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Diatoms in an extreme euxinic environment (Rogoznica Lake, eastern Adriatic coast)

Nikola Malešević[1*], Irena Ciglenečki[2], Elvira Bura-Nakić[2], Marina Carić[3], Iris Dupčić[3], Enis Hrustić[3], Damir Viličić[1], Zrinka Ljubešić[1]

[1] University of Zagreb, Faculty of Science, Division of Biology, Rooseveltov trg 6, 10000 Zagreb, Croatia

[2] Ruđer Bošković Institute, Division of Marine and Environmental Research, Bijenička cesta 54, 10000 Zagreb, Croatia

[3] University of Dubrovnik, Institute for Marine and Coastal Research, Kneza Damjana Jude 12, 20000 Dubrovnik, Croatia

Abstract – The Rogoznica Lake marine system is a small, karstic, naturally eutrophic and euxinic marine environment. Abundance and temporal distribution of phytoplankton was investigated in relation to environmental conditions in the period from 1998 to 2013. The 36 determined diatoms contributed 90% of the total phytoplankton abundance. The diatom composition is characterized by low species diversity and high single species abundance (up to 10^7 cells L^{-1}). There were, on average, 2.6 diatom species per sample (maximum 14 diatom species per sample) reflecting extreme environmental conditions. Dominant diatoms *Thalassionema nitzschioides*, *Cyclotella choctawhatcheeana*, *Dactyliosolen fragilissimus* and *Chaetoceros curvisetus* occurred repeatedly and were alternately dominant in the lake during the whole research period. Some diatoms were dominant only in limited period, like *Cyclotella choctawhatcheeana* (evident since 2001), and *Pseudo-nitzschia* spp. (evident in the period 2002 to 2009). It appears that the interplay of environmental conditions such as variability in thermohaline and redox conditions, nutrient and reduced sulphur concentration influence the phytoplankton development and abundance in the lake.

Keywords: diatoms, extreme environmental conditions, marine lake, phytoplankton

Introduction

An increased level of reduced sulphur species (RSS, including sulphide, polysulphide, elemental sulphur and thio-componds) and seasonal changes between oxic and anoxic conditions have long been recognized in the Rogoznica Lake marine system, central Dalmatia (Ciglenečki et al. 2005, 2013, Kršinić et al. 2013).

* Corresponding author, e-mail: nikola712@gmail.com

The thermohaline conditions in this lake are mainly regulated by solar heating, evaporation and rainfall, which influence surface salinity variations (CIGLENEČKI et al. 2005, 2013). Surface water could be well oxygenated (oxygen saturation up to 300%), while hypoxia/anoxia occurs in the bottom water layer (STIPANIČEV and BRANICA 1996, CIGLENEČKI et al. 1998, 2005, 2013). The boundary between oxic and anoxic water layers is usually situated below the depth of 9 m (CIGLENEČKI et al 2005, 2013). Although phytoplankton, zooplankton nauplii and larvae of benthic organisms may enter the lake through fissures between the rocks (KRŠINIĆ et al. 2000), few species are recorded in the lake.

Since the anoxic event in September of 1997, when the presence of hydrogen sulphide in the whole of the water column was detected, investigations of the lake have been intensive. This event, followed by massive mortality of all organisms, was taken as a zero point from which ecological recovery of the lake was monitored (BARIĆ et al. 2003, CIGLENEČKI et al. 2005, ŠESTANOVIĆ et al. 2005, SVENSEN et al. 2008, BURIĆ et al. 2009, ŽIC et al. 2010). Before the anoxic event in 1997, the dominant species in the phytoplankton was the diatom *Pseudo-nitzschia* spp., which accounted for 88% of the phytoplankton community. The microplankton usually was composed of about 30 species, among which the most frequent and abundant were the rare microflagellates *Prorocentrum arcuatum* and *Hermesinum adriaticum* (VILIČIĆ et al. 1996/1997, BURIĆ et al. 2009) and diatoms (*Chaetoceros curvisetus* and *Eunotia* sp.) (CIGLENEČKI et al. 2005, BURIĆ et al. 2009). Recently published papers reported that diatoms took over the domination of phytoplankton assemblages after 2001, accounting for on average up to 94%, recognizing *Chaetoceros curvisetus* and *Dactyliosolen fragilissimus* as dominant species until the end of 2005 (KRŠINIĆ et al. 2013). *C. curvisetus* and dinoflagellate *Ceratium furca* were found as dominant species in the lake in summer 2004 (SVENSEN et al. 2008). The calanoid copepod *Acartia italica* is the only metazoan plankton species commonly present in Rogoznica Lake surviving after anoxia episodes and reaching high abundance in the lake (KRŠINIĆ et al. 2000, 2013, SVENSEN et al. 2008). Before the disastrous anoxic event in 1997, top-down control governed the biological processes in the lake. This disappeared with anoxic stress conditions and it took several years for the full recovery of top-down control (KRŠINIĆ et al. 2013).

