>N. sigmoidea</i> (NITZSCH.) W. SMITH		+	
<i>Rhoicosphenia curvata</i> (KÜTZING) GRUNOW			+
<i>Stephanodiscus hantzschii</i> GRUNOW		+	+
<i>Synedra actinastroides</i> LEMMERMANN		+	
<i>S. acus</i> KÜTZING		+	
<i>S. ulna</i> (NITZSCH) EHRENBERG		+	+
<i>Tabellaria flocculosa</i> (ROTH) KÜTZING		+	
Chrysophyta			
<i>Chromulina</i> sp.			+
<i>Dinobryon divergens</i> IMHOF			+
<i>D. sociale</i> (EHRENBERG) EHRENBERG		+	+
<i>Mallomonas akrokomos</i> RUTTNER			+
<i>Mallomonas</i> sp.		+	+
<i>Ochromonas</i> sp.			+
<i>Pseudokephyrion conicum</i> SCHILLER			+
Xanthophyta			
<i>Ophiocytium capitatum</i> WOLLE			+
Euglenophyta			
<i>Euglena acus</i> EHRENBERG		+	
<i>Euglena oxyuris</i> SCHMARDA		+	
<i>Trachelomonas hispida</i> (PERTY) F. STEIN		+	
<i>T. volvocina</i> (EHRENBERG) EHRENBERG		+	+
<i>Phacus caudatus</i> HÜBNER		+	
<i>Ph. longicauda v. tortus</i> LEMMERMANN		+	
<i>Ph. pyrum</i> (EHRENBERG) STEIN			+
Pyrrhophyta			
<i>Ceratium hirundinella</i> (O.F. MÜLLER) DUJARDIN		+	+
<i>Gymnodinium helveticum</i> PENARD			+
<i>Peridinea</i> sp.		+	+
Cryptophyta			
<i>Chroomonas acuta</i> UTERMÖHL			+
<i>Cryptomonas erosa</i> EHRENBERG			+
<i>C. marsonii</i> SKUJA			+
<i>C. ovata</i> EHRENBERG			+
<i>Cryptomonas</i> sp.		+	+

Table 3. Phytoplankton taxa participating in the dominant complexes in different seasons of pre-invasion (after SAIZ, 1981) and post-invasion period

Season Taxon	Before invasion	After invasion
Spring	<i>Asterionella gracillima</i> <i>Cyclotella</i> sp. <i>Melosira islandica</i> <i>Stephanodiscus hantzschii</i>	<i>Asterionella formosa</i> <i>Cyclotella</i> sp. <i>Cyclotella ocellata</i> <i>Ankyra juday</i> <i>Ankyra lanceolata</i> <i>Merismopedia</i> sp.
Summer	<i>Microcystis aeruginosa</i> <i>Eudorina elegans</i> <i>Volvox aureus</i> <i>Carteria globosa</i> <i>Phacotus lenticularis</i> <i>Closterium aciculare</i> <i>Staurastrum gracile</i> <i>Asterionella gracillima</i> <i>Melosira granulata</i> <i>Ceratium hirundinella</i> <i>Peridinea</i> spp.	<i>Aphanoteche clatrata</i> <i>Aphanocapsa holsatica</i> <i>Ankyra juday</i> <i>Crucigeniella</i> sp. <i>Sphaerocystis</i> sp. <i>Oocystis</i> sp. <i>Asterionella formosa</i> <i>Fragilaria crotonensis</i> <i>Melosira granulata</i> <i>Cyclotella ocellata</i> <i>Cyclotella</i> sp. <i>Ceratium hirundinella</i> <i>Chroomonas acuta</i> <i>Cryptomonas</i> sp.
Autumn	<i>Microcystis aeruginosa</i> <i>Anabaena sheremetievi</i> <i>Closterium aciculare</i> <i>Staurastrum gracile</i> <i>Fragilaria crotonensis</i> <i>Melosira granulata</i>	<i>Woronichinia naegeliana</i> <i>Aphanizomenon</i> sp. <i>Staurastrum planctonicum</i> <i>Cyclotella ocellata</i> <i>Asterionella formosa</i> <i>Fragilaria crotonensis</i> <i>Chroomonas acuta</i> <i>Cryptomonas erosa</i> <i>Cryptomonas</i> spp.

