Article

Vanishing world: alkaline, saline lakes in Central Europe and their diatom assemblages

Csilla Stenger-Kovács,[1]* Edina Lengyel,[2] Krisztina Buczkó,[3] Franciska M. Tóth,[4] Luciane O. Crossetti,[5] Attila Pellinger,[6] Zsuzsa Zámbóné Doma,[1] and Judit Padisák[1,2]

[1] *University of Pannonia, Department of Limnology, Veszprém, Hungary*

[2] *MTA-PE Limnoecology Research Group of the Hungarian Academy of Sciences, Veszprém, Hungary*

[3] *Department of Botany, Hungarian Natural History Museum, Budapest, Hungary*

[4] *Eötvös Loránd University, Department of Physical Geography, Geoinformatics Research Group, Budapest, Hungary*

[5] *Universidade Federal do Rio Grande do Soul, Department of Ecology, Porto Alegre, Brasil*

[6] *Fertő-Hanság National Park, Sarród, Hungary*

* *Corresponding author: stenger@almos.uni-pannon.hu*

Abstract

European shallow, alkaline, saline lakes are potential indicators of climate change. Diatoms have often been reported as valuable proxies for different kinds of anthropogenic activities. Diatom assemblages and 14 environmental variables from shallow, alkaline lakes from 2 different regions of the Carpathian basin (Europe) were investigated for 3 years to (1) elucidate the physical and chemical parameters and diatom assemblages of these lakes, (2) select the principle variables affecting the diatom communities, and (3) show the relevance of diatoms as ecological bioindicators. Water chemical characteristics of the lakes in the 2 regions differ significantly in anion concentrations (HCO_3^-, SO_4^{2-}, and Cl^-), platinum (Pt) units (colour), and oxygen saturation. Dominance by the stress-tolerant, motile diatom ecological guild, represented mainly by *Nitzschia* and *Navicula* species, was characteristic in these saline, turbid environments. Indicator species of the 2 regions were found to be different. Diatom assemblage composition was chiefly determined by conductivity and HCO_3^- and SO_4^{2-} concentrations. Nutrient loads, extreme weather events, and consequences of habitat maintenance management were unequivocally identifiable by variations in the benthic diatom assemblage composition. Diatoms are valuable indicators for assessment of ecological status of these saline, alkaline lakes. Including these organisms in ecological status assessments of inland saline lakes may improve the effectiveness of directives for conservation management and might be useful in preserving these pristine habitats that depend on natural hydrological processes.

Key words: climate, diatoms, maintenance, management, saline lakes, status

Introduction

Endorheic, saline lakes are typically small (<50 ha) and shallow (<1 m). Their total area on the globe is large (0.006% of the total global water; Williams 1986), and their volume is not markedly different from that of inland freshwaters (0.007%; Shiklomanov 1990, Williams 1993). Most are found in arid and semiarid regions (Williams 2002). Their physical and chemical features depend on the local geomorphology, basin characteristics (Dargám

1995), geochemistry (Simon et al. 2011), and evaporation and precipitation (Langbein 1961). Lakes are relatively closed systems compared to running waters or terrestrial habitats and are therefore excellent sensors of environmental changes (Gottschalk and Kahlert 2012). Saline lakes are sensitive to unpredictable weather and climate changes (e.g., rainfall, UV radiation). Even relatively small variations cause large, even irreversible changes in the natural character of salt lakes (Hammer 1990). The ephemeral nature of these lakes results in a wide range of

salinity and a reduction in diversity (Moss 1994). Saline lakes have largely been neglected in recent limnological and hydrobiological research (Moss 1994).

Despite the economic and noneconomic value of these lakes, only a few are subjected to active conservation (Williams 1993). Climate change and catchment activities such as water course diversion, dredging, or excessive pumping of surface freshwater or ground water threaten their "good" ecological status (Williams 2002). In the Carpathian Basin, 90% of these waterbodies are found in protected areas (national parks); additionally, each alkaline, saline lake is under *ex lege* protection (by law). Pannonic saline steppes and marshes (Natura 2000 areas) are especially threatened by the lowering water table due to groundwater withdrawal, loss of periodic spring floods, and excessive drainage of the surrounding areas (VGT 2009). In the last few decades, the number of these distinctive, alkaline habitats has decreased in Hungary and Austria and are now restricted to only 2 regions: the Danube-Tisza Interfluve and the Fertő-Hanság regions (Boros 1999). A similar phenomenon was observed in Mexico and Spain (Alcocer and Escobar 1990). According to predictions, the extent of these seasonally filled saline lakes will further decrease by 2025 due to human-induced climate change (Williams 2002).

Diatoms commonly occur in saline and alkaline saline lakes (De Deckker 1988). Benthic diatoms can be found in considerable quantities in East African saline lakes (Gasse 1986a) where they are not light limited (Tuite 1981). In this type of lake in Bolivia, the algal biomass is dominated by diatoms (Servant-Vildary 1984). In a Romanian study on anthroposaline lakes (Ionescou et al. 1998), half of the identified algal taxa were diatoms. Despite their importance, there have been few studies on the ecology of these organisms. In contrast with the United States, South America, Africa, and Australia (Williams 1986), only sporadic or unpublished data are available on diatoms of saline lakes in Eurasia. Recognition of diatoms as useful indicator species of environmental changes initiated intensive research in the 1980s and 1990s (e.g., Hammer et al. 1983, Bradbury et al. 1989, Blinn 1990). Most of these published diatom studies on saline lakes were paleolimnological reconstructions (e.g., Gasse et al. 1997, Reed 1998), however, because preserved diatoms as proxies are applicable to reconstructing changes in salinity, ice cover, and water level (Spaulding and McKnight 1999, Fritz et al. 2010). Early publications on diatoms of inland saline lakes were mainly floristic (Hustedt 1959, Grunow 1862), and such works continued to appear (e.g., Grimes and Rushforth 1982, Sabbe et al. 2003). Ecological investigations of recent benthic/planktonic diatom assemblages are sporadic, not only in Europe (Padisák and Dokulil 1991, 1994, Buczkó and Ács

1996–1997, Nagy et al. 2008), but also on other continents (Sze and Kingsbury 1972, Blinn 1993).

