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Water usage and seasonality as primary drivers of benthic diatom assemblages in a lowland reservoir

Zsuzsanna Kókai[a], Gábor Borics[b,c], István Bácsi[d], Áron Lukács[d], Béla Tóthmérész[g], Eduárd Csépes[e], Péter Török[f], Viktória B-Béres[b,c,*]

[a] University of Debrecen, Department of Ecology, H-4032 Debrecen, Egyetem tér 1, Hungary
[b] MTA Centre for Ecological Research, Danube Research Institute, Department of Tisza Research, H-4026 Debrecen, Bem tér 18/c, Hungary
[c] MTA Centre for Ecological Research, GINOP Sustainable Ecosystems Group, H-8237 Tihany, Klebelsberg Kuno u. 3, Hungary
[d] University of Debrecen, Department of Hydrobiology, H-4032 Debrecen, Egyetem tér 1, Hungary
[e] Middle-Tisza Water Authority, Szolnok Tiszaliget 1, H-5000, Hungary
[f] MTA-DE Lendület Functional and Restoration Ecology Research Group, H-4032 Debrecen, Egyetem tér 1, Hungary
[g] MTA-DE Biodiversity and Ecosystem Services Research Group, H-4032 Debrecen, Egyetem tér 1, Hungary

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ABSTRACT

In general, reservoirs are multi-purpose objects and they often have to fulfil different tasks at the same time. The compliance with these different expectations is more manageable in reservoirs with well-separated heterogeneous basins than in homogenous ones. The Kisköre Reservoir is the second largest standing water in the Carpathian Basin. Its water level is artificially regulated which creates unique habitats with high nature conservation value. Furthermore, the Reservoir is also considered as an important recreation centre in the region. It consists of four basins with different protection degree and management strategy. Here, we tested whether spatial (usage-dependent) or seasonal (time-dependent) segregations characterized the benthic diatom composition in the Reservoir. We also tested the influence of different water usage of basins using diatom metrics and diversity indices. We hypothesized that spatial heterogeneity in diatom composition will be more pronounced than seasonal ones. We also supposed that composition and diversity of diatom assemblages as well as diatom based ecological status will clearly reflect to different management strategies in the basins, whereas we expected moderate ecological status and low diversity in basins with high level of human impact. Our first hypothesis was not confirmed by the results. While diatom composition was clearly heterogeneous in time, surprisingly no usage-dependent segregation was found. Furthermore, our second hypothesis was also only partially confirmed by the results. In early summer, diversity was significantly lower in basins with higher level of human impact, than in the other basins. In late summer, however, diversity was rather directly controlled by nutrients and light not by water usage. Moreover, diatom based ecological status positively correlated to the intensity of recreation activities and negatively to protection degree. Although these results were surprising at the first time, they clearly confirm that a balanced ecological-economical relation can be maintained with properly designed and performed strategies in artificial reservoirs. But protection strategies, because of their exclusive interest to habitat conservation of macroscopic not microscopic organisms, require careful revisions.

1. Introduction

The human society strongly links to water and wetland ecosystems in many ways (ICPDR, 2008; Alexander et al., 2012). Unexpected drastic changes of the water regime (e.g. floods, droughts) threatened human communities during the history, but due to the technological development from the 18-19th centuries, the problem could be resolved by effective human interventions (regulations, channelization, damming, creation of reservoirs, etc.). Although in usual these interventions lead to drastic environmental changes, their long-term ecological effects have not yet been clarified (Poff et al., 2007; Wu et al., 2010; Cibils Martina et al., 2013). It is especially true for reservoirs, since

* Corresponding author at: MTA Centre for Ecological Research, Danube Research Institute, Department of Tisza Research, H-4026 Debrecen, Bem tér 18/c, Hungary.

E-mail addresses: kokai.zsuzsanna@okologia.mta.hu (Z. Kókai), borics.gabor@okologia.mta.hu (G. Borics), lukacs.aron@okologia.mta.hu (Á. Lukács), beres.viktoria@gmail.com (V. B-Béres).

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long-term storage modifies the basic hydrological processes of the water currents i.e. flow velocity, discharge, water retention time, they change type (from stream to standing water) which coincides with changes in habitat composition and changes in the whole biota (Poff et al., 2007). Impoundments have various positive and negative effects on the biotic communities. There are evidences that impoundments can support spreading of invaders (Johnson et al., 2008) or can diminish diversity (Algarte et al., 2016; Braghin et al., 2018; Oliveira et al., 2018), other studies emphasize its positive influence on mature biofilm formation (Cibils Martina et al., 2013), or its importance as refuge (Clements et al., 2006).

In general, reservoirs are multi-purpose objects: they often have to fulfil different tasks at the same time, like flood control, irrigation, recreation activities (e.g. swimming, fishing) and/or contribution to diversity conservation (see more in review by Chester and Robson, 2013). These multi-purpose reservoirs can be considered as epitome of ecological engineering (Mitch and Jørgensen, 2003). The compliance with these different expectations is more manageable in large reservoirs with well-separated heterogeneous basins than in smaller, homogenous ones. However, all of these ecosystem services require good ecological status (or potential) of water bodies. If ecological status is not maintained, not only the ecological value but economic utility of reservoirs or basins can decrease within a short time (Vesterinen et al., 2010).

