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9 **Benthic Diatom-Based Lake Types in Hungary**

10 Ágnes Bolgovics^{1,2}, Éva Ács³, Gábor Várbíró¹, Judit Görgényi^{1,2}, Keve Tihamér Kiss³,
11 Angéla Földi², Zsolt Nagy-László⁴, Trábert Zsuzsa¹, Gábor Borics¹

12
13
14 ¹ MTA Centre for Ecological Research, Danube Research Institute, Department of Tisza Research, H-4026
15 Debrecen, Bem square 18/c., Hungary

16 ² University of Eötvös Loránd, H-1117 Budapest, Pázmány Péter Str. 1/A, Hungary

17 ³ MTA Centre for Ecological Research, Danube Research Institute, H-1113 Budapest, Karolina Str. 29, Hungary

18 ⁴ University of Pannonia, H-8200, Veszprém, Egyetem Str. 10, Hungary

19 **Abstract**

20
21 Hydromorphological and chemical properties of water bodies have pronounced influence on the occurrence and
22 distribution of biological elements in the aquatic ecosystems. Based on a series of abiotic characteristics,
23 seventeen lake types were established in Hungary for management purposes. Benthic diatom assemblages were
24 studied in shallow standing water bodies in Hungary in order to provide a biological validation of these types.
25 Species composition and abundance of the occurring taxa were analysed. By their diatom taxonomic
26 composition five basic lake types could be distinguished; two calcareous lake types, which differ in size and in
27 their trophic characteristics and three types within the group of high salinity lakes. In this latter group the astatic
28 and perennial lakes showed considerable differences. These results have great practical importance, because
29 biological validation of the hydromorphological lake typology is the first step for reliable assessment of the
30 ecological status of water bodies.

31 **Introduction**

32
33 Aquatic ecosystems are the most threatened ecosystems world-wide (Revena et al. 2000).
34 For managing the preservation and restoration of aquatic ecosystems across Europe the
35 European Commission implemented the Water Framework Directive (WFD, 2000/60/EC).
36 The directive is considered to be the most ambitious and comprehensive document of
37 European environmental legislation (Moss et al. 2003). WFD requires member states to

38 monitor and assess the quality of surface waters in order to identify and reverse negative
39 trends in the ecological state of water bodies. The WFD and the various supportive documents
40 (Anonymous 2003) provide guidance to ensure its implementation in a consistent way across
41 Europe; however, it is still a major challenge for the member states. Ecological state
42 assessment of water bodies has to be based on the evaluation of the actual status in
43 comparison to the type specific reference conditions (WFD, 2000/60/EC). Therefore,
44 establishment of river and lake typologies is the first step in the assessment process. It has
45 been known from the early decades of the last century that hydromorphological characteristics
46 of lakes basically determine the composition of lake biota (Murray et al. 1910). Ecoregions,
47 size, depth, altitude, hydrological regime and geology are considered as the most important
48 variables influencing distribution and abundance of biological elements. By combining these
49 variables, hundreds of lake types can be defined but forty-eight were proposed as “core types”
50 (Moss et al. 2003). Besides these variables other biologically important type descriptor
51 variables can also be applied in order to reach greater and clearer separation of the types.
52 Type of the stratification, lake residence time, acid neutralizing capacity, water level
53 fluctuation and several other properties were applied in the national typologies across Europe
54 (Borics et al. 2014). The resulted types, so-called top-down types, have been created
55 accordingly; while ecological similarities or dissimilarities of the types have not been
56 considered. However, biological elements used in ecological state assessment are not sensitive
57 to all the type descriptor variables and this makes possible the merging of the types, and thus,
58 the simplification of the typologies (Zenker and Baier 2009). Phytobenthos is one of the
59 biological elements that required by the WFD and included in ecological status assessments.
60 Benthic diatoms, being a species-rich and ecologically diverse group of algae, are used
61 increasingly in ecological monitoring as proxies for phytobenthos. Several diatom-based
62 metrics have been developed (Coste in Cemagref 1982, Rott et al. 1997, 1999) and used for
63 river quality assessment in European countries (Birk et al. 2012, Rimet et al. 2005, Van Dam
64 et al. 2007, Várbiro et al. 2012) and usefulness of these metrics in lake quality assessment has
65 been demonstrated (Ács et al. 2005, Bolla et al. 2010, Blanco 2004). A European scale
66 comparison of the diatom-based national assessment methods has been done for three
67 common European lake types (low, moderate and high alkalinity lakes) by Kelly et al. (2014).
68 However the number of hydromorphological lake types within countries is much higher
69 (Kolada et al. 2005, Borics et al. 2014), and only a few of them can be assigned to the
70 common intercalibration types.

71 Based on hydromorphological characteristics seventeen lake types were established in
72 Hungary (Szilágyi et al. 2008). As a result of the phytoplankton-based validation of these
73 types the numbers have been reduced to four (Borics et al. 2014). However in that study the
74 authors noted that there was no clear overlap between the biomass-based types and the types
75 based on phytoplankton composition. The four types were distinguished by their trophic
76 characteristics but in several types eutrophication may not be the key pressure (Hering et al.
77 2010). Large steppe lakes (Borics et al. 2014) and shallow, turbid soda lakes are characteristic
78 elements of the landscape in the Carpathian Basin (Felföldi et al. 2009). The common feature
79 of these lakes is that they are naturally eutrophic, or hypertrophic (Boros et al. 2006, Stenger-
80 Kovács et al. 2014), but other characteristics such as pH, conductivity, and macrophyte
81 composition show significant differences. However, it is still a question whether these
82 differences appear in the composition of the benthic microflora. Diatom based methods are
83 promising tools in lake quality assessment, but simplification of the top–down typologies and
84 establishment of diatom-based lake types are required. Therefore, the aim of the study is to
85 present a diatom-based bottom–up typology and simplification of the hydromorphology based
86 top–down typology for the lakes in the Carpathian basin.