Based on theory (Bhattacharyya and Volcani 1980), salinity may have only an indirect effect on diatom distribution by affecting thickness of the silica wall (Tuchmann et al. 1984) and pore size (Leterme et al. 2013). Specific surface area and pore size decrease with salinity (Vrieling et al. 2007, Leterme et al. 2010), influencing nutrient transport across the cell membrane and other physiological processes (Fritz et al. 2010). Salinity significantly affects the valve morphology of diatoms (Trobajo et al. 2011), and these morphological features may indicate changes of environmental drivers (Trobajo et al. 2004). Morphological plasticity of diatoms might also explain their ecological success in extreme environments (Leterme et al. 2013). Some species are associated with a given anion (e.g., *Cymbella pusilla* to bicarbonate because of its higher carbon requirement, or *Chaetoceros elmorei* to sulphate; Saros and Fritz 2002). Physiological or physiochemical processes determine these specializations because high salinity physioecologically excludes a number of species without osmoregulatory mechanisms and, consequently, their related traits (De Deckker 1988). The ionic concentration-dependent distributions have not been well studied (Saros and Fritz 2000). Accordingly, one of the recent goals of diatom research is to understand the diatom–salinity relationship using quantitative analyses of diatom distribution (Potapova 2011).

In Hungary, most diatom studies have focused on the 3 biggest, shallow, saline lakes: Lake Velencei (surface area 2600 ha, mean water depth 1.5 m), Lake Fertő/Neusiedlersee (surface area 30 900 ha, mean depth 0.7–1.5 m), and Lake Szelidi (surface area 360 ha, mean depth 3.5 m; Pantocsek 1912, Donászy et al. 1959, Szemes 1959, Buczkó 1986, Ács et al. 1991). Several algological studies (mostly of phytoplankton) of these soda pans were published (e.g., Kiss 1976, Padisák 1999, Fehér and Schmidt 2003, Fehér 2010), and some studies addressed the diatom floras, or at least included some records of diatom species (Grunow 1860, 1863, Cholnoky 1929, Uherkovich 1965, 1969, 1970, Kiss 1971, 1974, 1975, 1978, Schmidt and Fehér 1996). With the recognition of the scientific and conservation values of these alkaline lakes, a number of studies have recently been initiated to understand the hydrogeology (Simon et al. 2011), water chemistry (Boros 1999), bacterial communities (Rusznyák et al. 2011, Borsodi et al. 2013), picoplankton (Somogyi et al. 2011a, 2011b, 2012, Kürthy et al. 2012, Pálffy et al. 2013), zooplankton (Horváth et al. 2013a), macroinvertebrates (Horváth et al. 2013b), and waterfowl (Boros et al. 2008). Information on their benthic diatom communities and their ecology has remained scarce, however. Water chemical and biological characteristics of alkaline, saline

lakes would provide the ecological basis for their management, and the use of benthic diatoms as bioindicators to assess their ecological status and the impact of climate change is promising.

The aim of this study was to determine (1) physical and chemical characteristics and (2) diatom assemblages of shallow, saline, alkaline lakes located in 2 different regions (Fertő-Hanság and Danube-Tisza Interfluve) in the Carpathian basin (Europe); (3) to determine the principle variables that significantly affect the diatom communities in these special environments; and (4) to provide directives for ecological and conservation management.

Methods and materials

Samples for water chemistry and analysis of benthic diatoms were collected from 31 small, shallow, alkaline, saline lakes from 2 different parts of the "Hungarian lowlands" ecoregion (the 11th ecoregion of European lakes and rivers): (1) Fertő-Hanság (FH; distributed in Austria and Hungary) and (2) Danube-Tisza Interfluve (DT; in Hungary; Fig. 1; Table 1) in 3 different years (2006, 2008, and 2012). Following the recommendations for sampling littoral diatoms in lakes (King et al. 2006), 96 diatom samples were collected from macrophytes and mud, which represent the natural substrate type in these lakes. In 2006, sampling was conducted only in spring, the season when these lakes reach their maximum water volume. In 2008, sampling was extended to autumn, and in some cases in 2012, we could sample even in winter (Table 1).

Diatoms were removed from macrophytes with a toothbrush, and mud surface was sampled with a pipette. For analyses of siliceous algae, samples were prepared using standard digestion procedures (CEN 2003), then valves were embedded in Zrax. To determine the relative abundance of the species and diatom ecological guilds, a minimum of 400 valves per slide was counted using a Zeiss Axio Imager A1 with Planapochromat DIC lense at 1000× magnification. Small, difficult taxa were investigated with a Hitachi S-2600 N scanning electron
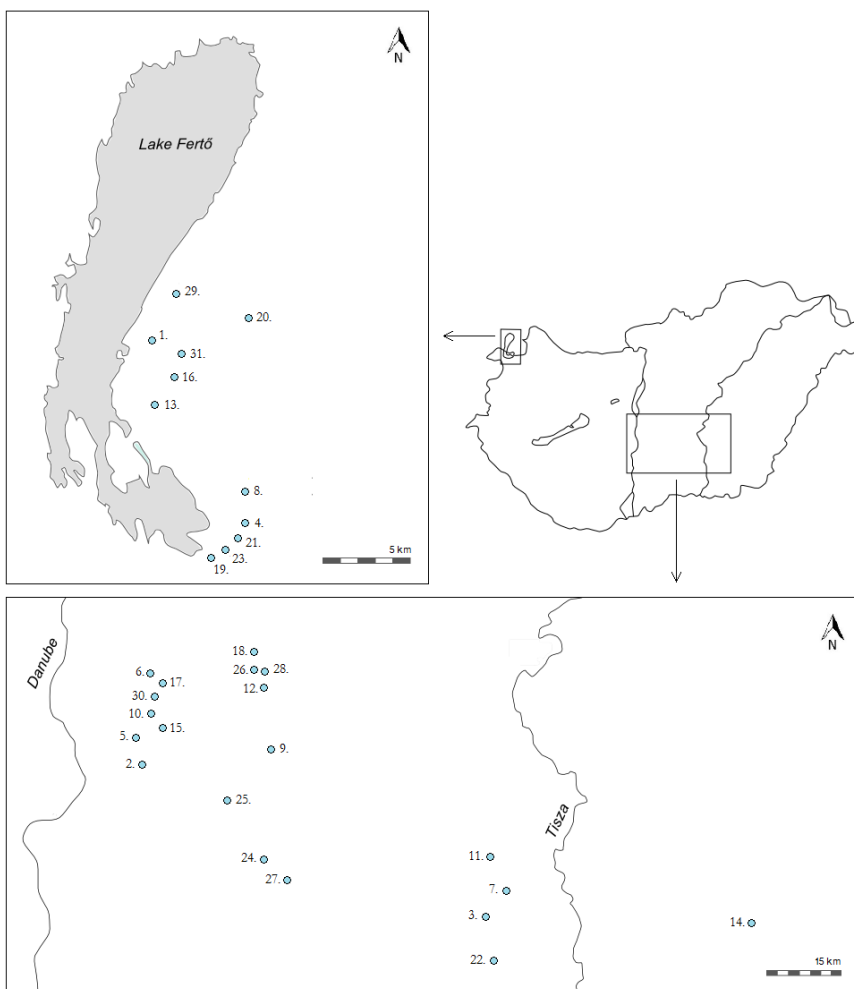