Traditionally pelagic phytoplankton is studied to assess ecological status of lakes and ponds (Padisák et al., 2006; Nõges et al., 2009), while benthic diatoms are considered as sensitive bioindicators in lotic ecosystems (Potapova and Charles, 2002; Várbíró et al., 2012). Most of the undesirable effects that affect the lakes (e.g. enhancing nutrient load due to fishing, or permanent physical disturbances due to water sports) first threaten the littoral zone of the standing waters. The increasingly occurring deteriorating conditions of littoral zone cannot be effectively monitored by using exclusively pelagic algae (Rimet et al., 2016). Benthic diatoms can play essential role in the early perception of these negative effects (Rosenberg et al., 2008; Rimet et al., 2016). In response to environmental disturbances as nutrient load, or physically disturbed conditions, the structure and function of the litoral assemblages significantly change (Berthon et al., 2011; B-Béres et al., 2014, 2016; Kókai et al., 2015). These changes, in turn, can be simply detected and assessed by using diatom indices (Coste, 1982; Kelly and Whitton, 1995; Rott et al., 1997, 1998; Várbíró et al., 2012). Although most of these indices were developed for rivers, not for lakes (for the exceptions see Stenger-Kovács et al., 2007; Bennion et al., 2014; Kelly et al., 2014), and there can be compositional differences between lotic and lentic diatom assemblages even with similar environmental background (Kahlert and Gottschalk, 2014), it has been also proved that several metric values can overcome these compositional differences and diatom indices provide reliable assessment results for lakes as well (Kahlert and Gottschalk, 2014).

The Kisköre Reservoir (Lake Tisza) is the second largest standing water in Hungary, and also in the Carpathian Basin. It possesses a particularly diverse wildlife which is similar to that of the late floodplain landscape. It was constructed in 1973 by damming of Tisza River. The Reservoir is an artificial shallow wetland complex with extended littoral vegetation. Its water level is artificially regulated: the Reservoir is filled up with water from the Tisza River during spring, and the water is drained off during the late autumn (ICPDR, 2008; Vasvári and Erdős, 2015). These special environmental conditions create unique habitats which represent high nature conservation value. The Reservoir is not only under national protection, but it is also an UNESCO World Heritage Site (UNESCO, 1999). But beside its nature conservation value, Kisköre Reservoir is also considered as an important recreation centre providing opportunities for swimming, fishing, boating, and water sport activities (ICPDR, 2008; Vasvári and Erdős, 2015). It consists of four differently managed basins: one highly protected basin with limited permit for boating and fishing but with no permission for sport activities and swimming. There are two moderately protected basins with options for fishing, boating and swimming with or without sport activities, and there is one basin with low protection and with extended opportunities for fishing, swimming and sport activities. Thus, Kisköre Reservoir is a good example for the design of sustainable ecosystem (Mitch and Jørgensen, 2003). It plays crucial role both in the water management and in the tourism in the Tisza valley. Its complex utilization needs very careful management maintaining the balance between nature protection (ecological interest) and recreation activities (economic interest).

Here, we tested whether seasonal (time-dependent) or spatial (usage-dependent) segregations in diatom compositions are characteristic in the Reservoir. The influence of different water usage in the basins was also tested using diatom based metrics and diversity indices. We hypothesised that the different levels of protection and water uses are reflected by the diversity and compositional differences of the benthic diatom assemblages. In a physically disturbed environment, where the amplitude of disturbances is constantly changing, sensitive taxa are overgrown by tolerant species and the diversity declines (B-Béres et al., 2016; Lange et al., 2016). Furthermore, diatom based ecological status is negatively influenced by increasing human impact (Rimet et al., 2016). That is, higher diversity and good diatom based ecological status is expected in the protected basins than in those ones which are exposed to higher level of human impact (sport activities, swimming, boating).

2. Materials and methods

2.1. Study area

Kisköre Reservoir is situated in the Middle-Tisza region of the Great Hungarian Plain (Fig. 1) (Vasvári and Erdős, 2015). It is 27 km long, its surface area is 127.34 km^2 and its total volume is 253,000,000 m^3. The average depth of the Reservoir is 1.3 m, while its largest depth is 17 m (K-Szilágyi et al., 2013). Mosaic patterns of habitats (extended macrophyte coverage, open water surfaces, islands) are characteristics for Kisköre Reservoir. It is divided into four, differently managed basins: the highly protected Tiszavalk basin (TV), the moderately protected Poroszló basin (PO) and Sarud basin (SA), and the Abadszalók basin (AB) with low protection and high recreation activities (Table 1). The Table 1 summarize the type and intensity of recreation activities and also the protection degree in the four basins.

2.2. Sampling setup and measurements

There are two relevant factors during the design of the sampling in Kisköre Reservoir: (i) The water level of the Reservoir is artificially regulated. It means that the filling up of the Reservoir usually starts in March and finishes in April. Further water level regulation happens in October/November for reaching the winter water level in the basins. (ii) The formation of the mature biofilm is a time-consuming process: at least 4–6 weeks are required for development of dense benthic assemblages (Tapolczai et al., 2016). Thus, epiphyitic diatom samples were collected twice a year, in June and in August during a four year period (from 2014 to 2017). Emergent macrophytes (common reed or reedmace) as characteristic plants of the Reservoir were the substrates we sampled. Samples were collected at the sunny part of the littoral zone in the four basins of the Reservoir, The samplings and preservations were performed according to the European standard (EN 13946). Environmental parameters such as conductivity (COND – $\mu S\,cm^{-1}$), dissolved oxygen (DO − %), pH and water temperature (T − °C) were measured in the field with a portable multiparameter digital meter. Water samples were also collected for further laboratory analyses to measure the following chemical factors: biological oxygen demand (BOD_5 − mg L^{-1}, iodometry, MSZ EN 1899-1), chloride ion (Cl^- − mg L^{-1}, argentometry, MSZ 1484-15), chemical oxygen demand (COD_{Cr} − mg L^{-1}, chromatometry, MSZ 12750-21), TP (total amount of P-forms −