Rogoznica Lake due to its relative isolation, semi-closed nature, environmental characteristics and size (10300 m^2 and maximum depth 15 m) can serve as natural laboratory for studying extreme environment and certain biogeochemical processes. In this paper changes of phytoplankton composition and low species diversity are studied in relation to physico-chemical conditions in the lake. The special focus is on the diatoms, with the regularity of specific species domination being discussed.

Materials and methods

Study area

Rogoznica Lake is situated on Gradina Peninsula (43°32'N, 15°58'E) in the vicinity of the settlement of Rogoznica and the city of Šibenik, on the eastern Adriatic coast (Fig. 1). It is a eutrophic, karstic lake with a surface area 10300 m^2 and a maximum depth of 15 m. Lake is round in shape and is surrounded by 4–24 m high porous karst cliffs with underground connections with the open sea visible through tides with a certain delay.

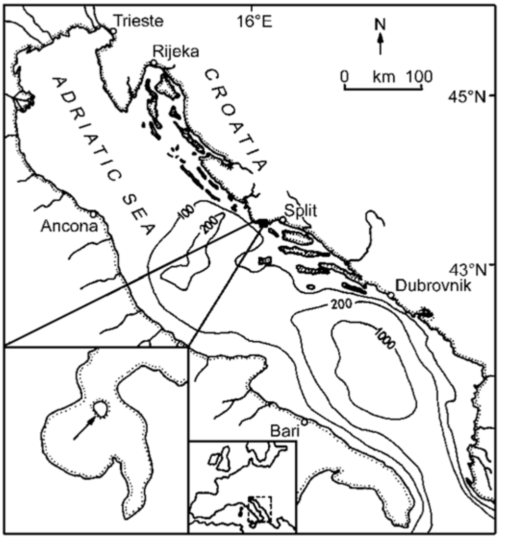

Fig 1. Location of Rogoznica Lake (marked by arrow) in the eastern Adriatic coast.

Sampling and analyses

Investigation of phytoplankton was conducted in the period from December 1998 to September 2013 (Tab. 1). Samples for phytoplankton and nutrient analyses were collected in 5 L Niskin bottles, from the water column in the center of the lake. Samples were taken from various depths from surface to the bottom (0, 2, 5, 7, 8, 9, 10, 11, 12, 13 m). Because

Tab. 1. Sampling of phytoplankton conducted in the period from December 1998 to September 2013. Sampling campaigns are marked with »+«.

Date	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1998												+
1999												
2000		+	+		+		+		+		+	
2001			+		+							
2002		+			+		+		+			
2003	+			+		+						
2004				+	+		+			+	+	+
2005	+		+									
2006						+	+				+	+
2007	+		+						+			
2008	+		+				+					
2009	+		+		+		+		+		+	
2010			+			+		+	+		+	
2011			+		+	+	+			+	+	
2012	+		+		+		+		+			+
2013		+		+			+					

of the appearance of anoxic conditions at depths below 9 m, in this research these phytoplankton data were excluded. The samples were preserved in a 2% (final concentration) neutralized formaldehyde solution. Cell counts were obtained by the inverted microscope method according to UTERMÖHL (1958). Nutrient concentrations were measured by standard methods (STRICKLAND and PARSONS 1972, IVANČIĆ and DEGOBBIS 1984). Software packages Grapher 7 and Statistica 12 were used for statistical and graphical analyses.