VANDER ZANDEN (2010) also reported a neutral effect of *Dreissena* spp. upon Cryptophyta. Our results, though opposite to the abovementioned, are consistent with the observations of other researchers, reporting that cryptophytes may be favoured by heavy grazing, which suggest a dynamic feedback between grazers and their prey (KLAIVENESS 1988).

Overall, the changes that occurred in the composition of phytoplankton in the Zhrebchevo Reservoir after infestation with *D. polymorpha* were observed on different taxonomic levels – on the division level (Cryptophyta dominated), on the order level (dominance of Chlorococcales instead of Volvocales), and on the genus level (*Aphanocapsa*, *Aphanothece*, *Woronichinia* instead of *Microcystis*; and *Cyclotella* instead of *Stephanodiscus*). Unfortunately, these results could not reveal to what extent exactly *D. polymorpha* is responsible for these changes and the precise mechanisms of its influence on the phytoplankton composition.

Phytoplankton numbers and biomass before and after *Dreissena* invasion in relation to nutrients

The total phytoplankton biomass after *D. polymorpha* invasion to the Zhrebchevo Reservoir was lower than in the pre-invasion period (Fig. 2), but the differences were not significant (M&W test, $P=0.22$). However, the numerical abundance was much higher after the invasion and the differences were statistically significant (Fig. 3). This substantial increase in numbers relative to the slight biomass reduction was associated with a statistically significant decrease in the average individual volume (AIV) of the phytoplankters (Fig. 4). AIV was significantly lower in both infested reservoirs Zhrebchevo and Ogosta than in uninfested Koprinka Reservoir (Fig. 5).

The above mentioned changes in the phytoplankton numbers, biomass and AIV were found not only in the deepest part of the reservoir, but also at the sampling site, close to the river inflow (Station 4). This contradicted the chemical and physical data, which did not show any differences between the compared periods at this sampling site (KALCHEV *et al.* 2013). This shows that neither the morphometric characteristics (water volume) of the reservoirs, nor the physico-chemical conditions determine the phytoplankton quantitative changes registered in this part of the reservoir. Therefore, we suppose that the phytoplankton might compensate for the influence of *D. polymorpha* by the reduction of size and increase in numbers, which is an r-strategy in the basic sense of the term as given by MACARTHER, WILSON (1967) after BEGON *et al.* (1989).

Significant negative linear regression was established between the phytoplankton numbers and biomass, on the one hand, and the soluble inorganic nitrogen, on the other (Fig. 6). The negative relation after the invasion between the numerical abundance and nitrogen could be interpreted as a consequence from the intensive uptake of the latter by the phytoplankton, which is more effective when the size of organisms is small because this corresponds to a higher total algal surface. This could explain why the relation of nitrogen with the numerical abundance seems to be stronger (steeper regression slope) than that with biomass (Fig. 6).

We found a discrepancy in the evaluation of trophic status of the Zhrebchevo Reservoir by the amount of phosphorus (eutrophic-hypertrophic state), on the one hand, and by the phytoplankton biomass (oligotrophic-mesotrophic), on the other (both after LIKENS 1975). This discrepancy existed both before and after the invasion, indicating also