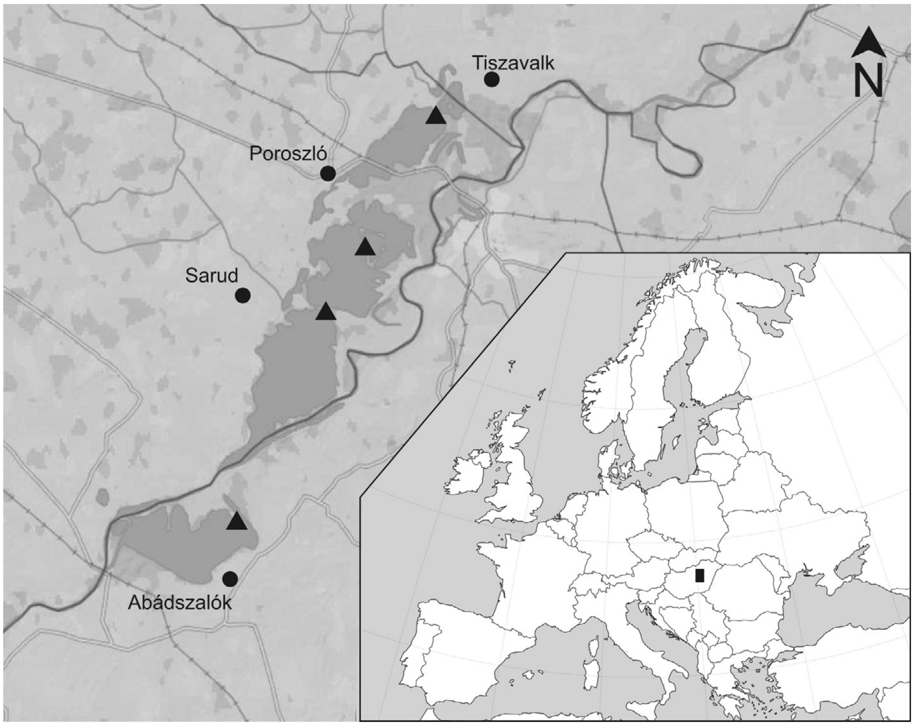

Fig. 1. Location of the Kisköre Reservoir and the sampling sites in the basins. Black triangles – sampling points; black circles – main cities and villages. Geographical positions of sampling sites: Tiszavalk basin – 47°40′14.7″N, 20°42′56.4″E; Poroszló basin – 47°36′39.2″N, 20°40′27.8″E; Sarud basin – 47°35′00.7″N, 20°39′11.5″E; Abádszalók basin – 47°29′53.1″N, 20°35′44.3″E.

mg L^{-1}, spectrophotometric analysis, MSZ 260-20), TSS (total suspended solids – mg L^{-1}, gravimetric analysis, MSZ 12750-6), TN (total amount of N-forms – mg L^{-1}, sum of the various N-forms, MSZ 260-12). These chemical parameters were measured in the laboratory of the Middle-Tisza Water Authority.

Benthic diatom sampling and preservation were performed according to the European guideline (EN 13946). After preparing the samples with hot hydrogen-peroxide, Naphrax resin was used for embedding (EN 13946). At least 400 diatom valves were identified and counted in each samples (EN 14407) using Leica DMRB microscope with 1000–1600-fold magnification. The following up-to-date references were used for identification: Krammer and Lange-Bertalot (1997a,b, 2004a,b), Potapova and Hamilton (2007), Bey and Ector (2013), Stenger-Kovács and Lengyel (2015).

2.3. Data processing and analyses

To define the diatom based ecological status of the basins Multimetric Index for Lakes (MIL) was calculated using by the following equation (Bolla et al., 2010):

$$MIL = \frac{IBD + EPI - D + TDIL_{1-20}}{3}$$

IBD: the Biological Diatom Index (Indice Biologique Diatomees; Prygiel and Coste, 1999)

EPI-D: the Diatom based Eutrophication Pollution Index (Dell'Uomo, 1996)

$TDIL_{1-20}$: the Trophic Diatom Index for Lakes (Stenger-Kovács et al., 2007)

Maximum value of MIL is 20, ecological status boundaries based on this metric are shown in Table 2 (Ács et al., 2016).

Berger-Parker diversity index was calculated using PAST software package (version 2.11; Hammer et al., 2001) to express the proportional abundance of the most abundant taxa. The Berger-Parker diversity index is a simple metric for measuring dominance (Berger and Parker, 1970; May, 1975). An increase in the value of the Berger-Parker index accompanies an increase in dominance and a decrease in diversity.

Monte-Carlo permutation test was used to decide which environmental parameters influenced significantly the taxonomical composition of diatom assemblages. These were conductivity (COND), pH, chemical oxygen demand (COD_{Cr}) and water temperature (T). In further, in the redundancy analyses we used only these parameters. To analyze the relationship between the assemblages' composition (relative abundances of taxa), and the environmental parameters such as physical and chemical parameters of water, intensity of recreation activities, protection degree, redundancy analysis (RDA) was used applying CANOCO 5.0 software package (ter Braak and Šmilauer, 2002). Monte-Carlo permutation test (default 499 permutations) was used to decide whether the detected pattern is significantly different from

Table 1
Management strategy of the basins of Kisköre Reservoir. The numbers indicate the intensity of recreation activities and the protection degree: 0 - not typical, 1–1-24%, 2–25-49%, 3–40-74%, 4–75-100%. Water usage data were provided by the Middle-Tisza Water Authority.

	Tiszavalk basin	Poroszló basin	Sarud basin	Abádszalók basin
Type of recreation activities	Intensity of recreation activities			
Fishing (FISH)	3	3	2	2
Boat with internal combustion engine (ICE)	2	3	2	3
Boat with electric motor (EC)	1	1	0	0
Swimming (SWIM)	0	1	1	1
Water sports (WS)	0	0	2	3
	Protection degree			
	4	2	2	1

Table 2
Boundaries of MIL values in Kisköre Reservoir.

Ecological status classes	High	Good	Moderate	Poor	Bad
MIL boundaries	≥13.9	12.3–13.89	8.2–12.29	4.1–8.19	< 4.1

Table 3
Results of one-way ANOVA analyses. Dependent variables were the physical and chemical parameters, the fixed factors were the four basins in June and in August. Bold letters represent significant correlations ($p < 0.05$). Abbreviations of basins: TV – Tiszavalk basin; PO – Poroszló basin; SA – Sarud basin; AB – Abádszalók basin.

