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Expanding the trait-based concept of benthic diatoms: development of trait- and species-based indices for conductivity as the master variable of ecological status in continental saline lakes

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Abstract

Shallow, saline inland lakes occur over large areas in Central-Europe and they bear exceptionally high biological conservation values. Climate change and anthropogenic activities threaten their natural conditions, or even their existence. These aquatic ecosystems are exposed to multiple stress like naturally high conductivity, pH and nutrient load with very low transparency for light. As they are subjects of criteria set by the EC Water Framework Directive and biological conservation managment, there is an urgent need for developing a suitable quality index for their ecological status assessment. As one major Biological Quality Element, benthic diatoms may provide a reliable basis for their ecological status indication. Here, in a large data set covering the soda lakes of the Carpathian basin, we developed a species- and a trait-based diatom ecological status index. First, based on the weighted average method, we developed a type specific, species-based diatom index (DISP = Diatom Index for Soda Pans) using conductivity as master variable of environmental constrains; and therefore the ecological status in soda lakes. Furthermore, by adapting and improving further the widely-used diatom ecological guild concept, we also developed an alternative trait-based index, which helps avoiding some limitations arising from the obvious complexity of the taxonomy-based approach. Our DISP index covered a significantly larger species pool for index calculation, and responded to conductivity in a more reliable way compared to other available indices. In the trait-based index (TBI) motility, small cell size, and less roundish, more elongated shape as functional and morphological traits indicated pristine ecological conditions (i.e high conductivity) of the soda pans. Planktic life form, high and low ecological guild profiles, as well as the large cell size indicated worse ecological conditions (e.g. lower conductivity). Our study highlights that benthic diatoms provide a reliable basis for ecological status assessment in soda lakes. While both the taxonomic and the functional trait approaches performed well in our analysis, the success of the trait-based approach may enable the use of our TBI index in biomonitoring and conservation management of soda lakes outside of the Carpahian basin, independently of the geographic location.

Introduction

Inland saline waters occur at each continent (Williams, 2005). On a European scale, extended saline lake districts are found e.g. in France, Spain, Serbia and Germany. In Hungary, the western margin of the Eurasian steppe zone, saline lakes are found on large areas (1,000,000 ha; Szabó, 1997) in two major hydrological basins: in the Duna-Tisza Interfluve, and in the sourrounding area of Neusiedlersee. The general, limnological explanation of development of such lake districts argues that in endorheic drainage basins precipitation and evaporation coequal in the long term, resulting in alkalization on the carbonaceous bedrock (Kalff, 2002). Besides precipitation, saline inland lakes in the Carpathian basin are fed by saline water from deep-layer aquifers (Mádl-Szőnyi and Tóth, 2009). These lakes are gems of the Earth's lake diversity and they serve as important refugia for biodiversity (e.g. Pálffy et al., 2014; Tóth et al., 2014). From an ecological point of view, these habitats with their extreme environmental characteristics (Boros et al., 2017) impose multiple stress on their biota. Most dries out completely by late summers; others dry out according to ~10-12 year mesoclimatic cycle (Padisák, 1998). Permanent water cover is more of exception than rule. When their basin is filled with water they are alkaline (pH: ~9-10), saline (conductivity may range from ~3,000 to ~60,000 $\mu S\ cm^{-1}$) and inorganically very turbid (Secchi transparency is measurable as few centimeters) (Boros et al., 2017). Since they serve as resting places of migratory birds (some species are also nesting), phosphorus load by the waterfowl can result in permanently high TP values (Stenger-Kovács et al., 2014). Such habitats allow only for low-diversity communities (Padisák et al., 2006; Horváth et al., 2014; Stenger-Kovács et al., 2016) due to pronounced environmental selectivity of best adapted taxa to multiple stress conditions. The role of biotic interactions in shaping community structure under such conditions has only minor importance; biotic communities are predominantly controlled by the physical environment (García et al., 1997).

Diatoms are abundant and widely distributed from freshwaters to marine ecosystems. The community composition of diatoms is well applicable in ecological status indication due to their high sensitivity to the physical and chemical constraints set by different kinds of natural and human impacts. The use of diatoms as ecological indicators can date back to the beginning of the 20th century (Kolkwitz and Marson, 1908). A number of paleoecological and ecological studies evidenced that diatom species composition indicated well past and current changes in the environment (Stoermer and Smol, 2010). Conductivity and pH are the most important variables determining diatom compositions (Soininen, 2007), and the variability of these parameters changes substantially not only on local but also on continental scale (Soininen et al. 2016).

A number of species-based diatom indices have been offered for ecological status assessment. Most of them were developed and tested for river phytobenthos and were included in the software "OMNIDIA" (e.g. IPS, IBD, EPI-D; Coste in Cemagref, 1982-91; Lenoir and Coste, 1996; Prygel and Coste, 2000; Dell'Uomo, 2004). Some of the indicies have been implemented into the ecological status assessment of lakes (Kelly and Whitton, 1995, Blanco, 2004, Bolla et al., 2010, Kelly et al., 2006, 2014) according to the requirements of the European Water Framework Directive (EC, 2000). However, diatom indices for lakes are less common and have only been published recently (Jüttner et al., 2010). In Europe, first the trophic diatom index (TI) was developed for German lakes based on alkalinity and trophic status (Hofmann, 1999), and was implemented according to the WFD in Germany (Schaumburg et al., 2004). In Hungary, the trophic diatom index (TDIL) was developed for shallow and freshwater lakes (Stenger-Kovács et al., 2007). Recently, an increasing number of diatom-based ecological analyses appeared for lakes (Crossetti et al., 2013; Kahlert and Gottschalk, 2014; Rimet et al., 2016), but with focus mainly on freshwater and brackish habitats (e.g. Wang et al. 2006., Gell et al. 2002, Della Bella et al. 2007). These indices, however, are „trained" to indicate high salinity levels as a result of human pollution due to e.g. sewage or industrial load, winter de-icing. The same applies for the Halobienindex of Ziemman et al. (1999), which approach has recently been implemented in Hungary applying an inverse scaling (Ács et al., 2015), but without a well-documented testing and details. Furthermore, the reliability of this index is highly questionable based on its poor species pool regarding soda lakes. When any of the aforementioned indices are applied in naturally highly saline habitats such as soda pans, they consistently report intolerable or bad ecological status (Stenger-Kovács et al., 2007). However, paradoxically, the most important harm on such lakes is the artificial freshwater input from alien watersheds, which results in decreasing salinity and in „improved" ecological status indicated by former diatom indices. In this context, the Sodic Conductivity Index for Lakes (SCIL; Ács, 2007) represented a great step forward, since it was able to assess the status of shallow, large, slightly alkaline lakes in a reliable way. Nevertheless, from an ecological and nature conservation point of view, there has been a compelling demand to develop a reliable diatom index for small, high salinity lakes (Stenger-Kovács et al., 2014, Lengyel et al., 2016; Bolgovics et al., 2017) as characteristic landscape components of the Carpathian region (Boros et al., 2013).

