

Characteristics of the pelagic phytoplankton in shallow oxbows

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Abstract Numerous oxbows of different sizes, depths and ages accompany alluvial rivers in the Carpathian basin. These water bodies provide various habitats for macroscopic and microscopic assemblages. Phytoplankton of 13 oxbows in the Tisza valley was studied between 2005 and 2008. In this article, we focussed on the following questions (i) do the oxbows have unique microflora? (ii) does the macrophyte coverage have a large effect on the composition and biomass of the algal assemblages? and (iii) does the higher plants dominated state result

in clear-water conditions in the oxbows? The studied oxbows were in different stages of the ageing process. We classified the sampled oxbows according to their macrophyte vegetation into five types. A total of 646 species of algae were recorded in the oxbows over the study period. The microflora was dominated by cyanophytes, chlorococcalean green algae, euglenophytes and diatom species. Phytoplankton species were allocated into 32 coda. For the determination of typical algal assemblages, we used Kohonen's Self Organizing Map (SOM) statistical analysis combined with *K*-means clustering, which has resulted five different types of phytoplankton associations. These types were dominated by coda **Y**, **L₀**, **W1**, **W_S** and **J**. Chlorophyll *a* data of the sparsely and densely vegetated oxbows did not differ, since a wide range of values characterised both types of the lakes. In this study, the composition of the microflora is similar to that of other eutrophic lakes, but some rarely occurring taxa such as *Peridinium gatunense* Nygaard and *Peridiniopsis elpatiewskyi* (Ostenf.) Bourrelly might play a key role in the phytoplankton succession of the oxbows. The effect of the macrophyte coverage was decisive in the composition of the algal assemblages, and our investigations indicated that, in the case of the oxbows, the macrophyte-dominated state does not necessarily result in a clear-water state.

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Introduction

Large- and medium-sized rivers, flowing across a flat area, are meandering. Over time, the meanders grow and develop into enormous loops. Eventually, during the flood periods, rivers break through the base of the loops (avulsion), cut off the meanders, and leave the curves behind as oxbow lakes. In addition to this natural process, man-made interventions can also result in the development of oxbows. The number of the oxbows created by the engineering and the natural processes exceeds 300 in the Carpathian basin (Pálfai, 2003). These lakes undergo a gradual ageing process (frequently referred as hydroséries in succession studies) that ultimately converts them into wetlands and then to terrestrial biotops. During the senescence of shallow basins the microflora undergoes considerable changes parallel with the macrophyte succession. Van den Berg et al. (1998) demonstrated the changes of the phytoplankton composition along a transect from the centre of a *Chara* stand to the open water. Development of extended macrophyte stands results in a number of physical, chemical and biological changes. Macrophytes reduce nutrient concentrations, shade the water column, increase sedimentation rate (Hasler and Jones, 1949), provide refuges for zooplankton grazers (Jeppesen et al., 1997) and release allelopathically active compounds (Gopal and Goel, 1993; Gross, 1999; Körner and Nicklisch, 2002). These changes result in lower phytoplankton biomass and induce changes in the composition of the microflora. In addition, macrophyte stands represent microhabitats and increase overall biodiversity (Borics et al., 1998, 2003). Possible impacts of the macrovegetation on the phytoplankton are well documented in the literature (Scheffer, 1998; Lau and Lane, 2002; Takamura et al., 2003; Qin et al., 2006); however, the general features of the long-term succession of algae in shallow, rapidly ageing ecosystems have not been studied in detail.

Our aim was to investigate how different macrophyte coverages influence the phytoplankton (both the composition and biomass) in the pelagial region of oxbow lakes. Phytoplankton of shallow oxbows with similar nutrient concentrations, but with different macrophyte vegetations, was studied.

The specific hypotheses of this study are that (i) the oxbows, as compared with other shallow lakes,

have a unique microflora, (ii) the macrophyte coverage has a great effect on the composition and biomass of the algal assemblages in the open water areas, (iii) as argued by the alternative equilibrium hypothesis (Scheffer et al., 1993), the plant-dominated state results in clear-water conditions in the oxbows.

Materials and methods

The investigated 13 oxbows are located in the Tisza valley, East Hungary (Fig. 1). Some physical and chemical characteristics of oxbows are shown in Tables 1 and 2.

For phytoplankton and water-chemical analyses, samples were taken with a tube sampler at the deepest part of the lakes monthly (except Tiszaugi-Holt-Tisza, Holt-Szamos Géberjén and Tunyogmatolcs) from May 2005 to October 2008. In shallow oxbows ($Z_{\max} < 2$ m) the whole water column was sampled; in the deeper ones we took samples from the epilimnion. All samples were collected from the unvegetated sites; therefore, differences in the illumination were negligible.