	June	August
	TV × PO × SA × AB	TV × PO × SA × AB
BOD_5	0.450	**0.047**
COND	0.891	0.482
Cl^-	0.955	0.587
COD_{Cr}	0.373	0.126
DO	0.630	0.268
TP	0.141	0.548
TSS	**0.044**	0.085
TN	0.754	0.751
pH	0.183	0.052
T	0.998	0.977

random. To compare the spatial and temporal characteristics of diversity and also the diatom based ecological status of the basins, one-way ANOVA was used (ter Braak and Šmilauer, 2002). The dependent variables were Berger-Parker diversity and MIL, the fixed factors were the four basins in June and in August. In addition, one-way ANOVA was also used for testing significant differences in physical and chemical parameters between basins in early and late summer.

3. Results

3.1. Environmental background

Spatially, only TSS (June) and BOD (August) differed significantly in the basins ($p < 0.05$; Table 3). Total suspended solids value was the lowest in Abádszalók basin in early summer, while low BOD characterised the Tiszavalk basin.

Seasonally, pH, BOD and TSS contents in Tiszavalk basin were significantly lower in August than in June ($p < 0.05$; Table 4). In Poroszló basin, pH was also lower in August than in June, while COND significantly increased with time ($p < 0.05$; Table 4). In the least protected Abádszalók basin, total nitrogen value was higher in June than in August ($p < 0.05$; Table 4).

Assessing temporal and spatial influences together, pH, DO and TSS contents differed significantly in basins (Table 4). The physical and chemical parameters of the basins are summarized in Supplementary Table 1.

3.2. Relationship between diatom assemblages, environmental factors and water usage

According to the Monte-Carlo permutation test in full models, water temperature ($p < 0.001$), pH ($p < 0.001$), chemical oxygen demand ($p < 0.05$) and conductivity ($p < 0.05$) affected significantly the taxonomical composition of benthic diatom assemblages. The RDA analysis showed, that temperature (-0.82) and pH (0.62) correlated highly with axis 1, while conductivity (-0.68), fishing (-0.48), boating with electric motor (-0.48) and water sports (0.43) strongly related to axis 2. A significant difference from random distribution was indicated by the Monte-Carlo permutation test (number of permutation = 499; $p = 0.002$ for all canonical axes). According to the RDA analyses, no spatial separation of diatom assemblages was found in the Reservoir (Fig. 2a), but the composition in differently managed basins differed from each other in time (Fig. 2b). The environmental parameters, the intensity of recreation activities and the protection degree explained 25.3% variance in the taxonomical composition of diatom assemblages for all canonical axes.

Clear seasonal pattern in composition was detected in the Reservoir. Some taxa, like the tube-forming *Encyonema* spp. (*E. caespitosum* Kützing, *E. silesiacum* (Bleisch) D.G.Mann), the pioneer *Achnanthidium minutissimum* (Kützing) Czarnecki, the fast moving *Nitzschia* spp. (*Ni. dissipata* (Kützing) Rabenhorst, *Ni. fonticola* (Grunow) Grunow), or the filamentous *Melosira varians* C. Agardh were characteristic in early summer. These species showed strong negative correlation to conductivity, while they positively connected to pH (Fig. 2c). Planktic taxa such as *Cyclostephanos invisitatus* (M.H. Hohn & Hellermann) E.C. Theriot, Stoermer & Håkasson and *Stephanodiscus hantzschii* Grunow also appeared in the epiphyton. They were characteristic members of the assemblages in June (Fig. 2b and c). In contrast, other species mainly occurred with high density in late summer (Fig. 2c). In this period, some monoraphid taxa with prostrate habit (e.g. *Amphora pediculus* (Kützing) Grunow, varieties of *Cocconeis placentula* Ehrenberg) clearly correlated to temperature, while taxa also with this habit (*Halamphora veneta* (Kützing) Levkov, *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot) related strongly to conductivity (Fig. 2c). Fast moving naviculoid and nitzschoid taxa (e.g. *Mayamaea atomus* var. *permitis* (Hustedt) Lange-Bertalot, *Nitzschia frustulum* (Kützing) Grunow) also preferred periods with increased conductivity (Fig. 2c).

Only *Diadesmis confervaceae* Kützing can be considered as clearly "usage dependent" species. It was a permanent and also a dominant member of diatom assemblages in basins with high fishing intensity and without water sport activities (Fig. 2c). But in other basins, its presence was only sporadic.

Table 4
Results of one-way ANOVA analyses. Dependent variables were the physical and chemical parameters, the fixed factors were the four basins in June and in August. Bold letters represent significant correlations ($p < 0.05$). Abbreviations of basins: TV – Tiszavalk basin; PO – Poroszló basin; SA – Sarud basin; AB – Abádszalók basin.

	TV_{June} × TV_{August}	PO_{June} × PO_{August}	SA_{June} × SA_{August}	AB_{June} × AB_{August}	temporality × spatiality
BOD_5	**0.023**	0.069	0.614	0.758	0.096
COND	0.329	**0.046**	0.157	0.397	0.249
Cl^-	0.172	0.134	0.083	0.081	0.087
COD_{Cr}	0.869	0.696	0.835	0.345	0.206
DO	0.093	0.185	0.501	0.099	**0.048**
TP	0.511	0.417	0.190	0.269	0.416
TSS	**0.003**	0.195	0.298	0.211	**0.003**
TN	0.229	0.499	0.069	**0.033**	0.191
pH	**0.015**	**0.047**	0.359	0.229	**0.004**
T	0.233	0.207	0.199	0.267	0.411