Results

Physico-chemical conditions

In the investigated period, seasonal variations in vertical gradients of salinity and temperature, together with changes between oxic and anoxic conditions indicated the existence of surface (0–2 m) and bottom water layers (12 m) with higher salinity and temperature values (Fig. 2). Mixing of the water layers (marked by arrows in Fig. 2) ending with the

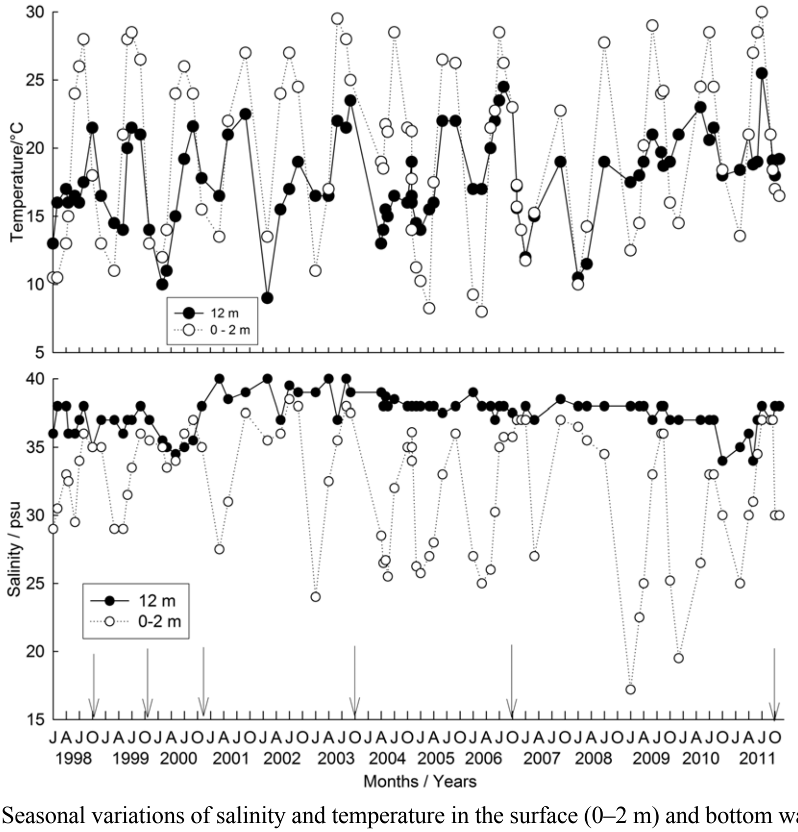

Fig. 2. Seasonal variations of salinity and temperature in the surface (0–2 m) and bottom waters (12 m) of Rogoznica Lake. Mixing of water layers is marked by arrows, months are denoted by abbreviations: J for January, A for April, J for July and O for October. In all these mixing occasions, except October 2011, hypoxic conditions (1–3 mg L^{-1}) within the whole water column with elevated concentrations of nitrite (up to 3.5 μM) and ammonium (31 μM) were recorded. In 2011 anoxia was present for more than 1 week in the whole water column of the lake.

formation of a chemically homogeneous water column, characterized by hypoxic or anoxic conditions, usually take place in autumn. All recorded mixing events in the investigated period except of the ones in October 2011, were characterized by hypoxic conditions (1–3 mg L^{-1}) within the whole water column accompanied with elevated concentrations of nitrite (up to 3.5 µM) and ammonium (up to 31 µM). Anoxic holomixis was present in the whole lake for more than a week in October 2011.

The maximum concentration of nitrate (44.21 µmol L^{-1}) was detected in January 2005 in the surface layer (0–1 m). Phosphate concentration varied from 0.01 µmol L^{-1} to 33.1 µmol L^{-1} with the minimum recorded in May 2004 in the surface layer. Silicate concentration varied from 0.34 µmol L^{-1} to 679 µmol L^{-1} (Tab. 3). Statistical analyses among nutrients showed a significant positive correlation between nitrite and: nitrate ($r = 0.15$; $p = 0.04$), ammonium ($r = 0.92$; $p = 0.00$) and phosphate ($r = 0.31$; $p = 0.00$).