Based on similar physiologies and functional characteristics of taxa, functional (e.g. guilds) and morphological traits may provide a reliable approach (Stevenson et al., 2010) to complete the traditional ecological indication based on taxonomic approach (Lange et al., 2011). On a global scale, diatom species composition may vary significantly among regions, but the guild composition may overlap in a more considerable way. Accordingly, functional approaches may enable us to compare diatom communities with different taxonomical compositions. Diatom guild composition has been found to highly relate to the environment, which approach therefore may enable expressing functional responses of the communities to global environmental changes (Soininen et al. 2016). Following the spread of trait-based approaches in phytoplankton ecology (e.g. Salmaso and Padisák, 2007, Kruk et al., 2010), trait-based ecological status assessments have also been developed for benthic diatoms (e.g. Tapolczai et al., 2017; B-Béres et al., 2017). At present, the diatom trait-based approach is applied principally in running waters (Lange et al., 2016, Trábert et al., 2017, Novais et al., 2014), whereas authors mainly related trait-based ecological groups of diatom to major environmental constraints such as nutrients, organic pollution, grazing, shear stress (e.g. Berthon et al., 2011, Lange et al., 2016, Soininen et al., 2016, Tapolczai et al., 2017). As to lakes, the trait-based approach of benthic diatoms has only been applied in very few cases (Gottschalk and Kahlert, 2012; Rimet el al., 2016; Riato et al., 2017; Zorzal-Almeida et al., 2017).

Our aim was (i) to develop a species-based benthic diatom index for small, shallow, naturally highly saline, alkaline lakes; (ii) adapt and further refine the widely-applied diatom ecological guild concept for diatoms of soda lakes in order to identify relevant traits (e.g. morphological) with clear ecological functions; and finally (iii) to develop a trait-based diatom index, which may substitute the taxonomy-based approach with its some obvious limitations. Here, we use the gradient of conductivity as the main proxy of environmental constraints in soda pans along which changes in the species and functional trait compositions may reflect relevant autecological adaptations and therefore indicate ecological functions.

Our hypotheses are that (i) our species-based diatom index performs better than the SCIL index developed for slightly saline lakes; (ii) functional characteristics (e.g. morphological traits, ecological guilds) of diatom taxa alter considerably with conductivity, as proxy for natural *vs.* degraded conditions; (iii) the trait-based diatom index performs as well or even outperforms our species-based diatom index.

Material and methods

Sampling sites, design and laboratory analyses

Altogether 338 parallel samples were collected for phytobenthos and water chemical analyses between 2006 and 2015 from 33 soda pans of the Carpathian basin. The sampling time and its frequency depended on the water supply of the lakes (Fig. 1). Diatom samples were collected each time from the characteristic substrates (macrophytes or mud) at the water depth of 5-10 cm in the littoral region of the pans. Epiphytic diatoms were collected by toothbrush, while epipelic diatoms by pipetting of ~10 cm^3 of superficial layer of the panbed (Cochero et al., 2013). Sample collection followed the recommendations of King et al. (2006) and Kelly et al. (2009). Diatom samples were preserved with ethanol and the samples were kept at pH ~7-8 by concentrated HCl to avoid the dissolution of the silica walls. For preparation of the samples, the hot hydrogen-peroxid method was applied (Battarbee, 1986), and then diatom valves were embedded in Pleurax®. Permanent slides were analyzed with light (Zeiss Axiovert A1, plan-apochromat lense with DIC) and electron microscopy (Hitachi S-2600N). A minimum of 400 valves were identified to species or even lower taxonomic levels in each sample (Stenger-Kovács and Lengyel, 2015). We used an updated nomenclature for diatoms according to AlgaeBase (Guiry and Guiry 2018). Water chemical parameters such as conductivity, dissolved oxygen, oxygen saturation and pH were measured *in situ* with a Hach Lange HQD40 multimeter. Soluble reactive silica (SRSi), nitrogen and phosphorus forms, and bicarbonate were determined in laboratory according to international standards (APHA, 1998; Wetzel and Likens, 2000).

Species-based community analyses

In a first step of developing a species-based diatom index, transfer function was applied to determine the optimum and tolerance values of the diatom species (Birks, 2010) with >3% in their relative abundance in each sample. Here, to get the best correlation, we used the weighted average method with inverse regression for deshrinking. The model development was based on 187 randomly chosen samples, and then tested on 151 samples using the program C^2 version 1.5 (Juggins, 2007). Root mean squared error of the prediction (RMSEP) was calculated directly from the calibration data set. Based on the optimum and tolerance of species, indicator (1-6) and sensitivity values (1-3) were defined (if the species were present at least in 3 samples) following the next scheme:

Indicator values: 1: conductivity optima of species ≤ 1999 μS cm^{-1}; 2: 2000 - 2999 μS cm^{-1}; 3: 3000 -3999 μS cm^{-1}; 4: 4000 -4999 μS cm^{-1}; 5: 5000 - 5999 μS cm^{-1}; 6: ≥ 6000 μS cm^{-1}.

Sensitivity values: 1 (sensitive): if the tolerance of species for conductivity was ≤ 499 μS cm^{-1}; 2 (less sensitive) 500 - 999 μS cm^{-1}; 3 (tolerant): ≥ 1000 μS cm^{-1}.

For the development of the species-based Diatom Index for Soda Pans (DISP) the Zelinka and Marvan equation (1961) was applied, where a_i= relative abundance of the taxon i, s_i= sensitivity value of the taxon i, and v_i= indicator value of the taxon i.

$$DISP = \frac{\sum_{i=1}^{n} a_i s_i v_i}{\sum_{i}^{n} a_i v_i}$$

The values of the DISP range between 1 and 6 where the higher the values, the better the ecological status.

Diatom indices (SCIL = Sodic Conductivity Index [Ács, 2007] and DISP) were calculated with the DilStore software (Hajnal et al., 2009). The relationship between diatom index values and conductivity was assessed by Pearson correlation.

Ttrait-based community analyses

Each species was classified into four diatom ecological guilds according to Passy (2007a) and Rimet and Bouchez (2012b) (Table 1). Furthermore, we classified all diatom taxa along two morphological traits based on categories: (i) biovolume according to Rimet and Bouchez (2012), and (ii) length/width ratio (L/W) (Table 1). Dimensions of diatom cells (length, width, thickness) were taken from our own datasets (see. Stenger-Kovács and Lengyel, 2015), where ~20 valves of each individual taxon have formerly been measured. Based on average values of length, width and thickness, biovolume was calculated according to Hillebrand et al. (1999). We tested the data for significant differences of L/W categories by ANOVA and post-hoc Tukey multiple comparisons at the level of significance p= 0.05 (Supplement 1).

Non-metric multidimensional scaling (NMDS) was conducted using Bray-Curtis dissimilarity index in order to ordinate 15 diatom functional and morphological traits (Table 1). By NMDS, we therefore visualized whether samples form ecological groups; i.e. with similar functional characteristics (traits) and therefore with similar ecosystem functions. To this end, a species x samples (n=338) data matrix was converted to binary form of trait x samples data matrix.