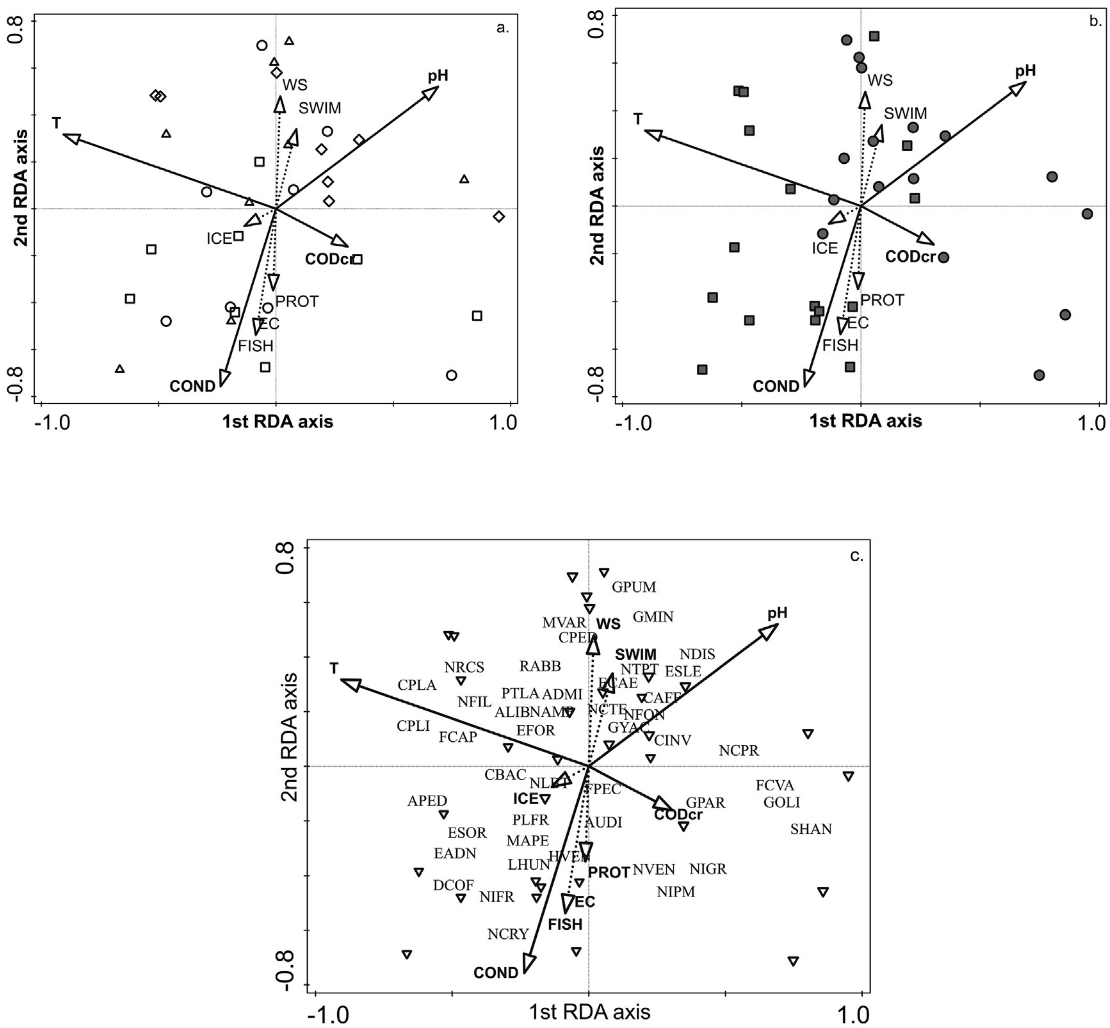

Fig. 2. Relation of diatom taxa, environmental variables and the intensity of recreation activities including protection degree displayed by RDA based on relative abundances of taxa. (a) Spatial heterogeneity in the Reservoir. Empty circles – samples from Tiszavalk basin; empty squares – samples from Poroszló basin; empty diamonds – samples from Sarud basin; up triangles – samples from Abádszalók basin. (b) Temporal heterogeneity in the Reservoir. Grey circles – samples in June; grey squares – samples in August; (c) Taxa distribution in the Reservoir – down triangles marked the samples; four letter OMNIDIA codes indicate the name of dominant diatom taxa (dominance > 5%). Abbreviations of environmental parameters: biological oxygen demand (BOD_5), conductivity (COND), chloride (Cl^-), chemical oxygen demand (COD_{Cr}), dissolved oxygen (DO), total amount of P-forms (TP), total suspended solids (TSS), total amount of N-forms (TN), pH and water temperature (T). Abbreviations of recreation activities: Fishing (FISH), boat with internal combustion engine (ICE), boat with electric motor (EC), swimming (SWIM), water sports (WS) and also protection (PROT).

3.3. Taxonomical diversity and diatom based ecological status in the differently managed basins

Spatially, the Berger-Parker index value was significantly higher in June in the Abádszalók basin suggesting low diversity here (Fig. 3a; $p < 0.005$). In contrast, there were no significant differences in taxonomical diversity of basins in late summer (Fig. 3b; $p > 0.1$). Temporally, the Berger-Parker index value was significantly higher only in Abádszalók basin in early summer than in late summer (Table 5; $p < 0.05$).

While a strong positive correlation was found between diatom based ecological status and intensity of recreation activities in the basins (Fig. 4a; $p = 0.002$), MIL value negatively correlated to the protection degree (Fig. 4b; $p < 0.0001$). The ecological status was significantly lower in the highly protected Tiszavalk basin both in early and late summer (Fig. 5a and b; $p < 0.005$ and $p < 0.05$, respectively).