Fig. 1. Saline, alkaline lakes sampled from the 2 regions (lake numbers in Table 1).

Table 1. The investigated saline, alkaline lakes, their country, region (FH = Fertő- Hanság, DT = Danube- Tisza Interfluve), GPS coordinates, number of samples, and sampling year and season (S = spring, SU = summer, A = autumn, W = winter).

Saline Lakes	Country	Region	GPS coordinates		Samples	Year	Season
1. Albersee	Austria	FH	47° 46.449 N	16° 46.177 E	2	2008	S
2. Bába-szék	Hungary	DT	46° 44.431 N	19° 09.019 E	5	2006, 2008	S, A
3. Bíbic-tó	Hungary	DT	46° 28.105 N	19° 58. 487 E	1	2006	S
4. Borsodi-dűlő	Hungary	FH	47° 40.891 N	16° 50.401 E	13	2008, 2012	S, A, W
5. Böddi-szék	Hungary	DT	46° 45.389 N	19° 08.373 E	4	2006, 2008	S, SU
6. Büdös-szék	Hungary	DT	46° 51.577 N	19° 10.943 E	1	2006	S
7. Büdös-szék Pusztaszer	Hungary	DT	46° 32.465 N	20° 15.815 E	1	2006	S
8. Cikes	Hungary	FH	47° 41.763 N	16° 50.459 E	3	2008	S
9. Csárda-szék	Hungary	DT	46° 45.326 N	19° 27.394 E	1	2006	S
10. Fehér-szék	Hungary	DT	46° 48.284 N	19° 11.159 E	1	2006	S
11. Fülöp-szék	Hungary	DT	46° 55.447 N	19° 99.420 E	1	2006	S
12. Hattyús-szék	Hungary	DT	46° 52.522 N	19° 26.350 E	1	2006	S
13. Herrnsee	Hungary	FH	47° 44.609 N	16° 46.210 E	3	2008	S
14. kardoskúti Fehértó	Hungary	DT	46° 28.245 N	20° 37.819 E	4	2006, 2008	S, SU
15. Kelemen-szék	Hungary	DT	46° 47.504 N	19° 10.591 E	4	2006, 2008	S
16. Kirchsee	Hungary	FH	47° 45.443 N	16° 47.299 E	3	2008	S
17. Kisréti-tó	Hungary	DT	46° 86.790 N	19° 19.360 E	1	2006	S
18. Kondor-tó	Hungary	DT	46° 53.471 N	19° 25.068 E	1	2006	S
19. Legény-tó	Hungary	FH	47° 39.793 N	16° 48.802 E	12	2008, 2012	S, A, W
20. Neubruch	Austria	FH	47° 47.162 N	16° 50.655 E	3	2008	S
21. Nyéki-szállás	Hungary	FH	47° 40.623 N	16° 49.970 E	7	2006, 2008	S, SU, A
22. Ősze-szék	Hungary	DT	46° 24.612 N	19° 59.418 E	1	2006	S
23. Paprét	Hungary	FH	47° 39.943 N	16° 49.597 E	6	2008, 2012	S, A
24. pirtói Nagy-tó	Hungary	DT	46° 31.623 N	19° 28.189 E	1	2006	S
25. Sárkány-tó	Hungary	DT	46° 44.481 N	19° 23.216 E	1	2006	S
26. Szappan-szék	Hungary	DT	46° 53.471 N	19° 25.068 E	1	2006	S
27. Szarvas-tó	Hungary	DT	46° 32.774 N	19° 29.012 E	1	2006	S
28. Szívós-szék	Hungary	DT	46° 52.751 N	19° 26.467 E	1	2006	S
29. Untersee	Austria	FH	47° 48.096 N	16° 47.051 E	3	2008	S
30. Zab-szék	Hungary	DT	46° 50.150 N	19° 10.112 E	6	2008	A
31. Zicklacke	Austria	FH	47° 46.075 N	16° 46.870 E	3	2008	S
Σ 31	Σ 2	Σ 2			Σ 96	Σ 3	Σ 4

microscope. Sorting species into high-profile, low-profile, and motile guilds followed the description by Cox (1996), Passy (2007), Rimet and Bouchez (2011), and Stenger-Kovács et al. (2013).

Dissolved oxygen, oxygen saturation, conductivity, pH, and temperature were measured *in situ* with an HQ40d Hach Lange multimeter at the sampling site. In laboratory analyses, concentrations of nitrogen and phosphorus forms were measured: nitrate (NO_3^-) by the UV spectrophotomet-

ric screening method; ammonium (NH_4^+) by the phenate method; soluble reactive phosphorus (SRP) and total phosphorus (TP) by the colorimetric method (APHA 1998); soluble reactive silica (SRSi) by the spectrophotometric method (Wetzel and Likens 2000); and chemical oxygen demand (COD) by the closed refluxe, titrimetric method (APHA 1998). The intensity of the brown colour in platinum (Pt) units used to assess the amount of humic substances was determined according to Cuthbert and del Giorgio (1992).