87

88

89 **Materials and Methods**

90 *Database*

91 Benthic diatom data derived from the Hungarian National Water quality monitoring survey
92 and from the database of the Danube Research Institute. To avoid mis-grouping, only data for
93 the least disturbed sites were considered during the analyses.

94 For selecting the least disturbed sites we applied type-dependent screening criteria. In case of
95 those lakes where there is only one lake within one lake type (Lake Balaton, Lake Velencei
96 and Fertő) we used data from last decade, because great improvement in lake quality could be
97 observed in this period (Istvánovics and Somlyódy 2001; Ács et al. 2005).

98 The following criteria were applied to the other lake groups: no point source pollution, no
99 intensive stocking of fish, no artificial modification of the shoreline, complete zonation of
100 macrophytes. Since very shallow high alkalinity soda lakes are considered naturally
101 hypertrophic (Boros et al. 2014) exclusion criteria for nutrients have not been applied in this
102 lake group. Although high alkalinity calcareous lakes can also be considered naturally
103 eutrophic (Borics et al. 2014), extreme values of nutrients unanimously refer to anthropogenic

104 load. Therefore, for the lakes in this lake group the following screening criteria were applied:
105 $P < 250 \mu\text{g l}^{-1}$ and $N < 2000 \mu\text{g l}^{-1}$ (lake mean values).

106 Land use is considered important screening criterion across Europe (Pardo et al. 2012; Kelly
107 et al. 2014), but this criterion has not been applied in this study, because previously it was
108 demonstrated that differences in land use appear not to be relevant for lake quality at this
109 region, because the importance of land use is exceeded by that of lake use, i.e., intensity of
110 fishing and fish stocking (Borics et al. 2013).

111

112 *Sampling*

113 Altogether six hundred thirty-nine samples were collected from one hundred forty-four
114 sampling sites belonging to seventy-five water bodies in the middle of the vegetation period
115 (from May to September) between 2010 and 2016. Benthic diatom samples were collected
116 from five reed stalks per sampling site from the well illuminated littoral zones of lakes.
117 Diatom samples were preserved with Lugol's solution and were stored in plastic containers
118 until processing.

119 *Sample processing*

120 The frustules were cleaned with hydrochloric acid and hydrogen peroxide, subsequently
121 washed in distilled water and mounted with Naphrax® mounting medium (MSZ EN
122 13946:2014). Identification was performed according to Krammer & Lange-Bertalot (1986–
123 1991), Krammer (2003) and Hofmann et al. (2011).

124

125 *Approaches of biological validation of the hydromorphological lake types*

126 There are two options for establishing lake types in which both hydromorphological and
127 biological characteristics of waters are considered (Fig. 1).

128 Option 1: during the implementation of the WFD one of the first steps is the establishment of
129 a water body typology. The typology proposed by the WFD has to be based on the broad scale
130 ecoregions, hydromorphological, physical and chemical characteristics of water bodies, and
131 thus, it can be considered as a top-down typology (Zenker and Baier 2009). This typology can
132 be simplified if biological characteristics of the hydromorphological types are compared
133 directly and types with no significant differences are merged. The disadvantage of this
134 approach is that biological homogeneity of the hydromorphological types is supposed *a priori*
135 (Mykrä et al. 2009), thus splitting off the hydromorphological types is not possible.

136 Option 2: when this option is applied the top-down typology is ignored because comparison
137 of the biological characteristics of lakes is done at lake (or site) level. During this process, the
138 whole lake population is separated into smaller groups in which lakes sharing similar
139 biological characteristics are pooled. This can be accomplished with a step by step process
140 (clustering), or with ordination techniques. This approach results in a so-called bottom-up
141 typology. These biological types have to be accommodated to the hydromorphological types.
142 Splitting of the hydromorphological types is feasible as long as it is corroborated by
143 biological evidences. During this study both options were combined.

144

145 *Statistical analyses*

146 Statistical analysis was based on species abundance data. Non-metric multidimensional
147 scaling (NMDS), using Bray-Curtis similarities, was applied for grouping of the
148 hydromorphological lake types (Option 1). In the second step this technique was applied to
149 data from entire lakes (Option 2). Statistical differences between the groups obtained by the
150 NMDS were tested by PERMANOVA (Anderson et al. 2008). Analysis was performed on
151 site level. The proposed biologically validated lake types were characterised by the diatom
152 species using Similarity percentage analysis (SIMPER; Clark 1993). SIMPER is a
153 multivariate, exploratory method that assesses the contribution of each taxon to the Bray-
154 Curtis dissimilarities between contrasted groups. Statistical analysis was performed using
155 PAST package (Hammer et al. 2001).

156 Species diversity was calculated by the Shannon formula (1948). The trophic state of the
157 proposed types was characterised by the trophic metric of the OMNIDIA software (Lecointe
158 et al. 1993) using the range zero to twenty. The highest values indicate lower trophic
159 conditions. The significance of the differences in diversity and TID values were tested by the
160 Kruskal-Wallis test. Analysis was done on a sample level.