Water temperature, pH and conductivity were recorded in situ. Transparency was measured by a Secchi disc [Secchi disc visibility depth (Zsd)]. Analyses of nitrate-nitrogen, nitrite-nitrogen, ammonium-nitrogen, soluble reactive phosphorus (SRP),

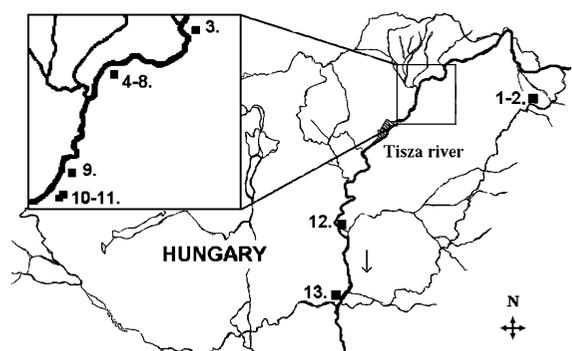


Fig. 1 Sampling sites: 1 Holt-Szamos Géberjén, 2 Holt-Szamos Tunyogmatolcs, 3 Szöglegelői-Holt-Tisza, 4 Szűcs-Tisza, 5 Malom-Tisza (pelagial part), 6 Malom-Tisza. part of floating island, 7 Falu-Tisza, 8 Darab-Tisza, 9 Miskafoki-Holt-Tisza, 10 Morotvaközi-Holt-Tisza, 11 Egyeki-Holt-Tisza, 12 Tiszaugi-Holt-Tisza, 13 Atkai-Holt-Tisza. Arrow shows the flow of the river

Table 1 Physical characteristics of the studied oxbows

Name	Geographic coordinates	Surface area (ha)	Mean depth (m)	Max depth/ depth of sampling point	Type	Macrophyte's cover (%)	Species number/ sample number
Miskafoki-Holt-Tisza	47°43'14" N 20°59'53" E	25	0.9	1/0.5	I	~10	124/9
Atkai-Holt-Tisza	46°22'58" N 20°11'50" E	83	3.5	2	II	~10	99/14
Falu-Tisza	48°01'15" N 21°11'10" E	23	3.6	4/2	II	~5	237/20
Holt-Szamos Géberjén	47°56'02" N 22°28'07" E	100	1.5	2/2	II	~5	152/7
Holt-Szamos Tunyogmatolcs	47°56'52" N 22°25'49" E	125	3.1	3.5/2	II	~5	159/7
Malom-Holt-Tisza (pelagical part)	48°01'14" N 21°11'27" E	30	3.5	10/2	II	~5	230/19
Tiszaugi-Holt-Tisza	46°51'46" N 20°03'10" E	50	2.3	2	II	~10	50/4
Darab-Tisza	48°01'18" N 21°11'17" E	9	1.7	2.5/1	III	~50	260/21
Egyeki-Holt-Tisza	47°38'32" N 20°52'19" E	40	1.5	2/1	IV	~80	172/22
Szűcs-Tisza	48°01'17" N 21°13'26" E	10	2.0	2/1	IV	~60	248/18
Morotvaközi-Holt-Tisza	47°39'51" N 20°56'57" E	71	1.4	2/1.4	IV	~80	127/16
Szöglegelői-Holt-Tisza	48°04'16" N 21°27'38" E	20	1.0	1.5/1	IV	~90	97/6
Malom-Holt-Tisza (part of floating island)	48°00'44" N 21°12'29" E	8	2.0	2/1	V	~80	308/19

total phosphorus (TP) and chlorophyll *a* were carried out according the Hungarian national guidelines (MSZ 12750-17:1974; MSZ 448-12:1982; MSZ ISO 7150-1:1992).

Phytoplankton samples were fixed with Lugol's solution. A minimum of 400 settling units per sample were counted with the LEICA DMIL-inverted microscope (Utermöhl, 1958). Phytoplankton biomass was calculated from biovolume data using appropriate geometric formulas, using Opticount programme (Opticount, 2008).

Uniqueness of the microflora has been evaluated by comparing our taxa list with that of the Hungarian Red List of Algae (Németh, 2005) and with other documented occurrences of the species published in national identification manuals (Uherkovich, 1995;

Németh, 1997a, b; Schmidt and Fehér, 1998, 1999, 2001; Grigorszky et al., 1999). Those species deemed to unique, which, according to the literature, occur principally in the oxbows. Functional groups were defined according to Reynolds et al. (2002) and Padisák et al. (2006, 2009).

The Kohonen's Self Organizing Map (SOM) was used to determine the typical algal assemblages (Kohonen, 2001; Park et al., 2003). For its ecological applications, we refer to Lek and Guégan (2000). SOM makes a projection of the data into a two-dimensional hexagonal map. Closely related communities are placed into neighbouring hexagons by their similarities, whereas samples with different communities are in distant hexagons. The SOM can display the groupings of samples and species together; therefore, each

Table 2 Chemical characteristics of the studied oxbows

Name	Secchi depth (m)		Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)		TIN ($\mu\text{g l}^{-1}$)		TP ($\mu\text{g l}^{-1}$)		SRP ($\mu\text{g l}^{-1}$)	
	Min–max	Mean	Min–max	Mean	Min–max	Mean	Min–max	Mean	Min–max	Mean
Miskafoki-Holt-Tisza	–	–	–	–	200–330	260	–	–	50–60	55
Atkai-Holt-Tisza	–	–	2.4–49	13.8	220–380	245	60–1070	340	–	–
Falu-Tisza	0.5–1.6	0.91	3.9–75.5	26.0	50–950	330	40–9450	692	3–50	20
Holt-Szamos Géberjén	0.6–0.9	0.72	14.5–62.5	35.0	50–1510	370	190–1660	557	20–270	140
Holt-Szamos Tunyogmatolcs	0.45–1.2	0.89	9.4–38.3	23.7	110–380	280	290–1510	654	110–690	361
Malom-Holt-Tisza (pelagical part)	0.8–2.5	1.34	4.1–70.2	19.8	50–990	320	30–2290	318	8–340	34
Tiszaugi-Holt-Tisza	–	–	41.0–610.0	390.0	220–480	290	50–460	287	50–140	87
Darab-Tisza	0.6–1.5	1.0	1.4–114.6	16.2	30–870	280	30–2160	320	7–160	25
Egyeki-Holt-Tisza	0.32–1.05	0.65	1.1–154.1	33.7	120–700	330	50–1860	507	10–130	33
Szűcs-Tisza	0.6–1.9	1.3	4.5–133.8	22.7	50–760	240	50–2430	236	3–100	21
Morotvaközi-Holt-Tisza	0.3–1.35	0.56	0.5–160.6	27.8	180–860	410	10–4140	712	11–750	63
Szöglegelői-Holt-Tisza	0.6–0.7	0.65	1.5–27.5	10.5	110–760	320	60–580	331	30–120	62
Malom-Tisza. part of floating island	1.0–2.1	1.46	2.3–44.9	17.4	60–650	260	40–1360	240	8–350	35