4. Discussion

4.1. Temporal heterogeneity characterizes diatom composition in differently managed basins

Benthic diatom assemblages have more obvious short time stability than the phytoplankton (Rimet et al., 2015). While planktic assemblages can be characterized with daily changes, chemical changes are followed only after 1 to 5 weeks by remarkable compositional modifications in phytobenthon (Lavoie et al., 2008; Rimet et al., 2015). Their spatial heterogeneity, however, is strongly forced by environmental conditions (Crossetti et al., 2013a; Rimet et al., 2015, 2016). Physical disturbances as well as nutrient supply play decisive role in dispersal and colonisation abilities of diatoms (Stenger-Kovács et al., 2013; B-Béres et al., 2016; Lukács et al., 2018). Thus, we supposed that different water usage of basins would lead to more pronounced heterogeneity in diatom assemblages than seasonality. The results did not confirm our hypothesis; only clear temporal differences in diatom composition were found. In June, relative abundance of planktic taxa was defined by the spring water level modification. In Tisza River,

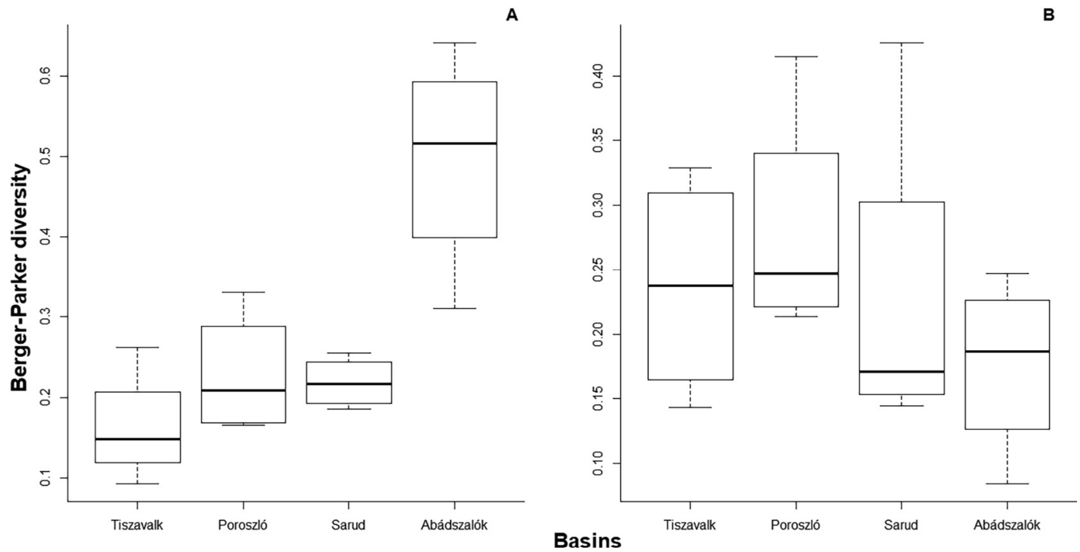

Fig. 3. Box plots of the Berger-Parker dominance in the four basins (A) in June and (B) in August. The box plots indicate the median (thick solid line), the 25th and 75th percentiles and the whiskers from minimum to maximum. Results of ANOVA tests were: F = 11.3578, p = 0.0008 (June) and F = 0.7635, p = 0.5360 (August).

Table 5
Results of one-way ANOVA analyses. Dependent variables were values of the Berger-Parker index, the fixed factors were the four basins in June and in August. Bold letters represent significant correlations ($p < 0.05$). Abbreviations of basins: TV – Tiszavalk basin; PO – Poroszló basin; SA – Sarud basin; AB – Abádszalók basin.

	p-value
$TV_{June} \times TV_{August}$	0.235
$PO_{June} \times PO_{August}$	0.419
$SA_{June} \times SA_{August}$	0.891
$AB_{June} \times AB_{August}$	**0.006**

centric diatoms are usually characteristic and dominant members of phytoplankton in spring (Hatvani et al., 2019). The increased TSS value in June also could be induced by the water level modification, especially in the Tiszavalk basin. Filling up of the Reservoir began with closing of the main dam and with opening the channels between the basins. Thus, increasing water level inundates the basins, at last the Tiszavalk basin. The stirring water collects particles from the basins below and it transports them to Tiszavalk basin.

Tube forming and filamentous taxa are able to produce extracellular enzymes or to extend the biofilm thickness to access nutrients in mats (Pringle, 1990; Rimet et al., 2015; B-Béres et al., 2017). In addition, they also have an advantage during high turbidity periods (Leira et al., 2015). Thus, they can be characteristic in spring or in early summer in turbid waters with low nutrient supply and/or conductivity (Stenger-Kovács et al., 2013; B-Béres et al., 2014, 2016; Leira et al., 2015; Rimet et al., 2016). In our study, these taxa correlated negatively to conductivity and they were dominant in early summer, when the TSS value was high (see above). In this period, the pioneer *A. minutissimum* was also common in the basins. Although in usual, this species showed strong negative relation to nutrients and/or conductivity (De Fabricius et al., 2003; Kovács et al., 2006; Berthon et al., 2011; B-Béres et al.,