161

162

163 **Results**

164 *Establishment of the biologically validated lake types*

165 Ordination of the hydromorphological lake types resulted in two distinct groups (Fig. 2). The
166 group of high salinity lakes (with Na⁺ and Mg²⁺ dominance) and the moderate salinity (Ca²⁺
167 dominated) lakes clearly separated from each other according to diatom composition
168 (Permanova of Bray-Curtis similarity p < 0.05). Further separation of the two subgroups was
169 based on site level data (Option 2). The NMDS ordination of the site level data displays two

170 groups in the moderate (Fig. 3) ($p < 0.05$), and three groups in the high salinity lakes (Fig. 4).
171 Diatom assemblages of Lake Balaton differed significantly from that of the other Ca^{2+}
172 dominated lakes (Fig. 3). Within the groups of high salinity lakes the following three groups
173 could be distinguished: 1. large steppe lakes (Lake Velencei and Lake Fertő), 2. Na^+
174 dominated perennial saline lakes, and 3. Na^+ dominated astatic saline lakes (PERMANOVA p
175 < 0.05) (Fig. 4). The proposed five bottom-up types could be accommodated to the
176 hydromorphological lake types (Table 1 and 2). Species characteristics for the given lake
177 types (identified by SIMPER analysis) are shown in Tables 3, 4 and 5. (Physical and chemical
178 characteristics of the proposed lake types are shown in Table 6.)

179

180 *Characterisation of the lake types*

181 Significant differences were found in the Shannon diversity values between the astatic [4] and
182 perennial [5] high salinity lakes (Fig. 5). The highest values were observed in the case of the
183 perennial lakes, while the lowest ones in the group of astatic lakes. Diversity of the large
184 steppe lakes Fertő and Lake Velencei (3rd biological type) did not show differences from the
185 others, and the values fell in the middle range of diversity (Fig. 5). In the two groups of
186 calcareous lakes (Balaton [1] and others [2]) differences in diversity could also be
187 demonstrated ($p < 0.05$) (data not shown).

188 The low values of the trophic metrics indicate that lakes in the Carpathian basin are eutrophic
189 or hypertrophic. Differences in the distribution of the trophic metric scores have also been
190 shown both for the moderate and high salinity lakes (Fig. 6). In the group of moderate salinity
191 calcareous lakes, metric scores calculated for Lake Balaton [1] samples were significantly
192 higher than those characterised in the other [2] calcareous lakes.

193 Significant differences were also found in the trophic metric scores among the three proposed
194 groups of high salinity lakes (Fig. 6). The lowest values were characteristic for the astatic
195 saline lakes [4], while the highest scores were obtained for the large steppe lakes (Fertő and
196 Lake Velencei [3]). Trophic scores of the perennial high salinity lakes [5] appeared to be
197 between the values of the two above mentioned types.

198

199 **Discussion**

200 *Establishment of the biologically validated lake types*

201 NMDS ordination of the species abundance data resulted in a clear and consistent distinction
202 between the highly saline sodium and magnesium dominated lakes and moderate salinity
203 calcareous ones. This result is consistent with that obtained in a recent study which was based

204 on the analysis of phytoplankton (Borics et al. 2014). Diatom flora of high salinity lakes
205 consists of species with wide ecological valence that enables their survival in extreme
206 environmental conditions (Hecky & Kilham 1973). In the highly saline lakes of the
207 Carpathian Basin species are subject to various types of extremities, such as high salt content
208 and high organic and inorganic load (Stenger-Kovács et al. 2014, Boros et al. 2006).
209 However, we note that from the present analysis separation of these extremities cannot be
210 made.

211 Separation of the two types of the moderate salinity calcareous lakes (Balaton and others) can
212 be explained partly by the trophic differences and partly by the unique microflora of the
213 Balaton (Bolla et al. 2010).

214 In the literature on saline lakes several halophilic species are mentioned such as *Nitzschia*
215 *frustulum*, *Rophalodia brebissonii*, *Halamphora veneta* (Hecky & Kilham 1973, Silva et al.
216 2010, Stenger-Kovács et al. 2014) and these taxa were also characteristic in the studied high
217 salinity lakes. However microflora of the lakes belonging to the highly saline lake group
218 appeared to be similar but the abundance of these taxa was remarkably different in the three
219 lake types (Table 5). These differences in abundance values are responsible for the separation
220 of the lake groups rather than unique species that might occasionally occur in one of the lake
221 groups.

222

223 *Characterisation of the lake types*

224 Although earlier it was believed that diversity of algae in eutrophic lakes is usually lower than
225 that of oligotrophic ones (Moss 1973), experimental studies proved that diversity is influenced
226 by the fluctuation of resources rather than the quantity of them (Sommer 1984). Both
227 experimental (Carrick et al. 1988) and field studies (Leira et al. 2009) demonstrated that
228 nutrient enrichment narrows the niche of some sensitive benthic diatom taxa, but
229 simultaneously creates favourable conditions for many specialised species. However, low
230 diversity values might be related to natural processes such as grazing or other disturbances
231 (DeNicola and Kelly, 2014). This means that higher nutrient concentration does not
232 necessarily coincide with decreasing species diversity. Therefore, the higher diversity
233 observed in the case of Lake Balaton, as compared to other calcareous lakes, cannot be
234 explained by its lower nutrient content. Results on the species/area relationship for algae
235 revealed the importance of lake size as a control of diversity (Bolgovics et al. 2016, Borics et
236 al. 2016), therefore the size differences between Lake Balaton and the other considerably
237 smaller lakes may be responsible for the observed differences of diversity.