species can be evaluated by its importance. The SOM Toolbox was used to implement the SOM under a MATLABs environment; the numbers of virtual units were determined according to Vesanto (2000) as $nVU = 5\sqrt{nS}$, where nVU , the number of virtual units and nS , the number of samples.

For clustering the SOM we used the *K*-means clustering technique, which is an algorithm to classify objects based on their attributes (in this case codon composition) into *K* number of group. The grouping is done by minimizing the sum of squares of distances between data and the corresponding cluster centroid as the square error of each data point is calculated and clusters reformed such that the sum of square errors is made to be minimum (Beccali et al., 2004).

The Structuring Index (SI) was originally developed to define species showing the strongest influence on the organization of the SOM map (Tison et al., 2008). Therefore, the set of species showing high SI (≥ 30) can be considered as indicator species (Park et al., 2005; Várbiro et al., 2007).

Results

Characteristic oxbow types

The sampling sites were classified on the basis of their location (outside or inside the dikes on the

floodplain) and macrophyte coverage. The main types of the oxbows are the following:

Type I—pelagial 1 type: macrophytes are found only in a narrow margin; the lakes are located on the floodplain (therefore, the microflora can be influenced by phytoplankton of Tisza river; Fig. 2a);

Type II—pelagial 2 type: macrophytes are only found in a narrow margin, located outside the embankments (therefore, the river does not have a direct effect on them; Fig. 2b);

Type III—floating-leaved type: *Trapa natans* L. or *Nymphaea alba* L. dominate the vegetation covering large portion of the surface of the oxbows (Fig. 2c);

Type IV—submerged-floating type: (*Ceratophyllum demersum* L. and *Stratiotes aloides* L. or *Nymphaea alba* L. are dominant in the water column (Fig. 2d);

Type V—floating island type: floating islands of *Thelypteris palustris* Schott and *Salix cinerea* L. dominate the water, *Myriophyllum* spp. are also present (Fig. 2e).

The percentage of the actual macrophyte coverage was estimated during sampling, along a transect perpendicular to the shoreline. The types listed above represent the stages of the ageing process (first phases of the hydroséries) of the oxbows. Most frequent

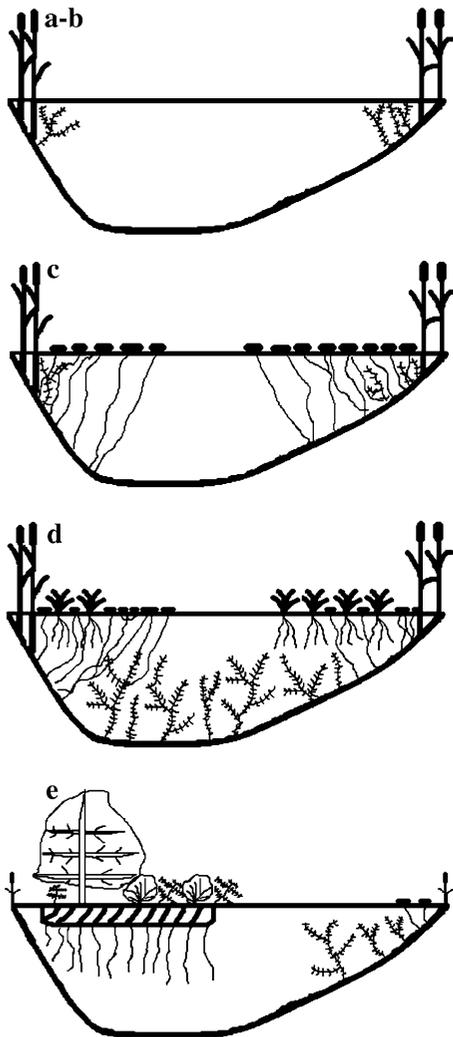


Fig. 2 Types of oxbows based on macrophyte coverage. **a–b** Types I and II; **c** Type III; **d** Type IV and **e** Type V. See type descriptions in [Materials and methods](#)

order of stages are I → II → III → IV or I → II → III → V.