After Hellinger transformation of the diatom relative abundance data, redundancy analysis (RDA) was run to discover the relationship between environmental factors and the ecological groups defined (G) based on 187 randomly choosen samples. A further RDA analyses was run using the trait composition of the most relevant ecological group characterising soda pans from the first RDA, in order to identify the most important traits of diatoms that can indicate high conductivity ranges, and therefore excellent or good ecological status. The identified traits were then tested along the conductivity gradient using generalised additive models (GAMs) with Gaussian distribution and identity function. GAMs is well-suited for analysing ecological data (Austin, 1987), and they give the relevant responses of the ecological groups/traits to the explanatory variables (conductivity) (Suarez-Seoane et al., 2002). Statistical analyses were carried out in R (R.3.1.2. R Development Core Team, 2014) using the 'vegan' (Oksanen et al., 2017) and 'mgcv' (Wood, 2017) packages.

Similarly to the Nygaard's (1956) and the ACID (Acidity index of Diatoms) index (Andrén and Jarlman, 2008), our trait-based index (TBI) was developed using the selected traits in the second RDA and GAMs.

$$\mathrm{TBI} = \log_{10}\left[\frac{T_1 + T_2 + \cdots + T_n + 0.003}{T_a + T_b + \cdots + T_m + 0.003}\right] + 4.5$$

where T_1, T_2, … T_n – relative abundance of diatoms under specific traits with strong positive relationship with conductivity. Such traits indicate the good or excellent ecological condition of soda pans; T_a, T_b, … T_m – relative abundance of diatoms under specific traits with strong negative relationship with conductivity. These traits indicate the non-characteristic, degraded ecological status of soda pans.

If the denominator is zero, it must be changed to 1 in order to avoid zero logarithm. The index values range between 0 and 9; the higher the values, the better the ecological status indicated.

Results

Species-based analyses

In the conductivity model of soda pans, the correlation was high between the diatom inferred and observed conductivity (r=0.78; RMSEP= 2376 µS cm^{-1}; n=187) (Fig. 2.). The correlation in the test set was close to that observed in the model (r=0.73; n=151). The conductivity optima and tolerance as well as the indicator and sensitivity values were determined for 143 dominant species (>3%) of the 194 total species number (Table 2.). *Inter alia Surirella hoefleri* and *Nitzschia bergii* indicated extreme high conductivity levels. However, *Nitzschia austriaca*, *Craticula elkab* and *Cylindrotheca gracilis* were also good indicators of high conductivity values. On the other side of the gradient, *Entomoneis paludosa* var. *subsalina*, *Navicula radiosa*, *Gomphonema clavatum* and some centric diatoms (e.g. *Stephanodiscus parvus*) were rather associated with freshwater characteristics. After calculation of the two indices (DISP and SCIL) in the test set, the reliability of the indices was obvious. Regarding the SCIL index, the used species number corresponded to 10% and 70% (mean = 37%) of the total available species number, while it was between 77% and 100% (mean = 93%) in the case of DISP. The correlation between these indices and conductivity was significant in both cases, however, the coefficient of determination was higher based on the DISP index than based on the SCIL (Pearson cor.; $r_{\text{DISP-conductivity}} = 0.69$, $p < 0.001$; $r_{\text{SCIL-conductivity}} = 0.25$, $p = 0.001$) (Fig. 3. a, b).

Trait-based analyses

The NMDS based on the 15 different traits indicated that some of the traits were highly related to each other. Seven different ecological groups with similar diatom trait characteristics could be distinguished. (Fig. 4a). Group 1 was the planktic guild, Group 2 and 3 contained species with the two extreme categories of the L/W ratio (LW1, LW6). Group 4 included diatoms from the high profile guild containing LW5 species, which type of species could only be found in this guild. Group 5 involved species from the S4 size class. Group 6 represented taxa from the low profile ecological guild. Group 7 was quite diversified including taxa with different traits like: S1, S2, S3, S5, LW2, LW3, LW4 and the motile ecological guild (Fig. 4a).

As the result of the RDA analysis of the seven ecological groups (Fig. 4b), Group 7 separated clearly and was connected to those features, which are typical for the naturally state of soda pans (like elevated conductivity, pH, bicarbonate and nutrient concentration). Other groups located on the opposite side of the RDA triplot indicated less saline conditions (Fig. 4b). Among seven different traits inside Group 7, in a subsequent RDA (Fig. 4c) showed, that the motile ecological guild with three characteristic morphological traits (S1, LW2, LW3) as Subgroup 1 were connected to the basically pristine features of our soda pans (Fig. 4c).

For the seven ecological groups defined by NMDS, and for the Subgroup 1 separated in the RDA (Table 3), the GAMs revealed that the conductivity had significant negative effect on the Groups 1, 4, 5, and 6; however, the explained variance was higher (17.3%) and p-value was lower ($p< 0.001$) when these groups were merged (Table 3., Fig. 5a). There was no significant relationship between the Group 2, 3 and conductivity. On the other hand, the conductivity had a significant positive effect on Group 7, however, the explained variance was higher (23.1%) in the case of the Subgroup 1 (Table 3., Fig. 5b).

Trait-based index was developed based on the results of the GAMs:

$$\mathrm{TBI} = \log_{10}\left[\frac{SG1 + 0.003}{G1 + G5 + G4 + G6 + 0.003}\right] + 4.5$$

with the substitution of the different traits, the equation is the next:

$$\mathrm{TBI} = \log_{10}\left[\frac{MS1 + MLW2 + MLW3 + 0.003}{P + S4 + H + L + 0.003}\right] + 4.5$$

where, in the numerator:

MS1: relative abundance of motile diatom species with biovolume < 100 μm^3

MLW2: relative abundance of motile diatom species with LW2 ratio ($2 \leq$ Length/Width < 4)

MLW3: relative abundance of motile diatom species with LW3 ratio ($4 \leq$ Length/Width < 6)

in the denominator (in settling order!):

P: relative abundance of diatoms under the planktic ecological guild

S4: relative abundance of diatom species with biovolume between 600 μm^3 and 1500 μm^3) independently of their ecological guild classification

H: relative abundance of diatoms under the high profile ecological guild

L: relative abundance of diatoms under the low profile ecological guild

In the test set, the TBI index showed significant postive correlation with conductivity (Pearson cor., $r_{\text{TBI-conductivity}}$=0.64, p<0.001) (Fig. 3c). Its correlation was almost similar to the correlation between the DISP index and conductivity (Pearson cor., $r_{\text{DISP-conductivity}}$=0.69, p<0.001) (Fig. 3b). The two indices (species-based [DISP] and trait-based index [TBI]) correlated positively and significantly with each other (Pearson cor., $r_{\text{DISP-TBI}}$=0.75, p<0.001) (Fig. 3d).