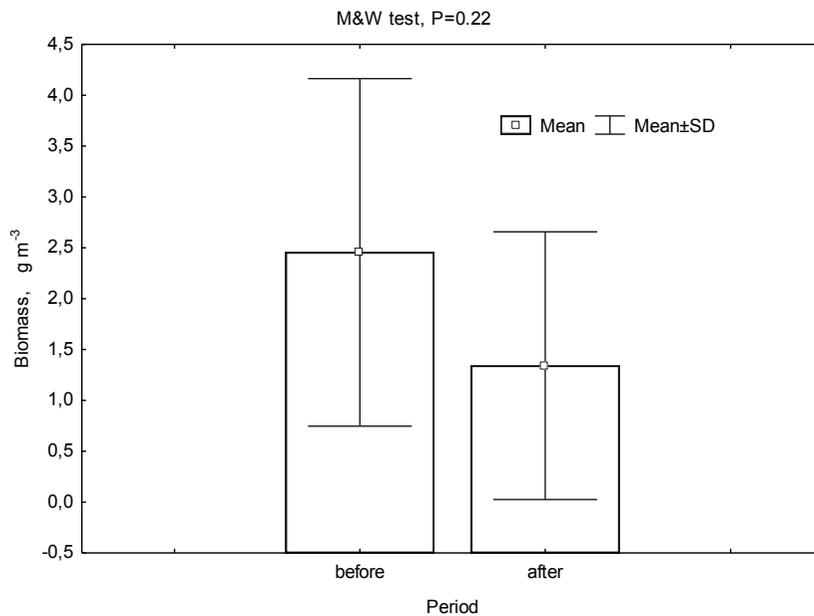


Fig. 2. Comparison (M&W test) of the phytoplankton biomass (g m^{-3}) in Zhrebchevo reservoir (sampling site 1) before and after *Dreissena* invasion

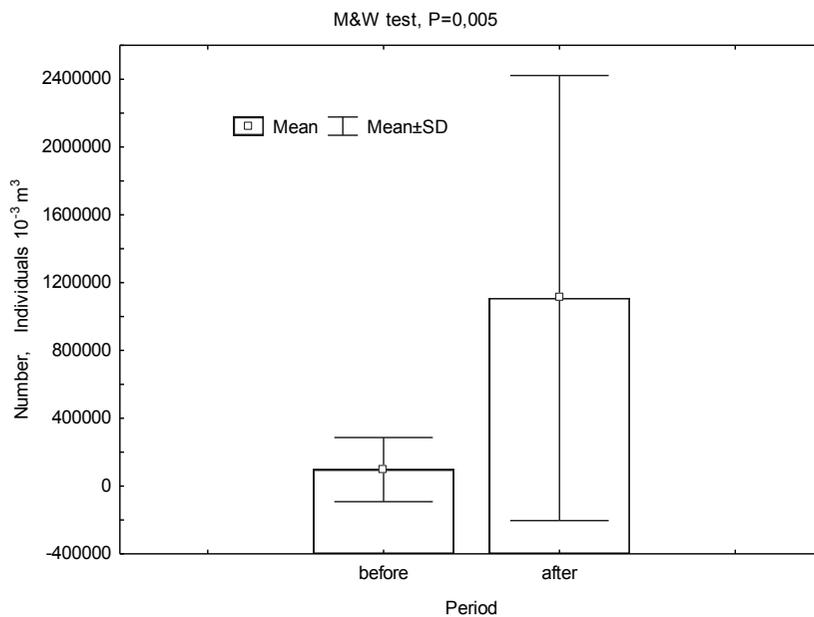


Fig. 3. Comparison (M&W test) of the phytoplankton numerical abundance (individuals 10^{-3}m^{-3}) in Zhrebchevo reservoir (sampling site 1) before and after *Dreissena* invasion

a possible nitrogen limitation. However, in the post-invasion period, the discrepancy between the increasing amount of phosphorus and the reduction of the phytoplankton biomass increased. This indicates that owing to zebra mussel, there is a high discrepancy between the trophic status estimated by the phosphorus concentration and that estimated by the phytoplankton biomass. In this respect, our results are in accordance with those of DZIALOWSKI, JESSIE (2009), who showed that the zebra mussel

masks the relationship between phosphorus and phytoplankton biomass, thus leading to underestimating the level of eutrophication obtained by phytoplankton. The main reason for this is the increase of light penetration in the depth as a consequence from *D. polymorpha* filtration effect, which shifts the major part of the energy flow from the pelagial to the benthal space, a fact revealed by many authors (FAHNENSTIEL *et al.* 1995, DE STASIO, RICHMAN 1998, LOWE, PILLSBURY 1995).