Taxonomic composition

A total of 646 species of algae were recorded in the oxbows over the study period. The microflora was dominated by chlorococcalean green algae (173), diatoms (114), euglenophytes (85), cyanophytes (70) and desmids (53). The ratio of the flagellated algae was high (31%). There are several chlorococcalean, euglenophyton and dinophyton species that are known exclusively from oxbows in Hungary, such

as *Nephrochlamys willeana* (Printz) Korshikov, *Trachelomonas woycickii* Koczw. var. *pusilla* Drez. f. *pusilla*, *Ceratium furcoides* (Levander) Langhans, *Peridinium gatunense* Nygaard. Occurrence of *Peridiniopsis elpatiewskyi* (Ostenfeld) Bourrelly, *Cystodinium cornifax* (Schilling) Klebs, *Woloszynskia pascheri* (Suchlandt) Stosch, *Scenedesmus pannonicus* Hortob. and *Cosmarium kjellmanii* Wille has been reported in other types of waters in Hungary; however, these can also be considered as typical oxbow-dwellers. Most of the species mentioned above occurred sporadically, but the planktonic dinoflagellates were dominant members of the phytoplankton.

In the case of those lakes where the number of samples is more or less similar (and relatively high, 18–20 samples), the flora consisted of more than 200 species (Table 1). An especially rich microflora (308 species) characterised the Malom-Tisza oxbow (floating island-type) where two regions, the pelagic and littoral join.

The average number of taxa was almost identical in types I, (28); II, (32) and III, (33), but in type IV, it decreased considerably (23). The highest taxa number was found in the case of type V (46).

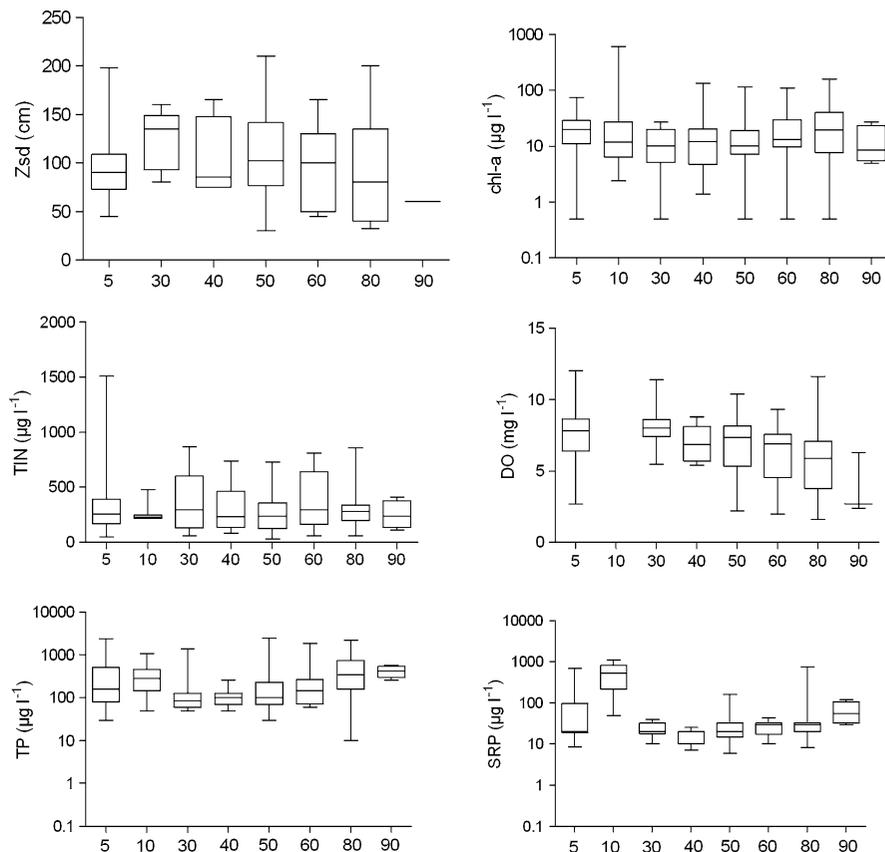
Physical and chemical characteristics

Changes of the relevant physical and chemical variables were investigated along the macrophyte coverage (Fig. 3). None of the nutrients (TIN, TP, SRP) showed close relationship with the coverage. Extremely high or low values occurred independently of oxbow types. It was also observed for the Secchi depth (Zsd) and the chlorophyll *a* concentration. Of the investigated variables, only DO showed consistent (decreasing) tendency towards the higher coverage.

Characteristic assemblages

The species were allocated into 32 coda. These were used to illustrate the phytoplankton assemblages in the different oxbow-types. The SOM and *K*-means clustering resulted in five different types of phytoplankton associations (Fig. 4a). These types were determined by the following coda with high structuring index **Y**, **L_O**, **W₁**, **W_S** and **J** (Fig. 4b). Type 1 was dominated by **D**, **H1**, **J**, **MP**, **S1** coda. The most frequent phytoplankton assemblage was the **W1** in

Fig. 3 Characteristic physical–chemical parameters along the different macrophyte coverages



Type 2. **L_O** codon dominated Type 3. The characteristic functional group of Type 4 is **W_S**, while of Type 5 is the **Y** codon (Fig. 4c).