Discussion

Traditional, species-based method (DISP index)

Inland saline lakes represent a challenge for scientific research, nature conservation and management on international level (Timms, 2005). In the Carpathian basin, they are unique (Padisák et al., 2006) and strictly protected in terms of legislation. Most of them are subject of ecological status assessment by recommendations of Biological Quality Elements (BQE) of the EC Water Freamework Directive. Harmonization of conservation request and those of the WFD called for the development of specific indicator/sensitivity values of diatoms characteristic in these environments. On the basis of conductivity model, optima and tolerances were defined for 143 diatom species of these special, low diversity ecosystems (Stenger-Kovács et al., 2016); and now applied in the newly developed species-based index (DISP). The advantages of the DISP index is that it is type specific (applicable in lowland, high salinity, <10 km^2, shallow [<3m depth] lakes with astatic water regime), and able to reflect the naturally high conductivity as a positive ecological characteristic of these lakes. The species pool of DISP is significantly larger than of the potentially available former indices (Ziemman et al., 1999, Ács, 2007). The usability of the Ziemann system by an inversed scaling — which has recently been implemented in Hungary (Ács et al., 2015) — as well as the SCIL index (Ács, 2007) is highly limited: species pool of these indices hardly overlap with those of the soda pans (24 in the Ziemann system, 63 in the SCIL index). This highlights clearly that ecological status based on former indices could not be evaluated in a reliable way. Moreover, the relationship of our DISP index with conductivity as a master variable of ecological status of soda lakes appeared also to be much stronger. Furthermore, a complete photo documentation about all species involved in our index is also available (see Stenger-Kovács et al., 2015; Lengyel, 2017; supplementary of the present study [Supplement 2]) for the "analysts" (biologists, assistants).

The usefulness of the traditional taxonomy-based indices with refined taxonomic resolutions cannot be questioned (Rimet and Bouchez, 2012a). However, they require time and expansive expertise with obvious limitations, disadvantages and uncertainties. These may include misidentification, availability of the continuously changing and exhaustive taxonomic literature, the elimination of rare species from statistical analyses, different expertise among labs, and different species compositions among ecoregions (Kahlert et al., 2012; Tapolczai et al., 2016, 2017). This huge effort taken, however, might be further constrained in ecological status assessments (Kelly, 2013). On the other hand, common DNA-based approaches develop fast in precision (Zimmermann et al., 2015; Leese et al., 2016). However, the ecological context for DNA-based approaches still remains to be explored. Accordingly, trait-based approaches may provide a "bridge" as potential solution for such difficulties.

Application of functional approaches (TBI index), and the ecological meaning of the trait community composition

The use of trait-based measures in ecological status assessments might potentially be favoured since they are related to functional properties of the biological elements of ecosystems directly (Larras et al., 2017). Initially, trait-based approaches have been suggested complementary (Bayona et al., 2014, Trábert et al., 2017, Algarte et al., 2017) since they are relatively rapid and simple (Algarte et al., 2017). Functional approaches may also enhance our ability in predicting the community composition from the environment (Mc Gill et al., 2006, Abonyi et al., 2018); also in context of ecological indication. Developing trait-based approaches in freshwater (e.g. Schwaderer et al., 2011), marine (e.g. Edwards et al., 2013) and terrestrial (e.g. Diaz et al., 2013) ecosystems is a recent trend in ecology. The number of studies using trait-based approaches in benthic algal communities has been rapidly increasing (e.g. Gottschalk and Kahlert, 2012, Rimet et al., 2016, Riato et al., 2017, Zorzal-Almeida et al., 2017). The first multimetric trait-based indices of benthic diatoms were developed without the geographical extension to Europe (Potapova and Carlisle, 2011; Tapolczai et al., 2017). By applying functional systems, uncertainties in species-based approaches may be avoided completely (Tapolczai et al., 2017) and the differences of taxonomic expertise of investigators or the change in investigator do not have crucial consequences on ecological status assessments (Hajnal and Padisák, 2008; Salmaso et al., 2015). Some useful traits, e.g. morphological ones can be measured relatively easily (B.-Béres et al. 2017); whereas the trait-based ecological classifications (e.g. ecological guilds, functional groups) may further simplify the understanding of mechanisms underlying community compositions (Salmaso et al., 2015).

Trait-based assessments ideally contain multiple traits, not only e.g. growth forms to understand main variables in determining the community composition (Lange et al., 2016). The application of small number of ecological guilds (e.g. in Passy, 2007a) may not be sensitive enough to follow all relevant changes of the environment (B.-Béres et al., 2014). In phytoplankton research, multiple morphological, physiological and behavioral traits have also been identified as key factors regulating success in the community composition (see Litchman et al., 2007). In benthic algal research, the first similar approach was the application of eco-morphological functional groups (combination of diatom ecological guilds and cell sizes; in B.-Béres et al., 2016). Combined ecological groups of diatoms provided strong relationships with environmental variables in multiple cases (B.-Béres et al., 2016, Tapolczai, 2017, Wang et al., 2018). One weakness of the existing trait-based classifications is that their data sets are based only on few sampling sites (B.-Béres et al., 2016), or on limited number of taxa (Lange et al., 2016; B.-Béres et al., 2016). In developing our trait-based diatom index, these disadventages were avoided. Here we used a multiple trait approach (15 functional and morphological traits), while former studies applyed simple trait combinations (B.-Béres et al., 2016; Tapolczai et al., 2016). Traits ideally represent specific environmental drivers (Petchey and Gaston, 2006); therefore, we identified traits responding to the main environmental drivers collectively. In saline ecosystems, conductivity is the master environmental variable representing an overall ecological status (Stenger-Kovács et al., 2014). The ecological groups associated with high conductivity and therefore the “pristine” ecological status may consist of motile diatom species with small cell size (MS1) and less roundish, more elongated shapes (MLW2, MLW3). *Nitzschia austriaca*, *N. aurariae*, *Craticula elkab*, *Halamphora dominici* are some examples for the representatives of MS1. MLW2 species were e.g. *Anomoeoneis sphaerophora*, *Craticula ambigua* and *Staurophora wislouchii*. In contrast *Halamphora kevei*, *Nitzschia salinarum* and *Navicula wiesneri* dominated among other species in MLW3. Our examples also confirm that for a given functional trait, examples from both phylogenetically close and distant species can be found (Tapolczai et al., 2016). Accordingly, the functional role identified may potentially be independent from the taxonomic position of diatom taxa.

On a global scale, the motile diatom guild is the most species rich group. Its richness may show a strong positive relationship with the concentration of nutrients (Soininen et al. 2016), organic matter and turbidity (Tapolczai et al., 2017). Species belonging to this guild are good competitors in resource-rich habitats (Van der Grinten et al., 2004, Lange et al., 2011) with stable nutrient availability (Soininen, 2007) without marked seasonality (Trábert et al., 2017). Motility of diatoms represents an important function in habitats with fine sediments, and an applicable indicator of siltation and land use of running waters (Stevenson et al., 2010; Smucker and Vis, 2010). They are characteristic in lakes under stable hydrodynamic conditions (Algarte et al., 2017); and in parallel with water abstraction, their relative abundance increases at high farm intensity (Lange et al., 2011). Therefore, besides the high salinity, all characteristic features of the soda pans such as high nutrient content, turbidity, the decreasing water level, or the temporary drying phases support the dominance of diatoms with characteristic functional traits in this guild. However, one single trait alone can also be in strong correlation with salinity and conductivity (Kókai et al., 2015). Our finding therefore may show that functional and morphological traits can respond to conductivity in a highly inter-connected way, supporting a multi-trait functional approach in diatom research.