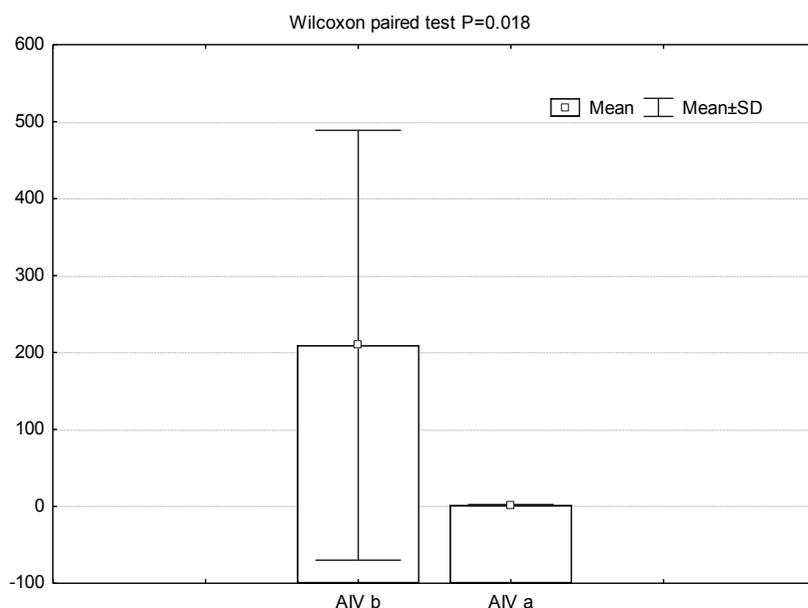


Fig. 4. Average individual volume (AIV) of the phytoplankters in the Zhrebchevo reservoir before (AIV b) and after (AIV a) *Dreissena* invasion

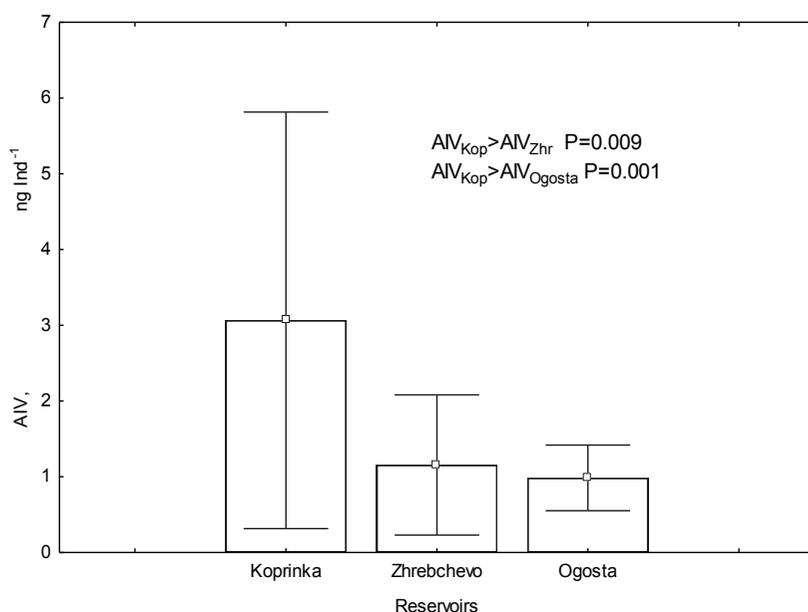


Fig. 5. Average individual volume (AIV, ng ind⁻¹) of the phytoplankters in the Zhrebchevo, Koprinka, and Ogosta reservoirs