On the basis of the SOM's results relative biomass abundances of the relevant coda were illustrated along the macrophyte coverage (Fig. 5). Where the coverage was low (5–10%, oxbow types I–II), **H₁**, **J**, **L_O**, **MP**, **P**, **Y** and **W₂** coda dominated the phytoplankton, of which the **Y** codon was notoriously dominating in some lakes. **L_O**, **W₁**, **W₂** and **Y** dominated assemblages were characteristic at 30–50% coverage (type III and early stage of type IV). In some of these oxbows the **H₁**, **J**, **MP** and **P** coda could also attain relatively high share (40–50%) in the phytoplankton. In the macrophyte-dominated lakes (coverage 60–90%, types IV–V.) the members of the **L_O**, **MP**, **W₁** and **Y** coda were well represented. The abundances of euglenoids (**W₁** codon) and dinoflagellates (**L_O** codon) was higher in the macrophyte covered oxbows, than in the pelagial-type oxbows. While the rate of the cryptomonads (**Y** codon) was relatively high in all oxbow

types, it was independent from the macrophyte coverage (Fig. 6). Characteristic species of the main coda (based on the SOM) are shown in Table 3.

An interesting assemblage was found in one of the pelagial oxbow (Type I oxbows, typical representative: Malom-Tisza). This is a deep, sheltered, consequently stably stratified lake that was characterised by the dominance of actively buoyant species such as *Limnotherix redekei* (Van Goor) Meffert (**S₁**) and *Peridinium gatunense* (*Peridiniopsis elpatiewskyi*) (**L_O**). This plankton started to develop in June and was found even in September in every year of the investigations.

Nutrient-phytoplankton relationship

The relationship between physical and chemical variables and the relative frequency of the relevant coda has been analysed. Significant relationships were not found. It also applies for phytoplankton biomass. The chlorophyll *a* was not found to have a statistical relationship with the TP and TIN values.

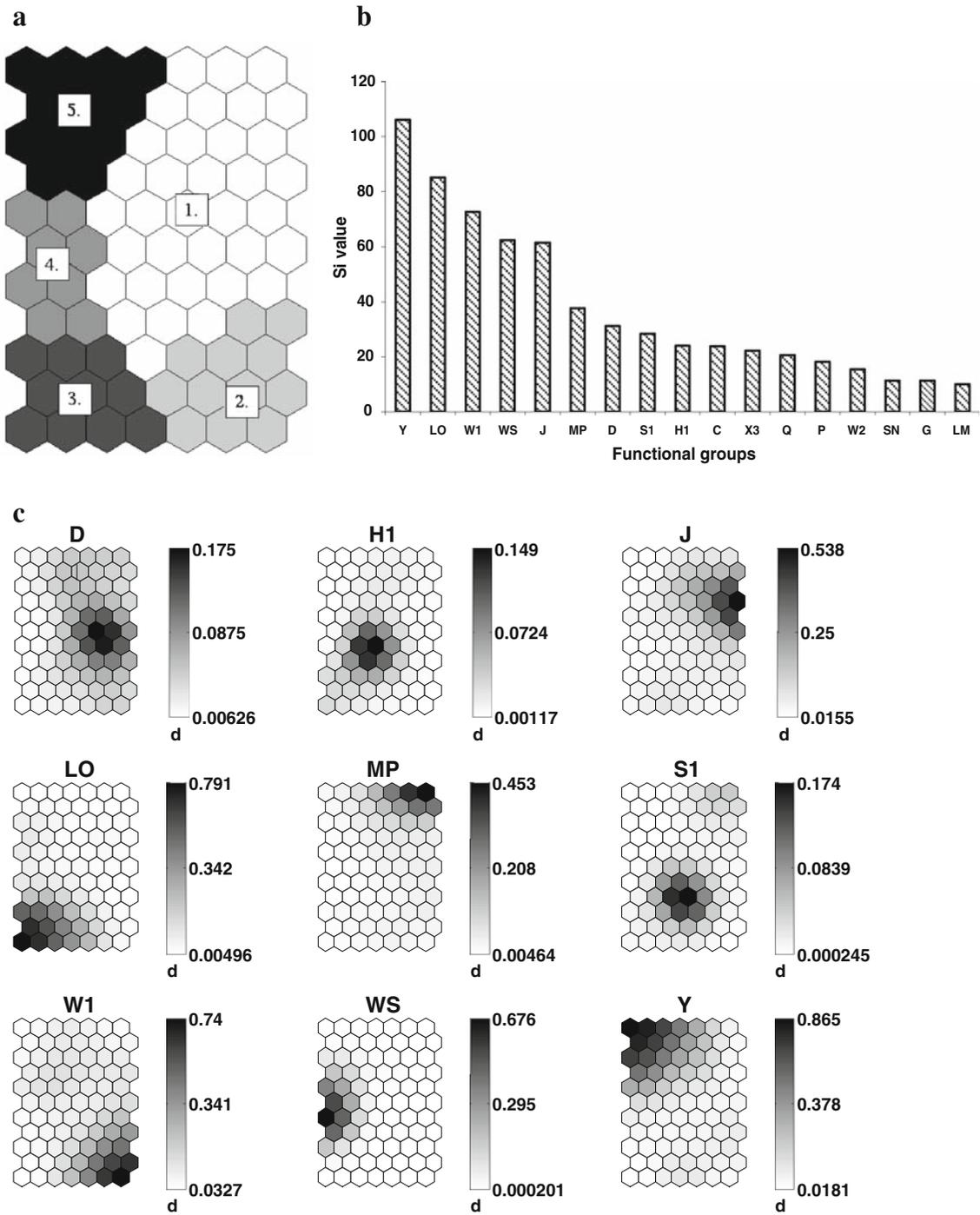


Fig. 4 **a** Clusters of the SOM resulted by the K-means clustering. **b** Coda with high structuring index (SI). The columns indicate the relative importance of each codon in determining the SOM patterns. **c** Gradient distribution of important coda on the SOM