238 The astatic/perennial distinction which was observed for Shannon diversity within the group
239 of saline lakes has also been demonstrated for the phytoplankton (Borics et al. 2014), which
240 indicates that desiccation puts a stress on both planktonic and benthic algae and thus coincides
241 with a decrease in diversity (Borics et al. 2013). In the group of high salinity lakes significant
242 differences in diversity were attributable to the very low values found in the astatic lake
243 group. In this group the biota is exposed to double stress i.e., desiccation of the lake basin,
244 and the extremely large salt content. Both phenomena exert strong selective pressure on the
245 species pool of the lakes, and results in very low Shannon diversity and species richness
246 values in pristine soda pans (Stenger-Kovács et al. 2016).

247 Desiccation means that for a considerable period of time the lake bed becomes a terrestrial
248 habitat where algae are subjected to heat and osmotic stress (Souffreau et al. 2010), and only
249 those taxa can survive which have special adaptations (i.e., migration, production of
250 extracellular polysaccharids) (McKew et al. 2011). Even in those periods when water is
251 present in the lake basin diatoms are under strong selection to adapt to pressures that the high
252 salinity and the dominance of sodium exert on them (Hecky & Kilham 1973).

253 The results of the characterisation of the nutrient status of lakes by trophic scores is in
254 accordance with that of a previous study (Borics et al. 2014) which suggest, that lakes in the
255 Carpathian Basin are in the mesotrophic – hypertrophic range. An elevated trophic state is
256 especially common in this group of saline lakes, because these lakes are endorheic (without
257 outlet). Their water cannot leave the lake basin and are continuously enriched with nutrients
258 mostly because of the birds which use the lakes for feeding and roosting (Boros et al. 2006).

259

260

261 **Conclusions**

262 The remarkable floristic and compositional differences in the benthic diatom flora of the
263 studied shallow lakes in Hungary enabled the separation of five bottom–up lake types. These
264 types could be clearly assigned to hydromorphological types, and this resulted in a rational
265 simplification of the hydromorphological typology. These results are in accordance with those
266 of previous studies which were based on the analysis of phytoplankton (Borics et al. 2014)
267 and of aquatic macrophytes (Lukács et al. 2015).

268

269

270

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274

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428 **Legends for figures and tables**

429

430 Fig. 1 Scheme of the applied biological validation options. The upper arrow indicates how the
431 17 hydromorphological lake types were established using a top–down approach.

432 Fig. 2 Nonmetric multidimensional scaling (NMDS) ordination of the hydromorphological
433 lake types (Ordination is based in the Bray-Curtis distances among the types).

434 Fig. 3 Nonmetric multidimensional scaling (NMDS) ordination of the sites belonging to the
435 groups of moderate salinity calcareous lakes.

436 Fig. 4 Nonmetric multidimensional scaling (NMDS) ordination of the sites belonging to the
437 groups of high salinity sodium and magnesium dominated lakes.

438 Fig. 5 Distribution of the Shannon diversity values in the five proposed biologically validated
439 types.

440 Fig. 6 Distribution of the trophic metric scores in the five proposed biologically validated
441 types.

442

443 Table 1 Hydromorphological lake types proposed for Hungary and the applied type descriptor
444 variables.

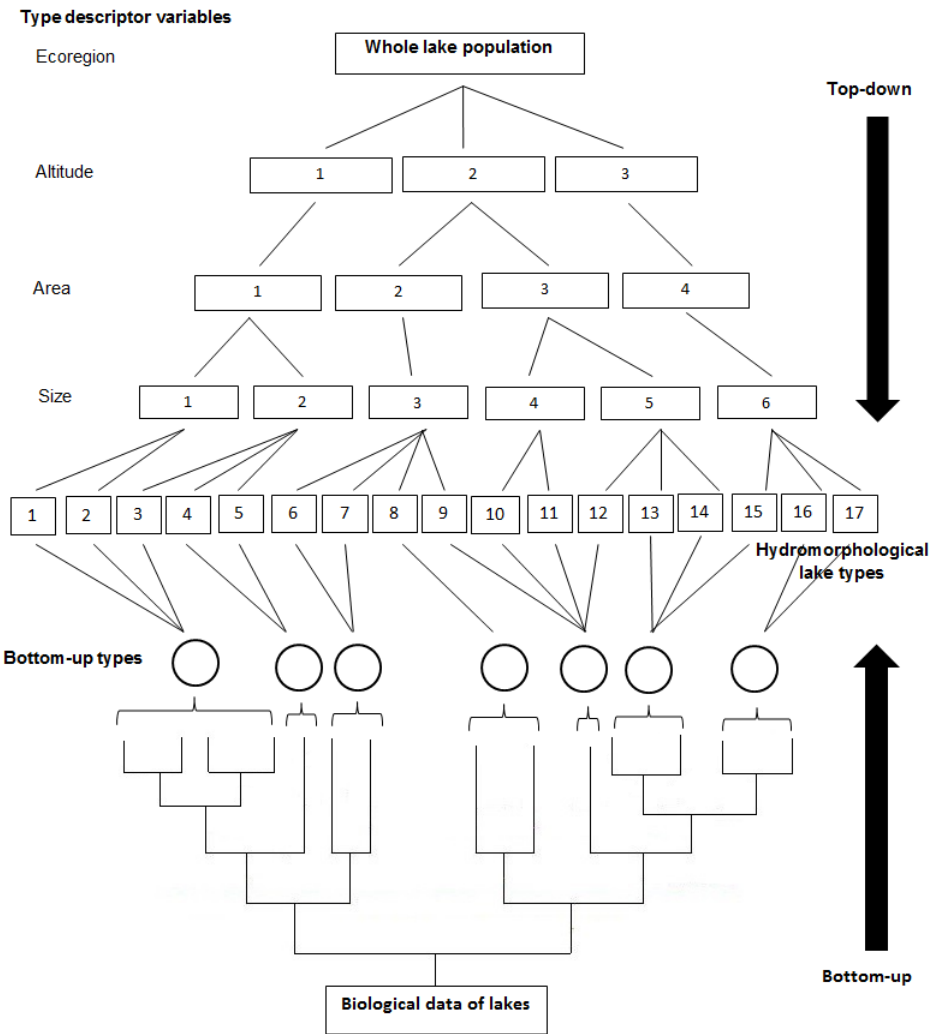
445 Table 2 Assignment of biological lake types to hydromorphological types.