Conclusions

The most qualitative changes observed in the phytoplankton of Zhrebchevo Reservoir in the post-invasion period (predominance of Chlorococcales instead of Volvocales, dominance of Cryptophyta, etc.) could hardly be determined uniquely as a result of *D. polymorpha* impact, although in the literature we find similar results, for example, an increase in the number of chroococcal species. However, these

results are important as a basis for further research in this direction. The quantitative results obtained are significantly more indicative, which can be considered with high probability as a consequence of the influence from *D. polymorpha*. The reduction of AIV in the phytoplankters, together with the increase in the total numerical abundance under the conditions of *D. polymorpha* presence suggests a shift of the phytoplankton to an r-selected strategy as the most adequate compensatory mechanism. Our

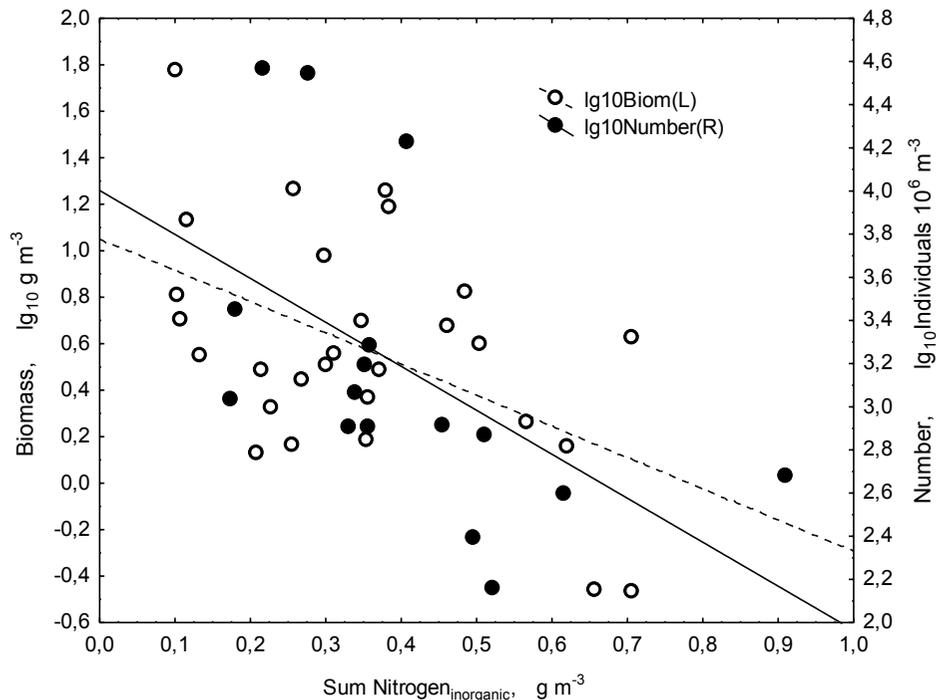


Fig. 6. Linear regressions: between phytoplankton biomass ($Lg_{10} \text{ g m}^{-3}$, \circ) and Sum of inorganic nitrogen (g m^{-3}) before *Dreissena* invasion ($Y = 1,0496 - 1,343X$; $R = -0,499$; $P = 0,006$) and between phytoplankton numerical abundance ($Lg_{10} \text{ ind.} \cdot 10^6 \text{ m}^{-3}$, \bullet) and Sum of inorganic nitrogen (g m^{-3}) after *Dreissena* invasion ($Y = 4,0 - 2,138 X$; $R = -0,529$; $P = 0,0352$)

results, like the findings of other researchers, also show that *Dreissena* can affect the positive relationship between the phytoplankton biomass and phosphorus, thereby leading to underestimation of the real trophic status of the reservoir.

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