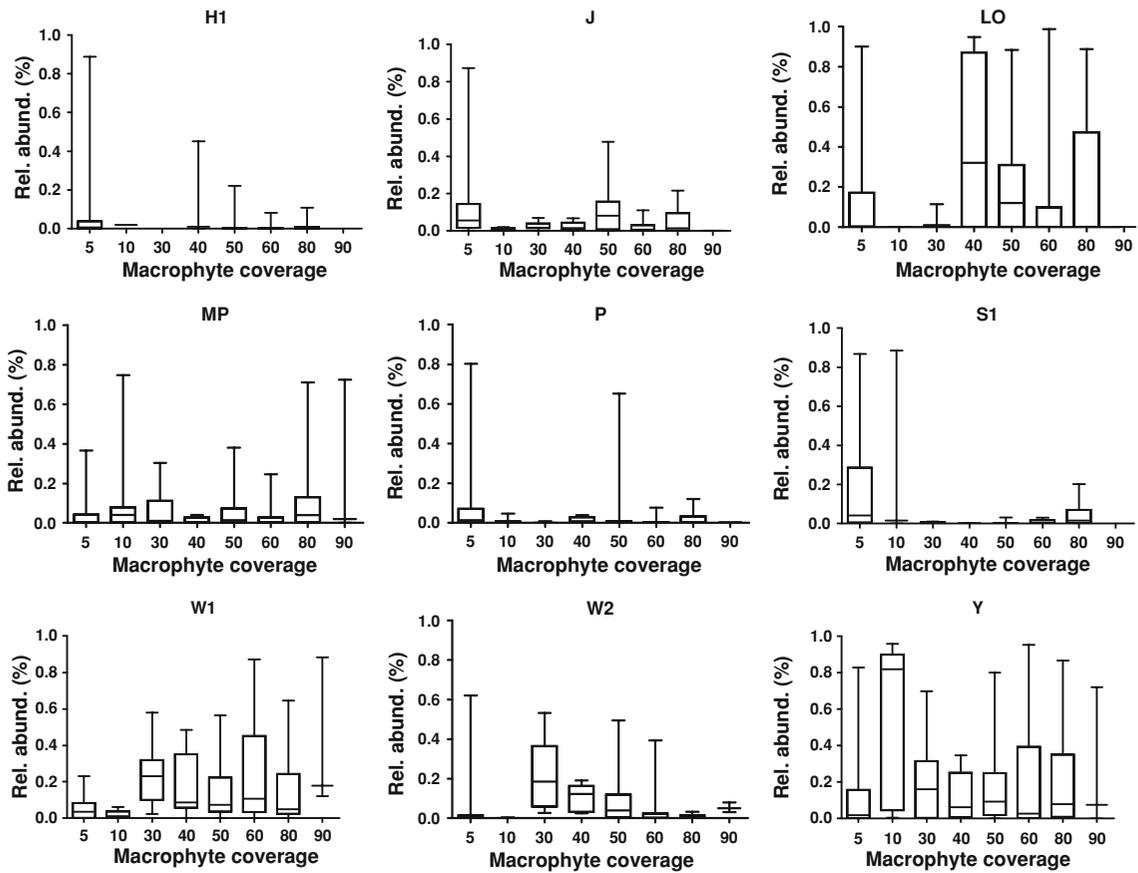


Fig. 5 Min, max, IQR data of relative biomass abundances of the relevant cota along the different macrophyte coverages

Fig. 6 Relative average biomass of the main cota along the different macrophyte coverages

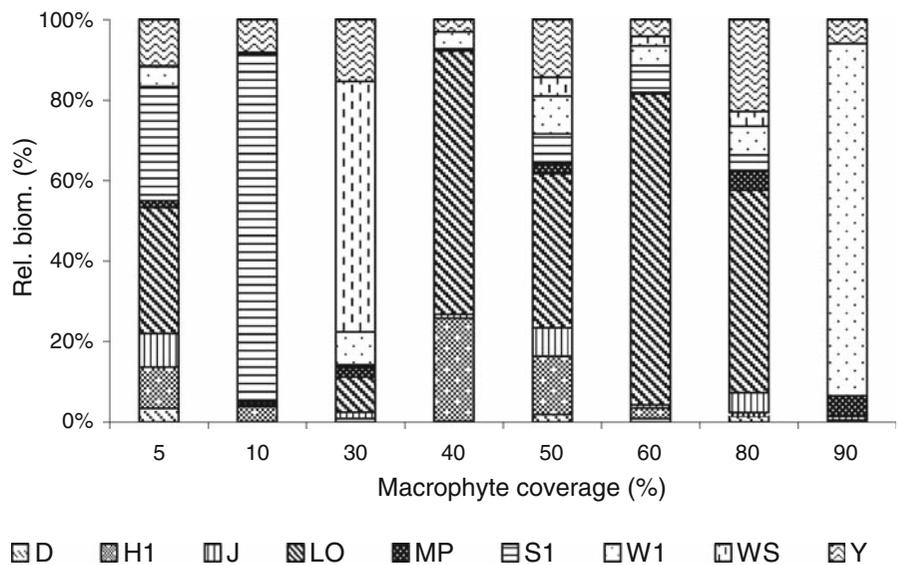
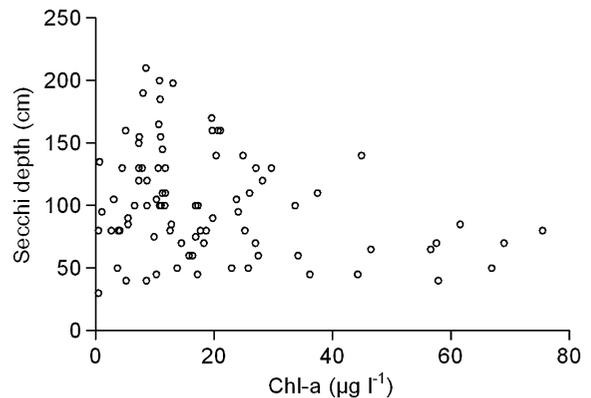