However, the question remains that what is the meaning of characteristic morphological traits of motile diatom species. Beside of the wide range covered by algal biovolumes (Tapolczai et al., 2017), the size is the easiest measurable feature of diatom species with several possible ecological meanings (Tapolczai et al., 2016). Body size influences the distribution of diatoms (Heino and Soininen, 2006; Passy, 2008), since small species have higher dispersal rates (Passy, 2012). Large species are rather sensitive for physical disturbances, in contrast to smaller ones with greater resilience (Passy, 2007b). Diatoms may also respond to environmental factors differently based on their cell sizes. The salinity has unequivocally significant effect on the size and surface area of the cell (Snoeijs et al., 2002, Neustupa et al., 2013). High conductivity soda pans impose high osmotic stress on algal cells; therefore, small size may be a physiological adaptation similar to the reduction of the surface area and pore size of the diatom valves under elevated salinity levels (Leterme et al., 2010). The function of this morphological trait can also be linked to other characteristics of the pans. Large species may have competitive advantage under higher light availability (Lange et al., 2011), while e.g. in afforested streams, small species may dominate with a more simple community structure (Cibils-Martina et al., 2017); similarly to communities of soda pans. Motile species with small cell size (S1) might hide easily among inorganic particles of mud in the drying period of lakes; similarly to cases observed in sedimanteted, drying streams (Lange et al. 2016).

Until now, elongated taxa with small L/W ratio were reported only from polluted habitats under high shear stress (Tapolczai et al., 2017). However, the shape of MLW2, MLW3 (less roundish, more elongated) indicated well the level of conductivity. A study on the photosynthetic activity of a *Nitzschia* species as one representative of this group showed outstandingly high conductivity optima (8599 μS cm^{-1}; Lengyel et al., 2015). Furthermore, this less roundish, more elongated shape similarly to small cell size may facilitate hiding among mud particles, or to move among sediment particles. Another potential mechanism underlying such functional characteristic in turbid environments is that elongated cells might serve as antenna/lighttrap in light-limited habitats.

In our study, S4 size as individual morphological trait appeared to indicate the worse ecological condition of the pans. In the low conductivity range (more freshwater habitats), the S4 size was connected to functional traits within the high, low, and motile ecological guilds. The abundance of diatoms under the LS4 and HS4 groups increased with decreasing conductivity, and the amount of LS4 and MS4 taxa were higher under higher pH (B.-Béres et al., 2016, 2017). Consequently, it seems that size S4 has alone ecological meaning independently of its ecological guild classification. Diatom species of size S4 may therefore prefer waters with low conductivity and high pH, which conditions in soda pans may characterize deteriorated ecological conditions.

The motile diatom ecological guild with special morphological features was representative for the excellent or good ecological status of the soda pans. However, other, well-known functional traits (planktic life form, high and low profile ecological guilds) may indicate lower conductivity values, similarly to S4 size. Trábert et al. (2017) showed already that the relative abundance of diatom taxa under the high profile and motile guilds correlated with each other negatively in lotic systems. The abundance of diatoms belonging to the high profile guild is not directly related to the nutrient level, rather to other habitat factors (Soininen et al. 2016) like high light intensity (Trábert et al., 2017). The dominance of low profile diatom taxa is characteristic in temporary and permanent water courses with frequent disturbance events and low nutrient content (Novais et al., 2014). Our analyses also showed that the separation of planktic taxa into an individual ecological guild has relevant ecological meaning; as suggested formerly by Rimet and Bouchez (2012b) and B.-Béres et al. (2017).

Summary

Naturally saline soda lakes are unique habitats in the Carpathian basin, and also in other regions. Their ecology-based management requires the development of 'easy to use', but reliable indices for local specialists, stakeholders, and policy makers. We showed that community composition of benthic diatoms enabled the development of such indices based both on the taxonomic and functional approaches.

The reliable identification of ecological funtions is the basis of functional approaches, which then may successfully be used in applied fields like ecological status assessment. Our study adapted and further improved a widely-used functional approach, the diatom ecological guild concept to naturally shallow, saline ecosytems. Our refined functional classification made possible to identify relevant functional characteristics, indicating natural (high salinity) *vs.* degraded (low salinity) ecological conditions in a meaningful way.

While both taxonomy and functional characteristics of benthic diatoms performed well in ecological status indication in our case, the trait-based approach based on simple morphological characteristics - 'easy to use' - may better fulfill cost and time efficiency, a feature highly required in biomonitoring. Therefore, the successful application of our trait-based benthic diatom index may not be restricted to the Carpathian basin, rather can be applied in biomonitoring and conservation management of soda lakes independently of the geographic location.

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Figures, tables and legends

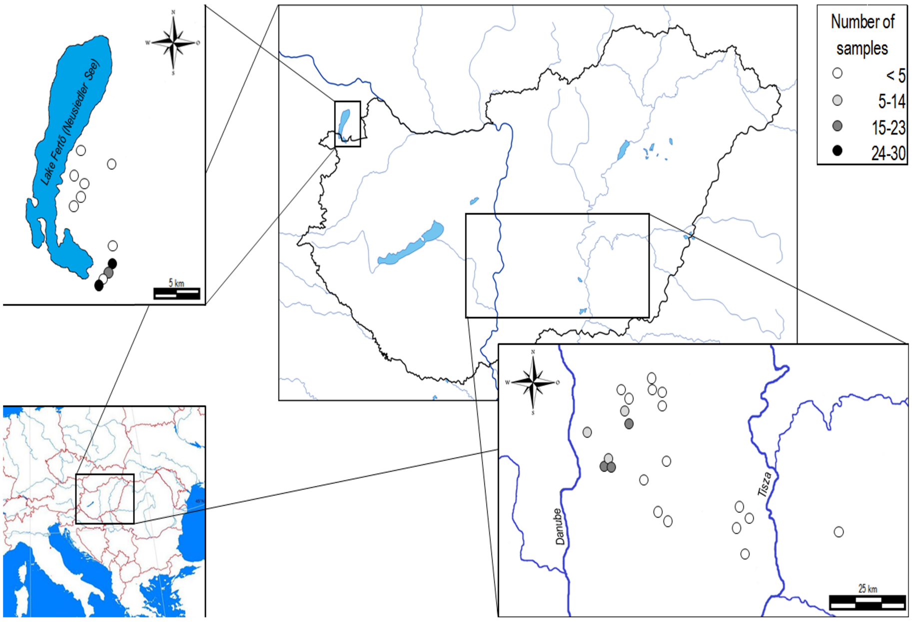

Fig.1 Sampling sites and the number of the samples in the Carpathian basin.

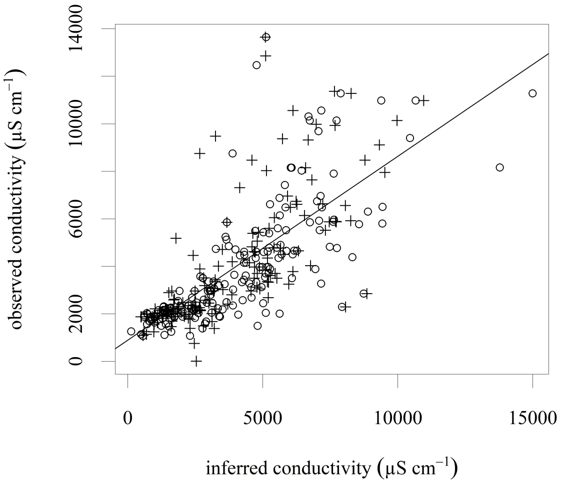

Fig. 2 Relationship between the diatom inferred and observed conductivity using weighted averaging tolerance downweighting regression (WAtol) with inverse deshdrinking. (empty circles: training set, where r = 0.78 [n=187]; cross signs: test set, where r = 0.73 [n=151]).