446 Table 3 SIMPER analysis results showing taxa contributing to 25% of the total similarity
447 within the groups of moderate and high salinity lakes.

448 Table 4 SIMPER analysis results showing taxa contributing to 25% of the total similarity
449 within the groups of Balaton and other calcareous lakes.

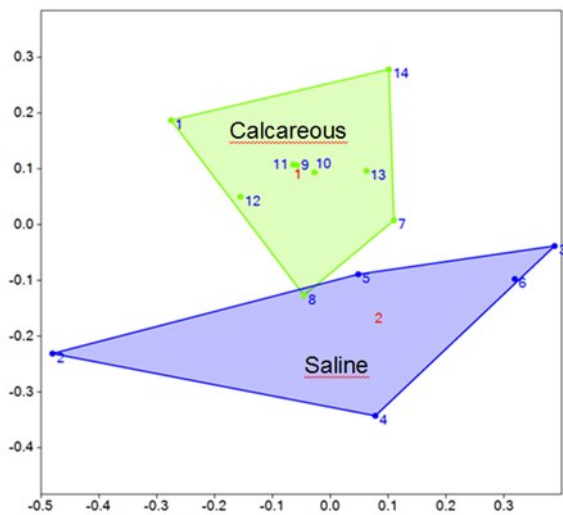
450 Table 5 SIMPER analysis results showing taxa contributing to 25% of the total similarity
451 within the three groups of high salinity lakes.

452 Table 6 Physical and chemical characteristics of proposed lake types.



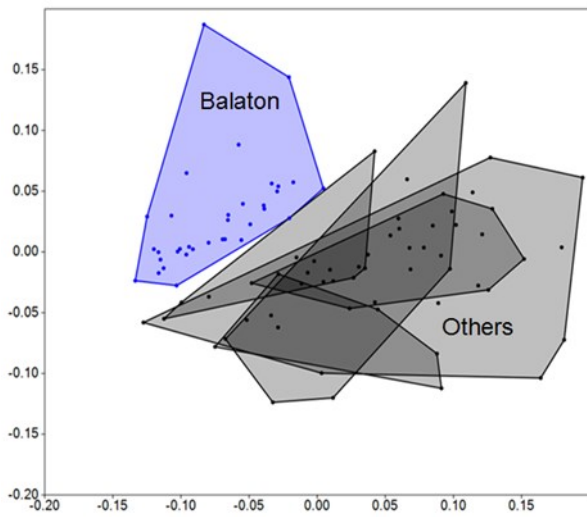
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454 Fig.1.



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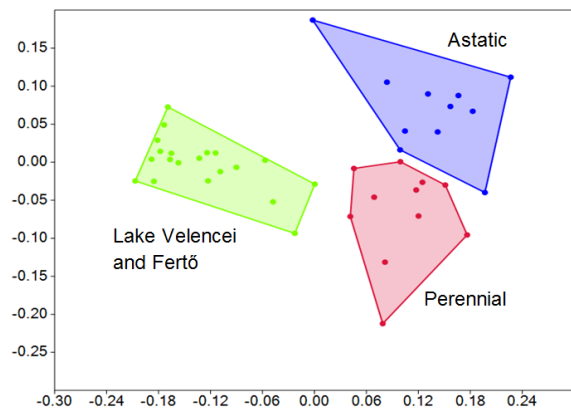
456 Fig.2.



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458 Fig.3.