Table 3 Characteristic species of the main coda based on the SOM analysis

Codon	Characteristic species
D	<i>Discostella pseudostelligera</i> (Hustedt) Houk et Klee, <i>Discostella stelligera</i> (Cleve et Grunow) Houk et Klee, <i>Nitzschia acicularis</i> (Kütz.) W. Smith, <i>Stephanodiscus minutulus</i> (Kütz.) Cleve & Möller
H1	<i>Aphanizomenon aphanizomenoides</i> (Forti) Hortob. et Komárek, <i>Aphanizomenon issatschenkoi</i> (Usacev) Proshk.-Lavr.
J	<i>Crucigenia tetrapedia</i> (Kirch.) West et West, <i>Pediastrum tetras</i> (Ehr.) Ralfs, <i>Tetraedron minimum</i> (A. Braun) Hansgirg, <i>Koliella tenuis</i> (Nygaard) Hindák, <i>Scenedesmus quadricauda</i> (Turp.) Bréb.
L _O	<i>Merismopedia glauca</i> (Ehr.) Kütz., <i>Peridinium gatunense</i> Nygaard
MP	<i>Achnanthydium minutissimum</i> (Kütz.) Czarnecki, <i>Fragilaria crotonensis</i> Kitton, <i>Navicula radiosa</i> Kütz.
P	<i>Aulacoseira distans</i> (Ehr.) Simonsen, <i>Closterium acutum</i> (Lyngbye) Bréb., <i>Staurastrum tetracerum</i> (Kütz.) Ralfs
S1	<i>Limnithrix redekei</i> (Van Goor) Meffert, <i>Planktolynghya limnetica</i> (Lemmerm.) Komárková-Legnerová et Cronberg, <i>Pseudanabaena limnetica</i> (Lemmerm.) Komárek
W1	<i>Chlorella</i> sp., <i>Euglena acus</i> Ehr., <i>Peridiniopsis elpatiewskyi</i> (Ostenfeld) Bourrelly, <i>Trachelomonas intermedia</i> Dangeard, <i>Trachelomonas planctonica</i> Svirenko
W2	<i>Trachelomonas volvocina</i> Ehr.
Y	<i>Cryptomonas erosa</i> Ehr., <i>Cryptomonas marssonii</i> Skuja, <i>Rhodomonas minuta</i> Skuja

Turbid versus clear-water state

Secchi transparency (Zsd) and chlorophyll *a* (Chl *a*) data were used to investigate the turbid *versus* clear-water state in the oxbows of different macrophyte coverages. At first, Zsd and Chl *a* data were plotted against the percentages of macrophyte coverages. No statistically significant relationship was found between the variables ($P > 0.05$). Descriptive statistics of the Zsd data (Fig. 3) has also been analysed. The interquartile range (IQR) was almost identical in each lake type and somewhat lower values characterised the lakes with low coverage (Types I–II). High (~ 200 cm) and low (~ 30 cm) values occurred in lakes with 5 and 80% coverage as well. As to the variation of Chl *a*, the IQRs were also shown to be independent from the lake type. The high values indicated eutrophic state (Chl *a* $> 75 \mu\text{g l}^{-1}$) even in lakes with 80% macrophyte coverage. An extremely high value ($610 \mu\text{g l}^{-1}$) was found in one of the lakes (10% coverage) during late summer due to a *Cylindrospermopsis raciborskii* (S_N codon) bloom. Secchi transparency values were plotted against the chlorophyll *a* concentrations (Fig. 7). The relationship was not statistically significant ($P > 0.05$). Nevertheless, the arrangement of the points indicate, if the Chl *a* concentration higher than $50 \mu\text{g l}^{-1}$ the Zsd must be less than 1 m. It might also be said that low Chl *a* values do not necessarily result in high water transparency.

**Fig. 7** Relationship between Secchi depths and Chlorophyll *a* concentrations

Discussion

The oxbows, similarly to other nutrient rich, productive ecosystems in the region, support various eutrophic assemblages (C, D, J, S1, and H1) (Grigorszky et al., 1998a, b; Borics et al., 2000). Comparison of the microflora with other occurrences published in the relevant literature (Uherkovich, 1995; Németh, 1997a, b, 2005; Schmidt and Fehér, 1998, 1999, 2001; Grigorszky et al., 1999) supported that there are some species known exclusively from oxbows in Hungary (Borics et al., 2002; Krasznai et al., 2008). The most interesting feature of the phytoplankton of the oxbows is that those assemblages that usually

play minor role in other eutrophic lake types (**S**, **Y**, **L_O**) can dominate. The elements of the **W_S** codon (*Synura* spp.) obligately use carbondioxide as an inorganic carbon source (Reynolds, 2006) and therefore avoid the eutrophic ecosystems with high pH. The members of this codon can prevail in macrophyte-dominated oxbows [sometimes with *Gonyostomum semen* (Ehr.) Diesing]. Cryptomonads (**Y**) that are susceptible to cladoceran filter feeding (Reynolds et al., 2002) can form stable populations in vegetated, as well as open water oxbows.