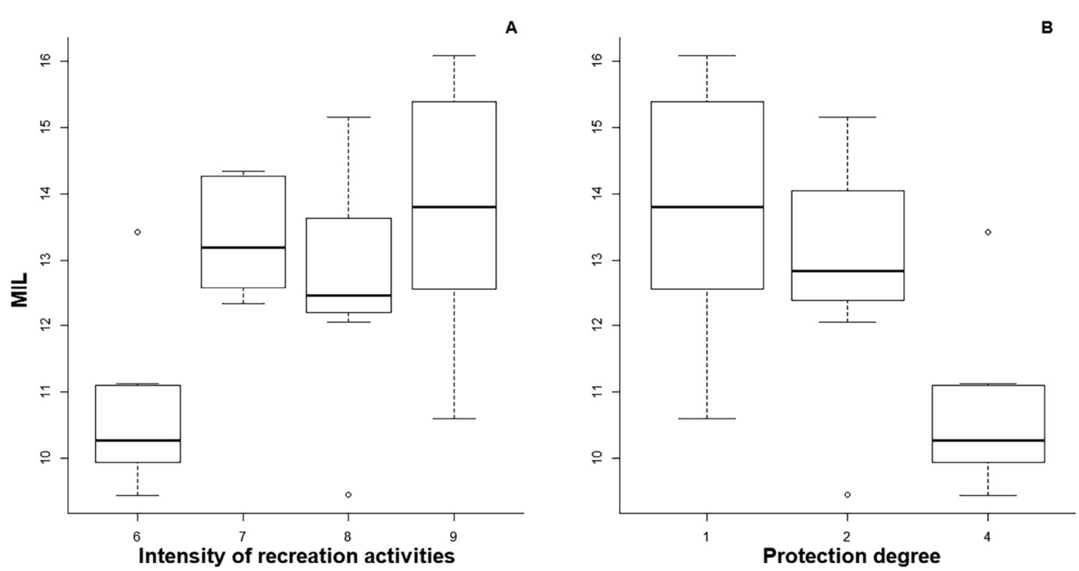

Fig. 4. Relations between MIL diatom index and (A) intensity of recreation activities; and (B) protection degree. The box plots indicate the median (thick solid line), the 25th and 75th percentiles and the whiskers from minimum to maximum. Results of ANOVA tests were: F = 6.9671, p = 0.0012 (A) and F = 10.0413, p = 0.0005 (B).

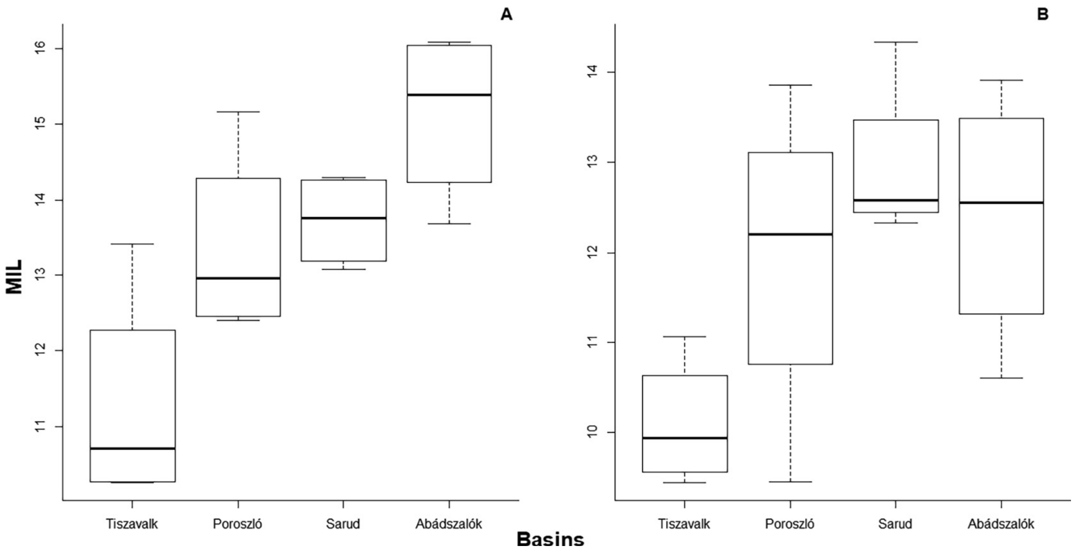

Fig. 5. The MIL diatom index in basins (A) in June and (B) in August. The box plots indicate the median (thick solid line), the 25th and 75th percentiles and the whiskers from minimum to maximum. Results of ANOVA tests were: F = 7.3904, p = 0.0046 (June) and F = 3.6445, p = 0.0446 (August).

2014; Kókai et al., 2015), its dominance is primarily determined by disturbances (e.g. Stenger-Kovács et al., 2006; Rimet et al., 2015, 2016). Here, one of the key disturbing factors could be the water level modification in spring, which could cause great possibilities for dispersal and colonization of this species. In usual, *Nitzschia* species characterize waters with high nutrient supply (Passy, 2007; Berthon et al., 2011; B-Béres et al., 2014; Kókai et al, 2015). However, our previous studies have already pointed out, that abundance of *Ni. dissipata* or *Ni. fonticola* are rather controlled by extreme water regime caused disturbances (B-Béres et al., 2014, 2016). In Kisköre Reservoir, these taxa were characteristic in June.

Due to the limited number of studies linked directly to seasonal changes in lentic diatom assemblages there are contradictory opinions whether succession is or is not clearly visible in periphyton (see more: Rimet et al., 2015). Here, seasonality had a clear regulatory force in shaping diatom assemblages. At ecosystem level, characteristic changes are induced mainly by the extension of macrovegetation during summer. The macrophyte density reaches its maximum in August. The most affected areas are the Tiszavalk basin (60–65% coverage) and the Poroszló basin (55–60% coverage), where water sport activities are not permitted. In contrast, increasing intensity in sport activities decreases the extension of macrophytes (~30–35% in Sarud and Abádszalók basins) (web 1). Extended macrophyte cover including mostly floating-leaved aquatic plants might interact to planktic algal assemblages causing lower TSS value and reduced intensity in photosynthesis (direct decrease in DO and indirect decrease in pH). The decrease in TSS content could induce an increase in light transmission through water column. Influence of light conditions on community composition is complex enough (Tapolczai et al., 2016). Even though prostrate diatoms can be considered as a priori shade-tolerant groups (Liess et al., 2009; Stenger-Kovács et al., 2013; Tapolczai et al., 2016), their dominance in assemblages might increase with rising light intensity (Leira et al., 2015). Here, prostrate taxa were characteristic members of assemblages in August. Obviously, light is not a single factor contributing dominance of these taxa. Predation also can be an important factor controlling and regulating the community composition (Jørgensen and de Bernardi, 1998; Jørgensen, 2009). In usual, grazing effect on benthic algal assemblages caused by macroinvertebrates enhances during summer. In Kisköre Reservoir, gastropods and chironomids are constant members of zoobenthos, and their dominance usually increases in summer (non-public data of MTW Authority). Prostrate diatoms, in turn, adapted well to this biotic pressure (Rimet et al., 2015). Furthermore, the strong positive relation between monoraphid, prostrate species such as *Halamphora veneta* and *Planothidium frequentissimum* and conductivity is also a known phenomenon (Kókai et al., 2015; Pfeiffer et al., 2015; Stenger-Kovács and Lengyel, 2015). Thus, we presume that combined effect of light, grazing and in certain cases conductivity was responsible for dominance of prostrate taxa in August. In usual, fast moving diatoms prefer physically undisturbed environments (Passy and Larson, 2011; Stenger-Kovács et al., 2013; B-Béres et al., 2014). But it is not clear, whether or not they require increased nutrient supply (see more in Lukács et al., 2018). Taxa such as *Mayamaea atomus* var. *permitis* and *Ni. frustulum*, however, successfully adapted to environments characterized by high conductivity, nutrient content and/or chloride concentration (Ziemann et al., 2001; Rimet, 2012; B-Béres et al., 2014; Kókai et al., 2015).