The t-test for unequal variances (Welch-probe) was used (1) to examine whether the lakes in the 2 regions (FH and DT) had different water chemistry and (2) to categorize the assemblages by guilds and identify the most characteristic diatom ecological guilds in all of the samples and in the 2 regions, separately. The Indicator Species Analysis (IndVal; Dufrêne and Legendre 1997) based on abundance values and relative frequency of occurrence (Legendre and Legendre 1998) was applied to identify species that can be used to separate FH and DT. For model building, a forward selection procedure of the redundancy analyses (RDA; Blanchet et al. 2008) was applied to identify master variables having the most significant effect on the diatom community composition and to reduce the number of the explanatory parameters. The stepping order of the environmental parameters to the model was based on the Akaike information criterion (AIC) with p-values (<0.05). The significance of all terms was assessed by ANOVA permutation test (permutations = 199, $p < 0.05$). Before the RDA analyses, species abundance data were Hellinger-transformed (Legendre and Legendre 1998) to reduce the significance of the most abundant species, a suggested method for multivariate approaches of compositional data containing a number of zero values (Legendre and Gallagher 2001). Rare species (occurrence <3 sampling sites) or species with small relative abundance (<5% in the total dataset) were excluded from the ordination analyses. Environmental variables were also transformed (see Table 2) to reach the normal distribution of the data; the best transformation of the individual variables was selected. All statistical analyses were performed in R computing environment (R 2.11.0; R Development Core Team 2010); model building was conducted using the package "Vegan" (Oksanen et al. 2012).

Results

The average conductivity of the lakes was >4000 µS cm^{-1}, with a maximum conductivity of 17 600 µS cm^{-1}. All lakes were alkaline, with an average pH of 8.9. The most abundant anion was bicarbonate (HCO_3^-, average concentration 941 mg L^{-1}), followed by sulfate (SO_4^{2-}, average 735 mg L^{-1}), and chloride (Cl$^-$, average 226 mg L^{-1}). Nutrient (N and P forms) concentrations, especially those for TP were high (average 1989 µg L^{-1}). Water temperatures varied between 5.3 and 36 °C, depending on the seasonal and daily variance of the air temperature. The water was usually oversaturated with oxygen (average 112%); the average COD was 43 mg L^{-1} (Table 2). Comparison of the chemical and physical features of the lakes in the 2 regions (Welch-test) identified several significant differences: HCO_3^- ($p < 0.001$), Cl$^-$ $p = 0.009$) ions, Pt colour ($p = 0.025$), and COD ($p = 0.013$) were

higher in the lakes of the DT (Table 2). In the FH, SO_4^{2-} concentration ($p < 0.001$) and oxygen saturation (135%, $p = 0.010$; Table 2) were higher than in DT.

The dominant diatom species were the members of the genera *Nitzschia* and *Navicula* of the motile diatom ecological guild. Of the 174 identified species, 107 were motile, 37 high profile, and 30 low profile. In the FH region, 120 species were found (81 motile, 21 low profile, and 18 high profile), similar to the DT, where 112 species were identified (68 motile, 13 low profile, and 31 high profile; Fig. 2). Based on the absolute numbers (Fig. 2a) and relative abundances (Fig. 2b) of species in the different ecological guilds, statistically significant differences were found between the high-profile and motile guilds ($p < 0.001$) and between low-profile and motile guilds ($p < 0.001$) on both the regional and whole sample sets (Fig. 2). No significant differences were found between the high- and low-profile guilds.
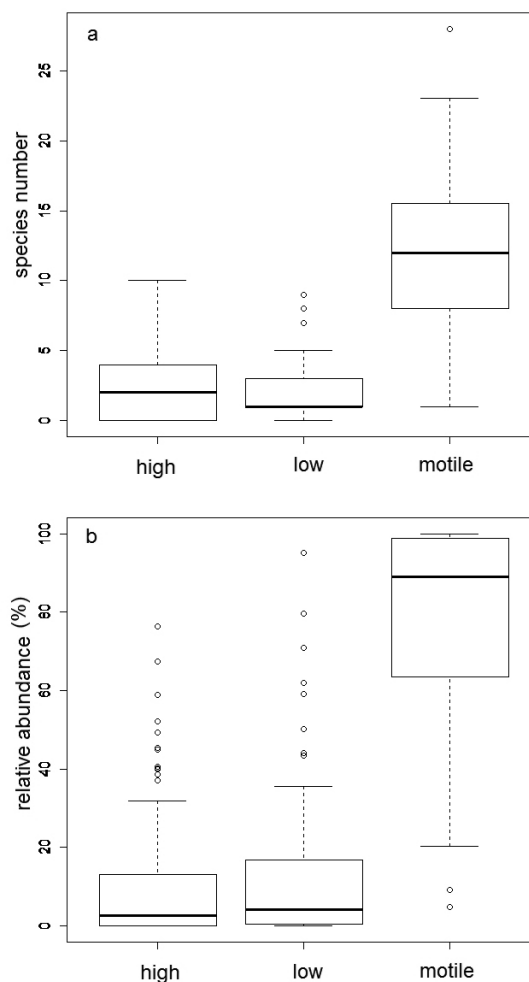

Fig. 2. Boxplots of the different diatomic ecological guilds based on (a) the number and (b) relative abundance of the species (high = high-profile guild, low = low-profile guild, motile = motile guild) in all lakes.

Table 2. Physical and chemical parameters and their differences based on Welch-test of the saline, alkaline lakes in the 2 regions, the Danube-Tisza Interfluve and the Fertő-Hanság.