The ratio of the flagellated algae both in terms of the number of species and of the relative share in the biomass was surprisingly high. It can be explained partly by the large numbers of metaphytic elements (euglenophytes and several volvoclean green algae) characteristic in macrophyte-dominated lakes (Borics et al., 2003), and partly by the fact that the oxbows are lentic habitats. In small forest lakes (most of the oxbows belong to this category), the wind shade, and consequently, the lack of wind-induced turbulences can be a major environmental factor. Species that do not have the capability of active buoyancy regulation settle from the water column. It might be the reason why dominance of large diatoms has never been observed (Fig. 5). Dominance of cryptomonads or the dinoflagellates like *Peridinium gatunense* and *Peridiniopsis elpatiewskyi* in the phytoplankton during summer indicates that due to their active vertical migration these organisms are successful competitors in this environment, where otherwise, dominance of elongated, cyanobacterial species possessing gas vacuoles are expected (Reynolds, 2002).

The long lasting dominance of the actively buoyant species like *Limnithrix redekei* (**S1**) and *Peridinium gatunense* (*Peridiniopsis elpatiewskyi*) (**L_O**) in the deeper and stratified oxbows allows to conclude that the phytoplankton was in equilibrium state (Sommer et al., 1993; Naselli-Flores et al., 2003; Padisák et al., 2003). Since the stable coexistence of these species was observed in every year, it cannot be considered as a simple mixture of the **L_O** and **S1** (**H1**) coda. Stable co-occurrence of the **L_O**–**H1** complex is characteristic also in Lake Balaton, and provided a reason (later unjustified, see Padisák et al., 2009) to include some of the **H1** species to **L_O** (Hajnal and Padisák, 2008). If examples are accumulating, description as new codon would be useful.

The numbers of the occurring taxa (200–300) belong to the range considered to be characteristic for smaller lakes (Reynolds, 2006). In ecosystems where the aquatic macroflora is diverse and morphologically structured, many microhabitats may develop (Borics et al., 2003). In compliance with it, in our survey the richest microflora was found in those lakes where the ratio of the pelagial and littoral zone was more or less similar. Towards the pelagial type, the number of metaphytic and benthic elements decreased, but towards the densely vegetated oxbows the decrease in the euplanktic elements was observed.

Nutrients are considered to play a critical role in regulating the composition and biomass of the phytoplankton. Nevertheless, their role in hypertrophic lakes is limited because in these systems the concentrations of the nutrients highly exceed those that can be considered as limiting (Sas, 1989; Reynolds, 2006). Since SRP and TIN values in the studied oxbows are considerably higher than the limiting values (Table 2), it is not surprising that neither the composition, nor the biomass had significant relationship with the nutrients.

Our results clearly demonstrate that among the investigated physical variables exclusively the macrophyte coverage influenced the composition of the phytoplankton assemblages. Where the coverage was higher than 40%, dominance of bloom-forming cyanobacteria (**S1**, **H1** coda) cannot be expected and in such environments dominance of the metaphytic **W1** species developed frequently (Fig. 5).

Due to the accumulating information on the shallow lakes during the last decades (Timms and Moss, 1984; Van den Berg et al., 1998), and especially from the publication of Sheffer's excellent book (Scheffer, 1998), it has become widely accepted that the eutrophic shallow lakes might be clear-water lakes dominated by macrophytes, or phytoplankton-dominated turbid lakes. In agreement with this, a clear relationship should exist between the macrophyte coverage and the Secchi transparency, moreover between macrophyte coverage and the chlorophyll *a* concentration. Surprisingly, our results did not support this theoretical consideration. In the case of the pelagial lake types, the low chlorophyll *a* and high Zsd values are explicable by the early sampling (May) and the early stage of phytoplankton succession, but the low Zsd and Chl *a* values in the case of the macrophyte-dominated lakes are unusual

and need more explanation. Because of the morphology (long, narrow) of the basin and the sheltering gallery forests, the fetch is very short in case of the oxbows. The wind-induced mixing is minimal and in the pools isolated by the macrophytes dense algal assemblages (usually dominated by euglenophytes; **W1** codon) developed. Nevertheless, low Zsd values were measured despite the low Chl *a* concentration. This phenomenon can be explained by the frequently occurring iron precipitation that coincided with the development of a planktonic assemblage dominated by iron bacteria. In these cases, the samples collected for phytoplankton analyses often contained ferritized cells of iron bacterium, *Ochrobium tectum* Perf.

In summary, the composition of the oxbow microflora is fairly similar to that of the other eutrophic lakes, but there are some rarely occurring species that are reported exclusively from oxbows. Species of the **S1** and **L0** coda co-occur with high fidelity in oxbow lakes which may provide a reason to define a separate codon if such observations accumulate. During the transition from lake systems to landscape, the direction and the main stages of macrophyte succession can be foreseen, but our results proved that it is not exclusive for the macroflora. The macrophyte coverage has a great effect on the composition of the algal assemblages. Nevertheless in case of the oxbows, the macrophyte-dominated state does not necessarily result in a clear-water state.

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