Phytoplankton composition

The phytoplankton composition in the lake is characterized by low species diversity and high single species abundance (up to 10^7 cells L^{-1}) (Tab. 2). During the entire research period diatoms were dominant, accounting, on average, for 90% of the whole phytoplankton (Fig. 3, Tab. 3). In all, 36 diatoms were recorded in the lake with a low average diversity of 2.6 diatom species per sample (maximal number 14 diatom species per sample). Dominant diatoms were: *Thalassionema nitzschioides, Cyclotella choctawhatcheeana*, *Dactyliosolen fragilissimus* and *Chaetoceros curvisetus* (Tab. 2). Those diatoms occurred repeatedly in the lake, and were alternately dominant in the phytoplankton assemblage over the research period (Fig. 3). The diatom *Cyclotella choctawhatcheeana* was found in the lake for the first time in May 2004, and was a permanent constituent of the phytoplankton assemblage until the end of the investigated period. *Pseudonitzschia* spp. was occasionally the dominant species from September 2002 to November 2009, and after that was not detected in lake (Fig. 3). In the first half of 2000, when stratification of the water column was very weak, and concentration of RSS increased in the upper layers the abundance of diatom species *C. curvisetus* decreased in the following period. In the summer of 2003, when thermohaline conditions in the lake water weakened again, the abundance of *C. curvisetus and D. fragilissimus* decreased, while the abundance of *T. nitzschioides* slightly increased. The next mixing of the water layers occurred in winter 2005 and probably triggered the decrease of abundance of all dominant species except of *C. choctawhatcheeana*. In the winter of 2007 mixing occurred again and consequently the abundance of the two dominant species *D. fragilissimus* and *T. nitzschioides* increased. In winter 2008 mixing resulted in a decreased abundance of the two dominant species *C. curvisetus* and *T. nitzschioides*, while the abundance of *D. fragilissimus* and of *C. choctawhatcheeana* increased. In autumn 2010 during isothermy in the lake, abundance of *C. curvisetus* and *T. nitzschioides* stayed almost the same, while the abundance of other two dominant species decreased (Fig. 2, Fig. 3).

Statistical analyses revealed a significant positive correlation of *D. fragilissimus* with nitrite ($r = 0.15$; $p = 0.03$) and with ammonium concentration ($r = 0.19$; $p = 0.01$). There was no significant correlation between the development of other dominant diatoms and nutrient concentration distribution. Diatom abundance and development responded to mixing as shown in Fig. 3. Every mixing event had as consequence a change in the diatom development. Furthermore, *D. fragilissimus* had positive correlation with the species *Pseudonitzschia* spp. ($r = 0.26$; $p = 0.00$) and *C. choctawhatcheeana* with *T. nitzschioides* ($r = 0.17$; $p = 0.02$).

Tab. 2. List of diatoms taxa found in the phytoplankton during the research period. MAX is for maximum abundance of cells per L and Fr is frequency of appearance (382 samples is 100%).

Taxa	Fr (%)	Max
Cerataulina pelagica (Cleve) Hendey	2	137960
Chaetoceros affinis Lauder	4	13300
Chaetoceros compressus Lauder	4	1122000
Chaetoceros curvisetus Cleve	51	1079090
Chaetoceros danicus Cleve	6	112530
Chaetoceros decipiens Cleve	2	28120
Chaetoceros diversus Cleve	2	6400
Chaetoceros lauderi Ralfs	2	1600
Chaetoceros perpusilus Cleve	2	560
Chaetoceros rostratus Lauder	2	800
Chaetoceros spp.	11	1165510
Cyclotella choctawhatcheeana Prasad	30	7926200
Cylindrotheca closterium (Ehrenberg) Reimann & J. C. Lewin	1	760
Dactyliosolen fragilissimus (Bergon) Hasle	30	2582210
Eunotia sp.	3	170808
Guinardia flaccida (Castracane) H.Peragallo	1	272790
Guinardia striata (Stolter.) Hasle	6	109730
Hemiaulus hauckii Grunow ex Van Heurck	1	1520
Hemiaulus sinensis Greville	1	380
Leptocylindrus danicus Cleve	6	313480
Leptocylindrus minimus Gran	2	7090
Licmophora sp.	3	1140
Microtabella interrupta (Ehrenberg) Round	2	760
Nitzschia longissima (Brébisson) Ralfs	10	63080
Pleurosygma sp.	6	380
Proboscia alata (Brightwell) Sundström	1	181060
Pseudo-nitzschia delicatissima (Cleve) Heiden	1	2974060
Pseudonitzschia spp.	6	622945
Rhizosolenia calcar avis Schultze	1	1890
Rhizosolenia delicatula Cleve	1	6400
Rhizosolenia fragilissima Bergon	1	4000
Rhizosolenia imbricata Brightwell	1	1140
Striatella unipunctata (Lyngbye) C. Agardh	3	22800
Thalassionema nitzschioides (Grunow) Mereschkowsky	30	1667885
Thalassiosira sp.	10	100475
unidentified pennate diatoms	25	812600