variables	units	transformations	Danube-Tisza Interfluve (n = 34)				Fertő-Hanság (n = 25)				Welch-test
			mean	SD	min	max	mean	SD	min	max	p-value
conductivity	µs cm^{-1}	$x' = \ln(x+1)$	4697	3808	520	17 600	4318	2716	1765	13650	ns
pH		—	8.9	0.4	8.1	9.7	8.9	0.4	8.3	9.4	ns
SO_4^{2-}	mg L^{-1}	$x' = \ln(x+1)$	118.9	140.0	0.0	731.0	616.4	593.8	91.9	2433.0	<0.001
HCO_3^-	mg L^{-1}	$x' = \ln(x+1)$	1182.4	508.4	435.0	2092.0	700.3	326.5	291.3	1866.6	<0.001
Cl^-	mg L^{-1}	$x' = \ln(x+1)$	325.9	374.5	0.9	1568.9	125.5	181.4	3.4	819.4	0.009
colour	mg L^{-1} Pt	-	525.0	276.2	243.1	926.9	96.6	72.7	40.9	352.2	0.025
NH_4^+	mg L^{-1}	$x' = \arcsin(x^{0.5})$	2.5	6.8	0.0	32.7	2.5	5.4	0.0	25.9	ns
NO_3^-	mg L^{-1}	$x' = (x/100)^{0,5}$	1.8	2.0	0.3	9.9	1.0	1.7	0.0	7.6	ns
SRP	µg L^{-1}	$x' = \ln(x+1)$	661.9	831.6	10.0	2985.0	354.8	449.9	6.3	1530.0	ns
TP	µg L^{-1}	$x' = \ln(x+1)$	2064.9	3954.4	50.0	21760.0	1913.1	3249.4	43.9	14720.0	ns
SRSi	mg L^{-1}	$x' = \ln(x+1)$	5.4	5.5	0.1	29.6	4.1	2.8	0.2	12.2	ns
temperature	°C	—	18.6	6.4	5.3	36.0	21.7	9.2	7.4	35.4	ns
O$_2$ saturation	%		89.8	44.4	1.2	184.2	135.0	71.8	18.1	293.9	0.010
COD	mg L^{-1} O$_2$	$x' = \ln(x+1)$	59.6	71.4	6.0	423.0	26.4	18.3	0.0	72.0	0.013

The indicator species analysis identified 5 indicator species with significant indicator values for the DT region (Table 3); *Nitzschia fonticola* (Grunow) Grunow and *Mayamaea atomus* var. *permitis* (Hustedt) Lange-Bertalot had the highest indicator values (IndVal = 25.90 and 20.70, respectively). Of the 16 indicator species in the FH region, *Navicymbula pusilla* (Grunow) Krammer, *Anomoeoneis sphaerophora* Pfitzer, *Nitzschia solita* Hustedt, and *Rhoicosphenia abbreviata* (C.Agardh) Lange-Bertalot had the highest indicator values (IndVal = 46.30, 41.20, 33.30 and 33.30, respectively; Table 3).

According to the RDA, separation of the 2 regions was most strongly determined by (Fig. 3a and 3c) HCO_3^-, SO_4^{2-}, COD, and NO_3^- along Axis 1 (10.3%; Fig. 3b). Along Axis 2 (9.8%), samples were grouped based mainly by Cl^- and TP concentrations (Fig. 3b). In the DT, one of the groups (DT1) included samples with higher NO_3^- and Cl^- concentrations (Fig. 3c), in contrast to the second group (DT2), which was characterized by higher conductivity, SRP, TP, NH_4^+ concentrations, pH, and temperature (Fig. 3b). In group DT1, *Nitzschia supralitorea* Lange-Bertalot and *Craticula halophila* (Grunow) D.G. Mann dominated, while in group DT2 *Nitzschia austriaca* Hustedt and *N. etoshensis* Cholnoky were characteristic (Fig. 3d). In the FH region, 2 groups were also distinguished. Group 1 (FH1) was characterized by high Cl^- and SRSi concentrations (Fig. 3b) with the following species (Fig. 3d): *Entomoneis paludosa* var. *subsalina* (Cleve) Krammer, *Nitzschia palea* (Kützing) W. Smith, *N. paleaceae* (Grunow in Cleve & Grunow) Grunow in

Van Heurck, *N. constricta* (Gregory) Grunow, and *Achnanthidium minutissimum* (Kützing) Czarnecki. Group 2 (FH2) was characterized by higher SO_4^{2-} concentrations and oxygen saturation (Fig. 3b), with assemblages dominated by *Nitzschia aurariae* Cholnoky, *N. frustulum* (Kützing) Grunow in Cleve & Grunow, and *Fallacia pygmaea* (Kützing) A.J. Stickle & D.G. Mann Fig. 3d). After the performance of the forward selection procedure in the reduced RDA model, 12 of the 13 environmental variables that had a significant effect on the diatom composition remained; only SRP was eliminated. The significance of the variables in descending order was: conductivity, HCO_3^-, SO_4^{2-}, temperature, COD, TP, pH, oxygen saturation, NH_4^+, SRSi, NO_3^-, and Cl^-.

Discussion

Water chemistry

The conductivity values (maximum 17 600 µS cm^{-1}) recorded in these saline alkaline lakes did not reach the previously reported maximum values (>30 000 µS cm^{-1}; Schmidt 2003). Total ionic concentrations calculated from conductivity values according to Boros and Vörös (2010) varied between 416 (corresponding to freshwater; Hammer 1986) and 14 080 mg L^{-1} (average 3606 mg L^{-1}), which falls into the hyposaline category (Hammer 1986). In contrast to seawaters, ionic composition was dominated by HCO_3^-, SO_4^{2-}, and Cl^-. Their concentration changed significantly with the precipitation of salts during the

Table 3. Most significant indicator species based on the Indicator Species Analyses (IndVal) using species abundance data for the Danube-Tisza Interfluve and for the Fertő-Hanság regions.

Regions	Species	Author	Mean abundance	Observed indicator value (IndVal)	p
Danube-Tisza	*Fistulifera saprophila*	(Lange-Bertalot & Bonik) Lange-Bertalot	0.39	9.50	0.030
	Fragilaria famelica	(Kützing) Lange-Bertalot	0.07	13.00	0.015
	Mayamaea atomus var. *permitis*	(Kützing) Lange-Bertalot	0.67	20.70	0.015
	Nitzschia communis	Rabenhorst	0.16	18.40	0.020
	Nitzschia fonticola	(Grunow) Grunow	0.37	25.90	0.005
Fertő-Hanság	*Amphora libyca*	Ehrenberg	0.12	16.70	0.005
	Anomoeoneis sphaerophora	(Ehrenberg) Pfitzer	0.58	41.20	0.005
	Cocconeis placentula var. *lineata*	(Ehrenberg) van Heurck	0.02	11.10	0.050
	Cyclotella meneghiniana	Kützing	0.60	16.70	0.005
	Cymbella cymbiformis	C.Agardh	0.05	11.10	0.055
	Gyrosigma sp.	Hassal	0.29	20.40	0.010
	Hippodonta capitata	(Ehrenberg) Lange-Bertalot, Metzeltin and Witkowski	0.06	12.30	0.050
	Hippodonta hungarica	(Grunow) Lange-Bertalot, Metzeltin and Witkowski	0.17	14.80	0.025
	Navicula salinarum	Grunow	0.24	22.20	0.005
	Navicymbula pusilla	(Grunow) K.Krammer	0.51	46.30	0.005
	Nitzschia elegantula	Grunow	0.28	22.20	0.005
	Nitzschia salinarum	Grunow	0.03	11.10	0.050
	Nitzschia solita	Hustedt	0.34	33.30	0.005
	Rhoicosphenia abbreviata	(C. Agardh) Lange-Bertalot	0.86	33.30	0.005
	Stauroneis wislouchii	V.S. Poretzky & Anisimova	0.09	16.70	0.010
	Surirella peisonis	Pantocsek	0.08	18.80	0.020