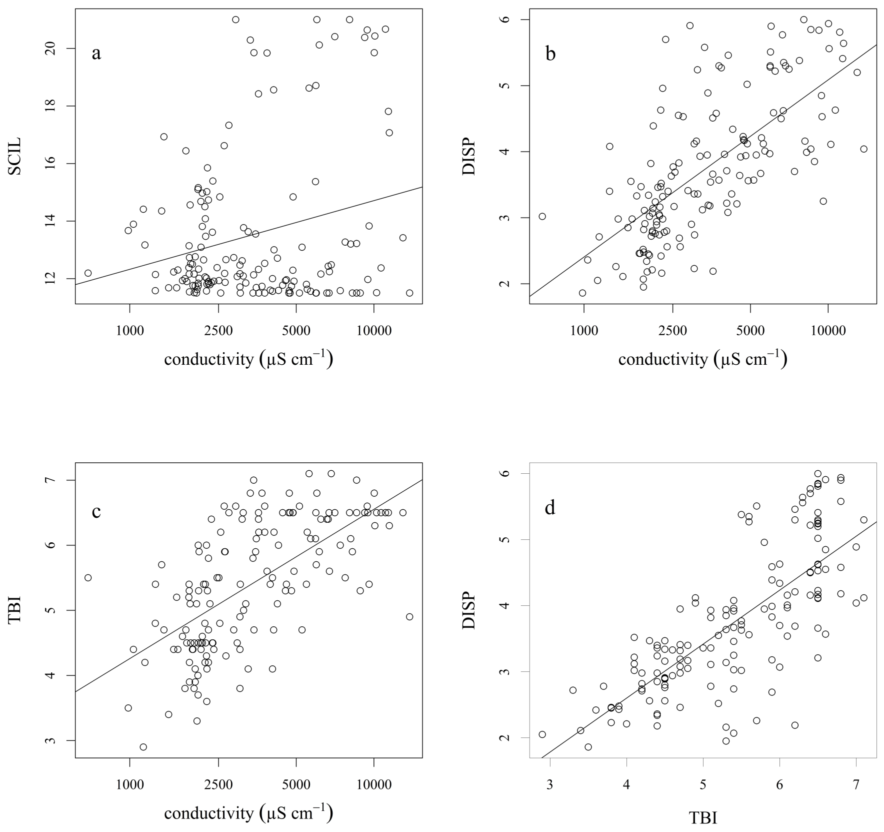

Fig. 3 Relationship between the conductivity and (a) SCIL [r=0.25, p=0.0024], (b) DISP [r=0.69, p<0.001], (c) TBI [r=0.64, p<0.001], moreover, (d) the DISP and TBI [r=0.64, p<0.001] in the test set (n=151) of the soda pans.

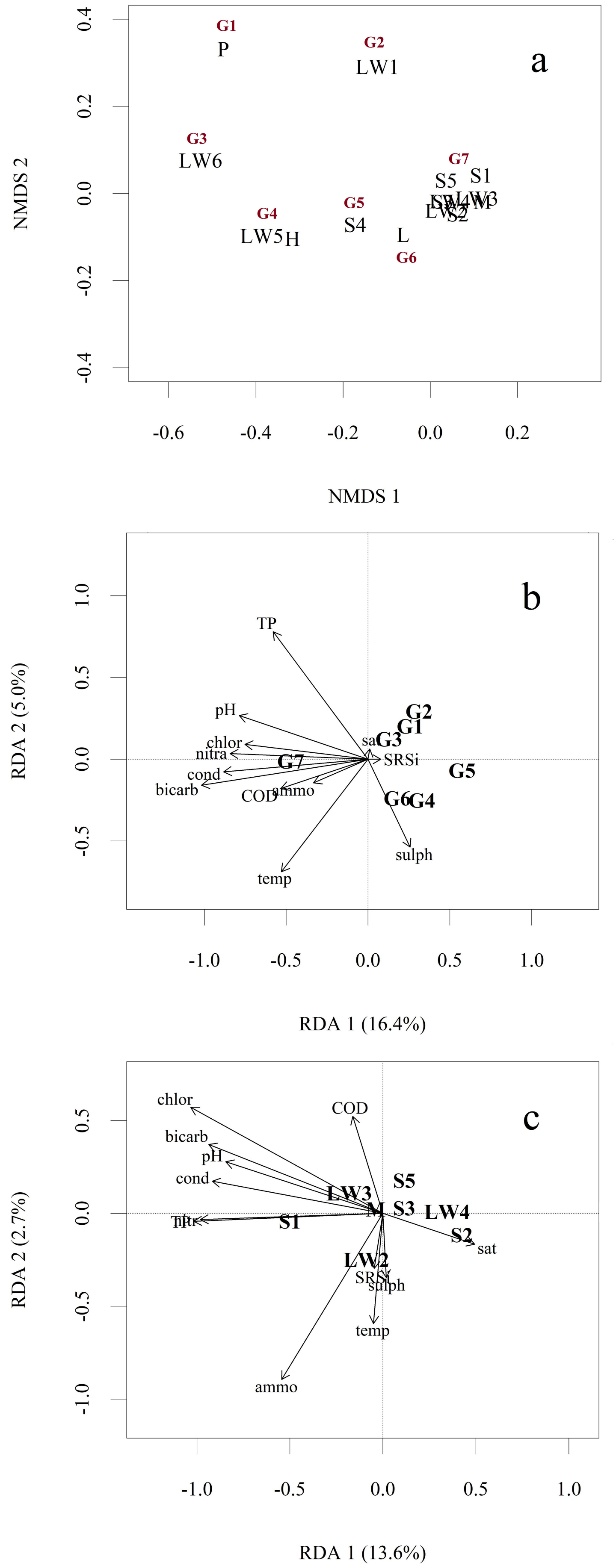
a
G1
P
G2
LW1
G3
LW6
G7
S5
S1
LW3
S2
G4
LW5
H
G5
S4
L
G6
NMDS 2
NMDS 1
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.4
-0.2
0.0
0.2
b
TP
pH
chlor
nitra
cond
bicarb
COD
ammo
sat
SRSi
sulph
temp
G2
G1
G3
G7
G5
G6
G4
RDA 2 (5.0%)
RDA 1 (16.4%)
1.0
0.5
0.0
-0.5
-1.0
-0.5
0.0
0.5
1.0
c
chlor
COD
bicarb
pH
cond
TP
nitra
S5
LW3
M
S3
LW4
S1
S2
sat
LW2
SRSi
sulph
temp
ammo
RDA 2 (2.7%)
RDA 1 (13.6%)
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0

Fig. 4 (a) Results of the NMDS (Bray-Curtis index, Stress = 0.11) for the binary data of the 15 functional and morphological traits based on the 338 diatom samples of the Central-European soda pans **(b)** Relationship between the relative abundance of the seven groups defined by NMDS and the water chemical variables in the biplot of the RDA analyses of the 187 samples **(c)** Biplot of the second RDA analysis (n=187) presents the connection the relationship the relative abundance of the different traits in Group 7 and the water chemical data. (explanatory variables: ammo=ammonium, bicarb=bicarbonate, chlor=chloride, COD= Chemical Oxygen Demand, cond=conductivity, nitr=nitrate, sat= oxygen saturation, SRSi= soluble reactive silica, sulph=sulphate, temp= temperature).