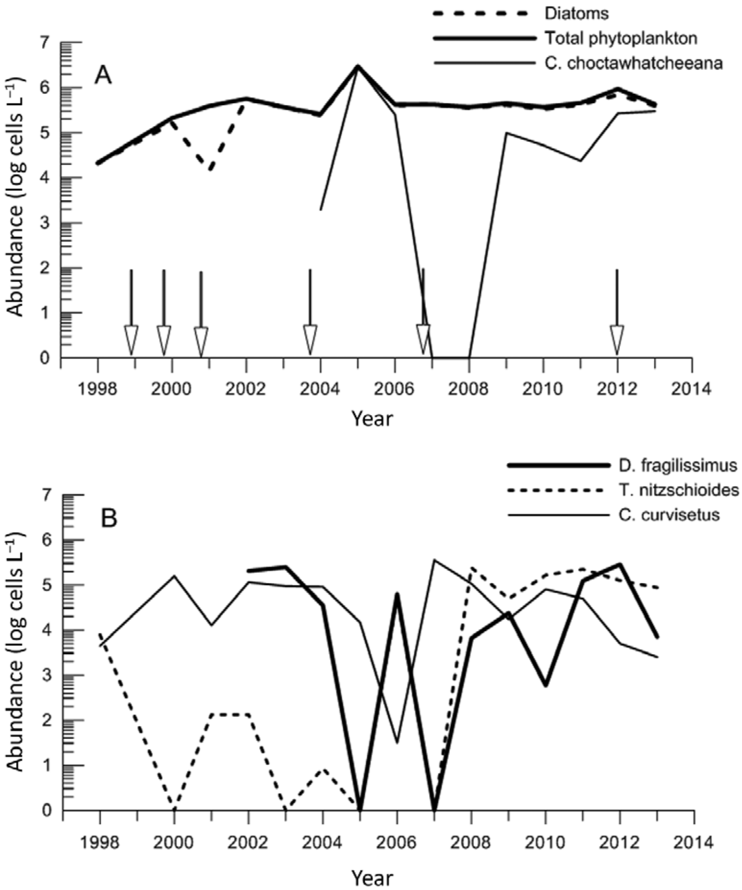

Fig 3. Temporal distribution of: A) diatoms, total phytoplankton and *Cyclotella choctawhatcheeana*; B) *Chaetoceros curvisetus*, *Dactyliosolen fragilissimus* and *Tthalassionema. nitzschioides* in Rogoznica Lake for the period 1998–2013. Diatom abundance is referring to average of 9 m water column. Mixing events are marked by arrows.

Tab. 3. Maximum (MAX), minimum (MIN) and average (AVG) of values of phytoplankton (during 1998–2013) and nutrients (during 2000–2008) in Rogoznica Lake. N – number of samples.

Parametar	AVG	MAX	MIN	N
Total microphytoplankton (cells L^{-1})	461 400	8 138 480	0	382
Diatoms (cells L^{-1})	451 360	7 926 200	0	382
Dinoflagelates (cells L^{-1})	10 040	840 910	0	382
NO_3 (µmol L^{-1})	2.03	44.21	0	476
NO_2 (µmol L^{-1})	0.26	3.7	0	478
NH_4 (µmol L^{-1})	14.84	315	0.23	457
Total inorganic nitrogen (µmol L^{-1})	17.21	315.83	0.31	440
PO_4 (µmol L^{-1})	1.98	33.1	0.01	496
SiO_4 (µmol L^{-1})	5.5	679	0.34	497

Discussion

The diatoms *Thalassionema nitzschioides*, *Cyclotella choctawhatcheeana*, *Dactyliosolen fragilissimus*, and *Chaetoceros curvisetus*, were found to be the most frequent and abundant phytoplankton species, and appeared recurrently during annual plankton succession in the Rogoznica Lake.

The maxima of species abundances in the lake are in the same order of magnitude as maxima of species abundances in other coastal regions of the eastern Adriatic Sea (Cetinić et al. 2006, Viličić et al. 2009, Bosak et al. 2009, Bužančić et al. 2012, Marić et al. 2012, Vidjak et al. 2012, Godrijan et al. 2013). The extreme environmental conditions (high seasonal variations in salinity and temperature; redox conditions and nutrients; periodically high RSS concentration in the whole water column) that characterize Rogoznica Lake govern the development of the above mentioned species that exist in the lake (Ciglenečki et al. 2005, 2013, Kršinić et al. 2013). During the research period (1998 – 2013) only 36 diatom taxa were recorded in the lake, as a significant difference from other coastal and semi enclosed basins along the eastern Adriatic coast; e.g. during one year of phytoplankton sampling in Šibenik Bay and Kaštela Bay in the middle Adriatic, 61 and 80 diatom taxa were recorded, (Bužančić et al. 2012) and 100 diatom taxa were found in the northern Adriatic fjord-like Lim Bay (Bosak et al. 2009).