In our study, *Diadesmis confervaceae* was the only species related strongly to water usage: it was a constant member of benthic assemblages in basins with high fishing intensity. This colonial taxon is considered to be an invasive, eutraphentic, salt-tolerant species (van Dam et al., 1994; Coste and Ector, 2000). In Hungary, it has become frequent from the early 2000′s (Szabó et al., 2004; B-Béres et al., 2014).

4.2. Taxonomical diversity and diatom based ecological status

Periphyitic assemblages as primary producers have an essential role in the food web (Potapova and Charles, 2002). Any negative changes in their structure and/or composition can damage the whole consumer-resource systems (Cantonati and Lowe, 2014). Use of diversity metrics in analyses contributes to follow and assess ecosystem processes (Stenger-Kovács et al., 2013). In this study, we hypothesized that diversity will scale with the intensity of physical disturbances, whereas the lowest diversity was expected in the most disturbed basin. Our results have confirmed this hypothesis only in the early summer period. In this time, diversity was significantly lower in Abádszalók basin. This basin is characterized by the most intense sport activities inducing strong disturbance pressure on diatom assemblages, and physical disturbances are basically responsible for reduction of diversity (Stenger-Kovács et al., 2013; B-Béres et al., 2014). In general, shearing effects caused by intense water movement can lead to overwhelming dominance of one or only a few tolerant taxa (Passy and Larson, 2011; Stenger-Kovács et al., 2013; B-Béres et al., 2014). In August, however, we did not found any spatial differences in diversity of basins. The shearing effect was as high in Abádszalók basin as in June. But this period was also characterized with high conductivity and low TSS value especially in basins with high fishing intensity and low water sport activity. Here, the low pressure on diversity due to lack of intense water movements was exceeded by direct or indirect effects of other physical and chemical parameters. This explains why no spatial differences in diversity were found in August. But this phenomenon does not explain why diversity did not decrease significantly seasonally. Since, increased conductivity and/or abundant nutrient supply induces a decrease in evenness of assemblages (Kókai et al., 2015), and it contributes to becoming a species more dominant (Stenger-Kovács et al., 2013; B-Béres et al., 2014). Liess et al. (2009), however, highlighted that "nutrient stress" alone are less effective in shaping community composition than in combination with other factors such as low light intensity, or high grazing pressure. Ecosystems can be characterized by large number of feedback mechanisms, where "everything is linked to everything" (Jørgensen, 1999, 2009). Thus, we think that negative effects of increasing conductivity and grazing intensity in August are masked by the increase in light transmission caused by low TSS content. These influences together can explain the similar diversity values of basins in June and in August.

Littoral benthic diatoms are considered to be strong indicators of ecological status changes in lakes (Stenger-Kovács et al., 2007; Rimet et al., 2015, 2016) and benthic diatom based indices are robust enough to reflect and assess ecological status here (Stenger-Kovács et al., 2007; Bennion et al., 2014; Kahlert and Gottschalk, 2014). Spatial heterogeneity of lakes might induce significant differences in ecological status between sampling sites (Crossetti et al., 2013b; Rimet et al., 2015, 2016). Here, we hypothesized that diatom based ecological status of basins will be influenced by the basin management, whereas the highest ecological status was expected in the least disturbed Tiszavalk basin. Our results have not confirmed this hypothesis at all, the lowest the recreation activity was, the lowest the calculated value of MIL index. In June, it was probably due to the strong biotic pressure by planktic algae. The elevated pH and TSS value as well as the dominance of planktic taxa in phytobenthon here also might imply this competitive relation. In August, however, conductivity was higher, while TSS value was lower in Tiszavalk basin than in early summer. In this period, salt tolerant, eutraphentic taxa (van Dam et al., 1994) such as *Diadesmis confervaceae*, *Mayamaea atomus* var. *permitis* or *Nitzschia frustulum* dominated the assemblages here.

5. Conclusion

In spite of the well-defined different water management strategies of basins in Kisköre Reservoir, our results revealed surprisingly a more pronounced temporal heterogeneity in phytobenthon composition than spatial ones. This phenomenon can be explained by the annual water level modification of the Reservoir, resulting in a clear spatial homogeneity in physical and chemical parameters of the basins. But in time, characteristic compositional changes were demonstrated in diatom assemblages induced by complex interaction based on disturbance tolerance and/or nutrient demand. In contrast to compositional characteristics of assemblages, diversity was strongly influenced by water usage and management of basins in early summer. In August, however, diversity was rather directly controlled by nutrient supply and light transmission. Diatom based ecological status also related strongly to water usage and protection level of basins. Surprisingly, the ecological status negatively correlated to protection level, suggesting the exclusive interest here to habitat conservation and restoration of macroscopic and not microscopic organisms. These results confirm that a balanced ecological-economical relation can be maintained with well-designed and properly performed water usage strategies in shallow reservoirs, but protection strategies require careful revisions with clearly defined objectives and ultimate goals.

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