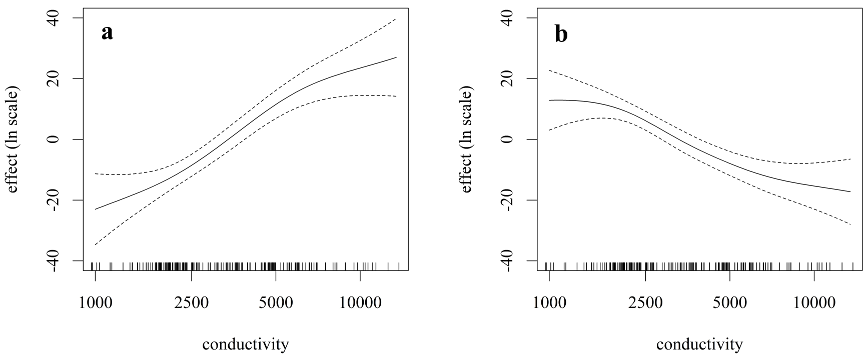

Fig. 5 (a) Smoothing curve of the additive effect for ln conductivity (μS cm^{-1}) applied on the combined Group 1, 4, 5, 6; and **(b)** on Subgroup 1. Dotted lines are the 95% confidence intervals. Marks along the horizontal axis represent the single observations (number of the samples).

Table 1. The applied traits in soda pans.

	Traits	
Guilds	Biovolume (S)	Length/width ratio (L/W)
high profile ecological guild	S1 < 100 μm^3	LW1 < 2
low profile ecological guilds	100 μm^3 ≤ S2 < 300 μm^3	2 ≤ LW2 < 4
motile guild	300 μm^3 ≤ S3 < 600 μm^3	4 ≤ LW3 < 6
planktonic guild	600 μm^3 ≤ S4 < 1500 μm^3	6 ≤ LW4 < 12
	S5 ≤ 1500 μm^3	12 ≤ LW5 < 20
		LW6 ≥ 20

Table 2. Indicator (v) and sensitivity values (s) of the diatom species in the DISP index and their presence (+) in the Ziemann's (1999) and Ács's (2007) studies. The photo documentation (PD) about the species are published in Stenger-Kovács and Lengyel, 2015 (*), Lengyel, 2017 (**) and in the supplemetary material of the present study (S).

Species	v	s	Ziemann (1999)	Ács (2007)	PD
Achnanthes brevipes var. *intermedia* (Kützing) Cleve	2	2	+		*
Achnanthidium minutissimum (Kützing) Czarnecki	2	3		+	*
Achnanthidium catenatum (Bily & Marvan) Lange-Bertalot	1	1			S
Achnanthidium saprophilum (Kobayasi & Mayama) Round & Bukhtiyarova	6	3			S
Achnanthidium straubianum (Lange-Bertalot) Lange-Bertalot	6	3			**
Adlafia minuscula var. *minuscula* (Grunow) Lange-Bertalot	2	2			S
Amphora copulata (Kützing) Schoeman at Archibald	2	1			*
Amphora indistincta Levkov	2	2			*
Anomoeoneis costata (Kützing) Hustedt	5	3			*
Anomoeoneis sphaerophora var. *sculpta* (Ehrenberg) Otto Müller	4	2			*
Anomoeoneis sphaerophora Pfitzer f. *sphaerophora*	5	3	+	+	*
Aulacoseira ambigua (Grunow) Simonsen	3	2			**
Bacillaria paxillifera (O.F.Müller) T.Marsson	2	3		+	*
Caloneis amphisbaena (Bory) Cleve	2	1	+	+	*
Caloneis silicula (Ehrenberg) Cleve	1	1			*
Campylodiscus bicostatus W. Smith	3	2			*
Cocconeis placentula Ehrenberg	1	2		+	*
Craticula ambigua (Ehrenberg) D.G. Mann	4	3			*
Craticula buderi (Hustedt) Lange-Bertalot	4	3			*
Craticula cuspidata (Kützing) D.G. Mann	3	2		+	**
Craticula elkab (Otto Müller ex Otto Müller) Lange-Bertalot, Kusber & Cocquyt	5	3			*
Craticula halopannonica Lange-Bertalot	4	2			S
Craticula halophila (Grunow) D.G. Mann	4	2	+	+	*
Craticula minusculoides (Hustedt) Lange-Bertalot	2	1			S
Craticula molestiformis (Hustedt) Mayama	4	3			**
Craticula sp. 1	5	1			S
Craticula subminuscula (Manguin) Wetzel & Ector	2	1			**
Ctenophora pulchella (Ralfs ex Kützing) D.M. Williams at Round	3	3	+	+	*
Cyclostephanos invisitatus (Hohn & Hellermann) Theriot, Stoermer & Håkasson	1	1			**
Cyclotella meneghiniana Kützing	2	2	+	+	*
Pantocsekiella ocellata (Pantocsek) K.T.Kiss & E.Ács	2	1		+	**
Cylindrotheca gracilis (Brébisson ex Kützing) Grunow	5	2	+		*

Cymbella hustedtii Krasske var. *hustedtii*	1	1			**
Cymbella neocistula Krammer	2	2			*
Diatoma moniliformis (Kützing) D.M.Williams ssp. *moniliformis*	3	3	+	+	**
Diatoma tenuis Agardh	2	2		+	*
Encyonopsis minuta Krammer & Reichardt	1	1			**
Entomoneis alata (Ehrenberg) Ehrenberg	1	1	+		**
Entomoneis costata (Hustedt) Reimer	1	1			**
Entomoneis paludosa var. *subsalina* (Cleve) Krammer in Lange-Bertalot & Krammer	1	1	+	+	*
Epithemia adnata (Kützing) Brébisson	2	1		+	**
Epithemia sorex Kützing	2	1		+	*
Fallacia pygmaea (Kützing) A.J. Stickle et D.G. Mann	3	2		+	*
Fallacia pygmaea ssp. *subpygmaea* Lange-Bertalot, Cavicini, Tagliaventi et Alfinito	4	3			*
Fistulifera saprophila (Lange-Bertalot & Bonik) Lange-Bertalot	3	2			S
Fragilaria rumpens (Kützing) Carlson	1	1		+	S
Fragilaria famelica (Kützing) Lange-Bertalot	3	2	+		*
Fragilaria nanana Lange-Bertalot	4	3			**
Fragilaria tenera (W. Smith) Lange-Bertalot	2	1		+	**
Fragilaria vaucheriae (Kützing) Petersen	6	3		+	**
Gomphonema clavatum Ehrenberg	1	1			*
Gomphonema micropus Kützing	3	2			**
Gomphonema olivaceum (Hornemann) Brébisson	2	2		+	*
Gomphonema parvulum (Kützing) Kützing var. p*arvulum* f. *parvulum*	3	3		+	*
Gomphonema saprophilum (Lange-Bertalot & E.Reichardt) Abraca, R.Jahn, J.Zimmermann & Enke	3	1			*
Gomphonema pseudoaugur Lange-Bertalot	4	2			**
Gyrosigma acuminatum (Kützing) Rabenhorst	2	2		+	*
Gyrosigma obtusatum (Sullivant & Wormley) C.S. Boyer	2	1			**
Halamphora dominici Ács et Levkov	4	2			*
Halamphora kevei Ács et Levkov	3	2			*
Halamphora oligotrophenta (Lange-Bertalot) Levkov	1	2			**
Halamphora paraveneta (Lange-Bertalot, Cavacini, Tagliaventi et Alfino) Levkov	4	2			*
Halamphora subcapitata (Kisselew) Levkov	3	1			*
Halamphora tumida (Hustedt) Levkov comb. nov.	2	2			**
Halamphora veneta (Kützing) Levkov	3	2			*
Hantzschia abundans Lange-Bertalot	1	1			*
Hantzschia amphioxys (Ehrenberg) Grunow	2	1			*
Haslea duerrenbergiana (Hustedt) F.A.S.Sterrenburg	2	1			*
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski	2	1			**
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin at Witkowski	2	1		+	*