evaporative concentration, as also observed by Eugster and Jones (1979). According to Simon et al. (2011), ionic composition of individual saline, alkaline lakes is related to the chemistry of groundwater. The composition of the groundwater of the catchment area is more important in saline than in freshwater lakes, which collect their water from surface flow (Comín et al. 1999). In the DT, the bicarbonate ion was dominant; most of these lakes are of a sodium bicarbonate (Na^+-HCO_3^-) type (Boros and Vörös 2010), in contrast to the FH region, which is characterized by the dominance of the SO_4^{2-} anion. COD and Pt colour were consistently higher in the DT region. Allochtonous organic substances are derived from decomposition of macrophytes and droppings (V.-Balogh et al. 2009, 2010). The lakes were oversaturated with oxygen due to photosynthetic activity of the algae because of the daytime sampling, but oxygen saturation is known to be low (16%) at night (Vörös and Boros 2010), and significant fluctua-

tions of saturated and unsaturated conditions may occur on a daily basis in these highly productive lakes (Wetzel 1983). Oversaturation was higher in the FH region (maximum 294%), although it did not reach the highest recorded maximum of 499% in Kelemen-szék in the DT region (Vörös and Boros 2010).

Diatom assemblages

Nitzschia and *Navicula* species were the most frequent in the saline lakes of the 2 regions in the Carpathian basin. At the generic level, they are dominant and characteristic in nonmarine (athalassic) saline lakes (Gasse 1986a, 1986b, Servant-Vildery and Roux 1990, Blinn 1993, Tibby et al. 2007, Blanco et al. 2013). These genera and other representatives of the motile ecological guild were significantly more abundant than those from the other 2 guilds. The reason for their abundance is that species in

soda pans must survive, either temporarily or permanently, and adapt to special conditions (Oren 1999) such as high salinity, high turbidity (Secchi-transparency of only a few centimeters; Horváth et al. 2013a), high nutrient concentrations, high daily temperature fluctuations (Vörös and Boros 2010), and ephemeral features (Cognetti and Maltagliati 2000). Under these conditions, the motile ecological guild has a competitive advantage over either the low- or the high-profile guilds. Parallel with increasing turbulence rates (Alvial et al. 2008) and decreasing underwater low irradiance levels, their contribution to the assemblages rises significantly (Stenger-Kovács et al. 2013) because of their ability to actively select the most suitable habitat (Passy 2007). Moreover, they are shade-

tolerant taxa; the photoadaptational parameter (I_k) of *Nitzschia* species is low (Padisák 2003). In addition, the motile guild largely prefers eutrophic and/or organically polluted waters and proliferates in nutrient-rich habitats (Passy 2007) such as the saline lakes in this study.

Indicator species of the regions were satisfactorily defined based on the IndVal analyses; suitable examples are *Nitzschia communis* for the DT region and *Anomoeoneis sphaerophora* for the FH region. *A. sphaerophora* indicated the saline type of lakes in the FH region by exhibiting a positive response to high pH and bicarbonate content (Blinn 1993). *Cyclotella meneghiniana* (indicator species of the FH region) is a suitable and well-known example of species that are physioecologically adapted to high salinity
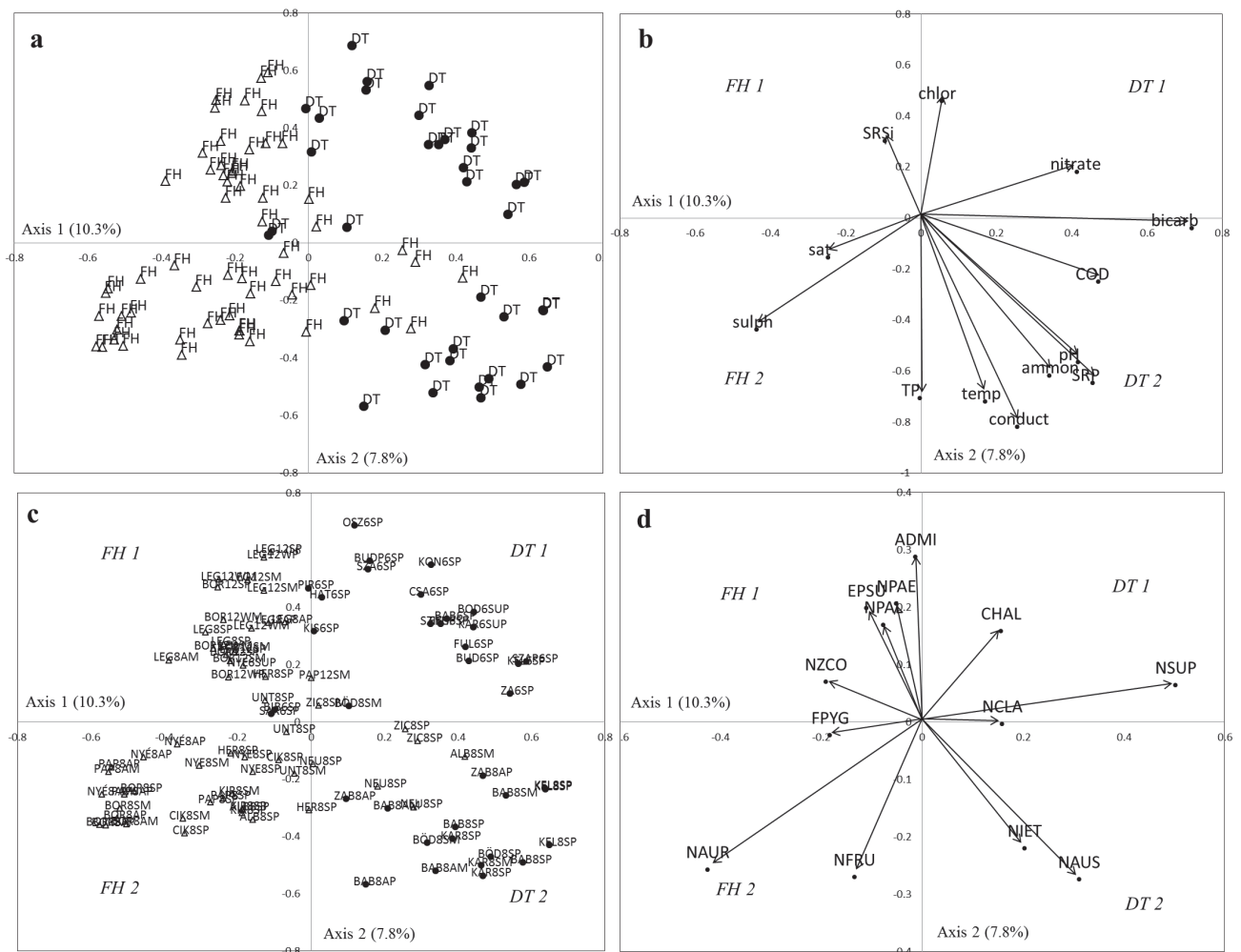