In comparison with other coastal regions of the Adriatic Sea, Rogoznica Lake is characterized by a high concentration of nutrients and their high variability within the water column (Ciglenečki unpublished data). In potentially eutrophic coastal areas like the Krka Estuary and Kotor Bay, the recorded maximal concentrations of total inorganic nitrogen and silicates were up to 17.70 and 44.1 µmol L^{-1} (Bosak et al. 2012; Šupraha et al. 2014), while in the Rogoznica Lake these numbers are several times higher, 44.21 and 679 µmol L^{-1}, respectively. However, registered mean values in the lake for total inorganic nitrogen, silicates and phosphate were 2.09 µmol L^{-1}, 55.5 µmol L^{-1} and 1.98 µmol L^{-1}, respectively. According to nutrient values Rogoznica Lake can be regarded as a highly eutrophic system. Such a high concentration of phosphate was registered only in the most eutrophic environments along the eastern Adriatic, e.g. in the Krka Estuary and Kaštela Bay (Vidjak et al. 2012). During stratification in the lake, the surface waters are poor in nutrients and phosphate limited (Ciglenečki unpublished data). Mixing events in the lake bring nutrient-rich bottom waters to the surface layer, which, accompanied by decomposition of dead organisms due to the anoxic stress, drastically change the concentration of nutrients and their ratios. It has a potential influence on the phytoplankton composition, abundance and diversity. However, it appears that the nutrients are not the main factor regulating the phytoplankton development in the lake. The impacts of redox conditions and light penetration might be crucial along with the mixing, concentration of nutrients and thermohaline conditions. Changes in the thermohaline conditions in favor of lower salinity recorded after 2001 in the surface and middle water layers (Fig. 2) (Ciglenečki et al. 2013) coincide with a change in phytoplankton composition. After 2001 diatoms took over the domination with four dominant species that were alternately dominant. Since *D. fragilissimus* abundance had a significantly positive correlation with nitrite and ammonium, it could be speculated that *D. fragilissiumus* could be a possible indicator of the mixing in the lake. Also, two dominant species *C. choctawhatcheeana* and *T. nitzschioides* had a positive correlation in the occurrence in the lake.

Mixing of the water layers depends on meteorological conditions, which highly influence the intensity of the process (Ciglenečki unpublished data). Due to the oxidation of a relatively high concentration of sulphide, which is rapidly transported to the surface, a sudden consumption of oxygen and the occurrence of anoxic conditions in the whole water column may be seen. Then the presence of RSS (sulphide, polysulphide and colloidal sulphur formed by oxidation) can be found through the entire water column (Ciglenečki et al. 2013). On the other hand, if the mixing is slow, oxygenated surface waters diffuse to the bottom of the lake, or the bottom waters, with plenty of sulphide and nutrients, diffuse to the surface layer of the lake (as was recorded in September of 2003 and November of 2006); the mixing process can last up to 7 days, while the surface layer remains rich in oxygen the whole time (Ciglenečki unpublished data). In most cases when RSS, i.e. sulphide, enters in the upper water layer, the abundance of phytoplankton species decreases because of the toxic effect which sulphur species could have on the phytoplankton community. On the other hand, those mixing events result in nutrient enrichment of the surface layer, stimulating phytoplankton development. Variability in the stratification conditions and the intensity of the mixing influence the phytoplankton development and domination of certain phytoplankton species. *C. curvisetus* usually reaches the highest abundance in spring during weak stratification. After the mixing in autumn, *D. fragilissimus* takes over the dominant position, probably due to the absence of *C. curvisetus* which prefers lower temperatures and nutrient concentrations (Burić et al. 2009).

Moderate phytoplankton abundance, extreme environmental conditions including high seasonal variations in salinity, temperature, mixing, periodically high RSS and nutrient concentrations characterize Rogoznica Lake as highly eutrophic system which can be regarded as natural laboratory for monitoring of the selected biogeochemical processes. The changes in the phytoplankton composition and variability coincide with changes of the thermohaline conditions in the lake; only species with high adaptability to stress using encystment can survive in such an extreme environment. It can be speculated that the species which dominated in the lake during the research period were adjusted to these extreme conditions, while they were alternately dominant due to the adaptation of each species to the rapid changes of the specific environmental conditions.

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