Mastogloia elliptica (C. Agardh) Cleve	2	1	+		**
Mastogloia sp. 1	2	1			*
Mayamaea permitis (Hustedt) K.Bruder & Medlin	4	2			*
Melosira varians C. Agardh	3	2			**
Navicula capitoradiata Germain	2	1	+	+	**
Navicula cryptocephala Kützing	3	3		+	**
Navicula cryptotenella Lange-Bertalot	2	2		+	*
Navicula cryptotenelloides Lange-Bertalot	1	2		+	*
Navicula oblonga (Kützing) Kützing	2	3		+	*
Navicula radiosa Kützing	1	1		+	*
Navicula salinarum Grunow var. *salinarum*	2	2	+	+	*
Navicula sp. 1	6	3			S
Navicula sp. 2	3	2			S
Navicula tripunctata (O.F. Müller) Bory	2	1		+	**
Navicula veneta Kützing	4	3		+	*
Navicula wiesneri Lange-Bertalot	2	2			*
Navicymbula pusilla (Grunow) Krammer	3	3			*
Nitzschia acicularis (Kützing) W. Smith	2	1		+	**
Nitzschia amphibia Grunow	2	1		+	*
Nitzschia aurariae Cholnoky	4	2			*
Nitzschia austriaca Hustedt	5	3			as Nitzschia sp. 1 in * (After Ács et al., 2017)
Nitzschia bergii Cleve-Euler	6	3		+	*
Nitzschia capitellata Hustedt	3	2	+	+	**
Nitzschia communis Rabenhorst	3	2			*
Nitzschia commutata Grunow	3	2	+		*
Nitzschia elegantula Grunow	2	1			*
Nitzschia fonticola (Grunow) Grunow	6	3		+	**
Nitzschia frustulum (Kützing) Grunow	4	3	+	+	*
Nitzschia gracilis Hantzsch	2	1		+	*
Nitzschia inconspicua Grunow	3	2	+	+	*
Nitzschia liebetruthii Rabenhorst	4	3		+	**
Nitzschia palea var. *debilis* (Kützing) Grunow	3	2			**
Nitzschia palea (Kützing) W. Smith var. *palea*	2	2		+	*
Nitzschia palea var. *tenuirostris* sensu Lange-Bertalot	2	1			*
Nitzschia paleacea (Grunow) Grunow	2	1		+	*
Nitzschia pusilla Grunow	5	3		+	*
Nitzschia reversa W Smith	3	1			*
Nitzschia solita Hustedt	2	2		+	*
Nitzschia sp. 2	3	2			*

Nitzschia sp. 3	3	3			*
Nitzschia supralitorea Lange-Bertalot	6	3			*
Nitzschia thermaloides Hustedt	1	1			*
Nitzschia valdecostata Lange-Bertalot et Simonsen	2	2			*
Nitzschia vitrea G. Norman var. *vitrea*	3	2	+		*
Pinnularia brebissonii (Kützing) Rabenhorst	1	1			*
Pinnularia kneuckeri Hustedt	1	2			*
Pinnularia oriunda Krammer morphotype2	2	1			*
Planothidium frequentissimum (Lange-Bertalot) Lange-Bertalot	3	2			**
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	2	1		+	**
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	5	3		+	**
Rhoicosphenia adriatica Caput Michalic & Levkov	2	2			**
Rhoicosphenia lacustris Levkov	2	3			*
Rhopalodia gibba (Ehrenberg) Müller	2	1	+	+	*
Rhopalodia operculata (Agardh) Håkansson	3	2			*
Scoliopleura peisonis Grunow	2	2			*
Sellaphora capitata D.G.Mann & S.M. McDonald	2	1			**
Staurophora wislouchii (Poretzsky et Anisimowa) D.G. Mann	3	2			*
Stephanodiscus hantzschii Grunow in Cleve & Grunow	1	1		+	**
Stephanodiscus hantzschii f. *tenuis* (Hustedt) H.Håkansson & E.F.Stoermer	1	1			**
Stephanodiscus minutulus (Kützing) Krieger	1	1		+	**
Stephanodiscus parvus Stoermer et Håkansson	1	1			*
Surirella brebissonii Krammer et Lange-Bertalot	3	3		+	*
Surirella brightwellii W.Smith	2	2			**
Surirella hoefleri Hustedt	6	3			*
Surirella ovalis Brébisson	2	2	+		*
Surirella peisonis Pantocsek	2	2		+	*
Surirella sp. 1	5	2			*
Tabularia fasciculata (Agardh) D.W. Williams et Round	3	2	+	+	*
Tryblionella apiculata W. Gregory	3	3			*
Tryblionella gracilis W. Smith	3	2			*
Tryblionella hungarica (Grunow) Frenguelli	2	2	+	+	*
Ulnaria acus (Kützing) Aboal	2	1			*
Ulnaria ulna (Nitzsch) Compère	2	3		+	*

Table 3. Results of the GAM modelling. Models included the defined seven Groups and the one Subgroup of the diatom functional and morhpological traits as response variable, and conductivity as explanatory variable.

GAM models	F-value	p-value	explained variance (%)
GAM (G1) = 2.68 + f (ln conductivity)	4	<0.001	6.8
GAM (G4) = 8.27 + f (ln conductivity)	3.38	=0.01	8.1
GAM (G5) = 4.59 + f (ln conductivity)	4.42	<0.05	2.3
GAM (G6) = 8.74 + f (ln conductivity)	4.813	<0.05	2.5
GAM (G1+G4+G5+G6) = 24.29 + f (ln conductivity)	**8.81**	**<0.001**	**17.3**
GAM (G7) = 69.97 + f (ln conductivity)	10.55	<0.001	19.1
GAM (SG1) = 50.731 +f (ln conductivity)	**13.98**	**<0.001**	**23.1**

Supplement 1. Photo documentation of diatom species involved in the DISP index:

in a separate file

Supplement 2. Results of the ANOVA and Tukey’s post hoc test among the L/W categories:

in a separate file