Fig. 3. Redundancy analyses (RDA) based on the water chemical and species abundance data emphasized (a) regions (Fertő-Hanság = FH; Danube-Tisza Interfluve = DT); (b) explanatory variables (chlor = chloride ion, bicarb = bicarbonate, ammon = ammonium, temp = temperature, conduct = conductivity, sulph = sulphate, sat = saturation); (c) samples (first 3 letters = beginning of lake name; number = year of sampling; next letter is season of sampling [S = spring, SU = summer, A = autumn, W = winter]; last letter is substrate type [P = macrophyte, M = mud]); and (d) dominant species. ADMI = *Achnanthidium minutissimum*, CHAL = *Craticula halophila*, EPSU = *Entomoneis paludosa* var. *subsalina*, FPYG = *Fallacia pygmaea*, NAUR = *Nitzschia aurariae*, NAUS = *Nitzschia austriaca*, NZCO = *N. constricta*, NIET = *N. etoshensis*, NFRU = *N. frustulum*, NPAL = *Nitzschia palea*, NPAE = *N. paleaceae*, NSUP = *Nitzschia supralitorea*.

(De Deckker 1988) because they are able to synthesise osmoregulators (like proline). As salinity increases, proline synthesis rates and nitrogen demand also increase (Schobert 1974). In East African alkaline, saline lakes the most common species was *Anomoeoneis sphaerophora*, accompanied by Centrales and *Navicula* species (Tuite 1981). *Nitzschia communis* (indicator of DT region) was present in 63% of the saline lake habitats of western North America and had the highest specific conductance index values and tolerated the highest ionic strength (Blinn 1993).

In general, indicator species of the 2 regions marked not only high conductivity (e.g., *Nitzschia fonticola* for DT and *Nitzschia salinarum* for FH) but also eutrophic conditions (e.g., *Fistulifera saprophila* for DT, *Hippodonta capitata* for FH). The high nutrient availability of these lakes is not necessarily the consequence of anthropogenic pollution; however, most are surrounded by agricultural areas and tilled down to their shorelines. Even so, because of the tens of thousands of birds that populate these lakes during migration (Harper et al. 2003, Boros et al. 2006, Horváth et al. 2013c) and the active maintenance of endemic beef cattle (*Bos primigenius*) and buffalo (*Bubalus bubalis*) farms in the regions, mammal and bird populations substantially increase plant nutrient levels through their droppings (Oduor and Schagerl 2007). The average TP concentration is 8 times higher (1989 µg L^{-1}) compared to the freshwater lakes (~225 µg L^{-1}) of the ecoregion, whereas the average NO$_3^-$ concentrations (1.4 mg L^{-1}) exceed twice that of freshwater concentrations (based on the database of the University of Pannonia, unpublished data). Accordingly, resource availability prevails, with minimal competition for nutrients among the species (Oduor and Schagerl 2007).

Main drivers of the diatom composition

Using RDA, lakes were separated into 2 subgroups in each of the 2 regions based on HCO$_3^-$ concentration. Subgroup DT2 inside the DT region is characterized by pristine saline lakes (Kardoskúti-Fehértó, Böddi-szék, Bába-szék, Kelemen-szék), which are turbid soda ponds with high levels of suspended inorganic solids (Boros 1999, Váradi and Fehér 2010). Their conductivity, pH, and nutrient concentrations (NH$_4^+$, SRP, and TP) are the highest of all the investigated lakes. Their ecological status is the highest because their conditions are the closest to the status considered as natural. In this group, *Nitzschia austriaca* and *Nitzschia etoshensis* were dominant. Subgroup DT1 (e.g., Fülöp-szék, Büdös-szék, Csárda-szék, Ősze-szék) is characterized by higher concentrations of Cl$^-$ and NO$_3^-$ and includes only samples collected in 2006, which was a meteorologically exceptional year. High precipitation and flooding occurred in spring 2006; therefore, conductivity was lower and

NO$_3^-$ concentration was higher than usual due to runoff from the surrounding agricultural areas. The lakes preserved their saline character, however; halophilic species like *Nitzschia supralitorea* and *Craticula halophila* were dominant. Nevertheless, changes in the ionic composition and in the dominant taxa clearly indicated the extreme weather conditions. The lakes in the DT area have a smaller surface area (e.g., Szappan-szék, Büdös-szék Pusztaszer) compared to those in other regions, which results in fewer waterfowl and lower TP.