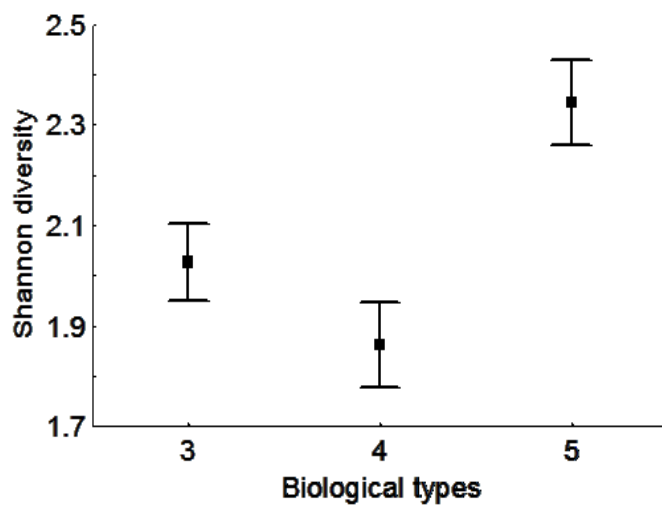
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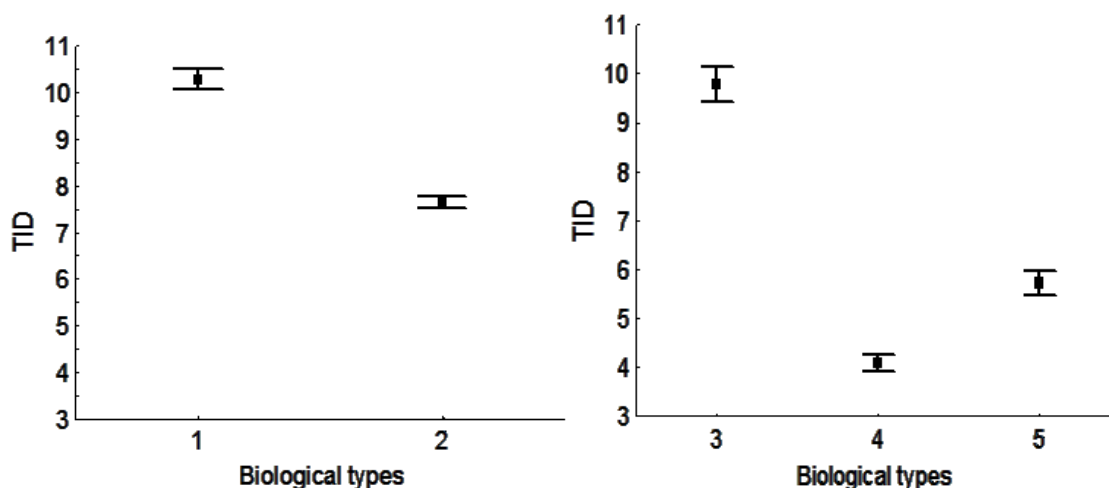
461 Fig.4.

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464 Fig.5.



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468 Fig.6.

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470

471 Table 1

Type	Altitude (m)	Hydrochemical character	Size (km ²)	Average depth (m)	Water regime	Biological types
1	< 200 m (lowland)	moderate salinity	> 10 (km ²)	> 3-6 m	perennial	1
2	< 200 m (lowland)	high salinity	> 10 (km ²)	< 3m	perennial	3
3	< 200 m (lowland)	high salinity	1- 10 (km ²)	< 1m	astatic	5
4	< 200 m (lowland)	high salinity	1- 10 (km ²)	< 3m	perennial	4
5	< 200 m (lowland)	high salinity	< 1 (km ²)	< 3m	perennial	4
6	< 200 m (lowland)	high salinity	< 1 (km ²)	< 1m	astatic	5
7	< 200 m (lowland)	moderate salinity	1- 10 (km ²)	< 3m	perennial	2
8	< 200 m (lowland)	moderate salinity	< 1 (km ²)	< 3m	perennial	2
9	< 200 m (lowland)	moderate salinity	1- 10 (km ²)	< 3m	perennial	2
10	< 200 m (lowland)	moderate salinity	1- 10 (km ²)	3-6 m	perennial	2
11	< 200 m (lowland)	moderate salinity	< 1 (km ²)	< 3m	perennial	2
12	< 200 m (lowland)	moderate salinity	< 1 (km ²)	< 3m	perennial	2
13	< 200 m (lowland)	moderate salinity	> 10 (km ²)	< 3m	perennial	2
14	< 200 m (lowland)	moderate salinity	> 10 (km ²)	< 3m	perennial	2
15	> 200 m (hill country)	moderate salinity	> 10 (km ²)	< 3m	perennial	2
16	> 200 m (hill country)	moderate salinity	> 10 (km ²)	< 1m	astatic	2
17	< 200 m (lowland)	moderate salinity	<1; 1-10 (km ²)	< 3m	astatic	2

472

473

474 Table 2

Codes of the proposed biological lake types	Names of the proposed biological lake types	Codes of the hydromorphological lake types
1	Balaton	1
2	Others	7,8,9,10,11,12,13,14,15,16,17
3	Lake Velencei and Fertő	2
4	Perennial	3,6
5	Astatic	4,5