Lakes in the FH region are characterized by lower bicarbonate content and can also be divided into 2 subgroups. Lakes in subgroup FH2 (e.g., Cikes, Pap-rét, Nyéki-szállás, Herrnsee, Albersee) are characterized by higher conductivity and dominated by SO$_4^{2-}$, with the diatom assemblages dominated by halophilic species like *Nitzschia frustulum* and *N. aurariae*. In addition to SO$_4^{2-}$, subgroup FH1 (Borsodi-dűlő, Legény-tó) is dominated by Cl$^-$ and has a higher SRSi content; the conductivity and TP concentration in these lakes were lower. Subgroup FH1 mostly includes samples from Borsodi-dűlő, which is located in the active reconstruction area of the national park. The water level is highly regulated, and therefore the characteristics of the water are modified and highly dependent on the management activities and conservation measures such as (1) flooding the area to supply water for the migratory birds and/or (2) draining the water through the established channel system of the FH to guarantee an adequate area for grazing of beef cattle and buffalo. Another example from this group is Legény-tó, which is in constant connection with a drainage system that maintains its permanent water level but considerably modifies its saline character. The lower TP concentration of the FH1 group is because most sampling occurred in winter when the water level was especially high and migratory waterfowl populations were reduced.

In the reduced RDA model, the explanatory variables determined by the composition of the diatom assemblage were, in descending order, conductivity, HCO$_3^-$, SO$_4^{2-}$, temperature, COD, TP, pH, saturation, NH$_4^+$, SRSi, NO$_3^-$, and Cl$^-$. In Turkish saline lakes, temperature, carbonate, conductivity, pH, silica, alkalinity, and SRP were the main environmental factors that explained variation in the diatom composition and the dominance of the assemblage by cosmopolitan species with high alkalinity tolerances (Koçer and Şen 2012). Except for SRP, this RDA model did not considerably reduce the number of the master variables. The statistically most significant factors were salinity (HCO$_3^-$ or SO$_4^{2-}$) and temperature. According to Williams (2002), conductivity and ionic composition determine the composition of biota, and these variables satisfactorily explained the differences in diatom assemblages of some Canadian lakes (Wilson et al. 1994).

Temperature is a key factor that determines the existence of saline lakes (Williams 2002) as well as the diatom assemblages identified in this study. For Central Europe, climate scenarios predict a substantial (6 °C) increase in temperature (Szépszó 2008) with modified precipitation patterns and increasing incidence of extreme weather events (high floods, heat waves, and droughts; Moss et al. 2009). The predicted effect of temperature increases or permanently higher summer water temperatures on diatom communities is not well understood. Some studies found that at temperatures >34.2 °C, diatoms are replaced by green algae as the dominant algae (Patrick 1969, Hickman 1982), or that the summer-dominant epipelic diatom species required higher temperatures for rapid cell division than the species that are dominant during the cold seasons (Eloranta 1982, Admiraal et al. 1984).

Because high pH (8.1–9.4) is a characteristic feature of these lakes, its effect on the diatom assemblages cannot be neglected. Although diatoms are more sensitive to pH changes in acid-neutral than in alkaline lakes (Blinn 1993), response of the diatom community to pH in these lakes was pronounced. Both pH and oxygen concentration influence the nutrient availability of algae in hypereutrophic lakes (Sondergaard et al. 1990). Nutrient levels are less important in the studied lakes than in the lakes of the Kenyan Rift Valley, where importance order of the key variables was nitrate, conductivity, phosphorous, and light supply (Oduor and Schagerl 2007).

In summary, diatoms of these saline lakes proved to be good indicators of climate-driven variables such as salinity, ionic composition (Saros and Fritz 2002), and temperature, as well as anthropogenic activities, including when these activities serve nature conservation purposes.

Management

Before water regulation, floods of the River Danube and River Tisza supplied the small saline lakes of the DT. At present, solely precipitation and groundwater provide their water supply. The scarcity of water in the DT has long been evident (VGT 2009) due to climate change and anthropogenic interventions (watercourse regulation, excessive drainage, and overpumping of groundwaters). Today the situation is critical. The area of lakes has decreased, some lakes have completely or partly dried out (e.g., Szappan-szék), and both abundance and diversity of biota have decreased.

There is an urgent need to assess lake values, to characterize threats, and to suggest management and conservation measures (Williams 2002). The lakes of the DT and FH regions are registered by the Ramsar convention and as Natura 2000 sites; however, lakes in these regions were not appointed and selected as waterbodies according to Water Framework Directive (EC 2000) because their surface areas rarely exceed the 50 ha threshold. Nevertheless, their significance cannot be measured by their size.

Changing agricultural methods, abandoning reduction of potential supply waters, and retaining water on the area can ensure the existence of these habitats (VGT 2009) and preserve the natural hydroperiod. Man-made (fresh) water supply as a replacement for natural groundwater sources would destroy the wildlife of these saline lakes.

Recent management of the saline lakes in the FH region was implemented for habitat restoration with a focus on the conservation of waterfowl (Comín et al. 1999) and beef cattle to maintain their populations (Korner 2012), which could result in losing the special saline character of the lakes of this group. Because this characteristic could be maintained by applying a different kind of conservation treatment, management efforts must consider the natural water coverage with simulation of natural water level fluctuations (Williams 2002) both seasonally and interannually (Talling 2001). Lack of natural salinization processes can lead to a number of floristic and faunistic changes in closed-basin lakes (Fritz et al. 2010). The typical saline diatom species are completely missing from lakes in FH1, and only one dominant species (*Entomoneis paludosa* var. *subsalina*) indicates the original or theoretically potential status. The presence of another species, *Nitzschia palea*, in the FH1 group is also reassuring because this species is defined as a characteristic species of saline lakes (Blinn 1993), although it is also common in freshwaters (Lange-Bertalot 2013). The dominant *Achnanthidium minutissimum*, however, is associated with electrolyte-poor environments at different pH (van Dam et al. 1994, Kovács et al. 2006) and trophic levels (Lange-Bertalot 2013).

Two saline lakes (Neubruch and Zicklacke in Austria) in the area were outliers from their own FH region, and they more closely resembled samples from the DT region because their bicarbonate content and COD were higher than characteristic in the FH region. Status assessment and evaluation of these 2 lakes may follow the method used in the DT region.

Threats to and impacts on saline lakes from anthropogenic activities involve special requirements for sustainable management. Development of management guidelines is difficult because experiences are scarce compared to freshwater lakes (De Bernardi et al. 1996). Both local and international management and conservation are needed to protect the natural character of these alkaline, saline lakes. Differences in hydrological patterns strongly determine the seasonal and long-term changes in salinity (Williams 2002), which should be considered during their maintenance.

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