475

476

477 Table 3

Taxon	DENOM	Av. dissim	Contribution (%)	Cumulative (%)	Moderate salinity	High salinity
ADMI	<i>Achnanthydium minutissimum</i> (Kützing) Czamecki 1994	1.786	2.532	2.532	12.1	9.87
NIS1	<i>Nitzschia</i> sp. Hassall 1845	1.726	2.446	4.978	6.32	7.93
EADN	<i>Epithemia adnata</i> (Kützing) Brébisson 1838	1.435	2.033	7.011	6.11	6.86
HVEN	<i>Halamphora veneta</i> (Kützing) Levkov 2009	1.381	1.958	8.969	2.24	10.8
RHOS	<i>Rhopalodia</i> species Müller 1895	1.24	1.757	10.73	0.561	7.87
NCLA	<i>Nitzschia clausii</i> Hantzsch 1860	1.182	1.675	12.4	0.284	8.19
NACI	<i>Nitzschia acicularis</i> (Kützing) W.Smith 1853	1.128	1.598	14	2.16	6.66
RBRE	<i>Rhopalodia brebissonii</i> Krammer in Lange-Bertalot & Krammer 1987	1.084	1.537	15.54	0.0606	7.89
NHAN	<i>Nitzschia hantzschiana</i> Rabenhorst 1860	0.8474	1.201	16.74	1.93	4.96
NLBT	<i>Nitzschia liebetruthii</i> var. <i>liebetruthii</i> Rabenhorst 1864	0.8303	1.177	17.91	1.45	6.98
CPLI	<i>Cocconeis placentula</i> Ehrenberg 1838	0.7983	1.131	19.05	3.48	5.33
ETUR	<i>Epithemia turgida</i> (Ehrenberg) Kützing 1844	0.7315	1.037	20.08	1.22	4.76
RGIB	<i>Rhopalodia gibba</i> var. <i>gibba</i> (Ehrenberg) Otto Müller 1895	0.7259	1.029	21.11	1.65	5.77
COCE	<i>Cyclotella ocellata</i> Pantocsek 1901	0.6806	0.9646	22.08	5.07	0.0436
SCON	<i>Stausosira construens</i> Ehrenberg 1843	0.6416	0.9094	22.99	3.36	3.73
AMIN	<i>Achnanthes minutissima</i> Kützing 1833	0.6384	0.9048	23.89	4.72	0
CPLA	<i>Cocconeis placentula</i> var. <i>placentula</i> Ehrenberg 1838	0.6314	0.8949	24.79	5.2	2.38
NIPU	<i>Nitzschia pusilla</i> Grunow 1862	0.6239	0.8842	25.67	0.467	4.48
APED	<i>Amphora pediculus</i> (Kützing) Grunow ex A.Schmidt 1875	0.6048	0.8572	26.53	5.94	2.4
GAFF	<i>Gomphonema affine</i> Kützing 1844	0.6013	0.8523	27.38	2.6	3.66
NDIS	<i>Nitzschia dissipata</i> var. <i>dissipata</i> (Hantzsch) Grunow in Van Heurck 1881	0.5676	0.8045	28.18	4.07	0.647
CYDE	<i>Cyclotella delicatula</i> Hustedt 1952	0.5664	0.8027	28.99	3.97	0
NPAL	<i>Nitzschia palea</i> (Kützing) W.Smith 1856	0.5085	0.7207	29.71	3.27	5.02
EBLU	<i>Eunotia bilunaris</i> (Ehrenberg) Schaarschmidt in Kanitz 1880	0.4995	0.708	30.41	2.28	3.17
LGOE	<i>Luticola goeppertiana</i> (Bleisch ex Rabenhorst) D.G.Mann in Round,	0.4962	0.7033	31.12	3.73	0.161
SHAN	<i>Stephanodiscus hantzschii</i> Grunow in Cleve & Grunow 1880	0.4768	0.6757	31.79	3.3	0.363
ESOR	<i>Epithemia sorex</i> Kützing 1844	0.4741	0.672	32.47	4.01	2.78
NISO	<i>Nitzschia solita</i> Hustedt 1953	0.4674	0.6625	33.13	0.234	3.4
AINA	<i>Amphora inariensis</i> Krammer 1980	0.4579	0.649	33.78	3.44	0.735
NRCS	<i>Navicula recens</i> (Lange-Bertalot) Lange-Bertalot in Krammer & Lange-Bertalot	0.4503	0.6382	34.42	0.593	3.21
NIPM	<i>Nitzschia perminuta</i> (Grunow) M.Peragallo 1903	0.4379	0.6207	35.04	1.19	3.85
GINA	<i>Gomphonema insigne</i> W.Gregory 1856	0.4373	0.6197	35.66	3.31	0.82
ADEU	<i>Achnanthydium eutrophilum</i> (Lange-Bertalot) Lange-Bertalot 1999	0.4327	0.6133	36.27	1.35	2.67
NVEN	<i>Navicula veneta</i> Kützing 1844	0.4302	0.6097	36.88	1.16	3.87
MAAT	<i>Mayamaea atomus</i> (Kützing) Lange-Bertalot 1997	0.4149	0.5881	37.47	1.4	2.49
NAMP	<i>Nitzschia amphibia</i> f. <i>amphibia</i> Grunow 1862	0.4104	0.5816	38.05	2.47	4.7

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479

480 Table 4

	Taxon	DENOM	Av. dissim	Contribution (%)	Cumulative (%)	Balaton	Others
1	ADMI	<i>Achnanthydium minutissimum</i> (Kützing) Czamecki 1994	8.694	10.68	10.68	33.4	13.8
2	CEXI	<i>Cymbella exigua</i> Krammer 2002	2.367	2.907	13.58	7.1	0
3	APED	<i>Amphora pediculus</i> (Kützing) Grunow ex A.Schmidt 1875	2.068	2.54	16.12	2.13	7.12
4	NDIS	<i>Nitzschia dissipata</i> (Kützing) Rabenhorst 1860	1.585	1.946	18.07	5.07	1.71
5	GPUM	<i>Gomphonema pumilum</i> (Grunow) E.Reichardt & Lange-Bertalot 1991	1.364	1.675	19.74	4.22	0.481
6	COCE	<i>Cyclotella ocellata</i> Pantocsek 1901	1.326	1.628	21.37	1.41	3.22
7	ESOR	<i>Epithemia sorex</i> Kützing 1844	1.238	1.52	22.89	1.36	3.17
8	FHUN	<i>Fragilaria hungarica</i> Pantocsek 1901	1.223	1.502	24.39	4.05	0
9	CPLI	<i>Cocconeis placentula</i> Ehrenberg 1838		1.399	25.79	1.63	3.77
10	ECPM	<i>Encyonopsis minuta</i> Krammer & E.Reichardt in Krammer 1997	1.106	1.359	27.15	2.09	2.1
11	NCTE	<i>Navicula cryptotenella</i> Lange-Bertalot in Krammer & Lange-Bertalot 1985	1.046	1.285	28.44	3.11	3.75
12	ENCM	<i>Encyonopsis microcephala</i> (Grunow) Krammer 1997	0.9935	1.22	29.66	2.98	0
13	EADN	<i>Epithemia adnata</i> (Kützing) Brébisson 1838	0.9336	1.146	30.8	0.208	3.07
14	SGRI	<i>Staurosira grigorszkyi</i> Ács, Morales & Ector in Ács et al. 2009	0.8726	1.072	31.87	2.87	0
15	HVEN	<i>Halumphora veneta</i> (Kützing) Levkov 2009	0.8714	1.07	32.94	0.0442	2.61
16	DMON	<i>Diatoma moniliformis</i> (Kützing) D.M.Williams 2012	0.8519	1.046	33.99	2.71	0.305
17	SBRV	<i>Staurosira brevistriata</i> (Grunow) Grunow 1884	0.8301	1.019	35.01	1.48	1.35
18	GOMS	<i>Gomphonema species</i> Ehrenberg 1832	0.8287	1.018	36.03	2.69	0.332
19	GOST	<i>Gomphonema olivaceum var. staurophorum</i> Pantocsek 1889	0.7915	0.9719	37	2.42	0
20	UUAC	<i>Ulnaria ulna</i> (Nitzsch) Compère in Jahn et al. 2001	0.7913	0.9717	37.97	0.978	1.95

481

482 Table 5

	Taxon	DENOM	Av. dissim	Contribution (%)	Cumulative (%)	Velencei -Fertő	Small astatic	Small high salinity perennial
1	ADMI	<i>Achnanthydium minutissimum</i> (Kützing) Czamecki 1994	7.935	8.91	8.91	176	6.46	15.3
2	HVEN	<i>Halumphora veneta</i> (Kützing) Levkov 2009	5.095	5.72	14.63	0.945	130	50.5
3	NCLA	<i>Nitzschia clausii</i> Hantzsch 1860	4.308	4.837	19.47	0	139	0.182
4	GPAR	<i>Gomphonema parvulum</i> (Kützing) Kützing 1849	3.573	4.011	23.48	1.46	89.4	35.3
5	CPLI	<i>Cocconeis placentula</i> Ehrenberg 1838	3.107	3.488	26.97	53.8	27	4.68
6	NPAL	<i>Nitzschia palea</i> (Kützing) W.Smith 1856	2.412	2.709	29.68	3.5	43.5	53.3
7	NLBT	<i>Nitzschia liebetruithii var. liebetruithii</i> Rabenhorst 1864	2.402	2.697	32.37	3.58	58.5	24.8
8	NIPU	<i>Nitzschia pusilla</i> Grunow 1862	2.142	2.405	34.78	0.2	72.8	2.05
9	RGIB	<i>Rhopalodia gibba</i> (Ehrenberg) Otto Müller 1895	2.081	2.337	37.11	12.4	2.85	56.4
10	EADN	<i>Epithemia adnata</i> (Kützing) Brébisson 1838	1.693	1.901	39.01	3.24	2.24	47.3
11	CMEN	<i>Cyclotella meneghiniana</i> Kützing 1844	1.625	1.824	40.84	1.17	20.5	36
12	ACHD	<i>Achnanthydium</i> F.T. Kützing	1.549	1.739	42.58	42.3	0	0
13	NIGR	<i>Nitzschia gracilis</i> Hantzsch 1860	1.545	1.735	44.31	1.88	1.33	52.1
14	NINC	<i>Nitzschia inconspicua</i> Grunow 1862	1.453	1.631	45.94	1.49	22.3	32.5
15	NAMP	<i>Nitzschia amphibia f. amphibia</i> Grunow 1862	1.367	1.535	47.48	6.71	14.7	31.7
16	NIFR	<i>Nitzschia frustulum var. frustulum</i> (Kützing) Grunow in Cleve & Grunow 1880	1.329	1.492	48.97	7.81	15.2	30.8
17	ESBM	<i>Eolimna subminuscula</i> (Manguin) Gerd Moser, Lange-Bertalot & Metzeltin 1998	1.325	1.487	50.46	0.275	5.94	33.3
18	ESOR	<i>Epithemia sorex</i> Kützing 1844	1.118	1.255	51.71	10.8	1.23	28.5
19	ADEU	<i>Achnanthydium eutrophilum</i> (Lange-Bertalot) Lange-Bertalot 1999	1.087	1.22	52.93	2.05	46.4	0.727
20	NCRY	<i>Navicula cryptocephala</i> Kützing 1844	1.087	1.22	54.15	1.32	24.7	7.67

483

484

485 Table 6

Type	1			2			3			4			5		
	n	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	21	718	6	157	647	25	27	2547	100	19	1930	142	38	5199	480
pH	24	8.5	0	139	8.02	0	6	8.56	0	19	8.63	0	37	9.13	0
Total phosphorus ($\mu\text{g}\cdot\text{l}^{-1}$)	24	48	3	152	175	18	30	71	4	19	695	243	38	4680	623
Total nitrogen ($\mu\text{g}\cdot\text{l}^{-1}$)	24	906	18	151	1583	96	30	2091	112	18	4719	992	38	10652	2058
Magnesium ($\text{mg}\cdot\text{l}^{-1}$)	24	61	1	35	37	4	30	214	11	18	64	7	30	23	4
Sodium ($\text{mg}\cdot\text{l}^{-1}$)	24	41	1	47	49	6	30	335	16	18	369	43	31	1222	127
Calcium ($\text{mg}\cdot\text{l}^{-1}$)	24	40	1	47	52	2	30	30	2	18	32	3	30	22	2
Potassium ($\text{mg}\cdot\text{l}^{-1}$)	24	8	1	47	7	1	30	48	2	18	20	3	31	17	3

486